



A review of soil tillage impacts on ground-nesting wild bees – mechanisms, implications, and future research perspectives

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ABSTRACT

The key role of wild bees in providing pollination services is well recognized. Most wild bees nest in the ground and need suitable nesting habitat to thrive. Despite covering 14 million km² of the world's surface, the potential of arable land as a nesting habitat has been largely neglected, although studies indicate that ground-nesting bees nest in arable soils. Therefore, it is important to understand the impact of tillage on bees' nesting and reproductive success. Here, we synthesize the existing knowledge of potential consequences and mechanisms underlying tillage effects on ground-nesting bees, identify knowledge gaps, and propose directions and approaches for future research. Our literature review has identified ten studies that directly or indirectly assessed impacts of tillage on ground-nesting wild bees in arable cropping systems, showing either no effect or a negative effect of tilled compared to no-till systems. Potential tillage effects include direct impacts related to physical injury of bees, offspring, and brood cells, destruction of nest burrow architecture, displacement of brood cells, and alteration of soil environmental conditions surrounding brood cells, as well as indirect effects related to soil cover, soil properties, and soil conditions. Our review highlights that we poorly understand how tillage influences bee nesting incidence, survival, emergence timing, offspring sex ratio, and, in the longer term, community composition. In particular, it remains unclear whether tilled arable soils are suitable nesting habitat or ecological traps for ground-nesting bees. To address these research gaps, we propose methods to directly quantify nesting and emergence of bees, and (semi-)field and laboratory experiments that allow to disentangle mechanisms driving tillage effects. Improved understanding of tillage effects and underlying mechanisms will help to develop more effective strategies to promote ground-nesting wild bees and the crop-pollinating and soil ecosystem services they provide through their foraging and nesting activities.

1. Introduction

The role of arable (mass-)flowering crops in providing floral food resources to a suite of wild bee species in agroecosystems has been relatively well studied (Diekötter et al., 2014; Holzschuh et al., 2013; Westphal et al., 2003). However, although arable land covers approximately 14 million km² of the world's surface (FAO, 2020), its potential as nesting habitat for ground-nesting wild bees has received surprisingly little attention. The few available field studies have found that at least some ground-nesting bee species do indeed nest in arable fields with flowering crops that they use as forage (Ullmann et al., 2020), such as sunflowers (Kim et al., 2006; Minckley et al., 1994; Sardiñas et al.,

2016b) and cucurbits (Hurd et al., 1974; Julier and Roulston, 2009; Mathewson, 1968), sometimes finding higher nest densities within cultivated fields than in undisturbed field margins (Julier and Roulston, 2009). Moreover, a variety of ground-nesting bee species have been found to nest in tilled and untilled winter cereal fields that provide no foraging resources to bees (Tschanz et al., 2023b). However, bees nesting in arable fields face additional, potentially interacting threats compared to those nesting outside of arable fields, such as exposure to pesticide residues in the soil (e.g., Rondeau and Raine, 2024a; Willis Chan and Raine, 2021), waterlogged or flooded fields caused by soil compaction (e.g., Batey, 2009; Fellendorf et al., 2004), and tillage (e.g., Ullmann et al., 2016), and arable land may thus act as an ecological trap

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if nests are destroyed and bee offspring killed (Antoine and Forrest, 2021; Christmann, 2022). More general threats to nesting bees not confined to those nesting in arable fields further include potential negative impacts by predators, parasites, and molds (e.g., Antoine and Forrest, 2021).

Ground-nesting bees spend most of their lives underground in a soft-bodied and immobile state, making them vulnerable to threats that are directly related to their life cycle (Harmon-Threatt, 2020; Ullmann et al., 2020). Agricultural soil management is therefore expected to have a major impact on the potential of such soils to provide suitable nesting habitat, on nesting conditions, as well as on the survival and emergence rates of bee offspring nesting in these soils. Tillage may be particularly detrimental to ground-nesting bees since many species construct their brood cells in the upper 20 cm of the soil (Cane and Neff, 2011; Harmon-Threatt, 2020), which is often within the tilled soil layer. Hence, conservation agriculture practices that minimize mechanical soil disturbance (particularly no-till) may have a strong potential to support ground-nesting bees in arable cropping systems. However, certain ground-nesting bee species may successfully survive conventional tillage practices, at least to some degree (Minter and Bessin, 2014; Ullmann et al., 2016), and it therefore remains unclear to what extent conventionally tilled arable crop fields represent an ecological trap for ground-nesting bees. Soil management practices also have profound impacts on soil properties, soil conditions, and vegetation cover (Soane et al., 2012), which can further affect ground-nesting bees in multiple ways – from nest site selection and population density to offspring survival and community composition (Antoine and Forrest, 2021; Harmon-Threatt, 2020; Ullmann et al., 2020).

Numerous studies have shown that tillage generally has negative effects on larger soil organisms, such as earthworms, spiders, ground beetles and other arthropods that spend part of their life-cycle in the soil, and that reducing soil disturbance by adopting no-till practices benefits many of these organisms (Green et al., 2023; Kladiivko, 2001; Rowen et al., 2020; Wardle, 1995). Surprisingly little attention has been paid to the effects of tillage on the nesting and reproductive success of ground-nesting bees and the potential of no-till practices to support them in arable cropping systems. The few existing studies have provided inconsistent evidence, showing either a positive effect of no-till (e.g., Appenfeller et al., 2020; Shuler et al., 2005) or no significant effect of no-till practices (e.g., Julier and Roulston, 2009; Tschanz et al., 2023b). Furthermore, most studies focused on a single species, the squash bee, *Xenoglossa pruinosus* (formerly *Eucera (Peponapis) pruinosus*; Freitas et al., 2023) (e.g., Skidmore et al., 2019; Ullmann et al., 2016) and the underlying mechanisms of tillage impacts on ground-nesting bees are largely unknown (Harmon-Threatt, 2020). However, a better understanding of the effects and underlying mechanisms of different tillage practices on ground-nesting bees is crucial to develop evidence-based management guidelines aimed at improving nesting conditions to support ground-nesting bees and their ecosystem services in arable crop dominated agroecosystems.

In addition to off-field pollinator promotion measures (e.g., improving field margins, establishing flower strips or floral-rich hedgerows, or adopting grassland extensification schemes), measures aimed at improving the nesting habitat quality for ground-nesting wild bees within fields can provide additional benefits. For example, in simplified agroecosystems characterized by large field sizes and low proportions of field margins and (semi-)natural habitats, improving within-field nesting habitat quality for ground-nesting wild bees may be particularly important to harness crop pollination services across the field without relying on purchased managed bees (Christmann, 2022; Cusser et al., 2023). Beyond benefits for crop pollination, increased nest density of ground-nesting bees in arable land also has implications for the health of arable soils. Many ground-nesting bees create large vertical and continuous pores, similar to anecic earthworms, that can persist for many months (Tschanz et al., 2023a). Such pores have a major impact on soil functions, such as soil aeration (e.g., Stepniewski et al., 1994),

water flow and nutrient transport (e.g., Jarvis, 2007), and root growth (e.g., Colombi et al., 2017). Most ground-nesting bee species also deposit excavated soil material on the soil surface (Danforth et al., 2019), contributing to the decompaction of compacted topsoils (Keller et al., 2021), which are often critically dense under no-till (e.g., Nunes et al., 2015). Thus, enhancing within-field nesting habitat quality for ground-nesting bees may contribute to the improvement and restoration of soil functions and their associated benefits to crops, which is particularly important in no-till systems that lack mechanical loosening of soils.

In this paper, we review the existing literature assessing the effects of tillage systems on ground-nesting bees in arable cropping system. We discuss hypothesized direct and indirect mechanisms underlying the effects of tillage systems on ground-nesting bees, review current evidence for some of these hypotheses, and identify important knowledge gaps. We also discuss factors that may enhance or mitigate tillage effects, including aspects of bee life history, tillage practices, and habitat characteristics, and highlight the implications of tillage effects for the conservation and management of ground-nesting bee pollinators to promote the multiple ecosystem services they provide. Finally, we address the identified knowledge gaps by providing recommendations to guide future research efforts to improve our understanding of the impacts and mechanisms by which tillage systems may affect ground-nesting bees. Such research is critical to assess the potential of arable land managed under different tillage systems, and to develop evidence-based management guidelines aimed at promoting the diversity and abundance of these important pollinators in agricultural landscapes.

2. Effects of tillage on ground-nesting bees

To identify published studies that examined the effects of different tillage systems (see [Supplementary Information Section 1](#) for an overview of tillage systems discussed in this review) on ground-nesting bees in arable land, we conducted a systematic search in the database Scopus using the following search terms: (tillage OR tilling OR plowing OR ploughing OR "soil management" OR cultivation) AND ((ground-nesting OR soil-nesting OR digger OR burrowing OR mining OR fossorial OR underground OR belowground OR below-ground) AND (bee OR bees)). We also screened for further potentially relevant studies cited within the literature identified by the Scopus search. This yielded a total of 20 potentially relevant studies. Our criteria for final inclusion of relevant studies were: (i) the study was empirical (excluding perspective, review, or modelling articles); (ii) the study compared different tillage systems against each other, against a control or used a before/after design; (iii) the study focused explicitly on ground-nesting bees (i.e., bees that nest in self-excavated burrows below ground); (iv) the study focused on arable cropping systems. Using this process, we identified ten studies that were included within this review (Table 1).

2.1. Evidence for tillage system effects on ground-nesting bee abundance using indirect methods

We are aware of three studies that quantified the abundance of ground-nesting bees in fields managed with different tillage practices using indirect methods, i.e., quantifying foraging bees rather than nesting bees (Table 1), yielding inconsistent results. All three studies focused on a single ground-nesting bee species (*X. pruinosus*) in cucurbit fields using an indirect measure of local bee abundance (i.e., flower-visiting bees) in the fields studied (Appenfeller et al., 2020; Julier and Roulston, 2009; Shuler et al., 2005).

Two of these studies found that reduced tillage was associated with higher local abundance of ground-nesting bees. Shuler et al. (2005) found that the number of *X. pruinosus* observed on cucurbit flowers was about three times higher in no-till fields than in tilled cucurbit fields. Similarly, Appenfeller et al. (2020) found that visitation rates of *X. pruinosus* on cucurbit flowers were about three times higher in no-till

cucurbit fields compared to tilled fields. Flower visitation rates in reduced tillage fields were similar to conventionally tilled fields. Tillage depth (0 cm, 3–14 cm, 15–25 cm) had no significant influence on flower visitation rates. Julier and Roulston (2009), however, found no significant difference in *X. pruinosa* abundance on pumpkin (*Cucurbita pepo*) flowers between no-till and tilled fields.

Possible explanations for the ambiguous results within the *X. pruinosa* squash cropping system between the study by Julier and Roulston (2009) and Shuler et al. (2005) are provided by Roulston and Goodell (2011). The authors argue that a sufficient reservoir of bees within fields may have survived tillage by nesting below the tillage depth (Hurd et al., 1974 reported *X. pruinosa* brood cell depths ranging from 9 to 69 cm, but mostly between 13 and 30 cm), or by nesting outside the fields at undisturbed sites, where they may nest in aggregations persisting for years. Further, they suggest that the inconsistency could be related to the fact that only pumpkins were grown in the study by Julier and Roulston (2009), whereas Shuler et al. (2005) studied different yellow-flowered *Cucurbita* species. Since pumpkin is grown later in the season and may not flower before *X. pruinosa* emerges from these fields, early bees may disperse rather than wait, and the foraging bees quantified in these fields may be predominantly from immigration.

2.2. Direct assessments of nest site selection and nest numbers across different tillage systems

While the above mentioned studies also provide some insights into nest site selection preferences, two studies specifically tested *X. pruinosa* nest site selection preferences using a choice experimental design, and another study, although not using a choice design, compared nesting incidence and nest density between different tillage systems (Table 1). Skidmore et al. (2019) found that bees nested in multiple tested tillage types, but nest densities were higher in tilled and strip-tilled soils than in untilled soils. Similarly, in a study by Julier and Roulston (2009), bees nested in both tilled and no-till nesting substrate treatments, but the difference was not statistically analyzed. One study quantified the nesting communities of ground-nesting bees in conventionally tilled (moldboard plow) and no-till winter cereal fields by directly measuring within-field nest density (number of nests per area searched for nests) and identifying bees by capturing nesting females (Tschanz et al., 2023b). The authors found that cereal fields are used as nesting sites by a suite of ground-nesting bee species, but there was no significant difference in ground-nesting bee nest density or nesting incidence in tilled compared to no-till cereal fields.

2.3. Effects on community composition

There is some evidence from a single study that different tillage systems may be associated with a distinct community assemblage of ground-nesting bees (Table 1). In the study by Tschanz et al. (2023b), they captured nesting females in conventionally tilled (moldboard plow) and no-till winter cereal fields. Of the fifteen species collected, eight occurred exclusively in tilled and three exclusively in no-till fields (see Table 1 in Tschanz et al., 2023b for a list of species captured by tillage system). However, no formal analysis was conducted due to small sample sizes for most species.

2.4. Effects on offspring survival

Anecdotal and experimental evidence suggests that ground-nesting bees can survive tillage, but that tillage reduces offspring survival (Table 1). Minter and Bessin (2014) reported that ‘many’ *X. pruinosa* emerged from plots subjected to heavy soil disturbance (moldboard plowing, rotary tillage, undercutting, surface tillage, and raised bed preparation). Mathewson (1968) reported that plowing a nesting aggregation of *X. pruinosa* that had persisted for two years in an undisturbed field margin resulted in a ‘drastic reduction’ in their population.

Quantitative evidence that tillage reduces offspring survival comes from a replicated semi-field experiment by Ullmann et al. (2016). In their study, the authors found that offspring survival of *X. pruinosa* kept in flight cages established on a squash field was around 50 % lower in cages subjected to tillage (disking to 15 cm and subsoiling to 40 cm depth) compared to control cages (no tillage but driven over by a tractor in the same way as the tilled plots).

2.5. Effects on emergence timing and sex ratio

Besides the more direct effects of tillage on nesting and survival, tillage has also been hypothesized to potentially affect bee emergence timing (e.g., by altering emergence cues) and sex ratio (e.g., when males and females nest at different depths) (Ullmann et al., 2016; Wuellner, 1999).

Two studies found some evidence that tillage can alter the timing of offspring emergence (Table 1). Wuellner (1999) found that *Dieunomia triangulifera* bees that nested in a bare road, which was then plowed and heavily vegetated, reached the peak of their emergence time about four days later than bees that nested in the still bare road. Delayed emergence of offspring due to tillage was also found by Ullmann et al. (2016); offspring in cages that were tilled (disked and subsoiled) emerged 0.55 (females) to 0.92 (males) days later than offspring in control cages, although the observed difference in emergence time of females was not statistically significant, and such a difference of less than one day is likely of minimal biological importance.

To date, there is no evidence that tillage can alter the sex ratio of bee offspring, but this has only been investigated in one study. In this experimental study by Ullmann et al. (2016), there was no significant difference in the sex ratio of emerging *X. pruinosa* offspring between cages that had been tilled (disked and subsoiled) and control cages.

3. Mechanisms underlying tillage effects

The documented effects of tillage on ground-nesting bees are likely causative rather than merely correlative with other management practices associated with the tillage system (e.g., crop rotation, insecticide use), as suggested by several authors (Appenfelder et al., 2020; Shuler et al., 2005). Evidence for this is provided by observational studies that found a negative effect of tillage on crop-flower visitation rates of the ground-nesting *X. pruinosa*, but not for bumblebees and honeybees that nested outside the field (Appenfelder et al., 2020; Shuler et al., 2005). Perhaps the best evidence for a causative relationship comes from the manipulative experiment by Ullmann et al. (2016), which showed that tillage reduced offspring survival. However, the relative importance of the different hypothesized mechanisms by which tillage may negatively affect ground-nesting bees is largely unknown (Antoine and Forrest, 2021; Harmon-Threatt, 2020), and the few studies that have assessed tillage effects were not designed to disentangle and quantify the role of such potential mechanisms. Hypothesized effects include direct (e.g., mechanical killing of offspring through contact with tillage implement) or indirect ones (e.g., through changes to soil properties) (Fig. 1).

3.1. Direct mechanical impacts of tillage and field traffic

3.1.1. Physical injury to nesting bees, offspring, and brood cells

The depth at which ground-nesting bees construct brood cells varies widely among species (from 1 cm to 530 cm) and even within some species (Cane and Neff, 2011), but the depth at which most ground-nesting bees typically construct brood cells ranges from 9–10 cm (upper median) to 20–23 cm (lower median) (Cane and Neff, 2011; Harmon-Threatt, 2020), which is often within the tilled soil layer. Offspring within the tilled soil layer are vulnerable to physical contact with a tillage implement and to compaction from vehicle traffic, which can injure or even kill nesting bees, developing or overwintering offspring, or may damage the structural integrity of the protective brood

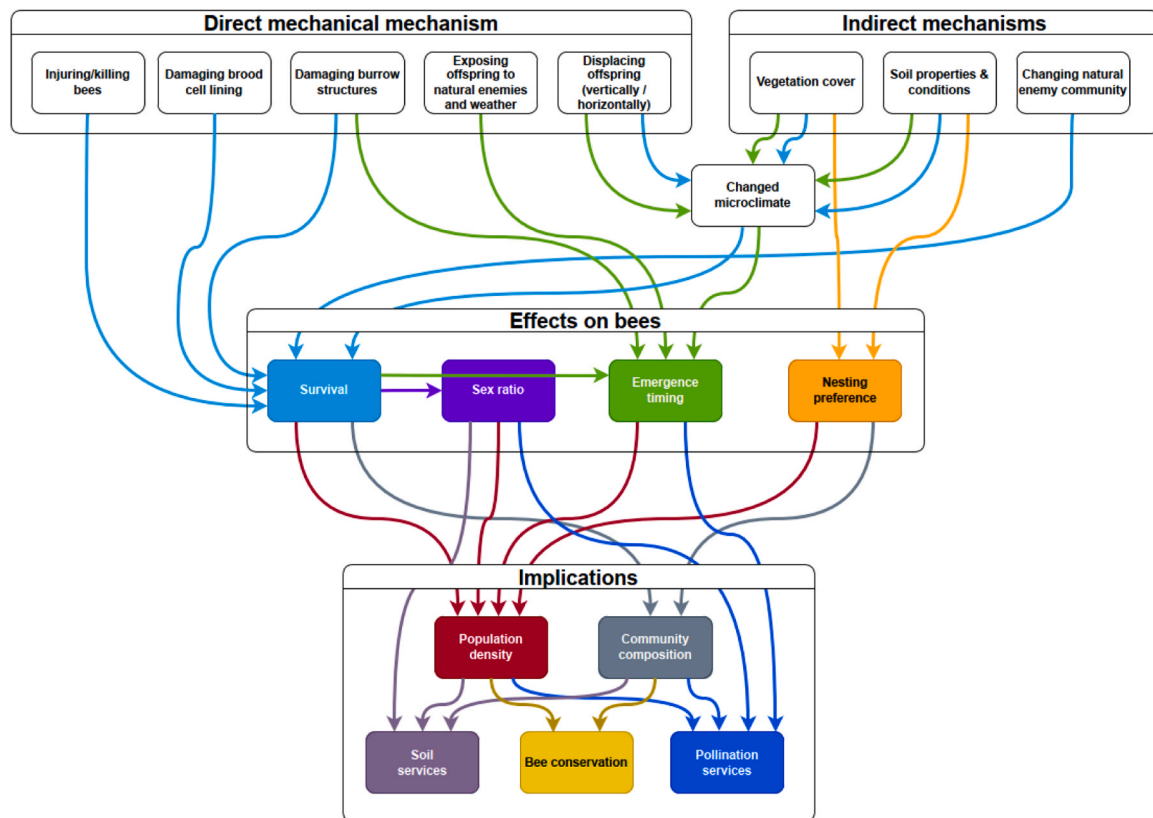


Fig. 1. Direct and indirect impacts underlying tillage effects and their implications for the conservation of ground-nesting wild bees and the pollination and soil services they provide.

cell lining, as suggested by several authors (Christmann, 2022; Harmon-Threatt, 2020; Roulston and Goodell, 2011; Ullmann et al., 2020).

To what extent nesting bees and their offspring can survive the mechanical disturbance of tillage within the tilled layer is still unknown. While the experimental study by Ullmann et al. (2016) showed that tillage reduced offspring emergence by about 50 % compared to control plots (subjected to agricultural traffic only), it is unclear to what extent this reduction was due to direct mortality within the tilled layer, either caused by physical contact with the tillage implement or by alternative mechanisms, such as inhibition of emergence or displacement of brood cells. It is also possible that bees within the tilled layer were able to partially survive the tillage operation itself, or that bees within the tilled layer did not survive but that bees from brood cells below the tilled layer were able to successfully emerge.

It is also conceivable that mechanical disturbance to soils is sufficient to damage the structural integrity of the brood cell wall lining, as hypothesized by Ullmann et al. (2020). Most ground-nesting bees smoothen their brood cell walls and then apply a waterproof film of glandular secretions, and some species also use plant-based materials (including leaves, flower petals, leaf trichomes, and floral oils) for this purpose (Antoine and Forrest, 2021; Danforth et al., 2019). This lining serves as a protective barrier against harsh environments, preventing desiccation in arid regions and high moisture in seasonally saturated environments, and hermetically sealing brood cells protects developing bees from biotic threats such as microbes, parasites, and predators (Albans et al., 1980; Almeida, 2008; Antoine and Forrest, 2021; Cane et al., 1983; Danforth et al., 2019). Damage to this protective sheath, even the smallest cracks, could leave offspring vulnerable to such threats. Such damage to the structural integrity could be caused by compaction from agricultural traffic, by physical contact with tillage tools, or by the physical trauma from displacement during tillage.

Whether and to what extent such mechanical stresses can cause damage to the impervious brood cell lining, and to what extent this plays a relevant role in the survival of ground-nesting bees in arable fields remains, to our knowledge, largely unexplored.

All tillage and cropping systems require some degree of field traffic for agricultural management, which could potentially crush offspring by compacting soils, as suggested by several authors (e.g., Roulston and Goodell, 2011; Ullmann et al., 2020). While field traffic has been shown to be able to kill, e.g., earthworms (Capowiez et al., 2012), it remains unknown whether it can also harm offspring or nesting females, and if so, to what soil depths.

3.1.2. Damage or destruction of nest structures

Traffic and tillage can damage or destroy existing nest structures. Damage or destruction of existing burrow structures could result in delayed emergence of offspring or even prevent successful emergence. Such a potential mechanism has been proposed by several authors (Christmann, 2022; Shuler et al., 2005; Ullmann et al., 2016; Vaughan et al., 2007), but to our knowledge, no study has yet examined whether, and if so to what extent, burrow destruction through soil management may contribute to reduced offspring emergence. Although Ullmann et al. (2016) found that offspring emerged later in tilled plots than in control plots, it was unclear whether burrow destruction contributed to delayed emergence. Delayed emergence could also arise if tillage altered emergence cues, such as soil temperature or moisture (Danforth, 1999; Wuellner, 1999), or if offspring only emerge from deeper brood cells if tillage destroyed the shallower brood cells, taking them longer to reach the soil surface (Ullmann et al., 2016). Emergence timing could also be affected by tillage practices that invert the soil (e.g., moldboard plowing) and thus move brood cells vertically (Fig. 2A), resulting in earlier or later emergence compared to untilled soil, depending on whether brood cells are predominantly moved upwards or downwards.

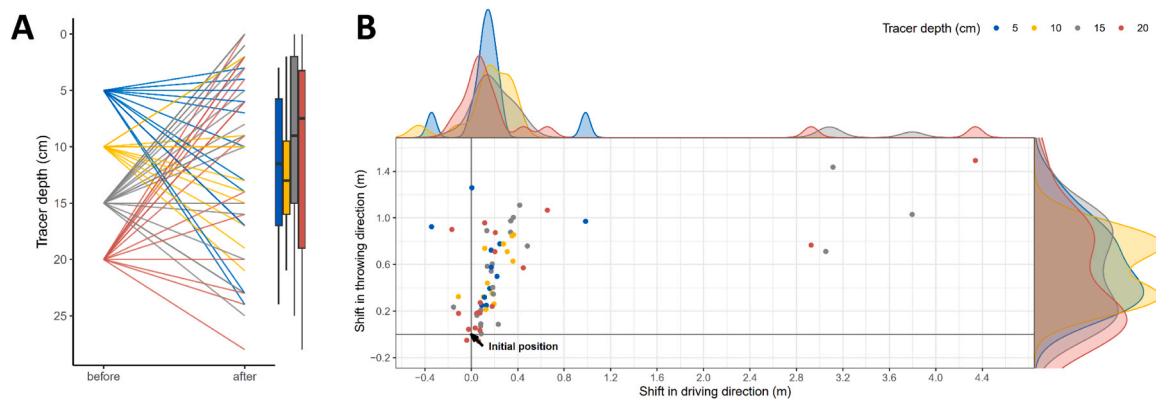


Fig. 2. Experiment to quantify the expected vertical and horizontal displacement of bee brood cells induced by conventional tillage. Shown are the vertical (A) and horizontal (B) displacements of metal tracers buried at four depths (5, 10, 15, 20 cm) induced by conventional tillage (moldboard plowing to 20 cm depth followed by rotary harrowing and sowing). A) Vertical position of tracers before and after tillage. B) Horizontal displacement of tracers relative to their initial position in driving direction (i.e., in the direction of field traffic) and in throwing direction (i.e., perpendicular to driving direction). See [Supplementary Information Section 2](#) for details.

In a pilot experiment, we demonstrated that, at least under certain conditions, offspring do not appear to depend on the integrity of pre-existing burrow structures for emergence ([Fig. 3](#); see [Supplementary Information Section 3](#) for details). Nevertheless, destruction of pre-existing burrow structures could potentially delay their emergence timing, reduce their emergence success, or reduce their reproductive success by depleting their energy reserves as a result of the increased effort required to dig themselves out. Furthermore, the effects of burrow destruction on emergence may depend on soil properties and soil conditions and may also differ among species. For example, clay-rich soils can become very hard when dry, which is known to prevent earthworms from burrowing ([Ruiz et al., 2021](#)), and this could similarly limit bees attempting to burrow out of the soil. Ground-nesting bees have been observed to delay digging until the soil becomes moist ([Minckley et al., 1994](#); [Wuellner, 1999](#)). It is therefore conceivable that soil properties and the hydromechanical state of the soil modulate such effects, but the burrowing mechanics of bees and how they are constrained by soil hydromechanical properties, which may be species-specific, have not been studied yet ([Ruiz et al., 2023](#)).

3.1.3. Displacement of offspring exposing them to altered soil conditions, environmental extremes, and natural enemies

Tillage displaces objects (including bee offspring) vertically and horizontally within the tilled layer to varying degrees depending on the type of tillage ([Fig. 2](#), [Figure S1](#); see [Supplementary Information Section 2](#) for details). It has been hypothesized that offspring displaced closer to the soil surface due to tillage may no longer be sufficiently buffered from environmental extremes, such as freezing or molding due to excessive exposure to moisture in temperate regions, or heat and desiccation in hot and arid climates, or, if displaced to the soil surface, bees may be more exposed to natural enemies or diseases ([Roger-Estrade et al., 2010](#); [Roulston and Goodell, 2011](#); [Ullmann et al., 2020](#)).

Vertical displacement of offspring may also have more subtle effects on offspring development and survival induced through altered soil conditions (e.g., moisture and temperature regimes, soil density). It appears that females modify the depth at which they place their offspring to accommodate for edaphic factors ([Harmon-Threatt, 2020](#)) with respect to, e.g., soil density ([Batra, 1970](#)) or soil moisture ([Miliczky, 2008](#); [Nye, 1980](#)), and possibly to buffer them against temperature extremes ([Westrich, 2015](#)). Thus, the brood cell depth chosen by the female may be an adaptive strategy to maximize her reproductive success, and altering the intended brood cell depth by tillage could likely have negative consequences for offspring development and survival.

3.1.4. Consequences of depth-dependent mechanical impact on sex ratio and emergence timing

Since the intensity of mechanical disturbance from tillage and field traffic decreases with depth, these perturbations could also alter the sex ratio of the nesting population, with implications for emergence timing, as hypothesized and investigated by [Ullmann et al. \(2016\)](#). This could occur in ground-nesting bee species in which male and female brood cells are located at different depths (e.g., *Calliopsis persimilis*; [Danforth, 1990](#)), with the shallower-nesting sex being more severely affected, thereby potentially leading to a biased sex ratio of the nesting population. Depending on whether tillage or field traffic destroys more males or females, and whether the nesting species is protogynous (females emerge before males) or protandrous (males emerge before females; [Danforth et al., 2019](#)), mechanical disturbance may result in earlier or later peak emergence timing.

3.2. Indirect impacts of tillage

The effects of tillage may go beyond the direct mechanical effects described above. Tillage systems can alter the nesting habitat of ground-nesting bees in a variety of ways, thereby indirectly affecting ground-nesting bees at multiple levels. Tillage operations can cause rapid changes in habitat characteristics (e.g., vegetation cover, soil properties, and soil microclimatic conditions) after bees have established their nests, to which their immobile offspring have limited ability to respond. Continued use of certain tillage practices can also induce longer-term changes in habitat characteristics that alter the attractiveness of the field for nesting ([Fig. 1](#)).

3.2.1. Alterations of soil surface features

Soil surface features modified by tillage have been associated with nesting preference (reviewed in [Antoine and Forrest, 2021](#)), including soil cracks (e.g., [Visscher and Danforth, 1993](#)), stones (e.g., [Potts and Willmer, 1997](#)), and vegetation cover (e.g., [Tschanz et al., 2023b](#)). These features are relevant to ground-nesting bees in several ways ([Antoine and Forrest, 2021](#)). They can act as visual cues to help bees locate their nest ([Brünnert et al., 1994](#)) or hide nest entrances from natural enemies ([Potts and Willmer, 1997](#)). Plants can stabilize nest structures ([Angers and Caron, 1998](#)), but their roots may also impede nest excavation and destroy brood cells ([Wuellner, 1999](#)).

Whether a particular tillage system results in soil surface changes that increase or decrease the attractiveness of arable land as nesting habitat for ground-nesting bees likely varies among species because of species-specific nesting preferences. For example, some ground-nesting

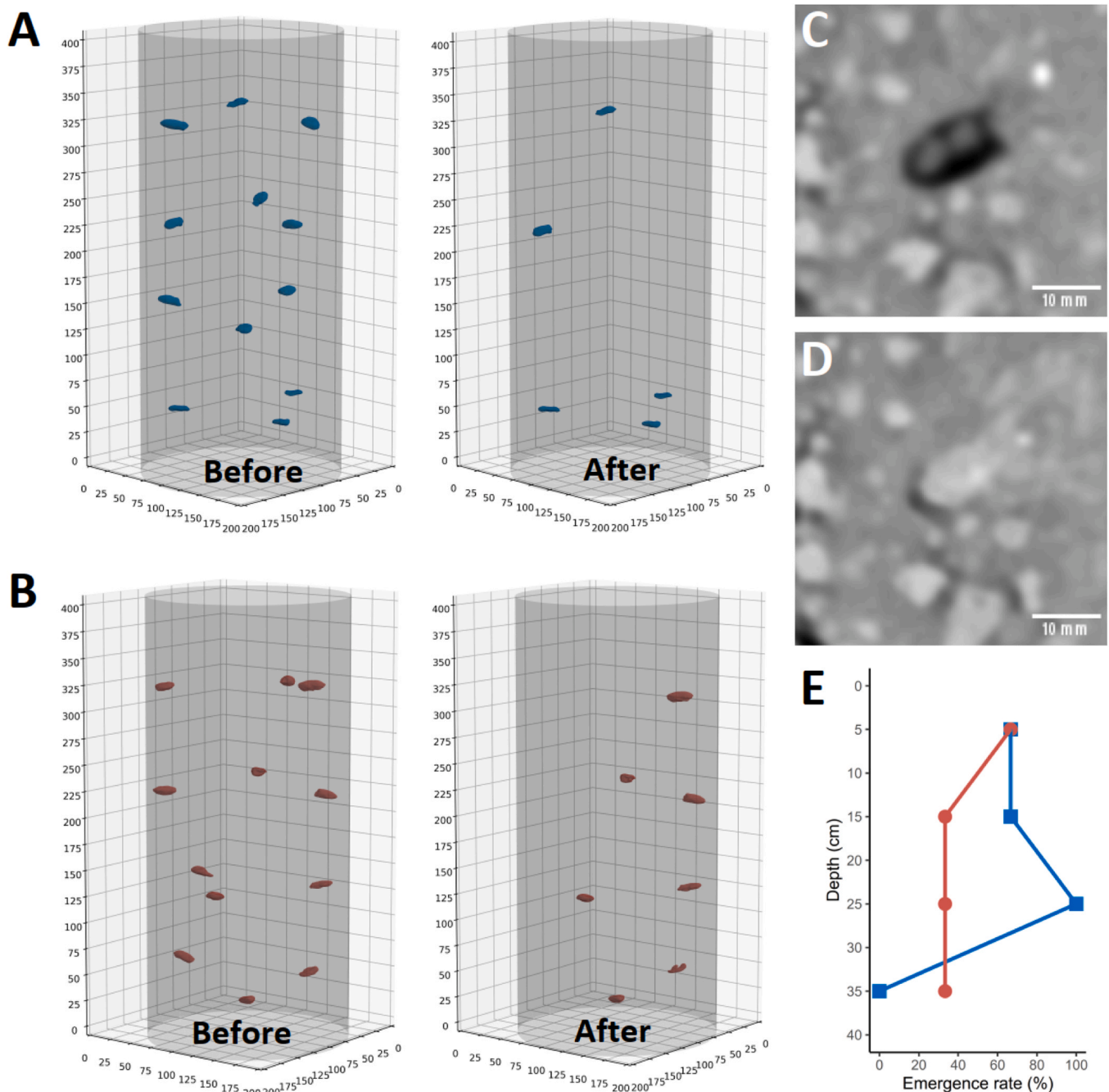


Fig. 3. Experiment to quantify the emergence success of translocated bee brood cells and to test whether bee offspring can successfully emerge in the absence of pre-existing burrow structures. Brood cells of *Colletes cunicularius* were buried in two soil columns at depths of 5, 15, 25, and 35 cm (three brood cells per depth). The soil columns were X-ray imaged before and after emergence, and brood cells were extracted from the 3D reconstructed images. A, B) Soil columns and extracted brood cells before and after emergence. C, D) Example of a brood cell containing an overwintering bee offspring before emergence (C) and after emergence (D). E) Emergence rates per brood cell depth for the two soil columns (blue line and squares represent soil column A; red line and dots represent soil column B). See [Supplementary Information Section 3](#) for details.

bees prefer to nest in sparsely vegetated areas (e.g., [Wuellner, 1999](#)), while others appear to be relatively indifferent to vegetation cover (e.g., [Kim et al., 2006](#)). Therefore, different tillage systems may have partially distinct communities of ground-nesting bees, thereby increasing their beta diversity across sites in arable cropping systems. There is some evidence that this may be the case. For example, in a nest site selection experiment, the ground-nesting bee *X. pruinosa* preferred to nest in tilled soil over untilled soil ([Skidmore et al., 2019](#)), and limited evidence based on uncomprehensive sampling of nesting bees in winter cereal fields indicates that no-till and tilled fields attracted different bee

communities ([Tschanz et al., 2023b](#)). Ground-nesting bees generally prefer bare ground ([Antoine and Forrest, 2021](#); [Harmon-Threatt, 2020](#)), and several studies have found a positive relationship between nest density and the amount of bare ground ([Albrecht et al., 2023](#); [Gardein et al., 2022](#); [Potts et al., 2005](#); [Sardiñas and Kremen, 2014](#); [Tschanz et al., 2023b](#)). This association of nesting with low vegetation cover, as demonstrated by systematic vegetation comparisons between nest and control sites ([Albrecht et al., 2023](#); [Gardein et al., 2022](#); [Tschanz et al., 2023b](#)), appears to reflect a genuine nesting preference rather than an observational bias due to difficulty finding nests in denser vegetation.

Because the soil surface in no-till systems is covered with residue from the previous crop, whereas conventionally tilled systems incorporate crop residue into the soil (Soane et al., 2012), tilled arable soils may provide more attractive nesting conditions due to their generally lower vegetation cover. There is, however, no clear evidence to support this hypothesis. Tschanz et al. (2023b) found no significant differences in nest densities or species richness of ground-nesting bees in tilled compared to no-till cereal fields. Furthermore, it is unclear whether and to what extent potentially favorable nesting habitat conditions in tilled fields, which may be enhanced by the proximity to floral food resources in and around such fields, are offset by subsequent tillage that reduces offspring survival (Ullmann et al., 2016), and tilled fields may act as ecological traps for ground-nesting bees.

3.2.2. Alteration of subsurface soil properties and conditions

Tillage, through mechanical manipulation of the soil, induces changes in soil properties that alter the microclimatic conditions experienced by bees. For example, while conventional tillage systems mix soils and create more homogeneous conditions, continuous no-till systems result in soil stratification due to the lack of soil mixing (House and Parmelee, 1985). Tillage affects many soil properties (e.g., aggregate stability, thermal conductivity, bulk density, macroporosity, organic matter concentration) with diverse consequences for the environmental conditions experienced by developing or overwintering bee offspring, such as soil moisture and temperature regimes, gas concentrations (O₂, CO₂), or soil diggability (Blanco-Canqui and Ruis, 2018; Soane et al., 2012). Changes in soil temperature and moisture regimes can also be induced by changes in soil surface features (e.g., reduced stone and vegetation cover due to incorporation into the soil; see Section 3.2.1) that affect the amount of solar radiation reaching the soil surface (Potts and Willmer, 1997). These changes in soil properties and conditions can occur over long periods of time or very rapidly after tillage (Blanco-Canqui and Ruis, 2018) and are likely to affect bees at various stages of their life cycle – from nest site selection, offspring survival, emergence timing, to community composition.

Changes in soil properties and conditions induced by tillage can potentially alter the attractiveness for ground-nesting bees as nesting habitat (see reviews: Antoine and Forrest, 2021; Harmon-Threatt, 2020). These include soil density (e.g., Potts and Willmer, 1997; Wuellner, 1999), soil moisture (e.g., Julier and Roulston, 2009; Wuellner, 1999), soil temperature (e.g., Potts and Willmer, 1997; Wuellner, 1999), and soil organic matter content (Osgood, 1972). As with soil surface features, different species have different soil-related preferences. For example, some species prefer to nest in softer soils (e.g., Potts and Willmer, 1997; Sardiñas and Kremen, 2014), while others prefer to nest in more compact soils (e.g., Wuellner, 1999). Therefore, tillage system-specific effects on soils may attract partially non-overlapping communities of ground-nesting bees, but predictions of species composition are hampered by a lack of knowledge about soil abiotic preferences of most ground-nesting bee species (Antoine and Forrest, 2021; Harmon-Threatt, 2020).

Changes in soil properties and conditions after nest establishment can have a wide range of consequences for developing and overwintering bee offspring. For example, no-till farming generally results in more compacted topsoils than conventional tillage (Soane et al., 2012). This, in turn, leads to changes in gas (O₂ and CO₂) concentrations and hydrological conditions, which affect the living conditions for bee offspring (Beylich et al., 2010). The effect of different gas concentrations on bees has not been studied (Antoine and Forrest, 2021; Christmann, 2022), but soil temperature and soil moisture are critical for bee offspring, and changes in them can affect bee development and survival rates, voltinism (number of generations in a year), body size, molding rates, food supply degradation, and more (Antoine and Forrest, 2021). For example, soil compaction reduces water permeability, which can lead to waterlogged or flooded fields (Batey, 2009). Such flooding events can severely decimate local ground-nesting bee populations (e.g.,

Fellendorf et al., 2004), but some species appear to be well adapted to survive prolonged periods in waterlogged environments as diapausing prepupae (e.g., up to six months: Norden et al., 2003) and even as diapausing adults (e.g., up to one week: Rondeau and Raine, 2024b). Soil temperature and moisture can also affect the timing of offspring emergence (Cane, 2021; Danforth, 1999; Forrest and Thomson, 2011; Wuellner, 1999).

3.2.3. Changes in soil community composition indirectly affect bees

Ground-nesting bees are exposed to a variety of natural enemies. These include predators (e.g., spiders, true bugs, ants), parasites (e.g., parasitic wasps, cleptoparasitic bees, nematodes), and microbes (e.g., bacteria and fungi) that can attack bees at various life stages (from eggs to adults) or reduce food resource availability or quality, thereby significantly impacting nesting bees (Antoine and Forrest, 2021; Danforth et al., 2019; Harmon-Threatt, 2020). By altering the physical and chemical environment of the soil, tillage has a broad impact on these natural enemy communities (Kladivko, 2001; Roger-Estrade et al., 2010; Wardle, 1995), thereby likely affecting the reproductive success of ground-nesting bees, but how tillage shape such impacts remains to be investigated.

3.3. Implications of tillage effects for bee conservation, pollination services, and soil services

The indirect and direct mechanisms of how tillage may affect ground-nesting bees outlined above have implications for ground-nesting bee conservation, as well as ecosystem functioning with respect to pollination and soil ecosystem services (Fig. 1). Aside from the obvious implications for conservation and ecosystem services as a consequence of impacts on nest numbers or offspring survival, tillage-induced changes in the sex ratio and emergence timing of the nesting population may also have less immediate and more hidden implications for population dynamics of ground-nesting bees and associated ecosystem services (Fig. 1).

Female nesting bees can determine the sex ratio of their offspring as an adaptive strategy (males are typically smaller and require less food resources) to cope with fluctuations in resource availability, foraging distances, and intrinsic factors such as body size and age (Danforth et al., 2019). Tillage-induced changes in the sex ratio of the nesting population are therefore likely to be maladaptive, with negative consequences for population dynamics of nesting bees. For example, shifting the sex ratio towards males results in an overall reduced reproductive output of the population over time, which could even lead to a downward spiral (extinction vortex) that drives local populations to extinction (Danforth et al., 2019). Since soil excavation to construct nests and pollination functions are primarily performed by females, a male-biased sex ratio could lead to a reduction in these ecosystem services.

Also, altered offspring emergence times could negatively affect bee populations and their services, as hypothesized by Ullmann et al. (2016). Bees that emerge later can have lower nutrient stores, which can reduce relevant fitness aspects (i.e., fecundity, longevity) (Dmochowska et al., 2013). Furthermore, altered emergence timing could lead to a phenological mismatch between bee activity and flowering periods of forage plants, which could be particularly detrimental to specialist bees due to their limited access to pollen and potentially impaired pollination services.

3.4. Potential factors mitigating or reinforcing tillage effects

Tillage effects are likely to depend on species-specific characteristics, tillage practices, and other agricultural management practices (e.g., crop residue management) that may be associated with specific tillage systems.

3.4.1. Bee characteristics

Bee characteristics that may influence how ground-nesting bees respond to disturbances from tillage and field traffic include aspects of their life history, such as sociality (e.g., solitary vs. social) and phenology (e.g., univoltine vs. multivoltine), their flexibility in nest site selection (e.g., strong vs. weak preferences for specific soil, vegetation, and other nesting habitat features), body size, and nesting depth (Harmon-Threatt, 2020; Roulston and Goodell, 2011; Ullmann et al., 2020, 2016; Williams et al., 2010). For example, social bee species were more vulnerable to tillage in vineyards than solitary bee species, possibly because of their longer activity period and because it may be more difficult for a colony with only one or a few reproductive females to repopulate after disturbance than for solitary species, where all females are reproductively active and construct their own nests (Kratschmer et al., 2018). Such species-specific differences in the ability to withstand disturbances could lead to distinct and tillage system-specific community assemblages of ground-nesting bees over time (Cárcamo, 1995; Kromp, 1999; Tschanz et al., 2023b).

Nesting depth in relation to tillage depth likely plays a critical role in driving tillage impacts and consequences for ground-nesting bee populations (Harmon-Threatt, 2020; Ullmann et al., 2016). Nesting depth of ground-nesting bees vary greatly between species, ranging from a few centimeters up to several meters, but for most species, nesting depths are about 9–10 cm (upper median) to 20–23 cm (lower median) (Cane and Neff, 2011; Danforth et al., 2019; Harmon-Threatt, 2020). Nesting depth can also vary within species in response to local edaphic factors (Harmon-Threatt, 2020), such as soil density (Batra, 1970) and soil moisture (Miliczky, 2008; Nye, 1980). Individuals nesting at greater depths are better shielded from physical disturbances through compaction by traffic, and nesting below tillage depth avoids direct contact of brood cells with tillage implements. Therefore, it seems likely that species nesting at greater depths are less at risk to be negatively affected by tillage (e.g., moldboard plowing), whereas shallow-nesting species should be more severely impacted by tillage and may only persist in largely undisturbed arable land (e.g., no-till). From the available literature on ground-nesting bees, however, it is unclear what role nesting depth plays for successful emergence after conventional tillage (moldboard plow: Minter and Bessin, 2014; three-shank subsoiler: Ullmann et al., 2016). It is possible that some offspring survived this disturbance despite nesting within the tilled layer, or it could be that all emerged offspring originated from depths below the tilled layer. Interestingly, Appenfeller et al. (2020) found no relationship between tillage depth and the abundance of foraging ground-nesting bees in the cucurbit fields studied. However, as they did not directly quantify nest density, it is also possible that observed flower visitation rates were not directly related to nest numbers and tillage practices.

Tillage is likely to pose the greatest threat to developing and overwintering offspring of ground-nesting bees because their immobile nature limits their ability to respond to threats such as tillage (Harmon-Threatt, 2020). Thus, conventional tillage practices may be especially harmful to univoltine species, which depend on nests being undisturbed for most of the year, and to overwintering generations of multivoltine species, while tillage may be less harmful to summer generations of multivoltine species, which spend only a few weeks in the soil (Shuler et al., 2005). There is also a great diversity in the developmental stages at which bees enter the overwintering phase, which may differ in their susceptibility to threats such as tillage (Danforth et al., 2019; Harmon-Threatt, 2020). For example, adults are thought to be less resistant to desiccation than prepupae, which have a thick, impermeable outer integument (Danforth et al., 2019), and may therefore be more susceptible to changes in soil microclimatic conditions induced by tillage.

Studies on other soil organisms have found that larger organisms, such as earthworms and beetles, are more sensitive to tillage than smaller organisms, such as nematodes (Kladivko, 2001; Wardle, 1995). Bee size could therefore also modulate tillage effects. For example,

smaller species may be less likely to be directly hit by the tillage tool than larger bees.

3.4.2. Tillage and related agricultural management practices

Tillage systems vary in various aspects that may dampen or strengthen their effects on ground-nesting bees. These include inversion and non-inversion tillage, type of tillage implement (and associated with it the degree of physical soil disturbance), the frequency of mechanical disturbance, tillage depth relative to nesting depth, and timing of tillage operations relative to the bee life cycle (Christmann, 2022; Kladivko, 2001; Ullmann et al., 2020, 2016). These factors may vary depending on crop, soil type, or region (Ullmann et al., 2016).

Comparisons of the effects of different tillage systems on ground-nesting bees have mostly focused on comparing the two extremes of disturbance intensity (i.e., no-till vs. conventional tillage; Table 1). Whether intermediate forms of tillage practices (e.g., reduced tillage) produce intermediate results, as has been suggested for other taxonomic groups (Kladivko, 2001), is unclear. Appenfeller et al. (2020) found no such intermediate effects; while flower visitation rates of the squash bee *X. pruinosa* were significantly higher in both no-till and reduced tillage than in conventionally tilled fields, they were not significantly different from each other. In contrast, intermediate forms of tillage (e.g., chisel plow) were less destructive to ground beetles than conventional tillage (e.g., moldboard plow) (Shearin et al., 2007). An intermediate tillage form that has received little attention, but may be of particular interest to ground-nesting bees, are strip-till systems. Strip-till systems share soil properties similar to both tilled and untilled soils (Skidmore et al., 2019), which could even attract more diverse communities of ground-nesting bees than either no-till or conventional systems by increasing small-scale spatial heterogeneity of nesting habitats, as has been found for other arthropod taxa (e.g., spiders; Samu et al., 1999). However, strip-till systems are also often accompanied by mulching practices, which may deter bees from nesting, although Appenfeller et al. (2020) found no negative effect of mulching practices on the abundance of flower visiting *X. pruinosa*. Because different tillage systems likely have species-specific effects, as demonstrated for ground beetles (Shearin et al., 2007), the interactions between tillage system and ground-nesting bees may be complex, as noted by Roulston and Goodell (2011).

Tillage-related agricultural management practices have further effects on ground-nesting bees (Antoine and Forrest, 2021; Harmon-Threatt, 2020; Kladivko, 2001). These include aspects that affect the amount of bare soil (e.g., crop residue management, crop row spacing, seed density, mulching practices, weed cover), crop rotations (e.g., whether root or tuber crops are included), timing of tillage/sowing practices (in relation to bee phenology), agrochemicals, and mechanical weeding. How these factors shape tillage effects are poorly understood.

4. Recommendations for future research

To improve our understanding of the suitability of arable soils as nesting habitat for ground-nesting wild bees and the underlying drivers, research efforts are needed that focus on direct measurements of nest density to quantify tillage and other management impacts on nesting preferences and nesting incidence across various cropping systems. Research is also needed that quantify tillage effects on bee survival and that aim at understanding the underlying mechanisms of tillage impacts and the factors that reinforce or mitigate them. In addition, the effectiveness of strategies that focus on improving nesting habitat quality within fields through improved agricultural management should be compared with measures that focus on improving nesting habitat quality outside fields, e.g., by increasing set-aside areas. Such research efforts allow to gain a more mechanistic and predictive understanding to provide solid management and policy recommendations for ground-nesting bee conservation and the pollination and soil ecosystem services they provide.

Here, we provide recommendations to guide future research efforts, focusing on largely underutilized established and novel approaches including: (i) field studies focusing on the entire nesting bee community using direct quantification methods for nest density; (ii) semi-field experiments to quantify the effects of tillage systems and to identify factors that mitigate or enhance such effects; and (iii) controlled experiments to identify the mechanisms behind tillage effects. We also highlight the potential of X-ray imaging as a valuable tool in such studies. Our recommendations are based on the knowledge gaps identified in the previous section with respect to impacts and underlying hypothesized mechanisms driving tillage effects on ground-nesting bees and include insights from partly unpublished data from recently conducted experiments to address them. We find it important to also share insights from experimental approaches that did not yield robust new findings, as we believe they provide valuable insights that can help guide future research efforts.

4.1. Field surveys to quantify the nesting habitat potential of arable land for entire communities of ground-nesting bees

Most field studies quantifying the effects of tillage systems on ground-nesting bees have relied on indirect methods such as sampling foraging ground-nesting bees (Table 1). However, it is unclear to what extent local abundance of foraging ground-nesting bees actually represents the density and reproductive success of ground-nesting bees nesting in the focal study field or patch under a particular soil management practice. Furthermore, species assemblages assessed using different methods to sample foraging and/or nesting bees can be highly dissimilar (Sardiñas and Kremen, 2014; Westphal et al., 2008). Appenfeller et al. (2020) argue that for the host plant specialist bee *X. pruinosa*, it is likely that flower visitation rates and nest densities are directly related because this species tends to nest close to its forage plants (Julier and Roulston, 2009), but this remains to be tested. We therefore recommend that at least studies aiming to assess nest densities or nesting habitat quality of less specialist ground-nesting bee species, or of multiple species or entire bee communities including less specialist species, should use direct methods to quantify nests in a focal field or patch of interest (Cope et al., 2019; Kim et al., 2006; Tschanz et al., 2023b).

Density and diversity of nesting bees in arable soils can be directly assessed using different methods, each with its respective advantages and disadvantages (see Antoine and Forrest, 2021; Klaus et al., 2024; Pane and Harmon-Threatt, 2017; Supplementary Information in Tschanz et al., 2023b for detailed discussions). Methods for direct quantification of nest density include: (i) searching for tumuli (i.e., mounds of excavated soil material) (e.g., Albrecht et al., 2023; Venturini et al., 2017), which can be combined with targeted placement of mini-emergence traps on detected nests (Tschanz et al., 2023b); (ii) random placement of emergence traps/tents installed at dusk and short deployment (<24 h) to capture nesting females at the time of sampling (Cope et al., 2019; Kim et al., 2006; Sardiñas et al., 2016a, 2016b); and (iii) random placement of traps/tents over an extended time period after the overwintering period to capture emerging offspring from previous years' nesting activity (Sardiñas and Kremen, 2014). While the use of emergence traps/tents had good success in habitats with high nest densities (Sardiñas and Kremen, 2014) or when deployed for longer periods (e.g., seven months; Sardiñas et al., 2016b), capture success rates in other habitats and short deployment periods (one to a few days) have typically been poor (Antoine and Forrest, 2021; Cope et al., 2019; Pane and Harmon-Threatt, 2017). Emergence traps are also relatively expensive and labor-intensive to install, which may limit the number of sites that can be sampled and also cover only a small sampling area (Antoine and Forrest, 2021; Pane and Harmon-Threatt, 2017). In areas where nest density is expected to be low, searching for nests may be more time and cost efficient to quantify nest density over a larger area and number of replicates (250 m² in 18 meadows: Albrecht et al., 2023;

400 m² in 25 cereal fields: Tschanz et al., 2023b), and, in combination with targeted placement of mini-emergence traps on detected nests, also lead to higher capture rates (e.g., 29 %; Tschanz et al., 2023b) compared to random placement of emergence traps (e.g., less than 4 % in Cope et al., 2019). However, searching for nests, unlike emergence traps, can be subject to observer bias and misclassification, does not include species that do not build a tumulus (e.g., *Andrena hattorfiana*; Larsson and Franzén, 2007), and is impaired by rain eroding tumuli (Tschanz et al., 2023b). Studies using the nest search method have also allowed to gain insights into local soil or vegetation characteristics associated with nest density or nesting incidence within and across differently managed fields by comparing local soil and vegetation characteristics quantified at nest locations with randomly selected control locations where no nest was found (e.g., Albrecht et al., 2023; Tschanz et al., 2023b). The size and selection procedure of such 'control' plots without nests (e.g., random, stratified random or specific selection criteria) should be determined by the specific study goals and take into account potentially confounding factors (e.g., distance from the field edge: Sardiñas et al., 2016b; Tschanz et al., 2023b).

Other aspects to consider when designing such studies include spatial and temporal factors. Ideally, sampling campaigns should cover the main activity period of known ground-nesting bee species in the study region. If nest density within a field is to be quantified in a representative way, the study design must take into account that nests may not be homogeneously distributed and can be concentrated, for example, towards field edges (e.g., Sardiñas et al., 2016b; Tschanz et al., 2023b). It is also important to ensure that a sufficiently large area and number of replicates is sampled. This also requires selecting the most appropriate method (e.g., emergence traps or nest search), which depends on expected nest density, among other factors. If the goal is to quantify post-tillage emergence/survival success by capturing emerging individuals from previously identified nests, trap designs must take into account that tillage displaces offspring from the original nest site (Fig. 2; see Section 4.2.3 for details).

4.2. Semi-field experiments to quantify tillage effects and identify key drivers

Surprisingly, replicated semi-field experiments have rarely been used to quantify the effects of different tillage systems on ground-nesting bees (but see Skidmore et al., 2019; Ullmann et al., 2016), despite their high potential to gain quantitative insights, particularly on the effects on offspring survival and reproductive success, but also to determine and disentangle the dominant mechanisms driving these effects, or to identify factors that mitigate or enhance these effects through. Depending on the focus, these experiments could vary in their level of perturbation (e.g., different tillage intensities) or in factors expected to modulate potential effects (see Section 3.4). For example, conventional tillage systems (e.g., moldboard plow) could be compared to conservation tillage systems (e.g., no-till) and/or other soil management treatments (e.g., doing nothing; or driving over with field machinery without tillage, as in Ullmann et al., 2016) to quantify the overall effects of different tillage systems on nesting and reproductive success of ground-nesting bees. In addition, such experiments could compare different levels of key modulating factors, such as nesting depth relative to tillage depth (e.g., within or below the tilled layer). Response variables of interest include nest numbers (see Skidmore et al., 2019), hatching success, sex ratio, and emergence timing (see Ullmann et al., 2016; Wuellner, 1999). Other variables of interest that have not yet been measured in tillage studies include body weight and nutrient stores, as suggested by Ullmann et al. (2016), which would allow quantification of potential adverse but sublethal effects of tillage.

In the following sections, we present and discuss two different semi-field experimental approaches, their respective advantages and disadvantages, as well as certain challenges associated with conducting such experiments, in particular the lack of suitable model ground-nesting bee

species and established experimental protocols, based on insights from recently conducted experiments. First, we discuss semi-field experiments using translocated adult ground-nesting bees kept in flight cages, similar to the experiment conducted by Ullmann et al. (2016). Second, we propose a novel alternative approach using translocated brood cells, which may allow to assess driving factors and mechanisms under even more controlled conditions.

4.2.1. Semi-field experiments using flight cages with translocated adult bees – the need for ground-nesting model species

The use of cavity-nesting bees (e.g., *Osmia bicornis* and *O. cornuta*) as model species in semi-field flight cage experiments is well established in experimental research (e.g., pesticide risk assessment: Franke et al., 2021; Knauer et al., 2022; Schwarz et al., 2022; Stuligross and Williams, 2020). Model bees for such experiments are commercially available, easy to handle in laboratory and field experiments, and guidelines have been established (EFSA, 2013). However, the use of ground-nesting bees as model species in such experiments has been largely neglected, and accepted guidelines for such studies with ground-nesting bees are largely lacking (reviewed in Leonard and Harmon-Threatt, 2019). The lack of ground-nesting bee model species is exacerbated by the fact that high adult nest failure is commonly observed in captivity, possibly due to high nest site philopatry of many ground-nesting bees (Antoine and Forrest, 2021; Leonard and Harmon-Threatt, 2019). Nevertheless, semi-field experiments have been successfully conducted with translocated adult ground-nesting squash bees (*X. pruinosa*) maintained in flight cages or other enclosures to study nesting preference (Julier and Roulston, 2009; Skidmore et al., 2019), to quantify the effects of tillage on offspring survival (Ullmann et al., 2016), and in pesticide risk assessments (e.g., Rondeau and Raine, 2024a; Willis Chan and Raine, 2021). Thus, *X. pruinosa* appears to be a suitable model species for semi-field experiments within its native distribution range (North America; López-Urbe et al., 2016). However, suitable model species outside its native range for such experiments have not yet been

established, but other ground-nesting bee species (e.g., various halictine bees; Plateaux-Quénu, 2008) have successfully nested under laboratory conditions (see Table S1 in Leonard and Harmon-Threatt, 2019 for a list of ground-nesting species that successfully nested under laboratory conditions).

Establishing new model species and protocols should be considered a key priority to advance research on tillage and other (soil) management drivers (e.g., Ullmann et al., 2016), as well as for risk assessment, such as the assessment of pesticide risks to ground-nesting bees (e.g., Rondeau and Raine, 2024a; Willis Chan and Raine, 2021). Ideally, a range of suitable model species should be established that differ in key life-history traits (e.g., sociality, nesting depth, voltinism), as these influence the species' response to disturbances (see Section 3.4.1), but may require different experimental protocols.

We conducted an experiment similar to the one by Ullmann et al. (2016), translocating adult bees to flight cages on conventionally tilled (moldboard plow) and no-till fields (Fig. 4A-B, Figure S2A; see Supplementary Information Section 4 for details). As a model solitary ground-nesting bee species, we used the spring mining bee *Colletes cunicularius*, which is a common and widespread solitary ground-nesting bee species in our study region (Greater Zurich Area, Switzerland) that nests in large aggregations and thus can be collected in sufficient numbers without threatening local nesting populations. Although soil properties were considered suitable for *C. cunicularius* nesting and ample floral resources were continuously provided to caged bees, the experiment was terminated due to very low nesting success of *C. cunicularius* within enclosures irrespective of tillage treatment (see Supplementary Information Section 4.3 for details and a discussion on potential reasons for failure). This example highlights the challenges associated with (semi-)field experiments with ground-nesting wild bees kept in flight cages, and the urgent need to establish suitable model species (in addition to *X. pruinosa*) and experimental protocols.

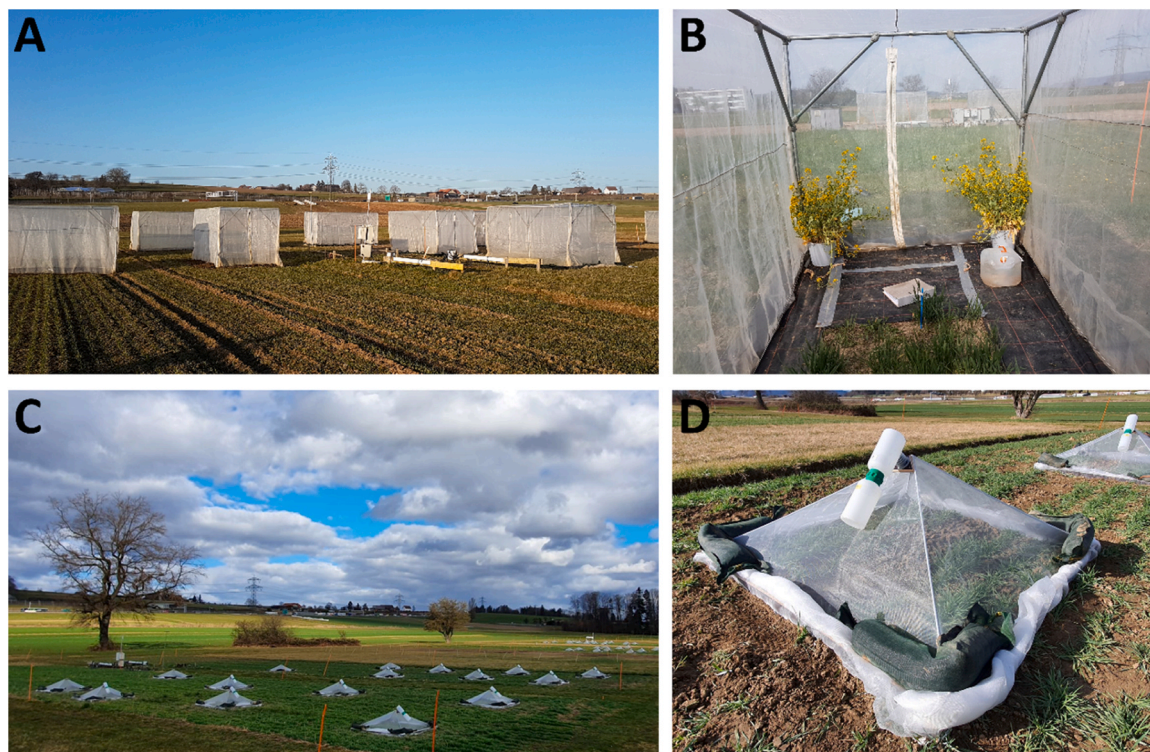


Fig. 4. Semi-field experiments to quantify the effects of tillage (conventional tillage versus no-till) on the survival of ground-nesting bee offspring using two different approaches. A-B) Experiment with translocated adult bees in flight cages. C-D) Experiment with translocated brood cells and emergence traps. See Supplementary Information Section 4 & 5 for details.

4.2.2. Translocation of offspring – a promising alternative approach

Semi-field experiments using adult ground-nesting bees collected from the wild and translocated into flight cages are costly and both labor- and time-intensive, especially when using a non-flowering crop that requires regular provision of floral resources. In addition, such experiments do not allow control of several factors that may have a significant impact on the number of emerged individuals and emergence time, such as the number of brood cells per nest and the depth at which brood cells are located. Without knowing the number of brood cells, survival rates cannot be accurately quantified. In addition, the number of brood cells per nest and brood cell depth may vary between (tillage) treatments because of tillage-related effects on soil properties (see [Section 3.2.2](#)).

Alternatively, instead of translocating adult bees into flight cages, brood cells from natural nest sites could be collected and transferred to an experimental site at which emerging bees can be quantified, e.g., through emergence traps, allowing better control of the factors mentioned above. Such an approach is also less costly (e.g., requiring only relatively small emergence traps rather than large flight cages), less laborious (requiring almost no maintenance after the initial experimental set-up), and may allow for a higher number of replicates or levels of experimental treatments of interest. In addition, translocation of brood cells allows to study specific drivers and mechanisms that are hypothesized to play important roles in the ability of ground-nesting bees to survive tillage. For example, half of the brood cells could be placed within the tilled layers, and the other half below tillage depth. This would allow us to address the open question of whether the documented emergence of bee offspring after tillage is ascribed to nesting below the tilled layer or whether offspring within the tilled layer are able to withstand the mechanical soil disturbance caused by tillage.

We designed such an experiment to evaluate the potential of this approach in general, and specifically to quantify effects of moldboard plowing versus no-till, and how these effects are modulated by nesting depth. Due to a lack of experience with such experiments in the scientific literature, we first conducted a pilot experiment (see [Supplementary Information Section 3](#) for details) in which we excavated brood cells of *C. cunicularius* in autumn and then buried them at their nesting aggregation site in large soil columns at depths ranging from 5 to 35 cm filled with the same soil material. The columns were scanned using X-ray computed tomography before and after their expected emergence date. Brood cells were extracted from the 3D reconstructed X-ray images. In addition, the soil columns were covered with a fabric and a trap was placed inside to capture emerging bee offspring. Out of a total of 24 buried brood cells, 12 emerged (50%), some from as deep as 35 cm ([Fig. 3](#)). Thus, the pilot experiment demonstrates the feasibility of such an approach in general and also demonstrates that bees can emerge even in the absence of pre-existing burrow structures (see [Section 3.1.2](#)).

In a next pilot experiment, we translocated *C. cunicularius* brood cells onto an experimental site where we buried them at different depths in experimental plots receiving different tillage treatments and measured the emergence rate using emergence traps ([Fig. 4C-D](#), [Figure S2B](#); see [Supplementary Information Section 5](#) for details). However, only one emerging offspring was captured out of the 144 translocated brood cells (see [Supplementary Information Section 5.3](#) for a discussion on potential reasons for the low emergence rate). We nevertheless believe that such an experimental approach has a great potential if suitable model species and experimental protocols can be established.

4.2.3. Ensuring capture of emerging offspring displaced by tillage using emergence traps

An important aspect to consider when designing field surveys or experiments to compare the effects of different tillage systems on emergence rates is the fact that tillage can displace soil and the bee offspring within it. If these displacements are not adequately accounted for in studies using emergence traps to quantify emergence rates, displaced bees may not emerge in the area covered by the emergence traps,

which would result in substantially underestimated emergence rates for tilled but not no-till treatments. For example, when comparing emergence rates between no-till and conventionally tilled fields and if the soil surface area covered by the traps is too small, then it is unclear whether a potentially lower emergence success in tilled compared to no-till fields is caused by a potential negative effect of tillage on offspring survival, or whether at least some emerging offspring in tilled fields were simply not captured, potentially leading to spurious results and wrong conclusions about the impact of the tillage system. Similarly, when conducting semi-field experiments with flight cages or translocated brood cells, treatment-specific differences in translocation effects must be accounted for, for example, by using sufficiently large emergence traps or by preventing bees from nesting near flight cage edges (e.g., by placing strips of landscape fabric onto the edge area of soils covered by flight cages; see [Ullmann et al., 2016](#)).

Tillage-induced translocation of objects (including bee offspring) in soils can be substantial and depends on several factors, including topography, soil type, soil conditions (e.g., moisture, bulk density, vegetation), tillage equipment, and tractor speed, and tillage direction (reviewed in [Van Oost et al., 2006](#)). To assess the correct spatial position and minimum emergence trap size required to ensure capture of all potentially emerging offspring, displacement vectors are ideally quantified prior to the actual experiment using the same tillage settings (tillage type, tractor speed, etc.) on the same site as planned for the ground-nesting bee experiment. For example, in the year before our flight cage and brood cell translocation experiment, we conducted a pilot experiment to measure the expected displacement of bee brood cells induced by conventional tillage (moldboard plowing followed by rotary harrowing and sowing) by measuring the translocation distance of aluminum tracers of approximately the size (but clearly heavier) of a *C. cunicularius* brood cell on the same site where the experiments were conducted. Translocation distance ranged from $-5-149$ cm (mean \pm SE = 55 ± 4 cm) in throwing direction (i.e., the direction perpendicular to the driving direction), and from $-45-434$ cm (41 ± 11 cm) in driving direction (i.e., the direction along which the tractor was traveling) ([Fig. 2](#), [Figure S1](#); details in [Supplementary Information Section 2](#)). These results were then used to design the dimensions of the emergence traps for the brood cell translocation experiment (see [Section 4.2.2](#)) and to determine the distance from the cage perimeter to exclude nesting activity in the flight cage experiment (see [Section 4.2.1](#)) so that at least 90% of the potentially displaced offspring would still be within the area covered by the emergence trap or flight cage.

4.3. Controlled manipulation experiments with soil columns and X-ray imaging to study tillage effect mechanisms

Disentangling the different mechanisms by which tillage affects ground-nesting bees also requires manipulative experiments under more controlled (albeit also more artificial) conditions than are possible in semi-field experiments. A particularly promising, but so far largely neglected, approach is the use of large soil columns containing bee offspring subjected to different experimental manipulations. Bee offspring could be translocated into the soil columns (as in our pilot experiment; see [Fig. 3](#) and [Supplementary Information Section 3](#)), or soil columns could be taken from naturally occurring ground-nesting bee nests (as done by [Tschanz et al., 2023a](#)). The soil columns can then be scanned by X-ray computed tomography before and after the experimental manipulation to study treatment effects.

Such an experimental procedure could be used to fill knowledge gaps with respect to tillage mechanisms. For example, soil columns could be subjected to soil compaction simulating field traffic to study the effects on bee offspring, brood cell lining, and nest structure, and how these effects are mediated by brood cell depth and soil aspects (e.g., texture, moisture). Other possibilities include: simulating soil inversion to study the effects of vertical displacement of bee offspring and associated exposure to altered soil temperature and moisture regimes; exposing soil

columns to field flooding scenarios to simulate tillage-induced changes in soil structure and associated effects on water drainage; comparing soil columns with intact burrow structures to those where burrow structures are artificially destroyed to determine effects on emergence success and timing, and body condition (energy storage). Such experiments could also be used to answer more fundamental questions about the behavior and ecology of ground-nesting bees that are potentially relevant to their resilience to disturbances such as soil management practices. In particular, nest depth is likely to play a critical role for the ability of ground-nesting bees to resist such disturbances (Harmon-Threatt, 2020), and understanding potential factors influencing brood cell depth (e.g., texture, soil moisture, climate) may allow to identify areas where ground-nesting bees may be more tolerant or particularly vulnerable to disturbances.

5. Conclusions

Our literature review reveals that there are very few studies on the consequences of tillage on ground-nesting bees and that we largely lack a quantitative understanding of the underlying mechanisms of tillage impacts. This is in part because most studies are associative, relating combined tillage system effects to indirectly estimated local bee abundance (e.g., local abundance of foraging bees), rather than quantifying nest density or reproductive success of ground-nesting bees. Furthermore, our synthesis shows that most of our knowledge of tillage effects on ground-nesting bees is based on a single crop–pollinator system (i.e., *X. pruinosa* in cucurbit fields). Thus, whether tilled arable soils act as ecological traps rather than suitable nesting habitats remains unclear. We highlight the need for novel research approaches to improve our understanding of the nesting habitat potential of arable soils and the underlying mechanisms that explain the impacts of tillage. In particular, we propose methods that directly quantify nest density and capture the entire nesting community to evaluate the nesting habitat potential of arable soils under different agricultural management practices. We suggest different (semi-)field and laboratory experimental approaches allowing to quantify the effects of tillage on ground-nesting bees and to disentangle key mechanisms driving such effects. Considering the increasing adoption of conservation agriculture practices and the fact that very large portions of the terrestrial surface are covered by arable land, future research efforts are warranted to quantify the potential of arable land as nesting habitat for ground-nesting bees, and to identify key soil and crop management factors associated with increased diversity and abundance of these bees. Such knowledge will help to provide evidence-based recommendations for agricultural land management policies to conserve and promote ground-nesting bees in agroecosystems and to harness their important contributions to crop pollination and soil health.

CRediT authorship contribution statement

Philippe Tschanz: Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Achim Walter:** Writing – review & editing, Supervision. **Thomas Keller:** Writing – review & editing, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization. **Matthias Albrecht:** Writing – review & editing, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization.

Declaration of Competing Interest

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

Data Availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.agee.2024.109224](https://doi.org/10.1016/j.agee.2024.109224).

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