



A systematic review of the nesting and overwintering habitat of bumble bees globally

Amanda R. Liczner¹ · Sheila R. Colla²

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Abstract

Some bumble bee species are in decline globally. Declines have been attributed to many factors including habitat loss. Habitat is an integral component of any species and should be a central focus of conservation efforts to protect at risk species. However, the habitat of bumble bee species is not fully understood. We conducted a systematic review of the peer-reviewed literature using Web of Science to summarize articles that have described the habitat of bumble bee species. In total, 55 nesting and 10 overwintering habitat studies are described in this review. We described common patterns associated with bumble bee studies including overwintering habitat, landscape type, and ground position. We found that bumble bee nests are more frequently found underground and that studies were biased towards the United Kingdom and agricultural habitats. There are some preferences in nesting and overwintering habitat, but further research is needed to draw any substantial conclusions. Detection of nesting and overwintering site studies may be improved using citizen science initiatives and possibly through employing detection dogs or radio-telemetry. Increasing the detection of nesting and overwintering sites is an important priority to improve our understanding of bumble bee habitat. It is critical that we identify all aspects of bumble bee habitat to ensure the protection, restoration and creation of important resources to ensure their conservation.

Keywords *Bombus* · Bumble bee habitat · Bumble bee nesting · Nest detection methods · Nesting resources · Overwintering habitat

Introduction

Some bumble bee species (34.7%) are in decline globally (Arbetman et al. 2017). Suggested threats that are contributing to bumble bee declines include climate change, pathogen spillover, pesticides, invasive species competition and habitat loss (Colla et al. 2006; Brown and Paxton 2009; Grixti et al. 2009; Goulson et al. 2015; Thomson 2016). Habitat loss especially has been cited as the main threat to bumble bees in Europe (Goulson et al. 2008; Williams and Osborne 2009). Bumble bee declines are problematic both to crop and wild plant systems, especially in temperate

regions. This is because bumble bees are efficient pollinators in conditions where other pollinators are not effective such as during cool and wet weather (Willmer et al. 1994; Bishop and Armbruster 1999). Bumble bees are also able to buzz pollinate plant species that require this method of pollination (Goulson 2003). To address these observed declines there has been a focus on protecting and improving pollinator habitat (Carvell 2002; Lye et al. 2009; Roulston and Goodell 2011). However, these efforts have mainly focused on increasing available forage (Carvell et al. 2007; Dicks et al. 2015; Moquet et al. 2017) and this is only one component of bumble bee habitat. Bumble bees require three main resources to complete a colony cycle: nesting, forage, and overwintering sites (Kearns and Thomson 2001). Overall, we lack understanding about what specifically characterizes bumble bee habitat besides describing very general ecosystem types where bumble bees are found and the types of forage species bumble bees utilize (Colla 2016). Nesting and overwintering requirements for bumble bees are extremely understudied likely due to the difficulty in locating these sites (Darvill et al. 2004; Waters et al. 2011; O'Connor et al.

✉ Amanda R. Liczner
aliczner@yorku.ca

Sheila R. Colla
srcolla@yorku.ca

¹ Department of Biology, York University, Toronto, ON, Canada

² Faculty of Environmental Studies, York University, Toronto, ON, Canada

2017). Compiling available literature, exploring patterns in previous research as well as outlining knowledge gaps are next critical steps for the conservation of bumble bees as we need to ensure we are protecting all aspects of bumble bee habitat. Additionally, this information is often needed when defining a species' critical habitat for legal protections. The nesting and overwintering requirements for bumble bees need to be better described to effectively address habitat protection for those in decline.

Methods

Literature review

A systematic literature review was conducted on February 5, 2018 using Web of Science. This search was part of a larger literature review for all of bumble bee habitat. The following search terms were used: (nest*) OR (forag* OR floral OR flower*) OR (overwinter* OR hiberna*) AND (bombus OR bumble bee OR bumblebee) AND (habitat OR resource*). A total of 955 articles resulted from this search. A preliminary refinement excluded 430 articles that were reviews, did not study bumble bees, or were not focused on bumble bee habitat. Of the remaining 525 articles, 53 appeared to be related to nesting or overwintering habitat (51 for nesting and 2 for overwintering) and were refined further for this review. These 53 studies were identified as potentially relevant to the review by reading the paper's title and abstract. These 53 studies were read in their entirety and we determined that 25 of these studies were not relevant (i.e. were focused on crop yields, did not actually involve finding nesting/overwintering sites or describing nesting/overwintering habitat), or we could not access (3 studies) due to no digital copy available. The literature cited section of the remaining 28 articles (26 nesting, 2 overwintering) was searched for additional relevant articles. This resulted in an additional 29 nesting and 8 overwintering studies that were included in this review. The search terms were then input into Scopus to locate any additional missing studies. The resulting papers from the Scopus search did not add any missing papers from our original Web of Science and literature cited searchers (i.e. all papers in the Scopus search results were already included in our literature review). The final total number of studies included in this review were 55 nesting and 10 for overwintering. Some of the studies included in the review looked at both nesting and overwintering habitat and were coded as separate studies even though they were from the same article. This was done to allow more efficient summaries of nesting and overwintering habitat. The 55 and 10 nesting and overwintering studies respectively, resulted from 59 separate articles (i.e. 6 articles looked at both nesting and overwintering bumble bee habitat) (Table 1).

Data extracted

The data extracted from each study was the study location (latitude and longitude), study species information (species, subgenus), and descriptions of the study site location (landscape and patch types, soil). If GPS coordinates were not provided in the study, we used description of the study site to approximate where the study took place and estimated the GPS coordinates using Google Earth. Ground cover (i.e. bare ground, litter, moss, etc.) was also described for overwintering studies. Additional information was extracted (when available) for nesting studies including the number of nests per species in each study, ground position of nests (aboveground, surface, underground), detection method used to find nests (detection dogs, molecular methods, nest searching queens, observational, and statistical modelling), nesting materials (i.e. what the nest was made from), and nest density. Molecular methods and some of the statistical models used to detect nests did not locate or describe the actual nest.

Data analysis

The data were summarized by subgenus, landscape type or ground position of nests to determine if there was a relationship between (i) where nests are located by landscape type and subgenus, (ii) ground-position of nests and landscape type and, (iii) subgenus and ground-position of nests. To examine these potential relationships the proportion of nests by subgenus, landscape type or ground position was compared. Landscape types were classified as: agricultural, alpine, forest, forest edge, grassland, tropical forest, urban or other. Agriculture includes all types of agriculture including intensive, conventional, and stewardship practices. It also includes non-arable areas such as hedgerows, pastures, woodlots, and grasslands. Grasslands included meadows, heathlands, and machair. The 'other' category includes landscape types that were not well represented across the studies: wetlands, dunes, shrublands, and human-associated (but not developed enough to be considered urban). If a range of nests were included in a study, the lowest number of nests in the range were assigned as the number of nests to keep a conservative estimate. If a study included more than one category (i.e. more than one ground position for the same species) the study was double coded. To determine if there was a relationship between subgenus, landscape type or ground position, three Chi square tests were performed comparing: (i) subgenus and landscape type, (ii) subgenus and ground-position, (iii) ground-position and landscape type.

Table 1 Bumble bee species information for all studies included in the literature review. Species are divided into subgenera. Numbers in brackets indicate the number of studies reported, square brackets are the number of overwintering studies. The IUCN red list status (IUCN, 2017) for each species is given. Bumble bee nest or overwin-

tering detection methods are shown under method and include detection dogs (dogs trained to find nests) molecular (i.e. genetic analysis), observational (i.e. transect visual surveys), Nest-searching queen surveys (as a proxy for bumble bee nest density), and modeling (i.e. predicting nest locations based on floral resources)

	Species	Continent	IUCN status ²	Method
<i>Alpigenobombus</i> (1)	<i>Bombus wurflenii</i> (1)	Europe	Not assessed	Observational ¹
<i>Alpinobombus</i> (8)	<i>Bombus alpinus</i> (1)	Europe	Vulnerable	Observational ²
	<i>Bombus balteatus</i> (3)	Europe ² North America ^{3,4}	Not assessed	Nest-searching queens ² Molecular ³ Observational ^{3,4}
	<i>Bombus hyperboreus</i> (2)	Europe ² North America ³¹	Not assessed	Observational ³¹ Nest-searching queens ²
	<i>Bombus polaris</i> (2)	Europe ² North America ³¹	Data deficient	Observational ³¹ Nest-searching queens ²
<i>Bombias</i> (3)[1]	<i>Bombus auricomus</i> (1)	North America	Least concern	Observational ⁵
	<i>Bombus nevadensis</i> (2)[1] ⁵	North America	Least concern	Observational ^{5,6}
<i>Bombus sensu stricto</i> (33)[4]	<i>Bombus affinis</i> (2)	North America	Critically endangered	Observational ^{7,8}
	<i>Bombus hypocrita</i> (1)	Asia	Not assessed	Observational ⁹
	<i>Bombus ignitus</i> (1)	Asia	Not assessed	Observational ⁹
	<i>Bombus lucorum</i> (10)[2] ^{55,56}	Europe	Not assessed	Detection Dogs ¹⁰ Nest-searching queens ^{2, 11–14} Observational ^{1,2,14–16}
	<i>Bombus occidentalis</i> (4)	North America	Vulnerable	Nest-searching queens ¹⁷ Observational ^{7, 18, 19}
	<i>Bombus terrestris</i> (14)[2] ^{55,56}	Europe ^{10–14, 20, 23} Asia ²⁶ Australia ^{27, 28}	Not assessed	Detection dogs ¹⁰ Molecular ^{20, 23} Nest-searching queens ^{11–14} Observational ^{14–16, 25–28}
	<i>Bombus terricola</i> (2)	North America	Vulnerable	Observational ^{7,8}
<i>Cullumanobombus</i> (46)[1]	<i>Bombus griseocollis</i> (1)	North America	Least concern	Observational ²⁹
	<i>Bombus melaleucus</i> (1)	South America	Data deficient	Observational ⁵⁹
	<i>Bombus rufocinctus</i> (4)[1] ³⁰	North America	Least concern	Nest-searching queens ¹⁷ Observational ^{18,29,30}
<i>Megabombus</i> (13)[3]	<i>Bombus diversus</i> (1)	Asia	Not assessed	Observational ⁹
	<i>Bombus hortorum</i> (9)[2] ^{55,56}	Europe	Not assessed	Detection dogs ¹⁰ Nest-searching queens ^{11–14} Observational ^{14,15,25,27}
	<i>Bombus ruderatus</i> (3)[1] ⁵⁶	Europe Australia	Not assessed	Observational ^{25,27,28}
<i>Melanobombus</i> (11)[2]	<i>Bombus lapidarius</i> (11)[2] ^{55,56}	Europe	Not assessed	Detection dogs ³² Molecular ^{22,23} Nest-searching queens ^{11–14} Observational ^{1,14–16,25}
<i>Mendaci-bombus</i> (1)	<i>Bombus handlirschianus</i> (1)	Asia	Not assessed	Observational ³³
<i>Pyrobombus</i> (46) [10]	<i>Bombus ardens</i> (4)	Asia	Not assessed	Observational ^{9,34–36} Statistical model ^{34–36}
	<i>Bombus beaticola</i> (1)	Asia	Not assessed	Observational ⁹
	<i>Bombus bifarius</i> (4)[1] ³⁷	North America	Least concern	Molecular ³ Nest-searching queens ¹⁷ Observational ^{18,37}
	<i>Bombus bimaculatus</i> (1)[1] ⁸	North America	Least concern	Observational ⁷
	<i>Bombus centralis</i> (1)	North America	Least concern	Observational ³⁷
	<i>Bombus flavifrons</i> (4)[1] ³⁷	North America	Least concern	Molecular ³ Nest-searching queens ¹⁷ Observational ^{18, 37}
	<i>Bombus frigidus</i> (2)[1] ³⁷	North America	Least concern	Observational ^{18,37}

Table 1 (continued)

	Species	Continent	IUCN status ²	Method
	<i>Bombus huntii</i> (2)[1] ³⁷	North America	Least concern	Nest-searching queens ¹⁷ Observational ³⁷
	<i>Bombus hypnorum</i> (2)	Europe	Not assessed	Nest-searching queens ² Observational ¹⁶
	<i>Bombus impatiens</i> (2)[2] ^{8,58}	North America	Least concern	Observational ^{7,8}
	<i>Bombus jonellus</i> (2)	Europe	Data deficient	Detection dogs ³² Nest-searching queens ²
	<i>Bombus lapponicus</i> (1)	Europe	Least concern	Nest-searching queens ²
	<i>Bombus melanopygus</i> (1)	North America	Least concern	Observational ³⁷
	<i>Bombus mixtus</i> (2)	North America	Least concern	Observational ^{18,37}
	<i>Bombus monticola</i> (1)	Europe	Not assessed	Nest-searching queens ²
	<i>Bombus pratorum</i> (9)[2] ^{55,56}	Europe	Not assessed	Molecular ²³ Nest-searching queens ^{2,11–14} Observational ^{12,14,16,25}
	<i>Bombus sylvicola</i> (2)[1] ³⁷	North America	Least concern	Molecular ³ Observational ³⁷
	<i>Bombus ternarius</i> (2)	North America	Least concern	Observational ^{18,37}
	<i>Bombus vagans</i> (3)	North America	Least concern	Observational ^{7,29,37}
Sibirico-bombus (1)	<i>Bombus niveatus</i> (1)	Asia	Not assessed	Observational ³⁸
Subterraneobombus (7)[2]	<i>Bombus appositus</i> (2)[1] ³⁹	North America	Least concern	Observational ^{18,39}
	<i>Bombus borealis</i> (2)	North America	Least concern	Nest-searching queens ⁷ Observational ³⁹
	<i>Bombus distinguendus</i> (2)	Europe	Data deficient	Detection dogs ³² Molecular ⁴⁰
Thoracobombus (41) [2]	<i>Bombus subterraneus</i> (1)[1] ⁵⁶	Europe	Not assessed	Nest-searching queens ¹²
	<i>Bombus brevivillus</i> (1)	South America	Data deficient	Observational ⁴³
	<i>Bombus deuteronymus</i> (1)	Asia	Data deficient	Observational ⁹
	<i>Bombus fervidus</i> (5)[1] ⁴⁴	North America	Vulnerable	Observational ^{7,8,18,29,44}
	<i>Bombus medius</i> (2)	North America	Vulnerable	Observational ^{45,46}
	<i>Bombus mesomelas</i> [1]	Europe	Not assessed	Observational ⁵⁵
	<i>Bombus mucidus</i> (2)	South America	Least concern	Observational ^{41,42}
	<i>Bombus muscorum</i> (1)	Europe	Not assessed	Detection dogs ³²
	<i>Bombus pascuorum</i> (15)	Europe	Not assessed	Detection dogs ¹⁰ Molecular ^{20–24} Nest-searching queens ^{11–14} Observational ^{1,14,16}
	<i>Bombus pensylvanicus</i> (1)	North America	Vulnerable	Observational ²⁹
	<i>Bombus pseudobaicalensis</i> (1)	Asia	Not assessed	Observational ⁹
	<i>Bombus pullatus</i> (3)	South America	Data deficient	Observational ^{47–49}
	<i>Bombus ruderarius</i> (2)	Europe	Not assessed	Nest-seeking queens ¹³ Observational ²⁵
	<i>Bombus schrencki</i> (2)	Asia	Not assessed	Observational ^{49,50}
	<i>Bombus transversalis</i> (5)	South America	Least concern	Observational ^{51–54}
Psithyrus [5]	<i>Bombus barbutellus</i> [1] ⁵⁵	Europe	Not assessed	Observational
	<i>Bombus campestris</i> [1] ⁵⁵	Europe	Not assessed	Observational
	<i>Bombus sylvestris</i> [1] ⁵⁵	Europe	Not assessed	Observational
	<i>Bombus vestalis</i> [2] ^{55,57}	Europe	Not assessed	Observational

Table 1 (continued)

- ¹Dramstad (1996)
- ²Svensson and Lundberg (1977)
- ³Geib et al. (2015)
- ⁴Hobbs (1964)
- ⁵Hobbs (1965a, b)
- ⁶Rao and Skyrms (2013)
- ⁷Plath (1922)
- ⁸Plath (1927)
- ⁹Sakagami and Katayama (1977)
- ¹⁰O'Connor et al. (2012)
- ¹¹Lye et al. (2009)
- ¹²Svensson et al. (2000)
- ¹³Kells and Goulson (2003)
- ¹⁴O'Connor et al. (2017)
- ¹⁵Osborne et al. (2008)
- ¹⁶Lye et al. (2012)
- ¹⁷Bowers (1985)
- ¹⁸Richards (1978)
- ¹⁹Gamboa et al. (1987)
- ²⁰Darvill et al. (2004)
- ²¹Knight et al. (2009)
- ²²Goulson et al. (2010)
- ²³Knight et al. (2005)
- ²⁴Herrmann et al. (2007)
- ²⁵Fussell and Corbet (1992)
- ²⁶Inoue et al. (2010)
- ²⁷Barron et al. (2000)
- ²⁸Palmer (1968)
- ²⁹Harder (1986)
- ³⁰Hobbs (1965a, b)
- ³¹Milliron and Oliver (1966)
- ³²Waters et al. (2011)
- ³³De Meulemeester et al. (2011)
- ³⁴Suzuki et al. (2007)
- ³⁵Nakamura and Toquenaga (2002)
- ³⁶Suzuki et al. (2009)
- ³⁷Hobbs (1967)
- ³⁸Rasmont et al. (2008)
- ³⁹Hobbs (1966a)
- ⁴⁰Charman et al. (2010)
- ⁴¹Sakagami et al. (1967)
- ⁴²Gonzalez et al. (2004)
- ⁴³de Oliveira et al. (2015)
- ⁴⁴Hobbs (1966b)
- ⁴⁵Michener and Laberge (1954)
- ⁴⁶Rau (1941)
- ⁴⁷Chavarria (1996)
- ⁴⁸Hines et al. (2007)
- ⁴⁹Janzen (1971)
- ⁵⁰Sakagami and Nishijima (1973)

Table 1 (continued)⁵¹Taylor and Cameron (2003)⁵²Olesen (1989)⁵³Ramirez and Cameron (2003)⁵⁴Cameron et al. (1999)⁵⁵Alford (1969)⁵⁶Sladen (1912)⁵⁷Bols (1937)⁵⁸Szabo and Pengelly (1973)⁵⁹Hoffmann et al. (2004)

Results and discussion

A total of 59 unique articles studies were retained for analysis. Ten studies examined overwintering habitat and 55 examined nesting habitat (some studied described both nesting and overwintering habitat) (Table 1). The lack of studies investigating nesting or overwintering is apparent when comparing the number of primary articles related to bumble bee habitat in general (525 articles identified from our preliminary refinement). Since most studies were focused on nesting habitat, most analyses in this review were focused on nesting habitat. These studies spanned five continents with most studies based in the United Kingdom (Fig. 1). Three overwintering studies took place in Europe while the others were in North America (Fig. 1). The small sample of articles examining bumble bee nesting habitats makes deriving substantive conclusions about the requirements for nesting and overwintering habitat challenging. To overcome this limitation somewhat, we summarized our findings at the subgeneric level. By summarizing our data this way, however, we may be confounding potential regional preferences in nesting or overwintering habitats and this should be considered. Additionally, the presence of a bumble bee nest or overwintering queens does not necessarily mean that the surrounding areas are high quality or preferred habitat. However, the available content provides an important summary of our current knowledge on bumble bee nesting habitat and areas of focus for future studies.

Overwintering habitat

The 10 overwintering studies occurred in North America and Europe with publication dates spanning from 1912 to 1973. These studies included 23 different bumble bee species and nine subgenera (Table 1). These studies described different aspects of bumble bee overwintering habitat including the landscape and patch characteristics, ground cover, soil type as well as the depth, density, depth, distance from the nest, that overwintering queens were found. Finally, a

single study examined the temperature during overwintering and spring emergence of *Bombus impatiens* queens at the University of Guelph, Ontario, Canada (Szabo and Pengelly 1973).

The overwintering studies took place in mountainous areas, grasslands, forests as well as a university campus (surrounded by urban development and agricultural areas). All overwintering queens were found underground. Overwintering queens were most often observed in shaded areas usually near trees and in banks without dense vegetation (Sladen 1912; Plath 1927; Bols 1937; Hobbs 1967; Alford 1969). There were a few observations by Alford (1969) and Sladen (1912) where queens were found in the open (*B. lapidarius* (Sladen 1912)) or away from trees (*B. mesomelas*, *B. lucorum*—found both away and under trees, (Alford 1969)). Overwintering queens were most often found in north-facing slopes (Sladen 1912; Bols 1937; Hobbs 1967; Alford 1969), but they were also found in slopes facing east, west and south by Hobbs (1967), and few overwintering sites were flat, namely for *Bombus impatiens* (Plath 1927), *B. pratorum* and *B. mesomelas* (Alford 1969). Alford (1969) noted that bumble bee queens may preferentially overwinter in north-facing slopes to prevent emerging too early on a warm or sunny day in the winter. The soil type was often described as sandy, well-drained, or loose where queens were found overwintering (Bols 1937; Plath 1927; Hobbs 1967; Alford 1969), however, *B. huntii* was found only in moist soil by Hobbs (1967). Whether this pattern of queens preferentially selecting shaded north facing banks is consistent across species would be an important future study question.

The ground cover where bumble bee queens overwintered was similar across the studies. Overwintering queens avoid areas with dense vegetation and will overwinter in bare-earth, moss, under tree litter, or in bare-patches within short grass (Sladen 1912; Plath 1927; Bols 1937; Hobbs 1965a, b, 1967; Alford 1969). Whether there are preferences for a certain ground cover at the species or subgenus level cannot be determined with the current level of overwintering studies, however, this would be an interesting avenue of future research.



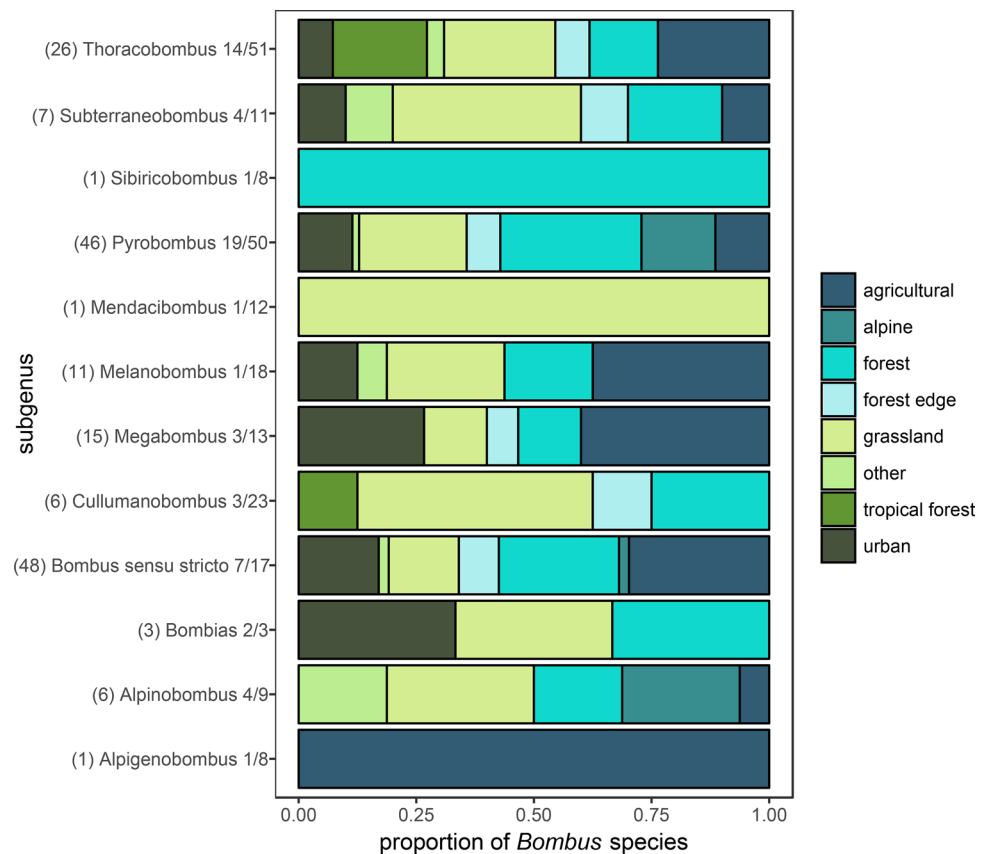
Fig. 1 Map of study locations. Blue circles=overwintering study locations, green=nesting study locations, turquoise=studies that described both overwintering and nesting habitat. The numbers correspond to the study number found in Table 1). 1. Dramstad (1996) 2. Svensson and Lundberg (1977) 3. Geib et al. (2015) 4. Hobbs (1964) 5. Hobbs (1965a, b) 6. Rao and Skyrn (2013) 7. Plath (1922) 8. Plath (1927) 9. Sakagami and Katayama (1977) 10. O'Connor et al. (2012) 11. Lye et al. (2009) 12. Svensson et al. (2000) 13. Kells and Goulson (2003) 14. O'Connor et al. (2017) 15. Osborne et al. (2008) 16. Lye et al. (2012) 17. Bowers (1985) 18. Richards (1978) 19. Gamboa et al. (1987) 20. Darvill et al. (2004) 21. Knight et al. (2009) 22. Goulson et al. (2010) 23. Knight et al. (2005) 24. Herrmann et al. (2007) 25. Fussell and Corbet (1992) 26. Inoue et al.

(2010) 27. Barron et al. (2000) 28. Palmer (1968) 29. Harder (1986) 30. Hobbs (1965a, b) 31. Milliron and Oliver (1966) 32. Waters et al. (2011) 33. De Meulemeester et al. (2011) 34. Suzuki et al. (2007) 35. Nakamura and Toquenaga (2002) 36. Suzuki et al. (2009) 37. Hobbs (1967) 38. Rasmont et al. (2008) 39. Hobbs (1966a) 40. Charman et al. (2010) 41. Sakagami et al. (1967) 42. Gonzalez et al. (2004) 43. de Oliveira et al. (2015) 44. Hobbs (1966b) 45. Michener and Laberge (1954) 46. Rau (1941) 47. Chavarria (1996) 48. Hines et al. (2007) 49. Janzen (1971) 50. Sakagami and Nishijima (1973) 51. Taylor and Cameron (2003) 52. Olesen (1989) 53. Ramirez and Cameron (2003) 54. Cameron et al. (1999) 55. Alford (1969) 56. Sladen (1912) 57. Bols (1937) 58. Szabo and Pengelly (1973) 59. Hoffmann et al. (2004). (Color figure online)

Overwintering queens hibernate at varying depths within the soil, at large densities, and they may or may not hibernate close to their nest. Queens were found to overwinter at depths between 2 and 15 cm. The depth queens hibernate at may vary by ecosystem type and region in order to best regulate temperature to optimize emergence time (Hobbs 1966a, b, 1967; Alford 1969; Szabo and Pengelly 1973). The average overwintering depths of queens reported are: *B. nevadensis* 11.43 cm in loose soil, 7.62 cm in compact soil (Hobbs 1965a, b); *B. rufocinctus* 4.32 cm (Hobbs 1965a, b); *B. flavifrons* and *B. bifarius* 10 cm, *B. frigidus* and *B. sylvicola* 2.54 cm (Hobbs 1967); *B. appositus* 6.35 cm (Hobbs 1966a); *B. fervidus* 2–4 cm (Hobbs 1966b). The overwintering studies reported finding large densities of queens hibernating in the same location and sometimes multiple queens

were found in the same hibernation chamber (Hobbs 1965a, b). Alford (1969) also reported that the same overwintering site may be used repeatedly. There were conflicting reports as to whether the overwintering sites were located near nests. Plath (1927) found 103 hibernating queens of *B. impatiens* that chose overwintering sites very close to their nests, however, they could not find any hibernating queens of *B. affinis* or *B. fervidus* close to their nests. Alford (1969) stated that queens do not preferentially overwinter close to their nests. A more recent study by Carvell et al. (2017) reported varying dispersal distances of spring queens from natal nests with a positive correlation observed between spring queen dispersal and habitat quality at various spatial scales. It may be possible that there are species-specific preferences in

Fig. 2 Landscape-level nesting habitat for the bumble bee subgenera. Values are the proportion of nests found for each subgenus by landscape type. The number of studies that included each subgenus is indicated in brackets. Fractions denote the number of species represented in the review per the total number of species within the subgenus



relation to nest distance, but it may also depend on whether there is suitable overwintering habitat near the nest location.

The soil temperature measured in the *B. impatiens* overwintering sites at the University of Guelph (Ontario, Canada) varied between -2.5 and 1.1 °C depending on the air temperature and snow pack (Szabo and Pengelly 1973). Soil temperature was found to have a strong influence on queen emergence in the spring with emergence occurring at temperatures between 13 and 17 °C. It is unclear whether the temperature range for overwintering and emergence as determined by Szabo and Pengelly (1973) would be similar across other bumble bee species and this should be the focus of future physiological studies of bumble bee overwintering.

Nesting habitats

Bumble bees exhibit a generalist nesting pattern across landscape types with no clear preferences in landscape types for nesting within subgenera (Fig. 2). Wild nests, artificial domiciles and nests in human structures were collectively considered. Bumble bee nests were found in eight landscape types: agricultural, alpine, dune, forest, forest edge, grassland, tropical forest and urban. Wild nests were found in more landscape types (agriculture, alpine, dune, forest, shrubland, tropical forest, urban and wetland) than nests found in human structures or artificial domiciles (agriculture, alpine, forest,

forest-edge, grassland, urban). Although the Chi square test showed that there was a significant relationship between bumble bee subgenera and locations of nests within the different landscape types (Chi squared = 148.91, $df = 70$, $p < 0.001$), there were large differences in the number of studies that reported each subgenus that likely contributed to this result. The most common landscapes for bumble bee nests were grasslands, agriculture and forests. Wild nests were found most commonly in forests followed by agriculture, grasslands, urban areas, tropical forests, alpine, dunes, shrublands, wetlands. Artificial domiciles and nests in human structures were also found most commonly in forested areas followed by urban areas, grasslands, forest-edge, alpine, and agriculture. There is a need to expand studies across more landscape types and geographical locations especially in alpine, dune, and urban habitats. Studies in semi-arid areas, dunes, tundra, and alpine are especially needed because we found no or few studies on bumble bee nesting in these habitats but bumble bees are found in these areas (Shelly et al. 1991; Koch et al. 2012; Eidesen et al. 2017). This should allow a clearer understanding of the nesting preferences of bumble bees across all habitats where bumble bees.

Most studies on the nesting habitat of bumble bees had at least part of their observations occur in agricultural landscapes (81.8%), but few nests were found within arable land. Most bumble bee nests (79.5%) within agricultural

landscapes were found in field margins/hedgerows, in surrounding patch types (woodlands, meadows, gardens) or pastures. Five of the eleven studies that found nests within arable lands used molecular techniques to determine nesting density (Darvill et al. 2004; Herrmann et al. 2007; Knight et al. 2009, 2005; Goulson et al. 2010; Geib et al. 2015). Since these studies did not locate the nests, it may be that nests were not actually within arable lands, but rather the surrounding landscape. The remaining six studies that found bumble bee nests in arable lands used observational methods to detect the nests (Rau 1941; Chavarría 1996; Janzen 1971; Barron et al. 2000; Rao and Skyrn 2013; de Oliveira et al. 2015). Nests were found within arable lands in these studies because planting and harvesting of crops was not highly disruptive, e.g. no tilling (Rao and Skyrn 2013) such as banana or coffee plantations (Chavarría 1996; Janzen 1971; de Oliveira et al. 2015), or through supplementation of nesting sites using artificial domiciles (Barron et al. 2000). Previous studies have indicated that arable lands are not suitable habitat for bumble bees and expansion of intensive arable lands without creating or protecting natural habitat patches or margins may be contributing to the decline in some bumble bee species (Svensson et al. 2000; Kells and Goulson 2003; Carvell et al. 2007; Lye et al. 2009). However, some crop types may increase the availability of nest sites for bumble bees. Rao and Skyrn (2013) found that rye fields attract voles who make their burrows within the field. The increase in burrow availability may benefit bumble bees by providing additional nesting sites (Carreck et al. 2009). Field margins and other habitat patches within an agricultural area can provide suitable nesting habitats because they diversify the landscape, are less disturbed than arable land, can provide cover needed for some species, and are more complex in vegetation pattern and resource availability (Svensson et al. 2000; Lye et al. 2009; Kremen et al. 2015). Improving field margins may increase the available nesting habitat for bumble bees within agricultural environments.

The availability of forage resources influences nest density and colony survival. Nest-searching queens may choose nesting sites that are near areas with spring forage available to optimize their energy intake during foraging trips (Suzuki et al. 2007, 2009; O'Connor et al. 2017). Increasing floral resources in a landscape have been shown to increase bumble bee nest densities (Osborne et al. 2008; Knight et al. 2009; Goulson et al. 2010). Forests often have a high density of early-flowering plant species (Wray et al. 2014; Kaemper et al. 2016) and may attract early-emerging bumble bee species. Conversely, later in the season, forests often have lower floral resources compared to other landscapes such as grasslands or urban areas (Wray and Elle 2015). Although high floral availability may attract bumble bee queens, nests are usually not found in areas of high floral cover (O'Connor et al. 2017), but this pattern may reflect the difficulty in

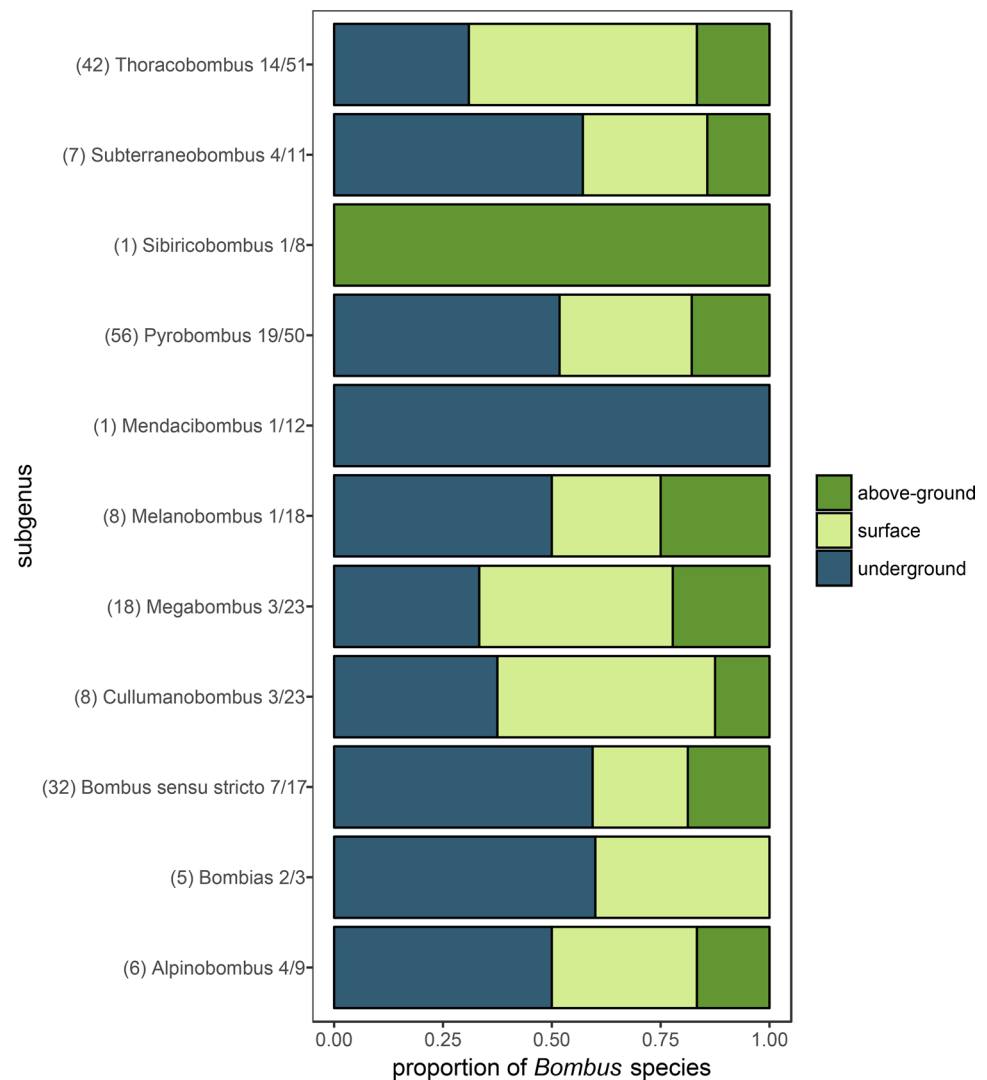
finding nests in highly vegetated areas and not nesting preferences. Suzuki et al. (2007) attempted to develop a statistical model to predict bumble bee nest locations using floral resource availability. Their model overall was not successful in predicting nest locations except for May forage. This low predictability may be because floral resource availability can change over the season. Seasonal fluctuations in floral resources can have negative effects on the survival of bumble bee colonies if sufficient food sources are not available (Bowers 1985; Moquet et al. 2017). Given that nesting, overwintering and foraging resources are all essential to bumble bee survival, efforts at predicting bumble bee nest locations and their survival throughout the season should consider temporal fluctuations in floral resources and investigate the potential influence of non-forage variables (i.e. forest cover, plant debris, animal burrows, ground cover, soil type, microclimates etc.) on nesting and overwintering habitat.

Ground position and materials of bumble bee nests

Bumble bees were found to nest underground, on the ground surface and aboveground. All three ground nesting positions were observed for most subgenera (Fig. 3) and in most habitats (Fig. 4). Underground nests were the most common ground position for wild nests, artificial domiciles and nests in human structures, followed by surface nests and aboveground nests. However, the proportion of nests found within each ground position differed between wild nests and artificial domiciles/nests in human structures. For wild nests: 52.1% were underground, 33.3% were on the surface, and 14.6% were aboveground. For artificial domiciles/nests in human structures: 39.1% were underground, 38.5% were on the surface and 22.3% were aboveground. Artificial domiciles/nests in human structures may be increasing the representation of aboveground nests. There is no significant relationship between ground position and subgenus (Chi square = 28.7, df = 20, $p = 0.09$), or ground position and landscape-type (Chi square = 16.9, df = 14, $p = 0.27$). Underground nests were the most commonly observed ground position for all subgenera and landscapes except *Thoracobombus*, *Megabombus*, *Cullumanobombus* and *Sibiricobombus* (although there was only one observation for this subgenus). The most common ground nesting position for *Thoracobombus*, *Megabombus* and *Cullumanobombus* were surface nests, while the one *Sibiricobombus* nest was found aboveground. Surface nests were more common in tropical forests and were as common as below-ground nests in agricultural landscapes (Fig. 4). Most bumble bee species were found nesting at one ground position (58.5%) and fewer species were found nesting at two (24.4%) or all three (17.1%) ground positions.

The materials used to construct bumble bee nests varied with the nest's ground position. Underground nests were

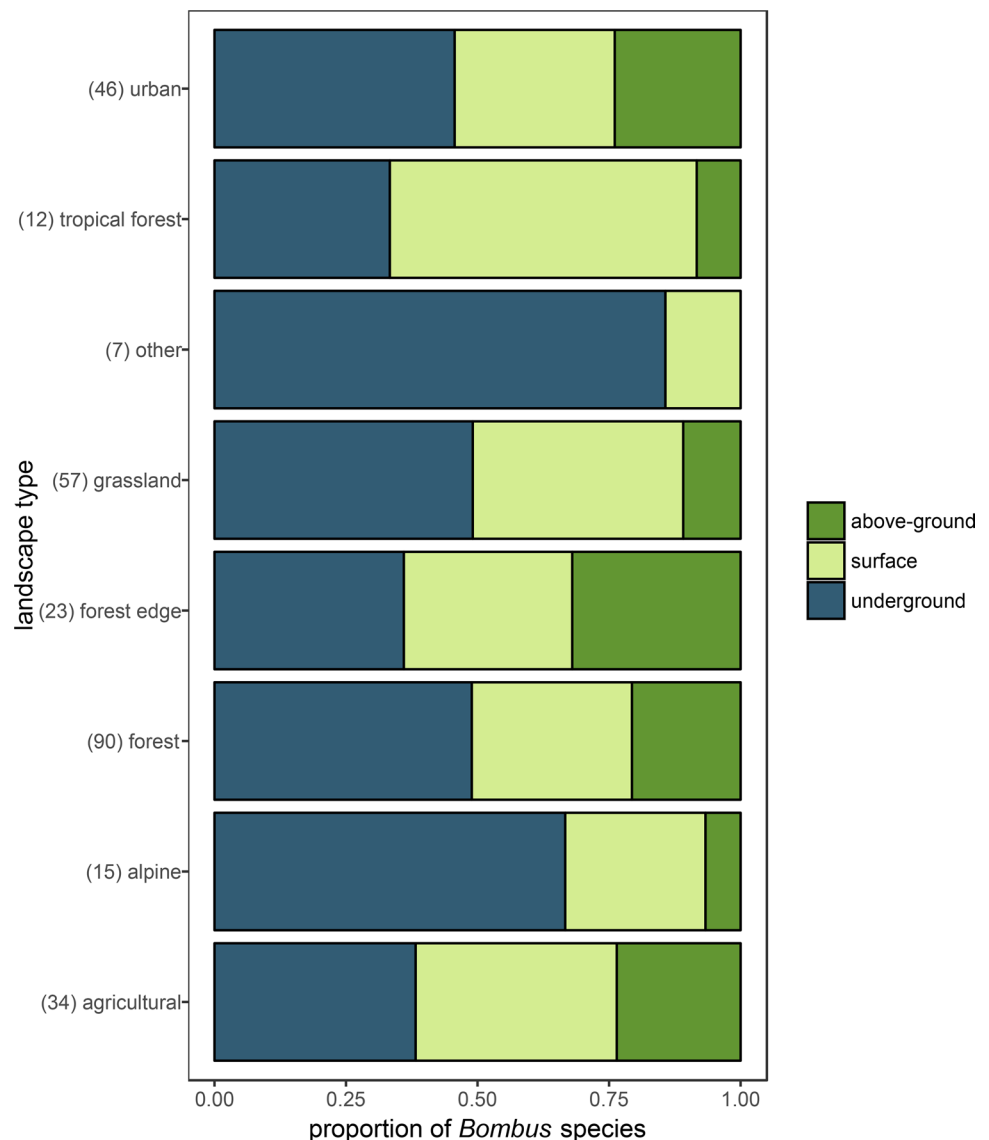
Fig. 3 The ground nesting position (underground, surface or aboveground) for the bumble bee subgenera. Values are the proportion of nests for each subgenus found per ground position. The number of instances where the ground position for each subgenus was described is shown in brackets. Fractions denote the number of species represented in the review per the total number of species within the subgenus. Not all nesting studies described the position of nests (i.e. molecular detection method studies)



often abandoned mammal burrows or nests (for example, Hoffmann et al. 2004; De Meulemeester et al. 2011; Rao and Skyrn 2013; Svensson and Lundberg 1977), or other cavities or holes in the ground (Fussell and Corbet 1992; Lye et al. 2012). These holes or cavities could include human-constructed materials including buried PVC pipe or underneath buildings (Fussell and Corbet 1992; Inoue et al. 2010; Lye et al. 2012). Some studies reported entrances to underground burrows would sometimes be covered with vegetation (either dried or living) and this is thought to help prevent the nest from being detected (Hoffmann et al. 2004; De Meulemeester et al. 2011; de Oliveira et al. 2015). Underground nests may also be particularly susceptible to flooding. For example, Harder (1986) reported that common ground nesting species were found infrequently in the late season possibly due to an unseasonably wet spring that may have resulted in colony failures. This may explain why underground nests are less common in tropical forests (Fig. 4).

Surface nests were either constructed of plant material or associated with certain vegetation. The surface nests found in tropical forests were constructed from dried grass, cut leaves, and twigs (Sakagami et al. 1967; Taylor and Cameron 2003; Hines et al. 2007). These nests were constructed by bumble bees in a dome-like shape to provide shelter for the colony. Additionally, the nests were often associated with other vegetation including shrubs or trees to act as structural support (Chavarria 1996; Taylor and Cameron 2003; Hoffmann et al. 2004). Non-tropical surface nesting bumble bees also construct nests under vegetation cover, especially tussock grasses, leaf litter, or log piles to protect their nests (Fussell and Corbet 1992; Sakagami and Katayama 1977; Svensson et al. 2000; Kells and Goulson 2003; Lye et al. 2012). Surface nests in human-developed areas included within buildings or walls (Fussell and Corbet 1992). Surface nesting bumble bees would be vulnerable to ground disturbances such as development and mowing, and in agricultural landscapes to tilling or grazing livestock (Harmon-Threatt

Fig. 4 Nesting position (underground, surface or above-ground) for bumble bees across eight habitat types as well as generalist species. Values the proportion of nests for each landscape-type found per ground position. The number of instances where the ground position for each landscape-type is shown in brackets. Not all nesting studies described the ground position of nests (i.e. molecular detection method studies)



and Chin 2016). Although surface nests are still detected in agricultural landscapes (Fig. 4), they are not likely to be found in arable lands. Indeed, the only study that found bumble bee nests within arable lands found them underground (Rao and Skyrm 2013). Setting aside undisturbed areas in agricultural areas (such as field margins) or in other developed regions (such as roadsides) may be a strategy to reduce impacts to surface nesting bumble bees, and underground nesting bees if tilling/soil disturbances occurs. Surface nesting species may also be susceptible to flooding or wet conditions.

Aboveground bumble bee nests were observed the least often and this could be because of the inherent difficulties in observing them. Most of the aboveground bumble bee nests included in this review were occupied artificial nest boxes (47% of papers). Most other observations of aboveground

nests (85%) occurred in gardens with bumble bees found in bird houses, within buildings/walls, in trees, tree cavities, and in cavities between rock piles/walls (for example, Janzen 1971; Richards 1978; Osborne et al. 2008; Lye et al. 2012). The remaining aboveground nests were in forest edge and urban sites as there would be naturally occurring or human-made cavities in trees, logs, exposed rock, and in buildings/walls. These aboveground nests may be going undetected as observational studies and the use of detection dogs focus on searching the ground for nests or search for low-flying nest-searching queens (Waters et al. 2011; O'Connor et al. 2012, 2017). Future studies should also attempt to search for nests aboveground particularly in forested habitat to help determine the true extent of aboveground nesting bumble bees.

Detecting bumble bee nests

Bumble bee nests are difficult to detect, and this has likely contributed to the lack of studies on nesting habitat. Some methods that have been employed to detect bumble bee nests include locating nests by observation—“observational”, using observations of nest-searching queens as a proxy—“nest-searching queens”, using genetic analysis to determine number of colonies in an area—“molecular”, using statistical modeling to predict nest locations—“modeling” and using trained detection dogs to locate nests—“detection dogs” (Table 1).

Observational studies vary from standardized (i.e. searching predetermined transects or areas (e.g. O’Connor et al. 2017) to opportunistic searches for nests (e.g. De Meulemeester et al. 2011). Observational studies have the advantage of identifying the exact location of bumble bee nests for further analysis of habitat preferences. However, the major disadvantage of observational studies is the amount of time and effort needed to find often difficult to detect nests. The most successful application of observational methods to detect nests was by Lye et al. (2012) who used citizen scientists to monitor their gardens for bumble bee nests across the United Kingdom. This study located an impressive 1022 bumble bee nests from ten species (including species classified as “other”, or “unknown”) between 2007 and 2009 versus an average of 21 nests for all other observational studies. The efficiency of using citizen science data to gather large amounts of data also comes at the cost of biased data towards areas readily surveyed by participants (i.e. gardens) and this should be considered when employing this method. Other observational studies monitored artificial nest-boxes or domiciles. This method can be useful for gathering information on the nesting habitat for bumble bees and be easier than looking for natural bumble bee nests. Occupancy of artificial domiciles is likely inversely related to the number of natural nest sites such as rodent burrows (Richards 1978). Finding natural nests would still be preferred for modelling nesting habitat to determine what natural materials are required for bumble bee nest sites (Waters et al. 2011; O’Connor et al. 2012). Detection dogs have the potential to significantly reduce human search effort and rapidly and accurately identify bumble bee nests, and they were successfully used in two studies thus far (Waters et al. 2011; O’Connor et al. 2012). In these studies, dogs were trained to locate bumble bee nests by scent. Once a nest is located, the dogs signal to their handlers the location of the nest in a non-destructive manner. Nests identified by dogs were also visually confirmed by researchers. However, the O’Connor et al. (2012) study which compared the nest detection ability

between humans and dogs concluded that dogs were no more efficient than trained humans, and given the cost involved with training dogs, they would recommend using humans over dogs. This is the only study that has compared the efficiency of using detection dogs as a method for identifying nests and more research into the potential use of this method is needed.

Another potentially useful method for locating bumble bee nesting and overwintering sites would be the use of radio-telemetry. Advances in radio-tracking technology has made it possible to track some insect species including bumble bees. Radio-telemetry and radio-frequency identification (RFID) has previously been used to study foraging and flight distances in bumble bees (Hagen et al. 2011; Minahan and Brunet 2018), but this method has not (to our knowledge) been applied to bumble bee nesting or overwintering studies. Spring queens or workers could be fitted with trackers so that researchers can follow individual bees back to their nest. Additionally, young queens can be tracked later in the season to find overwintering habitats. There are some challenges to radio-tracking that need to be considered when deploying this method. These are reviewed in Kissling et al. (2014) and include: short battery life, limited range of tracking, weight of the trackers, and the potential for the trackers to alter the behaviour of the individual.

Use of proxy measures to identify bumble bee nests can be an effective alternative, but with some limitations. Using nest-searching queens allows a greater sample size than looking for nests due to the easier detectability of nest-searching queens (Svensson et al. 2000; O’Connor et al. 2017). These methods can be inaccurate as a survey technique of bumble bee habitat because it does not actually find the physical location of nests. Molecular methods are likely the most rapid method of identifying many colonies within a given area (Goulson et al. 2010; Geib et al. 2015). Similarly, actual nests are not identified that can limit its applicability to more specifically determining nesting habitat especially at finer scale than landscape-level descriptions of habitat. Using a statistical modeling approach to predict nest locations have been applied to few studies thus far and have had limited success (Suzuki et al. 2007, 2009; Carvell et al. 2017). These studies have attempted to use forage availability to predict nesting or overwintering sites, with mixed results. If these models can be improved this could be an extremely powerful method to decrease survey times for nesting. However, these models likely are weakened by an incomplete understanding of bumble bee habitat. Future bumble bee nesting habitat studies may need to consider the trade-off between obtaining a good sample size with accurately predicting bumble bee nesting habitat.

Conclusions

Bumble bees appear to be generalists within and across subgenera in terms of nesting habitat preferences. Bumble bees may preferentially overwinter in shaded banks either with moss or in bare-ground but, more research is needed on overwintering habitat. Future studies should attempt to increase the knowledge available on the nesting habitat of bumble bees by investigating understudied habitat areas such as dunes, and alpine areas and by recording detailed descriptions of the habitat surrounding nests. For increased specificity in bumble bee habitat requirements it is suggested that observational methods especially citizen science projects be employed to increase the likelihood of finding a suitable number of nests and overwintering sites and look further into the efficiency of detection dogs. Increasing knowledge on the specific nesting and overwintering requirements for bumble bees is important to ensure their protection and aid in conservation efforts for declining species. Current management efforts focusing on bumble bee habitat are mainly interested in expanding the available forage for bumble bees. If nesting or overwintering habitat is limiting, focusing solely on forage will do little to protect or increase populations.

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Compliance with ethical standards

Conflicts of interest None to report.

Research involving human participants or animals This research did not involve human participants or animals.

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