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Influence of Nesting Characteristics on Health of Wild Bee Communities

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Abstract

Nest site availability and quality are important for maintaining robust populations and communities of wild bees. However, for most species, nesting traits and nest site conditions are poorly known, limiting both our understanding of basic ecology for bee species and conservation efforts. Additionally, many of the threats commonly associated with reducing bee populations have effects that can extend into nests but are largely unstudied. In general, threats such as habitat disturbances and climate change likely affect nest site availability and nest site conditions, which in turn affect nest initiation, growth, development, and overwintering success of bees. To facilitate a better understanding of how these and other threats may affect nesting bees, in this review, I quantify key nesting traits and environmental conditions and then consider how these traits may intersect with observed and anticipated changes in nesting conditions experienced by wild bees. These data suggest that the effects of common threats to bees through nesting may strongly influence their survival and persistence but are vastly understudied. Increasing research into nesting biology and incorporating nesting information into conservation efforts may help improve conservation of this declining but critical group.

INTRODUCTION

When nesting and foraging resources are both considered, nesting attributes can be the more important predictor of wild bee diversity and response to disturbance (87). Nevertheless, few studies assessing risks, patterns of species richness and occurrence, and conservation of wild bees have explicitly considered either the intrinsic nesting traits of the species (often referred to as functional traits) or nest site conditions. The result is an overall lack of direct evidence of the importance of nesting (93), which is surprising because wild bees spend most of their lives within the nest or in contact with nesting materials during the five primary stages of nesting: initiation, construction, development, overwintering, and emergence (**Figure 1**). Additionally, natural mortality while nesting of more than 80% has been observed (31, 62) and suggests increased consideration of how and where a nest is constructed may play a critical role in improving conservation of bees and ensuring pollination benefits (100). Although increasing attention is being paid to nesting traits and conditions, research considering the importance of nesting for predicting diversity, response to threats, and pollination still lags behind studies considering foraging due to limitations in our understanding of bee nesting and difficulties in observing nesting behaviors.

Incorporating nesting information into assessments of possible threats to bees is complicated by a general lack of information about most species and little knowledge of how ubiquitous functional nesting traits are across bee species within families or genera. As Michener (76, p. 227) keenly pointed out in 1964, "[a]lthough 20,000 or more species of bees exist in the world, nests of relatively few have been found and described. Even among those that have been described, it often happens that characteristics which one would especially like to know about have not been recorded." While nesting has been reviewed generally (68) as well as for some families, tribes, and genera (e.g., 1, 21, 92, 95, 97), these reviews can cover only a subset of species, and for most groups it is unknown how generalizable nesting traits or conditions are among species or even within species. Within the known characteristics of bee nests, significant differences in bee biology are often noted, including variance in time spent reaching or remaining in a life stage, location of overwintering, and nesting location or depth. For overwintering alone, bees can emerge and then overwinter in new locations or remain in natal nests (61) and may enter this phase in any stage from larva to adult (59, 61). These differences can affect how a bee experiences various threats, and generalizing across these traits and characteristics could affect our understanding of how bees may respond to disturbances. Nonetheless, in the absence of direct information about nesting, species are often assigned known or assumed nesting characteristics of their genus or family. Generally, nesting traits such as nesting guild (i.e., whether a species nests in cavities aboveground, nests belowground in soils, or parasitizes nests of other species) are used to group bee species and explore how they respond to anthropogenic threats while nesting (25, 58, 120), despite evidence that many species traditionally classified as aboveground cavity-nesting nest at or below ground level (21, 32). For example, in Megachilidae, which are characterized largely as aboveground cavity-nesting due to their presence in trapnests, two of the largest genera, *Osmia* and *Megachile*, often nest belowground in cavities (21, 32) and, in some cases, excavate their own belowground nests (45). This variance in nesting location alone could affect the type and severity of threats experienced by Megachilidae, and some of the discrepancy in bee responses to threats is presumed to be linked to nesting traits and conditions (122). Given the importance of nesting for bee survival, considering the range of possible nesting traits and environmental conditions for a bee species or community could provide critical insight into responses to threats.

The lack of integration of nesting information into many studies may be due to the large and diffuse literature on nesting, making it difficult to determine how generalizable nesting traits are among species and how these may be affected by environmental changes. In this review, to

Nesting stages	Threats experienced during stage	Life stage affected	Possible changes to nesting by threat
1 Initiation	Climate change, land-use change	Adult	Location of nest, available nesting habitat
2 Construction	Climate change, land-use change, parasitism, usurpation	Adult	Available nesting habitat, nest construction, survival, fecundity
3 Development	Climate change, land-use change, parasitism, pathogens	Egg, larva, pupa	Development speed, survival
4 Overwintering	Climate change, land-use change, parasitism, pathogens	Pre-emergent stages	Development speed, survival
5 Emergence	Climate change, land-use change	Adult	Survival, emergence time

Figure 1

Generalized belowground nests of bees, depicting major stages. Foraging and mating, which occur predominantly aboveground, are also depicted. Table summarizes the primary nesting stages and threats experienced during nesting. Although not pictured, cavity-nesting species are likely to experience similar threats during the same life stages. Image created by Jose Vazquez, ITG, Beckman Institute, UIUC.

facilitate increased consideration of nesting and the important role it may play in bee conservation, I quantify natural nesting traits and environmental conditions for a subset of bees to provide a more detailed body of knowledge on nesting traits. I then consider these traits and environmental conditions alongside common threats to bees to provide deeper insights into how previously documented threats may also affect bees while nesting (**Figure 1**). I devote particular attention to non-*Bombus* wild bees, which make up the majority of bee fauna but for which, compared with honey bees and bumble bees, comparatively few studies of their specific responses to threats have been performed. This discussion provides a basis for considering how biotic and abiotic changes may affect individual species and communities at large.

QUANTITATIVE ASSESSMENT OF NESTING TRAITS AND ENVIRONMENTAL CONDITIONS

To assess the prevalence of information on nesting functional traits and environments, I generated a list of the bees in America north of Mexico by using the Biodiversity Information Serving Our Nation (BISON) online database (see **https://bison.usgs.gov**). While the database excludes some genera and Stenotritidae, it provides a comprehensive and taxonomically updated list for a wide geographic area for which data on nesting are accessible. The database includes a total of 3,128 bee species across six families. All subspecies, and any records with fewer than two occurrences, were removed to prevent inclusion of species that may be taxonomically unresolved or misidentified, reducing the number of species to 2,633. I searched information on nesting for a randomly selected 20% (527) of the reduced species list in all databases of the Clarivate Analytics Web of Science (see **https://www.webofknowledge.com**) by using the species name, commonly used previous names, and the term "nest*" when initial searches yielded a large number of responses. I also obtained relevant literature cited in other sources. Invasive species were replaced with a randomly selected species in the same genus because invasive species are known to be skewed toward cavity-nesting (17) and may not reflect native species. I recorded information about nesting only when natural nests were observed or handled directly by the study authors rather than extrapolated on the basis of presumed nesting strategies for the family or genus. I excluded studies using trapnests and field domiciles, which may not reflect natural nesting conditions because nest site limitation may cause acceptance of unnatural nesting habitats (90). Cleptoparasites with confirmed hosts in natural nests were recorded as having the nesting attributes and location of the host, enabling assessment of how they may be affected by possible threats.

Information was recorded for nesting traits and environmental conditions. Nesting traits are intrinsic characteristics that likely have a biological basis and should be somewhat consistent regardless of location; they include nesting guild (i.e., whether a species is cavity nesting, ground nesting, or cleptoparasitic), nesting depth, and nest cell lining. Environmental conditions are site-specific characteristics that may change in time or space; they include soil texture, nest abiotic conditions, cavity size, and ground cover. It is likely that these two groups intersect with and influence each other and do not have clear boundaries. Many other characteristics were recorded but did not consistently appear in the literature and are not considered in this review.

Partial nesting or host information was found for 135 (26%) of the 527 species investigated. This number includes 113 nesting species and 22 cleptoparasites. Host information was found for four additional species, but these were recorded only in trapnests, so no natural nesting information was available; therefore, these species were excluded from further consideration. Notably, 77% of species (34/44) with information on nesting density form aggregations. This observation may suggest taxonomic, observational, or geographic biases (29) and may limit our understanding of both nesting traits and environmental conditions for wild bees.

Nesting Traits

Given that nesting information is available for only 26% of the 527 researched bee species, little is known about nesting traits for most species. Within the data, important information about nest traits and conditions is often absent, poorly described, or reported only for a single nest. For example, nest linings are often referred to as waterproof, but there is no mention of whether this was tested or presumed on the basis of visual inspection. Similarly, soil was often described as sandy, with no specific soil texture mentioned. Inconsistency in reporting of traits and conditions resulted in missing information for every trait. This lack of information for so many species may impede our understanding of the full extent to which known threats affect many species.

Nesting guild. Nesting belowground is considered the ancestral state of bees (76). Most bees retain this nesting strategy, with 83% (91/110) of nonparasitic bees nesting belowground and 91% (20/22) of parasitic bees found in belowground nests as well (**Table 1**). Six species (three cleptoparasites) were found both above- and belowground. These numbers are similar to those from a previous assessment of eastern North American bees (17), which found that 87% of species nest belowground; however, the assessment offered no details about how this number was derived, so direct comparisons cannot be made. Nesting aboveground was most common in Megachilidae, with some species in Apidae and Colletidae also using aboveground stems and holes. Species that can nest in cavities seem to commonly use belowground cavities created by other species or excavate their own nests belowground (105). Fifty percent of species (19/38) in Megachilidae nested belowground; for one of these species, there is evidence of nesting both above- and belowground. This pattern of belowground nesting in Megachilidae was in part driven by *Megachile*, 92% (11/12) of which nest belowground. *Megachile rubi* accepts trapnests (59), but two groups (32, 105) describe their natural nests as belowground, suggesting that the exclusion of trapnests may provide a very different picture of nesting guild for Megachilidae. The catholic tastes of this group for nesting cavities is well documented (32), but the assumption that their cavities are largely aboveground may be driven by observation biases toward nesting blocks and aboveground twigs and stems, as they are easier to observe and to open than belowground nests (75).

Nesting depth. Nesting depth may play a critical role in maintaining populations through disturbances, as individuals at greater depth may be shielded from changes in temperature (119), extreme events, and physical disturbance (114). Information about nesting depth was found for 68 species, which have a median upper nesting depth of 9 cm and a median lower nesting depth of 23 cm (**Table 1**). These depths were similar to the median depths reviewed earlier (23) for more than 400 ground-nesting species. The average difference between the upper and lower nesting depths for a given species was 21.8 cm. A similar difference in upper and lower nest depths affects many aspects of bee nest provisioning and colony development in *Lasioglossum malachurum* (119) and demonstrates that natural nesting depth may be key to understanding how bees are affected by climate change. In some locations, depth and orientation are related to edaphic characteristics, such that individuals avoid denser and rockier soils (94) or seek a particular moisture content (63, 77, 80, 117). However, this area has been poorly explored due to limited replication of nest descriptions for most species and unmeasured edaphic characteristics.

Nest cell linings. The advent of nest cell linings is believed to have been crucial in allowing bees to exploit various habitats, as they help protect developing larvae from adverse conditions (76). Linings are made of endogenous secretions from glands, exogenously gathered materials, or a combination of endogenous and exogenous materials. The source and composition of the linings

Table 1 Summary of nesting information from quantitative review of nesting traits and conditions for 527 researched species in America north of Mexico

	Number of species researched	Number with available nesting data	Percentage nesting belowground	Nest substrates and soil textures	Nest depth range (cm)
Andrenidae					
Andrena	71	12	100	Soil (S, LS, SiL, CL, SL)	5.5–107
Anthemurgus	1	1	100	Soil (SL)	11–15
Calliopsis	15	11	100	Soil (SCL, SL)	3–13
Macrotera	2	0	NI	NI	NI
Panurginus	3	1	100	NI	11–unknown[b]
Perdita	65	6	100	Soil (S, SL, SiL)	5.5–88
Protandrena	2	0	NI	NI	NI
Protoxaea	1	1	100	Soil (S)	24–50
Pseudopanurgus	3	0	NI	NI	NI
Apidae					
Anthophora	10	7	100	Soil (C, SiL, S), adobe walls	3–28
Anthophorula	6	0	NI	NI	NI
Bombus	14	11	55[a]	Soil, hole, grass	6–122
Brachynomada	3	1	100[a]	NI	NI
Centris	2	1	100	Soil (S)	8.3–unknown[b]
Ceratina	5	2	0	Stem	NI
Diadasia	8	6	100	Soil (S, SiL, SL)	7–37
Epeolus	2	1	100[a]	Soil	NI
Eucera	8	1	NI	NI	NI
Habropoda	2	1	100	Soil	28–71
Holcopasites	4	2	100[a]	Soil	NI
Melissodes	21	1	100	Soil (S)	NI
Neolarra	3	1	100[a]	Soil	NI
Neopasites	1	1	100[a]	Soil	NI
Nomada	23	3	100[a]	Soil	NI
Oreopasites	1	1	100[a]	Soil	NI
Ptilothrix	1	1	100	Soil	5.76–7.85
Svastra	5	1	100	Soil (S)	NI
Syntrichalonia	1	0	NI	NI	NI
Tetraloniella	4	0	NI	NI	NI
Triepeolus	2	1	100[a]	Soil	NI
Xylocopa	1	0	NI	NI	NI
Colletidae					
Caupolicana	1	0	NI	NI	NI
Colletes	21	5	100	Soil (C, S, SL)	7–60
Hylaeus	9	1	0	Stem	NI
Halictidae					
Agapostemon	3	1	100	Soil (SiL)	11.5–20
Augochlorella	1	1	100	Soil	NI
Conanthalictus	2	0	NI	NI	NI

(*Continued*)

Table 1 (*Continued*)

	Number of species researched	Number with available nesting data	Percentage nesting belowground	Nest substrates and soil textures	Nest depth range (cm)
Dufourea	16	1	100	Soil (S)	5–10
Halictus	6	4	100	Soil (SiL)	7.5–75
Lasioglossum	46	4	100[a]	Soil (SL)	5.31-unknown[b]
Protodufourea	1	0	NI	NI	NI
Sphecodes	10	2	100[a]	Soil	NI
Xeralictus	2	1	100	Soil	NI
Megachilidae					
Anthidium	6	2	50	Cavities, *Anthophora* nests, beetle burrows, yucca stalks	NI
Ashmeadiella	11	0	NI	NI	NI
Atoposmia	8	1	0	Attached to stone	NI
Chelostoma	3	2	0	Stem, wood, cavities	NI
Coelioxys	11	4	50[a]	Cavity, soil	NI
Dianthidium	5	4	50	Soil (S), wood	5–10
Dioxys	1	0	NI	NI	NI
Heriades	4	1	0	Stem	NI
Hoplitis	10	3	0	*Sceliphron* nest, cavity, stem	NI
Lithurgus	1	1	0	Wood	NI
Megachile	27	12	92	Soil (S, SL)	1.8–14
Osmia	18	6	17	*Anthophora* nest, cavity, wood, stem	NI
Protosmia	1	0	NI	NI	NI
Stelis	6	2	0[a]	Stem, cavity	NI
Trachusa	4	0	NI	NI	NI
Melittidae					
Hesperapis	2	1	100	Soil (S)	15–25
Macropis	1	1	100	Soil (SL)	2.5–6.5
Total	527	135	84		

[a]Includes cleptoparasites, which are assigned the nesting location of their host.

[b]For some species, only a single nest depth was reported and the nesting range is unknown.

Abbreviations: C, clay; CL, clay loam; LS, loamy sand; NI, no information; S, sand; SCL, sandy clay loam; SiL, silt loam; SL, sandy loam.

are considered such defining characteristics of individuals, species, and families that they are used to understand patterns of diversification (14, 44, 66) and kinship of bees (4). One presumed important role of secreted linings is maintaining moisture balance within cells (69); however, many nest caps are unlined, and there is evidence of water uptake into cells (69) and a wide variety of permeability of nest cell linings between populations (4) and possibly between individuals within the same species. Similarly, exogenously lined nests, which can be made of pebbles, resins, oils, leaves, petals, and plant hairs, protect developing larvae from possible threats and also vary in completeness; for example, some *Osmia* nests are lined only partially or not at all (73). Cell linings may play critical roles in providing protection from various biotic and abiotic threats, but in most cases these protections have not been parsed from other characteristics such as nest depth. In some cases, nest linings protect against predators (15) and parasites (20, 30) and serve as food for larvae (79), although the ubiquity of these benefits is unknown.

For 66 of the 113 nonparasitic bee species for which information about nesting is available, the nest descriptions indicate whether the nest cell is lined. The nest descriptions often do not explicitly mention nest cell linings or important characteristics such as the possible source of the lining and water permeability. Of these 66 species, 13 (20%) in the genera *Perdita*, *Diadasia*, *Chelostoma*, and *Melissodes* (although this was possibly overlooked) are described as having unlined nests. Many cavity-nesting species do not line nests unless they are required to modify their cavity, which may explain why this information was absent for many species in Megachilidae (108).

Environmental Conditions of Nests

The location of a nest can affect bees' exposure to various biotic and abiotic threats and may influence their survival and community composition. The most commonly reported environmental conditions are soil texture and ground cover, but a range of other soil abiotic conditions have been measured sporadically (e.g., pH, moisture content, slope). For cavity-nesting species, descriptions of natural cavities and conditions lack the details necessary to assess their relative importance for nesting success. Regardless of whether the species nests predominantly in cavities or excavates a nest, a lack of specific measurements and comparisons of nesting conditions between sites with and without nests present, with cavities selected or unselected, and at different depths limits our understanding of the importance of environmental conditions. For example, soil texture is often generalized with terms such as sandy or hard, but these qualitative descriptions cover a wide range of soil textures and provide little actionable information for conservation. Furthermore, little information on how conditions of the nesting location affect fecundity and survival is available.

Soil texture. Soil textures can affect water content, available oxygen, and temperature, all of which may influence survival in the nest. Additionally, soil texture may prevent some bees from initiating nests if soils are too hard or compacted (96). Some cavity-nesting species show a strong preference for certain soil textures in cell partitions, so the availability of required soil textures may limit nesting in some areas (84). Whether a species can manipulate certain textures and tolerate the conditions associated with those textures may partly explain the distribution of bee species, but to date this topic has received little attention, and information about soil texture preference throughout ranges is incomplete. Cavity-nesting species may have a possible advantage in areas where soils are difficult to manipulate by either using aboveground cavities or renting belowground cavities.

Soil texture was reported in 48 descriptions with 75% of bees nesting in either sand or sandy loam–textured soils (**Table 1**). This finding is in line with previous studies that found a strong association with sandy soils (16); however, evidence of at least four species nesting in clay soils was obtained in the quantitative review (**Table 1**), in contrast to previous observations. Similarly, experimental structures erected to test preferences for soil textures found no differences in richness for bees nesting in sand versus those nesting in clay soils (39), which also suggests that bees may accept a wide range of soil textures. Some species with multiple nest descriptions, including *Andrena macra* (91, 105) and *Agapostemon virescens* (31), use various soil textures, so although soil texture is generally considered an important characteristic for nest site selection, it is difficult to know how consistent it is within a species. The observed preference for sandy soils may be an observation bias, as sandy soils are also likely to have reduced ground cover, making nests easier to observe and excavate.

Ground cover. Greater amounts of bare ground have been repeatedly linked with increases in belowground bee nesting (99). Of the 44 nest descriptions that included mention of ground cover, 75% were in bare ground (**Table 1**). It is difficult to determine whether increased nesting in areas with little vegetation is a product of observation bias toward bare areas and aggregating species, or a genuine preference for unobscured soil. However, increased ground cover is associated with differences in temperature and moisture, as barer soils have greater sun exposure (2). Ground cover and landmarks can be important for nest site selection for some species (19) and can help bees locate nesting sites (124). Conservation efforts may consider practices that help increase bare ground, including burning and planting more diverse seed mixes (2), although it is unclear what level of bare ground is desirable.

Additional soil abiotic conditions. Soil abiotic factors that seem important for nest site selection include soil compaction (99), soil bulk density (81), humidity/moisture (51, 82), slope (97), ground cover versus bare ground (87, 124), pH (88), and aspect (88). Some of these abiotic conditions have been linked to differences in survival and development (106), although the use of these can shift depending on the size of the aggregation (88). Many of the studies in this area have focused on a single species, making it difficult to determine how generalizable these abiotic conditions are across species. In the quantitative review of abiotic conditions across species, few of these characteristics are consistently reported, and the recorded data often describe only a single nest or location, making it difficult to determine the within-species variability of nest site characteristics. Nest site conditions also interact with one another, so it is challenging to make a meaningful summary of this information across species. For example, some studies find increased nesting in drier areas (82), whereas others find increased nesting in wetter areas (117), but this likely intersects with other key features of a site (e.g., soil texture) and possibly traits of the species (e.g., nest cell linings). Understanding the types of abiotic conditions that a species can tolerate, and how they may alter nest construction in response to various edaphic or environmental characteristics that are important for successful nesting (5), can improve our understanding of how bees may survive emerging threats to nests. More consistent measuring and reporting of these abiotic characteristics for numerous species could provide more insight into the importance of these characteristics for nest site selection.

Cavity size and abiotic conditions. Little is known about the preferred nesting conditions of bees nesting in natural cavities. It is presumed that cavity-nesting bees must use available cavities, which can vary considerably in length, number of cells, size, and position. For example, *Anthidium illustre* nests in bee burrows, in beetle burrows, in plant stalks, and between rocks (46). Similarly, *Bombus vagans* nests in hollow trees, stone walls, bird's nests, attics, and even fur coats (85). Cavities can be lined with either soil or plant materials to alter their size (108), and to prevent modification bees may elect to lay male or female eggs depending on the size of the cavity available (48). Some preference for trapnest diameters similar to body size has been observed, which likely reduces the time bees spend modifying their cavities (59, 101). At least one species, *Chelostoma phaceliae*, rejects trapnests and is found only in living elderberry stems (83), but no statistical analysis has been conducted. Sun exposure is one of the few abiotic conditions known to be important in trapnest occupancy, with fully lit nests having increased occupancy for *Osmia bicornis* (36). Thus, cavity size, abiotic conditions, and availability may affect bee community composition and sex ratios, but little is known about the nest site conditions within or around natural cavities and how they may affect important aspects of bee survival.

COMMON THREATS TO BEES WHILE NESTING

Climate change, land-use change, parasites, and pathogens are some of the leading causes of declines in bee populations (121), but how these threats affect bees during development in nests or in contact with nesting materials depends both on how threats interact with nest site conditions and on species-specific nesting traits. Furthermore, many of these threats have additive or synergistic effects that could lead to negative outcomes for bee species and populations.

Climate Change

Global changes in temperature and precipitation can have drastic effects on bees, whose development (89), social structure (28), emergence (6, 110), and species interactions are directly affected by climate. While phenological mismatches with flowering resources have received significant attention (37), climate-mediated changes within nests have been less well studied, and our understanding of the physiological effects is poor. Most studies examining changes in climate on bees while nesting are restricted to a few species in trapnests or laboratory colonies (8, 38, 52), and there have been few direct measurements for ground-nesting species in wild conditions (but see 110, 116). For cavity-nesting species, increasing overwintering temperatures and the onset of winter affected fat storage, mortality, and size (11, 24, 55, 102), while increasing summer temperatures negatively affected eclosion and extended diapause (103), both of which could negatively affect survival. Similarly, in a laboratory experiment on a ground-nesting species, increasing temperature affected bee size and development rate (52). Depth of nests, soil texture, slope, orientation, and ground cover, however, may help buffer some effects by providing insulation or helping to maintain moisture content (63, 113). Nonetheless, increasing air temperatures and changes in snow cover will affect soil temperatures to depths relevant for most ground-nesting species (2). Lastly, for species that rely on plant resins, oils, and petals for nesting materials, phenological mismatches may have adverse effects on the availability of these necessary materials; however, there is no direct evidence for this type of phenological mismatch between plants and bees.

There is some evidence that ground-nesting bees may be robust to some climatic changes, as studies have found species resilient to hurricanes (18), complete and prolonged inundation (107, 118), fire (23), and drought (78). Some species regularly tolerate soil temperatures at nesting depths of 40°C (117), suggesting that there is some resilience to increased temperatures. However, few of these studies tracked changes in physiology, life span, or fecundity after extreme events, and many questions remain about the long-term effects of climate change. One strategy some species use to avoid adverse weather is to remain in diapause for up to 10 years, which may help populations persist under variable weather conditions (112). Additionally, some climatic changes, such as extreme cold, are still poorly studied. Nesting-site characteristics such as soil texture also interact with climate change and could cause a shift in nest site location in response to changes in abiotic conditions. Nesting-site characteristics such as slope, soil texture, and bare ground may be important for aiding bees to survive predicted differences in rain and temperature, but as mentioned above these characteristics have been poorly documented for many species across their range, making it difficult to determine how willing bees are to nest in these conditions.

Land-Use Change

Reduction in available natural habitat and changes in habitat quality are among the most significant causes of bee declines (86), but the direct effects of land-use change on aspects of bee nesting are poorly understood. Land-use change can shift available nesting habitat and disturbance patterns, changing the functional traits that can persist in these areas and the environmental conditions experienced by bees while nesting (35). Urbanization and agriculture, the two predominant examples of land-use change, can have different effects on nesting habitat by shifting the community to species with nesting traits suited for enduring new environmental conditions in these habitats.

Urbanization. Studies of differences in bee biodiversity in response to urbanization are mixed: Some find reduced diversity, and others find no response (22, 53). However, this discrepancy may depend on the nesting conditions necessary for bees, as urban areas affect environmental nesting conditions and nest site availability. Direct measurements of changes in important nesting environmental conditions are limited apart from the documented increases in impervious surfaces, human-made structures, and local temperatures. These habitat modifications negatively affect nest site availability for ground-dwelling species but may increase human-made cavities and the abundance of cavity-nesting bee species, causing shifts in community composition in urban environments (9, 22). Increases in impervious surfaces in urban areas also trap heat, affecting the rates of development (5) and parasitism of wild bees (49, 111), both of which could have negative effects on bee survival in urban areas. Recent research on thermal tolerance and desiccation limits found adults of some species closer to their critical thermal limit and others closer to their critical water limit in urban environments (13), suggesting that urban areas cause extreme stress on bees. Developing and diapausing species in nests could experience similar stress, but this may be buffered by nest site selection and soil depth, which may help reduce the effects in nests. Heavy-metal contamination in soils in urban areas has been recorded but thus far has been linked only to differences in foraging (74, 104). If heavy-metal contamination penetrates into nest cell linings and occurs at depths relevant for bee nesting, there could be other negative effects on bees, as observed in honey bees using contaminated nesting materials (47). Cavity-nesting species may be exposed to heavy metals in treated lumber or urban trees, which can have increased heavy-metal loads. Apart from changes in environmental conditions, urbanization can affect gene flow between populations of both solitary bees (67, 115) and bumble bees (50). Importantly, urbanization can increase bumble bee nesting (70), which, given reductions in the abundance and diversity of this group, could be important for conservation.

Agriculture. Studies to date have shown that agricultural disturbances such as tilling and grazing have only weak effects on bees (122), likely due to variance in intensity and frequency. These disturbances can alter a variety of environmental nesting conditions, including soil texture, hardness, availability of cavities and stems, ground cover, and other characteristics that are important for nesting. Grazed areas can have reduced bee diversity (54), but the role nesting traits or nesting conditions play in this relationship is unknown. Tilling reduces belowground-nesting species (120), but whether the loss of these species in tilled areas is due to direct mortality or to changes in the abiotic characteristics of soils remains unknown. Variance in nesting depth can be important for survival in agricultural areas (114), with deeper nests surviving tilling. Additionally, tilling may reduce the total number of cavities available to cavity-nesting communities, although flexibility in nesting location may mitigate some negative effects. Physical disturbances in agriculture are often accompanied by agrochemicals, which can also affect bees while nesting.

Many pesticides used in agriculture have detrimental effects on bees (12), but they have been tested mostly in feeding and application trials, which do not reflect all routes of exposure to bees while nesting. Contaminated soils and plant materials may expose larval and diapausing bees to pesticides (42, 57) when they are likely highly vulnerable, but little research has examined the direct effect of contaminated nesting materials on bees. While nest linings with glandular secretions should limit the introduction of external threats, the variance in permeability and structure, mentioned above, leaves many questions about how much protection such linings provide. Whether through unlined nests, semipermeable nests, or unlined nest caps, water uptake by larvae while nesting has been observed (69), suggesting that water-soluble pesticides could enter via this route and thereby affect bee survival in soils. In a simulated exposure to contaminated nesting resources, two solitary species showed highly variable responses in mortality and growth rates that depended on sex, species, and exposure concentration, further suggesting that contamination in nests may be an important route of exposure (3). For ground-nesting species, nesting depth, soil texture, and soil moisture may play a role in pesticide exposure and may intersect with other factors such as tilling, but this topic has not been well studied. Adult bees are exposed to contaminated nesting materials while preparing nests and have been observed gathering contaminated water to soften soils (117). Although nesting materials may have greater and more persistent amounts of pesticides (3), this route of exposure is understudied and limits our ability to adequately assess risks for many species.

Pathogens and Parasites

Pathogens and parasites can significantly reduce survival of bees while nesting (65). Pathogenic microorganisms including bacteria, fungi, protists, and viruses can be critical to honey bee health (40), but they are largely understudied and poorly described in most wild bee species (but see 7). Additionally, although parasitism can affect more than 50% of nest cells in some species (61), it is difficult to prove direct relationships with population stability, as high rates of parasitism are usually found in large stable populations. Nonetheless, current research suggests that anthropogenic threats such as climate change and land-use change may intensify pathogenic and parasitic interactions (98, 123), which could, in turn, intensify these threats to survival of bees while nesting.

Pathogens. Pathogens are poorly understood for most wild bees, as few studies have examined microbial associations in these species (43). Additionally, direct testing of solitary species for pathogenic bacteria and viruses is often performed for common honey bee and bumble bee viruses (72), leaving most other pathogens largely unexplored. In social species, susceptibility to infection has been linked to interactions that occur within the nest and microbiome (56). However, many wild bees lack these intimate social interactions (109), and there is limited information on their microbiomes (33), so it is difficult to understand how these factors may affect pathogen susceptibility and interactions with nesting materials. Aggregating species are expected to have more interactions with conspecifics, which may increase their risk for pathogen transmission in and around the nest, but this hypothesis has not been well studied. In social species, disease risk can interact with other threats such as climate change and agrochemicals (33), but these are underexplored in both social and solitary species. Molds are the best-documented pathogenic organisms in nests and can have significant effects on bee survival (65). Thus, limiting mold growth is key for survival of bees while nesting; bees select nesting characteristics (e.g., slopes and soil texture) that may help control mold growth. Nesting traits such as the type of nest lining, which can have antimicrobial effects, may help some species overcome pathogens or protect them from nest site conditions necessary for pathogen growth (15). Interestingly, characteristics such as philopatry, the tendency to return to nest in natal locations, could result in higher pathogen loads for bees, but whether nesting conditions or traits can prevent pathogens has been largely unexplored.

Parasites. Although a high level of belowground parasitism on larvae seems common for some bees (26, 48, 61, 62), it is unclear how parasitism directly affects population sizes and persistence, as it alters competition for nesting and floral resources. However, some evidence indicates that reductions due to parasitism may have negative effects on bee populations on the basis of reductions in pollination (26) and the deceleration of nest construction (10). While overwintering, adult bees can be inhabited by nematodes, but whether these have negative effects on bee survival or fecundity remains poorly understood for most bee and nematode species (41, 71). Mandibular secretions placed at nesting entrances can provide some deterrence against parasitism (15), although this process is poorly understood for most species. Nest site conditions influence parasitism rates and susceptibility: Higher temperatures increase the flight window for nest cleptoparasites, thereby increasing interactions with prey (38). Increasing temperatures also increase stress on nesting individuals, making make them more susceptible to a variety of infections (60). For philopatric species, returning to natal nesting grounds may increase parasitism rates because (*a*) some parasites can recognize nests and visit them repeatedly (75) and (*b*) some nematodes complete portions of their life cycles in soils. Clustering of parasites may explain the spatial variability in parasitism between populations. Interactions between threats could have various effects on parasitism rates for nesting bees, as there are fewer parasites in locations with high pesticide pressure (34) but greater parasitism in urban areas (49).

CONCLUSIONS

The documented declines of wild bees will require a deeper understanding of their ecology as well as better assessments of how threats affect bees during all life stages. Given that bees spend the majority of their life cycles in nests, both during vulnerable developmental stages and while initiating nests, specific knowledge about how common threats affect bee survival while nesting and interact with nesting traits and conditions is critical. Such knowledge is especially important because the greatest threats are to larvae and overwintering stages, which have a limited ability to respond to threats experienced while nesting. Thus, if nest site conditions experienced by adults change rapidly after nest initiation, nesting stages may be at increased risk. Unfortunately, most threats to bees have been poorly studied within the context of nesting, and extrapolation of aboveground responses in adult bees does not account for larval stages, nesting traits, or environmental conditions that could dampen or amplify these effects.

A major limitation is incomplete information about nesting traits for many species, which makes even general extrapolations difficult. Some nesting information has been recorded for only 26% of selected wild bee species, but important information is missing even for most of these species despite an established guide on traits to record for bees (64). In more poorly researched areas, less information is likely known about bee nesting characteristics than in the area covered in this review, which may put these lesser-known species and areas at even greater risk. This major knowledge gap is unlikely to be filled, however, given the sheer number of species that exist. More realistically, data on behavioral, physiological, survival, and reproductive differences in response to threats during nesting stages to ground-nesting species would provide significant insight into the relative importance of nesting for conservation and restoration. Such data would be especially important given the documented and expected interactions between the many threats that may place nesting bees at even greater risk. While many of these threats, such as parasitism and mold encroachment, are natural and cannot easily be ameliorated, mitigating some anthropogenic threats to nesting and improving nest site availability by increasing bare ground and cavities may make it possible to increase bee diversity, conservation, and ecosystem services. These actions may also provide some safeguard against the predicted interactions among various threats, such as climate change and parasitism.

By highlighting key nesting traits and environmental conditions for bees, this review hopes to encourage further research on the importance of bee nesting alongside the documented importance of floral resources. Bee nesting traits and environmental conditions can play an important role in species persistence in environments, and better recording of these characteristics could play an important role in predicting effects of environmental disturbances on bees. Such research may be especially important because some aspects of bee nesting biology, such as nesting depth, may be flexible enough to provide some protection against threats such as climate change.

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