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REVIEW

Beneath the buzz: Quantifying nest locations and densities of ground-nesting wild bees (Hymenoptera: Anthophila)

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Abstract

1. Wild bees (Hymenoptera: Anthophila) are important pollinators and essential for maintaining ecosystem health. The majority of bee species are ground-nesting, and all bees spend most of their lifetime inside the nest. Still, most studies and monitoring schemes assess wild bees during flower visitation, allowing no conclusion about their nest sites. Methods for locating and assessing the ground nests of bees are currently limited, hindering scientific progress and conservation efforts.
2. To evaluate and improve methods for locating and assessing ground nests, we combined information from a literature review and our own empirical studies. Methods ranging from established field methods (visual nest observations and emergence traps) to new technological approaches (marking and tracking individuals) are compared in terms of success in catching nesting bees and identifying nest locations, time effort required to implement the methods, and limitations.
3. We provide guidelines and recommendations on the use of the different methods depending on the data requirements and study locations. We also present a novel emergence trap design and two newly developed marking methods, using a radioactive tracer substance and a retroreflective pigment, and show that these methods can be used to successfully locate and assess ground-nesting habitats of bees.
4. With this work, we address gaps in current research methods and aim to enhance the efficiency of field research that explicitly targets ground-nesting bees and their nest sites in various environments. By providing a comprehensive overview for researchers and practitioners, we demonstrate how to improve knowledge about the ecology and life history of ground-nesting bees and thus support efforts for their conservation.

KEYWORDS
emergence traps, flower strips, ground-nesting wild bees, nest density, nesting habitat, overwintering, sampling methods, semi-natural habitat

Anne-Christine Mupepele and Felix Fornoff shared last authorship.

1 | INTRODUCTION

About 75% of all wild bee species nest below-ground (Harmon-Threatt, 2020) and depend on suitable below-ground habitat conditions for successful diapause and reproduction. They spend most of their life in their nests and are often active for only a few weeks a year (Danforth et al., 2019). Effective tools are needed to assess the location and suitability of nesting habitats to study wild bees and inform management and conservation. Given the recognized importance of wild bees for plant pollination, including crops (Klein et al., 2007), such tools are becoming increasingly relevant (Boetzl et al., 2021; Cope et al., 2019; Ganser et al., 2021; Williams et al., 2024).

Currently, pollinator populations are typically sampled through a combination of passive and active sampling, including transect walks and pan traps (Drummond & Stubbs, 1997; Klaus et al., 2024; Prendergast et al., 2020). These provide insights into pollinator activity (Kennedy et al., 2013; Senapathi et al., 2017) and have been used to inform conservation efforts (Gutiérrez-Chacón et al., 2020; von Königslöw et al., 2021). However, conservation efforts could not stop widespread wild bee declines (Aldercotte et al., 2022), which may be due to inadequate knowledge of suitable nesting habitats and, consequently, insufficient efforts to provide and protect them (Harmon-Threatt, 2020; Hudewenz & Klein, 2013; Potts et al., 2010). Without efficient approaches to assess ground-nesting habitats, wild bee research on successful conservation measures is hampered.

When studying ground-nesting bees, their diverse life histories (Danforth et al., 2019; Linsley, 1958), including the level of sociality, their voltinism, selection of nesting area or overwintering strategies, have to be considered. Many species are solitary ground-nesters, but some exhibit different levels of sociality, such as communal nesting or even complex divisions of labour similar to honeybees (Danforth et al., 2019). Although most species produce only 1 generation per year, some are multivoltine and can develop 2 or more generations in 1 year (Field, 1996; Kocher et al., 2014; Packer, 1990). Several species are known to nest in aggregations due to shared nesting substrate preferences or the desired presence of conspecifics, called communal nesting (Antoine & Forrest, 2021). Some bees overwinter with or without cocoons as preimaginal larvae or imagines in the natal nest, while others may overwinter as mated adults in a hole or crevice in the ground (Yanega, 1989). This variation dictates that different habitats and land uses have varying suitability to support these species within and across landscapes.

Similarly, contrasting life histories make sampling and the subsequent study of these bee species challenging, and different methods will be more appropriate than others depending on the focal species and context. Therefore, depending on the sampling method, timing and effort, different groups of bees are caught, all of which may not be relevant to the research question (Williams et al., 2024). For example, if the study focusses on influences of soil disturbances on overwintering bee survival, it will be misleading to count individuals that fully developed only after the disturbance occurred, for example, worker generations of eusocial species such as many Halictidae (Kocher et al., 2014). Furthermore, the choice of sampling unit (e.g. nest or bee individual counts) can impact the reliability of the conclusions drawn from the data. In ground-nesting bee studies, nest or individual bee counts are commonly used as proxies for the total number of nests (Albrecht et al., 2023; Buckles & Harmon-Threatt, 2019; Cane, 2003; Hudewenz & Klein, 2013; Sardiñas & Kremen, 2014; Tsiolis et al., 2022). However, since not every bee sampled corresponds to a single nest and not every nest found corresponds to a single bee, it is essential to consider additional factors, such as the level of sociality or phenology, when using nest counts to evaluate habitat nesting suitability (Brokaw et al., 2023).

Wild bees can be grouped by their shared preferences for nesting resources, and these can be used to inform suitable methods to study bees and their habitat requirements (Thompson et al., 2021). While studies related to cavity-nesting bees can utilize accessible nesting resources, for example, by assessing brood cells in trap nests (Fornoff et al., 2024) or performing pollen analysis (Dürrbaum et al., 2023; Ganser et al., 2021), ground-nesting bee studies rely on counting nests or collecting bees within a defined area of ground to address similar research questions (Antoine & Forrest, 2021; Ganser et al., 2019; Roulston & Goodell, 2011; Sarthou et al., 2014; Tschanz, Vogel, et al., 2023). Such studies can be considered ‘area-based’ when they involve knowledge of the extent of the sampling area. Most current wild bee sampling methods are not area-based; that is, they do not provide information about area-specific bee abundance, as the nest location of the sampled bees is unknown. Since bees are highly mobile species (Gathmann & Tscharntke, 2002), the sampled individuals may not necessarily be nesting in the sampling area. Consequently, such methods are unsuitable for quantitative assessments of nesting habitats, especially when the sampling relies on attraction via food resources (e.g. sampled during flower visits via sweep netting) or by the trap itself (e.g. pan traps). The only established methods for area-based sampling of ground-nesting wild bees or their nests are emergence traps (further referred to as ‘e-traps’) and visual nest searching (Bischoff, 2003; Brokaw et al., 2023; Pane & Harmon-Threatt, 2017; Sardiñas & Kremen, 2014; Williams et al., 2024).

Some other methods have been reported for the location of bee nests. These methods typically involve tracking bees back to their nests through repeated observation (Visscher & Seeley, 1989) or by using tags or marking substances (Kissling et al., 2014; Martins et al., 1999; Mola & Williams, 2019; Smith et al., 2021). Although such methods are not ‘area-based’ in the strictest sense, they still provide spatial information about the habitat, such as the distance between foraging and nesting sites (Ganser et al., 2021). None of these methods have been established for ground-nesting bee research yet.

The aim of this study was to combine literature and empirical data to review existing approaches and consider new approaches for studying ground-nesting bees, and compare them in terms of (1) the number of nests and bees sampled, (2) the estimated nest density and (3) their efficiency related to the time taken to implement the method and to the potential difficulties, such as habitat properties or weather.

Reviewing these methods will improve and increase the comparability of research on ground-nesting wild bees. Our goal is to assist researchers conducting studies on ground-nesting wild bees in selecting the most suitable sampling method depending on the available resources and research question being pursued. Our objective is to improve the methods by providing guidelines and recommendations to assess ground-nesting bees and their nests.

2 | MATERIALS AND METHODS

2.1 | Field surveys

All fieldwork was carried out in the Upper Rhine valley in Baden-Württemberg, South-West Germany. We selected a total of 20 study plots on newly sown and existing perennial flower strips to establish a heterogeneous vegetation density regime, ranging from bare ground to densely vegetated ground with forbs up to 2 m high.

The bees were sampled using one passive and three active sampling methods. Methods included (i) e-traps, (ii) visual searches for nests and (iii) marking of foraging bees with either (a) retroreflective powder or (b) a radionuclide containing liquid, and subsequent searching of the individuals or their traces. For all methods, we recorded the time needed for sampling (in hours) and the sampled area (in m^2) and classified vegetation density on plots categorically (sparsely vs. densely vegetated). For e-traps as a passive method, we also documented the time needed for preparation and duration of deployment. Fieldwork was permitted by the respective local authorities (LRA Emmendingen, Untere Naturschutzbehörde, 15.03.2023; Stadt Freiburg i.Br., Umweltschutzamt, 20.03.2023, AZ 364–660-03).

2.2 | Developing a soil emergence trap (e-trap) and its use

To cover a large and representative area while minimizing costs, we employed custom-built e-traps (Figure 1a). We modified commercially available hiking tents (Bestway Pavillo Monodome X2) to function as a soil e-trap by removing the tent floor (100 × 160 cm area) and attaching a trapping jar to the top (for a schematic figure, see Appendix S3). The sides of the tent floor were vertically buried in the ground to a depth of at least 20 cm to prevent bees from entering or exiting the e-trap once it was placed and to add stability to the construction. Each e-trap covered an area of approx. 2.2 m^2, which is much more than typically covered by commercially available e-traps (e.g., 'Soil Emergence Trap' by 'Bugdorm': 0.36 m^2). Before installing the trap, all vegetation at the trap position was cut clear and removed prior to installation using an electric hedge mower and a rake and regularly cut inside the trap throughout the season.

Between April and May, 160 e-traps were installed on the 20 study plots (8 traps per plot) and left until the beginning of August.

FIGURE 1 (a) E-traps on a flower strip. Traps were created from hiking tents from which floor material was removed to allow ground-emerging insects to be trapped in the bottles at the top. (b) 'Mini-E-Trap' used to sample bees that emerge from a nest entrance that was previously identified visually searching the ground. (Photographs by the authors).

Traps were placed semirandomly along two transects per plot, with intervals between traps depending on the plot length, ensuring spatial representation across the entire plot. The average duration that each trap was in place was 99 days (SD(n) = 19 days). The trapping jars of the e-traps were emptied every second week, constituting one sampling round. The trapping jars were filled with 100 mL of modified Renner solution (40% ethanol, 10% glycerol, odour-free dish soap) to kill and preserve insects.

In addition to permanent installations, we also installed 13 e-traps for 24 h, called 'short-term deployment'. In three further sampling rounds between the 3 and 15 August, e-traps were installed after sunset and emptied the following day after sunset. For each round of sampling, we selected a different plot for short-term deployment.

All bees caught in e-traps were dry mounted and identified to species level using the keys of Schmid-Egger and Scheuchl (1997) for Andrenidae and Amiet et al. (2017) for all other families.

2.3 | Visual nest searching

Visual nest searching was performed three times between the 3 and 15 August on different plots. The same observer systematically searched for bee nests identified through their characteristic tumuli (Figure 2). Searches were carried out before 7 AM to ensure that female bees had not left their nest for flower visitation yet. Searches were carried out only after at least 2 days without precipitation and with sufficient daytime temperatures (>20°C) for most bees to leave their nest and forage (Stone & Willmer, 1989). During each of the three sampling rounds, a random starting point was selected at the edge of the new survey plot and a straight transect was followed for 1 h. Throughout all rounds, a total of 66 m^2 were searched for nests.

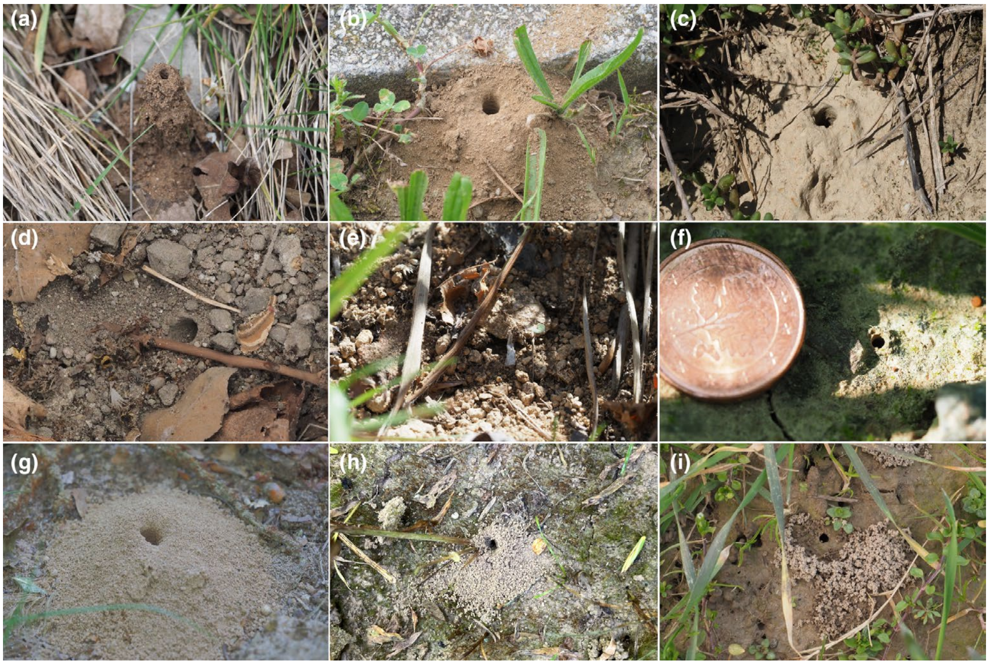

FIGURE 2 Bee nest or not? Some nests of ground-nesting bees, including (a) *Lasioglossum marginatum*, (b) *Halictus scabiosae* or (c) *Tetralonia malvae*, can be recognized by the characteristic tumulus around the nest entrance. But many nests are easily overseen when they do not have a tumulus, including (d) *Antophora plumipes* nest, are hidden below stones such as (e) *Dufourea dentiventris* nest or are simply too small to see, for example (f) *Lasioglossum morio* nest. They can also be easily confused with nests of other soil-dwelling organisms such as (g) sphecoid wasps (*Mellinus arvensis*), (h) ants or (i) beetles. Unlike other arthropod nests, bee nests often have more vertically symmetrical tumuli, without soil being spread more in one direction than another. (Photographs by the authors).

We thoroughly searched the ground within 0.5 m on either side of the transect and, when necessary, carefully removed plant litter and leaves to ensure diligent examination of the area. To minimize observer bias and focus on the effectiveness of the method, all searches were carried out by the same person.

If a nest was identified, a 'mini e-trap' (Figure 1b) similar to the one used by Tschanz, Vogel, et al. (2023) filled with Renner-solution was placed on the nest to collect emerging bees. All installed mini e-traps were checked for bees the following day.

2.4 | Developing bee marking methods and their use

Bee marking allows for the tracking of the bees from the flowers where they forage to their nests. Two marking methods were developed and tested: 1st marking bees with the radioactive substance Technetium-99 m (Tc-99 m), a short-lived (6 h half-life time) gamma emitter, and then locating nests using a hand-held contamination detection device in the evening hours; 2nd marking bees with retroreflective powder (Dipon Reflective White 1000 powder pigment), and locating them afterwards using an active light source. We always ensured that bees continued their activities after being marked. A detailed description of each method can be found in Appendix S4. We marked nine bees with Tc-99 m on two occasions and eight bees with retroreflective powder on three occasions between the 3 and 15 August. Only days of favourable conditions for bees to be active were used.

2.5 | Assessment of bee nesting activity

Bees sampled via e-traps were reviewed for wear of the mandibles and wings. Together with the expected phenology of bees, these parameters were used to classify whether bees collected with e-traps corresponded to a nest that was active or provisioned earlier in the year, emerged from overwintering, or were caught incidentally. These traits have been used before in bee studies, for example, to differentiate between freshly emerged and old bees or to designate caste (Hurd et al., 1974; Richards, 2000; Richards et al., 2010; Wittwer et al., 2017). Because both wing and mandible wear has been shown to correlate with bee activity (Albert & Packer, 2013), we considered any amount of wear on these body parts indicative of digging or foraging and thus nest building (Rehan & Richards, 2010). To ensure a systematic classification of bee nesting activity, we adapted and modified the protocol from Portman et al. (2022) to account for continuous e-trap sampling without rearrangement of traps and across multiple sampling rounds (replacement of trapping liquid; see Appendix S2 for the protocol). For example, we considered it unlikely to collect actively nesting bees after the first sampling round, which we subsequently define as 'two-week deployment'. To account for potential individual variation and environmental influences on wing and mandible wear, our protocol conservatively estimates nest type only when combined evidence from wear and phenology provides sufficient certainty. We calculated the relative abundance of nests as the sum of active nests, nests provisioned earlier the same year, and overwintering nests. For the purposes of this study, 'nests' were defined as both provisioned nests and overwintering sites of bee imagines that are not necessarily a natal nest. Additionally, we distinguished overwintering nests to assess the suitability of the methods for research questions related to overwintering.

For all methods, we standardized nest density to nests per hectare by dividing the number of observed (visual search) or estimated (e-traps) nests (*n*) by the sampling area (m^2) and then multiplying the result by 10,000 (see Appendix S5 for advantages and limitations of using nest density as a unit).

2.6 | Supporting literature review

We conducted a semisystematic literature review to identify studies that used emergence traps, visual searches or bee marking as methods to collect ground-nesting wild bees or locate their nests. For this, we searched the Web of Science Core Collection and Google Scholar databases for peer-reviewed publications (Hutchinson et al., 2022). We used 'bee' or 'bees' combined with either 'emergence trap*', 'visual search*', 'tracking', 'marking', 'UV*', 'fluorescent', 'retroreflective', 'quantify*', or 'nest* density' as keywords. Additionally, we used 'ground-nesting', 'ground nesting', 'soil-nesting', or 'belowground-nesting' to refine the search when necessary. We excluded studies focused solely on *Bombus* species due to their different nesting biology (Antoine & Forrest, 2021), but some search strategies used in these studies may still be useful for detecting nests of other ground-nesting species. Furthermore, we screened all studies identified by the search for references to identify additional studies using any of the methods. We grouped studies by sampling method (e-traps, visual search, bee marking). Information about the observed nests and wild bees, as well as the study area and duration, was extracted. When possible, the total nesting density per hectare was calculated.

3 | RESULTS

3.1 | E-traps

3.1.1 | Nest and bee sampling

We collected a total of 56 bees belonging to 20 different species (Appendix S1). Bees were found in each sampling round during the sampling period. All caught species are regarded as primarily ground-nesting, with most of the individuals belonging to the genera *Lasioglossum* (27 individuals) and *Andrena* (24 individuals). 57% of all bees (32 individuals) were collected during the first sampling round of each trap, which we use as a separate sampling approach and refer to it as 'two-week deployment'. No bees were caught during the short-term deployment of the e-traps in August.

3.1.2 | Nest density

We used bees collected from the first 2 weeks of e-trap deployment to calculate nest density after bee classification according to the adapted classification protocol (Appendix S2). We approximated a nest density of 426 nests per hectare (18 bees), of which 57 nests per hectare were used for overwintering (5 bees). With continued deployment for 3 months, these estimates increased to 710 nests per hectare (31 bees), of which 313 nests per hectare were used for overwintering (14 bees). Therefore, while the estimated total number of nests increased by 67% with longer deployment duration, the number of estimated overwintering nests increased by almost 450%. Twenty-four bees had to be classified as 'unknown' or 'incidental' because they could not be attributed to a nest or an overwintering location with sufficient certainty.

3.1.3 | Efficiency

The installation of e-traps included vegetation removal, trap set-up and burying of trap foil sides. Including these activities, we covered an average of 10.2 m^2 of ground per hour (about four traps) with e-traps. In sparsely vegetated habitats, our installation rate increased to 11 m^2 per hour, and in densely vegetated areas, the rate decreased to 8.8 m^2 per hour (−20%). During sampling, vegetation density did not affect our efficiency, allowing us to cover 30 m^2 per hour of trap-covered ground when emptying and refilling the e-traps.

3.2 | Visual search

3.2.1 | Nest and bee sampling

We counted 15 bee nests but were not successful in catching any bees that emerged from the nests using the mini e-traps. Therefore, we do not have any information about the nesting species except that they were always rather large species with nest hole diameters of at least 0.5 cm.

3.2.2 | Nest density

Nest counts allowed us to estimate a nest density of 2273 nests per hectare (Table 1). However, without information about the nesting species, we cannot determine whether nests were actively used, abandoned or belonged to non-bee organisms.

3.2.3 | Efficiency

During the search, the process was slower in areas with dense vegetation and accumulated plant litter. On average, we covered 32 m^2 per hour in sparse vegetation and 10 m^2 per hour in dense vegetation (−68.8%). Denser vegetation and littered ground occurred particularly in older habitats, where it had to be removed carefully to make the ground and any potential tumuli visible.

TABLE 1 Nest density (highlighted in orange) and number of bees per sampling area and sampling duration are provided for each sampling method based on our own research and the literature review.

	Emergence traps				
	Long-term deployment	Two-weeks deployment	Short-term deployment (24h max.)	Visual nest searching	Bee marking
Results from our own empirical study	710 nests/ha (313 overwintering nests/ha) 56 bees, 352 m^2, 4 months	426 nests/ha (57 overwintering nests/ha) 32 bees, 352 m^2, 2 weeks	no bees caught (30.8 m^2, 24 h)	2273 nests/ha (15 nests; 0 nests with bees, 66 m^2, 3 h)	Radionuclide/Reflective Powder Marking: no nest detection (Reflective Powder: 159 m^2, 3 h; Radionuclide: 1131 m^2, 2 h)
Results from the literature review	252 bees, 48 m^2, 6 months (Chaparral gray pine; 97% Halictidae; Sardiñas & Kremen, 2014) 21 bees, 17.28 m^2, 6 months (Open-canopy secondary forest; Ulyshen et al., 2021) 84 bees, 4.32 m^2, 5 months (Extensive green roofs; 99% Halictidae; Passaseo et al., 2020) 15 bees, 7.2 m^2, 3 months (Managed conifer forest; Rivers et al., 2018) 51 bees, 48 m^2, 5 months (Flight cages with pitfall traps on flower strips and winter wheat; Boetzl et al., 2022) *Targeted approach*: 271 bees, 2.5 m^2, 4 months (mainly *Epicharis picta* in Atlantic forest; Werneck & Campos, 2020) 2581 bees, 4 m^2, 9 months (mainly *Monoeca haemorrhoidalis* in Atlantic forest; da Rocha-Filho & Melo, 2017) 2046 bees, 4.25 m^2; 2 months (mainly *Calliopsis pugionis* in flood plain; Visscher et al., 1994) 185 bees, 180 m^2, 4 months (Flight cages with pan traps on artificial *Peponapis pruinosa* nest agg. in squash fields)	1478.82 nests/ha (only active nests; Tallgrass prairies; 507 bees, 1386.24 m^2, 6–10 days; Brokaw et al., 2023) 505 bees, 259.2 m^2, 2 weeks (open-canopy sec. forest; Ulyshen et al., 2021) 27 bees, 38.88 m^2, 1 week (Restored prairie; Pane & Harmon-Threatt, 2017) 121 bees, 65 female ground-nesting bees, 86.4 m^2, 1 week (Restored prairie; Grommes et al., 2021)	7750 nests/ha (only active nests; averaged over all years; Wildflower Strips; 453 bees, 486 m^2; Williams et al., 2024) 110 bees, 864 m^2 (Wildflower + fallow plots; Cope et al., 2019) 31 bees, 302.4 m^2 (Upland pine + hammock; Cope et al., 2019) 893 bees, 518.4 m^2 (Hedgerows; 99% Halictidae; Sardiñas, Ponisio, et al., 2016) 42 female bees, 72 m^2 (Sunflower Fields; Sardiñas, Yee, et al., 2016) 95 female bees, 129.6 m^2 (Sunflower fields; Sardiñas, Tom, et al., 2016) 252 bees, 1058.4 m^2 (Sunflower fields; Row cover fabric covering; Kim et al., 2006) 39 bees, 1089 m^2, 4 rounds (*Peponapis pruinosa* on pumpkin fields; Row cover fabric covering; Julier & Roulston, 2009) 1678 bees, 108 m^2 (Tallgrass prairie; Buckles & Harmon-Threatt, 2019)	3808.9 nests/ha (Managed Grassland; 1714 nests, 42 nests with bees, 4500 m^2, 4 rounds; Albrecht et al., 2023) 1013 nests/ha (Apple Orchards; 2289 nests, 58 nests with bees, 3450 m total tree rows, >11 sampling rounds, peak nesting mean from 2 years; Fountain et al., 2023) 101 nests/ha (28 nests with bees/ha; Winter cereal fields; 10,000 m^2; 2 rounds; Tschanz, Vogel, et al., 2023) 2.34 nests/ha (Protected mountain landscape; 96 nests, 410,000 m^2; Gascon et al., 2023) 459.14 nests/ha (*Peponapis pruinosa* on pumpkin fields; 50 nests, 1089 m^2, 4 rounds; Julier & Roulston, 2009) 2187 nests/ha (*Andrena* spp. on lowbush blueberry fields; 880.14 nests, 3700 m^2, 2 years mean; Venturini et al., 2017) 24688.87 nests/ha (Vertical streetside earth banks; 3928 nests with bees/ha, 1722 m × 1–4 vertical m, 24 rounds in 1 year; Michener et al., 1958) 93,000 nests/ha (mean peak nest density on artificial bare ground; Tsiolis et al., 2022) 221 nests with bees (Streetside earth banks; 1130.5 m × 1–4 vertical m, 24 rounds in 1 year; Pereira et al., 2021) Sidhu and Rankin (2018) (no reported abundance; Semi systematic nest aggregation mapping on an island) *Single-species aggregations*: 890,000 + − 660,000 nests/ha (Managed *Nomia melanderi*; 39,160 nests with bees, 440 m^2; J. H. Cane, 2003) 33,900 nests/ha (*Dieunomia triangulifera* on alluvial soil; 165.75 observed nests, 41.48 m^2; Wuellner, 1999) 410,000 nests/ha (*Epicharis picta* in Atlantic forest; no reported abundance; Werneck & Campos, 2020) 178,000 + − 105,250 nests/ha (*Epicharis nigrita* in urban environment, mean peak nest density of 4 years; 2990 observed nests, 168 m^2; Martins et al., 2019) 547,000+− 14,000 nests/ha (*Halictus rubicundus* in diff. locations; mean of max. density plots; 866 observed nests, 10 m^2; Potts & Willmer, 1997) 570,487 nests/ha (*Peponapis pruinosa* on lawns near squash plantings; 53 observed nests, 0.09 m^2; Hurd et al., 1974)	K. Tsiolis (personal communication, November 8, 2023): UV-Powder; no nest detection Sardiñas, Tom, et al. (2016): Fluorescent Powder; observed marked bees at nest entrance, but no systematic nest counting

3.3 | Bee marking

Eight female bees were marked with retroreflective powder and nine female bees with Tc-99 m during all sampling rounds. Searching for traces of reflective powder, we covered an average search area of 53 m^2 per hour, resulting in a total search area of 159 m^2. Using a contamination detector to search the ground for radiation levels above the environmental background level, we covered an average search area of 565.5 m^2 per hour, resulting in a total search area of 1131 m^2.

3.3.1 | Nest and bee sampling

Within the search area, we did not locate any of the marked bees on the ground. While searching the ground, we also detected increased activity in the surrounding vegetation and successfully located a marked bee (*Lasioglossum costulatum*) resting on a flower (*Malva sylvestris*) during the evening hours and two female bees (*Lasioglossum leucozonium*) clinging to the stems of the plant. All bees were located within 5 m of the release point.

3.3.2 | Efficiency

For both methods, we noticed a decrease in search area per time in densely vegetated areas by around 30%. For the search for retroreflective powder, we covered an average of 62 m^2 per hour in sparse vegetation and 43 m^2 per hour in dense vegetation (−30.6%). For radionuclide search, we covered 662 m^2 per hour in sparse vegetation and 468 m^2 per hour in dense vegetation (−29.3%).

3.4 | Supporting literature review

We found 34 studies that used at least one of the sampling methods, from which we extracted the numbers of bees and nests sampled, sampling area, and duration (Table 1). 18 studies used e-traps, 14 studies used visual searches and 2 studies used both. We did not find any study that successfully used bee marking for nest searches. [Correction added after online publication on 27 May 2025: The section heading “3.5 Method Comparison table” has been removed.].

4 | DISCUSSION

In this study, we evaluate methods for locating and assessing the nests of ground-nesting wild bees by comparing them with one another and with previous studies using the same approaches. Concluding from our own experiments and the literature, e-traps, if applied to large areas, are a promising and efficient tool to assess ground-nesting wild bees and their nest densities, potentially similar to trap nests for cavity-nesting bees (Staab et al., 2018). Furthermore, we highlight that visual nest search has multiple drawbacks and that finding nest locations using marked bees can be challenging. Therefore, while bee nesting can be studied with e-traps and visual searches, finding the nest location of foraging bees remains a challenge and subject of further methodological advances.

The efficiency in estimating nest density differed between e-traps and visual search approaches. Visual searching yielded higher nest density estimates with comparatively little effort, but comes with high uncertainty about which species or even organism was nesting or dwelling in the presumed nests. This is especially illustrated by our own empirical study in which we found nests, but no bees that could be linked to those nests. Previous studies have demonstrated that with a higher sampling effort and large numbers of sampled nests, some bee specimens can be collected at their nest burrows (Albrecht et al., 2023; Fountain et al., 2023; Tschanz, Vogel, et al., 2023); Yet, the number of sampled bees compared to the number of sampled nests always remained low (Table 1). This may be due to misidentification of bee nests, inactive bee nests due to the late sampling season, or nests where the bee had not returned for the night (Barthell et al., 1998). The efficiency of visual nest searching was also negatively influenced by vegetation density and ground litter, so besides observer bias, the time it takes to deploy this method increases with the inaccessibility of the soil surface. For example, Albrecht et al. (2023) searched for bee nests across 4500 m^2 of meadows. Covering the same area at our study sites would have taken us 200 h.

Short-term deployment of e-traps led to inconclusive results. Due to the later deployment time, the set-up targeted only nests active in late summer. As a result, phenological differences may have influenced our findings, limiting direct comparisons with longer deployment periods. Additionally, the short deployment duration and comparatively small sampling area may have contributed further to the lack of captured bees. In contrast, placing many e-traps for a long duration provides a viable approach for collecting ground-nesting bees: during the 3-month deployment, at least one bee was caught every sampling round. Although nest density estimations from e-trap sampling remain low compared to visual searches, they provide more reliable information.

The bees collected by e-traps also offer additional insights, revealing whether they were emerging from active nests, from nests provisioned earlier the same year, or from overwintering. Based on the analysis of wear and phenology, a proportion of the bees collected could be classified as having emerged after overwintering. However, because many e-traps were set up after typical emergence times of most overwintering bees (Westrich, 2018), the nest density of overwintering individuals remained lower than the density of active nests and nests provisioned earlier in the same year.

Our results also show that with longer continuous sampling, the share of bees emerging from overwintering increases compared to the share of bees from active nests (Pane & Harmon-Threatt, 2017). This is highlighted by the occurrence of typical summer emerging bees, such as *Melitta leporina* or *Andrena rosae*, in the e-trap samples in mid-June. The reason for this is that it is impossible for bees to use the

TABLE 2 Recommendations on when to use which method to sample ground-nesting wild bees in different habitats.

When the study…	and/or the target habitat…	…then choose
requires a before-after design (e.g., treatment, survival)	might be densely non-woody vegetated	
requires a passive, standardized sampling	allows permanent installations	➔ E-Traps
regards phenological questions	is even or slightly inclined	
needs to cover a larger area	is open or sparsely vegetated	
needs big sample sizes without species information	does not allow permanent installations	➔ Visual Search
regards species-specific studies	is inclined or vertical	
targets organisms that have a small range of movement	is open or sparsely vegetated	
aims to study foraging or dispersion ranges from nest	does not allow permanent installations	➔ Bee marking
aims to study behavioural questions	is inclined or vertical	

trapped area to start a new nest once the e-trap has been deployed. It illustrates that the assessment of bee abundances alone without appropriate classification can result in misinterpretations and the neglect of different types of bee activity, especially if traps are deployed for a longer duration and not before the start of any bee activity.

Although our efforts to locate bee nests by marking female bees with retroreflective powder or Technetium-99 m were unsuccessful in finding nests, they yielded valuable methodological insights. The fact that no nests were found is mainly due to the considerable amount of time needed to search the area for traces of the marking substance: The effective sampling area covered only a fraction of the theoretical flight range of the marked bees. We were still able to locate a marked female pollen-loaded wild bee (*Lasioglossum costulatum*) resting in a flower (*Malva sylvestris*) during sunset, supporting the observations by Barthell et al. (1998) that also female wild bees that currently provision a nest may spend the night outside on flowers. During a pilot experiment, the marking of a bee with Technetium-99 m yielded another interesting ecological insight: during the later search, we expected to locate the bee back in its nest, but instead discovered a common wall lizard (*Podarcis muralis*) nearby that clearly exceeded threshold radiation level, likely due to the consumption of the marked bee. Therefore, we consider this marking technique to be a promising method for studying ecological interactions and behavioural questions on smaller scales.

Depending on effort, habitat, timing, and methodology, resulting sample sizes of other studies that performed sampling of nests or emerging bees vary significantly. The comparability of these results is very limited due to the use of differing units (number of emerging bees vs. number of nests) and approaches to analysis, even though the study objectives are typically similar, such as assessing treatment effects, comparing habitats, or evaluating habitat preferences. Standardizing sampling methods and analytical frameworks can increase consistency and comparability between studies, allowing for more reliable and robust assessments and conclusions.

The growing interest in the comprehensive study of wild bees shows the need for methods to locate and further investigate ground-nesting bee nests. Based on our conclusions, we provide a decision framework for choosing the appropriate sampling method based on research focus and habitat context (Table 2). For example, to study the effects of soil disturbances during diapause on overwintering bee survival, visual search would not be an appropriate method because observed nests and collected bees do not correspond to overwintering bees. The following section is intended to support the decision about when to use which method.

4.1 | Emergence traps as a passive sampling method

E-traps are a passive sampling method designed to sample ground-nesting organisms as they emerge from the ground. E-traps have potential for a variety of applications, ranging from phenological studies on single bee species (da Rocha-Filho & Melo, 2017; Visscher et al., 1994; Werneck & Campos, 2020) to ecological studies on the community level, such as wild bee habitat preferences and effects of treatments (Sardiñas, Yee, et al., 2016; Ullmann et al., 2016; Williams et al., 2024), the interactions between hosts and parasitoids (Moore, 2001; Werneck & Campos, 2020) as well as studying the competition between honeybees and wild bees (Hudewenz & Klein, 2013).

Various e-trap designs have been reported, of which some are commercially available. The design generally consists of a fabric that covers a portion of the ground from which insects are expected to emerge. However, it can also vary from the common construction type with a trap container on top, for example, by using flight cages with pan traps, equally delimitating the sampling area but using colour attraction instead of phototaxis as the behavioural principle for attraction (Boetzl et al., 2022; Ullmann et al., 2020). Similarly, row cover fabric used in agriculture has been used to trap bees after emergence, but without a passive collection fixture, timely collection of trapped bees is required (Kim et al., 2006).

Unlike trap nests, sweep netting, or coloured pan traps, which either lure or actively target bees, e-traps provide an unbiased and passive method for sampling. They capture only bees naturally present in the landscape, without influencing their concentration, making them spatially representative. The bee community captured through e-traps typically differs from those observed in other assessments, first because e-traps exclusively collect ground-nesting bees, and second because certain species—particularly smaller ones—may be underrepresented in other sampling methods (Pane & Harmon-Threatt, 2017; Prendergast et al., 2020). Because migrants are excluded from the sampling area, collected bees can be attributed to the exact area where the trap has been placed (McCravy, 2018). This makes the method particularly useful when data need to be specific to an area. For example, little is known about overwintering survival rates of ground-nesting wild bees in temperate regions (Harmon-Threatt, 2020; Roulston & Goodell, 2011; Yanega, 1989). E-traps could be used to catch bees that emerge only from the exact location where a nest was recorded the previous season, allowing estimates of nest mortality or reproductive success to be made. Since the exact time of emergence is unknown, e-traps as a passive method also have the advantage of being deployable for any duration. It is important to note that e-traps, like any other sampling method, are not equally effective for every species, for example, due to behavioural differences (Lammers, 1977). A primary drawback of e-traps is that, compared to common wild bee research methods such as sweep netting or pan trapping, the collected bee sample sizes are generally low. More effort is required to collect a sufficient number of bees, although the capture rates of e-traps may be higher when nest locations are targeted (Pane & Harmon-Threatt, 2017; Tables 1 and 3).

E-traps allow the estimation of nest densities (Sunderland et al., 1995; Werneck & Campos, 2020), if collected bees can be attributed to either active nesting or recent emergence with high probability. To do so, it is always necessary to classify the collected bees regarding their nesting activity using a standardized procedure (Brokaw et al., 2023; Williams et al., 2024). Our classification protocol accounts for continuous deployment of e-traps over a longer period (>10 days) and allows for an emphasis on research questions related to overwintering diapause, such as survival rates or effects of soil disturbance. Our own data showed that the timing and duration of trap deployment influence which groups of bees are collected. For example, two-thirds of the bees that were included in the nest density estimation as having emerged from overwintering were caught before mid-May; therefore, if the study focuses on overwintering bees, e-traps should be deployed before the start of any bee activity and for longer periods to increase the probability of deployment coinciding with emergence. Accordingly, if the study focuses only on actively nesting bees, e-traps can be deployed later in the season and for shorter periods, because actively nesting bees leave their nests regularly at short intervals for foraging and provisioning. For this, e-traps can also be moved regularly to allow bees to utilize the area for constructing nests, potentially increasing sample sizes (Ulyshen et al., 2021). However, it should be noted that higher numbers of collected bees may not necessarily translate to a higher number of nests, since many bees, especially social bees, may have originated from the same nest. Without appropriate classification, such samples would inevitably skew study results (Passaseo et al., 2020).

In addition to bees from nests established in the previous season and active nests, e-traps can also collect bees emerging from nests established previously in the same season (eusocial or multivoltine species), bees that do not overwinter in' nests' ensu stricto (e.g., some Halictidae), and incidental bees (Brokaw et al., 2023). Especially when e-traps are deployed only for a short duration or are emptied for the first time, care must be taken to minimize the chance of collecting incidental bees. This can be partly overcome by setting up traps outside of daily, or even better, seasonal bee activity periods to prevent the collection of foraging bees (Pane & Harmon-Threatt, 2017; Ulyshen et al., 2021). It is not yet clear whether cutting vegetation to set up e-traps also reduces incidental catches. Like their male counterparts, female bees may spend nights outside of their nests on flowers or clinging to leaves, particularly during the prenesting period (Hurd et al., 1974; Schäffler & Dötterl, 2011; Willis Chan & Raine, 2021) but also while actively nesting (Barthell et al., 1998; Westrich, 2018). These bees may be collected by the trap the next day if it was placed over the resting bees. However, many bees drop to the ground when disturbed in a resting situation, for example, during cold weather or at night (pers. obs.) and might therefore still be collected by the trap. The possibility of catching incidental bees also persists after the e-trap has been deployed for a longer period. Bees may make it into the e-trap through holes in the fabric or through crevices in the ground that may develop after warm and dry periods (pers. obs.). There may also be a chance of multiple nest entrances inside and outside of the trap (Giovanetti et al., 2003). Therefore, a classification of the collected bees should always consider additional factors beyond the sex of the individual to prevent accidentally relating incidental bees to nests.

E-traps are not taxon-specific, meaning they also collect individuals from other taxonomic groups, such as flies, beetles, wasps, or moths. To mitigate the collection of non-target specimens, automated camera systems could be mounted on top of the traps instead of trap containers to capture images of emerging individuals (Wittmann et al., 2024). However, many bees cannot be identified to the species level without the specimen, and since bee nesting activity also cannot be classified from images alone, the information gain from this approach may be limited.

4.2 | Visual search as an active sampling method

Visual search for wild bee nests can be effective for assessing active nests (Ullmann et al., 2020), when nests are clearly identifiable. This method can be used for various research objectives, such as natural history studies (Barthell et al., 1998; Tschanz, Koestel, et al., 2023), ecological studies related to habitat preferences (Wuellner, 1999), or citizen science initiatives (Maher et al., 2019). The method is not suitable for assessing hibernation densities or overwintering

TABLE 3 Constraints identified for every sampling method.

	Emergence traps	Visual nest searching	Bee marking
Site-specific constraints and factors affecting search time	Permanent elements and steep slopes may prevent trap installation Long-term deployment in areas that are under active use poses challenges (Pane & Harmon-Threatt, 2017) Without adequate labelling, traps in exposed areas may be confused with recreational sites (own obs.) Installing traps on compact soils becomes time-consuming if trap sides need to be buried	Dense vegetation and ground litter increases search time (Tschanz, Vogel, et al., 2023) and makes it challenging to spot nests	Dense vegetation, structures and objects obstruct reflecting light and impede detector movement Dew reflections distract from reflecting targets at night searches
Temperature	Emergence of bees is linked to overwintering temperatures (Fründ et al., 2013) and thermoperiodism (Wuellner, 1999; Yocum et al., 2016). Trap-induced changes in microclimate might therefore influence emergence phenologies to varying degrees (Forrest & Thomson, 2011; Southwood & Siddorn, 1965) Daily bee activity is reduced at lower temperatures (Corbet et al., 1993; Stone & Willmer, 1989); Extended sampling durations reduce the impact of temporary cold periods on sampling success.	Cold periods reduce bee activity and thus formation of characteristic tumuli (Corbet et al., 1993; Stone & Willmer, 1989; pers. obs.)	No bees are active when temperatures are outside of their activity spectrum (Corbet et al., 1993; Stone & Willmer, 1989; pers. obs.) Reduced soil heat conduction in late summer facilitates the formation of dew, which obscures visual searches at night.
Wind	No direct effect Strong winds may damage traps	No effect	Strong wind may affect marked bees in their activity
Precipitation	No direct effect Moisty soils serve as cue for emergence for some ground-nesting bees (Danforth, 1999) Damp soils make trap installation easier if trap sides need to be buried	Characteristic nest tumuli are getting washed away by rain (Venturini et al., 2017). Several days of favourable conditions for bee foraging are needed to make nest entrances recognisable	Bee activity is decreased during rainfall Water drops distract from reflecting targets at night searches Wetter soils attenuate gamma rays, decreasing detection range
Other constraints	E-traps usually yield smaller nest sample sizes than visual nest searching Sampled bees can represent different nesting activities (Brokaw et al., 2023). Therefore, it is necessary to define clear study objectives Timing of trapping (e.g., spring or summer) influences the types of bees caught (Brokaw et al., 2023) Longer sampling duration reduces the influence of species-specific phenologies on sampling success Bees do not always indicate the presence of a nest, but may also emerge from a hibernaculum, which is not always the natal nest (Westrich, 2018) The capture of incidental bees (e.g. resting in vegetation) can be minimized, but not prevented if traps are set up outside of bee activity periods (night, bad weather, early spring (Sardiñas, Tom, et al., 2016; own obs.)) Long exposure to UV radiation can damage trap fabric (own obs.) Commercially available e-Traps are expensive and typically cover only a small area Permanent trap installation on subsidized land may lead to conflicts with the terms of the subsidy	Observed nests solely correspond to newly nesting female imagines Increased observer bias; success strongly depends on expertise (Tschanz, Koestel, et al., 2023; Tschanz, Vogel, et al., 2023; K. Tsiolis, personal communication, November 8, 2023) Many bees do not build tumuli (Larsson & Franzén, 2007; Westrich, 2018) or use old burrows where the tumulus has vanished (Cane, 2003) If nesting individuals are not observed or captured, species information will be incomplete. Mini e-traps can be used to verify bee nests and avoid misclassification. To catch bees leaving their nest, mini e-traps need to be installed before the bee activity period and left for at least one day (Tschanz, Vogel, et al., 2023)	Observed nests solely correspond to active nests Bees need to be checked for sex before marking (only females correspond to an active nest) Flight ranges of many solitary bees may extend the feasible search area Dark nights facilitate detection of reflecting targets Short half-time of Tc-99 m (6 h) limits searching time Tc-99 m availability is linked to specialized medical facilities Specific regulations apply depending on country. Germany: 10 MBq limit (Anl. 4 StrlSchV)

Note: Bold indicates different constraints categories.

reproductive success, as it only identifies nests that are obvious or actively provisioned.

Since visual search of the ground covers a specific area, nest densities can be estimated if the sampled area is documented (Table 1). As an active method, it requires the right timing for favourable environmental conditions (Albrecht et al., 2023) and sufficient expertise for sampling. In order to minimise observer bias, it is advantageous to have the same person conduct the searches or to ensure that all observers have a similar level of effort and expertise.

The method has some constraints (Table 3). First, the visual identification of nests always carries the chance of misidentification if a nest is not distinguishable with certainty from holes of other soil-dwelling organisms such as ants, beetles, or earthworms (Figure 2). Making a distinction is only possible by the characteristic tumulus, which may not always be present: Many bees actually do not build a tumulus around their nest or have it only occasionally (Larsson & Franzén, 2007; Westrich, 2018; own observation). Also, nests of many smaller species such as many *Lasioglossum* species may simply be too small (often just 1 mm) to recognize, potentially biasing the method towards larger species. It is also important to note that some species may create inconspicuous nests among dense vegetation (Fountain et al., 2023), under shrubs (Hurd et al., 1974) or dead leaves (Julier & Roulston, 2009); others may reuse existing nest burrows (Cane, 2003). Therefore, even when putting a lot of effort into nest searching, visual search alone cannot fully represent the ground-nesting bee species community and their nests.

Second, the method does not provide species information if nesting individuals have not been observed or captured in their nest, or if the study is not focused on single-species aggregations. Since knowledge about species and community composition is essential for most wild bee studies, additional efforts are necessary to obtain this information. Bees can be captured right after emerging from their nests using a mini e-trap that is installed outside of the daily bee activity period (Albrecht et al., 2023; Wuellner & Jang, 1996), though capture rates are typically very low (e.g., 2%–3%; Table 1) and a large number of nests is needed to sample any bees. Another way to obtain species information is to observe the nest during daily bee activity hours and to catch the individual after leaving its nest or returning from a trip using a hand net. The mean duration of a pollen collection trip is species-specific and depends on the surrounding habitat, but typically lasts between 5 and 30 min (Ganser et al., 2021; Gathmann & Tscharntke, 2002; Klein et al., 2004). Optimally, one would observe a nest for 30 min to encounter the individual. As with e-traps, automated camera systems could also complement this method by monitoring nest entrances over extended periods, allowing nest searches outside the bees' active hours (Wittmann et al., 2024). In any case, these are time-intensive approaches. In turn, visual nest searching is an effective method when the study focuses on a single species with a nest that is easy to identify. Information about its nesting requirements can be gathered without sampling other species or an unnecessarily large number of individuals (Cane, 2003; Hurd et al., 1974; Julier & Roulston, 2009; Potts & Willmer, 1997; Wuellner & Jang, 1996).

Third, the method is less effective in densely vegetated or littered areas, where the visibility of the ground is obstructed. Consequently, the method is most effective in areas with low vegetation density or bare ground (Tsiolis et al., 2022). Additionally, the method can be utilized on sloped and vertical surfaces (Michener et al., 1958).

4.3 | Bee marking as a method to locate nests of ground-nesting bees

Directly tracking bees to their nests through visual observation is extremely difficult due to their small body size and rapid movements. Following recurring bees from the same nest successively back to their nest is possible and known as "bee-lining", but appears only successful with social bees that are flower-constant (e.g., *Apis mellifera*) (Visscher & Seeley, 1989). Marking wild bees with a visual cue and following them to their nest has been reported (Martins et al., 1999), but such attempts mostly remain unsuccessful due to the above-mentioned constraints. Nests have also been successfully located using search-and-rescue dogs trained on olfactory cues (Liczner et al., 2021), but this method lacks the efficiency to be repeatedly applied independently. Tracking bees with electronic tags that are either passively detectable, for example via harmonic radar or radio frequency identification, or actively emitting radio signals has also been tested (Carreck et al., 1999; Kissling et al., 2014), but such attempts are generally limited by the weight and size of the tags (Mola & Williams, 2019).

The marking or tagging of ground-nesting bees with substances that are later relocated at or in their nest is an indirect approach to locate nests, since it is primarily targeting the location of the marking substance and not the bee itself and is therefore fundamentally different from mark–recapture methods (Bischoff, 2003; Hofmann et al., 2020; Martins et al., 1999; Yamamoto et al., 2014). Bee marking approaches have made successful use of fluorescent powder to assess flower visits (Sardiñas, Tom, et al., 2016), but its successful use for nest searching remains to be demonstrated (K. Tsiolis, 2023, pers. comm.). One advantage of retroreflective powder is its increased detectability, which improves with the amount of reflected light. However, the requirement for the detection of reflections is an undisturbed view, which was generally not given in the densely vegetated habitats we investigated. It remains to be tested whether fluorescent or retroreflective powder is better suited for the purpose of nest detection in open habitat.

Arthofer et al. (2016) demonstrated the feasibility of marking and tracking even smaller fruit flies with permission-free amounts of the radionuclide Technetium-99 m in a comparatively small search area. Our own results underline the feasibility of this method for studies on smaller spatial scales and its great advantage of being detectable through material like soil or plant litter. However, a considerable preparation effort is needed to perform this method.

If nest detection is the main goal, it is important to select only female bees that are currently on a provisioning flight (indicated by pollen loads) for marking. As flight ranges of wild bees often exceed the feasible search area for both methods, we recommend preselecting search areas based on any available knowledge about the nest preferences of the tagged species or focusing on species with a manageable maximum flight range.

5 | CONCLUSIONS

Effective methods for locating and assessing the nesting habitats of ground-nesting bees are essential to gain ecological knowledge and identify habitat requirements of these mostly cryptic living species, and to guide and monitor efforts for their conservation. Our study compares the trade-offs between the three most common and promising approaches, guiding the choice between visual nest searches, emergence traps, and marked bee tracking for locating and assessing ground nests across different vegetation regimes. Visual searches require expert knowledge and efficiently yield nest numbers, but may miss species-specific data and are not suitable for all habitats or research questions. E-traps provide unbiased, comprehensive information on nesting individuals across space, but are effort intensive and yield small nest sample sizes. Marking methods are promising for studying ecological aspects in smaller areas and sparsely vegetated habitats, although further method developments are necessary for nest site location. Regardless of the chosen method, the life history of the target species must be considered to draw meaningful conclusions from the observations. This method overview may stimulate further research on ground-nesting bees, particularly in their most important partial habitat, the place of reproduction and diapause.

AUTHOR CONTRIBUTIONS

Christopher Hellerich, Anne-Christine Mupepele, Felix Fornoff, and Alexandra-Maria Klein conceived the idea and designed the field experiment. Christopher Hellerich conducted the literature review and carried out the experiments with support from Anne-Christine Mupepele, Felix Fornoff, Michael Garratt, and Michael Mix, who contributed to the Tc-99 m marking method. Christopher Hellerich performed the analysis; Anne-Christine Mupepele and Felix Fornoff contributed to the analysis. Christopher Hellerich wrote the manuscript with input from all authors who approved the final manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare that there are no conflicts of interest regarding the publication of this paper.

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DATA AVAILABILITY STATEMENT

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1: Emergence traps (e-traps) bee species list.

Appendix S2: Revised classification key.

Appendix S3: Schematic illustration of custom emergence traps.

Appendix S4: Detailed description of the bee marking methods with Technetium-99m and retroreflective powder.

Appendix S5: Advantages and limitations of using nest density in ground-nesting bee studies.

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