

Resurrecting Historical Observations to Characterize Species-Specific Nesting Traits of Bumblebees

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ABSTRACT: In recent years, ecological research has become increasingly synthetic, relying on revolutionary changes in data availability and accessibility. In spite of their strengths, these approaches may cause us to overlook natural history knowledge that is not part of the digitized English-language scientific record. Here, we combine historic and modern documents to quantify species-specific nesting habitat associations of bumblebees (*Bombus* spp. Latreille, 1802 Apidae). We compiled nest location data from 316 documents, of which 81 were non-English and 93 were published before 1950. We tested whether nesting traits show phylogenetic signal, examined relationships between habitat associations at different scales, and compared methodologies used to locate nests. We found no clear phylogenetic signals, but we found that nesting habitat associations were somewhat generalizable within subgenera. Landcover associations were related to nesting substrate associations; for example, surface-nesting species also tended to be associated with grasslands. Methodology was associated with nest locations; community scientists were most likely and researchers using nest boxes were least likely to report nests in human-dominated environments. These patterns were not apparent in past syntheses based only on the modern digital record. Our findings highlight the tremendous value of historic accounts for quantifying species' traits and other basic biological knowledge needed to interpret global-scale patterns.

Keywords: *Bombus*, functional traits, habitat, hierarchical analysis, historic data, non-English.

Introduction

Many high-impact ecological studies published in recent years have leveraged “big-data” approaches to characterize large-scale patterns of species occurrence or widespread declines in abundance (Thomas et al. 2004; Powney et al.

2019; Engelhardt et al. 2022). To understand the mechanisms that drive these patterns, we need to understand the basic biology and natural history of species of interest. Unfortunately, collecting natural history information can be time-consuming, especially for animals that are cryptic, small-bodied, or otherwise difficult to track. Many species of insects meet all three of these criteria, at least during certain stationary life cycle stages, such as overwintering or pupation. These difficulties in monitoring have led to gaps in our understanding of basic natural history, even for model organisms (e.g., *Drosophila melanogaster* Meigen, 1830; see Markow 2015; Morimoto and Pietras 2020).

Written accounts of natural historians are an underutilized source of ecological data. These publications are not always included in the modern digital record; in our experience, many manuscripts may be obtainable only in hard-copy form or digitally as nonsearchable images. However, these records often contain relevant, place-based information, including detailed reports of singular observations (e.g., Le Souëf 1893; Howard 1918). Historic accounts have been used in combination with contemporary field studies to identify changes in avian community composition and species distribution (Lanctot et al. 2002; Alderson and Sander 2022) and have played an important role in characterizing phenomena like mass migrations of bumblebees (*Bombus* spp. Latreille, 1802 Apidae; Fijen 2020). These publications can also offer a wealth of natural history information for threatened species, which can be challenging to study in the modern era because of reduced occurrence. Summaries of natural history data may be found in modern books, which may or may not be available in digital form. In recent decades, groups such as the Biodiversity Heritage Library (established 2006; <https://www.biodiversitylibrary.org/>) have made a concerted effort

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to digitize older natural history notes, monographs, and expedition reports (e.g., Kalfatovic et al. 2019), creating greater opportunity to incorporate these documents into modern syntheses. However, as efforts to fully digitize these documents are currently underway, many historical documents are not yet part of the modern digital record.

In this study, we use a combination of historic naturalist notes and modern records to investigate the nesting ecology of bumblebees (*Bombus* spp.). Bumblebee conservation and habitat management are areas of growing research interest, as multiple bumblebee species have undergone dramatic declines over the last half century (Colla and Packer 2008; Graves et al. 2020). These large-bodied, highly charismatic insects have captured the interest of numerous natural historians and are relatively well studied in comparison to other bee taxa (Orr et al. 2022). However, the fact that bumblebee nest sites can be very difficult to find has created a major hurdle in studying these insects at the colony level (e.g., Liczner et al. 2021), leading to gaps in our understanding of critical stages of the bumblebee life cycle (US Fish and Wildlife Service 2018). To consolidate what is known about bumblebee nesting ecology, Liczner and Colla (2019) recently completed a systematic review of peer-reviewed publications focused on bumblebee nesting and overwintering, primarily targeting articles within the modern digital record. They could not characterize nesting habitat at the species level because of low sample sizes in the 55 articles they found. At the subgeneric level, bumblebees exhibited no clear preferences for landcover types or ground positions (e.g., belowground, on surface, aboveground). There were also no significant relationships between landcover associations and ground positions of nests.

Systematic literature reviews are generally considered to be less subjective and more exhaustive than traditional reviews based on author knowledge (Haddaway et al. 2015; Koutsof et al. 2019; Schmid et al. 2020). However, the methods relied on by modern literature reviews and meta-analyses also have significant limitations. First, these studies often rely on search engines like Web of Science and sets of standardized keywords to locate relevant articles (Tonietto and Larkin 2018; Schmid et al. 2020; Orr et al. 2022), which can bypass older natural history articles that have not been digitized. Second, thinning articles obtained via systematic reviews based on titles or abstracts can exclude those that include relevant information but do not explicitly mention the target of the search in the title or abstract. Third, many authors choose to exclude modern articles that are not written in English (Schmid et al. 2020), which may exclude relevant publications written in other languages (e.g., Pugsek et al. 2023). Last, publication biases may reduce the accessibility of some datasets; data that are not deemed worthy of publication could still be available in unpublished government reports (i.e., gray literature) or academic

dissertations but would not be included in a citation database (Schmid et al. 2020). Modern reviews of insect natural history that rely on these methodologies could thus be missing key historic information.

Here, we leverage a broad array of sources to characterize species-specific nesting habitat associations of bumblebees and explore the notion that nesting habitat associations of bumblebees are generalizable across evolutionary or ecological contexts. Using both modern and historic publications, we conducted an analysis of bumblebee nesting ecology using hierarchical mixed models. We used our dataset to evaluate (1) whether nesting habitat associations differ among subgenera or as a function of relatedness (i.e., phylogeny) and (2) whether nesting substrate associations are related to habitat associations at the landcover scale. From a methodological standpoint, we were also interested in quantifying (3) whether the strategies authors rely on to find bumblebee nests impact where nests are generally found. Our study is unusual in that we attempted to comprehensively synthesize historical natural observations across studies and combine them with modern data in a single analysis. To our knowledge, our study is the first to formally relate phylogenetic relationships to nesting habitat associations of bumblebees.

Material and Methods

Literature Search

We relied on several methods to compile articles that describe bumblebee nests or nesting habitat. Most articles were identified via a “snowball” literature review; this review method uses citations and reference lists of known articles to identify additional articles or documents (including books, theses, scientific papers, and unpublished research reports). We began our snowball search with a recently published review of *Bombus* nesting ecology (Liczner and Colla 2019), which used Web of Science to identify 55 articles focused on *Bombus* nesting habitat (44 of which described nest sites). To identify articles published after Liczner and Colla’s review, we performed a similar search of Web of Science for articles published between February 5, 2018, and February 9, 2022, using the keywords (nest*) AND (bombus OR “bumble bee” OR bumblebee) AND (habitat OR resource*). We scanned the abstracts of these articles ($N = 108$) to identify additional articles that described nest sites. Last, we identified documents via less formal methods, including prior knowledge of the literature, keyword searches of Google Scholar, and suggestions from social networking sites. We excluded all articles written before 1850, as language referring to habitat types was often ambiguous in relation to modern English.

We ceased our literature review after reading and extracting usable records of bumblebee nests from

316 documents (for a full list of citations, see the supplemental PDF, sec. A). At this point, most of the new material we encountered duplicated studies we had found, included no usable data, or were too degraded to translate. Of these 316 documents, 263 were identified via the snowball search starting with the Liczner and Colla (2019) review, 10 were identified via Web of Science, and 43 were identified via less formal methods (i.e., keyword searches of Google Scholar). We did not keep a complete record of the number of documents we identified as potentially relevant to our review; however, we approximate that usable data were extracted from ~75% of the documents we read in their entirety and ~50% of the documents that we identified as “potentially relevant” and at least skimmed or read in part. In some cases, the same nests were described in multiple documents (see, e.g., Matsumura et al. 2004; Inoue et al. 2008). To ensure potential duplicates were excluded from our dataset, we read articles by the same authors in sets within the same week and cross referenced the data described in each document. We were fairly conservative with these calls; if there was any possibility a nest was described more than once, the nest was considered a duplicate observation.

The majority of documents included in our meta-analysis were published in English ($N = 235$) or German ($N = 37$), in which we are fluent. For the remaining documents ($N = 44$), which were published in languages not spoken and read by the author group, we relied on volunteer colleagues who synthesized the data presented using a standardized form ($N = 12$) or used DeepL or Google Translate to extract data ($N = 32$). DeepL or Google Translate was also used occasionally to translate German-language documents.

Data Extraction

For each nest referenced in a document, we recorded the *Bombus* species using the nest site as well as a description of nesting habitat. Where applicable, we assigned each record to a modern species name, using the assumption that the taxon in each study was identified correctly (including names now placed into synonymy; see the supplemental PDF, sec. B). If the species using the nest site was not clearly referenced, we recorded that the nest was used by an unknown *Bombus* species (see the supplemental PDF, sec. B). Species IDs were used to assign each record to a subgenus, using the simplified subgenetic classification of Williams et al. (2008). Nesting habitat was defined at two spatial levels: (1) the nest position and (2) the landcover category where nests were found. Nest positions were classed into three broad categories: “belowground,” “surface,” and “aboveground” (supplemental PDF, sec. C, table C1). Landcover types were classed into six broad categories: “woodland or forest,” “grassland or shrubland,” “developed open space,”

“cropland,” “structure,” and “other” (supplemental PDF, sec. C, table C1). In cases where the colony was parasitized or usurped by another bumblebee species, we made two records of the nest site (one for each species that used the nest). If the exact number of nest sites located was not described (i.e., the author referenced finding “several” or “multiple” nests with similar nesting habitat associations), we approximated sample sizes (e.g., if the author referenced finding “several” or “a few” nests, we duplicated the observation by three).

Each record of a nest site was assigned to a study region, using latitude and longitude obtained from publications or approximated from descriptions of study sites. Study regions were classed into 10 categories: “polar,” “tropical New World,” “tropical Old World,” “temperate North America,” “temperate South America,” “temperate Europe or Middle East” (excluding the United Kingdom and Ireland), “UK/Ireland,” “temperate Asia” (excluding Japan), “Japan,” and “Oceania.” (Note: areas classed as temperate may also include alpine tundra as well as areas with dry or continental climates; see, e.g., Kottek et al. 2006).

We also made note of the methodology investigators relied on to find nests. Although many nests were found incidentally, investigators also used more systematic methods to find nests. We classed the methodologies used to locate nests into three categories: “surveys or incidental encounters by researchers” (where a researcher found a nest incidentally or via formal plot/transect survey), “surveys or incidental encounters by community scientists” (where data collected by nonscientists were reported by researchers), or “nest box studies” (where researchers put out nest boxes and recorded whether the box was occupied by bumblebees).

Records of nest positions and landcover-type associations were converted into binary datasets prior to statistical analyses in order to analyze data using binomial mixed models (there are no standard approaches for multinomial mixed models with the phylogenetic and random effects needed for our analyses; see “Statistical Methods” below). Nest positions were converted into three binary variables: aboveground (=1) or other (=0), surface (=1) or other (=0), and belowground (=1) or other (=0). Landcover associations were converted into five binary variables using the same strategy (excluding observations classed as other). In some cases it was obvious a nest did not fall within a certain category, although we could not confidently assign the nest to one of the remaining categories. For example, from the phrase “the nest was found in a haystack” it is clear that the nest is not subterranean, but it is unclear whether the nest is on the surface of the ground or aboveground. For these observations, we extracted whatever data we could by recording other (=0) for categories that could be excluded and not applicable (=NA) for other categories.

Thus, the proportion of nests found in each nest position or landcover type was not constrained to sum to 1.

Statistical Methods

To identify taxonomic and phylogenetic patterns in the nesting habitat associations of bumblebees, we used generalized linear mixed effects models (GLMMs) and phylogenetically corrected generalized linear mixed effects models (binomial family, logit link). All statistical analyses were performed in R version 4.0.2 (R Core Team 2020). For these analyses, we excluded data collected by community scientists or during nest box studies in order to better represent wild nests (see “Results”). For each binary response variable related to nest position ($N = 3$) and landcover type ($N = 6$), we ran a set of four models with different random effects structures. All models in each set included random effects of study region and author ID: model 1 (the null model) included no additional random effects, model 2 included an additional random effect of species ID, model 3 included additional random effects of species ID and subgenus, and model 4 included a phylogenetic covariance matrix. GLMMs were fitted using the command `glmer()` in the R package `lme4` (Bates et al. 2015). Phylogenetically corrected GLMMs were fitted using the command `phylo_glmm()` in the R package `phyloglmm` (Li and Bolker 2022). We used the most comprehensive phylogenetic tree for *Bombus* (Cameron et al. 2007; Hines 2008), which represented a global collection of 218 *Bombus* species. We loaded this tree (tree ID Tr2906) from <https://treebase.org> using the R package `treebase`. We pruned the tree to include only species represented in our historic datasets (87 species specifying nest position and 77 species specifying landcover associations). We used the R package `ape` to calculate branch lengths using Grafen’s (1989) method with power (ρ) set to 1. The four models in each set were ranked and compared using the Akaike information criterion (AIC) implemented using the `ICtab()` function in R. Because model comparison requires analyzing the same dataset, we removed records that could not be included in phylogenetically corrected models from datasets prior to model fitting, including observations of unknown *Bombus* species and of five *Bombus* species (*B. brevivillus* Franklin, 1913; *B. glacialis* Friese, 1902; *B. inexpectatus* Tkalců, 1963; *B. cullumanus* Kirby, 1802; *B. pyrrhopygus* Friese, 1902) that were missing from the phylogenetic tree. We repeated all analyses using a tree with branch lengths based on genetic divergence that did not include three additional species (supplemental PDF, sec. C, tables C2, C3). These analyses led to similar conclusions and are not discussed further.

To obtain species-specific probabilities of being found in a given nest position or landcover type, model coefficients were extracted from the species ID model for each response

variable (model 2 above; see extended description in the supplemental PDF, sec. D). Because species coefficients were estimated as random variables, species-specific probabilities were calculated using partial pooling. Thus, we were still able to generate estimates for species that were encountered infrequently, although we note that estimates for species with few observations were based partially on data from common species. For ease of interpretation, model coefficients were corrected for Jensen’s inequality (supplemental PDF, sec. D).

We used the model coefficients extracted from the species ID model to explore relationships between bumblebee habitat associations at different scales. Separate univariate linear models were fitted to each combination of predictor (logit-scale estimations of the proportion of nests found in grasslands/shrublands, forests/woodlands, and structures) and response variable (logit-scale estimations of the proportion of nests found aboveground, belowground, and on the surface of the ground). Associations with two landcover categories (croplands and developed open space) were not included in this set of analyses, as relatively few species were ever encountered in either of these landcover types. We used Wald χ^2 tests implemented with the `Anova()` function in the package `car` (Fox and Weisberg 2019) to obtain P values.

To test whether the methodologies investigators relied on to obtain data were related to nesting habitat associations, we used generalized linear models (binomial family, logit link). For all models, the methodology used to locate nests was used as a predictor variable, while author, region, and bumblebee species were included as random effects. We ran separate models for each binary response variable associated with nest position ($N = 3$) and landcover ($N = 5$). For these analyses, we included all records (including those for unknown *Bombus* species) in our dataset, as records collected by community scientists were often presented according to color groupings (e.g., Fussell and Corbet 1992). We used Wald χ^2 tests implemented with the `Anova()` function in the package `car` (Fox and Weisberg 2019) to obtain P values. For ease of interpretation, model coefficients corrected for Jensen’s inequality (see the supplemental PDF, sec. D) are reported.

Results

Nest Record Overview

We obtained descriptions of 9,564 nests, representing 102 different bumblebee species (i.e., approximately 40% of globally recorded species within the genus *Bombus*). The majority of nests ($N = 9,201$) were found in temperate regions; 67 nests were found in tropical regions, 208 nests were found in polar regions, and 16 nests were not assigned to a specific region. These records represent a total of 45 countries (fig. 1). Of the 9,564 total nest records,

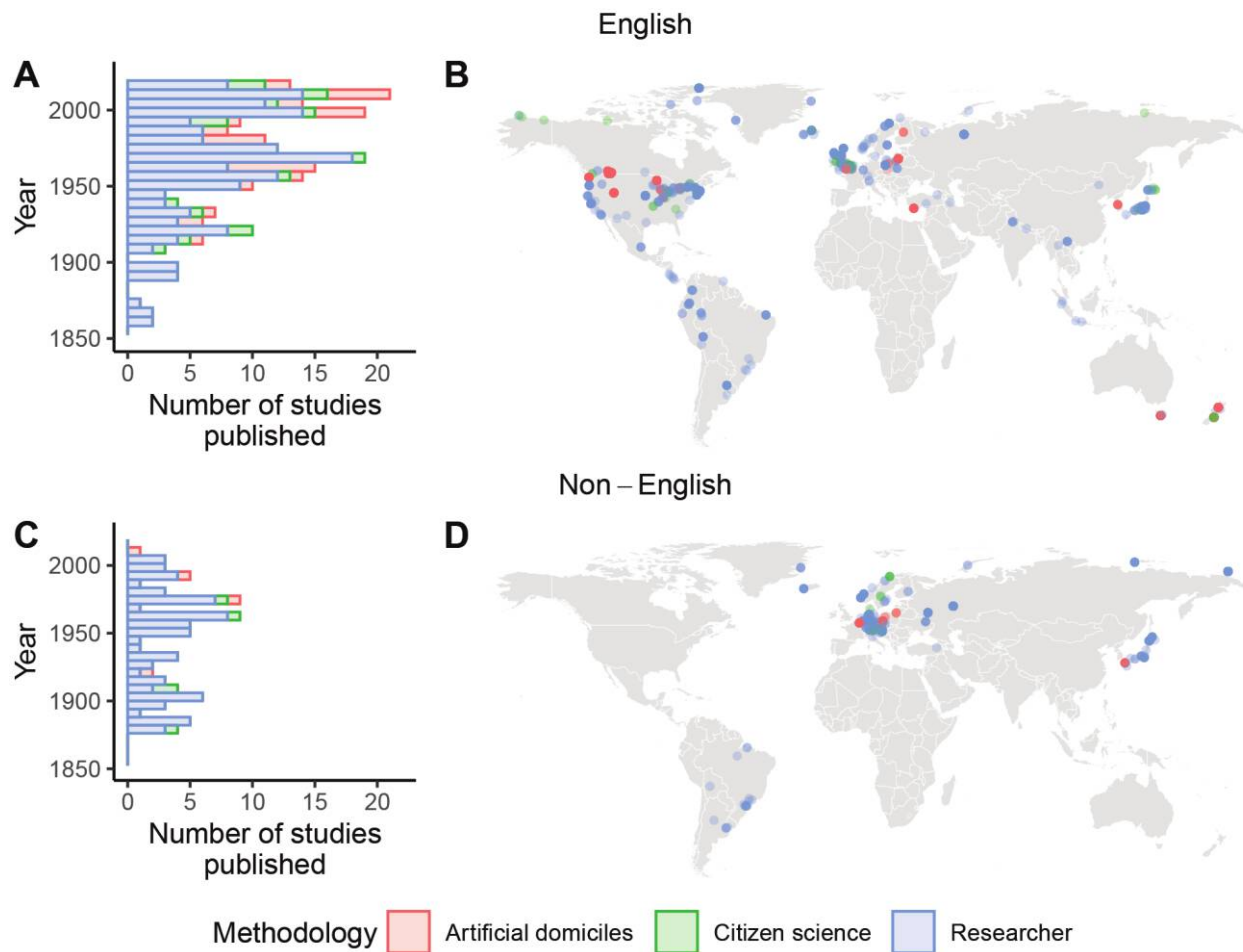


Figure 1: Histogram of the number of studies published each year and maps of study locations for publications written in English (A, B) and publications written in languages other than English (C, D). Each point on the map represents a nest site location; red points represent nests found in nest boxes, and blue and green points represent nests found by researchers and community scientists, respectively.

9,077 could be assigned to a specific landcover or substrate category. Of these relevant descriptions, 3,453 were of nests obtained using nest boxes (representing 44 species), 3,114 were of nests located by community scientists (representing 30 species), and 2,510 were of nests located by researchers or natural historians (representing 97 species). Of the 97 species encountered by researchers or natural historians, substrate-level associations were recorded for 92 species (~65% of which were represented by five or more nests; see fig. 2), whereas landcover-level associations were recorded for 80 species (~50% of which were represented by five or more nests).

Associations with Ground Position

Ground position associations of nesting bumblebees were species specific (fig. 2). For all sets of models, models that included species as a random effect ranked bet-

ter than the null model, which did not include species as a random effect (i.e., nesting habitat associations differed significantly among species; table 1). Ground position associations were highly variable across species. Species-specific estimates of the proportion of nests found belowground, on the ground surface, and aboveground ranged from 0.02 to 0.97, from 0.01 to 0.94, and from 0.03 to 0.81, respectively (see fig. 2; supplemental PDF, sec. C, table C4).

Ground position associations also differed among subgenera. For the sets of models used to estimate the probability that nests were found on the ground surface and the probability that nests were found below the ground, the highest-ranking models included random effects of species and subgenus (for all model comparisons, $\Delta AIC > 2$; table 1). Most notably, species belonging to the subgenus *Thoracobombus* Dalla Torre, 1880, were most likely to nest on the surface of the ground, whereas species belonging to the subgenus *Bombus* s. str. Latreille, 1802, were most likely

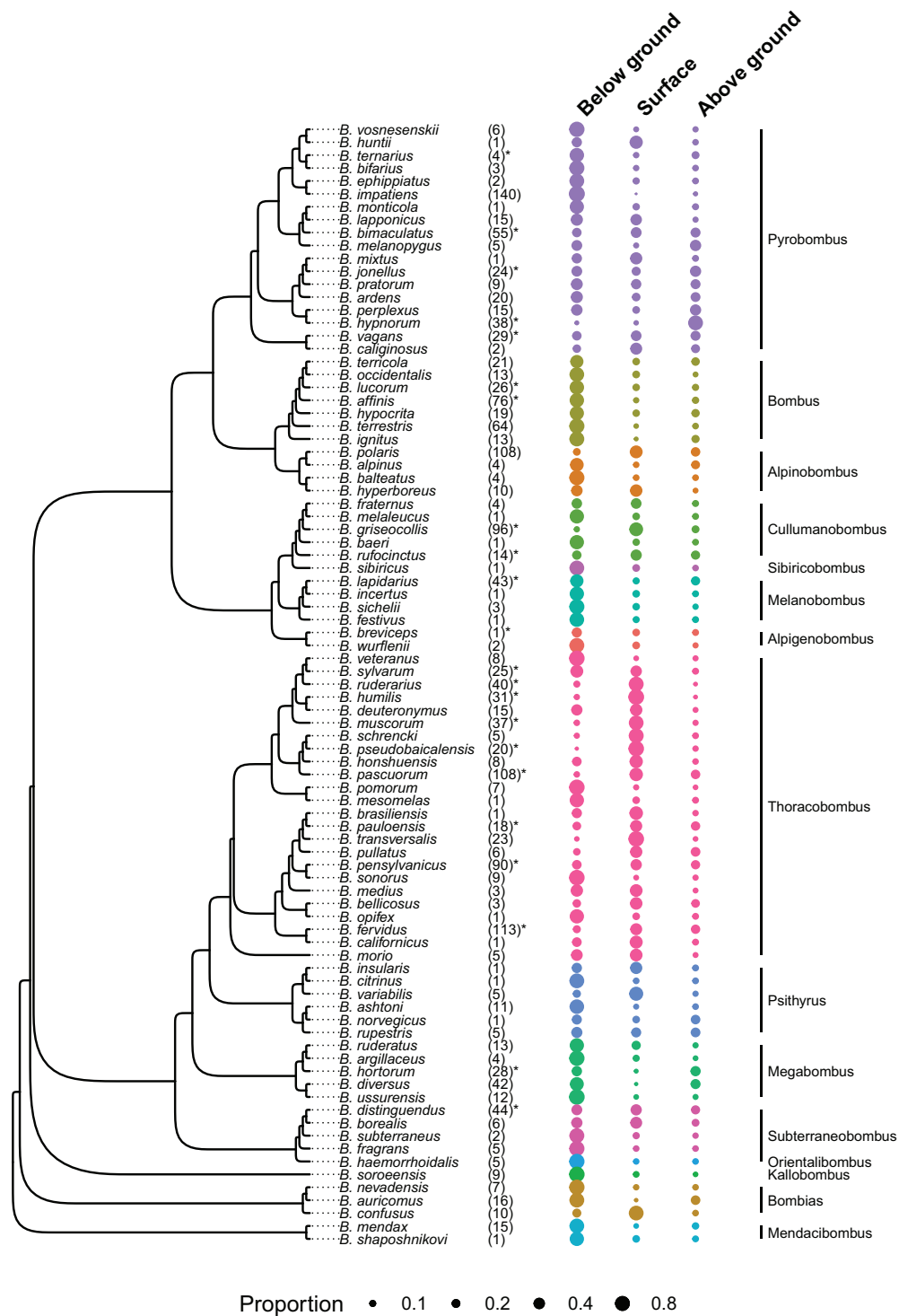


Figure 2: Ground positions of bumblebee nests mapped to a phylogeny. Colored points depict species-specific estimates of the proportion of nests found in each nest position extracted from mixed models that include random effects of geographic region, author ID, and species ID (for all predictors, this model was among the highest ranking). Values presented were corrected for Jensen's inequality. Sample sizes (i.e., the number of nests) are presented as values alongside species names. For 23 species, sample sizes were not equivalent for each set of models; for these species, the lowest sample size is listed and denoted by an asterisk.

Table 1: Akaike information criterion (AIC) statistics for competing generalized linear mixed models and phylogenetically corrected models (family = binomial) used to estimate the proportion of nests found in each ground position or landcover type

Response, model ^a	AIC/ΔAIC	df	Weight	Random effect variance			
				Author	Region	Species	Subgenus
Belowground:							
M_{AR}	1,970.9 (558.0)	3	.00	3.07	.39	...	...
M_{ARS}	1,416.9 (4.1)	4	.11	1.79	.04	7.57	...
M_{ARSS}	1,412.8 (.0)	5	.89	1.77	.01	5.65	1.29
M_{ARP}	1,438.3 (25.5)	4	.00	2.01	.00	64.01	...
Surface:							
M_{AR}	1,760.4 (552.2)	3	.00	3.35	.84	...	...
M_{ARS}	1,222.0 (13.7)	4	.00	3.27	.00	10.46	...
M_{ARSS}	1,208.3 (.0)	5	1.00	3.16	.00	5.44	2.62
M_{ARP}	1,233.0 (24.7)	4	.00	3.05	.00	75.94	...
Aboveground:							
M_{AR}	1,013.5 (129.8)	3	.00	4.95	.00	...	...
M_{ARS}	883.7 (.0)	4	.55	5.93	.00	4.57	...
M_{ARSS}	884.2 (.4)	5	.45	5.82	.00	3.66	.36
M_{ARP}	902.2 (18.5)	4	.00	4.62	.00	15.63	...
Grassland and shrubland:							
M_{AR}	1,111.3 (147.0)	3	.0	10.34	6.17	...	...
M_{ARS}	964.3 (.0)	4	.73	11.69	4.33	5.51	...
M_{ARSS}	966.3 (2.0)	5	.27	11.68	4.33	5.51	.00
M_{ARP}	990.5 (26.2)	4	.0	12.15	6.89	39.05	...
Forest and woodland:							
M_{AR}	835.2 (83.3)	3	.00	4.36	3.31	...	...
M_{ARS}	752.0 (.0)	4	.73	5.38	.00	7.67	...
M_{ARSS}	754.0 (2.0)	5	.27	5.38	.00	7.67	.00
M_{ARP}	772.3 (20.3)	4	.00	5.11	.00	80.83	...
Structure:							
M_{AR}	731.0 (89.4)	3	.00	7.90	.91	...	...
M_{ARS}	641.6 (.0)	4	.63	13.66	.49	6.11	...
M_{ARSS}	642.6 (1.1)	5	.37	12.83	.56	5.26	.51

Table 1 (Continued)

Response, model ^a	AIC/ΔAIC	df	Weight	Random effect variance			
				Author	Region	Species	Subgenus
M_{ARP}	663.5 (21.9)	4	.00	9.65	2.11	19.52	...
Developed open space:							
M_{AR}	410.8 (12.9)	3	.00	35.00	.07	...	...
M_{ARS}	398.5 (.6)	4	.43	39.69	.00	2.44	...
M_{ARSS}	397.9 (.0)	5	.56	58.09	.15	1.41	1.13
M_{ARP}	405.8 (8.0)	4	.01	11.60	5.96	2.95	...
Cropland:							
M_{AR}	219.5 (13.1)	3	.00	156.90	7.54	...	...
M_{ARS}	206.4 (.0)	4	.72	419.8	.00	230.4	...
M_{ARSS}	208.4 (2.0)	5	.27	419.7	.00	230.3	.00
M_{ARP}	214.9 (8.5)	4	.01	188.18	9.34	1.65	...

^a All models included random effects of author ID and study region: model 1 (M_{AR}) included no additional random effects, model 2 (M_{ARS}) included an additional random effect of species ID, model 3 (M_{ARSS}) included additional random effects of species ID and subgenus, and model 4 (M_{ARP}) included a phylogenetic covariance matrix.

to nest belowground (for all subgenus-specific estimates of the proportion of nests found at each ground position, see the supplemental PDF, sec. C, table C5). In contrast, for the set of models used to estimate the probability that nests were found above the ground, the highest-ranking model included only random effects of species (table 1). *Bombus hypnorum* Linnaeus, 1758, which belongs to the subgenus *Pyrobombus* Dalla Torre, 1880, was the only *Bombus* species found to generally nest aboveground (fig. 2).

Associations with Landcover

Landcover associations of nesting bumblebees were species specific, and there were no obvious phylogenetic or taxonomic signals in these associations. For nearly all sets of models, the model with the lowest AIC included species, author, and region as random effects (table 1). For the set of models that estimated the proportion of nests found in developed open space, the model with the lowest AIC included subgenus as a random effect; however, the AIC for this

model was nearly equivalent to the one without subgenus ($\Delta AIC = 0.6$; table 1). Landcover associations were highly variable across species; species-specific estimates of the probability that nests were found in a given landcover type ranged from 0.07 to 0.69 for grasslands/shrublands, from 0.02 to 0.72 for woodlands/forests, from 0.06 to 0.58 for structures, from 0.10 to 0.23 for developed open spaces, and from 0.11 to 0.33 for croplands (fig. 3; supplemental PDF, sec. C, table C4).

Relationships between Ground Position and Landcover

Associations with specific ground positions were related to habitat associations at the landcover scale. *Bombus* species that tended to nest above the ground were more likely to be associated with structures ($F = 63.21$; $df = 1, 76$; $P < .0001$; fig. 4) and were less likely to be associated with grasslands/shrublands ($F = 4.75$; $df = 1, 76$; $P = .03$; fig. 4) relative to other landcover types. In contrast, *Bombus*

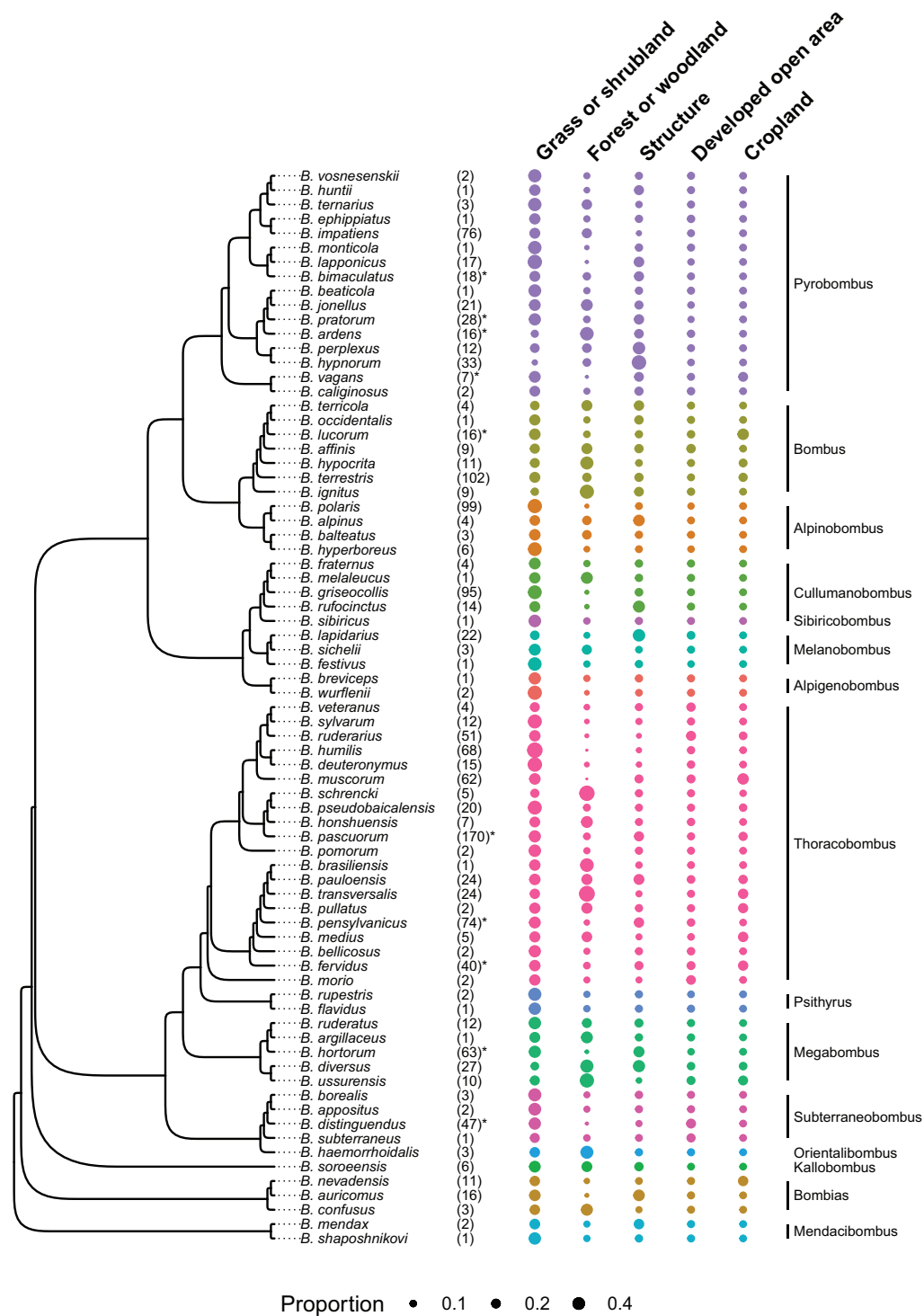


Figure 3: Landcover associations of bumblebee nests mapped to a phylogeny. Colored points depict species-specific estimates of the proportion of nests found in each landcover type extracted from mixed models that include random effects of geographic region, author ID, and species ID (for all predictors, this model was among one of the highest ranking). Values presented were corrected for Jensen's inequality. Sample sizes (i.e., the number of nests) are presented as values alongside species names. For 10 species, sample sizes were not equivalent for each set of models; for these species, the lowest sample size is listed and denoted by an asterisk.

species that tended to nest on the ground surface were more likely to be associated with grasslands/shrublands ($F = 10.12$; $df = 1, 77$; $P = .002$; fig. 4) and were less likely to be associated with structures ($F = 9.64$; $df = 1, 77$; $P = .003$; fig. 4) relative to other landcover types. For *Bombus* species that tended to nest belowground, there were no obvious associations with specific landcover types, nor were there any obvious associations between *Bombus* species that tended to nest on the ground surface or aboveground and forests/woodlands (for all models, $P > .05$; fig. 4).

Relationships between Nest Locations and the Methodology Used to Find Nests

Habitat associations differed among nests obtained via nest boxes, nests found by community scientists, and nests found by researchers. Methodology was a significant predictor of the probability that nests were found in four of the five landcover types tested (grasslands/shrubland, forests/woodland, structure, croplands) as well as all ground positions (aboveground, belowground, and on the ground surface; $\chi^2 > 7$, $P < .03$ for all comparisons; see the supplemental PDF, sec. C, table C6).

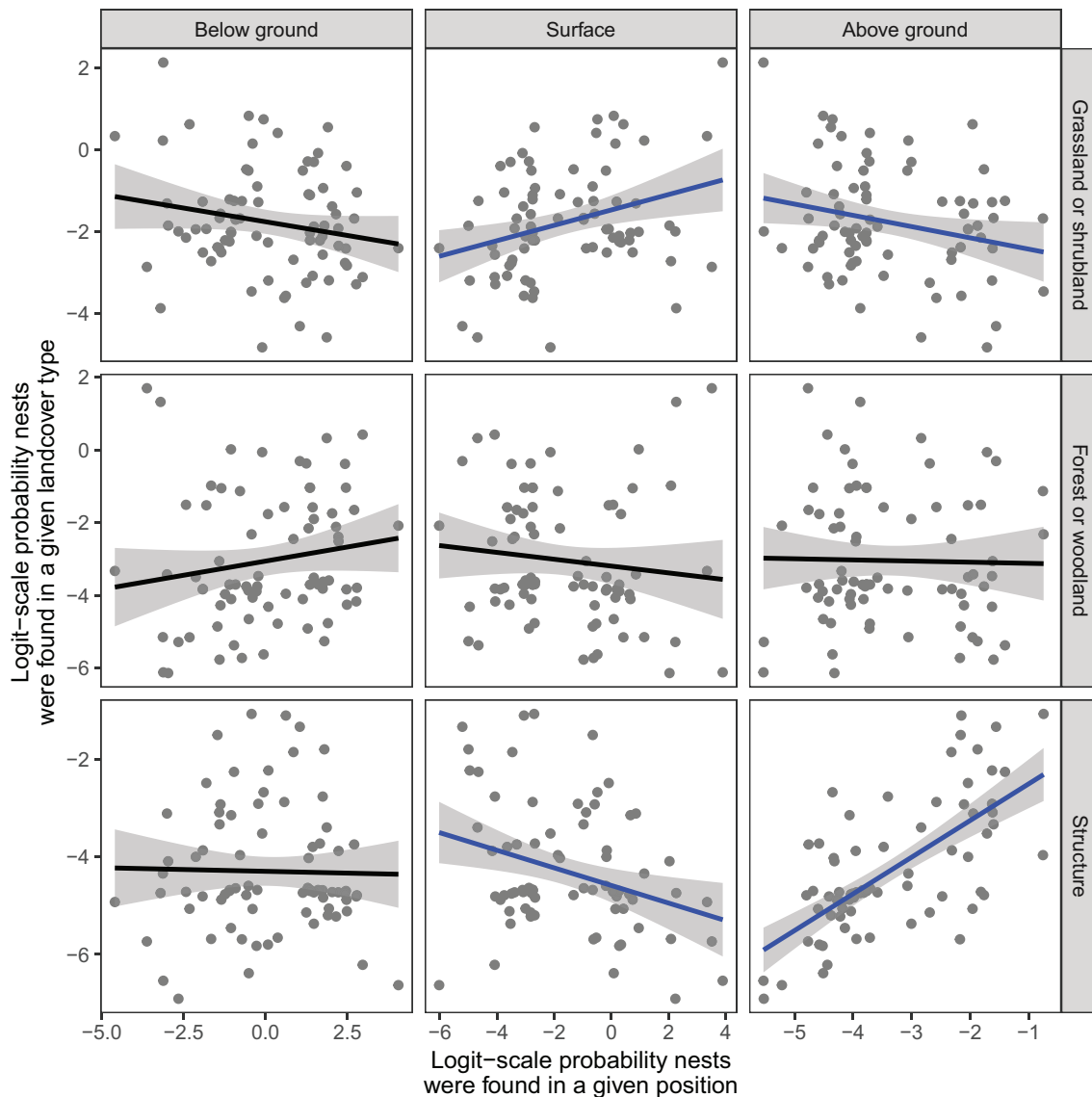


Figure 4: Relationships between landcover associations and nest positions among bumblebee species. Each point represents a single species; significant and nonsignificant relationships are represented by blue and black lines, respectively. Species-specific estimates of the proportion of nests found in each landcover type and in each position were calculated from coefficients extracted from mixed models that include random effects of geographic region, author ID, and species ID (see “Methods”). Model coefficients are presented on a logit scale.

Nests obtained via nest boxes were the most dissimilar from other groups. Specifically, nests in nest boxes were more likely to be found in natural areas (e.g., grasslands and forests) and were less likely to be found in highly modified environments (e.g., croplands) relative to naturally established nests located by community scientists or researchers (fig. 5B). There were also differences in substrate-scale nesting habitat associations between nests found via nest boxes and other groups. Compared with nests found by researchers, nests obtained via nest boxes were more likely to be found above the ground and were less likely to be found on the surface of the ground (fig. 5A). Compared with nests found by community scientists, nests obtained via nest boxes were less likely to be found below the ground (fig. 5A).

There were also differences in nesting habitat associations of nests found by researchers and by community scientists at both the substrate and the landcover scale. Compared with nests found by researchers, nests found by community scientists were more likely to be found above the ground (fig. 5A) and in structures (fig. 5B) and were less likely to be found in grasslands/shrublands (fig. 5B).

Discussion

In recent years, there have been repeated calls for ecologists to revitalize the discipline of natural history, often with emphasis on recording contemporary observations (Tewksbury et al. 2014; Anderson 2017). Our study showcases the importance of revisiting historical publications and other records to ensure that natural history information is not lost or forgotten by the broader scientific community. By leveraging records of bumblebee nests from a variety of sources, we were able to identify species-specific nesting habitat associations for 94 species of bumblebees, including several listed as vulnerable (e.g., *B. pensylvanicus* De Geer, 1773; *B. medius* Cresson, 1863) or endangered (e.g., *B. affinis* Cresson, 1863; *B. fraternus* Smith, 1854; *B. inexpectatus* Tkalců, 1963) by the IUCN Red List (IUCN 2023) and more than half of which were represented by five or more occurrences. We found that patterns of nesting habitat use are highly variable across species. This result challenges a paradigm related to bumblebee nesting ecology proposed by other authors: that bumblebees are nesting habitat generalists at the species (Lye et al. 2012), subgeneric (Liczner and Colla 2019), and regional (Bruninga-Socular et al. 2022) levels. Many bumblebee species are flexible in their nesting habitat use; however, this plasticity does not mean that other species do not have specific habitat requirements or preferences or that habitat requirements are interchangeable. Documenting differences in patterns of habitat use is a first step in understanding life history differences among bumblebee species and in informing species-specific management guidelines.

Over the past 20 years, there has been growing recognition in the field of evolutionary ecology that it is important to quantify phylogenetic signals in assessments of functional traits (see, e.g., Blomberg et al. 2003). We found that model fit was never improved by including a phylogenetic covariance matrix compared with models that included species and subgenus as a random effect. This result is consistent with the generalization that phylogenetic signals of behavioral functional traits tend to be poorly conserved, in comparison to morphological or physiological traits such as body size, thermal minima and maxima, and so on (Blomberg et al. 2003; Eterovick et al. 2010; Kamilar and Cooper 2013). At the same time, we found that including subgenus as a random effect improved model fit for nest position, suggesting that bumblebee nesting habitat associations are at least somewhat generalizable among related taxa. This finding contrasts with the findings of Liczner and Colla (2019), who detected no clear taxonomic patterns of bumblebee nesting habitat use. Our results suggest some niche similarities between closely related species, which implies that observations of closely related taxa may be used to better understand the habitat needs of rare species, at least in some contexts.

We found that the ground position associations of bumblebee nests were related to landcover associations, at least in some cases. It is particularly notable that surface-nesting bumblebee species were associated with grasslands and shrublands, as similar patterns have been noted for bumblebees by individual studies. For example, in North America several surface-nesting *Bombus* species have been characterized as grassland associated (e.g., *B. pensylvanicus* [Liczner and Colla 2020]; *B. fervidus* Fabricius, 1798 [Mola et al. 2021]). Aboveground nesting species, in contrast, tended to be associated with structures. The tree bumblebee (*B. hypnorum*) was one of the few species to show a strong association with aboveground nest sites (fig. 2); this species has been associated with suburban areas and forests by other authors (Prŷs-Jones 2014, 2019; Mola et al. 2021). It is likely that these patterns are at least partially driven by differences in nesting substrate availability across landcover types. For example, naturally occurring aboveground nest sites were almost always found in tree cavities or in bird's nests in trees and were thus rarely encountered in grassland systems. Further research is needed to tease apart the relationships between bumblebee substrate preferences and local landscape or management context.

Interestingly, we found that patterns of nesting habitat use were similar across geographic regions. Bumblebees are a diverse clade; although bumblebee diversity is highest in temperate regions, bumblebees can be found in many biomes, including arctic tundra and tropical lowland rainforest. Random effects of geographic region accounted for little to no variation in our models; however, it is

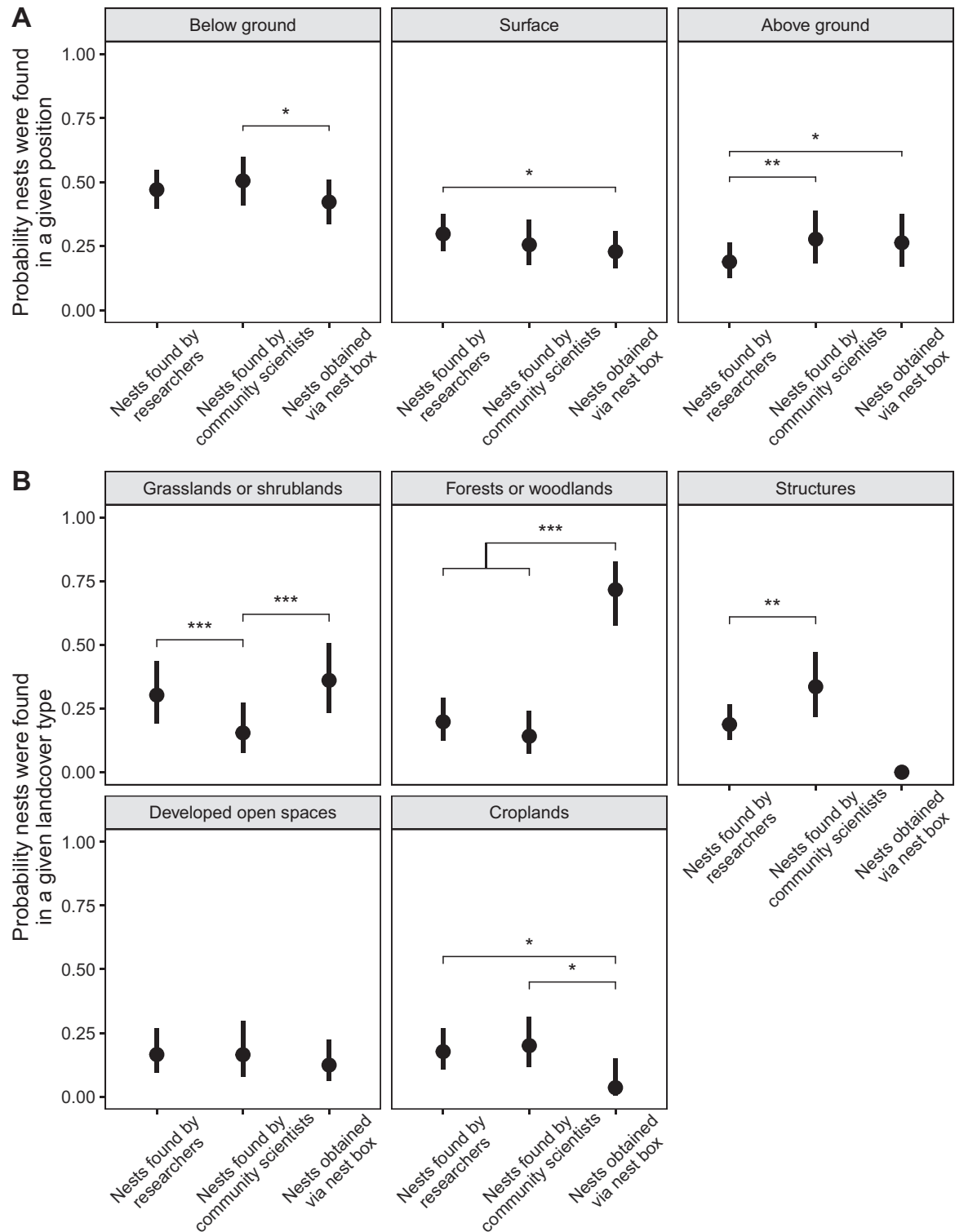


Figure 5: Proportion of nests found in each ground position (A) and in each landcover type (B) across methodologies. Estimates were corrected for Jensen's inequality (see "Methods"). Asterisks indicate significant pairwise comparisons (one asterisk represents P values between .01 and .05, two asterisks represent P values between .001 and .01, and three asterisks represent P values less than .001).

difficult to disentangle variance attributable to region versus subgenus. For example, past authors have noted that belowground *Bombus* nests are less common in tropical rainforests, potentially because subterranean cavities are susceptible to flooding (Licznier and Colla 2019). However, only a handful of *Bombus* species are present in the tropics of South America, many of which belong to the subgenus *Thoracobombus*, a group of surface nesters (supplemental PDF, sec. C, table C7). Improved coverage of geographic regions like the rainforests of Asia as well as dryer areas of the United States could be useful in understanding the relationships between bumblebee habitat associations and climatic and geographic variables.

Non-English documents contained valuable natural history information; as expected (Konno et al. 2020; Amano et al. 2021), the inclusion of these publications in our analysis improved our coverage of several geographic regions, including Japan, mainland Europe, and South America. Nonetheless, the majority of our observations were from majority English-speaking countries (the United Kingdom, the United States, New Zealand, Australia, and Canada): 53% of nests found by researchers, 83% of nests found in nest boxes, and 98% of nests found by community scientists. Geographic skew may be partly due to high bumblebee diversity in temperate regions, although bumblebee diversity is also high in several regions poorly represented in our study (e.g., China; Williams et al. 2017). Geographic skew could have also arisen because of challenges in obtaining data from non-English language articles, as we encountered several language-based barriers in extracting data from non-English documents. First, locating digitized copies of non-English-language documents was more difficult than locating English documents. Although articles from journals based in the United Kingdom or the United States were often readily found via the Biodiversity Heritage Library, locating non-English articles often required librarian assistance. Second, both strategies we used to translate articles came with challenges. Volunteers who could read articles were difficult to recruit and, as nonexperts, were sometimes uncomfortable in interpreting scientific descriptions of nests. Oppositely, using translation software likely led to more errors in translation but allowed experts to interpret descriptions. It was particularly difficult to translate documents written in non-Latin alphabets (e.g., Russian and Japanese). A valuable next step could be for scientists from multiple regions of the world to work cooperatively (e.g., Orr et al. 2022) to synthesize natural history information at a global level.

Although our approach substantially expands taxonomic breadth and sample sizes, many reports of bumblebee nests were anecdotal and sample sizes for some taxa were low. Using a hierarchical modeling framework was advantageous in that all observations could be included in our analyses.

Within this framework, however, coefficient estimates for taxa with low sample sizes are strongly informed by the group mean, a phenomenon commonly referred to as shrinkage (see, e.g., Gelman et al. 2013). Given that approximately half of the species included in our study were represented by fewer than five occurrences, model coefficients for species poorly represented in our dataset (e.g., *B. huntii* Greene, 1860; *B. mixtus* Cresson, 1879) should be interpreted with caution. Even for species that are well represented in the dataset by anecdotal observations, reports are still likely subject to survey bias, as are other forms of presence-only data (e.g., eBird data; Scher and Clark 2023). Bumblebee nests are harder to detect in some landcover types than others; for example, Pugsek and Crone (2021) reported lower detection rates of nests in forests than grasslands, which is consistent with lower incidences of nests in forests in our current cross-species analysis. Some natural historians may also have been inclined to describe encounters that they found especially interesting (“an unusual bumblebee nest”; Howard 1918).

Finally, we found that nest locations depended on the methodology used to obtain nests: community science, nest boxes, or researcher-collected data. Community science programs are widely regarded as an important component of “next-generation natural history” (Tosa et al. 2021), a trend that may be especially appealing for bumblebees (e.g., Fussell and Corbet 1992; Osborne et al. 2008; Lye et al. 2012; Boone et al. 2022). Nonetheless, data collected by community scientists often overrepresent urban or suburban areas (e.g., Ward 2014; Wolf et al. 2022). In our data, community scientists often described nests located in human-made substrates, including birdhouses, compost piles, and so on, whereas researchers were more likely to encounter nests in natural substrate, likely because these individuals were searching for nests in nature preserves and rural areas (e.g., Harder 1986). Similarly, our results suggest that nest boxes do not always lead to a representative sample of bumblebee communities, at least compared with the presence-only observations made by researchers and natural historians. Nest box studies are generally systematic and have proven useful in exploring habitat preferences of vertebrates (Goldingay et al. 2020; Kamm and Reed 2020). Nonetheless, researchers who study avian nesting ecology have raised concerns that nest boxes may bias understanding of target species ecology and natural history (Møller 1994). For bees, the difference between habitat associations of nests in nest boxes and researcher observations could reflect a bias in either direction. To assess the cause of these discrepancies, we would need systematic searches of different habitat types, with a record of search effort (Pugsek and Crone 2021). Of course, this recommendation comes with the caveat that systematic searches are highly labor intensive with current methodologies (see, e.g., O’Connor et al. 2012; Iles et al. 2019; Licznier et al.

2021). At a minimum, minor shifts in collection protocols, such as designating survey locations via BioBlitz activities or using systematic protocols (e.g., UK National Bumblebee Nest Survey; Osborne et al. 2008), could make community science efforts more representative of landcover types outside suburban or urban areas.

Understanding natural history is an essential first step in understanding the mechanisms that drive patterns of abundance and in designing effective conservation strategies for threatened species. Our study showcases the value of historic written records for enhancing basic biological knowledge, especially in the early stages of identifying critical habitat. Our work could directly benefit local governmental and intergovernmental entities responsible for defining legal protections for threatened species. We are hopeful that similar efforts to consolidate natural history information will be equally valuable in understanding other aspects of bumblebee life history and the habitat requirements of other taxa. Reviews of natural history information are particularly valuable in that they can draw from many sources, including non-English-language documents and knowledge derived from diverse methods that might not make it into peer-reviewed journals. In addition to filling critical knowledge gaps for conservation, utilizing this knowledge base can at least partly help overcome geographic biases that have generally led to the overrepresentation of high-income, English-speaking nations in our global understanding of biology, ecology, and conservation.

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Statement of Authorship

All authors contributed to the study's conception and design. Review of the literature was performed by G.P. and U.M. Data analysis was performed by G.P. and E.E.C. The first draft of the manuscript was written by G.P.; all authors commented on subsequent versions and read and approved the final manuscript.

Data and Code Availability

To better ensure reproducibility of results, code and data associated with this article have been deposited in Figshare (<https://doi.org/10.6084/m9.figshare.23552739.v1>; Pugsek et al. 2024). To improve reusability of datasets, we include information extracted from documents that was not used in our statistical analysis (e.g., detailed notes on nest locations and substrate used by nesting bumblebees, descriptions of study sites, notes on the elevation at which nests were found). Note that our results are not fully reproducible from the code and datasets uploaded to Figshare, as data from one unpublished report protected by copyright (Montgomery 1958) has been excluded from datasets.

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