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REVIEW PAPER

A review of global trends in the study types used to investigate bee nesting biology

Michael C. Orr[a,*], Mirjam Jakob[b], Alexandra Harmon-Threatt[c], Anne-Christine Mupepele[b]

[a]*Key Laboratory of Zoological Systematics and Evolution, Institute of Zoology, Chinese Academy of Sciences, Beijing, China*
[b]*Nature Conservation and Landscape Ecology, University of Freiburg, Freiburg, Germany*
[c]*Department of Entomology, University of Illinois Urbana-Champaign, Urbana, IL, USA*

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Abstract

Nesting resources are key inputs for the survival and reproduction of bees. However, relatively little work has been done on threats bees face from a nesting-biology perspective, with most studies focusing on floral resources. Much of what is known about bee nesting is thought to come from opportunistic observations within descriptive, natural history studies, but the relative contribution of these and ecological or artificial experimental studies remains unquantified. Via a systematic literature search, we quantified the contribution of different study types to our current knowledge on bee nesting biology and how bees face threats related to their nesting habits. From 2000 screened articles, we found that all study types contributed to our total knowledge in complementary ways. Natural history studies constituted most studies (~60%) and were the primary study type investigating specific nest site characteristics, nest architecture, and nesting behavior. Conversely, ecological studies (27%) provided more information about threats bees face, while artificial experimental studies (13%) predominantly tested mechanisms or highly-specific behaviors. Ground-nesting species were underrepresented in all study types (33%), especially in ecological and artificial experimental studies. Overall, natural history studies form the foundation of our knowledge on bee nesting, and ecological and artificial experimental studies enable us to extend and test related hypotheses in rigorous frameworks. Future work will benefit greatly from efforts to synthesize and standardize measurements and methods both within and across these study types, enabling a more comprehensive assessment of threats bees face and more effective management and conservation.

Keywords: Apoidea; Hymenoptera; Bee biology; Life history; Natural history; Traits; Trap nests

Introduction

Bees are important pollinators, crucial in both managed and natural ecosystems for their role in plant reproduction (Klein et al., 2007). There are many recent reports of bee declines, but these are geographically and often taxonomically restricted (Bartomeus et al., 2013; Biesmeijer et al., 2006). There are >20,000 species of bees worldwide and little is known of most of them or their relative importance to managed or natural systems (Michener, 2007). For most of these species, their conservation status remains unknown, as

*Corresponding author.
E-mail address: michael.christopher.orr@gmail.com (M.C. Orr).

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the data necessary to assess them do not publicly exist (Orr et al., 2021a), and the future of many species even remains uncertain because we lack data on their habitat and resource requirements (Michener, 2007; Nieto et al., 2015).

Floral resources and nesting resources are key inputs necessary for bee survival and reproduction. A great deal of research has been done on floral resources (Roulston & Goodell, 2011), especially in management to enhance pollination services, but most bee species spend the majority of their time within nests both as growing larvae and then while waiting to emerge the next season or year, and during this time they cannot actively avoid any threats. Studies on nesting biology aspects (e.g. Buckles & Harmon-Threatt, 2019; Cane, 1991; Chan & Raine, 2021; López-Uribe et al., 2015; Potts et al., 2005; Williams et al., 2010) have been synthesized, but these reviews either targeted a selected species group (Almeida, 2008; Cane et al., 2007, Roubik, 2006) or chose a different approach by either qualitatively and unsystematically summarizing selected nesting aspects (Antoine & Forrest, 2021) or synthesizing information about species and genera without focus on the kind of studies contributing to this knowledge (Harmon-Threatt, 2020).

Much of what is known about bee nesting comes from natural history studies, dating back in some cases well over 100 years ago (Michener, 2007). These studies are based on observation of single or few species, often opportunistically, and they are largely exploratory rather than foundationally question-driven, in contrast to ecological studies that typically explore themes such as how nesting traits might structure whole communities. On the other end of the spectrum, targeting finer-scale behavioral responses, some studies are done in controlled lab environments, and these might best be considered artificial (hereafter artificial experimental). There are clear synergies between these study types, as natural history studies contribute a large proportion of our most basic knowledge in ecology and behavior (used to design experiments), and remain important because only small parts of all autecological phenomena can ever be formally and rigorously experimentally tested, given the effort and time required for such validations (Tewksbury et al., 2014; Travis, 2020). Consequently, ecological and evolutionary research may be hindered if natural history data are unavailable to implement meaningful experimental designs (Guidetti et al., 2014; Travis, 2020; van der Niet, 2020).

Here, we aim first at identifying how different study types contributed to the current knowledge about bee nesting biology. We separated studies into natural history, ecological, and artificial experimental to identify the relative contribution of each type of study to our knowledge of nesting while considering changes over time and the global distribution of knowledge. Second, we explored the knowledge provided about nesting biology to identify how many studies are dedicated to cavity- versus ground-nesting bees as well as their study focus, such as nesting resource required for nest construction, site conditions or the threats bees face related to nesting, to highlight future research needs and possible conservation measures useful for protecting bees from such threats.

Materials and methods

Literature search

A systematic literature search covered articles related to wild bees and nesting biology from the Web of Science (Box 1, Appendix A: Fig. S1, Data S1). A random subsample of 2000 studies (of 8197 total) was screened by first looking at title and abstract and second reading the full text (CEE, 2018). Studies were excluded if they did not fulfill a-priori inclusion criteria (Box 2, Appendix B). One author performed the screening after an assessment of the inter-rater reliability kappa-test showing an agreement of 83% (Cohen's kappa based on n = 100) with another author.

Box 1. Search string used in the Web of Science (Clarivate Analytics) on December 17, 2020. The search string covered the databases: Web of Science Core Collection, BIOSIS Citation Index, BIOSIS Previews, Current Contents Connect, Data Citation Index, Derwent Innovations Index, KCI-Korean Journal Database, MEDLINE, SciELO Citation Index, Zoological Record. Search options in the Web of Sciences were set to 'all years' and 'all languages,' but excluding document types "patent" and "data set." Search terms were determined with step-wise best practices to maximize the return of relevant results (Appendix B).

"TOPIC: (bee OR bees OR Apidae OR Andrenidae OR Colletidae OR Halictidae OR Megachilidae OR Melittidae OR Stenotritidae OR Anthophila) AND TOPIC: (nest OR nests OR nesting) NOT TITLE: (apis OR "honey bee*" OR honeybee* OR honey* OR pheromon*) NOT TOPIC: ("bee eater*" OR varroa OR "hive beetle*" OR propolis OR danc*)"

Box 2. Inclusion criteria for studies to be included in this review (all must be met).
- study was about non-honey bees
- study provided information about nesting
- study is not about fossil nests
- study does not provide information about bees that could not be distinguished from other taxonomic groups (e.g., wasps)
- study was included if it fulfilled one of the inclusion criteria, including data on nesting architecture, nesting location, nesting resources, nesting behavior, impacts on or threats to nesting, or other aspects specifically regarding bee nesting biology in detail
- literature in English, German, French, Italian, Spanish, and Portuguese
- the article was accessible through the University of Freiburg or University of Illinois Urbana-Champaign (USA).

Data extraction and definitions

We extracted information about publication year; study country; taxonomy (according to Ascher & Pickering, 2021); nesting strategy (cavity- vs ground-nesting) and nesting resource (artificial human-made nest offers, e.g. trap nests, versus natural material). Articles were then tagged based on the information provided about nesting biology, such as nest site descriptions, nest architecture, nesting behavior, as well as threats to bee nesting or potential impacts nesting bees may face. Half of the studies (248) were analyzed to gain more detail about the kind of information given on nest sites, nest architecture, nesting behavior, and threats. All studies fulfilling the inclusion criteria (542) were used for other analyses.

We additionally classified all studies into three study types: natural history studies, ecological studies, and artificial experimental studies. This classification was done by two researchers (inter-rater reliability showing an agreement of 91% (Cohen's kappa, n = 100), during an initial round used to refine and improve classifications, see CEE, 2018 for further details on the process). We defined natural history studies as observational and descriptive studies that typically focus on just one species, or a few, and their associates (parasitoids, etc.). They take place in the natural environment of bees, often at a single site given opportunistic nest discoveries. Natural history studies are typically not singularly question-driven and do not follow a specific pre-planned framework, nor do they usually include statistical tests, making them qualitative at their core in most instances (Guidetti et al., 2014; Tewksbury et al., 2014; Travis, 2020; van der Niet, 2020). If they do include statistical tests, they are almost always applied in a post hoc manner to further test observations (e.g., Orr et al., 2016). Ecological studies, meanwhile, explore broader community interactions among species or species in relation to environmental treatments. They take place in natural or sufficiently representative settings and often revolve around land-use comparisons. Ecological studies are hypothesis-driven and studies are planned and realized to statistically test these. Artificial experimental studies take place in completely artificial or strongly manipulated natural environments, such as laboratories, greenhouses, or flight cages with controlled resources and settings. These studies often aim at providing insights about specific behaviors and focus on one or few species. They include statistical tests and are based on an experimental setup.

Statistical analysis

Chi^2-tests and Fisher's exact tests were implemented to identify whether study types differed in their contribution to our knowledge on various aspects of bee nesting biology (Agresti, 1990). We adjusted p-values when testing the contribution of study type on nest site, nest architecture, nesting behavior, and threats to nesting according to Holm (1979) to counteract problems of multiple testing. Statistical analysis was done with R (Version 4.0.4, R Development Core Team, 2021).

Results

Our search string identified 8197 studies. Out of our random subset of 2000 studies, we identified 542 references dealing with bee nesting biology and meeting our inclusion criteria. The majority of them were natural history studies (323 studies, i.e. 59.6%) followed by 145 ecological studies (26.8%) and 74 artificial experimental studies (13.6%). 73 studies were published prior to 1970 and only 23 before 1950, but their frequency has continuously increased. Natural history studies have long comprised the majority, but ecological studies are becoming more common and have recently overtaken natural history studies (2018, 2019, 2020). During the last decade (2011−2020), the number of annually published natural history studies remained almost constant, while ecological studies drastically increased and for the first time outnumbered natural history studies (Fig. 1). Artificial experimental studies have consistently played a minor role in comparison to the other two study types (Fig. 1), varying over time but showing a slight increase recently.

The geographic distribution of studies was skewed toward the North America and Europe, with most studies from the United States of America (n = 140, 26%), Germany (n = 39, 7%), Canada (n = 29, 5%), and Australia (n = 28, 5%) (Appendix A: Fig. S2, Data S2). Brazil was the only country in the tropics that contributed many studies to our analysis (n = 90, 17%). North America and Europe showed a higher proportion of ecological studies (30.6% and 35.2%, respectively, in comparison to 19.7% elsewhere) than was generally seen elsewhere, where natural history remained more dominant and they remain, by far, the primary source for information on bee nesting biology.

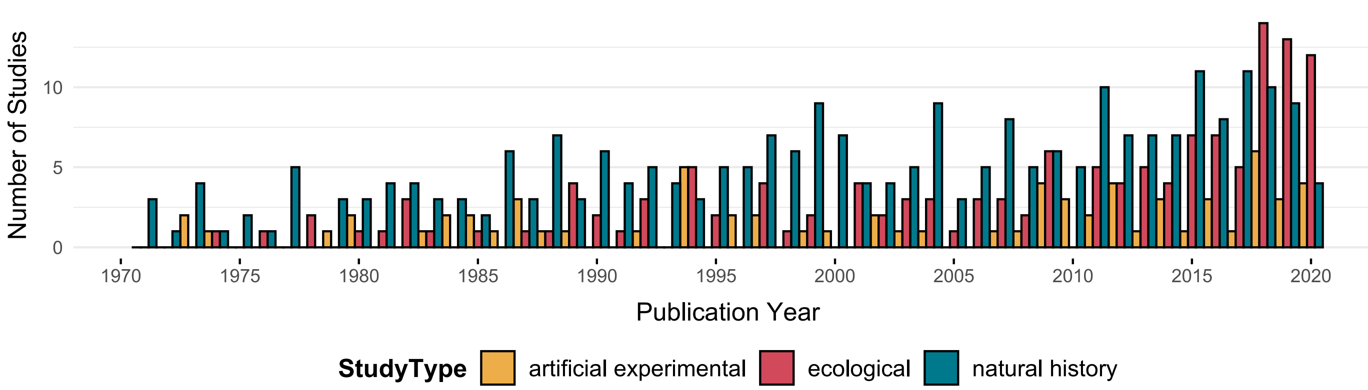

Fig. 1. Contribution of study types over time. Shown are 50 years from 1970 to 2020.

Nesting strategies: cavity- versus ground-nesting species

Cavity-nesting bees were studied more often than ground-nesting bees (365 versus 155 studies, 22 investigating both). The difference was particularly striking in ecological and artificial experimental studies (Fig. 2). In line with these findings, nest resources involved were proportionally more often of an artificial nature (i.e., mostly trap nests) in ecological studies than in natural history studies (Fig. 2).

Types of bee nesting knowledge and threats nesting bees face

Most of our knowledge on bee nesting biology across nest site description, nest architecture, and nesting behavior derives from natural history studies (Fig. 3, χ^2_{site}= 289.09, df=2, p_{adj}=3.74e^{-15}, χ^2_{arch}=360.29, df=2, p_{adj}=3.74e^{-15}, χ^2_{beh}=132.34, df=2, p_{adj}=3.74e^{-15}, respectively). Interestingly, research on threats and impacts on nesting was dominated by ecological studies (Fig. 3, χ^2_{impact}= 53.938, df=2, p_{adj}= 1.36e-^{11}).

For nest site description, the information most often provided was related to the nest substrate (*n* = 83, 34% of all studies giving a nest site description), i.e. the material used at the nest site, such as the soil composition for ground-nesting bees (e.g. Rayment, 1948; Youssef & Bohart, 1968) or the material used by cavity-nesting bees (e.g. Yogi & Khan, 2014). Nest density was also frequently investigated (*n* = 39, 16%), followed by slope (*n* = 30, 12%); vegetation cover (*n* = 29, 12%), such as bare versus grass-covered ground; and direction of exposure to sun (*n* = 28, 11%), a critical determinant of thermoregulation (Fig. 4). Other aspects mentioned in lower quantities were the presence of water bodies (*n* = 4, 2%), soil properties, i.e. pH (*n* = 2, 1%), and temperature of the soil surface or the upper soil (*n* = 2, 1%).

The category nest architecture summarizes aspects of nest shape and structure. Studies looked predominantly at brood-cell details (*n* = 85, 33% of all nest architecture studies), describing the number of cells (e.g. Danks, 1971; Roberts, 1973) or their size (e.g. Andrade-Silva & Nascimento, 2012; Camargo, 1996). Nest shape was almost equally frequently described (*n* = 81, 31%). For ground-nesting bees (*n* = 36, 14%) they mainly described shape and structure of the tunnel system, and burrow size and angle (e.g. Michener, 1963; Rozen, 1983; Youssef & Bohart, 1968). For cavity-nesting species (*n* = 44, 17% of all nest architecture studies), cavity dimensions, such as diameter, length, height, or volumes of cavities were mentioned, as well as their shape or their possible origin. Other studies investigated the nest entrance (*n* = 70, 27%), such as form or plug material, nest provision (*n* = 66, 26%), e.g. number or type of pollen grains, sugar content in honey pots, or source plant of pollen, or the depth of nests (*n* = 41, 16%).

Regarding nesting behavior, most studies reported on collection flights (*n* = 53, 18% of all studies looking at nesting behavior), such as the duration of foraging and nesting material collecting trips. Nest construction activities were also well-represented (*n* = 36, 12%), as were studies on nest site fidelity (*n* = 19, 7%), and nest guarding or defense against intruders (*n* = 18, 6%). There were a few studies on homing behavior to find and recognize nests (*n* = 9, 3%). Interactions with conspecifics (*n* = 7, 2%) including aggressive or avoidant behaviors were also documented (e.g., Flores-Prado et al., 2012). Intracolonial aggressive behavior was especially observed by dominant, reproductive females

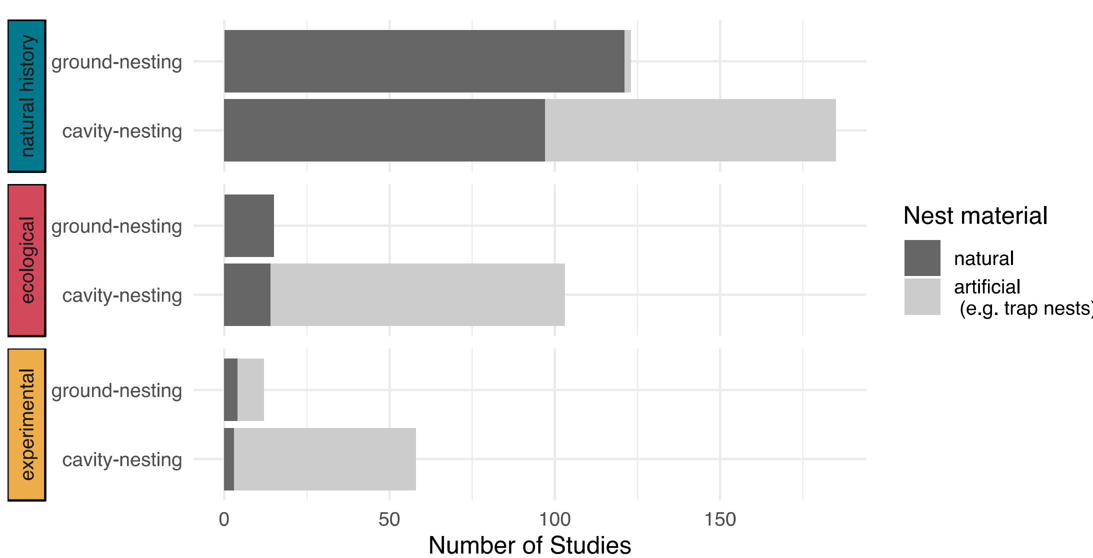

Fig. 2. Number of studies by type (natural history, ecological, artificial experimental), strategy (ground-nesting vs. cavity-nesting), and nest resources (natural vs. artificial).

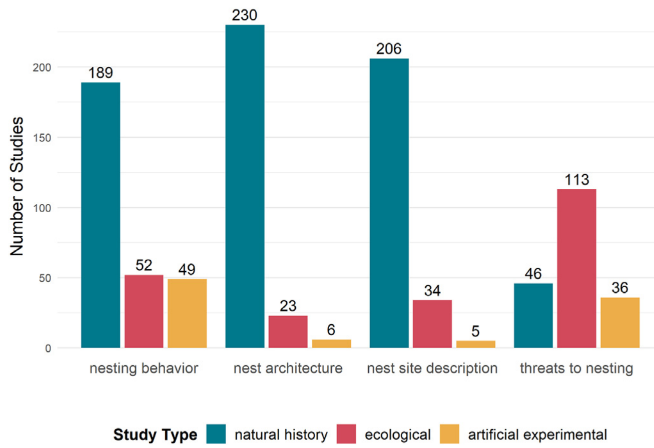

Fig. 3. Numbers of studies for nesting biology categories and nesting impacts by study type. Color code reflects the study types: natural history (blue), ecological (red), and artificial experimental studies (yellow). Sums are given above the bars.

against subordinate females in eusocial colonies (Andrade-Silva & Nascimento, 2012). Other studies looked at oviposition (n = 6, 2%), providing information about the time needed for oviposition and when it occurred (e.g. Augusto & Garófalo, 1998; Andrade-Silva & Nascimento, 2012).

Aspects impacting bees during their nesting activity were subsumed under the term ‘threats to nesting.’ They looked at the effect of landscape management and land-use change (n = 26, 13% of all studies looking at threats to nesting) on bee nesting site availability, such as the amount of

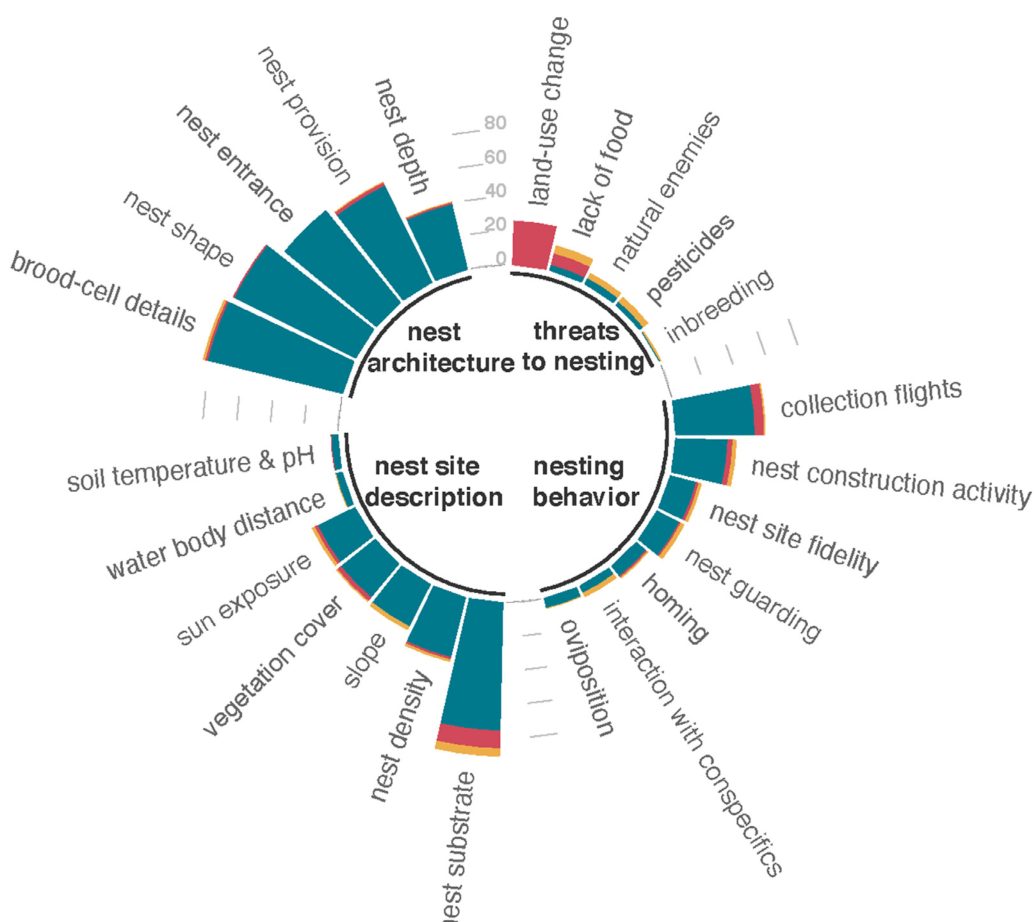

Fig. 4. Contribution of study types on aspects of bee nesting biology. Natural history studies in blue, ecological studies in red, and artificial experimental studies in yellow. Bars represent the number of studies per variable found within the content analysis subset.

intensively managed cropland or forest fragmentation. Many studies also investigated the benefit of agri-environmental schemes or other conservation measures such as semi-natural habitats increasing bee diversity. Studies investigating landscape management were primarily on cavity-nesting bees (*n* = 15, 58% of all 26 studies looking at landscape management), rarely on ground-nesting bees alone (*n* = 2, 8%), and sometimes on both (*n* = 9, 34%) (χ^2= 9.7692, df=2, *p* = 0.007562). Studies investigating the lack of food and the influence of floral resources on bee nesting (*n* = 15, 8% of all studies looking at threats to nesting) showed clearly that pollen or nectar availability had an impact on reproductive nesting success of both solitary (e.g. Goodell, 2003; Minckley et al, 1994) and social bee species (e.g. Maia-Silva et al., 2016). Cavity-nesting species were more commonly investigated (*n* = 13, 87% of all 15 studies looking at floral resources) than ground-nesting species (*n* = 2, 13%) (χ^2=8.0667, df=1, *p* = 0.0045). Other studies looked at natural enemies (*n* = 7, 4% of all studies looking at threats to nesting), such as parasitism (e.g. Moure-Oliveira et al., 2019) as a potential threat to bee nesting success, the effect of pesticides (*n* = 6, 3%) mainly neonicotinoids (*n* = 4, 2%) resulting in a loss of orientation (Woodcock et al., 2017), or inbreeding (*n* = 1, 0.5%).

Taxonomic coverage and resolution

The largest bee family, Apidae, was best represented in our subset (48.3%, *n* = 241), followed by Megachilidae (28.3%, *n* = 141), Halictidae (10.8%, *n* = 54), Andrenidae (7.0%, *n* = 35), Colletidae (3.6%, *n* = 18), Melittidae (2.0%, *n* = 10). Natural history studies showed a greater evenness across families (Apidae (49%, *n* = 160), followed by Megachilidae (24%, *n* = 77), Halictidae (10%, *n* = 33), Andrenidae (9%, *n* = 30), Colletidae (5%, *n* = 17), and Melittidae (3%, *n* = 9)) compared to ecological (Megachilidae (47%, *n* = 46), Apidae (41%, *n* = 40), Halictidae (9%, *n* = 9), Andrenidae (2%, *n* = 2), Colletidae (1%, *n* = 1)) or artificial experimental studies (only Apidae, Megachilidae, and Halictidae).

Studies on single species were most common (71.8%, *n* = 389), followed by those looking at two (7.7%, *n* = 42) or more than two species (6.7%, *n* = 36). Studies at the group level focused mainly on *Bombus* (*n* = 12, 46%) or stingless bees (*n* = 7, 27%). Natural history and artificial experimental studies worked seldomly at the group or community level (*n* = 14 (4.3%), *n* = 3 (4.1%), respectively). In contrast, ecological studies were more often conducted at the group or community level (40%, *n* = 58). Across all study types, 430 total species were covered across 126 genera (dominated by *Osmia* (*n* = 76 studies, 14% of all studies), *Megachile* (*n* = 60, 11%), and *Bombus* (*n* = 59, 11%)). Most species were covered by only one study (80.7%, *n* = 347).

Discussion

What we know about bee biology ultimately determines how well we can support them. Natural history studies provide a major contribution to our knowledge about bee nesting biology worldwide. Their numbers have not declined over the decades, but ecological studies have become roughly equally common more recently. Ground-nesting bees are understudied compared to cavity-nesting species which is most apparent in ecological and experimental studies. Natural history studies provided the most detailed, species-specific basic knowledge regarding nest site preferences, nest architecture, and nesting behavior, providing a foundation for other lines of research. As ecological and experimental studies mostly contribute to the threats nesting bees face, they are essential to identify and reverse bee declines.

For almost all categories, the vast majority of papers investigating specific aspects of nest sites, nest architecture, and nesting behavior were classified as natural history. Without these studies, we would know very little of the actual structure of bee nests, including how they might be emulated, and this would severely hinder efforts to manage pollinators (Bosch & Kemp, 2002; Pitts-Singer & Cane, 2011) and to provide nesting resources for bees in natural habitats for conservation (Harmon-Threatt, 2020). Ecological and artificial experimental studies are vital for connecting natural history knowledge to real-world outcomes and testing causal links and relationships between an intervention, such as a management strategy, with outcomes for bee health. There are clear synergies present between the study types, with each approach capable of enhancing others. For example, natural history is the primary source of associations between bees and the cleptoparasites that invade their nests, but ecological and experimental studies can be used to test the impact of their natural enemies in a rigorous statistical framework, better informing management and conservation. Going forward, it will be critical to seek out these synergies, as they can provide mechanistic, species-level, and community-level information vital for effective conservation planning and action.

One major challenge of investigating nesting is that over 80% of native bee species nest belowground (Harmon-Threatt, 2020). Thus, gathering critical information on nesting is difficult due to challenges in locating nests, excavating them, and manipulating them (but see Fortel et al., 2014), not to mention the training needed to effectively perform these studies. Although nest architecture can theoretically be studied in different land use types across species, the difficulty of getting sufficient, verified replicates for multiple species might generally be prohibitive under most circumstances with current methods. Thus, nest-based experimentation for the majority of bee species is rare (with some exceptions, Leonard & Harmon-Threatt, 2019). For the remaining 20% of species that nest in cavities aboveground, artificial and experimental studies have been conducted to assess behavioral and ecological responses to nesting materials and climatic factors for some species, but most remain poorly known (Staab et al., 2018; Tscharntke et al., 1998). This is only further complicated by the fact that many species require specific, sometimes uncommon resources for nest construction (Requier & Leonhardt, 2020), which must be factored in for effective conservation. Therefore, to design experimental frameworks that can meaningfully test ecological phenomena, we must ultimately know the life history of species (Travis, 2020).

Perhaps the biggest barrier to leveraging the vast literature on bee nesting biology is the sheer volume of information available, spread across countless papers and books. Although search engines such as Google Scholar or Web of Science enable much quicker searches than when all records were printed, there are still numerous articles that may not be digitized or properly indexed. In many cases, new nesting information is off-handedly reported in brief, making them much harder to find. This is further complicated when the articles are in languages other than English, as some languages such as Chinese even have their own species names (akin to common names, but used by scientists with preference under many circumstances). The majority of studies in other languages here were of the natural history type, and this may be tied to the ongoing devaluation of natural history studies combined with the infrequent consideration of non-English publications overall and especially for conservation (Amano et al., 2021; Konno et al., 2020). We expect this trend would hold if a broader search term using multiple languages were enacted, but it is still important to acknowledge that important historical and contemporary literature exists in other languages (many publications in addition to Malyshev, 1936; Sakagami & Michener, 1962, for example). A more difficult, but very important aspect to consider is indigenous knowledge, which often includes insights otherwise unknown to scientists (Wilder et al., 2016). Although such efforts on solitary bees remain limited, much work has been done on stingless bees that have long been cultivated, leading to many new insights about their biology (Ayala et al., 2013; Gonzalez et al., 2018).

What we know about bees defines our ability to ensure the ecosystem services that they provide in natural and managed environments. Information such as slope, sun exposure or soil characteristics, are only reported in a minority of studies. Consequently, for many species there is no information on their habitat requirements and the existence of or causes for long-term trend changes are difficult to identify. There have been calls for standard reporting and more recently a systematic monitoring of populations (Linsley et al., 1952; Meiners et al., 2019; Portman et al., 2020). A framework, including standards of terminology and metrics, is needed because measurements must be taken in similar enough ways to enable meaningful comparison. Ideally, experimental studies should be done to determine the best type of soil and other classifications to use meaningfully for bees, targeting those which correctly delineate between types of soil that are significantly different enough to impact bee nest choice or survival, then these should always be used to ensure comparability. In general, we suggest as a minimum that researchers should strive to report the following in nesting biology studies: all relevant habitat features, nest-placement-related factors such as vegetation presence/cover, soil type (various facets possible, including pH, moisture, density), sun exposure and orientation of entrance, slope or aspect, phenological timing, and others like depth of nest, use/type of nest cell lining, at least minimal recording of nest layout, and other individuals or species associated with the nests. We strongly encourage the collection of all data possible, as a fuller picture of species enables better management, but under limitations it is hoped that at least those details can be reported.

With so many papers on bee nesting, synthesis is becoming increasingly important, and reviews do thankfully exist for some groups or topics (Almeida, 2008; Antoine & Forrest, 2021; Cane et al., 2007; Harmon-Threatt, 2020; Liczner & Colla, 2019). However, many groups remain unsummarized, and a centralized database on bee nests could greatly improve prospects (Orr et al., 2021b). These records would be extracted from the literature and could even be reported newly via a community science friendly interface, enabling both researchers and the general public to contribute new information (Lye et al., 2012). An immense amount of work would be required, and, unfortunately, data generation is now devalued (Orr et al., 2021b), as is training in the type of natural history methods necessary (Tewksbury et al., 2014). Yet there is great potential for integrating new technologies and analyses with traditional methods, thereby enabling otherwise impossible, high-impact studies on bee nesting biology (Crall et al., 2018; Orr et al., 2016; Ostwald et al., 2021). Fundamental changes in the way we value scientific contributions and encourage interdisciplinary research are needed to enable scientists to not only innovate but also to synthesize and make available what is already known, otherwise, if this knowledge remains inaccessible and ignored, it may be functionally lost and unavailable for conservation decision-making.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found in the online version at doi:10.1016/j.baae.2022.03.012.

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