

Toward a functional trait approach to bee ecology

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Introduction

Inferring generalizable patterns in species dynamics, distributions, and functional variation are central aims of ecology and evolutionary biology (MacArthur, 1972). Trait-based approaches, which quantify phenotypic characteristics that impact organisms' fitness and/or functional role, provide a tractable comparative framework for understanding communities, ecosystems, and evolutionary processes (Mcgill et al., 2006; Violle et al., 2007). Functional trait studies have proliferated over the past two decades, addressing foundational questions in community ecology (Cadotte et al., 2015; Mcgill et al., 2006; Violle and Jiang, 2009), biogeography (Violle et al., 2014), and conservation biology (Cadotte et al., 2011; Wellnitz and Poff, 2001) across taxonomic groups. These works emphasize the promise of trait-based research for generating novel insights into central ecological concepts and theories.

Increasingly, bee researchers are recognizing the utility of trait-based approaches for a wide variety of applications in ecological research. Bees (Hymenoptera: Apoidea: Anthophila) represent more than 20,000 species worldwide and display dramatic interspecific variation in morphology and behavior (Figure 1), including traits that mediate pollination services and responses to global environmental change (Supplementary Table 1). Exploration of functional traits has long been a cornerstone of bee research, yet only recently have these traits been systematically applied in bee ecological studies as a comparative framework for understanding community-level processes. Given their major functional role as the primary animal pollinators of terrestrial ecosystems (Ollerton et al., 2011), the bees represent a group ripe for exploration through a functional ecological lens.

Here, we review an emerging body of literature that quantifies functional traits across bee communities to address questions in bee ecology. In doing so, we address the following questions: How have functional traits been used to study bee ecology? What have been the major outcomes and limitations in bee functional trait research? How might this framework be leveraged to address urgent questions in the study of global bee declines? We review the variety of methods used to quantify bee trait variation, highlight common methodological problems and inconsistencies, and recommend best practices. Additionally, we describe geographic, taxonomic, and trait biases across the body of bee functional trait work, and highlight research areas that merit particular attention in future studies. Finally, we emphasize the value of open trait data sharing, and propose a roadmap toward a global bee functional trait database, including an initial aggregated dataset of 3369 morphological measurements from 1209 bee species.

Trends, methods, and biases in bee functional trait research

To survey the literature on bee functional traits, we searched for publications on the ISI Web of Science, the SciELO database, and Google Scholar using combinations of the terms “bees” and “traits” or “functional traits,” as well as in the cited literature of relevant papers. We included studies that used methods that conformed to our definition of a functional trait approach to an ecological question, i.e., which analyzed multiple functional traits comparatively across a sample of multiple bee species in a given environmental

context. Correspondingly, we excluded taxonomic revisions and the large body of studies that report or describe bee traits for single species, which provide useful trait data but which do not use functional traits as a comparative framework. We extracted metadata from each of these publications, including information on the focal traits measured, the authors' definitions of these traits, and the sources of trait data (Supplementary Table 2). All reviewed publications are listed under the Data Sources section.

We found and analyzed 97 papers assessing bee functional traits comparatively across species, published between 2006 and February 2023 (Figure 2a; Supplementary Table 2). Half of the studies examined bees in agroecosystems (48 studies; 49.5%); the remainder were divided between natural landscapes (18 studies; 18.6%), urban landscapes (14 studies; 14.4%), and comparisons across multiple landscape types (17 studies; 17.5%); (Figure 2b). The focal topics of these studies were highly variable, but with a particular emphasis on landscape change (e.g., urbanization, habitat fragmentation, land management); (Figure 2c). These studies sampled bees from 32 different countries, but were overwhelmingly conducted in North America (36 studies; 37.1%) and Europe (39 studies; 40.2%), with only nine studies (9.2%) conducted in Africa and Asia combined, and only 13 (13.4%) in Central and South America (Figure 3).

On average, each study quantified 4.37 functional traits (range = 2 - 10; std. error = 0.18) across a sample of 118.9 bee species (range = 5 - 638; std. error = 11.09). The most commonly studied functional traits were body size (in 85 or 87.6% of studies), nesting biology (either nesting location, nesting ability, or both; in 72 or 74.2% of studies), diet breadth (66 studies; 68.0%), and sociality (64 studies; 66.0%). Also common were measurements of tongue length (28 studies; 28.9%), seasonality (29 studies; 29.9%), and voltinism (12 studies; 12.4%). Nearly a quarter of the studies (22 studies; 22.6%) assessed other, less common functional traits, including measures of pilosity (hairiness), foraging range, colony size, native vs. exotic status, reproductive strategy (parasitism), and the use of different pollen-carrying structures (Figure 2d). Studies sourced their trait data from the literature and published data records (80 studies; 82.5%), from their own measurements and observations (52 studies; 53.6%), and, less commonly, as estimations from allometric equations (10 studies; 10.3%). Below, we discuss measurement strategies, terminology, and possible quantification pitfalls for the most commonly assessed traits in these studies.

Body size

Body size is among the most widely studied functional traits across animal taxa. Because it correlates with important life history, physiological, and behavioral attributes (e.g., growth rates, lifespan, fecundity, etc.); (Angilletta et al., 2004; Blueweiss et al., 1978; Glazier, 2008; Woodward et al., 2005), body size is often a strong predictor of macroecological patterns (Blackburan & Gaston, 1994; Chown & Gaston, 2010; Peters, 1983). Further, in bees, links between body size and pollination traits suggest important functional consequences of size variation at the ecosystem scale (De Luca et al., 2019; Benjamin et al., 2014; Jauker et al., 2016). In the studies we surveyed, body size was overwhelmingly estimated from the distance between wing pads (tegulae) that cover the base of the forewing (intertegular distance or ITD; in 64 of 85 studies or 75.3%); (Supplementary Table 2). Intertegular distance is simple to measure and has predominated as a method for estimating bee body size since Cane (1987) established the allometric relationship between this measure and dry mass in female specimens of 20 North American bee species. The ubiquity of ITD measurement in bee ecology could enable meta-analyses of size effects in different ecological contexts, where raw data are available. However, caution should be taken to address confounding effects of sexual dimorphism and other sources of intraspecific variation in body size. Recently, Kendall et al. (2019) revisited the question of ITD as a proxy for body size, and found that this metric is a robust predictor of interspecific size variation when the effects of phylogeny, sex, and biogeography are accounted for. These predictive allometric models are available in the *R* package “pollimetry” made available by the authors, which was used by one study in our analysis to improve size estimates from ITD (Kammerer et al., 2021). Efforts like these to account for variation in body size can help improve the predictive power of size proxies, especially considering practical constraints of obtaining direct mass measurements from specimens (e.g., due to damage to older specimens or the error introduced by accounting for pins). Indeed, only one study in our analysis measured specimen mass directly (Harrison et al., 2018). Still, we emphasize the advantages of

ITD over other, less accurate size proxies like body length (measured in 9 of 85 studies; 10.6%), which is affected by telescoping of abdominal segments. Finally, about a quarter of studies (22 of 85 studies; 25.9%) classified size categorically (e.g., “small,” “medium,” and “large”), either following ITD measurements or, less commonly, in subjective reference to a size standard (e.g., relative to the size of a honey bee). Categorical metrics should be determined objectively rather than subjectively, and accompanied by numeric data where possible to facilitate data reuse.

Nesting biology

Nesting biology is highly variable in bees, with consequences for habitat preferences and exposure to environmental stressors. For example, ground-nesting bees may be better insulated from extreme temperatures and fire than are twig- or wood-nesting bees, yet may be more vulnerable to habitat loss under certain environmental pressures (e.g., urbanization). As such, nesting traits have figured prominently in bee functional trait studies (Figure 2d). Most studies reviewed here categorized nesting biology at the species level according to nest location (e.g., “ground,” “cavity,” “stem,” etc.), though others additionally or alternatively considered nesting ability, i.e., whether a given species excavates its own nest or occupies pre-existing cavities. More so than other categorical traits like sociality and diet breadth, nesting trait analysis prompted the use of a large number of unique terms, reflecting the sheer diversity of bee nesting strategies, especially when considering data on tropical bees (e.g., nesting in termite mounds or in exposed nests, Borges et al., 2020; Giannini et al., 2020; Munyuli, 2014); (Supplementary Table 3). By far the most common method of assigning bee species to nesting categories was by distinguishing broadly between above-ground and below-ground nesters. Importantly, several authors create categories (e.g., “variable” or “mixed”) that account for within-species variation in nesting location, for example, bumble bees that can nest either in below-ground soil cavities or above-ground tree cavities. Nesting information was predominantly sourced from the literature and only about half of the studies provided source information for their nesting trait data. Importantly, nesting categories were often inferred from literature observations at the generic or family level; these inferences may obscure important species-level variation. Finally, definitions for nesting categories were rare. Of the 62 studies that categorized bee species by nesting location, only 13 (21.0%) provided some definition (whether written or by referencing a previous paper’s definition) for at least one of their nesting states. We recommend that authors specify the sources of their nesting data, rigorously define the boundaries of their categorizations, and clarify whether data is inferred from the species or generic level.

Diet breadth

Diet breadth is another trait with important implications for bees’ functional roles and responses to environmental change. Because this trait indicates a bee species’ range of floral host species, it can determine susceptibility to habitat loss, pollination services, and vulnerability to phenological mismatch. Two thirds (66 studies; 68.0%) of the studies in our analysis considered the diet breadth of their focal species (Figure 2d). The majority of these studies classified diet breadth categorically (60 of 66 studies; 90.9%). Most commonly, studies classified bee species as either oligolectic or polylectic, sourcing data from the literature and adhering to the definition that oligolectic species collect pollen from within a single plant family (Supplementary Table 3). Definitions varied, however, and less than half of studies defined these terms at all, whether through written definitions or citations (26 of 60 studies; 43.4%). Importantly, diet breadth can be conceptualized as a continuous variable with large variation in the degree of specialization (Cane and Sipes, 2006; Danforth et al., 2019). Several studies accounted for the diversity of diet specialization states by additionally including such terms as “mesolectic” and “monolectic” (Hall et al., 2019; Hung et al., 2019; Hung et al., 2021; Moretti et al., 2009; Ricotta & Moretti, 2011; *sensu* Cane & Sipes, 2006). A minority of studies made efforts to account for the continuous nature of diet breadth by treating it as a numeric variable (in 6 of 66 studies; 9.1%). Studies varied in their approaches to quantifying diet breadth numerically, whether as simply the number of host plant species (Rader et al., 2014), through network analysis (Raiol et al., 2021), or by diversity metrics that consider the phylogenetic breadth of host plant species (Bartomeus et al., 2018; Campbell et al., 2022; Lichtenberg et al., 2017). It is important to note that these metrics often depend on detailed visitation data, and can be sensitive to effects of sampling bias (Blüthgen, 2010). Providing details

on the data source (e.g., pollen load data, expert knowledge, visitation data) is crucial for promoting data reuse in future studies.

Sociality

Sociality is another predictor of ecological patterns in bees, both because of its role in shaping fitness outcomes and environmental interactions, and because of the sheer diversity of social forms in bees (Michener, 1974; Wcislo and Fewell, 2017). Social bees may be more resilient than solitary bees to some forms of environmental change, due to advantages of communication strategies, resource sharing, and social behavioral thermoregulation (Ostwald et al., 2023). Defining the lexicon to describe bee sociality has been ongoing and contentious endeavor (Costa and Fitzgerald, 1996; Dew et al., 2016; Richards, 2019; Wcislo, 2005, 1997). This complexity was reflected in the diversity of methods for classifying social forms in the functional trait studies assessed here (Supplementary Table 3). A common classification method was to divide bees into “social” and “solitary” species, but studies differed in whether “social” referred to all non-solitary bees, or only to eusocial bees. Fewer studies explicitly distinguished eusocial bees from non-eusocial bees that are not solitary, and these differed widely in their classifications. Further, certain inconsistencies in terminology suggested misunderstanding of these lesser studied, “intermediate” forms of sociality, i.e., bees that are neither obligately solitary nor obligately eusocial. Examples of problematic classifications of these bees include categorizing all intermediate forms as “semisocial,” or classifying nest aggregations of solitary bees as “communal/semisocial.” Importantly, many bee species exhibit intraspecific variation in social organization (Michener, 1974; Shell and Rehan, 2017). Indeed, Michener (1974) and others have argued that social labels are often not applicable at the species level because they obscure this intraspecific variation, which tends to be underestimated (Wcislo, 2005, 1997). This issue presents a problem for functional trait studies examining sociality, which are generally comparative at the species level and for which it would be prohibitively challenging to assess social organization at the individual or colony level, due to the observation-intensive nature of this work. Several studies in our analysis addressed this through the use of unique terms for species known to exhibit social polymorphism (e.g., “multiple,” “variable,” “facultatively social”; Bartomeus et al., 2013, 2018; Davis & Comai, 2022; Graham et al., 2021; Jacquemin et al., 2020; Moretti et al., 2009; Ricotta & Moretti, 2011).

These considerations emphasize the need to clearly define social terminology, particularly because social categorizations may differ according to the question of interest (Wcislo, 2005, 1997). Nevertheless, only a quarter of the studies that measured sociality as a functional trait defined the social terms they used (16 of 61 studies; 26.2%). Several authors have argued that inconsistency in bee social terminology has presented an obstacle to synthesis in phylogenetics (Dew et al., 2016; Kocher and Paxton, 2014; Richards, 2019); the same is likely to be true in comparative bee functional ecology in the absence of clearly and consistently defined social terminology.

Other traits

Beyond the four most commonly assessed functional traits, several others warrant methodological consideration. Parasitism status, i.e., whether or not a given species is a brood parasite or social parasite, was commonly but inconsistently classified, and often excluded from analyses. Studies varied considerably in whether they classified brood parasitism (a reproductive strategy) as a trait state under sociality, nesting biology, diet breadth, multiple of these traits, or as its own trait (e.g., parasite: yes or no). Indeed, parasites may be considered functionally distinct from non-parasitic bees with respect to sociality, nesting, and diet; the appropriate classification scheme will depend in part on the research question. For example, a comparative study assessing impacts of nest microclimate on bee thermal ecology might be better served by assigning parasitic species to the nest type they occupy (e.g., stems), rather than to their own category. Importantly, however, divergence in classification methods across studies will present obstacles to meta-analysis.

Studies also varied in their approach to measuring tongue (proboscis) length, a functional trait strongly implicated in pollination ecology because it mediates access to diverse floral host species. Tongue length presents measurement challenges because it can require dissection of fresh specimens, a tedious process which can compromise subsequent identification (Cariveau et al., 2016). Likely for this reason, only seven of

the 28 studies measuring tongue length used actual specimen measurements (Bartomeus et al., 2018; Beyer et al., 2021; Ibanez, 2012; Laha et al., 2020; Persson et al., 2015; Ramírez et al., 2015; Roquer-Beni et al., 2021). More commonly, species were categorized as “short” vs. “long” tongued according to the literature, sometimes including an intermediate category (e.g., “medium”). However, this approach may obscure important variation within short- and long-tongued groups, and so may not always be appropriate for testing functional hypotheses in pollination ecology. These classifications typically rely only on family information, and so do not capture within-family variation related to body size. To overcome these limitations, Cariveau et al. (2016) described an allometric equation that explains 91% of the variance in bee tongue length, and produced an R package that allows users to predict tongue length from bee family and ITD (“BeeIT” package). Allometric scaling relationships have been instrumental for developing predictive models to estimate biological measurements, especially in plant ecology (McHale et al., 2009; Montagu et al., 2005; Roxburgh et al., 2015). Since its publication, the BeeIT package was used to estimate tongue length in nine of the functional trait studies we surveyed, suggesting that this approach has reduced quantification barriers (Bartomeus et al., 2018; Beyer et al., 2020; Evans et al., 2018; Hass et al., 2018; Hung et al., 2019; Kratschmer et al., 2021; Lane et al., 2022; Staton et al., 2022; Steinert et al., 2020). This approach will enable analysis of older specimens that cannot be dissected, which will be particularly useful for rare and endangered species. However, caution should be taken when applying this approach broadly, as relationships between body size and tongue length vary across regions and taxa. For example, tongue length varies dramatically in neotropical orchid bees (Apidae: Euglossini), with species of similar body size exhibiting both short and very long tongues, sometimes more than twice their body length. Although over-reliance on proxy calculations introduces error that could potentially obscure functional relationships, allometric approaches such as these can represent improvements upon categorical assignments based on bee family alone. However, where possible, actual tongue measurements are preferable for advancing our documentation and understanding of the functional consequences of tongue length variation.

Outcomes, limitations, and frontiers in bee functional ecology

Functional traits are increasingly providing a popular framework for making generalizable predictions about the impacts of global change on bee biodiversity. The majority of studies analyzed here reported significant effects of environmental variables on functional trait diversity or composition. These findings have helped to clarify patterns of community change in response to environmental disturbances. For example, one generally consistent finding in functional trait studies of urbanization is the tendency for urban environments to favor generalist, cavity-nesting species (Ayers and Rehan, 2021; Banaszak-Cibicka and Żmihorski, 2012; Buchholz and Egerer, 2020; Cane et al., 2006; Normandin et al., 2017). In other contexts, however, trait-mediated responses to environmental change variables may be weak or conflicting across systems (Bartomeus et al., 2018; Williams et al., 2010). The extent to which functional trait effects are generalizable across systems appears to be context- and trait-dependent.

Toward open science and community data standards for bee trait data

Meta-analyses have the potential to clarify patterns in bee functional ecology across biological scales (Bartomeus et al., 2018; Coutinho et al., 2018; Garibaldi et al., 2015; Poulsen and Rasmussen, 2020; Woodcock et al., 2019). However, while bee trait data is prolific in the literature, we currently lack community data standards for sharing trait data that would enable such meta-analyses. Trait databases are increasingly emerging as tools for functional exploration within a taxonomic group, with valuable examples from Lepidopteran (Shirey et al., 2022), spider (Pekár et al., 2021), amphibian (Oliveira et al., 2017), plant (Kattge et al., 2011), and bird databases (Tobias et al., 2022); (with many other examples registered in the Open Traits Network; Gallagher et al., 2020). Progress toward aggregated bee trait data will depend on researchers adhering to principles of FAIR (Findable, Accessible, Interoperable, Reusable; Wilkinson et al., 2016) data. Just over half (64.9%) of studies in our review made their trait data available online.

Equally important for making trait data usable in future analyses is clearly describing trait measurement methods, defining trait terms, and providing comprehensive metadata. Where appropriate, researchers should consider adhering to prevailing measurement protocols (Moretti et al., 2017). For example, measuring body

size as ITD can help ensure compatibility of data with past and future studies, due to the ubiquity of this measurement method. Importantly, even when using standardized methodologies, methods should still be defined and/or cited to enable future use of data. Our analysis also revealed the diversity of adopted trait terminology for categorical traits such as nesting biology, sociality, and diet breadth. These terms were rarely defined, presenting obstacles to data harmonization. In the absence of a controlled vocabulary for bee trait classifiers, terminology should be defined, whether by written definitions or citations of existing definitions, including links to ontologies (e.g., the Hymenoptera Anatomy Ontology; Yoder et al., 2010). Importantly, trait data should be shared as raw data to facilitate use in future analysis. Many datasets in our analysis aggregated trait data at the species level, such that information on within-species variation was lost. Associated geographic and taxonomic data should likewise adhere to community data standards (e.g. Darwin Core). In our review, we found that taxonomic information was at times incomplete, inaccurate, or ambiguous, and geographic data was poorly linked to specimen-level trait data and/or formatted according to outdated standards (Degrees, Minutes, Seconds format) To resolve ambiguity and promote machine-readability across datasets, taxonomic information should be linked to taxonomic identifiers (e.g., GBIF Backbone Taxonomy; 2023) and sampling coordinates should be reported in decimal-degree format.

We have compiled and harmonized the primary morphological data presented in the studies we reviewed, where data were available and interpretable, available at <https://zenodo.org/doi/10.5281/zenodo.10139286> as Supplementary Table 4 and registered in the Open Traits Network. This dataset presents body size, tongue size, and pilosity data for 1209 bee species along with geographic and other metadata. Behavioral trait data (e.g., nesting biology, sociality, diet breadth) in the studies we analyzed were generally extracted from the literature (secondary data), and so do not feature in this primary dataset. Data classes are defined in the metadata, and where possible, are mapped to the Darwin Core (Wieczorek et al., 2012). We have mapped taxon names to taxonomic identifiers and have introduced new trait definitions to the Hymenoptera Anatomy Ontology (Yoder et al., 2010) to link functional trait data to unique, persistent identifiers (e.g., tongue length: http://purl.obolibrary.org/obo/HAO_0002606). Importantly, this dataset provides a template (Supplementary Table 5) for organization of bee trait data that ensures compatibility among datasets by facilitating semantic interoperability and resolving ambiguity in terminology.

What are the gaps in our understanding of bee functional ecology?

Our analysis revealed critical knowledge gaps in the field of comparative bee functional ecology. While a subset of morphological and behavioral traits was well represented, phenological traits were more rare and physiological trait data was nearly absent. Despite a wealth of physiological research on honey bees and bumble bees, physiological trait data for other bee species has lagged. In other insect taxa, comparative physiological trait data (e.g., thermal tolerance and desiccation resistance) has been usefully leveraged to understand and predict performance under climate change (Baudier et al., 2015; Bujan et al., 2020, 2016; Roeder et al., 2021). Interest in quantifying these traits in non-*Apis* bees is increasing (Burdine and McCluney, 2019; Gonzalez, 2020; da Silva et al., 2021), yet they are still rare in comparative functional trait studies (Hamblin et al., 2017), due perhaps to the labor-intensive nature of quantifying these traits, especially relative to better-studied traits that can be sourced from the literature. Prioritizing physiological trait data collection and data sharing will vastly expand opportunities to predict performance under future climate scenarios. Phenological traits, especially flight seasonality, also merit increased attention in future functional trait studies. Despite known links between bee seasonality and vulnerability to environmental change, this trait was poorly represented in the studies we analyzed. While we emphasize the need to fill these trait gaps, we equally stress that trait selection should generally be hypothesis driven.

Urgently, future work should also expand the topical and geographic breadth of functional trait studies. The vast majority of functional trait studies were conducted in Europe and North America (80.4% of studies), mirroring a larger bias in ecological research (Archer et al., 2014; Martin et al., 2012; Pyšek et al., 2008). The geographic bias in bee functional trait research is even more extreme than the one reported by Winfree et al. (2011) for studies of native pollinators in human-altered landscapes (52% of studies conducted in Europe and North America). Preserving global crop pollination is a top priority for sustaining food security,

yet relevant data is concentrated in wealthy regions that are lowest priority for this aim. Over-reliance on geographically-restricted data will undercut our ability to predict bee responses to environmental change globally. Finally, these studies were dominated by research on agroecosystems and agricultural/land use questions. This contrasts with a broader pattern in terrestrial ecology, where natural systems tend to be overrepresented in ecological studies (Martin et al., 2012). Climate change questions, in particular, were poorly represented in the studies analyzed here. Increasing attention to these topical gaps will help balance the body of functional trait literature better in line with conservation priorities.

Synthesis and concluding remarks

Variation in bee functional traits significantly predicts patterns of community change across a wide range of systems and contexts. As such, this framework has become an increasingly popular tool for predicting species-level consequences of global change. Our review highlights common approaches to morphological trait measurement (e.g., ITD), but also reveals knowledge gaps in bee trait data and terminological inconsistency in classifiers applied to behavioral traits, namely diet breadth, nesting behavior, and sociality. We do not prescribe a particular terminology structure here, but rather emphasize that when authors clearly define terms their data becomes useful beyond its original publication. Increasingly, ecologists have called for the development of ecological trait data standards and the application of open science principles to functional trait research (Gallagher et al., 2020; Keller et al., 2023; Schneider et al., 2019). Our analysis highlights the need for integration of these practices into bee functional ecology research. To promote data reuse, researchers should rigorously define trait terminology and make trait data openly accessible with clear metadata and methodological descriptions. Our template for bee functional trait data sharing, along with the compiled primary data from these studies, represents the first step toward a consolidated database of bee functional traits. Future work toward this aim will promote synthesis across diverse study systems and questions in bee functional ecology.



Figure 1. Bees represent an impressive diversity of functional trait states, varying dramatically in morphology (e.g., size, coloration, pilosity, tongue length); (top) and behavior (e.g., nesting biology); (bottom).

Hosted file

image2.emf available at <https://aurea.com/users/515590/articles/690106-toward-a-functional-trait-approach-to-bee-ecology>

Figure 2. Descriptive metadata from 97 functional trait studies in bee ecology, including (a) the number of bee functional trait studies published each year (excluding one publication in the analysis from early 2023), the distribution of publications across (b) landscape contexts and (c) research topics, and (d) the frequencies of focal functional traits in these studies. Each study assessed multiple functional traits (mean = 4.39 traits), so the total number of publications containing each trait sums to greater than the 96 publications analyzed.

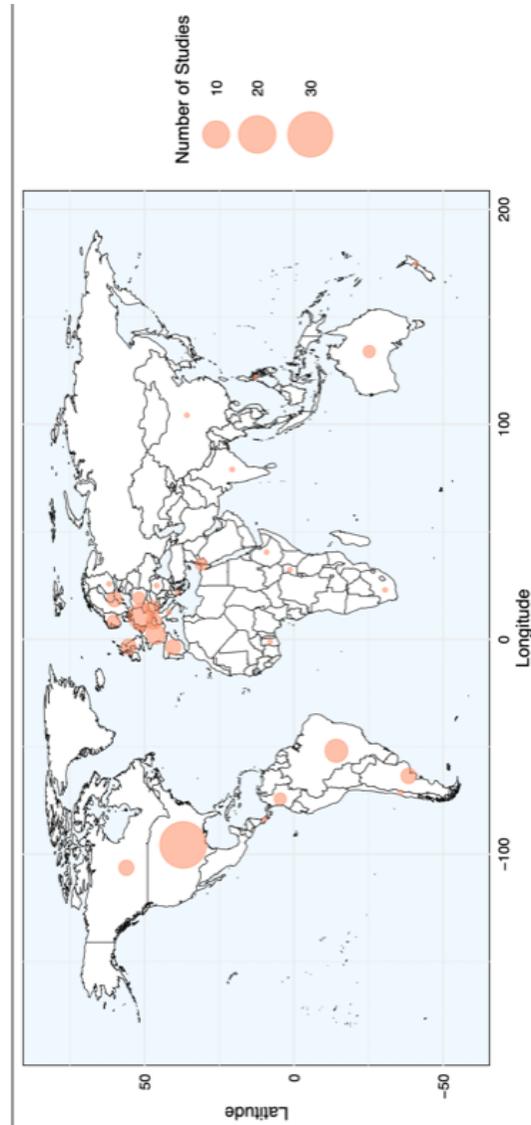


Figure 3. Geographic biases in bee functional trait studies. Circle size indicates the number of published studies assessing traits of bees sampled from a given country. Large-scale meta-analyses of existing published functional trait studies across countries are excluded from this map, to prevent double-counting.

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