





# Concentrated vulnerabilities in bees: Diet specialists have smaller geographic ranges

Charles N. Thrift<sup>1,2</sup>  | Thomas J. Wood<sup>3</sup>  | An Bui<sup>2,4</sup>  | Hillary S. Young<sup>2</sup>  |  
Katja C. Seltmann<sup>1</sup> 

<sup>1</sup>Cheadle Center for Biodiversity and Ecological Restoration, University of California Santa Barbara, Santa Barbara, California, USA

<sup>2</sup>Department of Ecology, Evolution, and Marine Biology, University of California Santa Barbara, Santa Barbara, California, USA

<sup>3</sup>Naturalis Biodiversity Center, Leiden, the Netherlands

<sup>4</sup>Environmental Studies Program, University of California Santa Barbara, California, Santa Barbara, USA

## Correspondence

Charles N. Thrift, Cheadle Center for Biodiversity and Ecological Restoration, University of California Santa Barbara, CA, USA

Email: [cnthrift@ucsb.edu](mailto:cnthrift@ucsb.edu)

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## Abstract

1. Wild bees are widely believed to be in decline, yet most species remain unassessed for IUCN extinction risk. Geographic range size is used in risk assessments under the assumption that species with smaller ranges are more vulnerable to anthropogenic impacts. Narrow diet breadth can also increase vulnerability but is not currently incorporated into assessments.
2. Niche breadth theory predicts a positive association between range size and diet breadth, which could concentrate risk among dietary specialists, but this relationship is not well established for bees and may differ among taxa.
3. Here, we combined pollen-use data from natural history collections with global occurrence records to test the relationship between diet breadth and range size across bees and among bee families. We assigned diet breadth using three metrics (categorical, numerical and phylogenetic) and estimated range size as the extent of occurrence for 633 species from six families.
4. Across bees, range size increased with diet breadth, and diet specialists tended to occupy smaller ranges. These results suggest that range size and diet breadth jointly contribute to increased vulnerability in bees, indicating that some specialist species may merit conservation prioritisation.
5. Our findings support the integration of trait-based approaches for assessing extinction risk and highlight the high value of natural history data in identifying patterns of vulnerability among pollinators.

## KEYWORDS

Anthophila, oligolecty, pollen diet, range size, species assessment

## INTRODUCTION

Wild bees (Hymenoptera: Anthophila) are key pollinators worldwide and have enormous impacts on agricultural production, global food supply and economics (Potts et al., 2010, 2016). Bees are widely believed to be in decline, largely due to anthropogenic change (LeBuhn & Vargas Luna, 2021; Wagner et al., 2021; Winfree, 2010).

Despite suspected declines, bees remain underassessed for extinction risk. Fewer than 3% of bee species have been assessed and assigned a non-data-deficient designation according to the IUCN Red List (IUCN, 2025), likely because insect species assessments are inherently challenging (Didham et al., 2020). Geographic range size, used in many IUCN assessments, is a widely recognised predictor of extinction risk, with smaller-ranged species facing greater vulnerability (Baillie

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et al., 2004; Gaston & Fuller, 2009). Diet breadth can also inform vulnerability to anthropogenic change, with dietary specialists (species with narrow diet breadths) considered more vulnerable than generalists across a wide range of taxa (Clavel et al., 2011; Colles et al., 2009), including bees (Bommarco et al., 2010; De Palma et al., 2015). Species with both restricted diets and limited geographic ranges may be especially at risk, yet the relationship between these traits is not comprehensively understood across taxa. If diet breadth and range size are independent, extinction risk may be more evenly distributed across species. However, if these traits are positively correlated, vulnerability would be concentrated in a subset of species, potentially amplifying extinction risk. While such a positive correlation would pose conservation challenges, it would also provide an opportunity to target conservation actions more precisely to species in need.

Niche breadth theory characterises the range of resources and environmental conditions a species can use and uses niche width to classify species and explain patterns of distribution (Hutchinson, 1957). Niche breadth theory predicts a positive association between diet breadth and range size, such that diet specialists tend to have smaller ranges (Brown, 1984; Gaston et al., 1997). Empirical studies, however, indicate that the magnitude and direction of this relationship vary across taxa. Positive associations between diet specialisation and smaller ranges have been observed in moths and butterflies (e.g., Beck & Kitching, 2007; Brändle, Öhlschläger, & Brandl, 2002; Dennis et al., 2005; Garcia-Barros & Romo, 2010, including when controlling for relatedness among species, Seifert et al., 2022; Seifert & Fiedler, 2024), rodents and shrews (Rickart et al., 2011) and primates (Eeley & Foley, 1999; Harcourt et al., 2002). In contrast, no relationship has been found in bats (Boyles & Storm, 2007), the opposite trend has been found in frogs, where diet specialists have larger ranges (Williams et al., 2006), and bird studies have shown conflicting patterns (Brändle, Prinzing, et al., 2002; Shkedy & Safriel, 1992). Despite their ecological and economic importance, this relationship has not been comprehensively examined in bees (Hymenoptera: Anthophila), aside from a study of 23 oil-collecting species which found no trend (Martins et al., 2015).

One challenge in conducting such an assessment is that bees, like most herbivorous insects, are typically classified into broad categorical diet bins, such as specialist (oligolectic diet) or generalist (polylectic diet; Ostwald et al., 2024). In this system, specialists feed on pollen from a single botanical family (*sensu* Robertson, 1925) while generalists feed on pollen from two or more families. While practical in the absence of quantitative data, this approach overlooks substantial variation within each category, which may instead be exhibited using numerical (counts of host plant taxa) or phylogenetic (breadth of host plant taxa) diet metrics (Ostwald et al., 2024). When broad categories obscure internal variation among specialists and generalists, they may also mask meaningful relationships between diet and range size. Similar issues have been shown in birds, where broad diet categories revealed no relationship between diet and range size (Brändle, Prinzing, et al., 2002), but finer scale diet information (species determinations via stomach content analysis) revealed a positive

relationship between diet and range size (Shkedy & Safriel, 1992). This suggests that quantitative measures of diet breadth (e.g., numerical or phylogenetic) can better capture the relationship between diet breadth and range size, two critical traits for evaluating extinction risk (Slatyer et al., 2013).

Here, we examine the relationship between diet breadth and geographic range size in 633 bee species across six families by combining pollen use data (Wood et al., 2023) with a global, 6.79 million record bee occurrence dataset (Dorey et al., 2023). Specifically, we asked: What is the relationship between geographic range size and diet breadth across bees? We predict that as diet breadth increases (i.e., becomes more general), range size also increases, because niche breadth theory predicts a positive correlation between niche breadth and range size. Establishing the strength and consistency of this association will support conservation prioritisation by enabling inference about vulnerability when only diet breadth or range size is available.

## METHODS

To answer our question, we assigned diet breadth in three ways: categorical (specialist or generalist), numerical (counts of host plant families) and phylogenetic (breadth of host plants). We calculated the extent of occurrence for each bee species as a proxy for range size. We compared range size between categorical diet breadths using a generalised linear model and mean ratio and determined the relationships between range size and numerical and phylogenetic breadth using Spearman's correlation and generalised linear models. We also accounted for bee phylogeny using phylogenetic generalised least squares regression.

### Pollen processing and filtering

To assign diet breadths to bee species, we utilised a bee-pollen association dataset published by Wood et al. (2023) and standardised sample sizes using rarefaction. Methodology for pollen sourcing, quantification and identification is described in Wood et al. (2023). In brief, for each bee specimen, pollen load size was visually estimated, pollen was removed from scopae with a clean entomological pin, pollen grains were transferred to a drop of water on a microscope slide, and the slide was heated to evaporate excess water and allow grains to achieve maximum size. Molten stained glycerine jelly was added and the slide was sealed with a cover slip. The proportion of different pollen taxa constituting the load was estimated along three random lines across the slip at  $\times 400$  magnification. Because different pollens can vary widely in grain size and hence volume (Cane & Sipes, 2006), the proportion of the load for each plant pollen was estimated as the relative area of the slide occupied by each plant taxon rather than the number of grains. This was achieved by calculating pollen-grain volume from measured diameter (assuming that the average pollen grain is spherical), then counting pollen grains and applying a volume-based correction to obtain more accurate proportional estimates.

Pollen grains were identified to the lowest taxonomic level possible using reference collections and then assigned to botanical families following APG IV (2016).

We filtered observations to remove plant taxa with 2% or less representation in a pollen load, as percentages lower than this could have arisen from contamination (Kleijn & Raemakers, 2008; Wood et al., 2023; Wood & Roberts, 2017, 2018). To account for uneven sampling between bee species, we standardised sample sizes using rarefaction. For each of 1000 iterations, we randomly selected 10 pollen loads per species without replacement, and excluded species with fewer than 10 pollen loads, following the procedure of Wood et al. (2023). Similar rarefaction procedures have allowed for comparison of bee-pollen associations in other studies with differing sample sizes between bee species (Bartomeus et al., 2018; Kleijn & Raemakers, 2008; Williams, 2005; Wood & Roberts, 2017, 2018) and thus avoid confounding rarity with diet specialisation (Blüthgen et al., 2008; Winfree et al., 2014).

### Categorical diet breadth

Using the filtered bee-pollen association dataset described above, we assigned each bee species as either a specialist or generalist, where specialists feed on pollen from a single botanical family, sensu Robertson (1925).

### Numerical diet breadth

To assign numerical diet breadths, we counted the number of plant families each bee species collected pollen from, using the filtered and rarefied bee-pollen association dataset described above. Due to rarefaction, numerical diet breadths are expressed as continuous (decimal) values rather than whole numbers.

### Phylogenetic diet breadth

To quantify phylogenetic diet breadth in bees, we first constructed a pruned phylogenetic tree for all plant hosts in our diet dataset. We began with a tree inferred from Smith and Brown (2018), pruned to one tip per family with R package *ape* (Paradis & Schliep, 2019). We further pruned this tree to retain only the plant families in our diet dataset. This resulted in one tree with 104 plant families.

We calculated the phylogenetic breadth of plant hosts for each bee species using this tree based on phylogenetic Hill diversity with  $q = 2$  to calculate inverse Simpson index, following Smith et al. (2025), using R package *hillR* (Li, 2018). This metric accounts for proportional abundance of plant taxa for each bee species, with the following equation as described by Chao et al. (2010).

$$PD = \frac{1}{1 - \sum_{ij}^S d_{ij} p_i p_j} \quad (1)$$

here,  $PD$  is the phylogenetic diet value for a bee species,  $i$  and  $j$  are plant families,  $d_{ij}$  is the distance between two plant families,  $p_i$  and  $p_j$  are the branch lengths of plant families  $i$  and  $j$ , respectively, and  $S$  is the number of plant families in the assemblage with an association with a given bee species. For singletons (bee species which only visited one plant taxon), the calculated phylogenetic breadth is the branch length of their single plant taxon.

### Calculating species range sizes with occurrence data

We chose to approximate range size as extent of occurrence (EOO), defined as the area contained by an imaginary boundary surrounding all known occurrences of a species, which may contain habitat discontinuities (IUCN, 2001). EOO differs from area of occurrence (AOO), which is the area within EOO actually occupied by a species, excluding areas where the species is absent (IUCN, 2001). EOO and AOO are both commonly employed to assess species conservation status and can each estimate species range size. When estimating range size, EOO is better suited when sampling is extensive, while AOO is better suited when sampling is intensive (Gaston & Fuller, 2009). As our chosen dataset of bee occurrences is extensive (Dorey et al., 2023), we opted to use EOO rather than AOO in approximating range size.

To estimate range size, we utilised a globally synthesised and cleaned bee occurrence dataset (6.79 million records) from Dorey et al. (2023). We cropped this dataset to our target species (species for which we also have diet breadth data). We only included species that were associated with three or more records in this occurrence dataset, resulting in 3.27 million records from 633 species for analysis. The median number of records per species was 476, though with a wide range (minimum: 4, maximum: 307,511). We built convex hulls for each species, or the minimum convex polygons over which each occurrence point would be contained, using the R package *sf* (Pebesma, 2018). Some species with large distributions had their convex hulls cross oceans. While guidelines to quantify EOO typically discourage excluding discontinuities, exceptions exist for extreme circumstances; an ocean basin from the perspective of a bee would seem to clearly meet such a threshold (IUCN Standards and Petitions Committee, 2024). Thus, we removed all ocean regions from convex hulls using the R package *naturalearth* (Massicotte & South, 2023) but we did not exclude any other regions with potential habitat discontinuities, as doing so would not accurately reflect EOO and instead approximate AOO (Gaston & Fuller, 2009). Then, we calculated the resulting area in square meters and square kilometres for each species.

Because convex-hull EOO can be sensitive to sampling density and spatial outliers (Meyer et al., 2017), we conducted sensitivity analyses using minimum record thresholds and an occurrence rarefaction approach; conclusions were qualitatively unchanged. To assess sensitivity to record number availability, we re-ran analyses including only species with more than 15 records, following Rivers et al. (2011; Supporting Information Table S2). To further reduce potential confounding between rarity in the occurrence dataset and small range size, we

**TABLE 1** Number of bee species comprising our botanical family-level dataset, by bee family and bee genus (total  $n = 633$ ). Numbers in cells indicate the number of species within the dataset.

Andrenidae	188	Apidae	108	Colletidae	83	Halictidae	85	Megachilidae	150	Melittidae	19
<i>Andrena</i>	168	<i>Amegilla</i>	1	<i>Colletes</i>	47	<i>Agapostemon</i>	2	<i>Afranthidium</i>	1	<i>Capicola</i>	1
<i>Arhysosage</i>	1	<i>Anthophora</i>	7	<i>Euryglossa</i>	2	<i>Augochlora</i>	1	<i>Anthidiellum</i>	2	<i>Dasypoda</i>	11
<i>Camptopoeum</i>	3	<i>Bombus</i>	52	<i>Hylaeus</i>	32	<i>Augochlorella</i>	1	<i>Anthidium</i>	16	<i>Meganomia</i>	1
<i>Clavipanurgus</i>	1	<i>Centris</i>	1	<i>Scrapter</i>	2	<i>Dufourea</i>	7	<i>Chelostoma</i>	16	<i>Melitta</i>	5
<i>Flavipanurgus</i>	1	<i>Ceratina</i>	3			<i>Halictus</i>	10	<i>Eoanthidium</i>	2	<i>Samba</i>	1
<i>Macrotera</i>	1	<i>Chalepogenus</i>	1			<i>Lasioglossum</i>	55	<i>Haetosmia</i>	1		
<i>Melitturga</i>	1	<i>Diadasia</i>	9			<i>Lipotriches</i>	4	<i>Heriades</i>	1		
<i>Panurginus</i>	3	<i>Diadasina</i>	1			<i>Patellapis</i>	1	<i>Hoplitis</i>	20		
<i>Panurgus</i>	7	<i>Eucera</i>	16			<i>Rophites</i>	2	<i>Icterantheidium</i>	4		
<i>Perdita</i>	1	<i>Euglossa</i>	1			<i>Systropha</i>	2	<i>Lithurgus</i>	1		
<i>Protomelitturga</i>	1	<i>Eulaema</i>	1					<i>Megachile</i>	11		
		<i>Melipona</i>	1					<i>Osmia</i>	57		
		<i>Melissodes</i>	3					<i>Othinosmia</i>	1		
		<i>Melitoma</i>	1					<i>Protosmia</i>	1		
		<i>Melitomella</i>	1					<i>Pseudoanthidium</i>	4		
		<i>Peponapis</i>	3					<i>Rhodanthidium</i>	5		
		<i>Ptilothrix</i>	2					<i>Stenoheriades</i>	2		
		<i>Xenoglossa</i>	3					<i>Trachusa</i>	4		
		<i>Xylocopa</i>	1					<i>Wainia</i>	1		

also ran a separate rarefaction procedure to estimate EOO from exactly 15 occurrence records per species. We excluded species with fewer than 15 occurrence records, randomly selected 15 occurrences per species, calculated EOO and repeated this procedure 100 times using independent random draws (Supporting Information Figure S2).

For our final dataset after all filtering steps, all 633 species from six families (Andrenidae, Apidae, Colletidae, Halictidae, Megachilidae and Melittidae) were assigned a range size and three diet breadth classifications: numeric (count of plant families from which pollen was collected), categorical (specialist/generalist) and phylogenetic (phylogenetic breadth of host plant families). The only bee family not represented, Stenotritidae, is the smallest with just 21 species, all restricted to Australia (Danforth et al., 2019). Counts of species per bee genus and bee family are available in Table 1. The full dataset is available in Supporting Information Table S1. In a subset of these bees, 174 species from 3 families (Andrenidae, Apidae and Halictidae), we also had finer resolution diet association data: pollen grains identified to plant genera rather than families. We repeated all analyses with this subset and found qualitatively similar results (Supporting Information Table S3). Within our full dataset, 81% of species are solitary and 19% are social (Wood et al., 2023). This is comparable to the proportion of sociality in all non-parasitic bee species, in which 89% are solitary and 11% are social (Danforth et al., 2019). Repeating the analyses with only solitary or only social species yielded qualitatively similar results for solitary species but some differences for social species (Supporting Information Table S4).

## Data analyses

All analyses were conducted in R version 4.5.0 (R Core Team, 2025). Code and data are available on Zenodo: [10.5281/zenodo.18853330](https://zenodo.org/record/18853330) (Thrift et al., 2026).

Range size and numeric diet breadth were right-skewed, with relatively long tails of increasing area and numbers of plant families. Therefore, for all models we used a generalised linear model (GLM) with a gamma error distribution and log link. We compared range size between categorical diet breadths (specialists and generalists) using a GLM as outlined above. Model parameters were estimated by maximum likelihood. We used a mean ratio to quantify the magnitude of the difference between categorical diet breadths. We calculated a mean ratio by exponentiating model predictions.

To quantify the correlative association between range size and diet breadth, we used Spearman's rank correlation coefficient ( $\rho$ ) which evaluates monotonic relationships without assuming normality. To determine the predictive relationship between range size and numeric diet breadth, we constructed a GLM as described above with numeric diet breadth and bee family as predictor variables. We compared two models, one that had an interaction between numeric diet breadth and bee family and one that did not, to examine whether the effect of diet breadth on range size was consistent across bee families (additive model) or differed across bee families (interactive model). We evaluated model residuals using simulated residuals from the *DHARMA* package (Hartig, 2024). We chose the best model based on conformity to assumptions of residual uniformity and homoscedasticity

in addition to Akaike's Information Criterion (AIC) to select the most parsimonious model that explained the greatest variation in range size (Burnham & Anderson, 2002).

To determine the relationship between range size and phylogenetic diet breadth, we constructed a similar GLM with phylogenetic diet breadth as a predictor (as opposed to numeric diet breadth, as above). Because phylogenetic diet breadth was similarly right-skewed, we constructed a GLM with the same error distribution as above.

To account for phylogenetic autocorrelation when investigating the relationship between range size and diet breadth in bees, we used phylogenetic generalised least squares (PGLS) regression. We used a comprehensive species-level bee tree from Henríquez-Piskulich et al. (2024). We rooted this tree with a beewolf wasp (Philanthidae: *Philanthus*) outgroup using the R package *ape*. Then, we pruned the tree to our bee species of interest. The resulting tree contained 520 of our original 633 bee species. To make this tree ultrametric, we used the 'chronos' function in *ape*. Finally, we fit two PGLS regressions with R package *caper* (Orme et al., 2023), one with numeric diet and one with phylogenetic diet as predictor variables of range size. Each PGLS regression estimates Pagel's  $\lambda$  by maximum likelihood, which quantifies the degree of phylogenetic dependence in the residuals through scaling the phylogenetic variance-covariance matrix. PGLS with  $\lambda = 0$  reduces to a standard linear model (when the tree is ultrametric) and a PGLS with  $\lambda = 1$  performs a model equivalent to phylogenetic independent contrasts. An intermediate  $\lambda$  indicates partial phylogenetic signal remaining in the residuals after accounting for diet breadth.

## RESULTS

When analysing categorical diet breadths, where specialists feed only on one plant family ( $n = 202$ ) and generalists feed on more than one ( $n = 431$ ), specialists had smaller range sizes (predicted mean =  $5.3 \times 10^6$  km<sup>2</sup>, 95% CI [ $4.3 \times 10^6$  km<sup>2</sup>,  $6.5 \times 10^6$  km<sup>2</sup>]) than generalists (predicted mean =  $1.6 \times 10^7$  km<sup>2</sup>, 95% CI [ $1.4 \times 10^7$  km<sup>2</sup>,

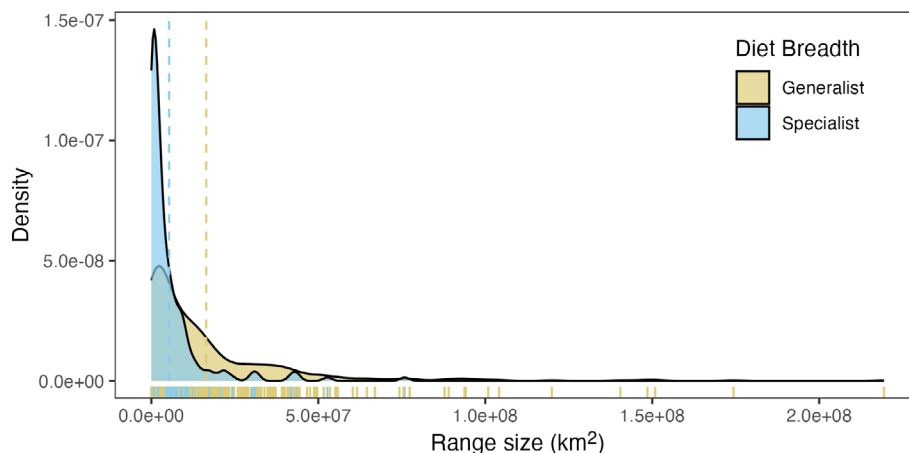
$1.9 \times 10^7$  km<sup>2</sup>]) (Figure 1; Supporting Information Table S5). Generalists had larger range sizes than specialists (mean ratio = 3.09), corresponding to an approximate 209% increase relative to specialists.

Overall, there was a moderately strong, positive correlation between range size and numeric diet breadth (Spearman's rank correlation,  $\rho = 0.42$ ,  $\alpha = 0.05$ ,  $p < 0.001$ ).

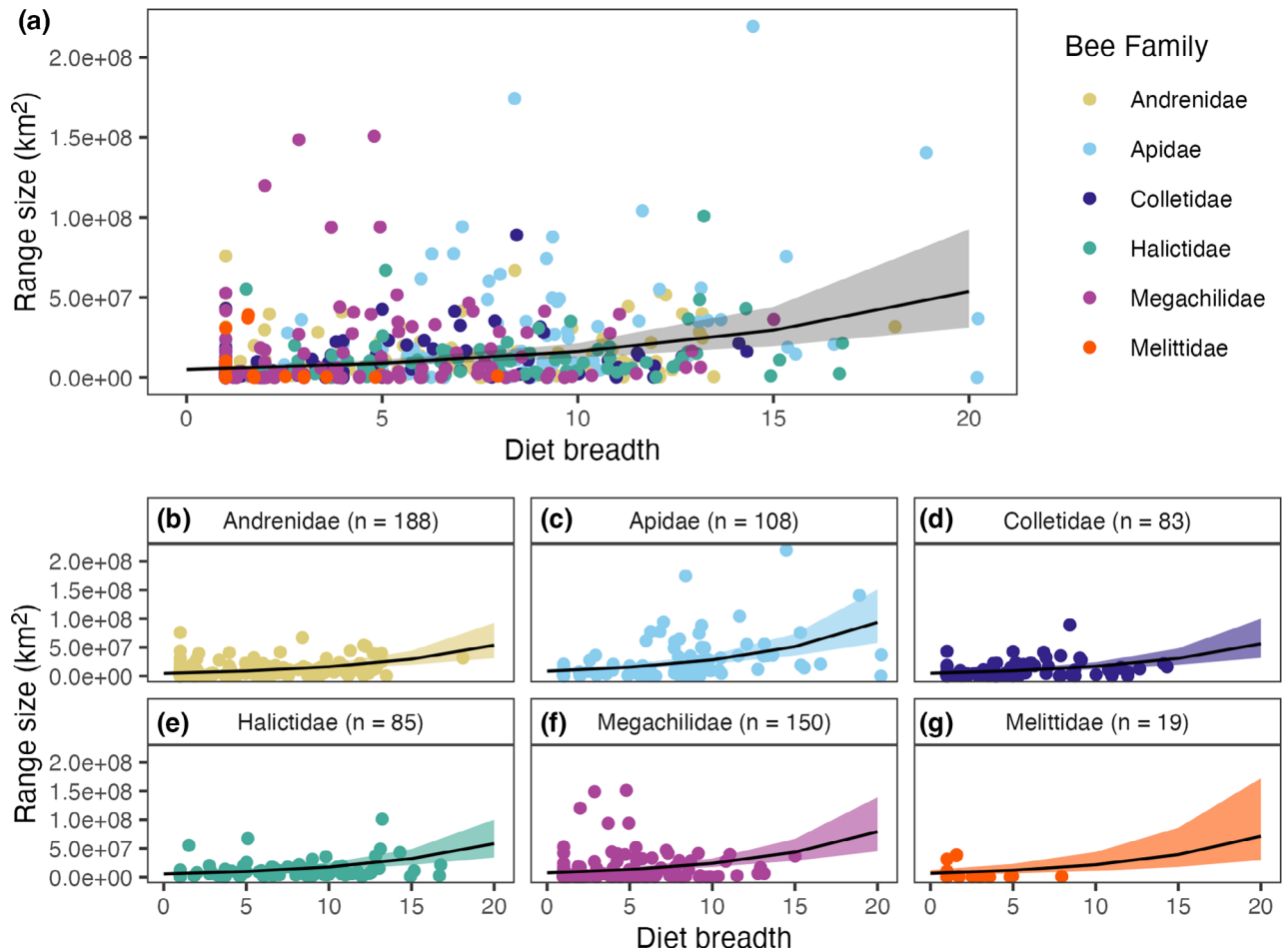
We found that the best model describing the predictive relationship between numerical diet breadth and range size included an additive effect of bee family (Supporting Information Tables S6 and S7) because this model conformed to GLM assumptions. The model with an interactive term did not conform to model assumptions, and because the  $\Delta$ AIC was not substantially greater than 2 (AIC additive: 38960.70, AIC interactive: 38958.15,  $\Delta$ AIC = 2.55), we report and interpret the results of the simpler, additive model. Broadly, range size increased as diet breadth increased and this effect was consistent across bee families (Figure 2; Supporting Information Table S6). While the relationship between numerical diet breadth and range size was the same for all bee families, bee families differed in their average range size (Supporting Information Figure S3).

We found a similarly positive relationship between range size and phylogenetic diet breadth in 633 bee species (Supporting Information Table S8). Likewise, when accounting for bee phylogeny in 520 bee species we found a positive relationship between range size and numeric diet breadth (Supporting Information Table S9; PGLS,  $R^2 = 0.04$ ,  $F(1, 518) = 20.03$ ,  $p < 0.001$ ,  $\lambda = 0.15$  [0.05, 0.32]), and range size and phylogenetic breadth (PGLS,  $R^2 = 0.02$ ,  $F(1, 518) = 13.42$ ,  $p < 0.001$ ,  $\lambda = 0.17$  [0.07, 0.33]). These low but non-zero values of  $\lambda$  indicate partial phylogenetic signal remaining in the residuals after accounting for diet breadth in these PGLS models.

We achieved similar results when restricting analyses to species with more than 15 records (Supporting Information Table S2) and when analysing species for which EOO was calculated from exactly 15 records using a rarefaction procedure (Supporting Information Figure S2). We achieved similar results when restricting analyses to solitary species but not when restricting analyses to social species, as



**FIGURE 1** Bee range size differs among categorical diets: Specialists have smaller range sizes (predicted mean =  $5.3 \times 10^6$  km<sup>2</sup>, 95% CI [ $4.3 \times 10^6$  km<sup>2</sup>,  $6.5 \times 10^6$  km<sup>2</sup>]) than generalists (predicted mean =  $1.6 \times 10^7$  km<sup>2</sup>, 95% CI [ $1.4 \times 10^7$  km<sup>2</sup>,  $1.9 \times 10^7$  km<sup>2</sup>]). Dashed vertical lines indicate predicted means.



**FIGURE 2** Bee range size increases as numerical diet breadth increases across 633 bee species (a). Points represent bee species; colour denotes bee family. Diet breadth is the rarefied number of plant families pollen is collected from and range size is the estimated EOO in km<sup>2</sup>. Black lines are the predicted trends from the gamma GLM, and shading surrounding lines represents 95% confidence intervals. Panels b–g divide bee families.

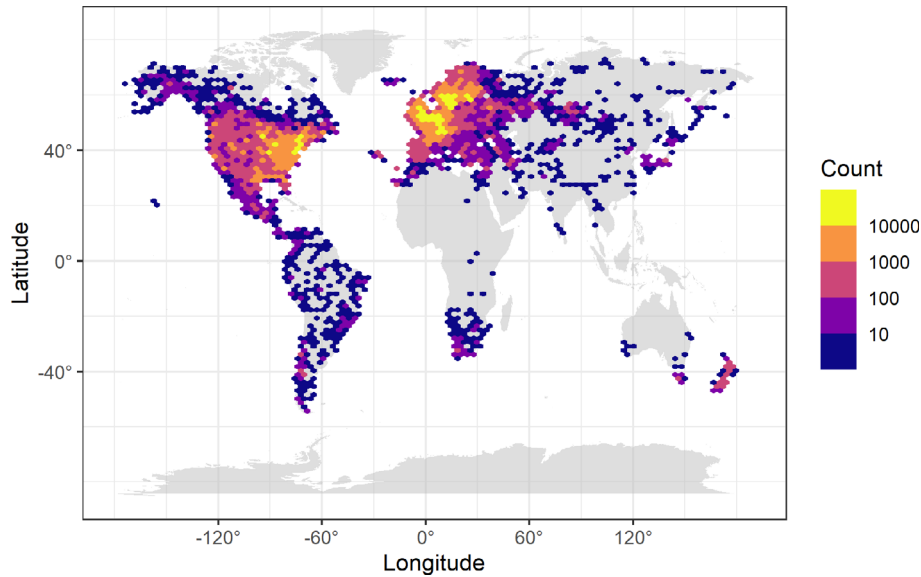
some tests within the social-only subset yielded insignificant results (Supporting Information Table S4).

## DISCUSSION

Understanding how diet breadth relates to geographic range size helps identify which bee species may be most vulnerable to habitat and host-plant loss and therefore most likely to require targeted conservation action. We found a significant positive correlation between range size and diet breadth across 633 bee species from six families, indicating that dietary specialists tend to occupy smaller geographic ranges. This relationship was consistent across all measures of diet breadth (categorical, numeric and phylogenetic) and after accounting for bee phylogeny, suggesting that it reflects an ecological pattern rather than shared ancestry. Although the PGLS models predicting range size by diet breadth yielded low  $R^2$  values, they still support the inference that range size and diet breadth are positively correlated in bees after accounting for shared ancestry. We also found evidence of

phylogenetic signal in diet breadth among bees, such that closely related bee species are more similar in diet breadth than expected under independence.

Ecologically, generalist bees likely achieve broader distributions through their ability to exploit diverse floral resources across habitats and phenological periods, whereas specialists are constrained by the spatial and temporal availability of their host plants (Danforth et al., 2019). In our study, we found that generalists had larger range sizes than specialists, which aligns with niche breadth theory (Brown, 1984) and parallels results in other taxonomic groups such as butterflies and moths (Beck & Kitching, 2007; Brändle, Öhlschläger, & Brandl, 2002; Dennis et al., 2005; Garcia-Barros & Romo, 2010; Seifert et al., 2022; Seifert & Fiedler, 2024), birds (Shkedy & Safriel, 1992), rodents and shrews (Rickart et al., 2011) and primates (Eeley & Foley, 1999; Harcourt et al., 2002). Additionally, we found a moderate difference in range size between generalists and specialists, which is comparable to effect sizes reported in other studies (Beck & Kitching, 2007; Brändle, Öhlschläger, & Brandl, 2002; Dennis et al., 2005; Eeley & Foley, 1999; Garcia-Barros & Romo, 2010; Harcourt et al., 2002).



**FIGURE 3** Geographic distribution of records used to estimate range size for each bee species with EOO. Lighter, more yellow hexagons show areas with more bee records, while darker, more purple hexagons show areas with fewer bee records.

All six bee families exhibited a consistent positive relationship between diet breadth and geographic range size. This consistency suggests that the association between broader resource use and larger ranges is not driven by a single lineage but instead reflects a general pattern that holds across major bee clades in our dataset. Regardless of family identity, species that use a wider diversity of plant families tend to occupy larger geographic ranges. However, the six bee families differed in mean range size (Supporting Information Figure S3). Family-level differences in historical biogeography and trait composition may influence mean range size among bee families. Historical biogeography may contribute to these differences by structuring where bee lineages have diversified and which regions they have been able to colonize over evolutionary time (Brown, 1984; Hines, 2008). Traits not analysed here may include sociality, body size, disturbance tolerance and nesting requirements. Social and large-bodied species are more mobile (Greenleaf et al., 2007; Osborne et al., 2008) and therefore may have larger range sizes independent of diet breadth. Species that tolerate anthropogenic disturbance and persist in human-modified habitats, such as many Halictidae (Harrison et al., 2017), may also have larger range sizes. Nesting requirements, which may include particular soil conditions or the availability of pre-existing cavities (Antoine & Forrest, 2021; Danforth et al., 2019), may influence range size because suitable nesting conditions can be spatially variable and thus increase or limit species occupancy. Because these traits can vary among families, they may help explain differences in mean range size across families and could be evaluated in future studies. Importantly, differences in mean range size among families did not alter the positive relationship between range size and diet breadth when all families were analysed together.

Examining relationships between diet breadth and range size can be challenging because uneven sample sizes can lead to rarity being interpreted as specialisation (Cardillo et al., 2019; Gaston et al., 1997;

Slatyer et al., 2013). Efforts to control for sample size effects have diminished or negated a positive correlation between niche breadths in some studies (e.g., Burgman, 1989; Kolb et al., 2006). To minimise the risk of such confounding in our study, we assigned range and diet from independent datasets. Additionally, we implemented a rarefaction procedure for both the diet data (main text) and range size data (supporting materials). A positive correlation between diet breadth and range size persists in bees with independent, rarefied data, indicating that this correlation is driven by ecological or evolutionary history, not statistical confounding.

The bee species we analysed have distributions biased towards the Northern Hemisphere, especially Europe and North America (Figure 3; Supporting Information Figure S1). This geographic bias in precise bee pollen-load data is consistent with the current distribution of available bee occurrence records and museum specimens (Dorey et al., 2023). Though bees live on every continent except Antarctica, there is a stark reduction in available bee occurrence data south of the equator. The 633 species analysed here represent the most comprehensive analysis of the relationship between diet breadth and range size in bees, yet this represents only 3.03% of the approximately 20,925 bee species worldwide (Ascher & Pickering, 2025). We proxied range size as the extent of occurrence (EOO) for each bee species with minimum convex polygons built from occurrence data, similar to Martins et al. (2015) and Smith et al. (2025). EOO can be less informative in conservation contexts when calculated from a low number of observations (e.g., fewer than 15, Rivers et al., 2011). However, the number of records used to construct EOO did not seem to influence our results: we achieved similar results when only analysing species for which there were more than 15 records (Supporting Information Table S2), and when analysing species for which EOO was calculated with exactly 15 records following a rarefaction procedure (Supporting Information Figure S2). While EOO can overestimate the

area actually occupied by a species, it is an appropriate metric for our question due to its conservation relevance and use in IUCN species assessments.

The three diet breadth metrics in this study (numerical, categorical and phylogenetic) each showed significant and consistent relationships with range size. This increases confidence in our findings and lends support for using either of the three metrics in other studies, depending on the scope of the research question and data available. To promote data reuse and comparisons across studies, we recommend that authors clearly define their diet breadth criteria and methodologies, and provide raw data (Ostwald et al., 2024). Open data are especially important, given that less than 5% of pollen-collecting bee species have known diet breadths (Wood et al., 2023). Further research considering bee diets can be facilitated by constructing and utilising public trait data resources such as the Big-Bee project (Seltmann, 2021) within the Open Traits Network (Gallagher et al., 2020). Natural history collections and bee-plant visitation datasets (e.g., GLoBI, Poelen et al., 2014; Noori et al., 2026) can be used for this effort via pollen analysis (e.g., Wood et al., 2023) or predictive modelling (Smith et al., 2025). While broad diet categories may help identify overall trends in other studies or inform a general understanding of risk associated with anthropogenic change, targeted conservation actions will require precise dietary niche information (i.e., knowledge of host plants). Mechanistically, bee declines are not driven merely by specialisation, but by the loss of key host plants (Scheper et al., 2014), and diet specialists have fewer host plant taxa available than generalists.

From a conservation perspective, the convergence of narrow diets and small ranges underscores the need to integrate trait data into risk assessments for bees. Trait-based indicators like diet breadth can serve as early-warning metrics for extinction risk, particularly for data-deficient insect taxa. Incorporating diet-range relationships into predictive frameworks may allow conservationists to identify vulnerable species even in the absence of population data, a critical step given that 97.4% of bee species remain either data-deficient or unassessed by the IUCN (IUCN, 2025). Aside from range size, IUCN criteria require knowledge of population size (IUCN Standards and Petitions Committee, 2024), which is notoriously difficult to quantify in insects, partially due to inherent population fluctuations which impede a search for declines (Didham et al., 2020). Additionally, because bees and flowering plants are mutualistic partners, the coupling of narrow diets and restricted ranges may heighten extinction vulnerability for both groups, as declines in bees can in turn increase extinction risk for their host plants, when mutually specialised (Colles et al., 2009; Koh et al., 2004; Raiol et al., 2021; Rezende et al., 2007).

We found diet specialist bees have smaller range sizes, in agreement with niche breadth theory. This study represents the first comprehensive analysis of this pattern in bees, which are key pollinators experiencing declines. Our results support the use of trait-based metrics to inform species conservation assessments. Expanding trait datasets via digitised collections and predictive modelling will be essential to identify and protect these vulnerable pollinators before their declines become irreversible.

## AUTHOR CONTRIBUTIONS

**Charles N. Thrift:** Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; visualization; writing – review and editing; writing – original draft. **Thomas J. Wood:** Conceptualization; data curation; methodology; writing – review and editing; writing – original draft. **An Bui:** Formal analysis; methodology; writing – review and editing; writing – original draft. **Hillary S. Young:** Methodology; writing – original draft; writing – review and editing. **Katja C. Seltmann:** Conceptualization; funding acquisition; formal analysis; methodology; writing – review and editing; writing – original draft.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Zenodo at <http://doi.org/10.5281/zenodo.17466214>. (Thrift et al., 2026).

## ORCID

Charles N. Thrift  <https://orcid.org/0000-0002-4257-6951>

Thomas J. Wood  <https://orcid.org/0000-0001-5653-224X>

An Bui  <https://orcid.org/0000-0002-9548-7776>

Hillary S. Young  <https://orcid.org/0000-0003-0449-8582>

Katja C. Seltmann  <https://orcid.org/0000-0001-5354-6048>

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## SUPPORTING INFORMATION

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

**Table S1.** Whole dataset (CSV,  $n = 633$  species). Includes columns for range size, diet breadth and bee family.

**Table S2.** Re-run main-text analyses on species for which we have 15 or greater occurrence records used to estimate EOO.

**Table S3.** Comparison of results in subset of bee species for which genus-level diet information is available compared to family-level in the same species ( $n = 174$ ).

**Table S4.** Comparison of results within solitary-only ( $n = 515$ ) and social-only ( $n = 118$ ) species to those presented in the main text.

**Table S5.** Model summary from categorical diet GLM.

**Table S6.** Model summary from numeric diet and bee family GLM, additive.

**Table S7.** Model summary from numeric diet and bee family GLM, interactive.

**Table S8.** Model summary from phylogenetic diet GLM, additive effect with bee family.

**Table S9.** Phylogenetic generalised least squares model table.

**Figure S1.** Map of convex hulls used to estimate range sizes.

**Figure S2.** Rarefaction of occurrence data to estimate EOO with exactly 15 occurrence records per species shows similar results to those presented in the main text.

**Figure S3.** Estimated marginal means of predicted range size by bee family.

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