




## OPINION PAPER

## Beyond pollination – The neglected contribution of ground-nesting bees to soil functions

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## ARTICLE INFO

## Keywords:

Soil functions  
Ecosystem services  
Bioturbation  
Wild bees  
Soil engineers  
Biopores  
Soil erosion  
Infiltration  
Aeration  
Melittosphere

## ABSTRACT

While the pollination services provided by wild bees are now well recognized, their importance as soil ecosystem engineers has been largely overlooked, despite the fact that most species nest in the soil in self-excavated burrows. Here we provide an overview of the many direct and indirect effects of ground-nesting wild bees on the physical, chemical and biological properties of soil, soil functions, and ecosystem services. In particular, we discuss how ground-nesting bees move and mix substantial amounts of soil during nest construction, thereby altering soil physical properties (e.g., soil pore architecture, soil porosity, density) and soil functions (e.g., water and gas exchange), and act as geomorphic agents at larger scales (affecting, e.g., surface runoff and soil erosion). We also review how ground-nesting bees affect soil chemical and biological properties through their nesting activity, leading to the redistribution and accumulation of organic carbon and nutrients in the soil, providing hotspots for microbial activity, and introducing a range of organisms into the soil. Furthermore, we discuss the large-scale indirect effects on soils through their pollination functions, which shape plant communities and soil functions modulated by plants. Lastly, we highlight the role of ground-nesting bees as soil ecosystem engineers that complement the activity of other bioturbators in both space and time by occupying biogeographical niches where other bioturbators are largely absent, and by complementary activity peaks during the season. We emphasize the distinctive position of ground-nesting bees among soil fauna, acting as both pollinators and soil bioturbators, and conclude that ground-nesting bees deserve greater attention and recognition in future research and conservation policy as part of soil biodiversity and for their role as soil ecosystem engineers.

## Introduction

Animal pollination is critical for the functioning of natural and managed ecosystems. Approximately 88 % of all flowering plant species (Ollerton et al., 2011) and three-quarters of the world's food crops (Klein et al., 2017) depend on or benefit from animal-mediated pollen transfer. Animal pollination accounts for 5–8 % of global crop production (Aizen et al., 2009), corresponding to an annual market value of US \$235–577 billion in 2015 (IPBES, 2016; Lautenbach et al., 2012). Additionally, pollinator-dependent crops play a particularly important role in global micronutrient supply and thus human health (Chaplin-Kramer et al., 2014). In most ecosystems, bees – both managed and wild – are the most important pollinators (Garibaldi et al., 2013; IPBES, 2016; Michener, 2007). Wild bees contribute about half of the

global economic value of crop pollination (Kleijn et al., 2015).

While the pollination services provided by wild bees are now well recognized, the ecosystem services they provide beyond pollination are undervalued (Christmann, 2019, 2022). The vast majority of wild bees are ground-nesting species, i.e., they nest below ground in self-excavated burrows (Cane & Neff, 2011; Danforth et al., 2019; Harmon-Threatt, 2020; Michener, 2007), thereby significantly influencing soil structure and functioning. Most ground-nesting bee species create vertical macropores similar to those formed by anecic earthworms that can persist for many months (Danforth et al., 2019; Tschanz et al., 2023), thereby improving water flow and gas transport in soil. Ground-nesting bees can move soil to the surface at higher rates (Cane, 2003; Watanabe, 1998) than many other soil-dwelling organisms recognized as soil ecosystem engineers (Bétard, 2021; Paton et al., 1995;

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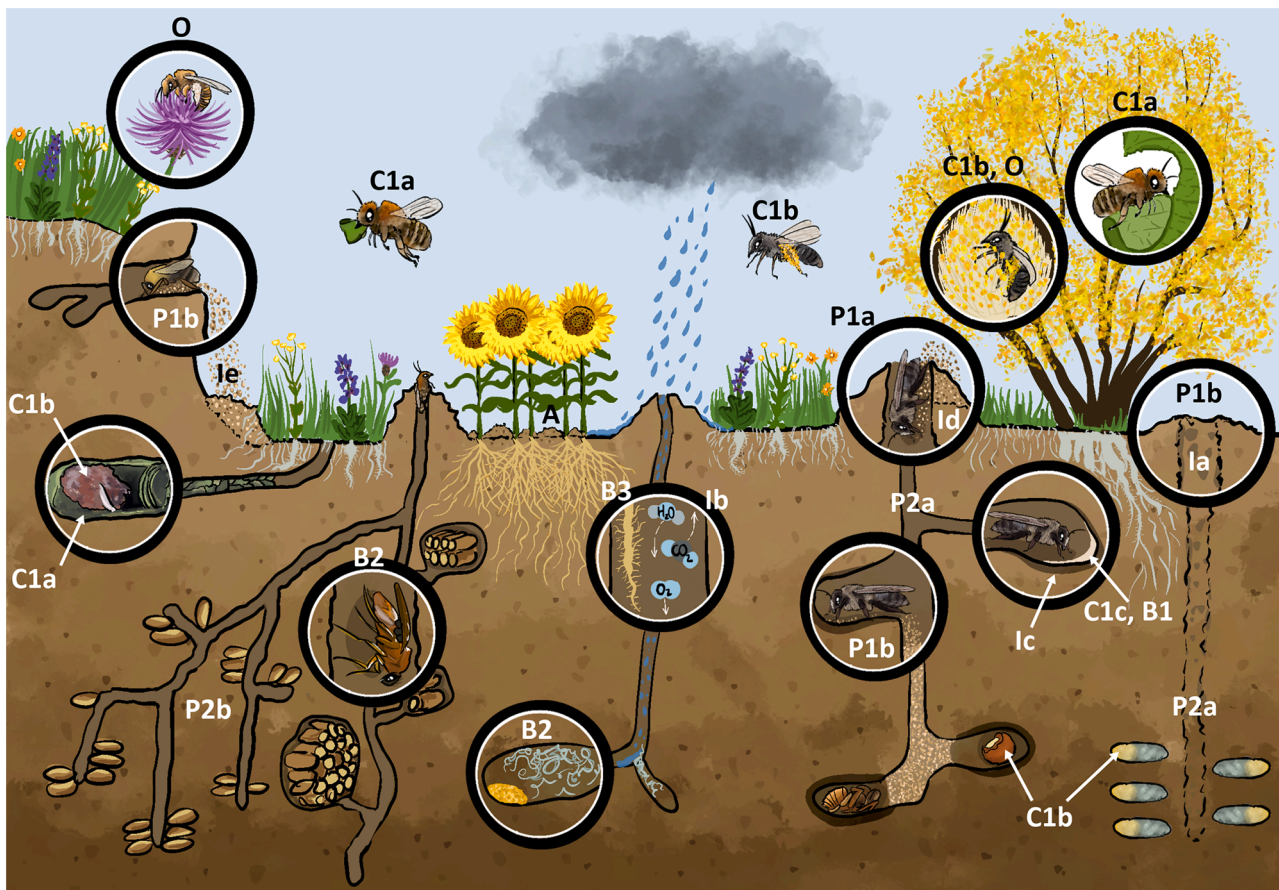
Wilkinson et al., 2009). Moreover, through their pollination functions, bees shape local communities of pollinator-dependent plants, which play a fundamental role in providing soil ecosystem services (Christmann, 2019). It is therefore surprising that ground-nesting bees have been largely overlooked in reviews of the impact of soil fauna on soil ecosystem services (e.g., Bottinelli et al., 2015; Gabet et al., 2003; Lavelle et al., 1997, 2006; Prather et al., 2013; Wilkinson et al., 2009), though some authors mention them briefly (e.g., Butler, 1995; Hole, 1981; Paton et al., 1995). Moreover, despite most ground-nesting bee species spend the vast majority of their lives in the soil (Danforth et al., 2019; Harmon-Threatt, 2020), ground-nesting bees are rarely considered as part of soil biodiversity and are not included in relevant soil biodiversity policies (e.g., FAO et al., 2020). As a consequence, bee conservation policies have primarily targeted the life history stages and requirements of bees outside the soil (e.g., floral resource needs) rather than those during their life stages in the soil (Christmann, 2022; Orgiazzi, 2022). Therefore, the importance of ground-nesting bees and the consequences of their decline for ecosystem services beyond pollination are greatly underestimated (Christmann, 2019, 2022).

Here, we describe the multiple effects of ground-nesting bees on soil

and define the soil volume directly influenced by ground-nesting bee activity as the 'melittosphere'. We discuss the implications of their activity for soil functions and soil ecosystem services, identify key knowledge gaps, and highlight the role of ground-nesting bees as bioturbators that are spatiotemporally complementary to other soil ecosystem engineers. Our analysis raises awareness of the largely neglected contribution of ground-nesting bees to soil health and highlights the role of ground-nesting bees as soil ecosystem engineers.

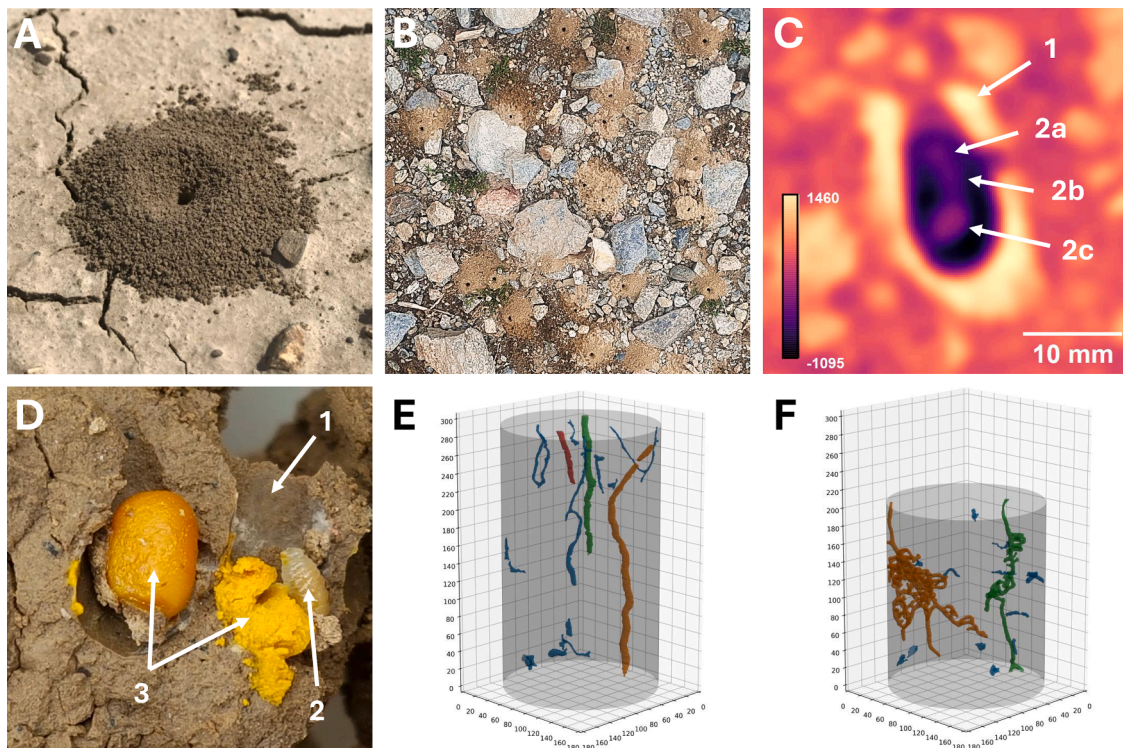
### The melittosphere – How ground-nesting bees affect soils

Ground-nesting bees modify soil physical, chemical, and biological properties, thereby affecting soil functions and ecosystem services (see Fig. 1 for an overview). Ground-nesting bees affect soils directly through their nesting activity, similar to the burrowing activity of earthworms, ants, termites, and other bioturbators. Unlike most other bioturbators, all pollinating bees also affect soils indirectly by providing pollination functions, which shape plant communities and thus soils. While the functional domains, i.e., the volume of soil under the influence of an organism, have been defined for earthworms (drilosphere), ants



**Fig. 1. Schematic illustration of the melittosphere – the volume of soil directly influenced by the activity of ground-nesting bees.** Ground-nesting bees directly affect physical (P), chemical (C) and biological (B) properties of soil, with implications (I) for soil functions, and ecosystem services. Physical effects include: (P1) movement and mixing of soil, e.g., by (P1a) depositing excavated soil material at the surface (mounding) and (P1b) excavation and refilling of burrows; (P2) altering soil pore architecture by excavating (P2a) simple to (P2b) complex burrow systems. These effects have implications for soil functions and properties, e.g., (Ia) soil textural profiles through soil mixing, (Ib) water and gas exchange between soil and the atmosphere, (Ic) local soil density profile through wall compaction, (Id) soil decompaction through soil mounding, and (Ie) soil erosion and soil creep. Chemical effects include: (C1) enhancement of soil organic carbon and nutrients, e.g., by bringing (C1a) leaves for nest construction or (C1b) pollen and nectar as food resources for offspring, or by (C1c) excretion of endogenous biochemical compounds for brood cell lining. Biological effects include: (B1) stimulation of microbial activity through excretions of endogenous substances, (B2) introducing and attracting organisms into the soil, and (B3) providing channels for plant roots. Effects may be particularly high where they nest in dense aggregations (A). Other, indirect effects on soils are provided by (O) bee pollination functions shaping plant communities and soil functions modulated by plants. Note that the drawing is not to scale and does not represent the exact behavior/nest structure of any particular species, but rather integrates aspects of several species for illustrative purposes. Illustration created by Noëlle Klein.





**Fig. 2.** Examples illustrating the effects of ground-nesting bees on soils. A) A mound of excavated soil material (so-called ‘tumulus’) formed by the social sweat bee, *Lasioglossum malachurum*. B) A nesting aggregation of an unidentified *Lasioglossum* species. C) X-ray image of a soil column containing a brood cell, presumably of *Andrena vaga* with an overwintering adult bee, showing (1) compacted soil around brood cell walls; and (2) the bee body (a: head, b: thorax, c: abdomen). Color scale in Hounsfield Unit (i.e., linear scale of radiodensity, where  $-1000$  represents air and  $0$  represents distilled water at standard temperature and pressure). (D) An opened brood cell of *L. malachurum* showing (1) the smoothed brood cell wall; (2) the larvae; and (3) pollen and nectar supply. (E–F) 3D reconstructed X-ray computed tomography images of soil columns containing nests of ground-nesting bees. Shown are the air-filled pores (red, green, and orange) created by (E) the solitary spring-mining bee, *Colletes cunicularius* and (F) the social *L. malachurum*. Grid lines represent 20 mm. Figures E–F adapted from Tschanz et al. (2023).

(myrmecosphere), termites (termitosphere), plant roots (rhizosphere) and others (Brown et al., 2000), an equivalent terminology is lacking for bees. Here, we propose to name the volume of soil directly influenced by the activity of ground-nesting bees the ‘melittosphere’ (from the Greek word μέλιττα, melitta, meaning ‘bee’).

### Physical engineering

Female ground-nesting bees are prolific diggers. They excavate a subterranean burrow system that contains brood cell chambers and food supplies for their offspring (Danforth et al., 2019; Michener, 2007). During this burrow construction process, they move and mix significant amounts of soil in a short period of time, thereby altering the local soil pore network architecture and soil density and texture profiles. Particularly where populations occur in dense aggregations (i.e., groupings of individual nests; Fig. 2B), bee nesting activity can greatly modify soil physical properties and associated soil functions and ecosystem services.

### Soil movement, mixing and alteration of soil texture profiles

Ground-nesting female bees bring larger amounts of soil per unit area to the surface each year than many other mound-building animals (Bétard, 2021; Paton et al., 1995). The few available estimates show that soil excavation by ground-nesting bees nesting together in local aggregations can bring to the surface the equivalent of several tonnes of soil per hectare and year, with reported values of  $5.5 \text{ Mg}$  (*Nomia melanderi*; Cane, 2003) up to  $27 \text{ Mg}$  (*Andrena prostimias*; Watanabe, 1998). These annual bee mounding rates exceed those of many other mound-building animals, including most of the reported rates for ants and termites. Termite mounding rates are typically  $<1 \text{ Mg ha}^{-1} \text{ yr}^{-1}$  and rarely exceed  $5 \text{ Mg ha}^{-1} \text{ yr}^{-1}$  (Bétard, 2021; Lobry de Bruyn & Conacher, 1990; Paton

et al., 1995; Wilkinson et al., 2009). Ant mounding rates are typically in the range of  $1\text{--}5 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ , although mounding rates exceeding  $50 \text{ Mg ha}^{-1} \text{ yr}^{-1}$  have been reported (Bétard, 2021; Paton et al., 1995; Viles et al., 2021; Wilkinson et al., 2009). While bee mounding rates are in a similar range to typical earthworm casting rates in temperate habitats of  $10\text{--}50 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ , earthworms casting rates can exceed  $100 \text{ Mg ha}^{-1} \text{ yr}^{-1}$  in tropical regions (Edwards & Arancon, 2022; Paton et al., 1995; Wilkinson et al., 2009). However, it is remarkable that the reported annual bee mounding rates were achieved within just a few days during the brief nest excavation period of the univoltine species (Cane, 2003; Watanabe, 1998), whereas mounding by, e.g., earthworms and ants, occurs over most of the year (e.g., Humphreys, 1981; Roy, 1957). Thus, the daily mounding rate of a dense ground-nesting bee aggregation during the nest-building period may even exceed the daily mounding rates of earthworm populations in productive habitats. Furthermore, annual mounding rates for nesting aggregations of multivoltine bee species may even exceed those of univoltine species.

By bringing soil material from deeper soil horizons to the soil surface (Fig. 2A), but also by refilling parts of their burrow system with excavated soil material, as reported for some bee species (e.g., Batra, 1964, 1968), ground-nesting bees mix soil material from different soil depths and thereby alter local soil textural profiles (Paton et al., 1995). While we are not aware of quantitative estimates of soil mixing rates or measurements of soil texture changes by ground-nesting bees, their effects on soil texture are evident from their soil mounds (so-called tumuli), which sometimes look conspicuously different in color and particle size from the soil surface (Danforth et al., 2019). In addition, erosion of bee tumuli may change soil texture by leaving larger particles behind while fine material is carried away by wind or water, as suggested for the soil mounds created by other species (Cammeraat & Risch, 2008; Reichman

& Seabloom, 2002). Unlike other bioturbators, however, ground-nesting bees appear to change soil texture rather inadvertently. The digestion and regurgitation of soil (e.g., earthworms, some termites) or the transport of soil particles with the mandibles (e.g., termites, ants) has been shown to result in the preferential movement of soil particles of certain size ranges in earthworms, ants, and termites, which can lead to the formation of entire soil horizons of specific particle sizes (Cammeraat & Risch, 2008; Hole, 1981; Paton et al., 1995). In contrast, soil excavation by bees is unlikely to result in particle size-dependent sorting of soil, because bees generally use their legs and body parts (head, thorax, abdomen) to push loose soil out of nests to the soil surface (e.g., Batra, 1968; Martins & Antonini, 1994).

#### Soil pore architecture, porosity, and soil density

Ground-nesting bees alter the local pore network architecture through their burrowing activity for nest construction, leaving behind a fascinatingly high diversity of pore network architectures (Fig. 2E–F). They create pores ranging from 2 to 10 mm in diameter (Rozen, 2016; Sarzetti et al., 2013; Westrich, 2018). Pores created by nesting bees can be several meters deep (up to 530 cm; Cane & Neff, 2011; Danforth et al., 2019), although the depth at which most ground-nesting bee species typically construct brood cells ranges from about 10 cm (upper median) to about 20 cm (lower median) (Cane & Neff, 2011; Harmon-Threatt, 2020). The architecture of bee burrows varies widely among species (Malyshev, 1936; Sakagami & Michener, 1962; Stephen et al., 1969). Nests of solitary species (which make up about 77 % of wild bee species; Danforth et al., 2019) typically consist of a main vertical burrow with lateral branches leading to brood cells (Antoine & Forrest, 2021; Danforth et al., 2019; Ullmann et al., 2020), resembling vertical burrows made by anecic earthworm species (Edwards & Arancon, 2022; Lee & Foster, 1991) (Fig. 2E). However, some species excavate only a main vertical burrow with no lateral branches ending directly in a single brood cell chamber (e.g., *Perdita maculigera*; Michener & Ordway, 1963), while others, especially social bee species, form an intricate network of branching horizontal and vertical burrows, sometimes with brood cells clustered in chamber-like structures (e.g., *Lasioglossum malachurum*; Sakagami & Michener, 1962) (Fig. 2F).

The lifespan of these burrow networks can be highly variable. Solitary species typically do not maintain their nests once the brood cells have been provided with food and oviposition, whereas social species can engage in nest-building for multiple generations over several months, gradually expanding their burrow network (e.g., Tschanz et al., 2023). Also, while some species leave their main burrow largely open (e.g., *Colletes cunicularius*; Malyshev, 1927), others refill their burrow system with soil material (e.g., *Lasioglossum versatum*; Batra, 1968) or form a solid soil plug to close the nest entrance at the soil surface (e.g., *Diadasia rinconis*; Neff & Simpson, 1992) after nests construction. However, even when burrows are no longer maintained after nest completion, burrows can persist largely intact for many months (Tschanz et al., 2023). Many ground-nesting bees coat burrow walls with a hydrophobic film of glandular secretions (e.g., Cane, 1981; Lybrand et al., 2020), or they compact walls by tamping excavated soil material into burrows walls (e.g., *Nomia melanderi*; Batra, 1970), which likely increases the stability of bee burrows. Biopores created by ants and earthworms have been shown to be more stable than pores formed by abiotic processes (Cheik et al., 2021; Pelíšek, 2018), and this increased stability is thought to be partly related to organic substances secreted by the organisms (e.g., plant root mucilage and earthworm mucus) (Czarnes et al., 2000, 2000; Gray & Lissmann, 1938; Leue et al., 2015) and wall compaction (Cheik et al., 2021; Ruiz et al., 2017). Hence, it can be expected that bee burrows will be more stable than abiotically formed soil pores.

By relocating soil material, the burrowing and soil mounding activity of ground-nesting bees alters the local bulk density profile (Fig. 2C) and can also change the overall porosity and bulk density of the soil. Ground-nesting bees generally act as soil ‘decompactors’ (Keller et al., 2021), i.

e., they reduce the average soil bulk density by depositing excavated soil material on the soil surface (Danforth et al., 2019; Westrich, 2018) (Fig. 2A), thereby increasing the total soil pore volume. The magnitude of the decompaction effect varies between species, e.g., due to differences in excavated burrow volume or the extent to which the nest is refilled after completion (e.g., Batra, 1968) or excavated soil material is tamped into burrow walls rather than disposed at the surface (e.g., Batra, 1970). Unlike some earthworm species, which can also reduce overall soil porosity and increase soil compaction by accumulating compact aggregates (Blanchart et al., 1999; Lavelle et al., 2004), such consequences are generally not expected for bees, apart from minimal local compaction effects along burrow walls or within brood cells (Fig. 2C), leading to the formation of biopores with compacted walls similar to those shown in earthworms (e.g., Rogasik et al., 2014). Because some ground-nesting bees nest within crop fields and sometimes form dense aggregations (Tschanz et al., 2024; Ullmann et al., 2020), ground-nesting bees could play a role in the decompaction of agricultural fields. Decompaction through biotic activity could be particularly relevant in continuous no-till fields that often suffer from compacted topsoil (e.g., Nunes et al., 2015), but the contribution of ground-nesting bees to soil recovery remains to be quantified.

#### Water and gas exchange between soil and atmosphere

Macropores formed by ground-nesting bees are likely to have significant effects on water and gas transport between the soil and the atmosphere. To our knowledge, these effects have not yet been quantified, but Colloff et al. (2010) found that invertebrate macropore density enhanced soil infiltration rates. While the contribution of each invertebrate taxonomic group was not quantified, ground-nesting bees nested at high densities (>50 holes m<sup>-2</sup>) in some of the measured sites and were likely a major contributor to the increased infiltration rate.

The typical vertical and continuous main burrows created by most ground-nesting bee species (Antoine & Forrest, 2021; Danforth et al., 2019) (Fig. 2E) connect the soil surface to the subsoil, similar to burrows created by anecic earthworms (Edwards & Arancon, 2022; Lee & Foster, 1991). Such macropores are particularly efficient at enhancing water infiltration and soil aeration (extending oxic conditions deeper into the soil) by creating preferential pathways for water and gas flow (Jarvis, 2007; Lee & Foster, 1991; Ruiz et al., 2023; Stepniowski et al., 1994). However, the effects of bee nesting activity on gas and water dynamics, as well as their duration, may be highly variable between species due to species-specific differences related to life history traits (sociality, voltinism), burrowing behavior, and nest architecture (cf. Fig. 2E and Fig. 2F). For example, hydraulic conductivity in earthworm burrows is influenced by earthworm behavior, such as burrow refilling behavior (Capowiez et al., 2014), and by burrow morphological characteristics, such as their length, surface area, diameter, inter-connectivity, tortuosity, and branching rate (Blouin et al., 2013; Bouché & Al-Addan, 1997). Thus, while the nesting activity of ground-nesting bees is likely to have generally positive effects on soil water and gas exchange dynamics, these effects may vary considerably among species.

#### Geomorphic effects at the landscape scale

Ground-nesting bees act as geomorphic agents through their nesting activity, with effects that extend far beyond the immediate vicinity of their nests. Similar to earthworms, ants, and termites, bees have both direct and indirect effects on geomorphology: directly through the formation of soil mounds that create micro-landforms, and indirectly through their effects on soil processes such as infiltration, surface runoff, soil erosion, and soil creep (Bétard, 2021; Butler, 1995).

The soil mounds formed by many ground-nesting bee species are mostly loose accumulations of excavated soil material (Danforth et al., 2019) (Fig. 2A). These are easily eroded by wind and rain (e.g., Cane, 2003; Watanabe, 1998), similar to the ephemeral mounds (type-I sensu Humphreys & Mitchell, 1983) formed by earthworms (casts) and some ant species (Bétard, 2021). Soil loss from eroded bee mounds may be



particularly high in sparsely vegetated areas, as shown for ants (Cerdà et al., 2009; Li et al., 2019), or on sloping terrain, and may contribute to soil creep, as known for earthworms (Nooren et al., 1995). On the other hand, biopores formed by ground-nesting bees likely increase water infiltration rates, which reduce surface runoff, and thus soil erosion rates, similar to the macropores created by earthworms, ants, termites, and other soil-dwelling species (Edwards & Arancon, 2022; Jouquet et al., 2014; Viles et al., 2021). In addition, some ground-nesting bee species build more stable mounds by lining/cementing parts of their mounds to form turrets (Antoine & Forrest, 2021; Danforth et al., 2019). Although still relatively ephemeral compared to the highly persistent mounds (type-II sensu Humphreys & Mitchell, 1983) produced by some ants and termites (termitaria) (Bétard, 2021; Paton et al., 1995; Wilkinson et al., 2009), these reinforced bee mounds may help slow down surface runoff and soil erosion by increasing surface roughness (Lavelle, 1997). Ultimately, whether ground-nesting bees are net mitigators or contributors to soil erosion is not clear and may depend on several factors, including species-specific behaviors (e.g., biopore refilling/closing and soil mounding behavior) and environmental conditions, as has been shown for ants (Cerdà & Jurgensen, 2011; Viles et al., 2021).

### Chemical engineering

To build their nests, ground-nesting bees move and mix the soil, and enrich it with various endogenous and exogenous biochemical compounds, thereby redistributing and accumulating organic carbon and nutrients in the soil. Most ground-nesting bees line their brood cells (and some also line the burrow walls) with exocrine gland secretions containing a wide range of biochemical compounds (Albans et al., 1980; Cane, 1991; Fellendorf et al., 2004; Lybrand et al., 2020). Some ground-nesting bees also incorporate external organic and inorganic substances into their nests, such as collected plant materials (including leaves, flower petals, leaf trichomes, resins, floral oils) and abiotic elements (mud, stones, or soil) (Danforth et al., 2019; Michener, 2007). After nest construction, ground-nesting bees introduce primarily pollen and nectar (Fig. 2D), and sometimes floral oils, into the soil as food resources for their offspring (Danforth et al., 2019; Michener, 2007). These food supplies are often only partially consumed or remain unconsumed, e.g., due to larval mortality (Danforth et al., 2019), thereby contributing to the spatial redistribution of substantial amounts of organic carbon and nutrients from above-ground vegetation into the soil across potentially large distances (up to >1 km; Gathmann & Tschardt, 2002; Greenleaf et al., 2007; Zurbuchen et al., 2010). Finally, organic matter and nutrients can also be incorporated into the soil via adult bee mortality and feces. To our knowledge, these contributions of ground-nesting bees to soil biochemical properties and cycling have not been quantified, although they could be substantial in dense nesting aggregations with far-reaching implications given the key role of soil organic matter in soil health. Soil organic matter plays an important role in maintaining and enhancing soil physical (e.g., water retention, soil structure, aggregate stability), chemical (e.g., soil fertility, nutrient release), and biological (e.g., soil microbial populations, soil enzymes) properties, with beneficial consequences for the various functions and services provided by soils, including crop productivity, erosion control, and climate resilience (reviewed in Bashir et al., 2021; Blouin et al., 2013; Lavelle et al., 1997).

### Biological engineering

Nesting and foraging activities of ground-nesting bees can also affect other soil organisms and plants (i.e., biological engineering: Lavelle et al., 2006), with potentially substantial consequences for soil functions and ecosystem services locally, but also over larger spatial scales within their foraging ranges. By moving significant amounts of soil during their extensive burrowing activity, soil invertebrates can help microorganisms to reach new substrates (Lavelle et al., 1997). Endogenous

substances excreted by ground-nesting bees may stimulate microbial activity, similar to root exudates, earthworm mucus, and termite saliva (Lavelle et al., 2006). This can lead to local hotspots of microbial activity where microbes may release substances that can have beneficial or detrimental effects on other organisms (Lavelle et al., 2006).

Ground-nesting bees introduce a range of organisms into the soil through various routes (reviewed in Danforth et al., 2019). For example, viruses, bacteria, and fungi enter the brood cell chambers through pollen and nectar, nematodes through the reproductive tract and glandular secretions, and mites by hitchhiking on the bee's body. Because of the remarkable diversity of (sometimes interacting) organisms found in brood cells of ground-nesting bees, they have been referred to as 'microcosms' or miniature ecosystems (Biani et al., 2009; Danforth et al., 2019). However, research to date has largely focused on the impact of these organisms on bee health, but little is known about the consequences for soil processes.

Plants benefit from the burrowing activity of ground-nesting bees. Biopores, including bee burrows, can serve as paths of least mechanical resistance for plant roots, allowing them to access nutrient and water resources in deeper soil layers, improving plant growth and productivity (Colombi et al., 2017; Wendel et al., 2022). Perhaps even more important, however, are the effects on plants through the pollination functions of all pollinating bee species, with large-scale consequences for soils (Christmann, 2019, 2022). Plants play a crucial role in providing soil functions and ecosystem services (Faucon et al., 2017), such as stabilizing soils and reducing soil erosion (Gyssels et al., 2005), enhancing nutrient availability and soil fertility (Dotaniya & Meena, 2015), carbon sequestration (Kumar et al., 2006), and maintaining soil structure with implications for soil water retention and aeration (Bronick & Lal, 2005). Thus, by shaping plant communities within their foraging range through their pollination functions, bees have profound indirect effects on soils (Christmann, 2019, 2022).

### Ground-nesting bees complement the bioturbation activity of earthworms both spatially and temporally

In this section, we highlight how bees complement the activity of other bioturbators in both space and time by occupying biogeographical niches where other bioturbators are largely absent, and by complementary activity peaks during the season. Because earthworms are the dominant bioturbators in most climatic regions (Paton et al., 1995), the focus is primarily on comparing activity patterns of bees with those of earthworms, but other faunal groups (especially ants, termites, and small burrowing mammals) can be more important bioturbators than earthworms in some environments (Paton et al., 1995).

#### *Spatial complementarity – from global biogeographic patterns to local habitat preferences*

Although the tropics are known as biodiversity hotspots (Hillebrand, 2004; Rosenzweig, 1995) and are particularly rich in insect species (Stork, 2018), including ants (Economo et al., 2018; Kass et al., 2022), termites (Eggleton, 2000; Eggleton et al., 1994), and pollinators (Ollerton, 2017), this is not the case with bees and earthworms. Bee species diversity follows a bimodal latitudinal distribution, peaking at mid-latitudes, particularly in the Northern Hemisphere (~30°–40°) and to a lesser extent in the Southern Hemisphere (~30°), with lower species diversity in the tropics (Bystrakova et al., 2018; Danforth et al., 2019; Michener, 1979, 2007; Ollerton, 2017; Ollerton et al., 2006; Orr et al., 2021). This distribution pattern is even more pronounced for solitary and ground-nesting bee species, which are underrepresented in the tropics compared to other groups of bees (Cheng & Ashton, 2021; Danforth et al., 2019; Michener, 1979, 2007). Similar to bees, earthworm diversity peaks at mid-latitudes in the Northern Hemisphere (~35°–45°), but unlike bees, a less pronounced secondary peak occurs in the tropics (Phillips et al., 2019; Ruiz et al., 2021). The relative

abundance of earthworm functional groups changes along a thermo-latitudinal gradient, shifting from detritivorous (epigeic in the northernmost latitudes to anecic in temperate regions) to soil-feeding endogeic earthworms in the tropics (Lavelle, 1983; Lavelle et al., 1997). Thus, in terms of latitudinal patterns of species diversity, the functional groups most relevant for the formation of vertical biopores, i. e., solitary ground-nesting bees and anecic earthworms, complement the tropical peaks of ant and termite diversity and share the mid-latitude peak, particularly in the Northern Hemisphere.

However, while earthworms and bees share their biogeographic distribution peaks in the temperate zone, they have largely opposite preferences for temperature and soil moisture conditions, leading to significant spatial niche differentiation. In general, bees prefer warmer and drier soil conditions (Antoine & Forrest, 2021; Danforth et al., 2019), and thus, hotspots of bee species diversity occur in warm and dry climates (Danforth et al., 2019; Michener, 1979, 2007; Orr et al., 2021). In contrast, earthworms require adequate soil moisture levels and generally prefer wetter and cooler soil conditions (Edwards & Arancon, 2022; Ruiz et al., 2023). These contrasting preferences result in partially complementary geographic distribution patterns within the mid-latitude peaks of the Northern Hemisphere. For example, bee species richness is particularly high in the arid region of southern Europe (Orr et al., 2021), whereas earthworm species diversity and abundance are particularly high in northern Europe (Phillips et al., 2019). In North America, earthworm species diversity and abundance are generally rather low and concentrated in the humid northeastern United States (Phillips et al., 2019), while North America, especially the arid southwestern United States, is a major hotspot for bee species diversity (Orr et al., 2021).

In conclusion, ground-nesting bees partially occupy regions and habitats around the world, particularly in water-limited environments, where their burrowing and soil mounding activity complements the reduced earthworm activity. In these environments, the effects of ground-nesting bees on soils, together with other soil-dwelling insects (Bétard, 2021), may play an important and underappreciated role in providing soil functions and services.

#### *Temporal complementary – how bees fill in periods of low earthworm activity*

Even where ground-nesting bees coexist with other soil bioturbators, their burrowing and mounding activity may be temporally complementary to that of other coexisting bioturbators. For example, bees and earthworms have largely opposite preferences for temperature and soil moisture conditions (Antoine & Forrest, 2021; Danforth et al., 2019; Edwards & Arancon, 2022; Ruiz et al., 2023), resulting in seasonally complementary mounding and casting activity patterns similar to the seasonally complementary casting and mounding activity patterns of ants and earthworms (Humphreys, 1981).

Adequate soil moisture is critical for earthworm activity because their thin skin offers little protection against fluctuating soil conditions (Edwards & Arancon, 2022), and dry soils can become too hard for earthworms to penetrate (Ruiz et al., 2023; Ruiz & Or, 2018). Earthworm casting and mounding activity is generally characterized by a maximum during cool and wet seasons (Edwards & Arancon, 2022). During periods of adverse soil conditions, particularly during the hot and dry summer months in temperate climates, earthworm bioturbation and soil mounding activity is reduced or even absent due to diapause (Edwards & Arancon, 2022). In contrast, bees, like all arthropods, possess an exoskeleton with a hard outer layer (cuticle) covered by a waxy layer composed of hydrophobic lipids that help them limit water loss and prevent desiccation (Blomquist & Bagnères, 2010). Bee activity in temperate climates, similar to that of other insects (e.g., Shi et al., 2021; van Dijk et al., 2024), is concentrated around the warmer months from early spring to late fall, including the hot and dry summer months, when floral food resources are abundant and air temperatures are high

enough for bees to fly (Danforth et al., 2019; Westrich, 2018; Willmer & Stone, 2004). Some bees actively moisten and soften the soil under dry conditions by regurgitating liquids from their crop (collected water or nectar) or by salivating (Malyshev, 1936; Rau, 1929; Rozen et al., 2019; Rust, 1980). This behavioral capacity to actively modify soil conditions may extend the soil hydromechanical limits under which bees can burrow compared to other soil-dwelling insects that use a similar excavation process (e.g., ants and termites; Espinoza & Santamarina, 2010; Ruiz et al., 2023) or bioturbators that burrow through the soil using a penetration-cavity expansion process (e.g., earthworms; Ruiz et al., 2017) (Ruiz et al., 2023).

In conclusion, ground-nesting bees in temperate climates complement earthworm biopore formation and soil mounding activity during periods of hot, dry weather when soils can become dry and hard. During such periods, ground-nesting bees, along with other soil-dwelling insects (Bétard, 2021), may make a particularly relevant contribution to improving soil functions and soil-related ecosystem services.

#### **Conclusions and perspectives**

We highlight how ground-nesting bees contribute to soil functions and ecosystem services through their manifold direct and indirect influences on the physical, chemical, and biological properties of soils that extend well beyond the immediate vicinity of their nesting sites. Ground-nesting bees not only enhance the bioturbation and soil mounding activity of other soil organisms with which they co-occur, but also complement them in space and time due to specific aspects of their biology and ecology, allowing them to occupy distinct spatio-temporal niches. Ground-nesting bees have not traditionally been considered as soil ecosystem engineers or regarded as part of soil biodiversity, and their role in supporting soil functions has been largely neglected. Consequently, we have very little quantitative data on the impacts of ground-nesting bees on soil functions and ecosystem services. As a further consequence, bees are currently not considered in relevant soil biodiversity conservation policies, nor are the protection and conservation needs of ground-nesting bees during their life stage in the soil adequately integrated into bee pollinator conservation policies.

We call for more attention of the role of ground-nesting bees as soil ecosystem engineers, and a better recognition of the protection needs of ground-nesting bees as part of soil biodiversity in national and global policies and management action plans. Future research could focus on quantifying the effects of ground-nesting bees on soils across a range of natural and human-modified habitats, and comparing them to those of other coexisting bioturbators. This will help to identify the spatio-temporal niches in which ground-nesting bees play a particularly dominant role in shaping soil functions and services, and to determine the potential consequences of the ongoing pollinator decline beyond pollination functions.

#### **CRedit authorship contribution statement**

**Philippe Tschanz:** Conceptualization, Writing – original draft, Visualization, Writing – review & editing. **Matthias Albrecht:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization. **Thomas Keller:** Writing – review & editing, Supervision, Project administration, 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.

#### **Acknowledgements**

We thank Noëlle Klein for creating the illustration shown in Fig. 1.

We also thank two anonymous reviewers for their valuable suggestions that helped improve this article. This study was funded by the Swiss National Science Foundation (SNSF, grant number 185273).

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