Habitat associations of ground-nesting bees, with a focus on soil characteristics

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J'aimerais dédier cette thèse à toutes les abeilles de ce monde,

qui m'émerveillent et m'inspirent chaque jour…

Abstract

Bees are a diverse group of insects responsible for pollinating plants in agricultural and ecological landscapes. Wild bees are impacted by anthropogenic activity and associated habitat loss. Although 75% of bee species nest underground, this nesting strategy has been overlooked. In my thesis, I explored the nesting habitat requirements of ground-nesting bees by studying the relation between bees and edaphic factors. First, I reviewed existing literature about ground-nesting bee nesting characteristics (Chapter 2). I found that certain abiotic factors (e.g., soil texture, temperature, moisture, compaction, slope, and soil surface features), as well as biotic factors (e.g., floral resources, conspecifics, predators), could be key in nest-site selection. I also discuss possible explanations for the choice of these nesting characteristics, particularly edaphic factors. Secondly, in Chapter 3, I assessed relationships between specific soil factors (soil texture, compaction, slope and ground cover) and the wild local ground-nesting bee communities on 35 farms around Ottawa throughout 2018 and 2019. I found that higher percentages of sand and bare ground were linked to increased total ground-nesting bee abundance and species richness, whilst slope and diversity (Simpson's index) were negatively correlated. Furthermore, associations with soil factors were found to be species-specific, especially for associations with sand content, which were either positive, negative, or non-significant. Ground-nesting bee community's composition was influenced by sand content, slope, soil compaction and bare ground in sampled agroecosystems. Finally, in Chapter 4, I experimentally tested nesting preferences of ground-nesting bee species for soil texture. Based on one season of sampling, there was no association between bee abundance or species richness and soil texture. Together, my research sheds light on the influence of soil characteristics on species-specific nesting-habitat associations for ground-nesting bees. Along with floral resources which have received far more

study, nesting habitat is vital for the well-being and persistence of bee populations, and therefore for their conservation.

Résumé

Les abeilles constituent un groupe d'insectes diversifié, responsable de la pollinisation des plantes dans les paysages agricoles et naturels. Les abeilles sauvages sont touchées par l'activité anthropique et la perte d'habitat qui en découle. Bien que 75% des espèces d'abeilles nichent sous terre, cette stratégie de nidification a été négligée. Dans ma thèse, j'ai exploré les exigences de l'habitat de nidification des abeilles terricoles en étudiant la relation entre ces abeilles et des facteurs édaphiques. Tout d'abord, j'ai passé en revue la littérature existante sur les caractéristiques de nidification des abeilles nichant au sol (chapitre 2). J'ai constaté que certains facteurs abiotiques (la température, l'humidité, la texture du sol, la compaction, la pente et les caractéristiques de la surface du sol), ainsi que des facteurs biotiques (par exemple, les ressources florales, les congénères, les prédateurs), pourraient jouer un rôle clé dans le choix du site de nidification. Je discute également des explications pouvant régir le choix envers ces caractéristiques de nidification, en particulier les facteurs édaphiques. Deuxièmement, dans le chapitre 3, j'ai évalué la relation entre certains facteurs pédologiques (texture du sol, compaction, pente et couverture végétale) et les communautés locales d'abeilles sauvages terricoles dans 35 fermes autour d'Ottawa tout au long de 2018 et 2019. J'ai constaté que les pourcentages de sable et de sol nu étaient associés à une augmentation de l'abondance totale des abeilles terricoles et la richesse en espèces, tandis que la pente et la diversité (indice de Simpson) étaient négativement corrélées. En outre, les associations avec les facteurs du sol se sont avérées spécifiques aux espèces, en particulier pour les associations avec la teneur en sable, qui étaient soit positives, soit négatives, soit non significatives. La composition de la communauté d'abeilles nichant au sol a été influencée par la teneur en sable, la pente, la compaction du sol et le sol nu dans les agroécosystèmes échantillonnés. Enfin, dans le chapitre 4, j'ai testé expérimentalement les

préférences de nidification des espèces d'abeilles nichant au sol pour la texture du sol. Avec une saison d’échantillonnage, il n’y avait pas d'association entre l'abondance des abeilles ou la richesse des espèces et la texture du sol. L'ensemble de mes recherches met en lumière l'influence des caractéristiques du sol sur les associations nidification-habitat spécifiques aux espèces d'abeilles terricoles. Avec les ressources florales qui ont été beaucoup plus étudiées, l'habitat de nidification est vital pour le bien-être et la pérennité des populations d'abeilles, et donc pour leur conservation.

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Land Acknowledgement

Ni manàdjiyànànig Màmìwininì Anishinàbeg, ogog kà nàgadawàbandadjig iyo akì eko weshkad. Ako nongom egawìkàd kì mìgiwewàdj.
Ni manàdjiyànànig kakina Anishinàbeg ondaje kaye ogog kakina eniyagizidjig enigokamigàg Kanadàng eji ondàpinangig endàwàdjin Odàwàng.
Ninisidawinawànànig kenawendamòdjig kije kikenindamàwin; weshkinìgidjig kaye kejeyàdizidjig.
Nigijeweninmànànig ogog kà nìgànì sòngideyedjig; weshkad, nongom; kaye àyànikàdj.

"We pay respect to the Algonquin people, who are the traditional guardians of this land. We acknowledge their longstanding relationship with this territory, which remains unceded. We pay respect to all Indigenous people in this region, from all nations across Canada, who call Ottawa home. We acknowledge the traditional knowledge keepers, both young and old. And we honour their courageous leaders: past, present, and future."

With this statement (provided by the University of Ottawa Indigenous Affairs webpage), I would like to acknowledge the inherent sovereignty of the Algonquin Anishinaabe People, on whose territory my sampling sites and university campus were situated. As an ecologist, I am an advocate of species conservation and would like to promote the habitat of all species—human and non-human—on earth.

I believe in the importance of Land Acknowledgement to inform and remind us about the presence and histories of Indigenous people here in Ottawa (Odaawaa) and elsewhere. As international student, I have learned a lot about the history of this country since I got here, five years ago, and I therefore include this statement to be thankful to this land original caretakers.

Statement of Contributions

Chapter 2 of this thesis is adapted from an article published in *Ecological Entomology* (Antoine and Forrest 2021). The pronoun "we" is used within the manuscript to include additional authors—here: Jessica Forrest (JF)—however this chapter was produced by myself. I researched the literature and compiled by myself extensive information from nearly 200 published papers for this review chapter. I wrote the manuscript in collaboration with JF.

Chapter 3 of this thesis is being adapted to be submitted for publication in a peer-reviewed journal. The pronoun "we" is used within this chapter to include additional authors—here: Etienne Normandin (EN) and Jessica Forrest (JF)—but I entirely produced this chapter by myself. I designed the study, conducted field work and lab work, analyzed the data, prepared the figures, and wrote the manuscript by myself. I contacted the 35 farmers involved in the study and got their approval to have land access on their properties. I was helped by several undergraduate students (Genevieve George, Sherry Xiaoyue Wu and Luca Fiorindi) to collect and prepare the bee collection as well as to run soil textural analysis in the lab. I was helped by EN and JF to identify bees to species-level for the most complicated genera (i.e., *Andrena* spp. and *Lasioglossum* spp.), I did the rest of the ground-nesting bee genera identification by myself and asked EN for verification when needed. I had feedback from both JF and EN on the manuscript.

Chapter 4 of this thesis will be adapted for submission as a research article (adding more years of data). I conceived the study: worked in collaboration with the National Capital Commission to get land access, got access to emergence tents for the sampling, collected and analyzed data by myself. I had the help of Emma Gaudreault and lab members to set up the sites (filling the planters with soil) and from undergraduate students (Sarah Knoerr and Lori Fernandez) to sample the bees. I designed this experiment and wrote the manuscript in collaboration with JF.

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Chapter 1: General introduction

1.1. Insect biodiversity and functions, and threats posed to them

Biodiversity, defined as the variety of life on Earth, is essential for maintaining ecosystem functions (Tilman et al. 1996) and providing ecosystem services that benefit humans (Mooney et al. 2005). Insects constitute a major part of this biodiversity, due to their taxonomic and ecological diversity (Wilson 2002, Schowalter 2016), with more than 5.5 million estimated species globally and many more species that have yet to be described (Stork 2018). Among the services provided by insects are the decomposition of organic matter, pest control, food provisioning, and pollination, which are together worth at least $57 billion USD (Losey and Vaughan 2006). Besides their economic value, their interactions with the environment and other living organisms are also key components of ecosystem functioning (Cardoso et al. 2020).

A growing number of scientific papers have raised alerts concerning declines in insect abundance, biomass, and range sizes. These declines vary among taxa and regions (Wagner et al. 2021) but have been reported worldwide in both terrestrial and aquatic habitats (Conrad et al. 2006, Van Dyck et al. 2009, Parmesan et al. 2013, Fox 2013, Dirzo et al. 2014, Hallmann et al. 2017, Leather 2017, Wagner 2020), with terrestrial insects more severely threatened (van Klink et al. 2020). Most threats are caused by human activities (Wagner 2020): The major drivers of insect declines include habitat loss due to agricultural intensification and urbanization, as well as climate change (Sánchez-Bayo and Wyckhuys 2019, Raven and Wagner 2021).

1.2. Insect habitat

Insects are found in all terrestrial, freshwater, and coastal marine habitats worldwide. Even in the harshest terrestrial environments (e.g., deserts, tundra, mountaintops), insects have developed strategies to overcome extreme cold, heat, aridity, and salinity. The abundance and richness of

insect species varies among biomes, reflecting species' preferences for certain environmental factors given their specific requirements (e.g., physiological limits) (Chase and Leibold 2003). Understanding the environmental factors insects favour can help predict their distributions as well as species abundance and richness patterns.

What factors limit animal species distribution was one of the major questions asked by early ecologists (Wallace 1876, Andrewartha and Birch 1954). Generally, species distribution patterns are dependent on biotic (e.g., predators, competitors) (Brown 1984, Robertson 1996, Boulangeat et al. 2012) and abiotic (e.g., temperature, precipitation) variables (Root 1988, Hawkins et al. 2003). Insects have evolved morphological (e.g., colour), physiological (e.g., diapause) and behavioural adaptations that allow them to survive, grow, and reproduce successfully in a given environment. Most insects are ectothermic, meaning that many aspects of their life-histories (e.g., activity levels, metabolic and developmental rate, fecundity, survival) are dependent on ambient temperatures. A number of species have evolved tolerance for either very low (e.g., Arctic and alpine species) or very high temperatures (Lundheim and Zachariassen 1993, Hadley 1994, Chapman 2012). For example, some chironomid (Diptera) larvae can live in hot spring water at temperatures of 49-51ºC (Chapman 2012). Insects may also need to balance their water content to prevent desiccation—a possible risk for many insect species because of their small size and high surface area to volume ratio. Therefore, moisture availability seems to be another key element in determining where insect species may occur (Schowalter 2016). For example, desert *Drosophila* (Diptera), that live on rotting cactus, can survive high temperatures (exceeding 40ºC) and humidity below 10% RH, and demonstrate greater desiccation resistance and have lower metabolic rates than mesic *Drosophila* (Marron et al. 2003). While certain insect species may occupy regions characterized by extreme abiotic conditions, most insects live in variable conditions subject to

seasonal patterns. Although they experience environmental variability, insects can choose habitats that buffer their exposure to environmental changes.

A common strategy among insects is to live in underground burrows, which can provide a moister microclimate and can mitigate heat penetration or loss (Schowalter 2016). For example, termites use air convection through cavities and side tunnels while they construct their nest to optimize temperature and moisture conditions, as well as oxygen levels (Lüscher 1961). Some insects live under the soil surface throughout their whole life, except during foraging activity (e.g., ants, springtails) whereas others only spend a portion of their lives underground, mostly during their immature stages (e.g., cicadas, beetles, flies, some wasps and bees) (Marshall 2007). The amount of time a species spends underground and the life stage at which the insect occurs underground can determine which abiotic conditions are most important with regards to habitat selection.

1.3. Bee diversity and habitat requirements

Bees, with more than 20,000 species described worldwide (Michener 2007), are part of the Hymenoptera order, in the clade Anthophila from the subfamily Apoidea, which they share with apoid wasps (Debevec et al. 2012, Sann et al. 2018). Following the current phylogenetic hypothesis, bees are sisters to a small group of thrips-hunting wasps called Ammoplanina (Sann et al. 2018). However, contrary to their sisters, bees are herbivorous, feeding on pollen and nectar from flowering plants. Bees and plants have co-evolved mutualistic relationships, where these insects harvest floral rewards, while incidentally effecting pollination. About 88% of all angiosperms benefit from animal pollination (Ollerton et al. 2011), mostly provided by bees, which have evolved morphological structures (e.g., branched hairs) and behaviours (e.g., dietary specialisation) well-adapted to the pollination of flowers (Danforth et al. 2019). Bees are pollinators of more than 87 crop types—including fruits, vegetables and seeds (Klein et al. 2007)—

worth billions of dollars annually (Gallai et al. 2009, Breeze et al. 2016, Porto et al. 2020). Despite their immense contributions to both wild ecosystems and the global human food supply (Khalifa et al. 2021), they are threatened by a number of anthropogenic factors (Goulson et al. 2015, Potts et al. 2016) which have led to regional population declines (Potts et al. 2010, Zattara and Aizen 2021). Paradoxically, one of the main threats bees face is linked to agricultural intensification through the use of agrochemicals, land-use changes, and pathogen transmission from domesticated species (Winfree et al. 2009, Goulson et al. 2015, Potts et al. 2016, Brown et al. 2016).

To counteract habitat loss and facilitate wild bee persistence, management practices have been modified or implemented in order to restore habitat resources for bees—e.g., reducing pesticide use (Pecenka et al. 2021), planting hedgerows (Morandin and Kremen 2013), and sowing floral mixes for pollinators (Pywell et al. 2006, Wood et al. 2015, 2017). These conservation measures have proven to be effective in promoting bee populations (Kennedy et al. 2013), especially by providing sufficient floral resources throughout the season (Mandelik et al. 2012, Mallinger et al. 2016, Martins et al. 2018, Timberlake et al. 2019, Guezen and Forrest 2021). While floral resources are often considered in the context of boosting pollinator populations in agroecosystems, nesting resource availability is rarely considered (Winfree 2010, Roulston and Goodell 2011, Harmon-Threatt 2020), even though nesting resources are necessary habitat components in any effort to maintain or restore bee populations.

Bees are holometabolous and exhibit various life-history traits as they have specialised on different plant resources and on different nesting substrates. Wild bees may partition their habitats between their feeding sites, composed of flower patches the adults forage on, and nesting sites where mother bees construct their nests and where their offspring develop, both of which must be available within the home range of the bee (Westrich 1996). Mother bees may need to select habitats that meet

environmental requirements both for themselves and for their offspring. This puts them at risk in this context of habitat loss because they need both available food and suitable nesting sites to thrive (Winfree 2010, Roulston and Goodell 2011).

1.4. Nesting habitat of bees

Wild bees can be divided into three categories according to their nesting behaviour: parasitic, cavity-nesting and ground-nesting. Parasitic bees, also called “cuckoo” or kleptoparasitic bees, encompass species that invade the nests of heterospecific bees. Female kleptoparasitic bees lay their eggs in the nests of their hosts; the parasitic offspring then feeds on the food resources gathered by the host bee, in addition to killing the host offspring. These species are therefore not nest-builders per se, contrary to the other two categories. Above-ground cavity-nesters, as their name suggests, use either pre-existing cavities (e.g., in dead wood, hollow plant stems, old insect nests or snail shells) or cavities that they excavate in wood or pithy stems. These bees tend to use plant materials (leaves, petals, resin, fibers) or mud to partition their nest and separate offspring brood cells (Cane et al. 2007). The last nesting category—ground-nesting—is the most widespread among wild bees, as about three quarters of all species nest underground (Cane and Neff 2011, Harmon-Threatt 2020). It is also believed to be the ancestral trait, as close-relatives to bees (wasps, ants) are also ground-nesters (Danforth et al. 2019).

Ground-nesting bees usually dig a main gallery with lateral tunnels and excavate brood cells either at the end of the main shaft, at the end or on the side of each branch (see *2.3 Ground-nesting bee biology and life-history traits* for more details on the biology of ground-nesting bees, nest construction and examples of subterranean nest architecture). Because most female bees do not provide maternal care to their offspring after egg-laying, nest conditions must be optimal for offspring survival and development. The ground-nesting strategy may buffer their offspring from

adverse environmental conditions as the larvae of many species overwinter underground; however, it can also increase their vulnerability to ground conditions and risks such as fire (Grundel et al. 2010, Williams et al. 2010, Burkle et al. 2019, Galbraith et al. 2019, see review by Cane and Neff 2011) or flooding (Fellendorf et al. 2004). Indeed, juvenile bees are not mobile and therefore rely on the nest-site conditions chosen by their mother. We may then ask: what are the soil conditions preferred by ground-nesting bee for their nest sites? or, what soil characteristics are ground-nesting bees associated with when nesting?

1.5. Thesis outline

Most wild bee species nest underground, and although it is difficult to find and study their nest sites, there is growing interest in them, for pollination and conservation purposes. Understanding the factors that influence the nesting of ground-nesting bees allows us to better understand where ground-nesting bees can be found and what variables limit their distributions. I am particularly interested in the edaphic factors ground-nesting bees could be choosing because they have been overlooked for many years even though they were recognized early on as being important: Charles Michener et al. (1958) said "no one can doubt the importance of edaphic and other environmental factors in determining where bees nest".

The main objectives of my thesis were to (1) review the existing knowledge on the nesting habitat requirements of ground-nesting bees to identify specific soil characteristics these bees could be selecting, (2) quantify and determine the associations of ground-nesting bee abundance, species richness, diversity, and community structure with these potential soil factors, and (3) experimentally test ground-nesting bee preferences for one soil characteristic.

This thesis contains five chapters including this first introductory chapter. Chapter 2 answers the first objective through a literature review of the nest-site characteristics of ground-nesting bees, identifying soil texture, compaction, moisture, temperature, and ground surface features (slope, ground cover, and aspect) as important edaphic factors to look at when studying habitat selection of ground-nesting bees. There are a handful of papers studying the nesting habitat of these bees but a great number of biological notes and specialised articles in the entomological literature, so I had to search extensively to be able to write a comprehensive review encompassing a wide variety of examples. Chapter 3 is an observational study looking at associations between soil texture, compaction, slope, and ground cover and local ground-nesting bee communities, passively sampled on 35 farms around Ottawa, Ontario. I investigated relationships between these soil factors and the total abundance, diversity, and richness of ground-nesting bees, as well as the abundance of the main taxa caught. I used ordination techniques to test the effect of soil variables on the structure of the ground-nesting bee community, while accounting for spatial autocorrelation in the data. In Chapter 4, I designed an original experimental study to test preferences of ground-nesting bees towards one soil characteristic (soil texture) while holding other factors constant. I used a randomized block design testing different soil textures in planters called hereafter "soilboxes" at two sites, enriched with floral resources. Previous studies have established an association between ground-nesting bee nests and a higher sand proportion (Cane 1991). I tested whether this association was generally true among ground-nesting bees in Ottawa and whether preference for sand was, species-specific. In Chapter 5, I discuss the major results and identify areas for future research, concluding on management recommendations to enhance ground-nesting bee populations.

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Chapter 2: Nesting habitat of ground-nesting bees: a review

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2.1. Abstract

About 3/4 of all wild bee species nest in the soil and spend much of their life cycle underground. These insects require suitable environmental conditions for nest construction and for the development and survival of their offspring. However, there is little quantitative information on the nesting habitat requirements and preferences of ground-nesting bees. Moreover, there are almost no data on the effects of nesting conditions on these bees' fitness.

Here, to better understand the factors that influence nest-site selection in ground-nesting bees, we synthesize the literature on the nesting-habitat associations of these important pollinators. We also review techniques that can be used to study the nesting preferences of ground-nesting bees.

Our review reveals enormous variation among bee species in their associations with such nesting-habitat attributes as soil texture, compaction, moisture, temperature, ground surface features, and proximity to conspecifics or floral resources. However, more studies—particularly experimental ones—are needed to segregate the influence of each factor on bees' choices of nesting location, since multiple factors are often correlated. It is also unclear whether nesting-habitat associations vary geographically or seasonally within species, or phylogenetically among ground-nesting bee species, partly because we lack information on nesting habitat for many species.

We argue that studies using established habitat-selection methods are essential to properly identify nesting-habitat preferences of ground-nesting species. Finally, more research on nesting ecology is needed (especially in agroecosystems) to determine how best to support this diverse group of bees and the vital ecosystem service they provide.

2.2. Introduction

Bees (Hymenoptera: Anthophila) are a diverse group of insects with more than 20,000 species described worldwide (Michener 2007). Although bees provide critical pollination services in both agricultural (Klein et al. 2007) and natural ecosystems (Ollerton et al. 2011), they are threatened by a number of anthropogenic disturbances including habitat loss, reductions in floral resources, pesticide use, and spillover of parasites and pathogens from managed bee species (Potts et al. 2016). While virtually all bees share a diet of floral pollen and nectar, bee species exhibit differences in life-history traits and ecological characteristics, including their preferred nesting substrates. Yet many aspects of the nesting habitat requirements of bees remain unknown, and this is particularly true for the ground-nesting species. Better understanding the nesting characteristics of ground-nesting bees can help promote their populations by allowing land-owners and managers to provide or maintain their preferred habitat.

Many insects spend at least a portion of their lives underground (e.g. springtails; larvae or nymphs of root-feeding insects such as cicadas, beetles, and flies; moth and beetle pupae) and may have specific below-ground habitat requirements. A smaller number, including some earwigs, crickets, beetles, termites, wasps and bees, are true ground-nesters, in the sense that they excavate and provide for their young in subterranean burrows (Gullan and Cranston 2010). Underground nesting is common among bees: Cane & Neff (2011) reported that 64% of bee species construct nests beneath the soil surface; Harmon-Threatt (2020) calculates the number to be 83%. The below-ground-nesting condition is believed to be ancestral in bees, as it is shared with the crabronid wasps that are thought to be bees' closest relatives (Debevec et al. 2012, Sann et al. 2018). Females of ground-nesting bees and wasps excavate tunnels leading to brood cells in which they lay eggs on top of a food reserve. Other bee species, and many wasps, do not dig

underground nests, and may be called cavity-nesters. This group includes species that excavate their own nests in wood, as well as those ("renters") that use pre-existing cavities—in wood, pithy stems, stone walls or snail shells (reviewed by Cane *et al.*, 2007; Danforth *et al.*, 2019), or even below-ground, as in many bumble bees (*Bombus* spp.; Apidae). Even though they sometimes nest in underground cavities, we do not consider bumble bees and honey bees to be ground-nesters for the purposes of this review: because they do not dig burrows, their criteria for nest-site selection should differ from those of burrowing bees. Finally, a minority of bee species are parasites of other ground-nesting bees (see *Bee life history*, below); however, we do not consider these species to be ground-nesters themselves.

Although the ground-nesting strategy is observed in every bee family, in solitary and social species, and in every habitat in which bees occur, ground-nesting bees are proportionally far less studied than cavity-nesters (Winfree 2010). The latter can be observed using artificial nesting structures, but nests of ground-nesters are typically difficult to locate, and there are few easy methods for studying within-nest behaviour of these bees (but see Leonard & Harmon-Threatt, 2019). Field and laboratory studies of living ground-nesting bees are scarce relative to the number of species in this group, and there is nesting information for only 26% of the 527 bee species that were studied in a recent review (Harmon-Threatt 2020). This leaves us with serious gaps in our knowledge of the ecology and behaviour of these insects.

We begin with a brief overview of the biology of ground-nesting bees. We then synthesize the existing information on the characteristics of ground-nesting bee nests and the biotic and abiotic factors that influence where these bees choose to nest. For some of these factors, there has been little research on ground-nesters, and we therefore refer to relevant studies on ground-nesting wasps and cavity-nesting bees. By identifying literature gaps and key research questions, and

also highlighting useful methodological tools, we hope to encourage and direct new efforts to understand the ecology of ground-nesting bees. Greater knowledge of bee nesting preferences is required if we are to determine which habitats and soil characteristics require protection or restoration to benefit bee populations.

2.3. Ground-nesting bee biology and life-history traits

2.3.1. Bee life history

Bee life histories can be classified into three major types: solitary, social, and parasitic. More than 75% of described bee species are solitary, with females working alone to build their nest(s) and provide for their offspring (Michener 2007). However, there is a gradient of sociality, from solitary nesting to advanced eusociality, with the limits of each category not clearly defined; furthermore, some species are socially polymorphic (Soucy 2002, Richards et al. 2003). All eusocial species are characterized by overlapping generations and a permanent reproductive division of labour wherein a single female (the queen) produces worker offspring that build and defend the nest, forage for food, and care for the young. Highly eusocial bees, such as honey bees (*Apis* spp.), are not ground-nesters and are not considered here; but many primitively eusocial and socially polymorphic bees belong to the family Halictidae, which is made up primarily of ground-nesters (Danforth *et al.*, 2019). In these species, queens typically establish nests on their own before producing workers. Solitary bees sometimes live in communal nests sharing the same entrance but otherwise behave independently as solitary females, producing offspring in their own brood cells (e.g., *Andrena scotica* Perkins, Andrenidae; Paxton *et al.*, 1999). In temperate climates, queens of primitively eusocial species emerge from the ground at the beginning of the growing season and choose a nest location (which may be the same nest in which they were reared, as in the halictid *Lasioglossum versatum* (Robertson), in which mated

queens also overwinter in their natal nest; Michener, 1966). They then initiate nest building, constructing and provisioning a few cells until the first generation of workers takes over these tasks. Female workers continue digging galleries and creating new brood chambers for another generation of workers, males, and the next season's queens (Packer et al. 2007).

A minority of bee species are parasites (brood parasites and social parasites) that invade the nests of pollen-collecting bees; many of these parasitic bees specialise on ground-nesting hosts (Sick et al. 1994). Female brood parasites kill the host egg, or their larvae do so before eating the food resources in the brood cell. Social parasites usurp the nests of social bee species, causing the workers in the host nest to rear the larvae of the parasite and sometimes killing the host queen (Danforth et al. 2019). Brood parasites, also known as cuckoo bees, spend much of their time flying close to the ground, searching for host nests. As they do not build their own nests but rather depend on their hosts, we do not consider these species as having nesting preferences per se; however, these parasites could act as agents of selection on host bee nest-site preferences (see *Biotic factors*, below). We also consider cuckoo bees as tools for locating nests of ground-nesting bees (see *Methods…*).

2.3.2. Life cycle of ground-nesting bees

Bees are holometabolous, and their life-stages vary in duration depending on the species and its environment (e.g., temperature, length of the flowering season). Some species or populations are multivoltine, meaning they produce several generations per year (Michener 2007, Danforth et al. 2019), while others have just one, or take even more than a year to complete a generation (Forrest et al. 2019). For solitary ground-nesting bees, the activity period starts with the emergence of adults from their underground nests followed by mating, and the active period may last only a few weeks. Among social species, the active season can last for months, as successive

generations of adult workers are produced by the foundress. Females of all bee species store sperm in their spermathecae, which allows them to spend the rest of their life after mating building their nest, provisioning brood cells and laying eggs. Eggs hatch within a few days (up to six days for *Andrena vicina* Smith, Andrenidae; Miliczky & Osgood, 1995). The progeny then enter the larval stage, during which they consume the food reserves provided by their mother or their sisters (in social species). In temperate regions, many solitary bee species overwinter in the prepupal stage, sometimes within cocoons, before completing metamorphosis in the spring. Other species complete metamorphosis before overwintering as adults, again sometimes within their cocoons. Regardless of their developmental stage, solitary ground-nesting bees, as well as the foundresses of some social species, spend the winter in a dormant state within the larval brood cell; thus, the mother's choice of nesting site determines her offspring's overwintering location. Immature bees can spend several months (sometimes more than a year; Torchio, 1975; Danforth, 1999) of their lives below-ground, where they are susceptible to environmental hazards such as wildfires (reviewed by Cane and Neff 2011) and flooding (Roubik and Michener 1980, Fellendorf et al. 2004), before emerging as adults that are active for only a few weeks.

Female ground-nesting bees do not care for their offspring after provisioning and sealing brood cells. Consequently, the main way they can maximize the success of their brood is by providing high-quality food and a high-quality location for larval development and survival. The latter may include a nest site protected from adverse weather conditions, excessive humidity, and other incidental risks such as predators and parasites (Roulston and Goodell 2011). On the other hand, the more time a female spends searching for the ideal location and creating a nest, the less time she will have to provision and lay eggs in it or to construct additional nests. In other words, energy and time invested in nest-site selection and nest construction come with potential fitness

costs—just as energy and time invested in long foraging bouts can trade off against lifetime offspring production (Zurbuchen et al. 2010a). This means that nest-site selection may play a key role in female bee fitness (Brockmann 1979).

2.3.3. Nest construction

Nest architecture varies widely among ground-nesting bee species (Figure 1). Typically, nests are composed of a main vertical gallery with lateral tunnels leading to ovoid brood cells, with one offspring per cell. Depending on the species, lateral tunnels vary in length and in the angle at which they connect to the vertical shaft. Most halictid bees have no lateral tunnels at all, their brood cells being directly connected to the main gallery (Sakagami and Michener 1962). Nests can also contain chamber-like structures—larger than single brood cells—in which several cells are clustered together (Packer et al. 1989). Others contain loops that reconnect tunnels to the main gallery or sometimes dead ends (Rozen Jr. 1970, Wcislo et al. 1993, Wuellner and Jang 1996). The nests of most ground-nesting bee species have not yet been described, but based on a worldwide review of 449 species by Cane and Neff (2011), cell depth can range from 1 to 530 cm, with an average minimum cell depth of 17 cm beneath the soil surface.

Ground-nesting female bees initiate nest excavation using their mandibles and/or their forelegs and push out the soil using their hind legs and abdominal movements (Martins and Antonini 1994). Unlike cavity-nesting bees, ground-nesters have specialized pygidial (on the 6th segment of the female abdomen) and basitibial plates. These plates allow the bee to dig, pack soil, and move easily within the nest (Danforth *et al.*, 2019). Male ground-nesting bees do not participate in nest construction, although males of some *Perdita* (Andrenidae) species may dig temporary shallow burrows in which to spend the night or periods of bad weather. Males occasionally enter a female's nest before nightfall, as in *Perdita maculigera* Cockerell (Michener and Ordway

1963), *P. floridensis* Timberlake (Norden et al. 2003) and *Macrotera texana* Cresson (as *P. texana*; Neff & Danforth, 1991).

Solitary female bees typically construct and provision brood cells one at a time, although some exceptions exist (Danforth *et al.*, 2019). Most species construct multiple cells per nest, and cell size is correlated with bee body size (Kamm 1974). There may be a single cell per lateral tunnel, or cells may be clustered together, either arranged linearly as in some *Colletes* species (Michener 2007, Almeida 2008) or surrounded by a cavity as in some Halictidae (Sakagami and Michener 1962, Eickwort and Sakagami 1979). When excavating the cell, the digging bee usually uses her pygidial plate to smooth the walls and apply a shiny waterproof film. Even though not all bees line their brood cells (e.g. some *Perdita* spp. construct unlined brood cells; Danforth, 1989), most ground-nesting bees use glandular secretions that they brush on the cell walls (Batra 1964, Danforth 1991). This lining is a secretion product of the Dufour's gland, located at the base of the sting in female bees, and it forms a transparent, waxy coating around the brood cell (Cane 1981). Bees of the family Colletidae, which includes ground-nesting species, produce a unique cellophane-like membrane, also from Dufour's gland secretions, which is insoluble by many solvents (Almeida 2008). Regardless of its specific chemical make-up, the brood-cell lining probably helps protect the brood from microbial infestation and from water infiltration. After oviposition, the mother bee plugs the cell and begins to create a new one. Some species, though, such as *Perdita maculigera* (Michener and Ordway 1963), *Fidelia villosa* Brauns (Megachilidae; Rozen Jr., 1970), and *Diadasina distincta* (Holmberg) (Apidae; Martins & Antonini, 1994), create one-celled nests; individuals must therefore dig multiple independent nests. Michener & Ordway (1963) suggested that this behaviour might occur only in species whose nests are easily excavated (shallow or in soft substrates), requiring minimal investment of time and energy per

nest; but the one- or two-celled nests of some *Ptilothrix* species are constructed in hard-packed soil (Rust 1980, Martins et al. 1996). It therefore seems more likely that construction of single-celled nests is a strategy to minimize chances of accidental nest destruction or parasite invasion killing all of an individual's progeny.

Brood-inspection behaviour has been observed in some social ground-nesting bees (e.g., *Lasioglossum versatum*; Batra, 1968), in which females open the completed brood cell to check on the egg or larva. If the outcome of the inspection is satisfactory, they immediately reseal the cell. If not, they fill the cell with soil and plug it as if burying the larva, perhaps an adaptation to prevent movement of pathogens or parasites to other brood cells. *Lasioglossum versatum* also closes brood cells from which adult bees have emerged, perhaps because they contain fecal matter.

Excess soil can be used to reinforce the nest's structure, but it is usually brought to the surface, creating a "tumulus" (mound of soil) marking the entrance of freshly dug nests (Sakagami and Michener 1962). Multiple bee species build turrets, or "chimneys", at their nest entrances. Typically, turrets rise vertically from the nest entrance, although they are sometimes curved or horizontal, as in *Anthophora* sp. (Batra and Norden 1996), *Diadasina distincta* (Martins and Antonini 1994) and *Halictus confusus* Smith (Sakagami and Michener 1962). The turrets have consolidated and cemented inner walls, constructed from soil mixed with glandular secretions (Ordway 1984, Neff and Simpson 1992, Wcislo et al. 1993). The function of these turrets is unclear, but they may prevent soil particles or water from falling into the open entrance; they could help females locate their nest or recognize it among others in an aggregation; or they could keep parasites and predators, such as ants, from entering the nest. However, some species scatter the loose soil, perhaps to make the nest less conspicuous, and others plug the nest entrance with

the excavated soil after nest completion (Martins et al. 1996, Wuellner and Jang 1996). Some bees also plug the nest entrance temporarily after a provisioning trip (while inside), presumably to avoid predator invasion (Wuellner and Jang 1996). These different behaviours may be species-specific or may be adaptations to local environmental conditions.

2.4. Nest-site selection: which characteristics matter?

Although soil may seem an unlimited resource, female bees likely select specific soil features that limit their nesting habitat to a subset of the species' range. Here, we discuss environmental variables that may influence nest-site selection and provide examples (see Table 1 and Supplementary Table S1). Differences among species in environmental tolerances, predation pressures, and/or host-plant associations may explain why there is such interspecific variation in preferred environmental conditions for nesting.

2.4.1. Abiotic factors

Soil texture

Soil texture is thought to be a key factor influencing where ground-nesting insects choose to nest. A soil's texture is defined by its particle size distribution—that is, the relative amounts of sand, silt, and clay (in order of decreasing particle size). Particle size distribution affects soil hardness, which likely influences bee nesting-site preferences (see next section). Sand particles in particular are abrasive and could cause wear to the mandibles and wings. Nevertheless, most ground-nesting bee nests have been described as occurring in sandy or sandy loam soils, and it has therefore been inferred that they prefer these soil textures (Cane 1991).

An important early investigation of the textural preferences of ground-nesting Hymenoptera was conducted by Brockmann (1979), who studied the digger wasp *Sphex ichneumoneus* (L.). She

observed that wasps initiated nests in soils with high sand content (50–88%) and smaller amounts of silt and clay; they did *not* nest in nearby areas with finer soil texture (i.e., less sand). She concluded that wasps were generally choosing the sandiest soil available, which would provide better drainage, while still containing enough clay to support their large (1 cm diameter) burrows. Soil texture analysis in aggregations of *Halictus rubicundus* (Christ) (Halictidae) revealed a sand fraction between 35 and 100%, with a combined silt–clay fraction of less than 5%, the rest being gravel (Potts and Willmer 1997). This study found no association between sand or silt–clay fractions and nest density, but more nests were found in more gravelly soils. In a broad survey across the U.S.A., Cane (1991) measured sand percentages of 34 to 94% at the nest locations of 32 species of ground-nesting bees, with maximum sand content observed near nests of the genera *Hesperapis* (Melittidae) and *Colletes* (Colletidae). Larger bees tended to nest in more clay-rich soils (Cane 1991). In another study, *Colletes inaequalis* Say were found to nest in soils with a mean sand content of 64% and never less than 30% (López-Uribe et al. 2015). Another colletid, *Caupolicana yarrowi* (Cresson), has been observed nesting in 45–55% sand (Rozen et al. 2019). Unfortunately, none of the latter three studies compared soil texture between nesting sites and nearby areas without nests, making it difficult to be sure that the characteristics of the nesting locations reflect bees' preferences.

Although they do not demonstrate that ground-nesting bees prefer sand, the studies above do show that these bees' nests are often associated with sandy soils. However, there is also plenty of variation, with *Lasioglossum malachurum* (Kirby) nests recorded in soils containing only 10–41% sand (Polidori et al. 2010), and several *Anthophora* species (*A. abrupta* Say, *A. bomboides* Kirby and *A. walshii* Cresson) nesting in soil with 20–30% clay content (Cane 1991). *Anthophora abrupta* can even nest in bags of clay (Graham et al. 2015) and clay walls (Norden

1984). Alkali bees (*Nomia melanderi* Cockerell), which are sometimes managed for alfalfa pollination, are known for nesting in clay soils with a pH > 8 and a high moisture level (Cane 2003, 2008, Vinchesi et al. 2013). Fortel *et al.* (2016) found no influence of soil texture on species richness or abundance of ground-nesting bees in experimental plots set up for this purpose; however, this result could mask interspecific differences, since species likely differ in their soil-texture preferences (Leonard and Harmon-Threatt 2019). Seemingly contradictory results could also be due to the use of different methods for soil textural analysis, from sieving and weighing different soil fractions, to particle size analysis either with a hydrometer (Bouyoucos method) or a pipette (U.S. Department of Agriculture, Bureau of Plant Industry, Soils 1951).

Soil compaction

Soil compaction, or hardness, is a measure of compressive strength at the soil surface that can be taken using a penetrometer. Soils can be classified as soft (<1.5 kgf cm^{-2} = <147 kPa), medium (1.6–3.0 kgf cm^{-2}) or hard (>3.1 kgf cm^{-2}) (Kim et al. 2006). More compact soils have fewer pores and higher density, making them more difficult to excavate and impeding water percolation. Compaction is often the result of the passage of animals, vehicles, or machines such as the compressive rollers used in agricultural environments.

In theory, soil compaction should be an important factor affecting nest-site selection, as nest excavation appears to represent a major investment of time and energy for a ground-nesting bee. All else being equal, females should prefer softer substrates to limit these costs. Indeed, although Potts and Willmer (1997) observed *Halictus rubicundus* nesting in soils ranging in hardness from 0.6 to 5.5 kgf cm^{-2}, they found greater nest densities in softer soils at the site they studied in most detail. The bees avoided nesting in hard-packed substrate, as did the digger wasp *Sphex*

ichneumoneus (Brockmann 1979). Sardiñas & Kremen (2014) also found fewer ground-nesting bees in emergence traps placed over harder soils.

On the other hand, burrows in softer soils may be more prone to collapse or excavation by vertebrate predators. The greater structural integrity of burrows built in more compact soil may be particularly important for bees that nest in aggregations. As the distance between neighbouring nests decreases, the advantage of easy excavation may be outweighed by the disadvantage of possible nest collapse. Potts and Willmer (1997) reasoned that this phenomenon must account for the greater densities of *H. rubicundus* nests at sites with greater soil compaction. In contrast, Polidori *et al.* (2010) observed no association between aggregation size and soil hardness in *Lasioglossum malachurum*, although it should be noted that all five aggregations they studied were in hard-packed soils. Several gregarious species, including *Macrotera opuntiae* (Cockerell), *Colletes kincaidii* Cockerell, and *Anthophora pueblo* Orr, have even been reported to excavate nests in sandstone despite the presumed energetic costs and mandible wear (Bennett and Breed 1985, Torchio et al. 1988, Orr et al. 2016). As with other soil characteristics, soil-compaction preferences seem to be species-specific. For example, consider three common halictid taxa studied by Kim *et al*. (2006): *Halictus tripartitus* Cockerell nested in hard soils, whereas *H. ligatus* Say was found in highest densities at medium soil hardness, and there was no association between soil hardness and nest density in *Lasioglossum* (*Dialictus*) sp.

Soil moisture

With their broad geographical distribution, bees have been found nesting in situations that vary enormously in soil moisture. Cane (1991) measured in situ water content in 32 bee species' nests across the U.S.A. and found that soil moisture ranged from 2.7% to 37.8%. Other studies have reported nests in wetter soil (Packer and Knerer 1986a), with Potts & Willmer (1997) reporting a

mean soil moisture of 80%. Still others have documented nests that are temporarily submerged (Roubik and Michener 1980, Visscher et al. 1994, Norden et al. 2003) or even permanently waterlogged (Pietsch et al. 2016). The ability to nest in flooded sites may help bees avoid competition for nest sites, or the cover of water may help protect nests from attack by parasites or predators.

A common feature of the nests of ground-nesting bees is a waterproof brood-cell lining secreted by the Dufour's gland of the mother bee (May 1972, Cane 1981, Visscher et al. 1994). This waterproof lining may function to retain soil moisture within the cell, but its primary function is probably to exclude excess water (May 1972, Roubik and Michener 1980). Even when submerged in water for up to 24 hours, brood cells of *Diadasina distincta* and *Ptilothrix plumata* Smith experienced no water infiltration (Martins and Antonini 1994, Martins et al. 1996), showing that the cells are completely waterproofed and can withstand heavy rains or flooding.

There are costs and benefits to nesting in damp soils. Soil moisture is crucial for larval development because larvae take up water as a component of weight gain (May 1972), particularly during the later larval stages. This water is likely to come from moisture within the brood cell, as relative humidity inside the nest can approach 100% (Potts and Willmer 1997). However, moisture can also cause mould to develop inside the cells, degrading the food supply and jeopardizing offspring survival, as observed in *Diadasia opuntiae* Cockerell (Ordway 1984). Nesting populations of alkali bees (*Nomia melanderi*), which prefer soils with high moisture content, are sometimes maintained by sub-irrigation and application of NaCl (in part to prevent loss of soil moisture) to the nesting beds (Cane 2008). However, Stephen (1965) showed that high soil moisture in artificial *N. melanderi* beds led to the development of fungi that killed overwintering bees. Flooding of the nesting area during diapause can also delay emergence, as

shown in male *Calliopsis pugionis* Cockerell (Visscher et al. 1994). Even more dramatically, *Andrena vaga* Panzer offspring died during a prolonged inundation, leading to a local population decline (Fellendorf et al. 2004).

Other adaptations to avoid excess water include the excavation of a cavity around the cell cluster to increase the rate of soil water evaporation around the brood cells, as in the halictids *Halictus ligatus* and *Augochlorella striata* (Provancher) (Packer and Knerer 1986a, Packer et al. 1989). In swampy habitats, *Epicharis zonata* Smith (Apidae) build a double cell plug inside the nest (Roubik and Michener 1980), presumably for the same purpose. Most species of *Perdita* do not have a brood-cell lining, but Norden *et al.* (2003) reported that *Perdita floridensis* prepupae secrete a water-repellent coating on their cuticle that presumably protects them from drowning and sand abrasion.

While bees in moist habitats often exhibit traits that appear to minimize water infiltration and damage, ground-nesting bees in drier habitats may preferentially select sites with higher soil moisture. For example, female *Dieunomia triangulifera* (Vachal) in the U.S. Great Plains only began nest construction when soil was moist enough for excavation (Wuellner 1999), postponing nest establishment in drier years until rains softened the soil (Minckley et al. 1994). Some species, especially *Anthophora* spp., bring water from outside the nest (sometimes mixed with nectar) to moisten the soil while digging, as in *Anthophora abrupta* and *A. villosula* (Pallas) (as *A. pilipes*; Batra & Norden, 1996). This behaviour might be related to nest architecture: anthophorine bees sometimes nest in soil that is rich in clay and may need added moisture to construct the turrets that often mark their nest entrances. Similarly, the desert bee *Caupolicana yarrowi* uses regurgitated nectar to soften the soil and smooth the interior surface of nest cells

and walls—a behaviour that is probably an adaptation to the dry and hard-packed soil (Rozen et al. 2019).

Allowing for variation in local environment and species-specific moisture preferences, most ground-nesting bee species are probably searching for a soil patch that is well drained but not too dry (Potts and Willmer 1997). However, whether female bees select nest locations based on soil moisture or on soil texture (see above) is often unclear, because soil texture is a major determinant of water content: clay soils retain water, while sandy soils do not. Thus, distinguishing the influence of these two variables on bee nest-site selection may require manipulative experimentation.

Temperature

As with all ectotherms, temperature influences many aspects of the lives of bees, including activity rates (Borrell and Medeiros 2004, Woods et al. 2005), mating behaviour (Larsson 1991), timing of adult emergence, rates of larval development (Forrest 2017), and number of generations produced per year (Forrest et al. 2019). Temperature at the nest entrance can influence when a bee can begin foraging in the morning, while below-ground temperatures may affect whether larvae can complete development before the end of the growing season. Although adult bees are partially endothermic and can elevate their body temperature using thoracic flight muscles (Stone and Willmer 1989), female ground-nesters cannot control the temperature within the nest, nor can bee larvae thermoregulate. In addition, the metabolic costs of raising body temperature to the level required for activity are greater when ambient temperatures are lower (Willmer and Stone 2004). As such, we expect temperature to strongly influence nest-site quality for ground-nesting bees.

Female ground-nesting bees spend the night in their nests and forage when ambient temperature is warm, but below their maximum thermal tolerance (Westrich 1996). Despite their thermoregulatory abilities, bees rely on warm air and/or solar radiation to warm up. For example, Stone (1994) found that *Anthophora plumipes* (Pallas) females with warmer nest entrance tunnels began foraging more than 3 hrs earlier in the day than conspecifics nesting in cooler microhabitats. *Anthophora abrupta* females appear to use the turrets protruding from their nest entrances to warm up on cool mornings, because these heat up more quickly in the sun than do the nest interiors; individuals whose nests lacked turrets required up to an hour longer to begin foraging (Norden 1984). While flight is particularly temperature-dependent, even nest construction can be slowed by cool temperatures. Weissel *et al.* (2006) showed that cooler below-ground temperatures (at 20 and 40 cm) were associated with slower nest founding and construction in the eusocial bee *Lasioglossum malachurum*. Because of the limited season available to most bees for building and provisioning their nests, getting an earlier start may translate into more total reproductive output.

In addition to affecting adult activity, temperature also influences bee development. Warmer temperatures during each larval stage can increase developmental rate and survival (Jeanne and Morgan 1992, Whitfield and Richards 1992), at least as long as they remain below species- and stage-specific critical thermal maxima. For example, prepupal development of *Nomia melanderi* is fastest at 29˚C and inhibited below 17˚C and above 35˚C (Stephen 1965, Vinchesi et al. 2013). Consequently, temperature can also affect voltinism (the number of generations in a year). In the cavity-nesting bee *Osmia iridis* Cockerell and Titus, temperatures experienced early in larval development influence whether a bee adopts a one- or a two-year life cycle (Forrest et al. 2019). Variation in voltinism also occurs among ground-nesting species (e.g., *Diadasia rinconis*

Cockerell and *D. afflicta* (Cresson) are both partially bivoltine), but it is so far unclear whether temperature controls this variation (Neff et al. 1982, Neff and Simpson 1992). In multivoltine species such as *Lasioglossum malachurum*, warmer below-ground temperatures decrease the duration of the intervals between generations, which correspond to periods of larval development. When below-ground temperature is 2˚C warmer, more colonies produce three broods instead of two (although the effect is small, explaining less than 2% of the variance) (Weissel et al. 2006). While we normally expect faster development and shorter generations to translate into higher rates of population increase, high temperatures can also be associated with smaller adult body size and higher rates of mortality in ectotherms, such that the fitness consequences of nesting in warm microenvironments can be complex (Kingsolver and Huey 2008, Forrest 2017).

Temperatures near the soil surface vary over the course of a day (Xu et al. 2002), and they can also vary by several degrees over small (<50 m) spatial scales owing to variation in shading, vegetative cover, surface reflectance (albedo), and topography (Redding et al. 2003, Mikola et al. 2018, Davis et al. 2019). For example, in some termite and ant species, nest temperatures can be influenced by nest orientation, which affects the amount of solar radiation reaching the nest entrance and therefore the amount of solar heat absorbed by the nest (reviewed by Jones & Oldroyd, 2006). Ground-nesting bees may respond to this variation in soil-surface temperature and choose to nest in locations that experience higher or lower daily maxima, or that experience desirable temperatures at particular times of day, such as the early morning. Indeed, Sakagami & Hayashida (1961) demonstrated that nests of *Lasioglossum duplex* (Dalla Torre) (as *Halictus duplex*) in the Hokkaido University Botanical Garden, Japan, were preferentially located in areas

that received morning sunlight—even if these locations were similar to less favoured locations in terms of total duration of insolation.

Below-ground temperatures are generally correlated with, but much less variable than, surface temperatures, with the strength of the correlation decreasing with increasing depth (West 1952, Xu et al. 1997, Rajver et al. 2006). Heat penetration into the soil (i.e., the thermal diffusivity of the soil) increases with soil water content and decreases with increasing soil bulk density (Marshall et al. 1996), such that below-ground temperatures in drier, more compacted soils are less correlated with surface temperature than those in moister but better-aerated soils. Regardless, because temperatures below a certain depth (on the order of 20 cm) are not predictable from surface temperatures (see Rajver *et al.*, 2006), below-ground temperature is unlikely to influence the choice of nesting location for bees that construct brood cells much below this depth. However, for bees that nest closer to the surface, near-surface temperatures should be good indicators of the temperatures that would be experienced by brood and may be used in site selection for this reason. Indeed, Potts and Willmer (1997) found that the areas with the highest densities of *Halictus rubicundus* nests in their Scottish study sites were significantly warmer at 5 cm belowground (the mean depth of the brood cells of this species), compared to the ambient air temperature, than nearby areas without nests. Temperatures at 5 cm depth were strongly correlated with soil surface temperatures, meaning that females' assessments of surface temperatures could inform them about the likely thermal quality of nests constructed at different locations.

Overall, we expect bees that construct shallow below-ground nests in temperate regions to choose sites with maximum sunlight exposure, facing toward the equator or eastward if the ground is on a slope, to maximize heat at the nest entrance in the morning and in the brood cells

during larval development. In other regions (e.g. hot deserts), female ground-nesting bees could adopt the opposite strategy to avoid overheating the young and might therefore dig deeper burrows or select poleward-facing slopes to find cooler underground environments. Bees might assess surface temperature directly to determine where to nest, or they might use other cues, such as aspect or solar irradiation, that correlate with nest temperatures (see *Soil surface features*, below). In practice, it may be difficult to distinguish preferences for temperature per se from preferences for other factors that are correlated with temperature; however, given the potentially major fitness consequences of nest temperatures, it seems likely that temperature would be an important ultimate driver of nest-site selection, even if it is not the proximate driver.

Soil surface features

Other variables, such as cracks in the soil, stones, slope, and vegetation cover, have been reported to influence where bees nest, with specific associations depending on the study and the species. The North American bee *Calliopsis pugionis* sometimes nests within cracks in dry flood-plains (Visscher and Danforth 1993), as does the Australian bee *Leioproctus muelleri* Houston and Maynard (Colletidae; Houston & Maynard, 2012). Potts and Willmer (1997) observed a strong preference for stones among *Halictus rubicundus*, with 57% of the bees at one study site initiating a nest near or under stones. Other halictid bees (*Augochlorella striata, Lasioglossum* (*Evylaeus*) *cinctipes* (Provancher) and *L. comagenense* (Knerer and Atwood)) also locate their nest entrances near surface stones (Packer et al. 1989). *Halictus ligatus* nests often occur near rocks and pebbles (Packer and Knerer 1986b), and indeed a preference was demonstrated experimentally by Cane (2015), who added pebbles in a nesting area of this species: females consistently preferred to nest near stream pebbles instead of bare ground. However, Sardiñas & Kremen (2014) found that cavities and cracks in the soil predicted nest

occurrence for one species of *Lasioglossum (Dialictus)* but not for all *Lasioglossum* species, so this preference might again be species-specific or context-dependent.

It is often assumed that female bees prefer open bare ground to vegetative cover to initiate nests, as has been shown for *Dieunomia triangulifera* (Wuellner 1999), because bee nests are often found in sparsely vegetated areas. However, this might reflect the difficulty of finding nests among vegetation rather than bee preferences. Some species, such as *H. ligatus* (Packer and Knerer 1986a), have actually been observed nesting under vegetation. *Lasioglossum rohweri* (Ellis) nested in aggregations in sparsely vegetated areas, but not in bare ground, in dense vegetation, or under dead plant material (Breed 1975).

There could be multiple reasons for choosing to nest in cracks or near stones, pebbles, or vegetation. First, these features could act as visual cues, helping the bee to locate her nest when returning from a foraging trip (but see Wuellner, 1999). Indeed, ground-nesting bees learn and evaluate distance to visual landmarks to locate their nests (Brünnert et al. 1994). Second, pebbles and stones help regulate underground temperature by heating the soil and the nest entrance located next to it, as stones can absorb solar radiation and retain heat (Packer et al. 1989, Potts and Willmer 1997, Cane 2015). Stones, pebbles, and vegetation can also help soil to retain moisture, which can be advantageous in dry environments (see *Soil moisture*, above), and they could also help maintain nest structural integrity. In particular, dead vegetation or leaf litter may prevent desiccation of the soil surface and help regulate soil temperature. Finally, these features could serve to conceal nest entrances from predators and parasites (Potts and Willmer 1997, Wuellner 1999). Conversely, Wuellner (1999) suggested that *D. triangulifera* might select unvegetated areas for their nests because parasitic conopid flies use the tips of plant leaves or stems as perches from which to observe their bee hosts. Alternatively, bare ground may be

preferred because roots impede nest excavation, and might destroy completed cells or because vegetation makes it difficult for bees to find their nest entrances (Wuellner 1999).

Finally, slope is another factor that is likely important in nest-site selection. Many ground-nesting bees nest in embankments close to rivers or roads, which can be steep or even vertical. For example, *Anthophora abrupta* has been reported nesting in a clay wall (Norden 1984) and *Neocorynura fumipennis* Friese (Halictidae) in the vertical banks of a ditch (Michener et al. 1966). Maher et al. (2019) compared the slope—as well as vegetation and shade—of 236 nesting sites belonging to four different species and recorded by citizen scientists, and many nests of *Colletes hederae* Schmidt and Westrich (a greater proportion than in the other three species) were located on sloping ground. However, there was no evidence that these bees preferred sloping substrates, and their nests were found equally often on flat ground. Slopes could be favoured in some cases because they facilitate water drainage, and, when the area is exposed to the sun and south-facing, because they enable nests to be warmer (see *Temperature*, above). However, it is difficult to conclude from observations alone whether ground-nesting bees are selecting nest sites based on slope, solar radiation, or temperature, all of which can be confounded. To segregate the influence of each of these factors, experimental studies are required.

2.4.2. Biotic factors

Natural enemies

Biotic factors could have a strong influence on where bees nest, potentially acting both as proximate indicators of nest-site suitability and as ultimate drivers of habitat preferences. In particular, natural enemies (pathogens, parasites and predators) are thought to have played a major role in shaping the nesting habits of bees (Wcislo and Cane 1996). Numerous natural

enemies attack bees at their nests, including parasitic wasps and cleptoparasitic bees; bombyliid flies; clerid and meloid beetles; ants; and even insectivorous mammals (Minckley and Danforth 2019, Danforth et al. 2019). Bee brood cells and larvae can also suffer infection by fungal and other microbial pathogens (Gerdin and Cane 1983, Antonini et al. 2003). All of these can impose significant mortality on ground-nesting bees (Gerdin and Cane 1983, Wcislo 1996, Minckley and Danforth 2019), and, as such, have likely been major agents of selection on nesting behaviour (e.g., Batra & Bohart, 1969). As noted above, parasites or predators may be responsible for the tendency of some bees to nest in cryptic locations (e.g., Potts & Willmer, 1997). However, we know of no evidence so far that natural enemies have influenced bee preferences for specific below-ground soil features such as texture or moisture.

Presence of conspecifics

Many ground-nesting bees choose to nest near conspecifics, for reasons that are not always clear. Gregarious behaviour occurs among solitary, communal and social ground-nesters and leads to the aggregation of conspecific nests in the same area. In these aggregations, nest density can vary from a dozen to more than 300/m^2 in *Halictus rubicundus* (Potts and Willmer 1997) to 1650/m^2 in some aggregations of *Calliopsis pugionis* (Visscher and Danforth 1993). Aggregations can persist for many bee generations (Neff, 2003) and as long as 50 years (Cane 2008). Large nesting aggregations can be conspicuous; but even so, nesting in an aggregation may be a form of defence against parasites (reviewed by Rosenheim, 1990). The presence of large numbers of active bees entering or exiting their nests can prevent parasites from approaching undetected, and the activity may even distract or frighten some prospective predators. In rare cases, members of an aggregation may collectively attack intruders (Thorp 1969). On the other hand, areas of high nest density can also attract parasites and therefore suffer disproportionately from parasite attack

(e.g., Polidori *et al.*, 2005). In these cases, any adaptive value of nesting in aggregations seems unrelated to defence.

Regardless of their adaptive value, aggregations can form through three possible processes (reviewed by Cane, 1997): First, bees may nest in aggregations simply because conspecifics have similar preferences and many individuals therefore (independently) select the same place. Second, aggregations may arise because of natal philopatry (i.e., bees returning to nest at the site from which they emerged) combined with population growth (Crozier et al. 1987, Yanega 1990); or, third, because bees are attracted by the presence of conspecifics. In the latter two mechanisms, bees are choosing to nest at a location that has been deemed (or even proven) suitable by others, presumably because copying the choices of other individuals is less risky, or requires less investment of time or energy, than identifying a suitable site independently. There is in fact abundant evidence, discussed in detail by Michener (1974), that bees are attracted by conspecifics. The specific cues responsible for this attraction are generally unknown, although odour or visual signals are suspected (e.g., Roubik & Michener, 1980). One of the few experimental tests (Wuellner, 1999) found no evidence that the ground-nesting bee *Dieunomia triangulifera* was attracted to conspecific tumuli (here created "by hand" from soil taken from actual nest tumuli).

Floral and nesting resources

As central-place foragers, bees require food and nesting resources within flying range of their nests (Westrich 1996). Pollen and nectar are the primary food resources for ground-nesting bees, although some species also collect floral oils and resins (Michener 2007), while nesting resources can include abiotic elements (water, mud), resin (used as a cell-lining in *Trachusa* spp; Cane, 1981, 1996) or leaves (Requier and Leonhardt 2020). Female bees must complete several

foraging bouts to provision a single brood cell, and the flight distance within which those bouts are conducted is constrained by environmental factors (e.g., landscape configuration) and by the bee's physiological capabilities. Flight distances are generally correlated with body size in bees (Gathmann et al. 1994, Gathmann and Tscharntke 2002), with larger bees able to fly disproportionately further than smaller ones (Greenleaf et al. 2007). Small bees (smaller than 1 cm long) typically do not forage beyond 100–300 m from their nest (Zurbuchen et al. 2010b). Ground-nesting bees, many of which are small (as little as 2 mm long in some *Perdita* [Andrenidae]), therefore need adequate soil substrate close to floral resources, and, all else being equal, should prefer to nest near flowers. Furthermore, many solitary bees are dietary specialists that collect pollen only from certain plant taxa; these bees require appropriate nesting habitat within flight distance of their specific floral host-plants.

It is certainly the case that dietary specialists (oligoleges) nest near their host plants: squash bee (*Peponapis pruinosa* (Say), Apidae) nests occur in squash (*Cucurbita* spp.) fields (Julier and Roulston 2009, Skidmore et al. 2019); *Nomia melanderi* nest near alfalfa (*Medicago sativa* (Linnaeus)) (Cane 1997, 2008, Vinchesi et al. 2013); and *Dieunomia triangulifera* nest near sunflowers (*Helianthus annuus* (Linnaeus)) (Minckley et al. 1994). Oddly, however, it is not known whether bees actually use the presence or abundance of host-plant flowers or foliage when choosing where to nest: they may simply be found alongside their host-plants because of philopatry, or because they share substrate preferences with their host-plants. Experiments (such as those of Wuellner, 1999, and Julier & Roulston, 2009, or those suggested by Cane, 1997) are still needed to determine which factors are used by ground-nesting bees as proximate cues for where to nest, as opposed to those that are simply correlated with nest presence.

2.5. Methods for studying the nesting habitat of ground-nesting bees

A variety of techniques can be used to study the nesting behaviour and habitat of ground-nesting bees, depending on the researcher's objectives. Documenting habitat associations and responses to environmental perturbations can be done by sampling entire communities of bees (see *At the community level*, below), while studying nest construction or within-nest behaviour requires more targeted methods (see *At the nest level*). Accurately characterizing nest-site selection also requires locating individual nests—either in the field or in enclosed arenas. Finding nests is one of the main challenges in studying ground-nesting bees. Here we review the existing methods, both experimental and observational, used to study the habitat of ground-nesters, and we highlight some techniques that we hope will be used more broadly in future.

2.5.1. At the community level

One method to survey ground-nesting bees is to observe or sample the whole bee community. By identifying bees to the genus or even family level, it is often possible to sort them by nesting type, distinguishing above- from below-ground nesters. Assembling a list of species within a community permits studies of bee responses to their environment (including disturbances) based on their functional traits, of which nesting location is one (Williams et al. 2010). For example, several studies have examined the effects of different anthropogenic and environmental factors (agricultural management (Martins et al. 2018a), agricultural intensification (Williams et al. 2010, Renauld et al. 2016a, Carrié et al. 2018), fire (Burkle et al. 2019, Galbraith et al. 2019), habitat management (Buckles and Harmon-Threatt 2019), etc.) on ground-nesting bee abundance and diversity.

To sample a broad array of bee species, the use of multiple techniques is recommended (Sardiñas and Kremen 2014). Active sampling methods consist of visual observation followed by active

pursuit of the bee, and collection with a net or aspirator ("pooter"). Passive trapping involves installing pan traps (Kearns and Inouye, 1993), pitfall traps, window traps (Gullan and Cranston 2010), vane traps or malaise traps (Darling and Packer 1988) in a site and returning later to collect the captured insects. Unfortunately, these techniques are not specific to ground-nesting bees, and because they capture bees moving towards or between food patches, mates, or nesting sites, it is impossible to know if the nests of the captured bees are nearby. However, given the limited foraging ranges of most ground-nesting bees, most sampled bees' nests are presumably within a few hundred metres of the sampling location (see *Floral and nesting resources*, above).

At a smaller scale, assemblages of ground-nesting bees can be sampled in a more targeted fashion using tent-like emergence traps. These structures have an open bottom and an aperture at the top leading to an insect killing jar, and they can be placed haphazardly on the ground to opportunistically collect any bees emerging from a previous year's nest, or, if placed overnight, to capture nesting females as they exit their nests in the morning. Emergence traps are useful to examine the effects of substrate characteristics on the abundance and richness of ground-nesting bees (e.g. Sardiñas & Kremen, 2014). However, their efficiency is questionable, compared to other trapping methods (Cope et al. 2019), because they cover only a small area of the ground, and the tents are expensive; furthermore, their effectiveness in catching actively nesting bees decreases after 48 h of deployment (Pane and Harmon-Threatt 2017). Still, they have the advantage of allowing the researcher to link the occurrence of bee nests with habitat characteristics measured at a very local scale.

One way to collect extensive ecological data, including on ground-nesting bees, is by working with citizen scientists (Deguines et al. 2016), who can potentially sample on a broad spatial and temporal scale at low cost. When observers are trained to identify local pollinator taxa (or groups

of similar taxa), the quality of the resulting data can be similar to that of professionals (Kremen et al. 2011). Maher *et al.* (2019) used citizen science to investigate the nesting requirements of four European species of gregarious ground-nesters: *Andrena cineraria* (Linnaeus)*, A. fulva* (Müller)*, Halictus rubicundus* and *Colletes hederae*. To validate records, pictures were submitted to an online platform and checked by scientists. The researchers were able to gather data on several variables, including number of nests in the aggregation, extent of shading, and type of ground cover from 236 verified nests (out of 394 submitted records). This example shows how citizen scientists can help overcome the logistical difficulty of finding ground-nesting bee nests; however, these four species were targeted because of their gregariousness and ease of identification. Less gregarious species would be more challenging (Maher et al. 2019).

2.5.2. At the nest level

Relative to cavity-nesters, ground-nesters are challenging to study at their nests. Cavity-nesting bees occur naturally in wood cavities and hollow plant stems, and there is a simple method to monitor them using human-made infrastructure such as nest boxes, also called "bee hotels" or "trap nests" (reviewed by MacIvor 2017). These have been useful for studying nest provisioning and reproductive output in above-ground cavity-nesting bees (Steffan-Dewenter and Schiele 2008, Forrest and Chisholm 2017, Schenk et al. 2018). Analogous artificial nesting structures have not been successfully developed for ground-nesting bees; however, Fortel et al. (2016) had some success in attracting bees to nest in experimental plots of soil (1 $m^2 \times 0.5$ m deep). These authors obtained 232 individuals of 37 ground-nesting bee species across their 16 urban study sites (representing a total area of 36 m^2 of substrate from which bees were collected) over a two-year period (Fortel et al. 2016b). This method has not yet been widely deployed, but these results

suggest that it could be an effective technique for assessing bee soil preferences and even, perhaps, for enhancing bee habitat.

As noted previously, locating nests of ground-nesting bees in more natural settings can be a substantial challenge, especially for species that do not form aggregations. One way to locate those nests could be by following nest-searching cleptoparasites (e.g., *Nomada* spp., Apidae), which often fly slowly and close to the ground and are therefore more conspicuous and readily tracked than their hosts. By following parasites and noting how long they spend in an underground hole (cell parasitism takes more than 120 s), one could determine the location of the host species' nest (e.g. Sick *et al.*, 1994). López-Uribe *et al.* (2015) overcame the difficulty of finding nests by building a predictive spatial model to detect suitable nesting habitat for *Colletes inaequalis* based on ecological variables thought to be important for this species. The authors were able to identify 13 new aggregations thanks to this technique. More such models should be developed to assess habitat suitability for ground-nesting bees; however, this can only be achieved with species for which the important habitat variables are already known.

Once nests have been identified, various techniques can be used to study the nest interior or other aspects of the species' life history. Nest excavation techniques were first described in the 1930s by S.I. Malyshev (in Russian) and were published in English by Linsley *et al.* (1952). Excavation techniques have been improved and used since then to study nest architecture and reproductive output of many ground-nesting bees. Unfortunately, this procedure is both destructive and extremely meticulous, given the challenge of tracking tunnels in the midst of falling debris (Marinho et al. 2018). If internal nest architecture is not the focus, targeted emergence traps can be useful. A small tube or inverted transparent cup can be placed over the nest entrance when the mother bee is inside (at night or between foraging trips) (Wcislo 1993, Neff and Simpson 1997);

one can then wait for the bee to emerge, at which point she can be measured, identified, individually marked (e.g. *Andrena vaga*, *Anthophora plumipes*; Straka *et al.*, 2014), or collected (Linsley et al. 1952, Michener et al. 1955). Alternatively, the nest location can be marked and an emergence trap placed over it the following year to collect emerging progeny (or parasites), thereby quantifying the reproductive output from that nest.

Although ground-nesting bees can be found in many different natural environments, most are unwilling to nest in captivity. One exception is the squash bee, *Peponapis pruinosa*, which has consequently been used as a model species in many studies (Julier and Roulston 2009, Ullmann et al. 2016, Willis Chan et al. 2019). These bees tolerate a broad range of soil conditions, as long as they have access to their host plant, *Cucurbita* spp. (Cucurbitaceae), and have therefore been reared in cages or greenhouses to investigate the effects of agricultural practices on ground-nesting bees. A few species of ground-nesting bees have even been reared in the laboratory (reviewed in Leonard and Harmon-Threatt 2019), using observation chambers with glass windows to investigate their behaviour and nest architecture (Michener et al. 1955). These nest boxes, similar to the ones commonly used to study ants, kept below-ground or moved above-ground, have been used to observe *Lasioglossum zephyrum* (Smith) (Batra 1964, 1968, Michener and Brothers 1971), *Nomia melanderi* (Batra 1970), *Macrotera portalis* (Timberlake) (Danforth 1991) and *Anthophora* sp. (Batra and Norden 1996), among others (see Leonard and Harmon-Threatt 2019). However, this method works mainly with social and communal bees (mostly halictids), and even with these, attempts are sometimes unsuccessful (Michener et al. 1955). More research is needed on rearing other species, as these could eventually be integrated in agricultural practices, with populations sustained in nesting beds (as has been done with *Nomia melanderi*; Cane, 2008) for crop pollination purposes.

2.6. Future directions

Until the early 1990s, most studies of ground-nesting bees were field observations describing nest architecture, immature stages, and parasites, as well as taxonomic notes (see Supplementary Table 1). These papers helped build a body of knowledge on the nest structures and life histories of ground-nesters. Rearing projects yielded more knowledge of within-nest behaviour and daily activity patterns. Since then, studies have included more species, looking at the entire community of ground-nesting bees in the context of nesting habitat characteristics (Potts et al. 2005, Sardiñas and Kremen 2014). But only a handful of papers (e.g., Potts & Willmer, 1997) have actually focused on soil characteristics near nests in order to assess nesting preferences, and they have produced conflicting results (e.g. soil hardness in Kim *et al.*, 2006). As noted by Harmon-Threatt (2020), it is difficult to generalize about abiotic preferences across ground-nesting bee species. Furthermore, we still have no information on the nesting biology—including the soil preferences—of many species, probably due to the challenge of locating and excavating cryptic underground nests. It remains impossible to draw conclusions about geographic or seasonal patterns (e.g., do ground-nesting bees that are active in cooler conditions—due to an early flight season, or because they occupy high altitudes or latitudes—have stronger preferences for nesting in warm microhabitats?).

As nest-site characteristics for ground-nesting bees have received little quantitative study, there might be important factors influencing nest quality and nest-site selection that have never been identified. What about the effect of below-ground oxygen levels on larval survival? Or the effects of soil pH (as described for *Eucera nigrilabris* Lepeletier, Apidae, by Shebl *et al.*, 2016), organic matter, and chemistry (including salinity and the presence of pollutants)? Similarly, few studies have investigated the influence of natural enemies on nest-site selection. For example, do

certain soils create conditions more vulnerable to pathogen infection within the brood cell, or does the presence of predators or parasites influence where bees choose to nest?

To identify and isolate the habitat characteristics that influence nest-site selection in ground-nesting bees, an experimental or rigorous comparative approach is required. For example, comparing the attributes of nesting sites that are selected by females, with those investigated but not used—as in the study by Brockmann (1979) on the digger wasp *Sphex ichneumoneus*—provides stronger evidence of preference than merely quantifying the attributes of sites with nests. Well-developed methods to detect habitat selection (by comparing factors at the nest site and at unused sites nearby) have been reviewed for birds by Jones (2001) and for all animals by Montgomery & Roloff (2017). While these methods were developed for vertebrates, they are equally applicable to bees—yet have scarcely been employed. Once nesting-site preferences have been documented, they can be incorporated in predictive models (as in López-Uribe *et al.*, 2015), to create maps of suitable nesting habitat and to predict likely occurrences of the focal species. In all such studies, it is crucial to consider the scale at which the study organisms perceive their environment and within which they can select habitat (Johnson 1980). Studies that rigorously document the factors involved in nest-site selection would allow researchers to propose, and then test, adaptive hypotheses for the observed preferences.

More experimental research is needed to test which soil factors (texture, compaction, moisture, etc.) are selected by ground-nesting bees when choosing their nest location, and why. For example, to test the preference for texture, one could give female bees a choice among different soil textures—while holding all other factors constant—and document their preferences. In addition to documenting the mother's choice, measuring components of offspring fitness would be required to assess the performance of bee larvae under different conditions (i.e., the quality of

the nest location), which may not correspond exactly with the mother's preference. There is a huge gap in the literature regarding the fitness of ground-nesting bees in relation to the various soil characteristics we have reviewed.

Such research would be especially valuable in agricultural systems, where farming practices can involve mixing the soil to a depth of up to 40 cm during tillage, and the use of agrochemicals to combat insect pests. A few papers have investigated the effect of tillage (Ullmann et al. 2016, Skidmore et al. 2019), irrigation (Julier and Roulston 2009) and pesticides (Willis Chan et al. 2019) on ground-nesting bees, but more research is needed on different species of ground-nesters, other than squash bees, and their reproductive output. We still know little about the effects of agrochemicals on survival of ground-nesting bees, whether at the underground larval stages or as adults, but recent studies have begun to show impacts of pesticides on bees through exposure to contaminated soil (Anderson and Harmon-Threatt 2019, Willis Chan et al. 2019). There are also many unanswered questions related to the impacts on bee populations of agricultural machinery in settings that could be attractive nesting habitat for ground-nesters, but that could act as ecological traps if nests are subsequently destroyed. Similarly, we know little about the consequences of cover crops, mulch, plastic cover or straw on the soil surface for the reproductive success of ground-nesting bees. Knowing more about nesting requirements would allow farmers to supply patches of undisturbed habitat suitable for ground-nesting bees, along with the necessary floral resources. One practice to create nesting resources is the development of patches of bare ground (Severns 2004, Gregory and Wright 2005) or sandy areas (Wesserling and Tscharntke 1995). Such techniques are used by gardeners but could be developed at a broader scale in urban and agricultural environments if shown to be effective.

Finally, studies are needed to quantify the importance for ground-nesting bee populations of soil habitat relative to other factors such as floral resources or natural enemies (Roulston and Goodell 2011). To be sure, nesting sites and food are non-substitutable resources, but it is unclear how often each of these limits bee populations in nature (or in human-modified habitats). Better understanding the variables that have a major influence on ground-nesting bees will help decision-makers, as well as interested members of the public, to provide habitat and conserve targeted species.

2.7. References

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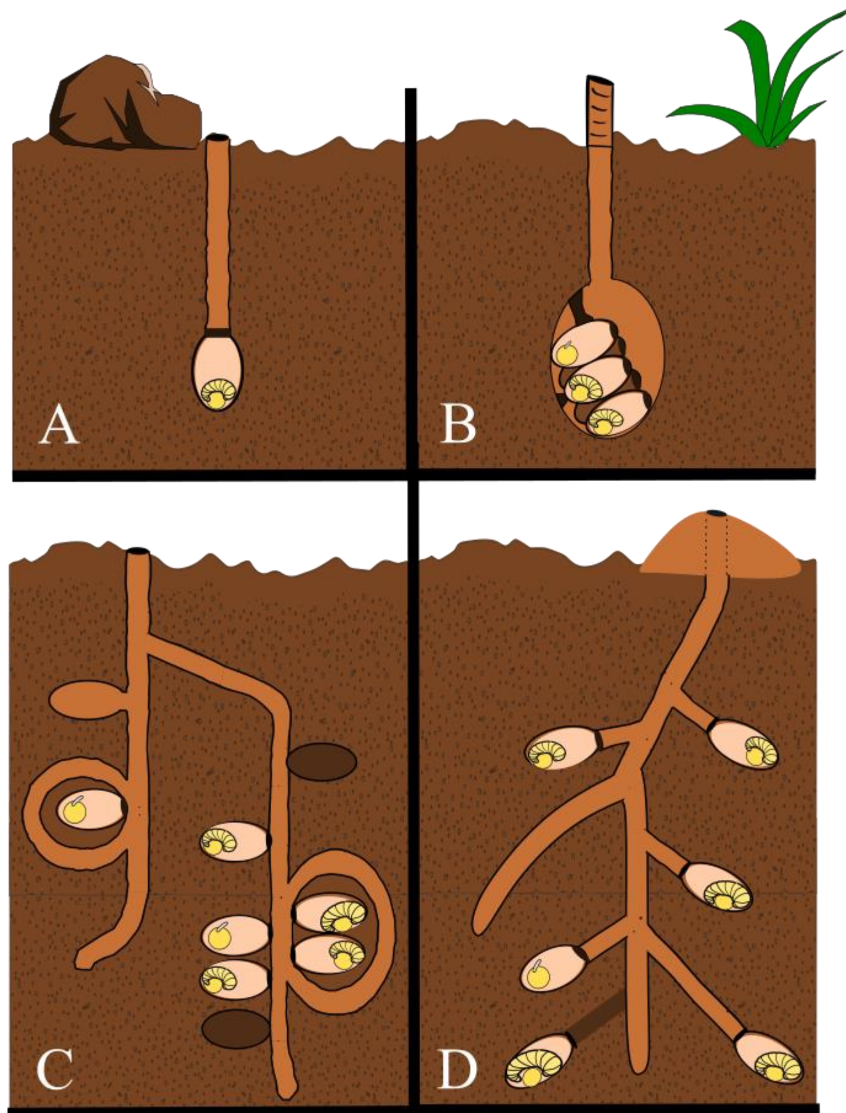

Figure 2-1: Variety of nest architecture seen in ground-nesting bees: A. One-celled nest with a plug as described by Roubik and Michener (1980) for *Epicharis zonata*. B. Turret forming the nest entrance, and brood cells piled in a chamber-like structure, as observed in halictid bees such as *Augochlorella striata*, following Packer et al. (1989). C. Nest composed of a main vertical gallery with lateral tunnels and brood cells directly connected to the main tunnels (cell in construction in lighter color and filled cells in darker brown). Some loops are surrounding a few cells as observed in *Halictus ligatus* by Packer & Knerer (1986) and as described for other Halictidae by Eickwort & Sakagami (1979). D. Nest entrance forming a tumulus and leading to brood cells connected to the main tunnel by short lateral tunnels, inspired by nests of *Peponapis pruinosa* described by Mathewson (1968) and some *Lasioglossum* sp. described by Sakagami & Michener (1962). Image created by Cécile Antoine and Philippe Tremblay.

Table 2-1: A non-exhaustive list of studies that have investigated the soil variables associated with ground-nesting (GN) bee nests, in reverse chronological order. Only studies that present quantitative data on soil variables (excluding soil disturbances such as tillage and fire) are included; see Supplementary Table S1 for a more comprehensive list. In 'Methods', 'manipulative' studies are those that experimentally modified one or more soil variables. Observational studies are listed as 'correlative' when the authors tested for an association between the response variable and one or more soil variables; 'descriptive' studies simply documented the values of one or more soil variables near nests (and therefore do not involve a response variable). We also note under 'Methods' any distinctive techniques that were used in the study (see *Methods for studying…*). Temp. = temperature; Abundance = abundance of adult GN bees; Richness = species richness of GN bees.

Study	**Species**	**Response variable(s)**	**Soil predictors**						**Method(s)**	**Region**
			Compaction[1]	Ground cover[2]	Texture	Temp.	Slope	Other:		
Maher *et al.* 2019	*Andrena cineraria* *Andrena fulva* *Halictus rubicundus* *Colletes hederae*			×			×	Shade	Descriptive Citizen science	Ireland United Kingdom
Olliff-Yang & Mesler 2018	*Habropoda miserabilis*	Phenology				×		Moisture	Correlational	California, USA
Pane & Harmon-Threatt 2017	Community of GN bees (18 species)	Nest presence		×				Moisture	Correlational Emergence traps	Illinois, USA
Fortel *et al.* 2016	Community of GN bees (37 species)	Abundance Diversity Richness			×				Manipulative Artificial habitat	France
Sardiñas *et al.* 2016	Community of GN bees (10 species) *Halictus* sp. *Lasioglossum* sp.	Abundance Nest presence Richness	×	×	×		×	Irregularities[3]	Correlational Emergence traps	California, USA
López-Uribe *et al.* 2015	*Colletes inaequalis*	Nest presence		×	×		×		Correlational Spatial modelling	New York, USA

Cane 2015	*Halictus rubicundus*	Nest number				×		Stones (pebbles)	Manipulative	Utah, USA
Sardiñas & Kremen 2014	Community of GN bees (54 species)	Abundance	×	×			×	Irregularities	Correlational Emergence traps	California, USA
Vinchesi *et al*. 2013	*Nomia melanderi*	Phenology				×			Manipulative	Washington, USA
Xie *et al*. 2013	*Andrena camellia*	Nest number	×	×	×	×		Moisture	Correlational	China
Polidori *et al*. 2010	*Lasioglossum malachurum*		×	×	×		×	Stones pH	Descriptive	Italy
Grundel *et al*. 2010	All bees (170 species)	Abundance Richness Community composition		×	×			Organic matter Shade	Correlational	Indiana, USA
Kim *et al*. 2006	*Halictus tripartitus* *Halictus ligatus* *Lasioglossum (Dialictus)* 6 species of GN bees	Nest number	×	×					Correlational Emergence traps	California, USA
Potts *et al*. 2003, 2005	All bees (116 species in 1999 and 170 over 1999–2000)	Abundance Richness	×	×			×	Irregularities	Correlational	Israel
Wuellner 1999	*Dieunomia triangulifera*	Nest number	×	×		×		Sun exposure Moisture Irregularities	Correlational	Kansas, USA
Potts & Willmer 1997	*Halictus rubicundus*	Nest number	×	×		×	×	Moisture Stones	Correlational	United Kingdom
Cane 1991	32 species of GN bees				×	×		Moisture	Descriptive	USA

[1] Also called soil hardness.
[2] Includes categories such as vegetation cover, bare ground, litter, etc.
[3] e.g., cracks in the soil and small cavities

2.8. Supplementary Information

Table 2-S1: A non-exhaustive list of primary research articles that have investigated the habitat associated with ground-nesting (GN) bees. Bee species names are given as reported in the original paper. Variables are listed as predictor (P) or response (R) where appropriate. Under 'Approach', 'manipulative' studies are those that experimentally modified one or more variables; 'method' studies focused on one method for studying GN bees; 'correlative' studies are observational studies where the authors tested for an association between the response variable and one or more predictors; and 'descriptive' studies generally documented the nesting biology of ground-nesting bee species (nesting behaviour, pollen provisions, developmental stages, etc.). Studies are listed in reverse chronological order of publication.

References	Bee sp. (from paper)	Bee family	# sp.	Region	Variables	Approach	Methods	Habitat
Melin & Colville (2019)	*Rediviva intermixta*	Melittidae	1	South Africa	Nesting biology	descriptive	Observations on a mound of harvester termite	desert
Skidmore *et al.* (2019)	*Peponapis pruinosa*	Apidae	1	Ohio, USA Kentucky, USA	Number of nests (R) Nest density: number of nests/m^2/female bee (R) Tillage type (P): strip tillage vs plasticulture	manipulative	Visual nest counts near squash plants Capture and release of males and females inside tunnel	agricultural fields greenhouse tunnel
Willis Chan *et al.* (2019)	*Peponapis pruinosa*	Apidae	1	Ontario, Canada	Mean pesticide residue concentrations (R) Matrix: soil, pollen, nectar (P) Developmental stage: adult vs larvae (P)	correlative	Pesticide residues in 18 farms growing squash	agricultural fields
Maher *et al.* (2019)	*Andrena cineraria* *Andrena fulva* *Halictus rubicundus* *Colletes hederae*	Andrenidae Halictidae Colletidae	4	UK Ireland	Number of nests (R) Soil characteristics (P): vegetation/bare ground, shade/sun exposure, flat/slope	correlative	Citizen science: observations made by participants; photographs checked by experts	urban and agricultural areas
Rozen *et al.* (2019)	*Caupolicana yarrowi* *Triepeolus grandis*	Colletidae	1	Arizona, USA	Nesting biology Nest architecture Developmental stages	descriptive	Nest excavation	desert
Marinho *et al.* (2018)	*Epicharis analis* *Epicharis fasciata*	Apidae	2	Brazil	Nest excavation techniques: powder of Paris vs rubber refill	method	Nest excavation	garden, urban area

Olliff-Yang & Mesler (2018)	*Habropoda miserabilis*	Apidae	1	California, USA	Nesting phenology: start, peak and end date (R) Nesting activity: active nests counts (R) Soil characteristics: temperature at 1 cm and 25 cm below surface (P), moisture at 1 cm below surface (P)	correlative	Observation of nesting activity at 17 aggregations found in previous years	coastal dunes
Hanson & Ascher (2018)	*Anthophora (Melea) bomboides*	Apidae	1	San Juan Islands, USA	Number of nests Nest density	descriptive	Observation of a known aggregation Nests counts + net surveys	coastal dunes
Rozen (2018)	*Protozaea gloriosa* *Oxaea flavescens* *Oxaea austera* *Mesoxaea nigerrima*	Andrenidae	4	New Mexico, USA	Nesting biology Developmental stages Nest architecture	descriptive	Nest excavation	desert
da Rocha-Filho & Melo (2017)	*Monoeca haemorrhoidalis* *Protosiris gigas*	Apidae	2	Brazil	Bee abundance (R) Cleptoparasite number (P) Bee sex ratio (P) Phenology: period of sampling (P)	correlative	Observation of a known nest aggregation (from da Rocha-Fillo and Melo 2011) Emergence traps	forest
Pane & Harmon-Threatt (2017)	GN bees		18	Illinois, USA	Bee species richness (R) Bee abundance (R) Floral abundance (P) Floral diversity (P) Soil characteristics: soil moisture (P), bare ground % (P)	method + correlative	Traps: emergence traps, pan traps, blue vane traps	prairies
Orr *et al.* (2016)	*Anthophora* (*Anthophoroides*) *pueblo*	Megachilidae	1	Utah, USA	Soil (sandstone) hardness Sandstone composition	descriptive	Sandstone samples were collected in the field and brought back to lab. Specimens of bees emerging from nests were collected. Description of a new species	desert, sandstone
Fortel *et al.* (2016)	GN bees + cavity-nesting bees		37	France	Bee abundance (R) Bee species richness (R) Soil characteristics: texture (P), shade (P), vegetation (P)	manipulative	Artificial nesting bed in field (soil squares) Capture with emergence traps and nets	urban area
Renauld *et al.* (2016)	*Andrena nasonii*	Andrenidae	1	New York, USA	Bee size: inter-tegular distance (R) and head capsule width (R) Agricultural intensification (P)	manipulative	Sweep netting	agricultural fields

Sardiñas *et al.* (2016)	*Halictus* spp. *Lasoglossum* spp.	Halictidae	10	California, USA	Bee incidence (R) Bee species richness (R) Soil characteristics: bare ground % (P), slope (P), compaction (P), soil texture (P)	correlative	Emergence traps, sweep netting	agricultural fields hedgerows
Ullmann *et al.* (2016)	*Peponapis pruinosa*	Apidae	1	California, USA	Number of emerging offspring (R) Sex ratio: proportion of male offspring (R) Mean emergence day (R) Tillage incidence or control (P)	manipulative	Flight cages: release 40 individual bees (2 females + 2 males per cage) Blue vane traps to capture emerging bees the next spring	agricultural fields greenhouse tunnel
Pietsch *et al.* (2016)	*Augochloropsis caerulans*	Halictidae	1	Brazil	Nesting biology	descriptive	Nest excavation (nests under water)	riverbank
Shebl *et al.* (2016)	*Eucera nigrilabris*	Apidae	1	Egypt	Soil characteristics: texture, hydraulic conductivity, bulk density, electrical conductivity, soil pH, soluble cations and anions	descriptive	Nest excavation + sweep netting	riverbank
Graham *et al.* (2015)	*Anthophora abrupta*	Megachilidae	1	Florida, USA	Number of nests	descriptive	Artificial nesting structure	
López-Uribe *et al.* (2015)	*Colletes inaequalis*	Colletidae	1	New York USA	Genetic diversity and relatedness in population (R) Nesting location (P) Geographic distance between nesting aggregation (P) Soil texture: % sand (P)	correlative	Surveys for nesting aggregations, sweep netting Females collected from each aggregation + microsatellite genotyping Predictive spatial model for suitable nesting habitat	urban area
Cane (2015)	*Halictus rubicundus*	Halictidae	1	Utah, USA	Number of nests (R) Soil characteristics: surface with pebbles or control (P) Soil temperature measured 5 cm below soil surface (P)	manipulative	Observation of a known aggregation (by author)	urban area
Sardiñas & Kremen (2014)	GN bees		15	California, USA	Bee species richness (R) Soil characteristics (P): bare ground %, vegetation, litter, cavities, cracks, slope, soil compaction	correlative	Traps: emergence traps, pan traps, nets	agricultural fields hedgerows
Ramos & Rozen (2014)	*Psaenythisca flavifrons* *Psaenythisca wagneri* *Psaenythisca punctata*	Andrenidae	3	Argentina	Nesting biology	descriptive	Nest excavation (up to 2 m below ground) Observation of adult voucher specimens from collections and comparisons with samples collected on the field	

Vinchesi *et al.* (2013)	*Nomia melanderi*	Halictidae	1	Washington, USA	Number of nests (R) Phenology: % emergence (R) Treatment (P): chalk charcoal dust, white chalk dust, clear plastic, control Soil temperature (P)	manipulative	Artificial nesting beds	agricultural fields
Xie *et al.* (2013)	*Andrena camellia*	Halictidae	1	China	Number of nests (R) Phenology: % emergence (R) Habitat type (P): base vs summit hill and near vs far from human settlements Vegetation (P): cover and height Soil characteristics (P): temperature, water content, bulk density, hardness	correlative	Nest counts near host plants	agricultural fields
Houston & Maynard (2012)	*Leioproctus (Ottocolletes) muelleri*	Colletidae	1	Australia	Nesting biology	descriptive	Sweep netting Taxonomic notes	natural habitat bushland
Sarzetti & Genise (2011)	*Diadasia hirta*	Apidae	1	Argentina	Nesting biology	descriptive	Nest excavation	agricultural fields
Kuhlmann & Timmermann (2011)	*Samba (Prosamba) spinosa*	Melittidae	1	South Africa	Nesting biology	descriptive	Nest excavation	agricultural fields semiarid area
Cane & Neff (2011)	GN bees + cavity-nesting bees	Megachilidae	2	USA	Offspring survival (R) Temperature (P) Developmental stages	manipulative + review	Laboratory: thermal tolerance experiments on *Osmia lignaria* and *Megachile rotundata* at different life stages: adult, larvae, egg. Cocoons were placed in moist sand and heated at different temperatures. Review on the cell depth of 449 GN bee species.	
Polidori *et al.* (2010)	*Lasioglossum malachurum*	Halictidae	1	Italy	Bee species richness (R) Soil characteristics (P): texture, organic matter, pH, vegetation cover, stones, slope, soil compaction Floral resources (P)	correlative	Survey for nests on site	agricultural fields

Grundel *et al.* (2010)	All bees		229	Indiana, USA	Bee abundance (R) Bee species richness (R) Habitat type (P) Floral resources (P) Soil characteristics (P): particles size, organic content, % bare ground, litter, canopy cover	correlative	Traps: pan traps, nets Bees identified and sorted by nesting habits	costal dunes savanna prairies woodland forest
Julier & Roulston (2009)	*Peponapis pruinosa* *Bombus impatiens* *Apis mellifera*	Apidae	3	Virginia, USA Maryland, USA	Bee abundance (R) Number of nests (R) Tillage vs no-till (P) Irrigation vs control (P) Vegetation cover (P) Clay content (P)	manipulative + correlative	Count of insects on squash flowers in transects on 20 farms Use of row covers in crop and edges in one farm Survey for nests under squash plants Use of a screenhouse on experimental farm. Release of 98 females and 45 males in a large screenhouse and nest surveys	agricultural fields screen house
Rozen (2008)	*Calliopsis zebrata*	Andrenidae	1	Arizona, USA Oklahoma, USA	Nesting biology	descriptive	Nest excavation Comparison of specimens with the collection from C. D. Michener Taxonomic descriptions	cemetery unpaved road
Cane (2008)	*Nomia melanderi*	Halictidae	1	Washington, USA	Number of nests (R) Nest density (R) Year (P)	correlative	56 artificial nesting beds: survey of population trends over 8 years 10-20 quadrats of 1 m^2 placed on aggregation to estimate population size	agricultural fields
Rozen (2008a)	*Nomioides patruelis* *Chiasmognathus pashupati*	Halictidae	2	Pakistan	Nesting biology	descriptive	Taxonomic descriptions	
Miliczky (2008)	*Andrena (Plastandrena) prunorum*	Andrenidae	1	Washington, USA	Nesting biology	descriptive	Nest excavation	urban area
Kim *et al.* (2006)	*Halictus tripartidus* *Halictus ligatus* *Lasioglossum (Dialictus)*	Halictidae	8	California, USA	Bee abundance (R) Bee species richness (R) Number of nests (R) Soil characteristics (P): vegetation cover, soil hardness Distance from farms: Near or Far (P)	correlative	Emergence traps made with row cover fabric	agricultural fields

Weissel *et al.* (2006)	*Lasioglossum malachurum*	Halictidae	1	Germany	Nesting activity: duration of pauses and activity periods (R) Soil temperature (P)	manipulative	Heated subterranean pipes allowed observations at higher temperature versus control	urban area
Celary (2006)	*Melitta leporina*	Melittidae	1	Poland	Nesting biology	descriptive	Nest site surveys along a transect in alfalfa field Nest excavation	agricultural fields
Gregory & Wright (2005)	ground-nesting bees + wasps		46	England	Bee species richness	descriptive	Artificial nesting area: creation of open ground for ground-nesting bees and wasps	natural habitat
Potts *et al.* (2005)	All bees		174	Israel	Bee abundance (R) Bee species richness (R) Soil characteristics (P): % bare ground, slope, soil compaction	correlative	Bee captures by sweep netting on transect walks	semiarid pine forest
Gonzalez & Chavez (2004)	*Anthophora walteri*	Megachilidae	1	Colombia	Nesting biology	descriptive	Nest excavation Taxonomic description	semiarid area
Richards (2004)	*Halictus ligatus*	Halictidae	1	Ontario, Canada	Nesting biology Daily activity Social behaviour	descriptive	Nest excavation, female individual marked	
Fellendorf *et al.* (2004)	*Andrena vaga*	Andrenidae	1	Germany	Female bees' number Offspring emerged number	descriptive	Emergence traps + nest sites surveys Test cell resistance submerging 9 brood cells in water	riverbank
Aguiar & Gaglianone (2003)	*Centris (Centris) aenea*	Apidae	1	Brazil	Nest architecture Nesting activity	descriptive	Nest sites surveys Nest excavation	tropical semiarid climate urban area
Antonini *et al.* (2003)	*Diadasia distincta*	Apidae	1	Brazil	Number of nests (P) Mortality rate (P) Population size (P) Parasitism ratio (R) Number of parasites (R)	correlative	Population size estimated by netting and marking bee individuals Fungi isolated from brood cells	unpaved road
Wcislo & Schatz (2003)	*Lasioglossum umbripenne*	Halictidae	1	Panama	Bee behaviour at the nest entrance Ant predation	descriptive	Observations at the nest entrances of female bees back from foraging trip	unpaved road
Cane (2003)	*Nomia melanderi*	Halictidae	1	Washington, USA	Number of nests	descriptive	Estimation of excess soil brought to surface	agricultural fields
Norden *et al.* (2003)	*Perdita (Alloperdita) floridensis*	Andrenidae	1	Florida, USA	Nesting biology Daily activity	descriptive	Nest site surveys Nest excavation	sandy pond

Potts *et al.* (2003)	All bees		174	Israel	Bee abundance (R) Bee species richness (R) Soil characteristics (P): vegetation cover, slope, soil compaction Floral resources (P)	correlative	Sweep netting on transect walks	semiarid pine forest
Neff (2003)	*Panurginus polytrichus* *Holcopasites rozeni*	Andrenidae + Apidae	2	Texas, USA	Nesting biology	descriptive	Nest excavation	savannah unpaved road
Soucy (2002)	*Halictus rubicundus*	Halictidae	1	Colorado, USA Utah, USA	Number of nests (R) Reproductive output (R) Proportions of male offspring (R) Year (P) Date (P)	correlative	Nest excavation Observations of behaviour	3 sites: alpine area unpaved road in agricultural fields urban area
Richards (2001)	*Halictus sexcinctus*	Halictidae	1	Greece	Number of brood Number of individuals/nests Bee size: head width, wing length Social behaviour	descriptive	Nest excavation Behavioural observations Dissection of females	semiarid area
Richards & Packer (2000)	*Lasioglossum malachurum*	Halictidae	1	Ontario, Canada	Nesting biology Colony survival Number of individuals/nests Weather conditions: degree-day accumulation + rainfall	descriptive	Nest excavation Behavioural observations	
Wcislo (1999)	*Calliopsis hondurasicus*	Andrenidae	1	Panama	Nesting biology	descriptive	Nest excavation Individuals marked	coastal area near tropical forest
Paxton *et al.* (1999)	*Andrena scotica* *Panurgus calcaratus*	Andrenidae	2	Sweden Germany	Nesting biology	descriptive	Laboratory Social behaviour	laboratory
Paxton *et al.* (1999a)	*Andrena agilissima*	Andrenidae	1	Italy	Nesting biology Mating behaviour Phenology: emergence patterns	descriptive	Emergence traps Emergence patterns: number of individuals/dates	semiarid area
Danforth (1999)	*Perdita portalis*	Andrenidae	1	Arizona, USA New Mexico, USA	Nesting biology Phenology: date of emergence (R) Sex (P) Body size (P) Number of larvae pupating per day (R) Early rainfall vs late rainfall (P)	correlative + manipulative	Nest excavation Laboratory rearing Museum collections: comparison of specimens	desert-grassland

Wuellner (1999)	*Dieunomia triangulifera*	Halictidae	1	Kansas, USA	Number of nestss (R) Soil characteristics (P): moisture, surface irregularities, compaction, vegetation cover, light, surface temperature Conspecifics: presence of tumuli (P) Distance to visual landmarks (P)	correlative	Observation of a known aggregation (in Minckley 1994) Handmade tumuli	agricultural fields
Barthell *et al.* (1998)	*Habropoda depressa*	Apidae	1	California, USA	Nesting biology Daily activity	descriptive	Observation of a known aggregation (in Fowler 1899) Nest excavation Museum collection	urban area coastal area
Potts & Willmer (1998)	*Halictus rubicundus*	Halictidae	1	UK	Number of nests (R) Distance to nearest neighbouring nest(P) Length of lateral tunnels (P)	correlative	Quadrats to study nest density and nearest-neighbour distances Nest excavation	agricultural fields
Mayer & Miliczky (1998)	*Nomia melanderi*	Halictidae	1	Washington, USA	Nesting biology Phenology: number of individuals emerged/date Sex ratio	descriptive	Artificial nesting bed Emergence traps	agricultural fields
Neff & Simpson (1997)	*Andrena (Callendrena) rudbeckiae*	Andrenidae	1	Texas, USA	Nesting biology Daily activity	descriptive	Nest excavation Individuals marked Emergence cups	riverbank + unpaved road
Potts & Willmer (1997)	*Halictus rubicundus*	Halictidae	1	UK	Number of nestss (R) Distance to nearest nest (P) Soil characteristics (P): soil compaction, slope, vegetation cover, stones, soil temperature, moisture, pH	correlative	Measures on 1 m^2 quadrats. Females marked in one site, natal nest and newly found nest marked to assess philopatry	agricultural fields
Cane (1996)	*Trachusa larreae*	Megachilidae	1	Arizona, USA	Nesting biology	descriptive	Nest excavation	desert
Mueller (1996)	*Augochlorella striata*	Halictidae	1	New York, USA	Nesting biology Sex ratio	descriptive	Nest searching: looking at returning females or "through the grass" to find new nests Individuals marked + measured Nest excavations	pond embankment urban area
Cameron *et al.* (1996)	*Melissodes rustica*	Apidae	1	Arkansas, USA	Nesting biology Daily activity	descriptive	Individual females marked; nest marked Nest excavations	urban area
Batra & Norden (1996)	*Anthophora abrupta* *Antophora pilipes villosula*	Megachilidae	2	Washington, USA	Nesting biology Daily activity	descriptive	Laboratory rearing	

Martins *et al.* (1996)	*Ptilothrix plumata*	Apidae	1	Brazil	Nesting biology Phenology: emergence patterns Nest density Soil characteristics: compaction, slope	descriptive	Observation of a known aggregation (from Martins and Almeida 1994; Martins and Antonini 1994) Individual females marked	sand banks, unpaved road
Wuellner & Jang (1996)	*Crawfordapis luctuosa*	Colletidae	1	Costa Rica	Nesting biology Daily activity	descriptive	Known aggregation (from Otis et al 1982) Individual females marked, nest marked Nest excavations	tropical forest
Miliczky & Osgood (1995)	*Andrena (Melandrena) vicina*	Andrenidae	1	Maine, USA Washington, USA	Nesting biology Daily activity	descriptive	Nest excavations	Agricultural fields Urban area
Richards & Packer (1995)	*Halictus ligatus*	Halictidae	1	Ontario, Canada	Nesting biology Sex ratio	descriptive	Known aggregation (from Packer 1986) Nest excavations	
Sick *et al.* (1994)	*Sphecodes* sp. *Lasioglossum malachurum* *Lasioglossum pauxillum* *Halictus maculatus*	Halictidae	9	Sweden Germany	Nesting biology Parasitism Daily activity	descriptive	Observations of nests in the field Laboratory rearing Artificial nests	
Brünnert *et al.* (1994)	*Lasioglossum malachurum* *Dasypoda hirtipes*	Halictidae	2	Germany	Nest location (R) Size (P) and distance from landmarks (P) Landmark height (P)	manipulative	Use of a black cylinder (of different sizes) near nest entrance as a landmark	
Martins & Antonini (1994)	*Diadasia distincta*	Apidae	1	Brazil	Nesting biology Daily activity	descriptive	Observation of a known aggregation (from Pimenta 1988) Nest excavation	urban area
Cane (1994)	*Habropoda laboriosa*	Apidae	1	Alabama, US	Nesting biology	descriptive	Emergence traps Nest excavation	agricultural fields
Minckley *et al.* (1994)	*Dieunomia triangulifera*	Halictidae	1	Kansas, USA	Nesting biology Phenology: number individuals emerged/date Sex ratio Daily activity	correlative	Known aggregation Traps: emergence traps, nets Nests excavation	agricultural fields
Visscher *et al.* (1994)	*Calliopsis pugionis*	Andrenidae	1	California, USA	Phenology: emergence patterns (R) Sex ratio (R) Soil humidity (P) Date (P)	correlative	Observation of a known aggregation (from Visscher and Danforth 1993) Emergence traps Nest excavations	riverbank

Wcislo (1993)	*Nomia tetrazonata* *Dieunomia heteropoda* *Triepeolus verbesinae* *Triepeolus distinctus*	Halictidae + Apidae	4	Arizona, US	Nesting biology Ground temperature	descriptive	Nest excavation Emergence traps with plastic cups over nest entrances	grassland semiarid area
Rozen (1993)	*Sphecodosoma dicksoni* *Conanthalictus conanthi* *Rophites trispinosus*	Halictidae	3	California, USA New Mexico, USA	Nesting biology	descriptive	Observation of a known nests (from Rozen and McGinley 1976) Nest excavation	desert unpaved road
Visscher & Danforth (1993)	*Calliopsis pugionis*	Andrenidae	1	California, USA	Nesting biology Soil moisture Daily activity Sex ratio	correlative	Nest searching in areas where bees were caught on flowers Nest excavations	desert urban area
Wcislo *et al.* (1993)	*Lasioglossum (Dialictus) figueresi* *Lasioglossum (Dialictus) aeneiventre*	Halictidae	2	Costa Rica	Nesting biology Daily activity	descriptive	Nest excavation	agricultural fields
Neff & Simpson (1992)	*Diadasia rinconis*	Apidae	1	Texas, US	Nesting biology	descriptive	Nest excavation	desert-grassland
Miliczky (1991)	*Perdita gerhardi* *Calliopsis coloradensis* *Pseudopanurgus rugosus*	Andrenidae	3	Illinois, USA	Nesting biology Daily activity	descriptive	Nest excavation	forest
Vinson & Frankie (1991)	*Centris aethyctera*	Apidae	1	Costa Rica	Nesting biology	correlative	Observation of a known nest site (from Vinson and Frankie 1977; Vinson and Frankie 1988) Nest excavation	savanna, volcanic rocks
Danforth (1991)	*Perdita portalis*	Andrenidae	1	New Mexico, USA	Nesting biology Mean number individuals/nests. Sex ratio Daily activity	manipulative + correlative	Nest excavation Laboratory rearing	desert-grassland
Neff & Danforth (1991)	*Perdita texana*	Andrenidae	1	Texas, USA	Nesting biology Mean number of females/nests Date Daily activity	descriptive	Nest excavation	desert-grassland

Cane (1991)	GN bees		32	USA	Bee species (R) Bee size (P) Soil characteristics (P): soil temperature, moisture, texture	correlative	Nest excavation Soil near shallowest provisioned cell sampled and analyzed	
Danforth (1990)	*Calliopsis (Hypomacrotera) persimilis*	Andrenidae	1	New Mexico, USA	Nesting biology Daily activity Nest architecture Sex ratio (R) % female produced (R) Date (P)	correlative	Nest excavations	desert-grassland unpaved road
Rozen & Buchmann (1990)	*Centris caesaliniae* *Centris pallida* *Ericrocis lata*	Apidae	3	Arizona, USA	Nesting biology Nest density Nest architecture	descriptive	Nest excavation	desert-scrubs
Chapman *et al.* (1990)	*Peponapis pruinosa*	Apidae	1	Ontario, Canada	Nest architecture	method	Method using fiberglass resin for nest excavation	
Osgood (1989)	*Andrena crataegi*	Andrenidae	1	Maine, USA	Nesting biology	descriptive	Nest excavation	agricultural field
Cane (1989)	*Perdita (Alloperdita) bradleyi*	Andrenidae	1	Alabama, US	Nesting biology Phenology: emergence patterns	descriptive	Nest excavation	
Danforth (1989)	*Perdita (Perdita) difficilis* *Perdita luciae* *Perdita (Cockerellia) coreopsidis* *Perdita (Cockerellia) albipennis*	Andrenidae	4	Arizona, USA New Mexico, USA Kansas, USA	Nesting biology Daily activity Phenology Mean number of females/nests	descriptive	Individual females marked Nest excavations	multiple sites: desert-grassland, agricultural fields
Packer *et al.* (1989)	*Augochlorella striata* *Lasioglossum (Evylaeus) comagenese* *L. (Evylaeus) cinctipes* *L. (Dialictus) laevissimum*	Halictidae	4	Nova Scotia, Canada	Nesting biology Number of nests Brood cells vs surrounding soil (R) Soil characteristics (P): temperature, moisture Nest architecture	correlative	Nest position marked Nest excavation Cell examination for sources of mortality	roadside
Torchio *et al.* (1988)	*Colletes kincaidii*	Colletidae	1	California, USA	Nesting biology Nest construction behaviour Nest architecture Developmental stages	descriptive	Nest excavation Removal of soil blocks containing overwintering larvae from nesting site to lab Laboratory rearing: artificial nest in glass tube	sandstone cliffs

Torchio & Burdick (1988)	*Colletes kincaidii* *Epeolus compactus*	Colletidae + Apidae	2	California, USA	Nesting biology Nest architecture Parasitism Developmental stages	descriptive	Nest excavation Cells found in the field (in blocks of sandstones) and brought to lab. Bee emergence monitored	sandstone cliffs
Crozier *et al.* (1987)	*Lasioglossum zephyrum*	Halictidae	1	Kansas, USA	Genetic relatedness (within and between aggregations)	descriptive	Bees sampled from aggregations Polymorphic allozyme loci	riverbank
Batra (1987)	*Dialictus laevissimus*	Halictidae	1	Maryland, USA	Nesting biology Nest architecture Daily activity Developmental stages	descriptive	Nest excavation Individuals sampled and dissected Females marked and recaptured to estimate population size	agricultural fields
Rozen (1987)	*Ashmeadiella holtii* *Stelis elongativentris*	Megachilidae	2	New Mexico, USA	Nesting biology Nest architecture Developmental stages	descriptive	Nest excavation Taxonomic description	desert-grassland unpaved road
Kukuk & Schwarz (1987)	*Lasioglossum (Chilalictus) erythrurum*	Halictidae	1	Victoria, Australia	Nesting biology Social behaviour	descriptive	Nest excavated and brought to lab	urban area
Schmidt & Schmidt (1986)	*Lasioglossum kinabaluense*	Halictidae	1	Borneo, Malaysia	Nesting biology Nest architecture	descriptive	Nest excavations	clay bank
Torchio & Trostle (1986)	*Anthophora urbana urbana* *Xeromelecta californica*	Apidae	2	California, USA Utah, USA	Nesting biology Nest architecture Parasitism Developmental stages	descriptive	Females caught and released in greenhouse	embankment greenhouse
Eickwort & Kukuk (1986)	*Dufourea novaeangliae*	Halictidae	1	New York, USA	Nesting biology Nest architecture Developmental stages Parasitism	descriptive	Nest excavation	lakeshore
Packer & Knerer (1986)	*Halictus ligatus*	Halictidae	1	Florida, USA	Nesting biology Social behaviour Phenology Bee size (head width)	descriptive	Nest excavation	coastal area

Packer & Knerer (1986b)	*Halictus ligatus*	Halictidae	1	Ontario, Canada	Nesting biology Nest architecture Vegetation cover Parasitism Pollen load	descriptive	Nest excavation	road bank
Brooks & Michener (1985)	*Tetralonia lepida*	Apidae	1	Oklahoma, USA	Nest architecture	descriptive	Nest excavation	prairie pasture
Bennett & Breed (1985)	*Perdita opuntiae*	Andrenidae	1	Colorado, USA	Nesting biology Floral resources Mating Parasitism Number of nests	descriptive	Nest site searching	sandstones
Rozen (1984)	*Ptiloglossa arizonensis* *Ptiloglossa fulvopilosa* *Ptiloglossa jonesi* *Ptiloglossa guinnae* *Crawfordapis luctuosa* *Policana albopilosa*	Colletidae	6	Arizona, USA	Nesting biology Nest architecture Developmental stages Parasitism	descriptive	Nest excavation	desert
Houston (1984)	*Ctenocolletes smaragdinus* *C. tigris* *C. ordensis* *C. centralis* *C. nicholsoni* *C. fulvescens* *C. albomarginatus* *C. rufescens* *C. tricolor*	Stenotritidae	9	Australia	Nesting biology Daily activity Floral resources Mating Nest architecture	descriptive	Nest excavation	desert
Ordway (1984)	*Diadasia opuntiae*	Apidae		Arizona, USA	Nesting biology Nest architecture Desert bee	descriptive	Nest excavation	

Norden (1984)	*Anthophora abrupta*	Apidae	1	Maryland, USA	Nesting biology Phenology Mating Soil surface temperature Floral resources Developmental stages	descriptive	Artificial nesting structures; screen cage made with a wood frame, filled with clay Laboratory rearing	agricultural fields
Coville *et al.* (1983)	*Centris segregata*	Apidae	1	Costa Rica	Nesting biology Nest architecture Developmental stages	descriptive + review	Nest excavation	Riverbank in tropical forest
Parker & Griswold (1982)	*Andrena haynesi*	Andrenidae	1	Utah, USA	Nesting biology Nest architecture	descriptive	Nest excavation	desert, sand dunes
Neff *et al.* (1982)	*Diadasia afflicta*	Apidae	1	Texas, USA	Nesting biology Daily activity Nest architecture Mating	descriptive	Nest excavation	urban area
Eickwort (1981)	*Agapostemon sericeus* *A. cockerelli* *A. texanus* *A. angelicus* *A. splendens*	Halictidae	5	New York, USA Arizona, USA California, USA Georgia, USA	Nesting biology Nest architecture	descriptive + review	Nest excavations Some aggregations were known by author	
Johnson (1981)	*Andrena dunningi*	Andrenidae	1	Indiana, USA	Nest architecture Nesting biology Floral resources Developmental stages	descriptive	Nest excavation	urban area
Rust (1980)	*Ptilothrix bombiformis*	Apidae	1	Delaware, USA	Number of nests Nest architecture Nesting biology Developmental stages Floral resources	descriptive + review	Nest excavation	coastal area
Batra (1980)	*Anthophora antiope*	Apidae	1	India	Nest architecture	descriptive	Nest excavation	riverbank
North & Lillywhite (1980)	*Diadasia bituberculata*	Apidae	1	California, USA	Nest architecture	descriptive	Turret excavation	unpaved road
Roubik & Michener (1980)	*Epicharis zonata*	Apidae	1	French Guiana	Nest architecture Nesting biology Developmental stages Floral resources	descriptive	Nest excavations	forest-savanna edge

Alcock (1979)	*Centris pallida*	Apidae	1	Arizona, USA	Nesting biology Nest architecture Body size	descriptive	Nest searching by finding tumulus Nest excavation	desert
Eickwort & Sakagami (1979)	*Rhinocorynura inflaticeps*	Halictidae	1	Brazil	Nesting biology Nest architecture	descriptive + review	Observation of a known site (from Sakagami and Moure 1967) Nest excavation	roadside bank
Rajotte (1979)	*Colletes validus*	Colletidae	1	Connecticut, USA	Nest architecture Mating Nesting biology Floral resources Developmental stages	descriptive	Nest excavation	riverbank
Batra & Schuster (1977)	*Centris transversa* *Centris anthracina* *Melissodes floris* *Colletes* sp.	Apidae + Colletidae	4	Guatemala	Nesting biology Nest architecture	descriptive	Nest excavation	roadside bank, subtropical forest
Eickwort (1977)	*Perdita octomaculata* *Perdita halictoides*	Andrenidae	2	New York, USA Florida, USA	Nest architecture Foraging and mating behaviour Daily activity	descriptive	Nest excavation	sand + gravel quarry
Alcock *et al.* (1976)	*Centris rhodopus* *Centris cockerelli resoluta* *Centris pallida*	Apidae	3	Arizona, USA	Nesting biology Nest architecture	descriptive	Nest excavation	floodplain site, desert
Bohart & Youssef (1976)	*Evylaeus galpinsiae*	Halictidae	1	Utah, USA	Nesting biology Floral resources Foraging activity Nest architecture Developmental stages Sex ratio	descriptive	Nest excavation	riverbank
Michener (1975)	*Paranthidium jugatorium* *Melitoma taurea*	Megachilidae + Apidae	2	Missouri, USA	Nesting biology Nest architecture	descriptive	Nest excavation	roadside bank

Houston (1975)	*Stenotritus pubescens*	Stenotritidae	1	Australia	Nesting biology Nest architecture Floral resources Daily activity Developmental stages Mating	descriptive	Nest excavation	arid region
Breed (1975)	*Lasioglossum rohweri*	Halictidae	1	Kansas, USA	Social behaviour Nest architecture Body size	descriptive	Nest excavation	prairies, roadside
Torchio (1975)	*Perdita nuda* *Sphecodes* sp.	Andrenidae + Halictidae	1	Idaho, USA	Nest architecture Developmental stages Parasitism	descriptive	Nest excavation	riverbank
Kamm (1974)	*Lasioglossum zephyrum*	Halictidae	1	Kansas, USA	Offspring body size (R) Temperature (P) Day length (P) Adult body size (head width) (P)	manipulative	Artificial nesting structures Laboratory rearing	
Bell *et al.* (1974)	*Lasioglossum zephyrum*	Halictidae	1	Kansas, USA	Nesting biology Social behaviour Nest defense Number of nests (R) Days (P)	manipulative + descriptive	Artificial nesting structure Laboratory rearing	
Eickwort & Eickwort (1973)	*Augochlorella edentata*	Halictidae	1	Costa Rica	Nesting biology Nest architecture Developmental stages Parasitism Social behaviour	descriptive	Nest excavation	roadside bank
Barrows (1973)	*Augochlora pura* *Lasioglossum coeruleum*	Halictidae	2	Kansas, USA	Nesting biology Nest architecture	manipulative + descriptive	Artificial nesting structure Laboratory rearing	
Clement (1973)	*Melissodes rustica*	Apidae	1	Wyoming, USA	Nesting biology Nest architecture Developmental stages	descriptive	Nest excavation	natural habitat
Roberts (1973)	*Oxaea flavescens*	Andrenidae	1	Colombia	Nest architecture Developmental stages	descriptive + review	Nest excavation	pasture near riverbank
May (1972)	*Augochlora pura*	Halictidae	1	Kansas, USA	Weight gain (R) Developmental stages (P) Moisture: % humidity (P Days (P)	manipulative	Cells collected from the field Laboratory rearing “Humidity chambers” made from small desiccator jars used for experiments	

Bohart *et al.* (1972)	*Emphoropsis pallida*	Apidae	1	Arizona, USA	Nesting biology Nest architecture Developmental stages	descriptive	Nest excavation	lakeshore, desert
Eickwort & Eickwort (1972)	*Augochlora nominata* *Augochlora pura* *A. cordiaefloris*	Halictidae	3	Costa Rica	Nesting biology Nest architecture Social behaviour Developmental stages Parasitism	descriptive + review	Nest excavation	unpaved road
Eickwort & Eickwort (1971)	*Dialictus umbripennis*	Halictidae	1	Costa Rica	Nesting biology Developmental stages Parasitism	descriptive	Nest excavation	unpaved roadside bank
Michener & Brothers (1971)	*Lasioglossum zephyrum*	Halictidae	1	Kansas, USA	Nesting architecture	method	Laboratory rearing Artificial nesting structure	
(Rozen 1970)	*Fidelia villosa*	Megachilidae	1	South Africa	Nesting biology Nest architecture Developmental stages	descriptive	Observation of a known nesting area (from Martinez 1968) Nest excavation	desert-grassland
Batra (1970)	*Nomia (Acunomia) melanderi*	Halictidae	1	Utah, USA	Nesting biology Nest architecture	descriptive + method	Laboratory rearing Artificial nesting structure	
Eickwort & Eickwort (1969)	*Agapostemon nasutus*	Halictidae	1	Costa Rica	Nesting biology Nest architecture Developmental stages Parasitism	descriptive	Nest excavation Marking of individuals	unpaved roadside
Youssef & Bohart (1968)	*Andrena candida*	Andrenidae	1	Utah, USA	Nesting biology Nest architecture Developmental stages	descriptive + review	Nest excavation	unpaved road
Torchio & Youssef (1968)	*Anthophora flexipes* *Zacosmia maculata*	Apidae	2	Utah, USA	Nest biology Nest architecture Developmental stages Parasitism	descriptive	Nest excavation	riverbank
Mathewson (1968)	*Peponapis pruinosa*	Apidae	1	Rhode Island, USA	Nesting biology Nest architecture	descriptive	Nest excavation	agricultural fields
Michener (1968)	*Nomia sp.* *Lasioglossum sp.* *Halictus jucundus*	Halictidae	9	South Africa, Cameroon	Nesting biology	descriptive	Nest excavation	Cameroon highlands, bush

Batra (1968)	*Lasioglossum (Dialictus) versatum* *L. zephyrum* *L. imitatum* *Halictus rubicundus* *Neocorynura fumipennis* *Augochlorella sp.*	Halictidae	6	Utah, USA	Nesting biology Nest architecture Nest construction	descriptive	Laboratory: artificial nesting substrate	
Torchio *et al.* (1967)	*Dufourea mulleri* *D. malacothricis* *D. pulchricornis* *D. trochantera* *Neopasites cressoni*	Halictidae	5	Arizona, USA Utah, USA	Nesting biology Nest architecture Developmental stages Parasitism	descriptive	Nests known to authors Nest excavation	desert-grassland riverbank
Michener & Kerfoot (1967)	*Pseudaugochloropsis costaricensisP. gramineaP. nigerrima*	Halictidae	3	Costa Rica	Nesting biology	descriptive	Nest excavation	
Ordway (1966)	*Augochlorella striata* *A. persimilis*	Halictidae	2	Kansas, USA	Nesting biology Nest architecture Phenology Social behaviour	descriptive	Laboratory rearing Nest excavation	
Michener *et al.* (1966)	*Neocorynura fumipennis*	Halictidae	1	Costa Rica	Nesting biology Nest architecture	descriptive	Nest excavation	riverbank
LaBerge & Ribble (1966)	*Agapostemon splendens* *A. radiatus* *A. texanus* *A. virescens*	Halictidae	4	Nebraska, USA	Nesting biology Nest architecture Developmental stages	descriptive	Nest excavation	lakeshore
Michener (1966)	*Lasioglossum versatum*	Halictidae	1	Kansas, USA	Nesting biology Floral resources Social behaviour	descriptive + review	Nest excavation	agricultural field
Batra (1966)	*Nomia capitata* *Nomia oxybeloides* *Nomia nasicana*	Halictidae	3	India	Nesting biology Nest architecture Social behaviour	descriptive	Nest excavation	

Torchio (1965)	*Colletes ciliatoides*	Colletidae	1	Utah, USA	Nesting biology Developmental stages	descriptive	Nest excavation	riverbank (drainage ditch)
Bohart (1964)	*Xenoglossa strenua*	Apidae	1	Maryland, USA	Nesting biology Nest architecture Developmental stages	descriptive	Nest excavation	agricultural field
Batra (1964)	*Lasioglossum zephyrum*	Halictidae	1	Kansas, USA	Nesting biology Social behaviour Nest architecture	descriptive	Laboratory rearing Artificial nesting substrate Nest excavation	
Blagovescenskaya (1963)	*Dasypoda plumipes*	Melittidae	1	Russia	Number of nests Nest architecture	descriptive	Nest excavation	
Michener & Ordway (1963)	*Perdita maculigera maculipennis*	Andrenidae	1	Kansas, USA	Nesting biology Phenology Nest architecture Developmental stages	descriptive	Nest excavation	riverbank
Sakagami & Hayashida (1961)	*Halictus duplex*	Halictidae	1	Japan	Nesting biology Nest architecture Sex ratio Developmental stages	descriptive + review	Based on nest excavations and published observations	
Michener (1960)	*Euryglossa subsericea* *Paracolletes incanescens*	Colletidae	2	Australia	Nesting biology Nest architecture Developmental stages	descriptive	Nest excavation	
Burdick & Torchio (1959)	*Hesperapis regularis*	Melittidae	1	California, USA	Nesting biology Nest architecture Developmental stages	descriptive	Nest known to authors Nest excavation	
Michener & Lange (1958)	*Paroxystoglossa jacosta*	Halictidae	1	Brazil	Nesting biology Phenology Nest architecture Developmental stages	descriptive	Nest excavation	

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Chapter 3: Associations between soil characteristics and ground-nesting bees on farms

A modified version is to be submitted for publication in a peer-reviewed journal.

3.1. Abstract

Much of the world's agricultural production depends on the pollination services provided by wild bees. Yet, agriculture changes landscapes and soils in ways that can alter bee habitat. Three-quarters of wild bee species nest underground, but little is known about their nesting requirements. In this study, we asked which soil factors (texture, hardness, slope, or ground cover) influence the abundance, species richness, diversity, and community composition of ground-nesting bees in agroecosystems around Ottawa, Canada. We measured soil characteristics and sampled the bee community at 131 plots on 35 farms (mostly orchards and market gardens) over a two-year period, and identified the ground-nesting bees to species. We collected 8,661 ground-nesting bees representing 102 species and 2,624 cavity-nesting bees, not identified to species level. Ground-nesting bee abundance and species richness were higher with increased percentages of bare ground and sand, while Simpson's diversity was negatively associated with slope. In contrast (but as expected), abundance of non-ground- nesting (cavity-nesting) bees was not related to any measured soil properties, suggesting that the associations between soil variables and ground-nesting bees reflect direct effects of soils on these bees, rather than indirect effects mediated by unmeasured variables. Only a small portion of the total variance in ground-nesting bee community composition was explained by soil factors; however, sand percentage, slope, soil compaction, and bare ground were all significant predictors. This result reflects the fact that relationships between soil predictors and ground-nesting bee taxa were species-specific; for example, *Eucera pruinosa* and *Lasioglossum leucocomus* were associated with sandier soils, while *L. versatum* and *L. hitchensi* were associated with less sandy soils. Compared to floral resources, soil characteristics have been neglected as components of bee habitat quality, but understanding the soil characteristics preferred by ground-nesting bees can assist in efforts to

protect this important group of pollinators (especially on farms) by creating or preserving suitable habitat.

3.2. Introduction

Crop pollination is a hugely valuable ecosystem service: 75% of global crop types depend to some extent on animal pollination (Klein et al. 2007), representing an estimated US$206 to US$387 billion per year globally (reviewed by Breeze et al. 2016, and Porto et al. 2020). Much of this service is provided by wild bees (Klein et al. 2003, Winfree et al. 2008, 2018, Garibaldi et al. 2011, Adamson et al. 2012), which are highly effective pollinators of most crop species (Delaplane et al. 2000, Garibaldi et al. 2013) and of >80% of all flowering plants (Ollerton et al. 2011). Yet, in agroecosystems, wild bees—like many other animals—are less abundant and diverse than in most natural habitats (Kremen et al. 2002, Koh et al. 2016). Declines in wild bee populations in agricultural settings are due to a combination of interacting factors including agrochemical use, lack of floral resources, and habitat loss (Potts et al. 2010, Mayberry and Elle 2010, Goulson et al. 2015).

At the local scale, bee habitat is limited by both food resources—nectar and pollen provided by flowers—and nesting resources. Although the importance of floral resources has been investigated for many years in agricultural settings (Carvalheiro et al. 2011, Blaauw and Isaacs 2014, Nayak et al. 2015, Saunders and Luck 2018, Eeraerts et al. 2019, Guezen and Forrest 2021), nesting resources have been far less studied (Winfree 2010, Roulston and Goodell 2011). Much of the research that has been done on bee nesting habitat has focussed on cavity-nesting bees, which occupy above- and below-ground cavities (in wood, pithy stems, or former rodent burrows) (reviewed by Cane et al. 2007, and Harmon-Threatt 2020). This bias towards cavity-nesting species has likely arisen because above-ground nests are generally easier to locate, and

there are specific tools such as trap-nests to study them (MacIvor 2017). However, most bee species are ground-nesters that excavate nests in soil, building underground tunnels and creating subterranean brood cells. Between 64% (Cane and Neff 2011) and 83% (excluding parasitic bees, (Harmon-Threatt 2020) of bee species belong to the latter category, and they make up an even larger proportion of the bee fauna on farms (Williams et al. 2010, Forrest et al. 2015, Harrison et al. 2018a). Because ground-nesting bees spend most of their lives belowground, soil-related characteristics might play an important role in their fitness (Antoine and Forrest 2021). However, studies on communities of ground-nesting bees and their nesting habitat are scarce (but see Potts et al. 2005, Kim et al. 2006, Grundel et al. 2010, Sardiñas and Kremen 2014).

Although soil resources may not appear to be a limiting factor in agricultural areas, ground-nesting bees may have species-specific preferences for particular soil characteristics, the availability of which could limit bee occurrences to portions of their geographic ranges (Harmon-Threatt 2020, Antoine and Forrest 2021). These soil characteristics could include slope, temperature, texture, compaction, moisture content, and presence of surface features such as rocks, stones, cracks, and groundcover. Many studies report nests of ground-nesting bees in sandy soil (Cane 1991), but nests of some species can occur in other types of soils (Harmon-Threatt 2020, Antoine and Forrest 2021); for example, a few *Anthophora* species will nest in clay substrate (Norden 1984, Cane 1991, Graham et al. 2015). Species might differ in their preferences for soil characteristics due to differences in body size, morphology, phenology, or physiology. For example, earlier-emerging bees (in temperate climates) might prefer relatively warm nesting sites and thus be associated with soil features that promote heat accumulation or retention (e.g., stones can retain heat, as suggested by Packer et al. (1989) and shown by Cane (2015)). Gregarious bees might prefer harder soils to avoid the collapse of their underground

galleries (Potts and Willmer 1998). Most ground-nesting bees line their brood cells with waterproof secretions, but those that do not (e.g., *Perdita* (Eickwort 1977, Danforth 1989), *Dasypoda* (O'Toole 2013) or *Melissodes* (Harmon-Threatt 2020)) might be associated with drier substrates. Soil surface features including vegetation may act as visual landmarks of the nest entrance or, conversely, conceal nests from predators or parasites; they can also affect other soil variables. However, these ideas remain speculative because little research has been done on the potential of soil factors to influence communities of ground-nesting bees (Antoine and Forrest 2021), and little is known about mechanisms governing nest-site selection among these insects.

In this study, we explored the ability of several edaphic factors (specifically, soil texture, compaction, groundcover, and slope) to predict the abundance, diversity, and community composition of ground-nesting bees on farms in eastern Canada. We determined which soil factors were most strongly associated with the abundance, species richness, Simpson's diversity, and community composition of ground-nesting bees. We also accounted for crop type and farm management, as these could affect soil characteristics and the bee community directly, potentially leading to spurious associations between soil variables and bees. Furthermore, in such an observational study, any association between bees and soil factors could be indirect, driven by effects of soils on vegetation (Forero et al. 2021), which in turn could affect the bee community, rather than by any direct effects of soils on bees (Buckles and Harmon-Threatt 2019). To test whether observed associations between ground-nesting bees and soil features reflect the latter, direct path, we used above-ground- (cavity-) nesting bee species as a sort of internal control or reference: Any associations between cavity-nesting bees and soil features must be driven by correlated variables such as plant community composition, while associations that are observed

only between soil features and ground-nesting bees are more likely to reflect direct effects of soils on bees.

3.3. Methods

3.3.1. Study sites

This study took place on farms within a 100 km radius of Ottawa, Ontario, Canada, on both sides of the Québec–Ontario provincial border (Figure S1 and Table S1 in Supplementary Materials). The landscape around Ottawa is a mix of forest, urban areas, and agricultural fields. Topography is flat to hilly, and elevations range from 38 m to 440 m above sea level. Although most of the field crops grown in this region are corn, soybeans, cereal grains, and hay, we focused on vegetable and fruit farms as these are likely to both support and, to varying extents, depend on, wild bee communities. We did not target a specific crop but rather sampled in a wide diversity of fruit and vegetable crops at 15 and 30 farms in 2018 and 2019, respectively. We sought sites sufficiently scattered throughout the region to maximize the variety of soils sampled, but we were also limited by the location of vegetable farms and by the willingness of growers to participate in the study. Some farms were sampled in a single year, and some were sampled in both years (Table S1, Figure 1 and S1), for a total of 35 farms sampled over the two years (Table S1 and S2). All farms were separated by at least 1.5 km from one another, a maximum foraging distance for most bee species (Zurbuchen et al. 2010b). Farms varied in management practices, with 20 following organic or integrated pest management practices (henceforth considered "organic") and 15 following conventional practices.

We visited each farm once per month from early May to late September for a total of 5 monthly sampling rounds in each year. We established three triangular sampling plots of ~10 m^2 per farm (Figure 1); each plot remained in the same location throughout the sampling year. Plots were

usually on field margins to avoid being destroyed by farm equipment, or within orchards. Each plot was in a different field (though sometimes of the same crop type), and they were separated from all others by more than 100 metres.

3.3.2. Bee sampling

We sampled the bee community using pan traps, a standard method for bee sampling (Westphal et al. 2008), although not one targeted to ground-nesters specifically. We set the traps on the ground and, as bees are central-place foragers, we assumed that most bees captured in the bowls were coming from or travelling to a nearby nest. Bee foraging distances are positively correlated with body size (Gathmann and Tscharntke 2002, Greenleaf et al. 2007), and maximum foraging distance has been estimated at up to 1400 m for large solitary bees (Zurbuchen et al. 2010b). However, maximum foraging distances can be misleading as bees tend to avoid long and energetically costly foraging bouts (Zurbuchen et al. 2010a); indeed, (Zurbuchen et al. 2010b) found that 50% of female bees tend to not travel further than 100–200 m (small bees), or 300 m (larger ones). Because most ground-nesting bees are small (e.g., most species in our dataset had an intertegular distance less than 2 mm), we reasoned that most ground-nesting bees caught in pan traps would have nests located within 100 m of the traps. We therefore measured soil features and sampled bees within ~10 m^2 plots, separated by at least 100 m from all other such plots, on the assumption that these plots provided a good representation of the soil conditions within the bees' foraging ranges. We opted not to use emergence traps, another passive method that can better target ground-nesting bees (Sardiñas and Kremen 2014), because it is labour-intensive and has low capture rates (Pane and Harmon-Threatt 2017, Cope et al. 2019, Grommes et al. 2021).

Each pan trap set consisted of yellow, blue, and white coloured plastic bowls (one of each colour to maximise attractiveness) filled with water and a few drops of soap to break the surface tension. Bees are attracted by the colour and shape of the bowl and drown in the water. We used three sets of three pan traps (350 mL capacity, 175 mm diameter, Festive Occasion®), placed in an approximately equilateral triangle defining the corners of the plot (Figure 1). We left the traps on the ground for 2–3 days (one day longer if there was rain during the sampling period). Then, we collected the insects, pooling the specimens from the 9 traps to yield one sample per plot. Samples were stored in 70% ethanol and the bee specimens were sorted, dried, pinned, and labeled. The proportion of traps recovered was high (median 8.4 out of 9 bowls), but two plots had a mean recovery rate of less than 6 out of 9 owing to traps being overturned by wind, animals or farming activities. To account for this variation in trap recovery rate, the total number of recovered pan traps (over the course of the season) was included in the model as a covariate. We excluded honeybees from the following analyses because their presence was linked to the presence of hives on the sampled or nearby farms instead of other environmental variables.

3.3.3. Bee identification and nesting traits

We identified all bees to genus and we classified each genus as ground-nesting, cavity-nesting, or parasitic based on (Normandin et al. 2017). We then identified specimens belonging to ground-nesting genera to species, using the following keys: Mitchell (1960, 1962) for *Andrena, Colletes*, *Mellissodes* and *Pseudopanurgus*, Gibbs (2010, 2011, Gibbs et al. 2013) for *Lasioglossum*, and Discover Life (Ascher and Pickering 2012) for *Calliopsis*, *Perdita*, and most Halictidae other than *Lasioglossum* spp. In addition, we used reference specimens from the Ouellet-Robert collection of the Université de Montréal. In our analysis, *Megachile* species were excluded from the ground-nesters, as their nesting strategy is not always known, and they may

sometimes switch between below- and above-ground cavities (Sheffield et al. 2011). Although *Bombus* species' nests can be found underground, they do not excavate their own nests but rather occupy a previously dug cavity (e.g., rodent holes) and were thus not included as ground-nesters either. See Supplementary Table S3 for a list of cavity-nesting bee genera and Table S4 for a complete list of the ground-nesting bee species in our dataset. Specimens are stored at the University of Ottawa (Forrest lab) and in the Ouellet-Robert collection of the Université de Montréal.

3.3.4. Soil sampling

We measured four soil variables once per year within each plot: compaction, slope, texture and ground cover. Ground cover was categorized as bare ground, live vegetation, or dead litter, and the percent cover of each category was assessed visually (using a grid) to the nearest 5% from photographs of a 1 × 1 m quadrat placed randomly within the ~10 m^2 plot (Figure 1). The sum of all ground-cover categories per plot was 100%. The other three soil variables were each measured at three haphazard locations per plot ("x"s in Figure 1); we then calculated the mean per plot of each variable from the three replicate measurements. Compaction was measured using a hand-held pocket penetrometer (G118H4200 Hoskin Scientific, Canada). Slope was measured as angle from the horizontal using an Abney level.

To measure soil texture (particle-size distribution), we sampled the top 15–20 cm of soil (depth depending on soil hardness) at the three soil-sampling locations within each plot using a 20 mm diameter corer (E121-Model LS Hoskin Scientific, Canada). The soil samples were placed individually in sealed plastic bags in 2018 and mixed in a single bag per plot in 2019 before being transported to the lab, then stored until texture analysis. Multiple soil textural analysis were carried out in order to make an average per plot: three textural measurements for each of

the three different sample taken per plot in 2018 and two to three analysis of sub-samples of the mix per plot collected in 2019. Samples were dried for 24 hours at ambient temperature in the lab and then weighed. Texture was measured for individual soil samples using the Bouyoucos (1927) method with a hydrometer (Day 1965). Rocks were first separated from the rest of the soil particles by passing the sample through a #10 sieve (2 mm); both fractions were then weighed. Only 50 g of finer particles were used for further analysis, and these were put in a jar with 250 mL of distilled water and 100 mL of sodium hexametaphosphate (a dispersing agent) at a concentration of 50 g/L. The mixed solution was left for 16 hours to disaggregate the soil particles. The day after, the soil–water suspension was placed in a 1 L cylinder with distilled water, mixed, and left to settle. We measured the density of the resulting suspension with the hydrometer at 60 s, 10 min, 30 min, 1 h and 7 h after mixing. The sedimentation technique allowed estimates of percentages of silt, clay, and sand (Carter and Gregorich 2007).

3.3.5. Statistical analyses

All analyses were conducted using R version 4.1.2 (R Core Team 2021). For each plot, we pooled the bee data over the whole annual sampling period, summing male and female bee abundance for all five rounds. Our three primary response variables were ground-nesting bee abundance, species richness, and species diversity calculated as Simpson's index (1/D). We also ran the abundance model using the cavity-nesting bee data to test whether any observed associations were specific to ground-nesters. We checked all data distributions for outliers and collinearity among our predictors as recommended by Zuur et al. (2010). To check for multicollinearity, we calculated Pearson correlation coefficients (Figure S2 in the Supplementary Materials). Two of the predictor variables (soil texture and ground cover) are each made up of three variables that sum to 100% (percentages of sand, clay, and silt; and percentages of bare

ground, vegetation and dead litter cover, respectively). For each of these, we could include only one or two of the three variables in the analysis. We chose to retain sand and bare ground, as we considered these the most biologically relevant (they are also the most frequently reported in past research); we excluded vegetation cover, percent clay, and silt, as all three were strongly correlated ($|r| \geq 0.75$) with percent sand or bare ground. Dead litter was not strongly correlated with bare ground ($r = -0.04$) and was therefore included. We tested for spatial autocorrelation by using the Mattern function from the spaMM package (Rousset et al. 2022). Autocorrelation among plots was apparent only at spatial scales less than 200 m and was 0 at 1 km, the minimum distance between farms. Spatial autocorrelation was therefore taken into account simply by including farm identity as a random effect. GLMM model diagnostics were assessed using the DHARMa package (Hartig 2022).

Abundance, richness, and diversity of ground-nesting bees

To model the abundance of ground-nesting bees in relation to soil predictors, we ran a generalised linear mixed model (GLMM; (Bolker et al. 2009, Zuur et al. 2010, Harrison et al. 2018b)) with a negative binomial distribution and log-link function, using the glmmTMB package (Brooks et al. 2017). Farm identity was included as a random effect. Year of sampling (categorical) and total number of traps sampled (continuous) were included as additional fixed effects. We also wanted to consider the effects of crop type and farm management on ground-nesting bee abundance and diversity; however, both variables were correlated with at least one soil factor (Figure S5 and S6) and therefore had to be excluded from this model. Instead, we ran separate models in which we substituted crop type (categorical, 7 levels) and farm management (categorical, 2 levels) for percentages of sand and bare ground (but retaining the other soil variables, year of sampling, number of traps collected, and farm identity). We assessed

significance of crop type and farm management using likelihood-ratio tests and ran post-hoc tests using the multcomp package (Hothorn et al. 2008) to compare crop types when a significant effect of crop type was detected. We used analogous models for ground-nesting bee species richness.

We calculated Simpson's index of diversity (1/D) for ground-nesting bees within each plot, and we analysed the association between diversity and soil variables using a linear mixed-effects model (as the response variable was normally distributed) with the package lme4 (Bates et al. 2015). We used the same predictors as in the other models: percentages of sand, bare ground and dead litter; slope; compaction; year of sampling; number of traps collected; and farm identity.

To check whether associations between ground-nesting bee abundance and soil predictors were directly related to soil characteristics or were instead due to an indirect mechanism (e.g., soils affecting floral resources), we ran the same abundance model as described above but instead using abundance of cavity-nesting bees as the response. We again included year and bowls as fixed effects and farm identity as a random factor.

Bee community composition

We ran a partial redundancy analysis (Legendre and Legendre 2012) using the vegan package (Oksanen et al. 2018) to test for associations between bee community composition and soil variables. We accounted for spatial autocorrelation among plots by calculating a distance-based Moran's Eigenvector Map (dbMEM; formerly called Principal Coordinates of Neighbor Matrices PCNM (Borcard and Legendre 2002), testing the significance of each MEM eigenvector in the RDA through permutation, and selecting the significant spatial predictors for the partial RDA. We therefore had two sets of explanatory matrices: the environmental variables (made up of the

soil predictors used in the GLMMs) and the spatial variables. We then selected explanatory variables (including both spatial and soil predictors) by forward selection (Blanchet et al. 2008). The response variable was the bee-species-per-plot matrix, corrected with a Hellinger transformation to mitigate the masking effect of dominant species on the ordination covariance structure (Legendre and Gallagher 2001). We tested the significance of the model, its constrained axes, and its terms by permutation (n = 999).

Species-specific associations

We used similar models to those described above for testing abundance and richness, to analyse the associations between individual ground-nesting bee species (all those represented by more than 200 individuals in our dataset) and soil variables. We ran one model testing the soil predictors alone and another one in which we substituted sand percentage and bare ground percentage by crop type and farm management. We ran models with and without a quadratic term for percentage sand, to check if relationships with this factor were non-linear—as would be expected if bees exhibit species-specific optima in terms of sand percentage. The quadratic term did not improve model fit, nor was it significant in any model output (even when percentage sand was significant); it was therefore excluded from analysis. A zero-inflated formula was used in the models for *Eucera pruinosa*. All GLMMs were run with a negative binomial distribution and using the glmmTMB package. We used likelihood-ratio tests and post-hoc Tukey HSD tests for pairwise comparisons among crop types.

As a result of testing eight species separately, each with two models, we had a total of 16 models just for species associations. This high number of models increases chances of Type I errors (false positives). We did not statistically correct for multiple testing but rather suggest that the results be interpreted with caution—especially those with p-values greater than 0.01.

3.4. Results

In total, 11,722 bees were collected over the two years of sampling (excluding honey bees, *Apis mellifera*), of which 8,661 were ground-nesters representing 102 species. This total includes a large number of ground-nesting squash bees, *Eucera (Peponapis) pruinosa*: 3,846 males and 288 females of this species were sampled on squash fields. Analyses were run with and without *E. pruinosa* to ensure that results were not driven by this species alone; results reported below refer to analyses excluding *E. pruinosa* except where specified otherwise. The remaining ground-nesters comprised 3,663 females, 770 males, and 94 incomplete specimens of unknown sex; all were included in analyses regardless of sex. After *E. pruinosa*, the most abundant ground-nesting species were *Halictus ligatus* (358 individuals), *Lasioglossum versatum* (357), *L. leucozonium* (300), *Augochlorella aurata* (295), *L. imitatum* (295), *L. leucocomus* (255), and *Andrena nasonii* (200) (Table S4). In addition, we collected 2,624 cavity-nesting bees from 11 genera (not identified to species level, Table S3), with the two most abundant genera being *Bombus* and *Ceratina*.

Means and ranges for the soil variables measured at each plot are summarized in Table 1. Textural analysis from the surface layer of the plots showed high amounts of sand at all sites, and small percentages of clay (Figure S2). There was substantial variation in bare ground and vegetation cover among plots, but typically small amounts of litter. Soil surface compaction ranged from 0.2 to 5.0 kg/cm^2, with the modal value around 1 (Figure S3), meaning many plots had soft soil (probably related to soil tillage and/or high sand content). Finally, slope in most plots was minimal (median = 2º), which is not surprising for an agricultural environment in a largely flat region.

3.4.1. Abundance, richness, and diversity of ground-nesting bees

Both the abundance and richness of ground-nesting bees significantly increased with the percentage of bare ground (abundance: $\beta = 0.19$, $z = 3.60$, $p < 0.001$; richness: $\beta = 0.08$, $z = 2.68$, $p = 0.007$, Table 2 and Figure 2,3) and the percentage of sand (abundance: $\beta = 0.14$, $z = 2.12$, $p = 0.034$; richness: $\beta = 0.09$, $z = 2.41$, $p = 0.016$, Table 2 and Figure 2,3). In contrast, Simpson diversity of ground-nesting bees was unrelated to soil texture or ground cover (Table 2) but decreased with increasing slope ($\beta = -0.63$, $t = -2.31$, $p = 0.017$, Figure 3). Models including *E. pruinosa* (squash bees) yielded the same significant predictors (Table S5).

In the models where we replaced sand percentage and bare ground percentage by crop type and farm management (the latter two variables being correlated with the former two), we found no significant associations (Table S6) between crop type or farm management and ground-nesting bee abundance (likelihood-ratio test for crop: $\chi^2 = 7.82$, df = 6, $p = 0.25$; for farm management: $\chi^2 = 0.25$, df = 1, $p=0.61$), richness ($\chi^2 = 5.37$, $p = 0.5$; and $\chi^2 = 0.34$, $p = 0.56$ respectively), or diversity (crop: $\chi^2 = 15.33$, $p = 0.018$, but no significant pair-wise differences between crop types; farm management: $\chi^2 = 1.74$, $p = 0.19$). Simpson diversity of ground-nesting bees (but not abundance or species richness) was negatively associated with slope ($\beta = -0.59$, $z = -2.33$, $p = 0.02$), as in the previous models testing all soil predictors.

The abundance of cavity-nesting bees was not explained by any of the soil variables in the soil predictors model (Table 2). In the model in which crop type and farm management were substituted for sand and bare ground (Table S6), number of traps was a significant predictor ($\beta = 0.21$, $z = 1.67$, $p = 0.05$), as was crop type ($\chi^2 = 15.6$, df = 6, $p = 0.016$). Post-hoc pairwise comparisons showed a significantly higher abundance of cavity-nesters in berry fields than in orchards ($z = 3.65$, $p = 0.0046$; Figure S7). Farm management had no effect on the abundance of cavity-nesters ($\chi^2 = 1.34$, df = 1, $p = 0.25$).

3.4.2. Ground-nesting bee community composition

Seven spatial eigenvectors explained significant variance in the sites-by-bee-species response matrix, and these were taken into account in the partial redundancy analysis as covariates. The RDA showed that the composition of the ground-nesting bee community (excluding *Eucera pruinosa*) was significantly associated with soil (proportion of variance explained: 0.073) and spatial predictors (proportion of variance explained: 0.118), with the full model explaining 19.2% of the variation in composition of the ground-nesting bee communities ($F_{5,117} = 2.12$, $p < 0.001$). Significant soil predictors were percentage sand ($F = 3.89$, $p < 0.001$), slope ($F = 1.99$, $p = 0.002$), compaction ($F = 1.83$, $p = 0.007$), and percentage bare ground ($F = 1.80$, $p = 0.010$). The model including *E. pruinosa* differed slightly, in that compaction was no longer a significant predictor of community composition; however, percent sand remained the strongest predictor (Table S10).

In the RDA without *E. pruinosa* (Figure 4), *Lasioglossum leucocomus, L. pectorale,* and *L. pilosum* were positively associated with percent sand, while *L. versatum*, *Calliopsis andreniformis*, and *L. hitchensi* were negatively associated with sand. The latter two species were also associated with harder soils. Three species (*Halictus ligatus, L. tegulare*, and *L. versans*) were positively associated with bare ground, whereas *Andrena wilkella* and *L. lineatulum* were correlated with higher vegetation cover. *Augochlorella aurata* and *L. admirandum* were positively associated with slope, while *Perdita octomaculata* and *L.versans* were associated with flatter soils. *Lasioglossum vierecki, L. imitatum, L. heterognathus*, and unidentified *Lasioglossum* sp. were found in softer and sandier soils. The RDA biplot including squash bees *E. pruinosa* (Figure S8) was similar.

3.4.3. Species-specific associations

The eight most abundant ground-nesting bee species in our dataset varied in their associations with soil variables (Table S8). Most of the individual species tested showed strong associations with soil texture, with some species positively associated with percent sand (i.e., *Lasioglossum leucocomus* $\beta = -0.53$, $z = -2.59$, $p = 0.01$, Figure 3-5D; *Eucera pruinosa* $\beta = 0.93$, $z = 2.85$, $p = 0.004$, Figure 3-5A), others negatively associated with percent sand (i.e., *L. versatum* $\beta = -0.36$, $z = -2.39$, $p = 0.017$, Figure 3-5C), and others not detectably associated with sand (i.e., *Halictus ligatus* $\beta = -0.06$, $z = -0.43$, $p = 0.66$, Figure 3-5B). *Augochlorella aurata* was more abundant at sites with more sloping ground ($\beta = 0.28$, $z = 2.17$, $p = 0.03$), and *Lasioglossum leucocomus* was negatively associated with soil compaction ($\beta = -0.53$, $z = -2.59$, $p = 0.01$). *Andrena nasonii*, *H. ligatus, L. imitatum,* and *L. leucozonium* were not associated with any soil factors (all $z < 2$, $p > 0.05$).

Abundance of *E. pruinosa* differed among crop types ($\chi^2 = 20.56$, df = 6, $p = 0.002$): these bees were more abundant in squash fields than in corn/soy/wheat fields (Tukey test: $z = 3.31$, $p = 0.015$) or pasture/forage fields ($z = 2.96$, $p = 0.04$), and they were more abundant in strawberry fields than in corn/soy/wheat ($z = 3.16$, $p = 0.02$). Abundance of *H. ligatus* also differed among crop types ($\chi^2 = 21.08$, df = 6, $p = 0.0018$); these bees were more abundant in strawberry fields than any other crops (all $z > 3$, $p < 0.02$). Although *L. leucozonium* seemed to be associated with certain crop types (Table S9), the likelihood-ratio test was non-significant. No species were associated with farm management.

3.5. Discussion

We assessed ground-nesting bees' associations with soil characteristics on farms in eastern Canada and found that soil texture and ground cover were the most important factors among those examined: Ground-nesting bee abundance and species richness increased with increasing

percentages of sand and bare ground, and these variables (particularly sand content) were also significant predictors of community composition. Slope was negatively associated with ground-nesting bee diversity and was a significant factor in community composition as well; however, this association is surprising in light of the minimal variation in slope among sampled plots. These results—identifying slope, sand content of soil, and bare ground as important factors for ground-nesting bee populations—are consistent with the existing literature (Cane 1991, Potts and Willmer 1997, Wuellner 1999, Potts et al. 2005, Sardiñas and Kremen 2014), although the direction of the relationship between ground-nesting bees and specific soil factors often varies among studies (see below).

Methods to study ground-nesting bees in the field vary, and all come with benefits and drawbacks. In this study, we used pan traps, a standard method to sample bees but one that can capture any bee flying through the area; it is not specific to bees nesting near the traps. We set pan traps on the ground to target ground-nesters and assumed that bees were nesting nearby, given the typically short flight distances of most ground-nesting bees. Because of this method, we cannot be certain that the associations we documented were driven by nesting habitat preferences; but the non-significant associations between soil factors and cavity-nesting bees mean that the associations we documented are specific to ground-nesters. We therefore assume that the soil factors found to be significant in our analyses are related to ground-nesting bee nesting biology. Emergence traps represent a different approach that allows researchers to make direct links between ground-nesting bees and their nesting habitat (see *2.5 Methods for studying the nesting habitat of ground-nesting bees*), but their many drawbacks (see Pane and Harmon-Threatt 2017, Cope et al. 2019, Grommes et al. 2021) led us to use pan traps, despite the biases

of the latter method (Portman et al. 2020). Future studies could use emergence traps, but at the cost of sampling a smaller area.

3.5.1. Which soil characteristics matter for ground-nesting bees?

Soil texture (defined by the relative amounts of sand, clay and silt particles) seems to have an important influence on ground-nesting bees, as discussed by Antoine and Forrest (2021). Many papers have described bees nesting in sandy areas (Burdick and Torchio 1959, Cane 1989, Miliczky 1991, Norden et al. 2003, Martins et al. 2019)—although the exact sand proportion is rarely reported—and have suggested that ground-nesting bees prefer sandy soils (Cane 1991, Harmon-Threatt 2020); however, other studies have found nonsignificant effects of soil texture on ground-nesting bee species abundance and richness (Sardiñas et al. 2016, Fortel et al. 2016). We found that even in our generally sandy landscape (with up to 97% sand), ground-nesting bees occurred in higher numbers—of individuals and species—in sandier soils. But this result cannot be generalised to all ground-nesting species: although several species showed a positive relationship with percentage of sand (e.g., *Lasioglossum leucocomus, Eucera pruinosa*, *L. pilosum*, *L. pectorale*), others showed a negative relationship (e.g., *L. versatum*, *L. hitchensi*) or no detectable association (e.g., *H. ligatus, Andrena nasonii, L. imitatum*). Associations with the sand fraction are therefore species-specific and could be driven by species-specific preferences for better drainage, ease of digging, or integrity of nest structure (Antoine and Forrest 2021).

Regarding ground cover, preference for bare soil has been shown previously in a few bee species (Wuellner 1999, Potts et al. 2005), and some studies have also found higher overall abundance of nesting bees in areas with more bare ground (Potts et al. 2005, Sardiñas and Kremen 2014). Indeed, we found higher abundance of ground-nesting bees and greater species richness in open bare ground, and we also observed that certain species (e.g., *L. tegulare*) were positively

associated with bare ground. However, some species (e.g., some *Andrena* and *Colletes* spp.) are known to nest in grassy areas (Maher et al. 2019), and in our study, some species (*L. lineatulum* and *Andrena wilkella*; Figure 5) were associated with higher vegetation cover. Preference for bare ground could be explained by the increased ease of locating and accessing nest entrances, the increased surface temperature thanks to increased absorption of solar radiation, the decreased density of roots in the soil, or the decreased risk of having predators hiding nearby (see Antoine and Forrest 2021). Of the 44 nests descriptions reviewed by Harmon-Threatt (2020), 75% were in bare ground, but the author noted that this finding might be the product of sampling bias, since nest entrances are easier to locate on bare soil. Our results, however, are not influenced by nest-detection bias, and they suggest that ground-nesting bees are indeed found at higher abundance and species richness in areas with more bare ground, at least in agroecosystems in our study region. Associations between ground-nesting bees and soil factors may be context-dependent: for example, bees might exhibit greater preference for bare ground in relatively cool climates where maximizing nest exposure to solar radiation is most likely to be beneficial.

Slope has previously been found to be negatively associated with ground-nesting bee abundance on farms (Sardiñas and Kremen 2014), but nest incidence, abundance, or density can sometimes be correlated with steeper soils (Potts and Willmer 1997, Potts et al. 2005, Sardiñas and Kremen 2014). In our study, slope was a significant predictor of community composition and of ground-nesting bee diversity, despite the minimal variation in slope among plots. These community-level associations with slope might be driven by the fact that several *Lasioglossum* species appear to be associated with flatter ground (based on the RDA). However, given the correlational nature of the dataset, another possibility is that an unmeasured predictor, correlated with slope, influenced bee diversity, e.g., floral resources or landscape features (trees, hedgerows etc.). A broader range

of slopes should be investigated in future studies to draw stronger conclusions about this soil predictor.

Soil compaction is believed to be an important factor for nest-site selection, owing to its effects on ease of digging and the energetic costs of nest construction (see Antoine and Forrest 2021). Other studies have either found more nests in softer soils (Potts and Willmer 1997, Sardiñas and Kremen 2014) or more ground-nesting bees associated with harder soils (Potts et al. 2005). Kim et al. (2006) found species-specific associations with soil hardness. Curiously, we detected no effect of compaction on ground-nesting bee abundance, species richness or diversity. However, compaction was a significant predictor of bee community composition, and several species (mainly *Lasioglossum* spp.) were primarily found in association with softer soil. Species-specific associations with compaction could be related to body size or other traits such as sociality or preference for nesting in aggregations. Gregarious bees might select more compact soils for nest structural integrity, rather than risking gallery collapse in softer but more easily excavated soils (Potts and Willmer 1998).

Overall, edaphic factors were statistically significant predictors of ground-nesting bee community attributes. However, they explained a relatively small amount of the variation in these attributes, suggesting that other unmeasured variables are also important. For example, there was only a 1.6% increase in ground-nesting bee abundance, and a 1.1% increase in species richness, from the smallest to the largest percent sand measured (62%–97%). Measured soil characteristics explained only 7.3% of the variation in ground-nesting bee community composition—in accordance with a previous study showing 5–10% of variance in bee community composition explained by nesting resources (Potts et al. 2005). Of course, non-edaphic factors, such as floral resources and landscape characteristics, also affect bee

communities (Roulston and Goodell 2011, Kennedy et al. 2013) and were not incorporated in our study. Other biotic factors, such as parasites, predators, or competitors for floral or nesting resources, may also influence ground-nesting bees' associations with soil resources. However, it should be noted that additional soil variables, such as temperature and moisture, percentage organic matter (Osgood Jr 1972, Grundel et al. 2010), presence of pebbles or rocks (Cane 2015), soil porosity, and soil chemistry, may also be important predictors of ground-nesting bee nest-site location (see Antoine and Forrest 2021) and were not included here (although most would probably be correlated with factors we did include). Thus, our analysis may underestimate the overall importance of edaphic factors. Studies analysing bee community composition using variance-partitioning approaches (Peres-Neto et al. 2006, Legendre 2008, Zellweger et al. 2017, Zwolicki et al. 2019) or structural equation modelling (Grace and Pugesek 1997, Dainese et al. 2017) would be useful for evaluating the importance of soil features (or nesting habitat features more broadly) relative to more frequently measured components of habitat quality like floral resources.

3.5.2. Are soil variables the true drivers of variation in bee communities?

Soil factors can regulate water availability, and, together with precipitation, affect plant community composition (Lane et al. 1998, Renne et al. 2019). Plant communities in turn have important impacts on bee communities, including both ground- and cavity-nesting species (Roulston and Goodell 2011). To determine whether our observed relationships between soil factors and ground-nesting bees were in fact driven directly by soil variables (or instead by correlated variables such as local floral resources), we also tested for associations between cavity-nesting bees and soil predictors. The lack of association between abundance of cavity-nesters and any of our measured soil predictors suggests that the observed relationships between

soils and ground-nesters are indeed direct, rather than mediated by vegetation. However, to conclusively demonstrate direct effects of soil factors on ground-nesting bees, an experimental approach would be necessary—i.e., manipulating soil variables while keeping other factors constant.

Although our results suggest direct effects of soils on abundance of ground-nesting bees, crop type (which is correlated with soil variables) undoubtedly influenced community composition as well. For example, the squash bee, *E. pruinosa*, was more abundant near populations of its host-plant, in squash fields and strawberry fields (the two crops usually occurred on the same farms, in neighbouring fields). Another ground-nesting bee species, *Halictus ligatus*, was associated with strawberries, with higher abundances in this crop than others (Table S9). Interestingly, cavity-nesting bees were more abundant in berry fields than in orchards. This result may appear surprising, given that wood-nesting mason bees (*Osmia* spp.) are known orchard pollinators (Bosch et al. 2002, Sheffield et al. 2008, Sheffield 2014), but our most abundant cavity-nesting genus was *Ceratina*. The latter often nest in Rosaceae twigs (Vickruck et al. 2011) and were probably using raspberry (*Rubus* spp.) shrubs as nesting sites.

Bee communities can also be associated with farm management styles (e.g., conventional vs. organic) (Forrest et al. 2015, Martins et al. 2018, Nooten et al. 2020), which influence ground cover and compaction (Figure S5), in turn affecting bee communities. Farming practices encompass different tillage or pesticide regimes, and ground cover types that may harm or benefit survival of ground-nesting bee larvae (Ullmann et al. 2016, Willis Chan et al. 2019, Appenfeller et al. 2020, Willis Chan and Raine 2021). Farming practices are also influenced by crop type. For example, fields of perennial crops, such as fruit shrubs and trees, undergo less soil disturbance than those of annual crops, such as corn. Soil disturbance might be expected to lead

to higher ground-nesting bee abundance in orchards than in corn fields. However, we found no associations between crop type or farm management and ground-nesting bees overall, perhaps because most of our sampled farms—including conventional ones—were highly diversified, usually including both annuals (e.g., vegetable crops, strawberries, squashes) and perennials (e.g., berry shrubs, fruit trees). Moreover, the landscape around Ottawa is characterized by patches of forests and semi-natural habitat (see land-cover map in Figure S1b), which could promote bee populations, regardless of local farm management. Although we were unable to identify relationships between crop types or farm management and the abundance or diversity of ground-nesting bees, such relationships would probably be detected if a more extensive range of farm types were considered (i.e., including monocultures).

3.5.3. Species-specific associations with nesting habitat

Our findings demonstrate the importance of studying bees at the species level, rather than using broader taxonomic groups, which may hide certain patterns of association with nesting resources. For example, the very common and diverse genus *Lasioglossum* (Halictidae) is famously challenging to identify at the species level (Gibbs 2010, 2011, Gibbs et al. 2013) and is therefore often identified only to subgenus (e.g., *Dialictus*, as mentioned by Gibbs (2009)) in ecological studies (Gezon et al. 2015, Galbraith et al. 2019). However, we show here the importance of distinguishing individual *Lasioglossum* spp., as they can have quite different—sometimes completely opposite—soil habitat associations. The related genus *Halictus* also showed species-level differences in their associations with soil predictors. Of course, testing numerous species individually comes with the risk of inflating the false discovery rate (Type I error); therefore, we consider associations with $p > 0.01$ (e.g., the association with less flat ground for *A. aurata*) to be potentially spurious. Nevertheless, there are many subtle differences in morphological,

phenological, and life-history traits among species, even within a single genus, that may drive interspecific differences in associations with soil characteristics. More research is needed to understand the ecology and evolution of species-specific nesting-habitat preferences in bees.

Although we were able to identify specific interactions with some soil factors for a few ground-nesting bee species, it is challenging to do this because many species are rare in datasets (e.g., 35 singletons in our dataset). In our community analysis, 21 species explained more than 5% of the variance among sites, but 80 species did not. The latter were either inadequately represented in the sample, or insufficiently influenced by the measured factors, to detect any pattern of association. In general, it is challenging to document habitat associations of rare species (Robinson et al. 2018), but identifying specimens to the species level is an essential first step.

3.6. Conclusion

Our results indicate that soil features should not be neglected as components of bee habitat, alongside floral resources. Creating patches of habitat suitable for ground-nesting bees—specifically, in our region, including areas of sandy, bare ground—will help in maintaining bee populations on farms, and therefore, maintain crop pollination services in the long run. However, given the species-specific nature of bees' soil associations, maximising heterogeneity of soil factors (e.g.., offering both vegetated areas and open ground, sloping and flat soil, etc.) is likely the best strategy for enhancing bee diversity.

Ground-nesting bees represent an important group of pollinators, thanks to their abundance and diversity, but also because they can nest within crop fields. It is still unclear whether farm fields are suitable nesting sites for ground-nesters or whether they act as ecological traps due to tillage (Ullmann et al. 2016, Skidmore et al. 2019); more research in needed on the effect of soil work

on bee survival. Studying the inherent quality of a nesting site, for example comparing crop field interiors to field edges (as in Sardiñas et al. (2016), will provide useful information to foster pollination services by wild bees for a more sustainable agriculture.

Table 3-1: Mean, median, and range of values of the soil predictors measured at each plot (N = 131), on 35 farms around Ottawa. Compact. = Compaction; BG = bare ground; Veg = living vegetation. Compaction is in kg/cm^2 and slope is in degrees from horizontal.

			Ground cover			Soil texture		
	Compact.	Slope	BG %	Veg %	Litter %	Sand %	Silt %	Clay%
Min	0.2	0.0	0.0	0.0	0.0	62.0	2.0	0.0
Mean	2.0	3.1	25.0	68.0	7.0	79.0	16.0	5.0
Median	1.7	2.0	10.0	80.0	0.0	80.0	15.0	3.0
Max	5.0	15.0	90.0	100.0	90.0	97.0	34.0	23.8

Table 3-2: Results of Generalized Linear Mixed Models (GLMM) of ground-nesting bee abundance, richness, and diversity, as well as cavity-nesting bee abundance. Fixed predictors were the uncorrelated soil predictors (slope, compaction, bare ground %, litter %, and sand %), number of traps, and year; farm was included as a random effect. All continuous predictors were scaled to mean = 0 and s.d. = 1. N = 131 observations (plots) from 35 farms. Z statistics are reported for abundance and richness, t statistics are reported for Simpson's diversity. Results in bold were significant at α = 0.05.

Response	Predictors	Coef.	SE	z or t	P
Ground-nesting bees					
Abundance	slope	−0.011	0.056	−0.201	0.841
	compaction	−0.022	0.054	−0.413	0.679
	bare ground	**0.189**	**0.053**	**3.599**	**<0.001**
	dead litter	0.019	0.054	0.345	0.730
	sand	**0.135**	**0.064**	**2.124**	**0.034**
	traps	**0.182**	**0.073**	**2.487**	**0.013**
	year (2019)	−0.159	0.169	−0.936	0.349
Richness	slope	−0.023	0.031	−0.751	0.452
	compaction	0.012	0.031	0.394	0.693
	bare ground	**0.077**	**0.029**	**2.681**	**0.007**
	dead litter	−0.001	0.029	−0.035	0.972
	sand	**0.092**	**0.038**	**2.414**	**0.016**
	traps	**0.103**	**0.043**	**2.397**	**0.017**
	year (2019)	−0.162	0.096	−1.685	0.092
Diversity (Simpson's)	**slope**	**−0.629**	**0.261**	**−2.410**	**0.017**
	compaction	0.166	0.258	0.641	0.523
	bare ground	0.142	0.244	0.582	0.562
	dead litter	0.028	0.240	0.116	0.907
	sand	0.357	0.299	1.192	0.236
	traps	0.473	0.339	1.393	0.166
	year (2019)	**−2.044**	**0.784**	**−2.607**	**0.010**
Cavity-nesting bees					
Abundance	slope	−0.032	0.078	−0.413	0.679
	compaction	0.110	0.076	1.448	0.148
	bare ground	−0.056	0.072	−0.774	0.439
	dead litter	0.073	0.068	1.072	0.284
	sand	−0.078	0.086	−0.904	0.366
	traps	0.185	0.110	1.680	0.093
	year (2019)	0.279	0.237	1.174	0.241

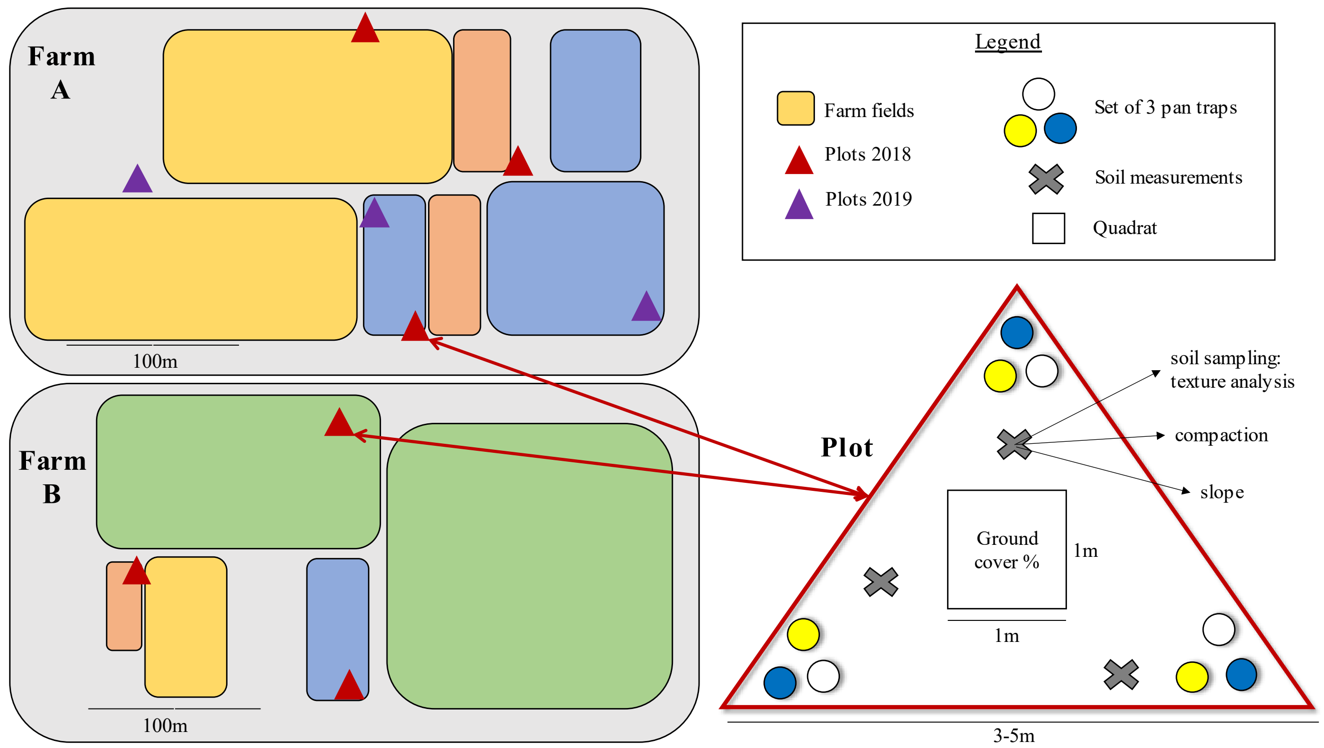

Figure 3-1: Schematic representation of sampling design on two hypothetical farms (A sampled in both years, 2018–2019; B sampled only in 2018). Coloured polygons represent fields with different crops; the red triangle shows a close-up of the plot level showing the three sets of pan traps in each corner (9 in total), three random locations (indicated by grey “x”s) within the plot for soil measurements (slope, compaction, and soil sampling for textural analysis), and the central quadrat in which ground-cover measurements were taken.

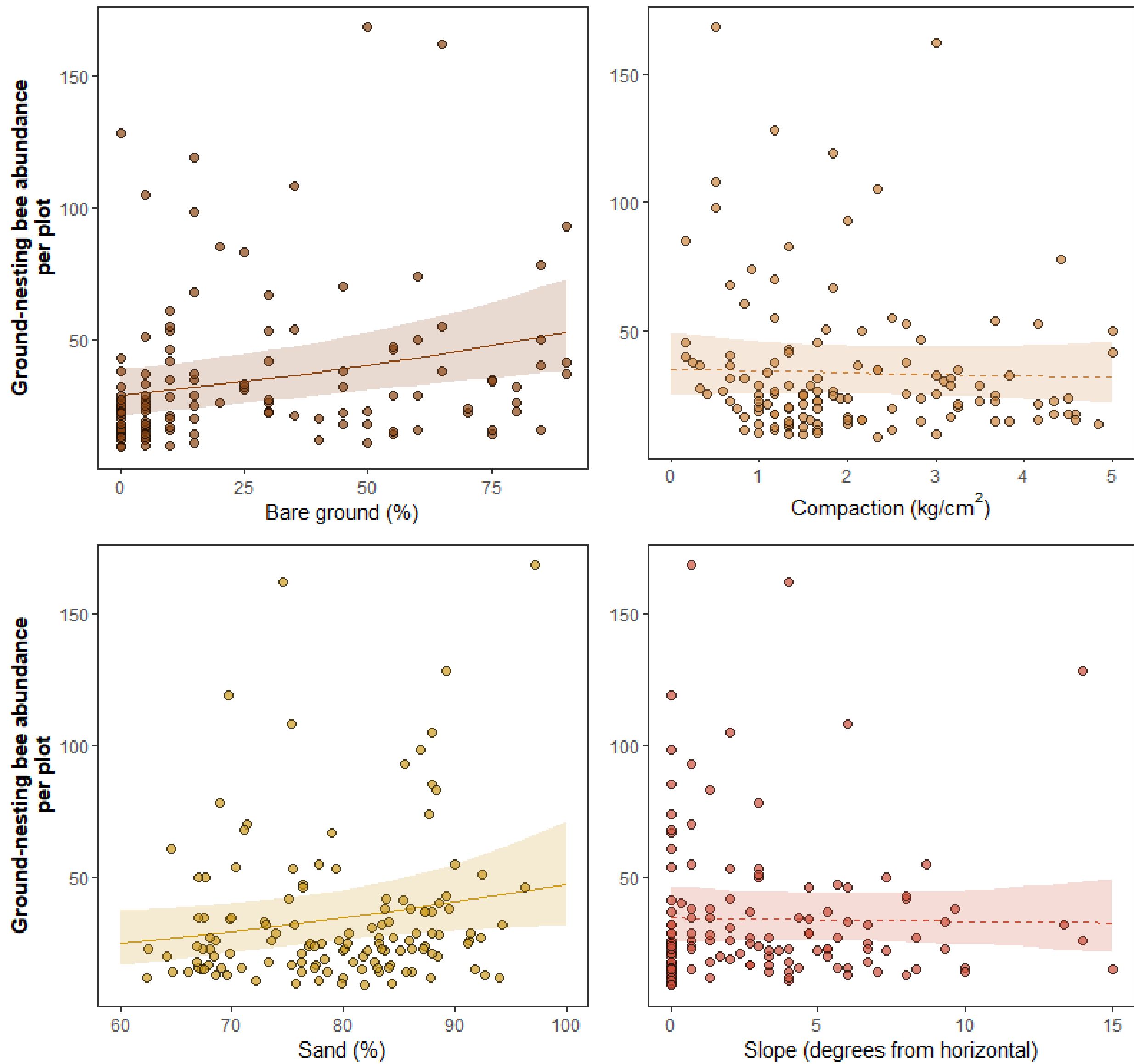

Figure 3-2: GLMM results showing the associations between the abundance of ground-nesting bees per plot and four soil predictors: bare ground cover, compaction, percentage sand, and slope. Points represent plots (N = 131) sampled at 35 farms over the two years of sampling (2018–2019). Shading represents 95% confidence intervals of model predictions. Solid lines represent significant relationships and dotted lines are non-significant ($p > 0.05$).

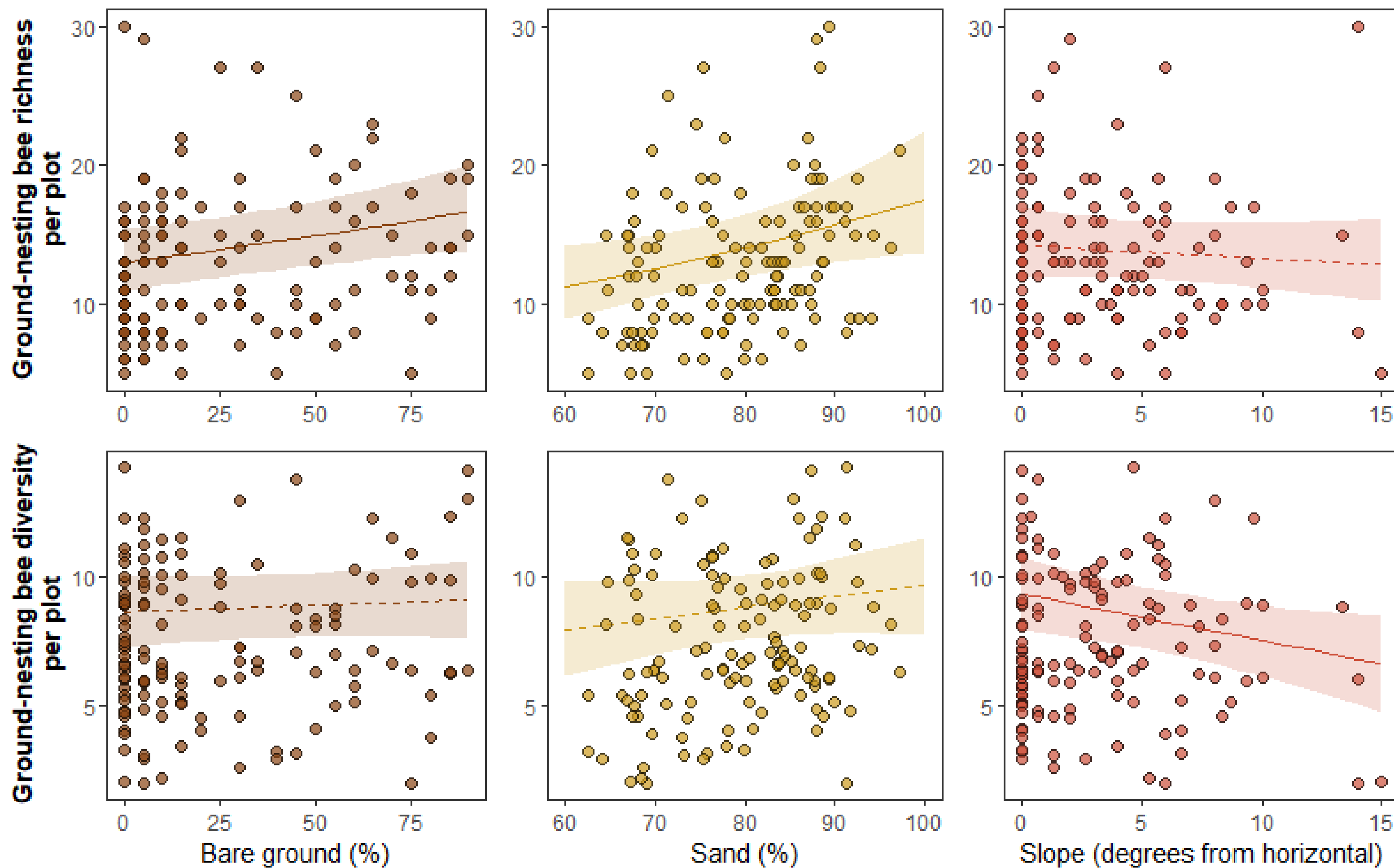

Figure 3-3: GLMM results showing the associations between three soil predictors and species richness (top panels) and diversity (1/D; bottom panels) of ground-nesting bees per plot. Points represent plots (N = 131) sampled at 35 farms over the two years of sampling (2018–2019). Shading represents 95% confidence intervals of model predictions. Solid lines represent significant relationships and dotted lines are non-significant ($p > 0.05$).

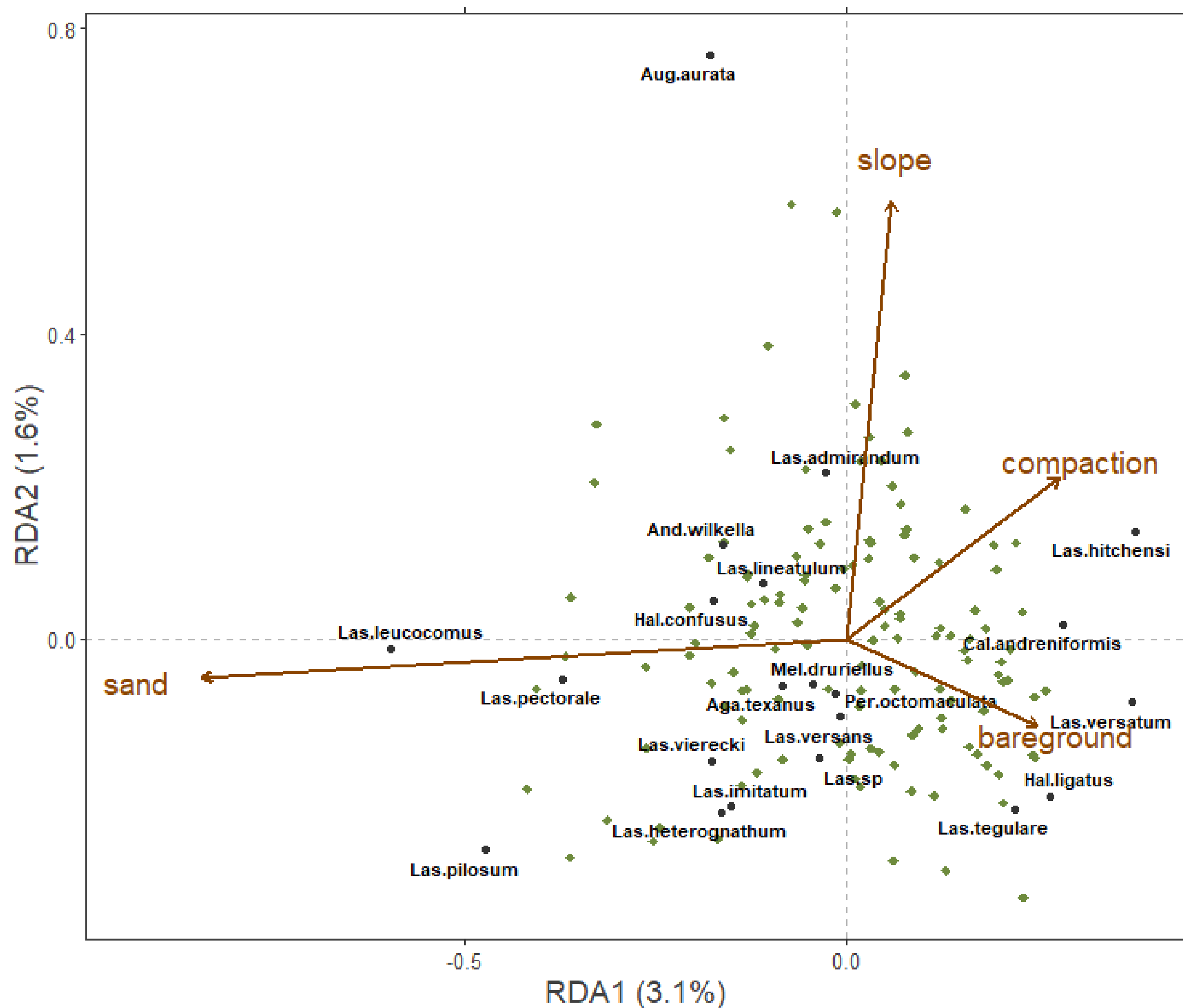

Figure 3-4: Redundancy analysis biplot showing associations between species and soil predictors for the 21 species that explain more than 5% of the variation among sites. The first and second axes are the only significant ones. RDA1 (F = 4.51, p = 0.001) explains 42.5% of the soil predictors' contribution (7.3% of the variance in bee community composition) and RDA2 explains 22.1% (F = 2.35, p = 0.011). Axis 1 was mostly a function of sand content (canonical coefficient: 0.095), and axis 2 was mainly defined by slope (canonical coefficient: 0.075). Significant soil predictors are represented by the brown vectors, sites by the green diamonds, and bee species by black points labeled with the species name (genus abbreviated with the first three letters).

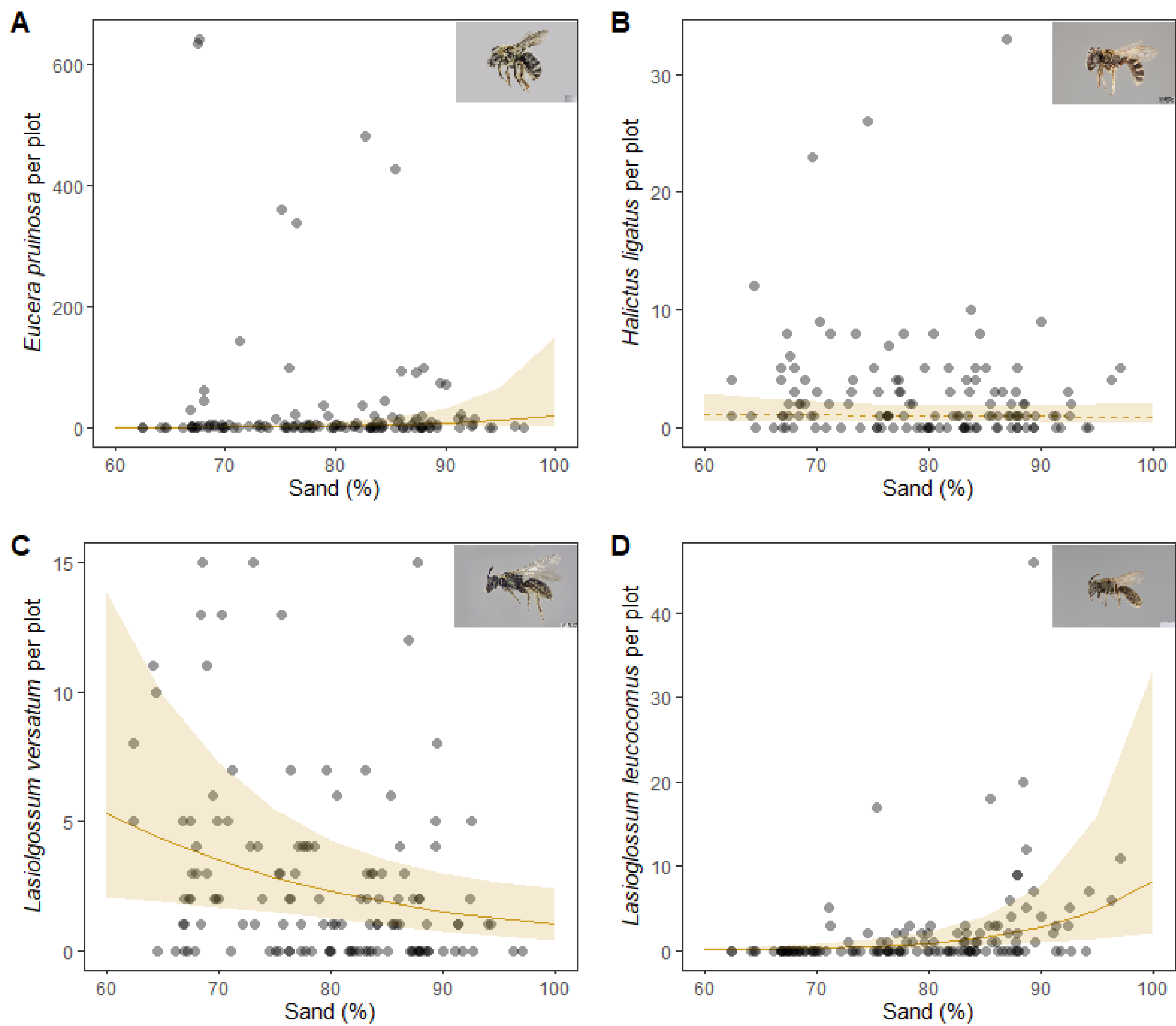

Figure 3-5: Associations between percentage sand and per-plot abundances of four ground-nesting bee species, chosen for their differences in their association—positive, negative, null—with sand (A: *Eucera pruinosa*, B: *Halictus ligatus*, C: *Lasioglossum versatum*, D: *L. leucocomus*). Points represent plots (N = 131) sampled at 35 farms over the two years of sampling (2018–2019). Shading represents 95% confidence intervals of model predictions. Solid lines represent significant relationships ($p < 0.05$) and dotted lines are non-significant. Photos © Laurence Packer.

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3.9. Supplementary Materials

Table S1: List of sites (n=131) used in the study with information on sampled farms, crops, and type of farming practices (conventional, organic) as well as geographic coordinates and nearest municipality. Some farms were sampled only in 2018, some only in 2019, and some were sampled in both years; but in the latter case, plots differed between years.

Site Code	Farm	Plot	Year	Crop	Farm Management	Latitude	Longitude	Locality
ORLE1	Orleans fruit farm	1	2018	orchard	conventional	45.456729	75.572757	Orleans
ORLE2	Orleans fruit farm	2	2018	strawberries	conventional	45.458795	75.555106	Orleans
ORLE3	Orleans fruit farm	3	2018	berries	conventional	45.46022	75.56456	Orleans
PROU1	Proulx Berry farm	1	2018	strawberries	conventional	45.486261	75.41941	Cumberland
PROU2	Proulx Berry farm	2	2018	strawberries	conventional	45.484974	75.417898	Cumberland
PROU3	Proulx Berry farm	3	2018	corn/soy/wheat	conventional	45.487464	75.408939	Cumberland
MILL1	Millers's Farm & Market	1	2018	strawberries	conventional	45.191788	75.650601	Manotick
MILL2	Millers's Farm & Market	2	2018	squash	conventional	45.190202	75.65219	Manotick
MILL3	Millers's Farm & Market	3	2018	veggies	conventional	45.190214	75.654242	Manotick
RIDE1	Rideau Pines Farm	1	2018	berries	conventional	45.176094	75.773695	North Gower
RIDE2	Rideau Pines Farm	2	2018	strawberries	conventional	45.175784	75.774902	North Gower
RIDE3	Rideau Pines Farm	3	2018	berries	conventional	45.175251	75.773775	North Gower
DEKO1	Dekok Berry Farm	1	2018	orchard	organic	45.368995	75.942022	Kanata
DEKO2	Dekok Berry Farm	2	2018	orchard	organic	45.36848	75.942075	Kanata
DEKO3	Dekok Berry Farm	3	2018	berries	organic	45.368163	75.941457	Kanata
HARV1	Harvest Moon Orchard	1	2018	orchard	organic	45.372173	76.094798	Carp
HARV2	Harvest Moon Orchard	2	2018	orchard	organic	45.372935	76.095435	Carp
HARV3	Harvest Moon Orchard	3	2018	squash	organic	45.375768	76.104555	Carp
WILS1	Wilson Kevin Farm	1	2018	corn/soy/wheat	organic	45.468799	76.08364	Woodlawn
WILS2	Wilson Kevin Farm	2	2018	pasture/forages	organic	45.466483	76.085084	Woodlawn
PINE1	Pine Hill Orchard	1	2018	orchard	conventional	45.416757	75.175763	Bourget
PINE2	Pine Hill Orchard	2	2018	orchard	conventional	45.417535	75.17747	Bourget
PINE3	Pine Hill/Lavoie Ferme	3	2018	corn/soy/wheat	conventional	45.415856	75.185369	Bourget

CAST1	Castor River Farm	1	2018	corn/soy/wheat	organic	45.243364	75.450495	Metcalfe
CAST2	Castor River Farm	2	2018	pasture/forages	organic	45.242587	75.452683	Metcalfe
ZAND1	Zandbelt Andrew Farm	1	2018	corn/soy/wheat	conventional	45.240358	75.445054	Metcalfe
ZAND2	Zandbelt Andrew Farm	2	2018	pasture/forages	conventional	45.243306	75.438762	Metcalfe
CANN1	Cannamore Orchard	1	2018	orchard	conventional	45.198191	75.247616	Crysler
CANN2	Cannamore Orchard	2	2018	strawberries	conventional	45.198276	75.246349	Crysler
CANN3	Cannamore Orchard	3	2018	squash	conventional	45.196049	75.247153	Crysler
GLEN1	Glen Haven Farms	1	2018	pasture/forages	conventional	45.191157	75.259597	Crysler
GLEN2	Glen Haven Farms	2	2018	corn/soy/wheat	conventional	45.193729	75.261733	Crysler
GLEN3	Glen Haven Farms	3	2018	corn/soy/wheat	conventional	45.196438	75.263293	Crysler
NOTR1	Notre Petite Ferme	1	2018	veggies	organic	45.594116	75.276338	Lochaber-Partie-Ouest
NOTR2	Notre Petite Ferme	2	2018	veggies	organic	45.594165	75.275464	Lochaber-Partie-Ouest
NOTR3	Notre Petite Ferme	3	2018	veggies	organic	45.594549	75.274195	Lochaber-Partie-Ouest
CROQ1	Croque Pomme	1	2018	orchard	organic	45.58778	75.304544	Thurso
CROQ2	Croque Pomme	2	2018	orchard	organic	45.586087	75.306645	Thurso
CROQ3	Croque Pomme	3	2018	squash	organic	45.585258	75.30638	Thurso
WILM1	Wilmont Orchard	1	2018	orchard	conventional	45.574113	75.350362	Gatineau
WILM2	Wilmont Orchard	2	2018	orchard	conventional	45.573063	75.351848	Gatineau
HAR1	Harvest Moon Orchard	1	2019	orchard	organic	45.372937	76.094371	Carp
HAR2	Harvest Moon Orchard	2	2019	orchard	organic	45.372068	76.095316	Carp
HAR3	Harvest Moon Orchard	3	2019	squash	organic	45.375314	76.105456	Carp
KIN1	Kinburn	1	2019	strawberries	conventional	45.405093	76.168445	Kinburn
KIN2	Kinburn	2	2019	corn/soy/wheat	conventional	45.40422	76.171481	Kinburn
KIN3	Kinburn	3	2019	strawberries	conventional	45.403386	76.170269	Kinburn
NEE1	Needhams Market	1	2019	veggies	conventional	45.391175	76.311099	Arnprior
NEE2	Needhams Market	2	2019	berries	conventional	45.391518	76.315707	Arnprior
NEE3	Needhams Market	3	2019	corn/soy/wheat	conventional	45.393678	76.312325	Arnprior
MAC1	MacLaren Orchard	1	2019	orchard	conventional	45.445044	76.649581	Renfrew
MAC2	MacLaren Orchard	2	2019	orchard	conventional	45.445729	76.642961	Renfrew
MAC3	MacLaren Orchard	3	2019	orchard	conventional	45.441529	76.64614	Renfrew
IND1	Indian Creek Orchard	1	2019	veggies	organic	45.26767	76.333919	Pakenham

IND2	Indian Creek Orchard	2	2019	veggies	organic	45.267371	76.33519	Pakenham
IND3	Indian Creek Orchard	3	2019	berries	organic	45.266527	76.33497	Pakenham
ROC1	Rock-n-Horse Farm	1	2019	veggies	organic	45.167638	76.225292	Almonte
ROC2	Rock-n-Horse Farm	2	2019	berries	organic	45.166822	76.224635	Almonte
ROC3	Rock-n-Horse Farm	3	2019	squash	organic	45.167004	76.226445	Almonte
AVO1	Avonmore Fruit Farm	1	2019	orchard	conventional	45.191605	74.979502	Avonmore
AVO2	Avonmore Fruit Farm	2	2019	strawberries	conventional	45.192907	74.977789	Avonmore
AVO3	Avonmore Fruit Farm	3	2019	berries	conventional	45.194542	74.977899	Avonmore
RUB1	Rubicon berries	1	2019	berries	organic	45.178928	74.973431	Avonmore
RUB2	Rubicon berries	2	2019	berries	organic	45.178928	74.974262	Avonmore
RUB3	Rubicon berries	3	2019	berries	organic	45.177477	74.973908	Avonmore
CAN1	Cannamore Orchard	1	2019	orchard	conventional	45.198415	75.247151	Crysler
CAN2	Cannamore Orchard	2	2019	strawberries	conventional	45.19504	75.25001	Crysler
CAN3	Cannamore Orchard	3	2019	orchard	conventional	45.1982	75.245809	Crysler
MOU1	Mountain Orchard	1	2019	orchard	conventional	45.028331	75.527499	Mountain
MOU2	Mountain Orchard	2	2019	orchard	conventional	45.030033	75.530352	Mountain
MOU3	Mountain Orchard	3	2019	orchard	conventional	45.031951	75.531007	Mountain
ARC1	Arc Acres	1	2019	veggies	organic	45.232604	75.612018	Greely
ARC2	Arc Acres	2	2019	pasture/forages	organic	45.233248	75.61172	Greely
ARC3	Arc Acres	3	2019	pasture/forages	organic	45.233272	75.610699	Greely
RID1	Rideau Pines Farm	1	2019	berries	conventional	45.176094	75.773416	North Gower
RID2	Rideau Pines Farm	2	2019	strawberries	conventional	45.176234	75.77598	North Gower
RID3	Rideau Pines Farm	3	2019	veggies	conventional	45.174763	75.777128	North Gower
MIL1	Millers's Farm & Market	1	2019	strawberries	conventional	45.193409	75.645704	Manotick
MIL2	Millers's Farm & Market	2	2019	strawberries	conventional	45.192826	75.652488	Manotick
MIL3	Millers's Farm & Market	3	2019	squash	conventional	45.189456	75.652289	Manotick
BEE1	Beetbox	1	2019	pasture/forages	organic	45.357649	75.871586	Ottawa
BEE2	Beetbox	2	2019	veggies	organic	45.358928	75.87068	Ottawa
BEE3	Beetbox	3	2019	veggies	organic	45.359309	75.87247	Ottawa
EKO1	Ekoroot	1	2019	veggies	organic	45.39322	75.558327	Ramsayville
EKO2	Ekoroot	2	2019	veggies	organic	45.393083	75.559144	Ramsayville

EKO3	Ekoroot	3	2019	pasture/forages	organic	45.39187	75.559311	Ramsayville
VAN1	VanVliet	1	2019	veggies	organic	45.42619	75.583142	Ottawa
VAN2	VanVliet	2	2019	veggies	organic	45.426404	75.58493	Ottawa
VAN3	VanVliet	3	2019	veggies	organic	45.425441	75.584962	Ottawa
ART1	Artisan Farm	1	2019	berries	organic	45.427657	74.951588	Fournier
ART2	Artisan Farm	2	2019	squash	organic	45.426967	74.953125	Fournier
ART3	Artisan Farm	3	2019	orchard	organic	45.425699	74.94976	Fournier
PIN1	Pine Hill Orchard	1	2019	orchard	conventional	45.419138	75.173654	Bourget
PIN2	Pine Hill Orchard	2	2019	orchard	conventional	45.41681	75.174481	Bourget
PIN3	Pine Hill Orchard	3	2019	orchard	conventional	45.418322	75.175876	Bourget
VIL1	Villeneuve verger	1	2019	berries	conventional	45.537615	75.159469	Saint-Pascale-Baylon
VIL2	Villeneuve verger	2	2019	berries	conventional	45.538309	75.158541	Saint-Pascale-Baylon
VIL3	Villeneuve verger	3	2019	orchard	conventional	45.539883	75.154901	Saint-Pascale-Baylon
PRO1	Proulx Berry farm	1	2019	berries	conventional	45.486659	75.417619	Cumberland
PRO2	Proulx Berry farm	2	2019	strawberries	conventional	45.486404	75.412469	Cumberland
PRO3	Proulx Berry farm	3	2019	strawberries	conventional	45.48767	75.407029	Cumberland
ORL1	Orleans fruit farm	1	2019	strawberries	conventional	45.458157	75.568545	Orleans
ORL2	Orleans fruit farm	2	2019	orchard	conventional	45.460604	75.56341	Orleans
ORL3	Orleans fruit farm	3	2019	strawberries	conventional	45.454989	75.565232	Orleans
NOT1	Notre Petite Ferme	1	2019	veggies	organic	45.594701	75.27637	Lochaber-Partie-Ouest
NOT2	Notre Petite Ferme	2	2019	veggies	organic	45.594589	75.27459	Lochaber-Partie-Ouest
NOT3	Notre Petite Ferme	3	2019	veggies	organic	45.593101	75.275298	Lochaber-Partie-Ouest
CRO1	Croque Pomme	1	2019	orchard	organic	45.590376	75.305682	Thurso
CRO2	Croque Pomme	2	2019	berries	organic	45.587042	75.306858	Thurso
CRO3	Croque Pomme	3	2019	orchard	organic	45.586002	75.304999	Thurso
WIL1	Wilmont Orchard	1	2019	orchard	conventional	45.573663	75.350377	Gatineau
WIL2	Wilmont Orchard	2	2019	orchard	conventional	45.574202	75.349836	Gatineau
WIL3	Wilmont Orchard	3	2019	orchard	conventional	45.575596	75.351029	Gatineau
CHA1	Chapeau Melon	1	2019	veggies	organic	45.592145	75.443302	L'Ange Gardien
CHA2	Chapeau Melon	2	2019	veggies	organic	45.593196	75.442619	L'Ange Gardien
CHA3	Chapeau Melon	3	2019	squash	organic	45.592617	75.439768	L'Ange Gardien

AGR1	Agricole	1	2019	veggies	organic	45.60251	75.439576	L'Ange Gardien
AGR2	Agricole	2	2019	veggies	organic	45.5997	75.439286	L'Ange Gardien
AGR3	Agricole	3	2019	veggies	organic	45.602203	75.436579	L'Ange Gardien
COU1	Courges et cie	1	2019	veggies	organic	45.532616	75.607996	Gatineau
COU2	Courges et cie	2	2019	squash	organic	45.533574	75.60609	Gatineau
COU3	Courges et cie	3	2019	squash	organic	45.529634	75.60519	Gatineau
LEV1	Leve Tot ferme	1	2019	veggies	organic	45.766119	76.028785	Alcove
LEV2	Leve Tot ferme	2	2019	veggies	organic	45.76644	76.027112	Alcove
LEV3	Leve Tot ferme	3	2019	veggies	organic	45.765248	76.027049	Alcove
ROO1	Roots and Shoots	1	2019	veggies	organic	45.660703	76.019451	Alcove
ROO2	Roots and Shoots	2	2019	veggies	organic	45.657813	76.019619	Alcove
ROO3	Roots and Shoots	3	2019	berries	organic	45.659186	76.018174	Alcove
JUN1	Juniper Farm	1	2019	veggies	organic	45.675348	75.950342	Wakefield
JUN2	Juniper Farm	2	2019	berries	organic	45.675544	75.948484	Wakefield
JUN3	Juniper Farm	3	2019	veggies	organic	45.674978	75.94683	Wakefield

Table 3−S2: Numbers of plots in each crop category, categorized by farming management

		Management		
Crop category	Crop included	conventional	organic	Total
berries	Raspberries, blueberries, red and black current, gooseberries	9	10	19
corn/soy/wheat	Sweet corn, soy, wheat, barley	7	2	9
orchard	Apple, cherry, plum, pear trees	23	11	34
pasture/forages	Pasture, alfalfa, mix clover/alfalfa	2	6	8
squash	Pumpkins and winter squashes	3	8	11
strawberries	Strawberries	17	0	17
vegetables	Asparagus, broccoli, cabbages, carrots etc.	3	30	33
Total		**64**	**67**	**131**

Table 3−S3: List of cavity-nesting bee genera (specimens were not all identified to species level) with the total number of individuals caught over the two years of sampling (2018-2019).

Genus	**n**
Anthidium	5
Anthophora	8
Augochlora	29
Bombus	939
Ceratina	958
Chelostoma	6
Heriades	13
Hoplitis	151
Hylaeus	301
Megachile	116
Osmia	98
Total	**2,624**

Table 3−S4: List of ground-nesting bee species identified (based on known ground-nesting genera; *Megachile* species were excluded because of their ability to nest in different substrates—underground and above-ground), with the total number of individuals caught over the two years of sampling (2018-2019), taxonomic keys used to identify specimens were Gibbs 2010, 2011, 2013, Mitchell 1960, 1962, and Ascher & Pickering 2020.

Family	Species	Individuals
Andrenidae	*Andrena arabis* Robertson 1897	5
Andrenidae	*Andrena canadensis* Dalla Torre 1896	3
Andrenidae	*Andrena carlini* Cockerell 1901	30
Andrenidae	*Andrena commoda* Smith 1879	17
Andrenidae	*Andrena crataegi* Robertson 1893	4
Andrenidae	*Andrena cressonii* Robertson 1891	10
Andrenidae	*Andrena dunningi* Cockerell 1898	9
Andrenidae	*Andrena erigeniae* Robertson 1891	8
Andrenidae	*Andrena erythronii* Robertson 1891	4
Andrenidae	*Andrena forbesii* Robertson 1891	2
Andrenidae	*Andrena frigida* Smith 1853	3
Andrenidae	*Andrena hippotes* Robertson 1895	1
Andrenidae	*Andrena imitatrix* Cresson 1872	10
Andrenidae	*Andrena integra* Smith 1853	1
Andrenidae	*Andrena macoupinensis* Robertson 1900	4
Andrenidae	*Andrena mandibularis* Robertson 1892	3
Andrenidae	*Andrena melanochroa* Cockerell 1898	5
Andrenidae	*Andrena miserabilis* Cresson 1872	17
Andrenidae	*Andrena morrisonella* Viereck 1917	3
Andrenidae	*Andrena nasonii* Robertson 1895	200
Andrenidae	*Andrena nivalis* Smith 1853	1
Andrenidae	*Andrena nubecula* Smith 1853	1
Andrenidae	*Andrena persimulata* Viereck 1917	13
Andrenidae	*Andrena rufosignata* Cockerell 1902	4
Andrenidae	*Andrena rugosa* Robertson 1891	1
Andrenidae	*Andrena sigmundi* Cockerell 1902	3
Andrenidae	*Andrena simplex* Smith 1853	10
Andrenidae	*Andrena* spp.	18
Andrenidae	*Andrena tridens* Robertson 1902	1
Andrenidae	*Andrena vicina* Smith 1853	4
Andrenidae	*Andrena wheeleri* Graenicher 1904	25
Andrenidae	*Andrena wilkella* Kirby 1802	71
Andrenidae	*Andrena w-scripta* Viereck 1904	7
Andrenidae	*Calliopsis andreniformis* Smith 1853	132

Andrenidae	*Perdita halictoides* Smith 1853	24
Andrenidae	*Perdita octomaculata* Say 1824	15
Andrenidae	*Pseudopanurgus andrenoides/labrosiformis*	14
Andrenidae	*Pseudopanurgus rudbeckiae* Robertson 1895	2
Andrenidae	*Pseudopanurgus solidaginis* Robertson 1893	1
Apidae	*Melissodes agilis* Cresson 1878	14
Apidae	*Melissodes denticulata* Smith 1854	2
Apidae	*Melissodes dentiventris* Smith 1854	3
Apidae	*Melissodes desponsus* Smith 1854	20
Apidae	*Melissodes druriellus* Kirby 1802	7
Apidae	*Melissodes illatus* Lovell & Cockerell 1906	5
Apidae	*Melissodes niveus* Robertson 1895	2
Apidae	*Melissodes trinodis* Robertson 1901	8
Apidae	*Melissodes trinodis/agilis*	8
Apidae	*Eucera (Peponapis) pruinosa* Say 1837	4134
Colletidae	*Colletes inaequalis* Say 1837	54
Colletidae	*Colletes latitarsis* Robertson 1891	1
Halictidae	*Agapostemon sericeus* Forster 1771	18
Halictidae	*Agapostemon texanus* Cresson 1872	53
Halictidae	*Agapostemon virescens* Fabricius 1775	68
Halictidae	*Augochlorella aurata* Smith 1853	295
Halictidae	*Augochloropsis metallica* Fabricius 1793	3
Halictidae	*Halictus confusus* Smith 1853	172
Halictidae	*Halictus ligatus* Say 1837	358
Halictidae	*Halictus rubicundus* Christ 1791	22
Halictidae	*Lasioglossum admirandum* Sandhouse 1924	40
Halictidae	*Lasioglossum albipenne* Robertson 1890	16
Halictidae	*Lasioglossum anomalum* Robertson 1892	60
Halictidae	*Lasioglossum atwoodi* Gibbs 2010	3
Halictidae	*Lasioglossum cinctipes* Provancher 1888	1
Halictidae	*Lasioglossum coeruleum* Robertson 1893	11
Halictidae	*Lasioglossum coriaceum* Smith 1853	48
Halictidae	*Lasioglossum cressonii* Robertson 1890	44
Halictidae	*Lasioglossum dreisbachi* Mitchell 1960	2
Halictidae	*Lasioglossum ellisiae* Sandhouse 1924	1
Halictidae	*Lasioglossum ephialtum* Gibbs 2010	21
Halictidae	*Lasioglossum foxii* Robertson 1895	10
Halictidae	*Lasioglossum heterognathus* Mitchell 1960	128
Halictidae	*Lasioglossum hitchensi* Gibbs 2012	193
Halictidae	*Lasioglossum imitatum* Smith 1853	294
Halictidae	*Lasioglossum laevissimum* Smith 1853	74
Halictidae	*Lasioglossum leucocomus* Lovell 1908	255
Halictidae	*Lasioglossum leucozonium* Schrank 1781	300

Halictidae	*Lasioglossum lineatulum* Crawford 1906	18
Halictidae	*Lasioglossum macoupinense* Robertson 1895	54
Halictidae	*Lasioglossum nelumbonis* Robertson 1890	2
Halictidae	*Lasioglossum nigroviride* Graenicher 1911	3
Halictidae	*Lasioglossum novascotiae* Mitchell 1960	1
Halictidae	*Lasioglossum nymphaearum* Robertson 1895	36
Halictidae	*Lasioglossum oblongum* Lovell 1905	3
Halictidae	*Lasioglossum oenotherae* Stevens 1920	1
Halictidae	*Lasioglossum paradmirandum* Knerer & Atwood 1966	11
Halictidae	*Lasioglossum pectorale* Smith 1853	51
Halictidae	*Lasioglossum perpunctatum* Ellis 1913	76
Halictidae	*Lasioglossum pilosum* Smith 1853	110
Halictidae	*Lasioglossum planatum* Lovell 1905	1
Halictidae	*Lasioglossum sagax* Sandhouse 1924	3
Halictidae	*Lasioglossum smilacinae* Robertson 1897	3
Halictidae	*Lasioglossum* spp.	184
Halictidae	*Lasioglossum subversans* Mitchell 1960	7
Halictidae	*Lasioglossum subviridatum* Cockerell 1938	5
Halictidae	*Lasioglossum tegulare* Robertson 1890	157
Halictidae	*Lasioglossum tenax* Sandhouse 1924	1
Halictidae	*Lasioglossum truncatum* Robertson 1901	1
Halictidae	*Lasioglossum versans* Lovell 1905	27
Halictidae	*Lasioglossum versatum* Robertson 1902	357
Halictidae	*Lasioglossum vierecki* Crawford 1904	48
Halictidae	*Lasioglossum viridatum* Lovell 1905	12
Halictidae	*Lasioglossum viridatum* complex	2
Halictidae	*Lasioglossum zephyrum* Smith 1853	31
Halictidae	*Lasioglossum zonulum* Smith 1848	83

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Table 3−S5: Results of GLMM of ground-nesting bee abundance, richness, and diversity including *E. pruinosa* (squash bees). Fixed predictors were the uncorrelated soil predictors (slope, compaction, bare ground %, litter %, and sand %), number of traps, and year; farm was included as a random effect. All continuous predictors were scaled to mean = 0 and s.d. = 1. N = 131 observations (plots) from 35 farms. Results in bold were significant at α = 0.05.

Response	Predictors	Coef.	SE	z or t	P
Ground-nesting bees					
Abundance including E. pruinosa	slope	−0.047	0.072	−0.650	0.516
	compaction	0.119	0.069	1.741	0.082
	bare ground	**0.237**	**0.069**	**3.417**	**0.001**
	dead litter	0.021	0.071	0.299	0.765
	sand	**0.242**	**0.087**	**2.783**	**0.005**
	traps	**0.193**	**0.097**	**1.991**	**0.046**
	year (2019)	−0.299	0.221	−1.353	0.176
Richness including E. pruinosa	slope	−0.023	0.031	−0.751	0.453
	compaction	0.013	0.030	0.438	0.662
	bare ground	**0.076**	**0.028**	**2.691**	**0.007**
	dead litter	−0.005	0.029	−0.164	0.870
	sand	**0.092**	**0.037**	**2.452**	**0.014**
	traps	**0.102**	**0.042**	**2.427**	**0.015**
	year (2019)	−0.146	0.094	−1.555	0.120
Diversity including E. pruinosa	**slope**	**−0.610**	**0.278**	**−2.193**	**0.030**
(Simpson's index 1/D)	compaction	−0.172	0.276	−0.625	0.533
	bare ground	−0.394	0.260	−1.519	0.132
	dead litter	−0.001	0.255	−0.003	0.998
	sand	−0.271	0.324	−0.835	0.406
	traps	0.203	0.361	0.561	0.576
	year (2019)	**−1.913**	**0.835**	**−2.289**	**0.024**

Table 3−S6: Results from the GLMM substituting sand percentage and bare ground percentage by crop type and farm management (organic vs conventional). Response variables for ground-nesting bees exclude *E. pruinosa*. Farm identity was included as a random factor. Bold indicates significant effects (p<0.05), SE is the standard error and z the z-score.

Response	Predictors	Coef.	SE	z or t	P
Ground-nesting bees	reference crop: berries				
Abundance	crop: corn/soy/wheat	0.35	0.25	1.43	0.15
	crop: orchard	0.02	0.18	0.13	0.89
	crop: pasture/forages	-0.10	0.26	-0.39	0.70
	crop: squash	0.07	0.22	0.33	0.74
	crop: strawberries	0.38	0.20	1.89	0.06
	crop: veggies	-0.09	0.19	-0.50	0.62
	management (organic)	0.09	0.18	0.50	0.62
	slope	-0.02	0.06	-0.38	0.70
	compaction	-0.07	0.05	-1.35	0.18
	traps	**0.18**	**0.08**	**2.37**	**0.02**
	year (2019)	-0.28	0.17	-1.62	0.11
Richness	crop: corn/soy/wheat	0.07	0.14	0.49	0.62
	crop: orchard	-0.08	0.10	-0.79	0.43
	crop: pasture/forages	-0.21	0.15	-1.40	0.16
	crop: squash	0.00	0.12	0.04	0.97
	crop: strawberries	0.02	0.11	0.19	0.85
	crop: veggies	-0.12	0.10	-1.17	0.24
	management (organic)	0.06	0.11	0.58	0.56
	slope	-0.02	0.03	-0.73	0.47
	compaction	-0.01	0.03	-0.25	0.80
	traps	**0.10**	**0.04**	**2.35**	**0.02**
	year (2019)	**-0.20**	**0.10**	**-2.03**	**0.04**
Diversity (Simpson's 1/D)	crop: corn/soy/wheat	-0.17	1.11	-0.15	0.88
	crop: orchard	-1.20	0.81	-1.48	0.14
	crop: pasture/forages	-1.40	1.19	-1.18	0.24
	crop: squash	0.40	1.00	0.40	0.69
	crop: strawberries	-0.53	0.90	-0.58	0.56
	crop: veggies	-1.12	0.83	-1.34	0.18
	management (organic)	-0.48	0.80	-0.60	0.55
	slope	**-0.59**	**0.25**	**-2.33**	**0.02**
	compaction	0.02	0.25	0.08	0.93
	traps	0.47	0.34	1.39	0.17
	year (2019)	**-1.99**	**0.78**	**-2.56**	**0.01**

Cavity-nesting bees					
Abundance	crop: corn/soy/wheat	-0.13	0.31	-0.41	0.68
	crop: orchard	**-0.84**	**0.23**	**-3.65**	**<0.001**
	crop: pasture/forages	-0.56	0.34	-1.65	0.10
	crop: squash	-0.21	0.29	-0.74	0.46
	crop: strawberries	-0.28	0.26	-1.10	0.27
	crop: veggies	-0.28	0.24	-1.19	0.24
	management (organic)	-0.26	0.22	-1.20	0.23
	slope	0.02	0.07	0.22	0.82
	compaction	0.11	0.07	1.44	0.15
	traps	**0.21**	**0.10**	**1.98**	**0.048**
	year (2019)	0.38	0.23	1.65	0.10

Table 3−S7: Results from the GLMM substituting percentage sand and percentage bare ground by crop type and farm management (organic vs conventional). Response variables for ground-nesting bees include *E. pruinosa*. Farm identity was included as a random factor. Bold indicates significant effects (p<0.05), SE is the standard error and z the z-score.

Response	Predictors	Coef.	SE	z	P
Ground-nesting bees	reference crop: berries				
Abundance including E. pruinosa	cropcorn/soy/wheat	-0.196	0.319	-0.614	0.539
	croporchard	-0.186	0.232	-0.802	0.423
	croppasture/forages	-0.371	0.338	-1.097	0.272
	cropsquash	0.395	0.277	1.429	0.153
	cropstrawberries	0.499	0.258	1.937	0.053
	cropveggies	-0.016	0.233	-0.069	0.945
	management (organic)	-0.207	0.243	-0.853	0.394
	slope	-0.059	0.071	-0.832	0.406
	compaction	-0.005	0.069	-0.067	0.946
	traps	0.182	0.098	1.857	0.063
	year (2019)	**-0.525**	**0.221**	**-2.375**	**0.018**
Richness including E. pruinosa	cropcorn/soy/wheat	0.053	0.134	0.398	0.691
	croporchard	-0.093	0.098	-0.954	0.340
	croppasture/forages	-0.226	0.150	-1.504	0.133
	cropsquash	0.007	0.114	0.058	0.954
	cropstrawberries	0.013	0.106	0.126	0.900
	cropveggies	-0.112	0.102	-1.106	0.269
	management (organic)	0.060	0.109	0.555	0.579
	slope	-0.022	0.030	-0.734	0.463
	compaction	-0.007	0.031	-0.237	0.813
	traps	**0.103**	**0.043**	**2.398**	**0.016**
	year (2019)	-0.185	0.095	-1.950	0.051
Diversity including E. pruinosa	cropcorn/soy/wheat	1.579	1.176	1.343	0.182
	croporchard	0.315	0.861	0.366	0.715
	croppasture/forages	0.375	1.257	0.298	0.766
	cropsquash	-0.852	1.064	-0.801	0.425
	cropstrawberries	-1.812	0.959	-1.889	0.062
	cropveggies	0.135	0.881	0.153	0.879
	management (organic)	0.248	0.846	0.293	0.771
	slope	**-0.546**	**0.266**	**-2.052**	**0.042**
	compaction	0.064	0.270	0.236	0.814
	traps	0.280	0.360	0.777	0.439
	year (2019)	**-1.459**	**0.823**	**-1.774**	**0.079**

Table 3−S8: Results of GLMMs with negative binomial distribution of the abundance of the most abundant ground-nesting bee species (those with more than 200 individuals). A zero-inflated formula was used in the models for *E. pruinosa* due to numerous zeroes in the data. Explanatory variables are the five soil predictors, number of traps collected, and year; farm identity was included as a random effect. Bold indicates significant effects (p ≤ 0.01), SE is the standard error and z the z-score.

Response	Predictors	Coef.	SE	z	P
Augochlorella aurata (n = 295)	slope	0.28	0.13	2.17	0.03
	compaction	0.13	0.14	0.89	0.37
	bare ground	-0.02	0.13	-0.15	0.88
	dead litter	0.01	0.12	0.12	0.90
	sand	0.13	0.17	0.79	0.43
	traps	0.28	0.19	1.47	0.14
	year (2019)	0.21	0.43	0.49	0.62
Andrena nasonii (n = 200)	slope	-0.21	0.19	-1.10	0.27
	compaction	-0.14	0.18	-0.78	0.44
	bare ground	0.04	0.17	0.22	0.83
	dead litter	0.12	0.16	0.73	0.46
	sand	-0.41	0.21	-1.93	0.05
	traps	**1.29**	**0.33**	**3.97**	**<0.001**
	year (2019)	**-2.32**	**0.66**	**-3.52**	**<0.001**
Eucera pruinosa (n = 4,134)	slope	-0.16	0.23	-0.70	0.48
	compaction	0.21	0.22	1.00	0.32
	bare ground	0.36	0.23	1.54	0.12
	dead litter	-0.12	0.26	-0.48	0.63
	sand	**0.93**	**0.33**	**2.85**	**<0.001**
	traps	0.47	0.34	1.37	0.17
	year (2019)	-0.23	0.70	-0.33	0.74
Halictus ligatus (n = 358)	slope	-0.28	0.15	-1.86	0.06
	compaction	0.18	0.13	1.42	0.16
	bare ground	0.13	0.13	0.97	0.33
	dead litter	0.05	0.12	0.39	0.70
	sand	-0.06	0.14	-0.43	0.67
	traps	0.03	0.18	0.17	0.86
	year (2019)	0.98	0.41	2.40	0.02
Lasioglossum imitatum (n = 294)	slope	-0.11	0.14	-0.81	0.42
	compaction	0.08	0.12	0.65	0.52
	bare ground	0.14	0.12	1.21	0.22
	dead litter	0.18	0.14	1.27	0.20
	sand	0.18	0.16	1.18	0.24

	traps	0.25	0.17	1.47	0.14
	year (2019)	-0.84	0.40	-2.08	0.04
Lasioglossum leucocomus (n = 255)	slope	0.04	0.17	0.23	0.82
	compaction	**-0.53**	**0.21**	**-2.59**	**0.01**
	bare ground	0.16	0.17	0.95	0.34
	dead litter	0.01	0.15	0.10	0.92
	sand	**0.99**	**0.23**	**4.36**	**<0.001**
	traps	0.57	0.32	1.82	0.07
	year (2019)	-0.56	0.58	-0.96	0.34
Lasioglossum leucozonium (n = 300)	slope	-0.11	0.14	-0.81	0.42
	compaction	0.08	0.12	0.65	0.52
	bare ground	0.14	0.12	1.21	0.22
	dead litter	0.18	0.14	1.27	0.20
	sand	0.18	0.16	1.18	0.24
	traps	0.25	0.17	1.47	0.14
	year (2019)	-0.84	0.40	-2.08	0.04
Lasioglossum versatum (n = 357)	slope	0.08	0.13	0.63	0.53
	compaction	-0.11	0.13	-0.85	0.40
	bare ground	0.18	0.12	1.51	0.13
	dead litter	0.05	0.12	0.43	0.67
	sand	-0.36	0.15	-2.39	0.02
	traps	0.18	0.17	1.09	0.27
	year (2019)	-0.18	0.40	-0.46	0.65

Table 3−S9: Results of the GLMM substitute models with negative binomial distribution of the abundance of the most abundant ground-nesting bee species (those with more than 200 individuals). A zero-inflated formula was used in the model for *E. pruinosa* due to numerous zeroes in the data. Explanatory variables are slope, compaction, crop type (model reference: berries), farm management (model reference: conventional), number of traps collected, and year; farm identity was included as a random effect. Bold indicates significant effects ($p \leq 0.01$), SE is the standard error and z the z-score.

Response	Predictors	Coef.	SE	z	P
Augochlorella aurata	**Slope**	**0.33**	**0.12**	**2.66**	**0.01**
	Compaction	0.05	0.13	0.34	0.74
	Crop corn/soy/wheat	0.46	0.59	0.79	0.43
	Crop orchard	0.01	0.43	0.02	0.98
	Crop pasture/forages	-0.01	0.62	-0.02	0.99
	Crop squash	0.39	0.50	0.77	0.44
	Crop strawberries	0.50	0.45	1.11	0.26
	Crop veggies	-0.32	0.43	-0.74	0.46
	Management (organic)	-0.05	0.41	-0.12	0.90
	Bowls	0.25	0.19	1.35	0.18
	Year (2019)	0.31	0.42	0.76	0.45
Andrena nasonii	Slope	-0.19	0.20	-0.96	0.34
	Compaction	-0.05	0.18	-0.29	0.77
	Crop corn/soy/wheat	0.80	0.76	1.04	0.30
	Crop orchard	-0.32	0.59	-0.55	0.59
	Crop pasture/forages	-1.02	0.94	-1.09	0.27
	Crop squash	0.75	0.65	1.16	0.25
	Crop strawberries	0.29	0.61	0.48	0.63
	Crop veggies	0.55	0.54	1.02	0.31
	Management (organic)	-0.09	0.51	-0.18	0.86
	Bowls	**1.37**	**0.35**	**3.96**	**<0.001**
	Year (2019)	**-2.26**	**0.68**	**-3.32**	**0.001**
Eucera pruinosa	Slope	-0.09	0.21	-0.41	0.68
	Compaction	0.12	0.19	0.63	0.53
	Crop corn/soy/wheat	**-2.76**	**1.02**	**-2.72**	**0.01**
	Crop orchard	-0.86	0.71	-1.22	0.22
	Crop pasture/forages	-2.84	1.29	-2.20	0.03
	Crop squash	1.02	0.71	1.43	0.15
	Crop strawberries	0.58	0.62	0.93	0.35
	Crop veggies	-0.19	0.65	-0.29	0.77
	Management (organic)	-0.06	0.99	-0.06	0.95

	Bowls	0.52	0.32	1.62	0.10
	Year (2019)	-0.41	0.61	-0.67	0.50
Halictus ligatus	Slope	-0.23	0.13	-1.74	0.08
	Compaction	0.16	0.12	1.41	0.16
	Crop corn/soy/wheat	0.98	0.54	1.82	0.07
	Crop orchard	0.27	0.40	0.69	0.49
	Crop pasture/forages	-0.60	0.62	-0.97	0.33
	Crop squash	-0.25	0.52	-0.49	0.63
	Crop strawberries	**1.57**	**0.44**	**3.59**	**<0.001**
	Crop veggies	0.16	0.37	0.43	0.66
	Management (organic)	0.60	0.35	1.73	0.08
	Bowls	0.02	0.17	0.14	0.89
	Year (2019)	**0.99**	**0.38**	**2.58**	**0.01**
Lasioglossum imitatum	Slope	-0.15	0.21	-0.69	0.49
	Compaction	-0.13	0.20	-0.63	0.53
	Crop corn/soy/wheat	0.19	0.85	0.22	0.83
	Crop orchard	-0.67	0.63	-1.06	0.29
	Crop pasture/forages	0.48	0.89	0.54	0.59
	Crop squash	-0.46	0.83	-0.55	0.58
	Crop strawberries	0.98	0.63	1.57	0.12
	Crop veggies	0.46	0.71	0.64	0.52
	Management (organic)	-0.68	0.84	-0.82	0.41
	Bowls	**0.99**	**0.33**	**3.05**	**0.002**
	Year (2019)	-1.41	0.68	-2.08	0.04
Lasioglossum leucocomus	Slope	0.07	0.17	0.42	0.67
	Compaction	**-0.72**	**0.22**	**-3.20**	**0.001**
	Crop corn/soy/wheat	-0.25	0.84	-0.30	0.76
	Crop orchard	0.06	0.58	0.11	0.92
	Crop pasture/forages	0.13	0.90	0.15	0.88
	Crop squash	-0.19	0.71	-0.27	0.79
	Crop strawberries	-0.47	0.76	-0.62	0.53
	Crop veggies	-0.13	0.63	-0.20	0.84
	Management (organic)	0.01	0.69	0.02	0.98
	Bowls	0.38	0.32	1.20	0.23
	Year (2019)	-0.62	0.60	-1.03	0.30
Lasioglossum leucozonium	Slope	-0.06	0.13	-0.46	0.65
	Compaction	0.02	0.12	0.14	0.89
	Crop corn/soy/wheat	1.00	0.54	1.85	0.06
	Crop orchard	**1.17**	**0.43**	**2.76**	**0.01**
	Crop pasture/forages	0.64	0.59	1.08	0.28
	Crop squash	0.59	0.51	1.16	0.25
	Crop strawberries	**1.19**	**0.45**	**2.63**	**0.01**
	Crop veggies	0.40	0.41	0.98	0.33

	Management (organic)	0.08	0.42	0.19	0.85
	Bowls	0.23	0.16	1.40	0.16
	Year (2019)	-0.84	0.40	-2.11	0.03
Lasioglossum versatum	Slope	0.05	0.13	0.42	0.68
	Compaction	-0.05	0.12	-0.36	0.72
	Crop corn/soy/wheat	-0.16	0.57	-0.29	0.77
	Crop orchard	0.06	0.42	0.14	0.89
	Crop pasture/forages	-0.36	0.59	-0.61	0.54
	Crop squash	0.37	0.49	0.76	0.45
	Crop strawberries	0.13	0.48	0.27	0.79
	Crop veggies	-0.01	0.42	-0.02	0.98
	Management (organic)	0.06	0.42	0.15	0.88
	Bowls	0.16	0.17	0.96	0.34
	Year (2019)	-0.23	0.40	-0.58	0.56

Table 3−S10: Results of the partial RDA of ground-nesting bee abundance (with and without *E. pruinosa*) and soil predictors, accounting for spatial autocorrelation. The two models are significant ($p \leq 0.001$), and bold predictors indicates significant effects ($p < 0.05$).

Model excluding *E. pruinosa*

Predictors	Df	Variance	F	p
bare ground %	**1**	**0.008**	**1.80**	**0.008**
compaction	**1**	**0.008**	**1.84**	**0.009**
sand %	**1**	**0.017**	**3.89**	**0.001**
slope	**1**	**0.009**	**1.99**	**0.005**
dead litter %	1	0.005	1.11	0.304
Residual	117	0.52		

Model including *E. pruinosa*

Predictors	Df	Variance	F	p
bare ground %	**1**	**0.008**	**1.85**	**0.012**
compaction	1	0.007	1.53	0.059
sand %	**1**	**0.016**	**3.69**	**0.001**
slope	**1**	**0.008**	**1.76**	**0.019**
dead litter %	1	0.005	1.21	0.216
Residual	118	0.52		

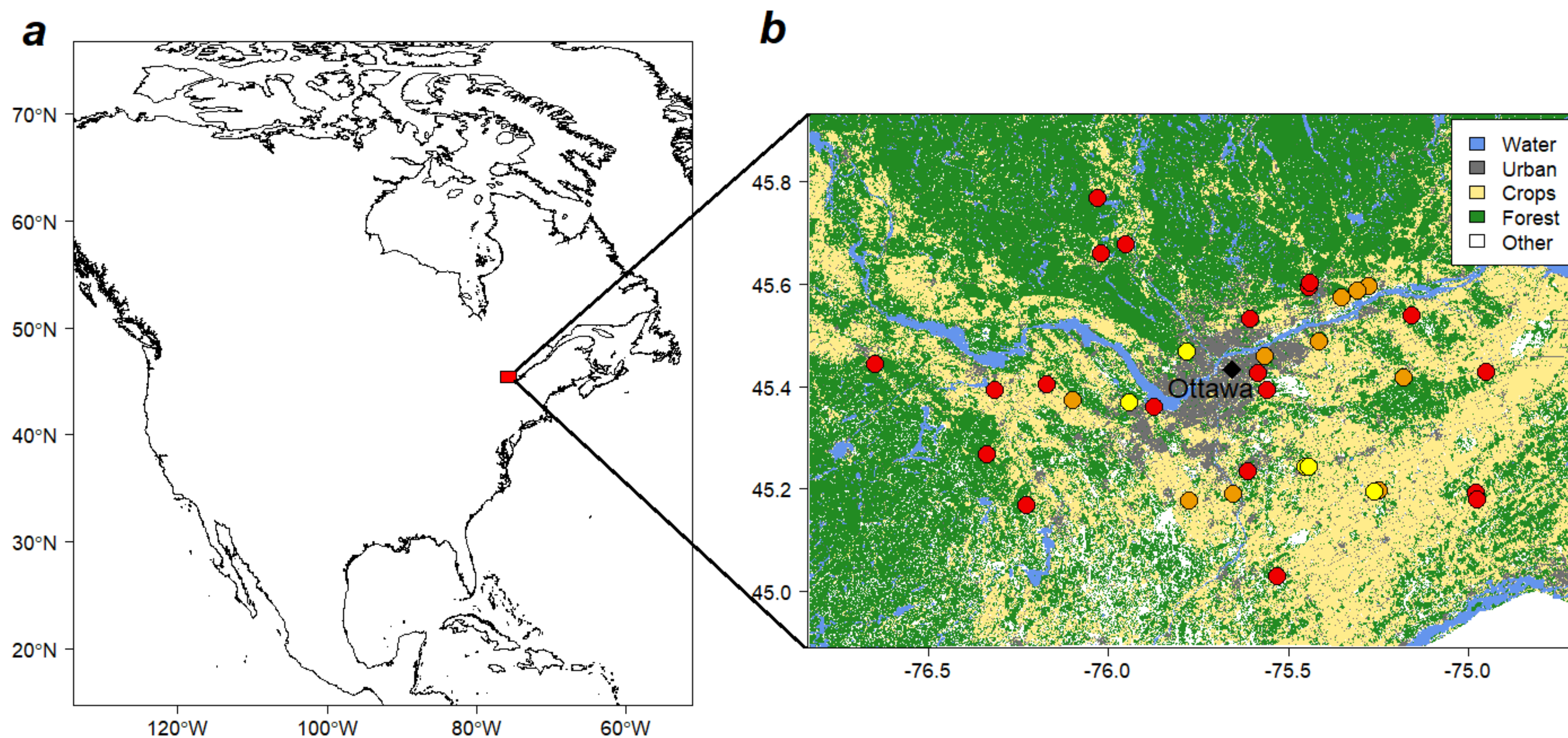

Figure 3−S1: Maps of the study region. (a) Location of the study region in North America. (b) Zoomed-in map showing locations of the study sites (n= 35 farms) colour-coded by year of sampling (yellow only = 2018, red only = 2019, orange = both years). Sites are located around the city of Ottawa, Canada, and are shown overlaid on a 30 m resolution 2019 land-cover map (Canada Centre for Remote Sensing 2015).

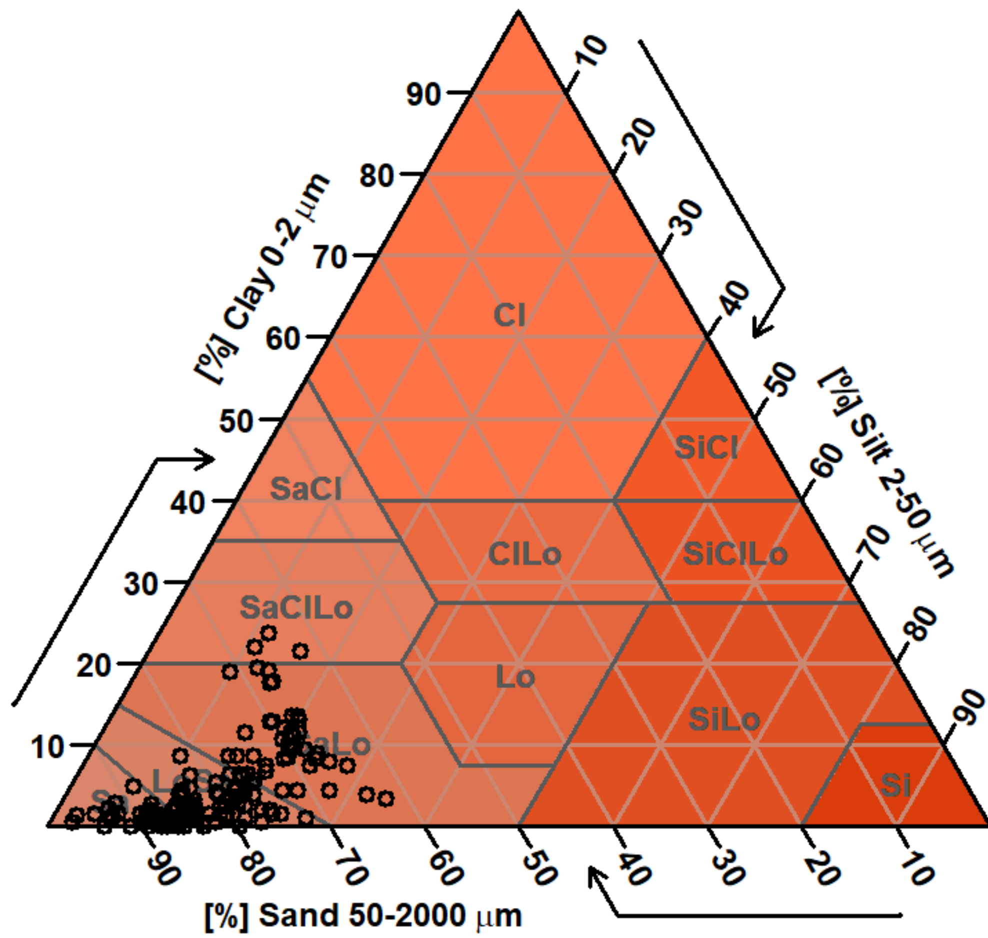

Figure 3−S2: Soil textural triangle representing the percentages of sand, silt and clay observed in samples from the surface layer (top 15-20 cm) of each plot (N=131), on 35 farms around Ottawa, Canada.

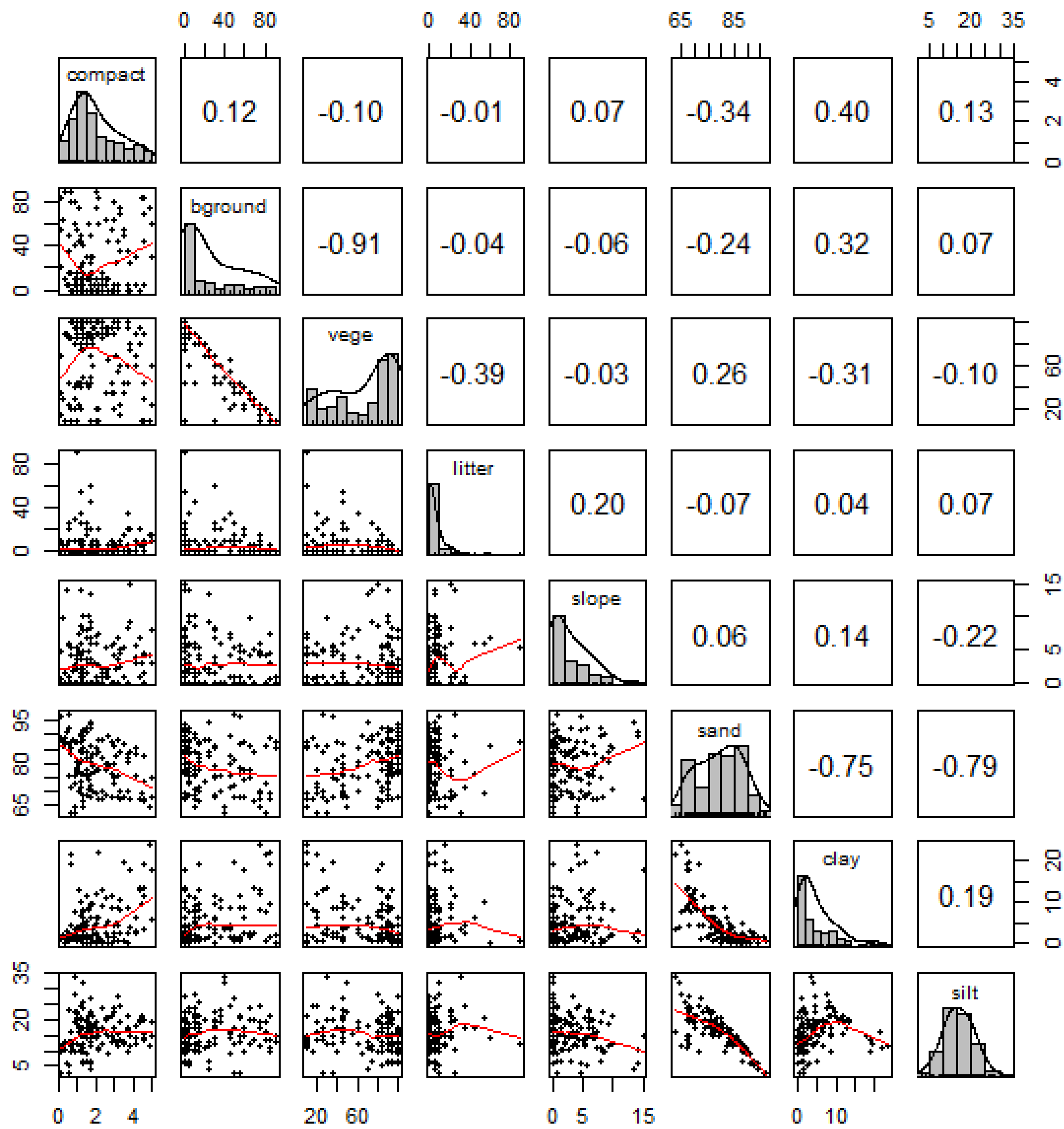

Figure 3−S3: Correlation matrix between all soil predictors with Pearson correlation coefficients in the upper right panels, histograms of the distribution of the raw data on the diagonal, and correlations in the lower left panels. Soil predictors are compaction (compact), bare ground % (bground), vegetation cover % (vege), dead litter % (litter), slope, sand %, clay % and silt%. Bare ground and vegetation (Pearson r = −0.91), sand and clay (r = −0.75), and sand and silt (r = −0.79) were highly correlated, therefore vegetation cover %, clay %, and silt % were not included in the models.

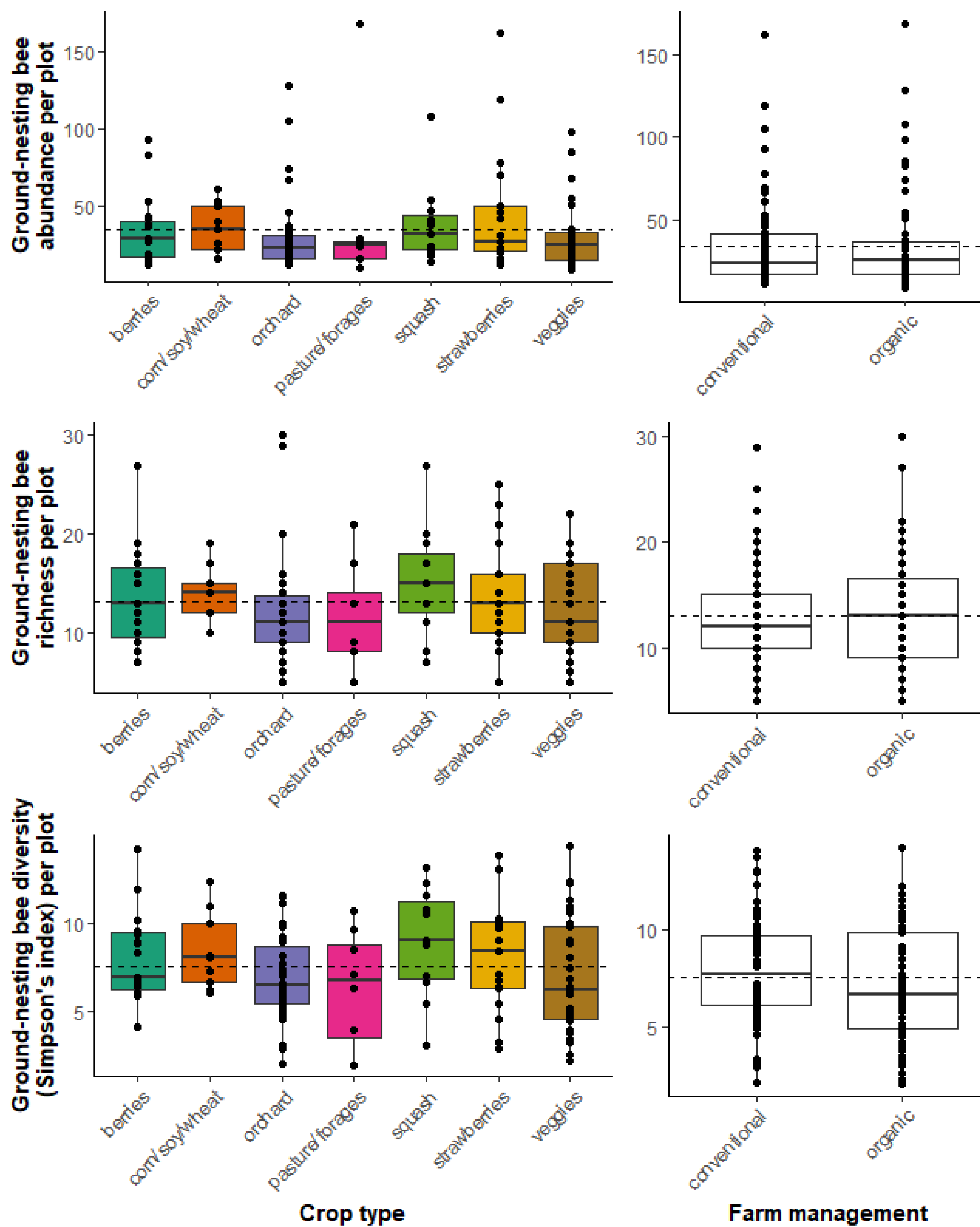

Figure 3−S4: Boxplots of the abundance, richness, and diversity (Simpson's index, 1/D) of ground-nesting bees per plot (excluding *E. pruinosa*) in relation to crop type and farm management. There was no statistical difference among crop types and farm management (see Table S2 for details on each category) according to a GLMM that included other variables (see Table S6). N=131 plots.

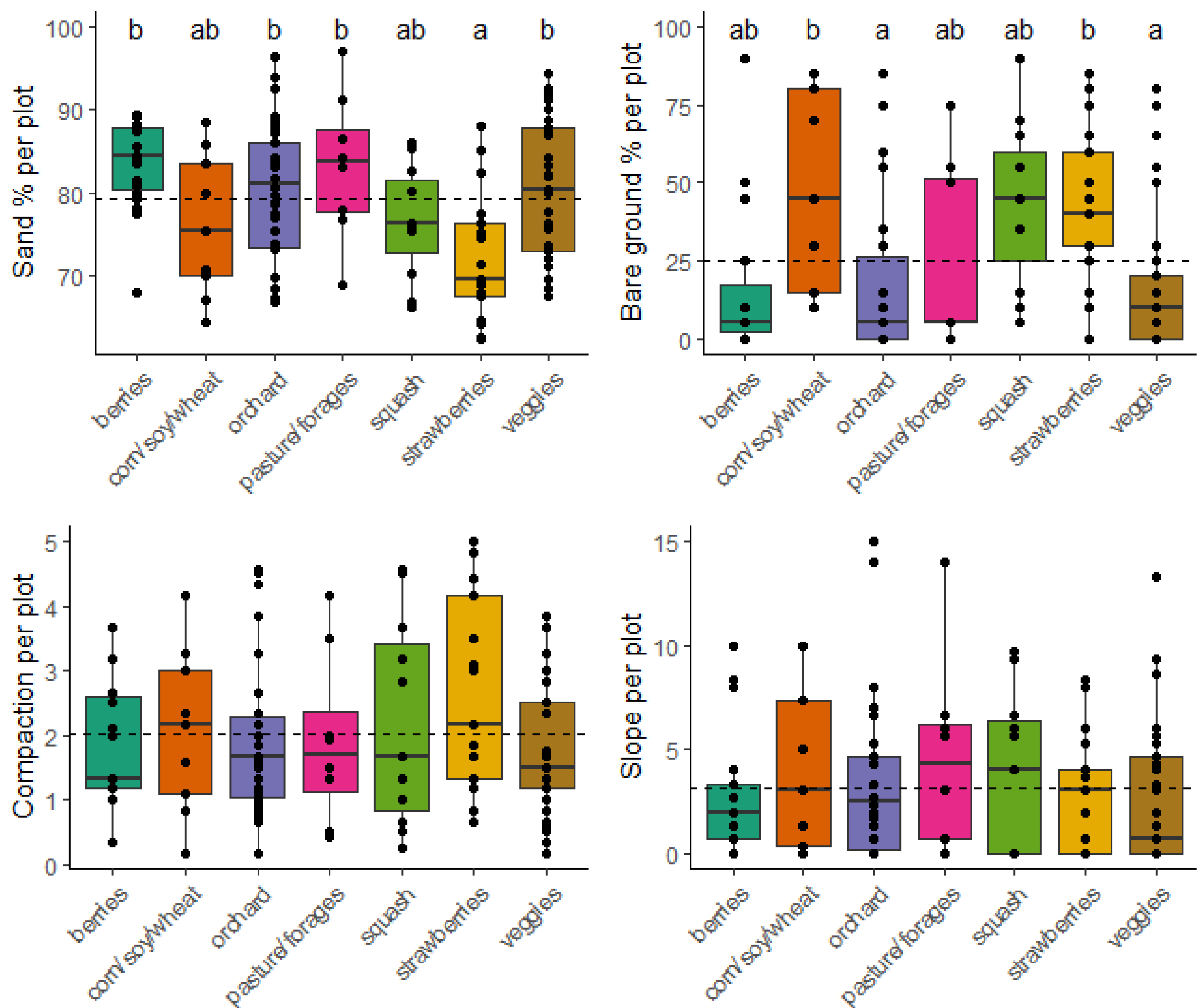

Figure 3−S5: Boxplots of soil variables—percent sand, percent bare ground, compaction and slope—in relation to crop type. Dotted horizontal line represents the mean across all plots. Significant differences according to Tukey HSD tests ($p < 0.05$) are indicated by letters. N=131 plots.

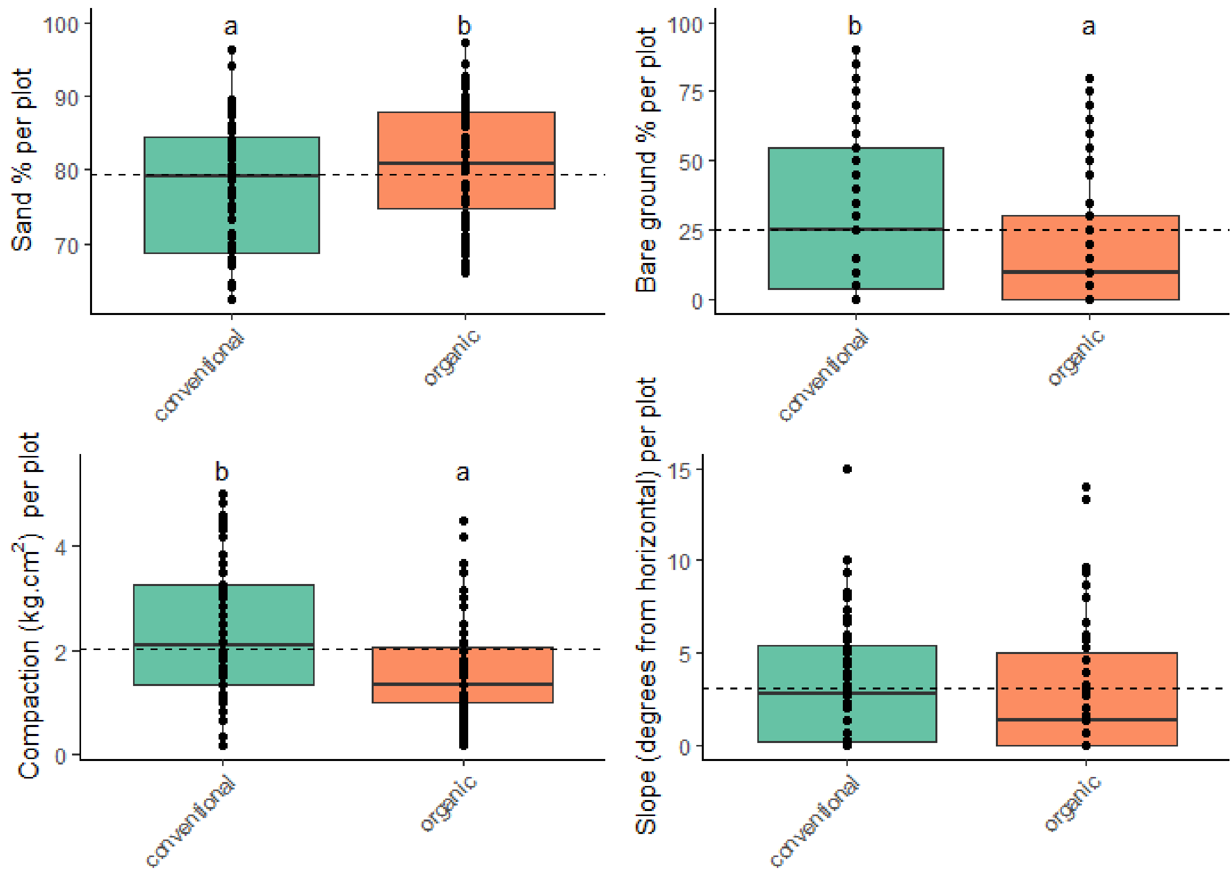

Figure 3−S6: Boxplots of the soil predictors—percent sand, percent bare ground, compaction and slope—per plot in relation to farm management. Dotted horizontal line represents the mean across all plots. Statistical differences ($p < 0.05$ based on ANOVA) are indicated by letters. N=131 plots.

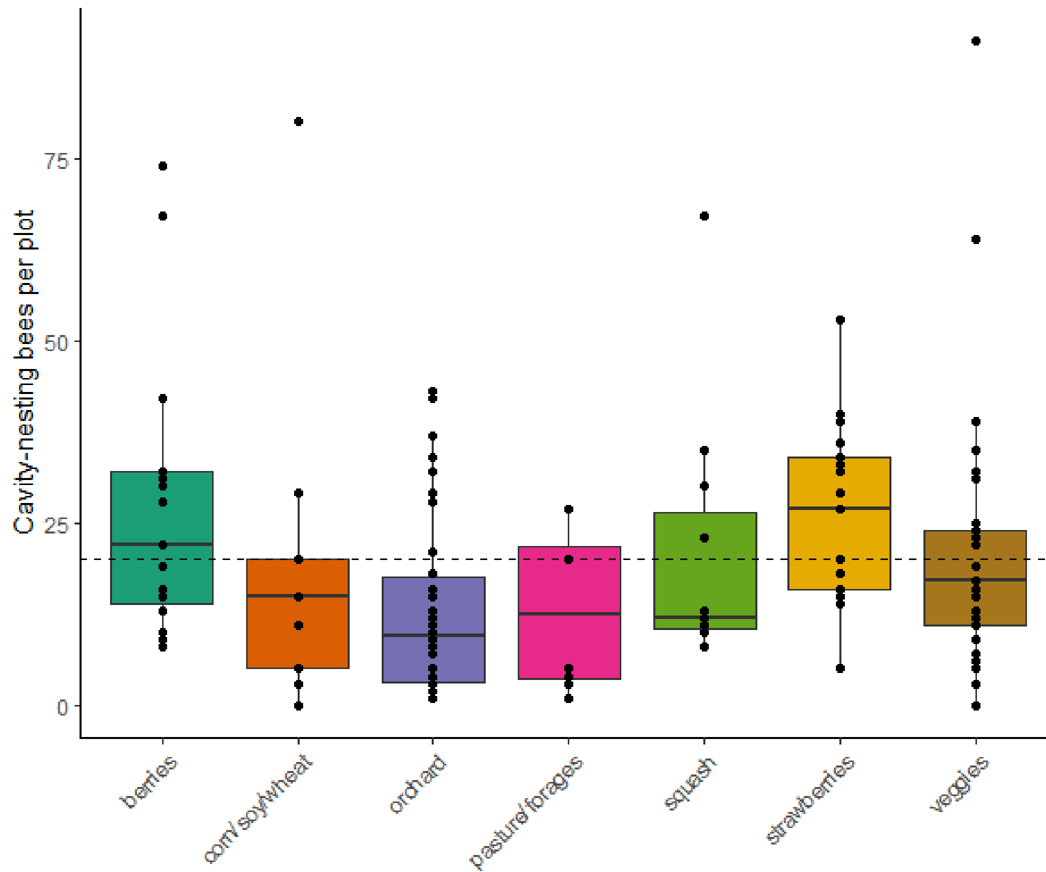

Figure 3‒S7: Boxplots of the abundance of cavity-nesting bees per plot in relation to crop type. Cavity-nesters were significantly more abundant in berry fields than in orchards (z = 3.65, p = 0.0046). N=131 plots.

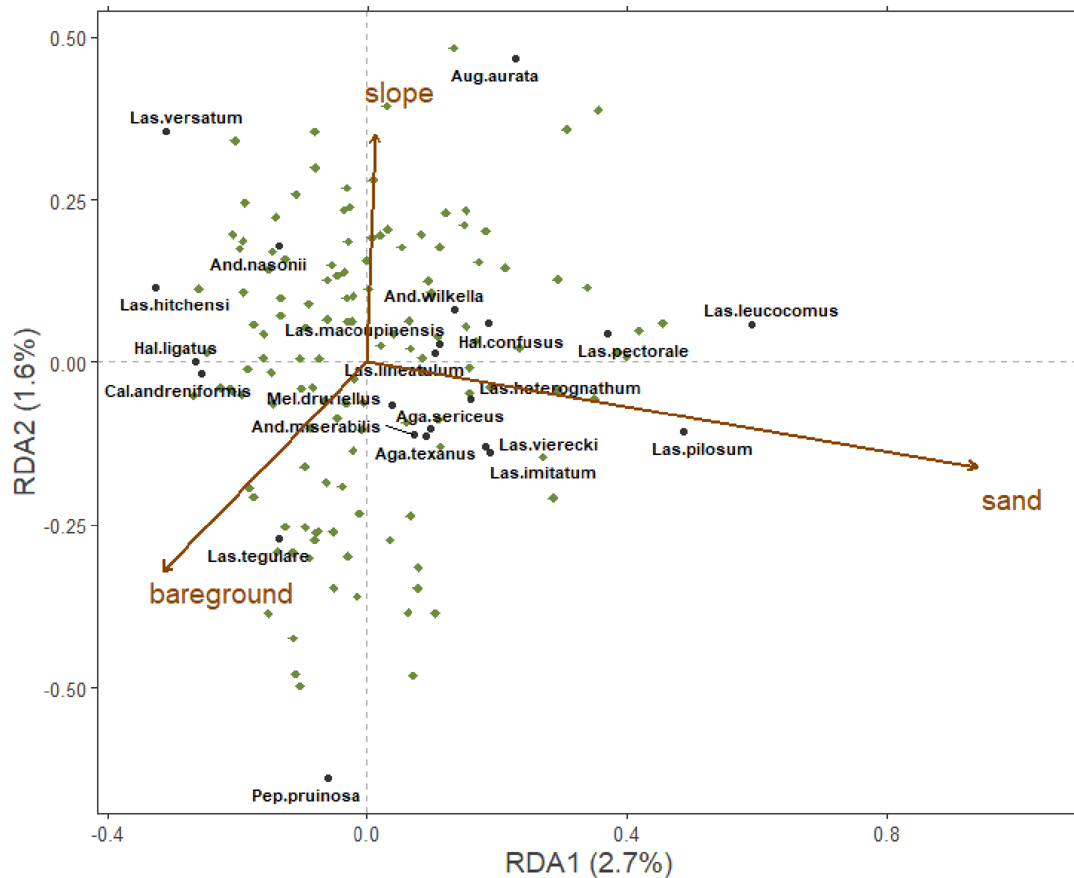

Figure 3−S8: Redundancy analysis biplot showing associations between species and soil predictors for the 22 species, including *E. pruinosa* (represented by "Pep.pruinosa"), that explain more than 5% of the variation among sites. The overall ordination was significant (F= 2.0, p=0.001), and significant individual predictors were percent sand (F=3.53, p=0.001), percent bare ground (F=1.90, p=0.020), and slope (F=1.75, p=0.027). The first and second axes are the only significant ones. RDA1 (F=8.24, p=0.001) explains 39.8% of the soil predictors' contribution (6.7% of the variance in bee community composition) and RDA2 explains 24.0% (F=3.33, p=0.012). Spatial predictors explained 13.4% of the variance in bee community composition. Significant soil predictors are represented by the brown vectors, sites by the green diamonds, and bee species by black points labeled with the species name (genus abbreviated with the first three letters). The two biplots (*E. pruinosa* included vs excluded, Figure 5 of main text) showed similar patterns of species associations with sand, bare ground and slope, although *Halictus ligatus* and *Lasioglossum versatum* are no longer found near the bare ground arrowhead in this figure.

Chapter 4: Soil texture preferences of ground-nesting bees: a field experiment

4.1. Abstract

Little is known about the nesting habitat of ground-nesting bees, including what soil factors these bees could be selecting when they establish a nest. There is a need to better understand the edaphic factors preferred by this important group of bees (representing ¾ of wild bee species) if we wish to promote their populations. We created a field experiment by providing artificial nesting habitat in two sites around Ottawa. We set up soilboxes (i.e., planters of approximately 1 m^2) filled with different soil textures (sand, topsoil and two mixtures of sand and topsoil: 50:50 and 75:25) in a randomized block design, to test the influence of soil treatment, while holding other factors constant. The following year, we caught emerging bees using emergence traps and assessed bee abundance and number of species in relation to soil treatments. Textural and loss-on-ignition analyses confirmed that our treatments differed in soil organic matter content and particle size distribution. We collected a total of 122 bees in the e-traps, but neither total bee abundance nor species richness varied among treatments. The most abundant ground-nesting bee species in our samples, *Lasioglossum foxii*, was more abundant in the topsoil treatment than in the sand, despite the general belief that ground-nesting bees prefer sandy soil. Adding more years of data will help shed light on bee species' soil textural preferences.

4.2. Introduction

Because of their diversity and distribution across continents, as well as their adaptation to various terrestrial habitats (from desert dunes to mountain peaks), wild bees display a wide range of life-history traits. Among them, nesting strategies can be divided into three categories: use of aboveground cavities, underground excavation, and brood parasitism. The underground-excavation (ground-nesting) strategy is widely shared among wild bees, with 67%–83% of species showing this behaviour (Cane and Neff 2011, Harmon-Threatt 2020). Females of these

species dig shafts leading to brood cells typically located 17–35cm under the soil surface (Cane and Neff 2011) where their offspring develop and, in cool climates, overwinter underground. Because ground-nesting bees spend most of their lives underground (Linsley 1958, Cane 1991), soil conditions must be key to their growth and survival (Harmon-Threatt 2020), likely leading to selection on females to choose the most suitable nest-site locations (Potts and Willmer 1997). However, although most wild bees are ground-nesters, their specific nesting habitat associations have been largely overlooked (Antoine and Forrest 2021), probably due to the difficulty of locating and studying underground nests. Because we know little about the habitat requirements of ground-nesting bees, particularly the soil characteristics that influence nest-site selection, it is difficult to create effective nesting habitat enhancements for these species, or even to know whether supplemental nesting habitat would be beneficial.

Soil is broadly defined as the combination of solids (minerals and organic matter), with liquids (mostly water) and gas (air) filling the spaces between physical components (FAO 1998, USDA 1999). The solid fraction determines soil's physical properties, which influence water retention and plant growth (McCarty et al. 2015). The organic matter is a mixture of organic compounds from dead organisms and their waste (Carter and Gregorich 2007). In most soils, the organic fraction is less than 5% of the total volume, but it is key to nutrient exchange and moisture retention (McCarty et al. 2015). Soil texture is a physical characteristic of the mineral matter and is defined by the proportion of sand, silt, and clay-sized particles (in order of decreasing size, ranging from 2.0 mm in diameter to less than 0.002 mm). Together, soil texture and organic matter affect other soil properties (colour, compaction, substrate temperature and moisture) (McCarty et al. 2015), and they are believed to be key factors in nest-site selection by ground-nesting bees (reviewed by Antoine and Forrest, 2021).

There have been few quantitative investigations of the nesting-habitat preferences of ground-nesting bees, and even fewer that have included soil texture. The most thorough study examined nesting habitat associations of *Halictus rubicundus* at 10 sites in the U.K. (Potts and Willmer 1997). The authors found that nest density was not generally correlated with soil particle size fractions, but the highest nest density at the one site they studied in detail occurred in the sandiest soils. In the United States, Cane (1991) studied the soil texture associated with nests of 32 ground-nesting bee species and found that most nested in sandy soils; but some species have been observed nesting in more clay-rich soils (e.g., *Anthophora* spp. in Cane 1991; *Anthophora abrupta*, Norden 1984; *Anthophora* spp., *Andrena* spp., and *Colletes* spp., Harmon-Threatt 2020), suggesting interspecific variation in nesting-substrate preferences. In another study using artificial habitat, the authors were unable to show any associations between bee abundance and soil texture; however, they did not evaluate individual species' preferences (Fortel et al. 2016a). So far, there have been no experimental demonstrations of female bees' soil texture preferences when creating new nests.

One reason for the shortage of studies of the nesting-habitat preferences of ground-nesting bees is that there are no easy and effective methods to study these nests. In contrast to the popularity of trap nests (artificial nesting structures for cavity-nesting species that nest above-ground; reviewed by MacIvor 2017), nest boxes for ground-nesting bees are not widely used. Fortel et al. (2016) successfully used human-made "soil squares" (1 m^2 plots of undisturbed soil, 0.5 m deep, surrounded by wooden frames) in urban areas in France to attract ground-nesting bees. The holes were either filled with "local soil" or a mix of local soil and varying proportions of clay or sand. The study showed that artificial nesting substrates can be used to study ground-nesting bees, as the authors were able to observe 232 bees of 37 species nesting in their soil squares. Still, even

with the use of soil squares, it can be challenging to locate the inconspicuous nests of ground-nesting bees. One way to overcome this difficulty is the use of emergence traps (Sardiñas and Kremen 2014, Fortel et al. 2016a, Pane and Harmon-Threatt 2017). These are open-bottomed tents covering the soil surface; a killing jar at the top captures insects emerging from the soil. Emergence traps have been used elsewhere to link soil characteristics with ground-nesting bee nests in natural substrates (e.g., Sardiñas and Kremen 2014). Here, we combine these tools (experimental soil boxes and emergence traps) to investigate soil characteristics that could affect nest-site selection in ground-nesting bees.

In this study, we assessed female ground-nesting bees' preferences for soil texture by giving wild bees a choice among different soils. Specifically, we provided planters filled with four different soil textures: topsoil, sand, and two mixtures of topsoil and sand differing in sand content. We set up the planters in the field in a randomized block design, at two restoration areas where floral resources were abundant. We asked the following questions: (a) Do ground-nesting bees show an overall preference among the four available soil textures? (b) Do species vary in their soil-texture preferences?

4.3. Materials and Methods

4.3.1. Study design

The study took place in 2020 and 2021, at two sites (Orleans and Kanata) near Ottawa, Ontario, Canada (Figure S1). Sites were in semi-natural habitat (the "Greenbelt") on National Capital Commission (NCC) land. The Orleans site (45°28'03"N, 75°34'57"W) is a 150 m x 30 m plot located near the Ottawa River, in an area containing a mix of native hardwoods and open fields. The Kanata site (45°20'44"N, 75°52'08"W) is 150 m x 90 m, with pine (*Pinus*) trees along with hardwoods and adjacent meadows. The Kanata site is a little drier than the Orleans site, due to

microclimate conditions. Both sites are restoration areas: the NCC seeded a plot at each site (75 m x 20 m in Orleans, and 130 m x 50 m in Kanata) with a pollinator-friendly mix of native plants the year before the start of our experiment, in 2019.

We used planters—called soilboxes hereafter—filled with four different soil textures, placed in groups of four ("blocks") following a randomized block design (Figure 1). Planters differed between the two sites: we used 16 black wooden planters (1.10 m x 1.10 m x 0.36 m) with solid wooden bottoms in Orleans, provided by the NCC, and 12 white plastic planters without bottoms (1.13 m x 1.13 m x 0.30 m) bought at Costco Wholesale® for the Kanata site (two planters were black originally and were spray-painted white). In each block, one box was filled with each soil treatment: topsoil, sand, an equal mixture (by volume using buckets) of both topsoil (½) and sand (½), and a mixture made of ¾ sand and ¼ topsoil. Soil was bought from a local supplier (Andre Taillefer Ltd, Navan, Ontario) and soil texture of each box was assessed in 2021 (see below) to determine the exact percentage of sand. Blocks were placed around each site such that each block was at least 30 m from all others and no more than 30 m from the flowering plot; all were in full sun. In Orleans, we set up 16 soilboxes (4 blocks) before May 15th, 2020, and in Kanata we set up 12 soilboxes (3 blocks) by June 15th, 2020 (differences between the two sites were related to the COVID-19 pandemic and delays in planter delivery).

Bees were allowed to nest in the soilboxes during the remainder of the spring (those in Orleans only) and summer 2020 (both sites). Since we wanted to eliminate the leftover sand pile in Orleans —which could have skewed the attraction for the boxes—we installed a tarp over the leftover pile during the rest of the 2020 season. We left the leftover sand pile uncovered in Kanata, as that site was only fully set up later. Maintenance work was done weekly to remove weeds. A protocol based on weekly observations was established following the set up of the

soilboxes, to record any nesting activity and the location of potential nests, but these data were not used in the following analyses due to a lack of species identification. Following this protocol, we noted whether bees were seen colonizing the nesting boxes and where as well as any activity related to nesting: nest initiation, nest construction, nest provisioning by mother bees, mating behaviour or patrolling activity by male bees, and even nest searching by parasitic bees. However, due to the difficulty of identifying flying bees, we decided not to use this data in this chapter and focused on the emerging bees instead.

4.3.2. Bee sampling

Ground-nesting bees (emerging progeny from nests built in 2020) were captured weekly during the 2021 season using emergence traps (BioQuip Products Inc., Compton USA). Each tent-like trap is made of polyester netting and supported by fibreglass poles, with a collecting bottle at the top filled with 70% ethanol to capture emerging insects, and an open base measuring ~60 x 60 cm. Traps were attached to the ground using tent pegs, and the flaps at the base of the tent were covered by soil. We set up the traps in early April 2021 (after snowmelt) and we placed one trap per soilbox (Figure 1.B). Because the traps were smaller than the area of the planters, we placed each trap over a random portion of a soilbox. At each site, we also placed a group of four "control" emergence traps in a haphazardly selected location within the surrounding area, about 5 m from a block of four planters. We placed two additional traps on top of the remaining sand pile at each site to check if bees had nested there.

Emergence traps were left in the same location for the whole season, targeting emerging offspring from the previous season's nests rather than actively nesting females, as in other papers (Pane and Harmon-Threatt 2017, Buckles and Harmon-Threatt 2019, Ulyshen et al. 2021). We collected samples weekly from April 8th to August 26th, 2021, and brought them back to the lab,

where we sorted the bees from other insects. Bees were then washed in distilled water, dried, pinned and labelled.

4.3.3. Bee identification

Bee specimens were identified using the Discover Life key (Asher and Pickering, 2021) as well as keys specific to some genera (*Lasioglossum*: (Gibbs 2011, Gibbs et al. 2013); *Andrena*: (Mitchell 1962)), and our reference collection. All bees were identified to species, except members of the brood-parasitic genus *Sphecodes* (three specimens), which were treated as a single species for analysis. Specimens were added to our collection at the University of Ottawa, and vouchers will be deposited at the Canadian National Collection of Insects, Arachnids and Nematodes upon publication of the manuscript.

4.3.4. Soil sampling and textural analysis

In summer 2021, we sampled soil from each of the soilboxes and at the locations of the "control" emergence traps. We extracted soil cores 20 cm deep using a 20 mm diameter auger (E121-Model LS Hoskin Scientific, Canada). Every soil sample was labelled and brought to the lab, where we ran texture analysis using, first, the sieving technique (to separate soil into gravel and sand particles of different size), and second, the Bouyoucos (1927) hydrometer method to separate sand (2.0−0.05 mm diameter), silt (0.05−0.002 mm) and clay (<0.002 mm) particles (Day 1965), as described below.

Sieving: We weighed 100 g of each sample and passed this subsample through a stack of sieves (#10, #35, #60, #230), shaking one sieve at a time for 3 mins, which allowed us to partition gravel (more than 2.0 mm, sieve #10) and sand particles between coarse (2.0−0.5 mm, sieve #35), medium (0.5−0.25 mm, sieve #60), and fine sand (0.25−0.05 mm, sieve #230). Silt and clay particles, which are smaller, passed through the last sieve. This technique was used to obtain

information on sand particle size distributions, but it is not sufficient to estimate quantities of silt and clay (Day 1965).

Hydrometer: The same subsample (combining all sand fractions, silt and clay) was used again but gravel was kept aside. The soil sample was weighted to have a 100 g (more was added to it to compensate for removed gravels). The remainder of the subsample was then added to a jar with 250 mL of distilled water and 100 mL of sodium hexametaphosphate (dispersing agent) at a concentration of 50 g/L. The suspension was left to disaggregate for at least 12 hours. The day after, the jar contents were placed in a 1 L cylinder filled with distilled water. We mixed this suspension and left it to settle, measuring density with the hydrometer at 40 s, 10 mins, 30 mins, 1 h and 7 h after mixing. This technique allows estimation of percentages of silt, clay and sand. “Sand” here comprises all sand particle sizes, from coarse to fine.

Organic matter was determined by applying the Loss-On-Ignition (LOI) technique, i.e., the loss of weight in a sample from being heated at a temperature high enough to burn the organic material. Samples were first air dried, then 20 g subsamples were gradually heated to 360 ^{o}C over a two-hour period in a high-temperature oven. The difference in weight, relative to the 20 g total, determined the percentage of organic matter present in the sample.

4.3.5. Data analysis

All analyses were conducted using R version 4.1.2 (R Core Team, 2021). To check whether treatments in fact differed in soil composition, we first ran linear mixed-effect models of each soil variable (sand, silt, clay and organic matter separately), with treatment (sand, topsoil, 50:50, or 75:25), site, and their interaction as fixed categorical predictors and block as a random effect. Because block did not explain any variance, we removed it from the models and ran linear

models instead. When there were significant differences among treatments, we ran post-hoc Tukey HSD tests using the multcomp package (Torsten et al 2008).

To test the effect of treatment on ground-nesting bees, we ran generalised linear mixed models (GLMM; Bolker et al. 2009) using the glmmTMB package (Brooks et al. 2017). For each soilbox, we pooled the bee data over the activity period, summing male and female bee abundance. We ran two models, one with number of bees (total count per soilbox) as the response variable and a negative binomial distribution, and another with species richness (total number of bee species per soilbox) with a Poisson distribution. We included treatment, site, and their interaction as fixed predictors and included block as a random effect. We checked model residuals with the DHARMa package (Hartig 2022).

We ran an additional GLMM with a negative binomial distribution to test whether the abundance of the most abundant taxon caught in the soilboxes (*Lasioglossum foxii*) differed among treatments. We used treatment and site as predictors (their interaction was not significant, so we excluded it from the final analysis) and accounted for blocks (random effect).

Finally, we ran post-hoc analyses to test associations between specific soil predictors (sand, organic matter, and gravel, here treated as continuous variables) and ground-nesting bee abundance. For these, we ran three separate GLMMs with negative binomial distributions, each with soil predictor (a continuous variable) and site as fixed effects and block as a random effect.

4.4. Results

We collected a total of 122 ground-nesting bees in the soilboxes, an additional five from emergence traps placed on top of the leftover sand piles in Kanata, and one from the surrounding ground (controls) at the Orleans site (Table 1). The total 128 bees included 71 females and 57

males and represented 15 species (Table S1), of which the most abundant by far was *Lasioglossum foxii* (83 individuals), followed by *L. laevissimum* (14 individuals) and *Agapostemon virescens* (6 individuals). Only bees sampled in the soilboxes were included in subsequent analyses. Bee emergence peaked in July (Figure S5), and as many of the bees were *L. foxii*, this spike is correlated to the phenology of this particular species.

Treatments differed in organic matter content and particle size distribution (Table 2, Figure S2, Figure S3). As intended, sand percentage differed significantly among treatments ($F_{3,20} = 21.27$, $p < 0.001$); however, this effect differed between sites (treatment x site interaction $F_{3,20} = 17.55$, $p < 0.001$; Fig. S2A). Specifically, sand amount (from the hydrometer method) did not differ significantly among treatments in Orleans nor between the 75% and 100% treatments in Kanata (Tukey HSD, Table S1, Figure S2). However, sand particle size (coarse, medium or fine, from the sieving method) differed significantly among treatments in Orleans (Figure S3). In Kanata, percentages of sand, silt and organic matter differed between the topsoil and the sand boxes. Overall, as planned, the topsoil treatment had more organic matter, gravel, and coarse sand than the sand treatments (Figure S2, Figure S3). All treatments contained high percentages of sand (77−90%) compared to the local soil (controls in Table 2), which was richer in clay in Orleans and silt in Kanata.

Bee abundance did not differ significantly between treatments (Wald $\chi^2 = 4.8$, df = 3, $p = 0.19$), nor did the effect of treatment differ between sites (treatment x site interaction $\chi^2 = 4.47$, df = 1, $p = 0.22$), but there were significantly more bees overall in Orleans than at the Kanata site ($z = 2.60$, $p = 0.009$, Table 3, Figure 2). Similarly, bee species richness (total = 15 species) did not differ significantly among treatments (Wald $\chi^2 = 1.6$, df = 3, $p = 0.66$), although marginally ($p < 0.1$) more species were detected in Orleans (Table 3, Figure 2). *Lasioglossum foxii*, which

represented 68% of all collected bees, was more abundant at Orleans than Kanata ($z = 3.02$, $p = 0.003$, Table 3) and less abundant in the sand soilboxes ($z = -2.41$, $p = 0.016$) compared to topsoil ones (Table 3, Figure S4).

Post-hoc analyses, in which soil variables were treated as continuous predictors, showed no association between bee abundance and total sand, organic matter, or gravel (Table S3). However, they did show a significant negative association between bee abundance and fine sand, and a significant positive association between bee abundance and coarse sand (Table S3).

4.5. Discussion

After one year of sampling, we found no effect of soil texture on ground-nesting bee abundance or richness. Bees were more abundant at the Orleans site, likely due to the delay in establishing the Kanata site in 2020. Because the soilboxes could not be set up at the Kanata site until June, while the Orleans site was ready for May 1st, we missed the nesting period of spring-active bees in Kanata, probably resulting in far fewer offspring emerging in 2021 than at the other site. More years of sampling (in which soilboxes are available for bee nesting throughout the growing season) will help answer our research questions about ground-nesting bee preferences among different soil treatments.

4.5.1. Soil texture preferences

We expected more ground-nesting bees in the soilboxes containing higher proportions of sand, and we expected species composition to differ between the sand and topsoil treatments. Even though we did not see any effect of soil treatments after one year of sampling, our bee numbers were low overall, and trends might appear with more data collection. The increase in bee abundance in relation to fine sand (posthoc analysis) as opposed to a decrease related to coarser

sand, might simply reflect a higher bee abundance in the Orleans topsoil treatment, which was richer in fine sand. We expected higher abundance in sandy soil vs topsoil as nest observations are often described in sandy areas (see Introduction section). Softer soils—less clayey and sandier—may be advantageous for ground-nesting bees as it could facilitate nest excavation (requiring less energy and less wear of wings and mandibles). Less costly nest excavation should increase foundresses' chances of being able to produce more brood, increasing their fitness (Danforth 1990). In theory, given the choice between multiple substrates, ground-nesting female bees should seek the optimal choice for their own fitness as well as that of their offspring (Potts and Willmer 1997). Indeed, sandy soils ensure better drainage, which would prevent the development of molds inside the nest cells. However, sandy substrates might also increase the risk of larval desiccation (May 1972).

Nest descriptions in research articles often give information on soil hardness, aspect and textural class; however, information on organic matter content is rarely included (see Pietsch et al. 2016). When information on the organic fraction is provided, it is usually for soils with higher organic content (than the 4−5% average of organic matter in soils, see Introduction): 7.2% humus content from a *Halictus duplex* aggregation in Japan (Sakagami and Hayashida 1961), 6.7%−10.6% organic carbon (organic matter = 1.724*organic carbon according to Polidori et al. 2010) and 25% organic matter content in waterlogged nests of *Augochloropsis caerulans,* in Brazil (Pietsch et al. 2016). Organic matter complements soil texture, and both factors influence soil hardness, colour, and water retention (McCarty et al. 2015), all of which impact soil temperature and moisture. Organic content also darkens the soil, which could increase absorption of solar radiation, resulting in warmer nest structures including brood cells where offspring develop. Temperature is believed to be a key factor for nest-site selection because it affects larval growth

(see Antoine and Forrest, 2021); therefore, higher organic matter could potentially be selected for due to its effect on colour. However, we have not yet observed any preference from ground-nesting bees for higher organic matter in soils (i.e., topsoil). It would be interesting to examine this relationship, especially for early-spring bees—under-sampled in this one-year collection and analysis—which might need warmer substrates for emerging and for their periods of activity (see Antoine and Forrest 2021).

4.5.2. Use of soilboxes as experimental nesting sites

Overall, this experiment was successful in attracting ground-nesting bees and providing them with nesting habitat. We caught 122 bees in the soilboxes while we were only sampling in a portion of them—emergence tents were covering about a third of the surface area—meaning emerging bees were probably three times more abundant. Several species from mostly the Halictidae and Andrenidae families chose to nest in the soil provided. Because ground-nesting bee species vary greatly in their morphology and behaviour, it would be interesting to see how species' traits influence species-specific preferences for soil type (if such preferences are observed).

It would have been interesting to document the number of offspring per female per nest, and how soil texture affects offspring survival, since this is not well known for ground-nesting bees (Harmon-Threatt 2020). Ground-nesting bees were seen colonizing the soilboxes as soon as they were set in 2020, however, it turned out to be impossible to record all nesting activity and sample emerging offspring from the whole available surface area (limitations due to trap size). To link the emerging offspring to the nests established by their mothers, we would have needed to identify the females supplying the nests—which proved difficult without collecting them—and it was impossible to distinguish the entrance holes of the small bees. We could not be sure if it was

a single mother or several females nesting in the same nest (communal and social species) or several females nesting in aggregation. Although more destructive protocols would be required (e.g., sampling of mother bees, nest excavation), the use of soilboxes combined with observations of actively nesting bees and nest excavation can allow us to study ground-nesting bee nest biology and fitness related to soil factors in the future.

Little is known about ground-nesting bee nest site conditions and how it influences parasitism or pathogens infection (Harmon-Threatt 2020). It would be interesting to monitor the bee community of the soilboxes over the years and assess ground-nesting bees' regulations by natural enemies (i.e. parasites, pathogens, predators). It has been shown before that parasitism is density-dependent in nesting aggregations of ground-nesting bees (Rosenheim 1990, Wcislo 1996, Antonini et al. 2003), so if nest density increases in the soilboxes, it might attract more parasites as well. It would also be interesting to measure whether a drier substrate (sand) would lead to less mold development in cells or more parasitism but to answer these questions, a destructive method to excavate nest cells and assess pathogens would be required.

4.5.3. Project limitations

The use of planters as artificial nesting habitat comes with its advantages (clear delimitation of the experimental area, ease of setup) but also its shortcomings—for example, the area made available to the bees was of limited size and elevated above the surrounding ground. In their study, Fortel et al. (2014) had dug their squares so that the experimental nesting sites were on the ground surface; but this would have required more work and approval from land managers. Another disadvantage could be the general appearance and soil conditions chosen that may have repelled some ground-nesting bee species. Some bees might prefer to nest near vegetation or on a slope, that would serve as visual landmarks or could be useful for drainage, but the ground

surface in the boxes was bare (weeded weekly) and flat, so this new nesting habitat might attract only a portion of the local bee community. Another drawback of the soilboxes is the limitation on the choice of soil filling: sand and topsoil quality and content might have not matched "natural" soil conditions and could have deterred bees from nesting in the boxes. But in general, the Ottawa region is very sandy, and the amount of sand provided in the boxes (76%−92%) is within the range of the area (62%−97% see Chapter 3).

To sample bees from our soilboxes, we set up emergence traps at the beginning of spring 2021 and removed them at the end of the season—keeping the traps in the same place throughout the bee activity period—to target bees emerging from the previous year's nests (as in Sardiñas and Kremen 2014, Sardiñas et al. 2016). By doing so, we missed the emergence of multivoltine species—bees that have more than one generation per season. Many halictid bees show social behaviour (Michener 1974) with a succession of broods in a year (Schwarz et al. 2007), and these would not have been collected with our sampling regime. For example, we observed many female *Halictus rubicundus* establishing nests in the Orleans soilboxes in 2020, yet none were captured the following year, suggesting either that traps were not placed on top of their nests (although at least one trap was placed on top of an observed active nest seen in 2020), offspring didn't survive, or, more likely, offspring emerged during the previous season (i.e., in summer 2020). To be more inclusive of multivoltine ground-nesting species, traps should be moved during the active period to allow bees to build a nest and then be able to capture the emerging offspring (called "short deployment" in Pane and Harmon-Threatt 2017). The downside of this approach is that foundresses will likely be caught in these short deployments, therefore both newly emerged bees and female establishing new nests will be mixed. However, the main advantage is that we will be able to sample bees from social species. It is possible (but difficult)

to separate the female emerging offspring from the female foundresses based on physical attributes (Packer and Knerer 1986a). In theory, females showing a lot of wing and mandible wear should be older and in the process of excavating a nest whereas newly emerged females should not show any wear (Portman et al. 2022).We can then link sampled (foundress) bees to the current soil conditions where their nests are found (Pane and Harmon-Threatt 2017).

Another limitation to consider is the impact of sociality and gregariousness—solitary species that often nest in close proximity to one another sometimes leading to large nesting aggregations—on observed bee abundance. Social species (including those that nest communally) would potentially be non-independent in the sample, due to the larger number of individuals (and potentially laying mothers) per nest, and thus a larger number of offspring. However, sociality is difficult to estimate because some species, especially in the family Halictidae, are labile and can be either solitary or social, depending on environmental conditions (Richards and Packer 1995a, Plateaux-Quénu et al. 2000). In our sampling, we caught many *Lasioglossum foxii*, and this species is presumed solitary (based on phylogenetic affiliations according to Gibbs et al. 2013) but is known to nest in aggregations (Knerer and Atwood 1962). *Lasioglossum foxii* individuals were caught in several different soilboxes in Orleans so there should not be dispersion issues for this species in our data. Although gregariousness and sociality might be difficult to include when analysing the total abundance on the soilboxes, these traits could be added as a factor in models analysing species preferences.

4.6. Conclusion

Although we were unable to establish a relationship between ground-nesting bee abundance or richness and the different soil treatments, the continuation of this project for additional years will allow us to better assess nesting trends and to see if there are species-specific preferences for

certain soil textures. This experimental design is useful to be testing one soil factor at a time, holding all other factors constant (e.g., no vegetation coverage, no slope, and a similar compaction between soilboxes). More such rigorous studies of species preferences for soil texture (and other soil features) are needed in order to make informed recommendations for habitat preservation and restoration.

4.7. References

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Table 4-1: List of ground-nesting bee species caught in the emergence tents and their abundance per treatment, as well as the numbers emerging from "control" locations and the leftover sand piles in the two sites, Orleans (ORL) and Kanata (KAN).

	Treatments ORL site							Treatments KAN site						
Species	0	50	75	100	control	sand pile	total	0	50	75	100	control	sand pile	total
Lasioglossum foxii	48	19	13	1	0	0	81	1	1	1	0	0	0	3
Lasioglossum laevissiimum	0	14	0	0	0	0	14	0	0	0	0	0	0	0
Agapostemon virescens	0	0	6	0	0	0	6	0	0	0	0	0	0	0
Lasioglossum oenotherae	0	2	0	2	0	0	4	0	0	0	0	0	0	0
Sphecodes sp.	1	2	0	0	0	0	3	0	0	0	0	0	2	2
Perdita halictoides	0	0	0	0	0	0	0	0	0	0	0	0	3	3
Calliopsis andreniformis	0	2	0	0	0	0	2	0	0	0	0	0	0	0
Halictus rubicundus	0	0	0	0	0	0	0	0	0	0	2	0	0	2
Andrena sp.	1	0	0	0	0	0	1	0	0	0	0	0	0	0
Andrena algida	0	0	1	0	0	0	1	0	0	0	0	0	0	0
Andrena cressonii	1	0	0	0	0	0	1	0	0	0	0	0	0	0
Andrena persimulata	0	0	1	0	0	0	1	0	0	0	0	0	0	0
Andrena sigmundi	0	0	0	0	0	0	0	1	0	0	0	0	0	1
Halictus confusus	1	0	0	0	0	0	1	0	0	0	0	0	0	0
Lasioglossum leucozonium	1	0	0	0	0	0	1	0	0	0	0	0	0	0
Lasioglossum tegulare	0	0	0	0	0	0	0	0	1	0	0	0	0	1
Megachile brevis	0	0	0	0	1	0	1	0	0	0	0	0	0	0
TOTAL	53	39	21	3	1	0	117	2	2	1	2	0	5	12

Table 4-2: Means of the different soil particle sizes and organic matter content (OM) estimated from the different techniques (loss-on-ignition (LOI), hydrometer, and sieving) for each treatment in Orleans (ORL) and Kanata (KAN). All values are the averaged estimated weights from a 100 g dried soil sample. $N_{ORL} = 4$, $N_{KAN} = 3$ (except for controls which represent a single sample from the ground near the soilboxes).

		LOI	Hydrometer			Sieving			
site	treatment	OM	sand	silt	clay	gravel	coarse sand	medium sand	fine sand
ORL	0	6.8	78.7	17.6	3.8	15.3	40.4	34.4	9.9
ORL	50	2.8	80.1	16.5	3.4	6.8	16.9	59.9	16.1
ORL	75	1.5	79.2	17.5	3.3	5.9	9.0	66.1	18.7
ORL	100	0.5	80.6	16.2	3.2	4.0	3.9	72.1	20.1
ORL	control	7.1	4.8	27.7	67.5				
KAN	0	6.8	77.8	17.9	4.3	12.8	25.4	49.9	11.5
KAN	50	3.1	84.3	11.6	4.1	6.1	12.7	71.5	9.6
KAN	75	1.4	89.1	8.2	2.8	4.7	6.8	79.0	9.2
KAN	100	0.5	90.8	7.1	2.1	2.9	4.4	83.5	9.0
KAN	control	0.4	29.5	56.2	14.3				

Table 4-3: Results of the Generalized Linear Mixed Models (GLMM) of ground-nesting bees sampled from soilboxes at two sites (ORL: Orleans and KAN: Kanata). Fixed predictors were treatment, site and their interaction; block was included as a random effect. A negative binomial distribution was used for bee abundance and a Poisson distribution for species richness.

Response variable	Predictors	Estimate	SE	Z	P
Bee abundance	Treatment 100	0.782	1.650	0.474	0.635
	Treatment 50	0.700	1.641	0.426	0.670
	Treatment 75	0.110	1.818	0.060	0.952
	Site ORL	**4.193**	**1.611**	**2.603**	**0.009**
	Treatment 100: site ORL	**-4.283**	**2.067**	**-2.073**	**0.038**
	Treatment 50: site ORL	-1.915	2.021	-0.948	0.343
	Treatment 75: site ORL	-1.875	2.174	-0.862	0.388
Bee richness	Treatment 100	0.693	1.225	0.566	0.571
	Treatment 50	0.693	1.225	0.566	0.571
	Treatment 75	0.000	1.414	0.000	1.000
	Site ORL	1.792	1.061	1.689	0.091
	Treatment 100: site ORL	-2.079	1.458	-1.426	0.154
	Treatment 50: site ORL	-0.981	1.339	-0.733	0.464
	Treatment 75: site ORL	-0.470	1.525	-0.308	0.758
L. foxii	**Treatment 100**	**-3.587**	**1.489**	**-2.409**	**0.016**
	Treatment 50	-0.415	1.103	-0.376	0.707
	Treatment 75	-0.668	1.142	-0.585	0.558
	Site ORL	**3.250**	**1.075**	**3.023**	**0.003**

(A) Orleans, April 2020

(B) Kanata, April 2021

Figure 4-1: Photographs of the sampling design with (A) a block of four soilboxes at the Orleans site—with the plot sown with native plants for pollinators in the background—and (B) a block from the Kanata site with the emergence traps placed on it. Each block comprised four soilboxes filled with sand, topsoil and two mixtures of topsoil and sand differing in sand content. Blocks in Orleans were painted black and made of wood; those in Kanata were white plastic. The Orleans site had four blocks whereas Kanata had three.

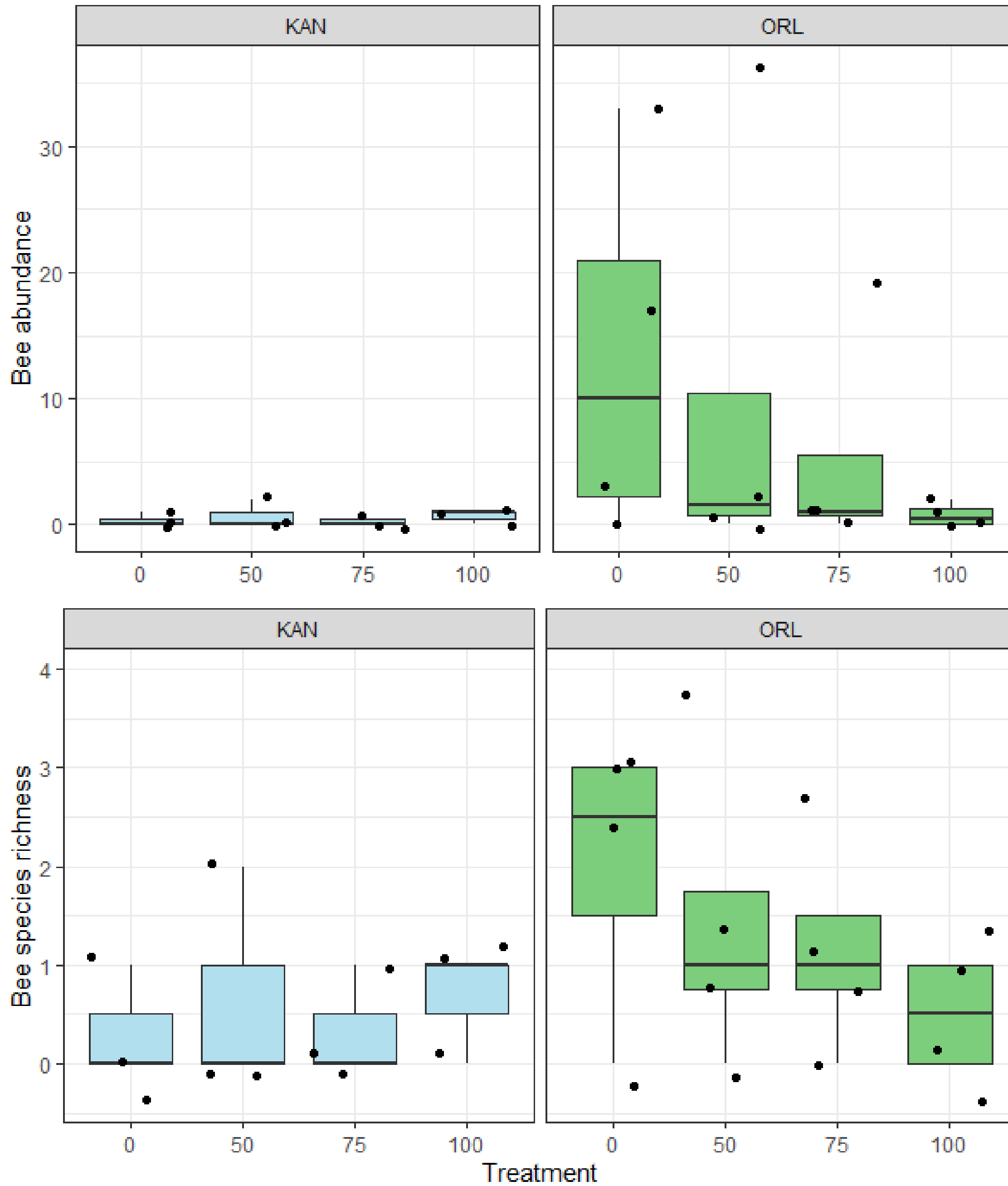

Figure 4-2: Boxplots showing bee abundance and bee species richness per soilbox in the four treatments at the two sites (KAN: Kanata and ORL: Orleans). Coloured boxes represent values from the first to the third quartile with the median represented by the thick line. Whiskers reach the minimum and maximum values within 1.5× the interquartile range. Treatments are: 0 = topsoil only, 50 = equal mix of topsoil and sand, 75 = ¾ sand, 100 = only sand. $N_{KAN} = 3$, $N_{ORL} = 4$.

4.8. Supplementary Materials

Table 4−S1: List of all ground-nesting bees caught in the emergence tents throughout the 2021 season, sorted by sampling date. Site code is as follows: site (ORL/KAN), box number (B) or control (C) or leftover sand pile (S). A total of 128 were identified; 1 bee was in a control tent in Orleans, and 5 were from the sand pile in Kanata.

Number	Sampling date	Site code	Species	Sex
1	04.vi.2021	ORLB10	*Lasioglossum oenotherae*	F
2	04.vi.2021	KANB1	*Lasioglossum foxii*	F
3	27.v.2021	ORLB10	*Lasioglossum oenotherae*	F
4	27.v.2021	ORLB9	*Agapostemon virescens*	F
5	27.v.2021	ORLB9	*Agapostemon virescens*	F
6	27.v.2021	ORLB9	*Agapostemon virescens*	F
7	27.v.2021	ORLB9	*Agapostemon virescens*	F
8	13.v.2021	ORLB5	*Halictus confusus*	F
9	20.v.2021	ORLB4	*Sphecodes* sp.	F
10	20.v.2021	ORLB14	*Lasioglossum leucozonium*	F
11	20.v.2021	ORLB9	*Agapostemon virescens*	F
12	20.v.2021	ORLB9	*Agapostemon virescens*	F
13	20.v.2021	ORLB9	*Andrena persimulata*	M
14	23.iv.2021	KANB12	*Halictus rubicundus*	F
15	11.vi.2021	ORLC	*Megachile brevis*	F
16	11.vi.2021	ORLB11	*Lasioglossum oenotherae*	F
17	11.vi.2021	ORLB11	*Lasioglossum oenotherae*	F
18	14.iv.2021	ORLB1	*Andrena algida*	M
19	14.iv.2021	ORLB5	*Andrena* sp.	F
20	14.iv.2021	ORLB10	*Lasioglossum laevissimum*	F
21	14.iv.2021	ORLB10	*Lasioglossum laevissimum*	F
22	14.iv.2021	ORLB14	*Andrena cressonii*	M
23	14.iv.2021	KANB3	*Andrena sigmundi*	F
24	14.iv.2021	KANB2	*Halictus rubicundus*	F
25	18.vi.2021	ORLB14	*Lasioglossum foxii*	F
26	25.vi.2021	ORLB10	*Calliopsis andreniformis*	F
27	25.vi.2021	ORLB10	*Calliopsis andreniformis*	F
28	01.vii.2021	ORLB4	*Lasioglossum foxii*	M
29	01.vii.2021	ORLB4	*Lasioglossum foxii*	M
30	01.vii.2021	ORLB6	*Lasioglossum foxii*	M
31	01.vii.2021	ORLB9	*Lasioglossum foxii*	M
32	01.vii.2021	ORLB10	*Lasioglossum laevissimum*	M
33	01.vii.2021	ORLB10	*Lasioglossum foxii*	F
34	01.vii.2021	ORLB10	*Lasioglossum laevissimum*	M

35	01.vii.2021	ORLB10	*Lasioglossum laevissimum*	M
36	01.vii.2021	ORLB10	*Lasioglossum foxii*	M
37	01.vii.2021	ORLB10	*Lasioglossum foxii*	M
38	01.vii.2021	ORLB10	*Lasioglossum laevissimum*	M
39	01.vii.2021	ORLB10	*Lasioglossum foxii*	M
40	01.vii.2021	ORLB10	*Lasioglossum laevissimum*	M
41	01.vii.2021	ORLB10	*Lasioglossum foxii*	F
42	01.vii.2021	ORLB10	*Lasioglossum foxii*	M
43	01.vii.2021	ORLB10	*Lasioglossum foxii*	M
44	01.vii.2021	ORLB10	*Lasioglossum foxii*	M
45	01.vii.2021	ORLB10	*Lasioglossum foxii*	M
46	01.vii.2021	ORLB14	*Lasioglossum foxii*	M
47	01.vii.2021	ORLB14	*Lasioglossum foxii*	M
48	01.vii.2021	ORLB14	*Lasioglossum foxii*	M
49	01.vii.2021	ORLB14	*Lasioglossum foxii*	M
50	01.vii.2021	ORLB14	*Lasioglossum foxii*	F
51	01.vii.2021	ORLB14	*Lasioglossum foxii*	F
52	01.vii.2021	ORLB14	*Lasioglossum foxii*	F
53	01.vii.2021	ORLB14	*Lasioglossum foxii*	M
54	01.vii.2021	ORLB14	*Lasioglossum foxii*	M
55	01.vii.2021	ORLB14	*Lasioglossum foxii*	M
56	01.vii.2021	ORLB16	*Lasioglossum foxii*	F
57	07.vii.2021	ORLB4	*Lasioglossum foxii*	F
58	07.vii.2021	ORLB4	*Lasioglossum foxii*	M
59	07.vii.2021	ORLB4	*Lasioglossum foxii*	F
60	07.vii.2021	ORLB4	*Lasioglossum foxii*	M
61	07.vii.2021	ORLB4	*Lasioglossum foxii*	M
62	07.vii.2021	ORLB7	*Sphecodes* sp.	M
63	07.vii.2021	ORLB7	*Sphecodes* sp.	M
64	07.vii.2021	ORLB10	*Lasioglossum foxii*	F
65	07.vii.2021	ORLB10	*Lasioglossum foxii*	F
66	07.vii.2021	ORLB10	*Lasioglossum foxii*	F
67	07.vii.2021	ORLB10	*Lasioglossum foxii*	F
68	07.vii.2021	ORLB10	*Lasioglossum foxii*	F
69	07.vii.2021	ORLB10	*Lasioglossum laevissimum*	M
70	07.vii.2021	ORLB10	*Lasioglossum laevissimum*	M
71	07.vii.2021	ORLB10	*Lasioglossum laevissimum*	M
72	07.vii.2021	ORLB14	*Lasioglossum foxii*	F
73	07.vii.2021	ORLB14	*Lasioglossum foxii*	F
74	07.vii.2021	ORLB14	*Lasioglossum foxii*	F
75	07.vii.2021	ORLB14	*Lasioglossum foxii*	M
76	07.vii.2021	ORLB14	*Lasioglossum foxii*	M
77	07.vii.2021	ORLB14	*Lasioglossum foxii*	M

78	07.vii.2021	ORLB14	*Lasioglossum foxii*	M
79	07.vii.2021	KANS1	*Perdita halictoides*	F
80	07.vii.2021	KANS1	*Perdita halictoides*	F
81	07.vii.2021	KANS2	*Perdita halictoides*	F
82	15.vii.2021	KANS1	*Sphecodes* sp.	M
83	15.vii.2021	KANB1	*Lasioglossum tegulare*	F
84	15.vii.2021	ORLB4	*Lasioglossum foxii*	F
85	15.vii.2021	ORLB4	*Lasioglossum foxii*	F
86	15.vii.2021	ORLB4	*Lasioglossum foxii*	F
87	15.vii.2021	ORLB4	*Lasioglossum foxii*	F
88	15.vii.2021	ORLB4	*Lasioglossum foxii*	F
89	15.vii.2021	ORLB4	*Lasioglossum foxii*	M
90	15.vii.2021	ORLB4	*Lasioglossum foxii*	M
91	15.vii.2021	KANB11	*Lasioglossum foxii*	M
92	15.vii.2021	ORLB5	*Lasioglossum foxii*	F
93	15.vii.2021	ORLB14	*Lasioglossum foxii*	F
94	15.vii.2021	ORLB14	*Lasioglossum foxii*	F
95	15.vii.2021	ORLB14	*Lasioglossum foxii*	F
96	15.vii.2021	ORLB14	*Lasioglossum foxii*	F
97	15.vii.2021	ORLB14	*Lasioglossum foxii*	M
98	15.vii.2021	ORLB14	*Lasioglossum foxii*	M
99	15.vii.2021	ORLB14	*Lasioglossum foxii*	M
100	15.vii.2021	ORLB10	*Lasioglossum foxii*	F
101	15.vii.2021	ORLB10	*Lasioglossum foxii*	F
102	15.vii.2021	ORLB10	*Lasioglossum foxii*	F
103	15.vii.2021	ORLB10	*Lasioglossum laevissimum*	M
104	15.vii.2021	ORLB10	*Lasioglossum laevissimum*	M
105	15.vii.2021	ORLB10	*Lasioglossum laevissimum*	M
106	15.vii.2021	ORLB10	*Lasioglossum foxii*	M
107	15.vii.2021	ORLB9	*Lasioglossum foxii*	F
108	15.vii.2021	ORLB9	*Lasioglossum foxii*	F
109	15.vii.2021	ORLB9	*Lasioglossum foxii*	F
110	15.vii.2021	ORLB9	*Lasioglossum foxii*	F
111	15.vii.2021	ORLB9	*Lasioglossum foxii*	F
112	15.vii.2021	ORLB9	*Lasioglossum foxii*	F
113	15.vii.2021	ORLB9	*Lasioglossum foxii*	M
114	15.vii.2021	ORLB9	*Lasioglossum foxii*	M
115	15.vii.2021	ORLB9	*Lasioglossum foxii*	M
116	15.vii.2021	ORLB9	*Lasioglossum foxii*	M
117	15.vii.2021	ORLB9	*Lasioglossum foxii*	M
118	21.vii.2021	ORLB14	*Lasioglossum foxii*	F
119	21.vii.2021	ORLB14	*Lasioglossum foxii*	M
120	21.vii.2021	ORLB10	*Lasioglossum laevissimum*	M

121	21.vii.2021	ORLB13	*Lasioglossum foxii*	F
122	28.vii.2021	KANS2	*Sphecodes* sp.	F
123	28.vii.2021	ORLB4	*Lasioglossum foxii*	M
124	28.vii.2021	ORLB4	*Lasioglossum foxii*	F
125	28.vii.2021	ORLB14	*Lasioglossum foxii*	F
126	28.vii.2021	ORLB14	*Lasioglossum foxii*	F
127	28.vii.2021	ORLB14	*Lasioglossum foxii*	F
128	13.viii.2021	ORLB14	*Lasioglossum foxii*	F

Table 4−S2: Tukey HSD results comparing percent sand among all treatments. Bold indicates a significant result ($p < 0.05$) and grey background is used when comparisons of treatments from the same site were not significant.

Pair comparisons	Coef.	Lower CI	Higher CI	P (adj.)
KAN 100-KAN 0	**13.00**	**8.48**	**17.52**	**<0.001**
KAN 50-KAN 0	**6.48**	**1.96**	**11.00**	**0.002**
KAN 75-KAN 0	**11.27**	**6.75**	**15.79**	**<0.001**
ORL 0-KAN 0	0.87	-3.36	5.09	0.996
ORL 100-KAN 0	2.82	-1.41	7.04	0.368
ORL 50-KAN 0	2.32	-1.91	6.54	0.599
ORL 75-KAN 0	1.40	-2.82	5.63	0.945
KAN 50-KAN 100	**-6.52**	**-11.04**	**-2.00**	**0.002**
KAN 75-KAN 100	-1.73	-6.25	2.79	0.891
ORL 0-KAN 100	**-12.13**	**-16.36**	**-7.91**	**<0.001**
ORL 100-KAN 100	**-10.18**	**-14.41**	**-5.96**	**<0.001**
ORL 50-KAN 100	**-10.68**	**-14.91**	**-6.46**	**<0.001**
ORL 75-KAN 100	**-11.60**	**-15.82**	**-7.37**	**<0.001**
KAN 75-KAN 50	**4.78**	**0.26**	**9.30**	**0.033**
ORL 0-KAN 50	-5.62	-9.85	-1.39	0.005
ORL 100-KAN 50	-3.67	-7.90	0.56	0.120
ORL 50-KAN 50	-4.17	-8.40	0.06	0.055
ORL 75-KAN 50	-5.08	-9.31	-0.85	0.012
ORL 0-KAN 75	**-10.40**	**-14.63**	**-6.17**	**<0.001**
ORL 100-KAN 75	**-8.45**	**-12.68**	**-4.22**	**<0.001**
ORL 50-KAN 75	**-8.95**	**-13.18**	**-4.72**	**<0.001**
ORL 75-KAN 75	**-9.86**	**-14.09**	**-5.64**	**<0.001**
ORL 100-ORL 0	1.95	-1.96	5.86	0.699
ORL 50-ORL 0	1.45	-2.46	5.36	0.907
ORL 75-ORL 0	0.54	-3.38	4.45	1.000
ORL 50-ORL 100	-0.50	-4.41	3.41	1.000
ORL 75-ORL 100	-1.41	-5.33	2.50	0.917
ORL 75-ORL 50	-0.91	-4.83	3.00	0.992

Table 4−S3: Results of the post-hoc GLMM analyses of total bee abundance as functions of site and soil predictors, treated as separate continuous variables.

Response variable (posthoc)	Predictors	Estimate	SE	Z	P
Bee abundance	Sand	-0.020	0.119	-0.168	0.867
	Site ORL	**2.524**	**1.160**	**2.176**	**0.030**
	OM (organic matter)	0.268	0.170	1.582	0.114
	Site ORL	**2.270**	**0.886**	**2.561**	**0.010**
	Gravel	0.164	0.086	1.917	0.055
	Site ORL	1.941	1.009	1.923	0.054
	Coarse sand	**0.062**	**0.031**	**2.025**	**0.043**
	Site ORL	1.876	0.972	1.930	0.054
	Medium sand	-0.049	0.029	-1.707	0.088
	Site ORL	1.561	1.069	1.461	0.144
	Fine sand	**-0.254**	**0.097**	**-2.625**	**0.009**
	Site ORL	**3.834**	**1.120**	**3.423**	**0.001**

Figure 4−S1: Map of the two sampling locations around Ottawa, eastern Ontario. Sites are represented as filled yellow circles and their abbreviated name. Base image is taken from Google Maps with the satellite imagery in background, Image © 2022 Terrametrics.

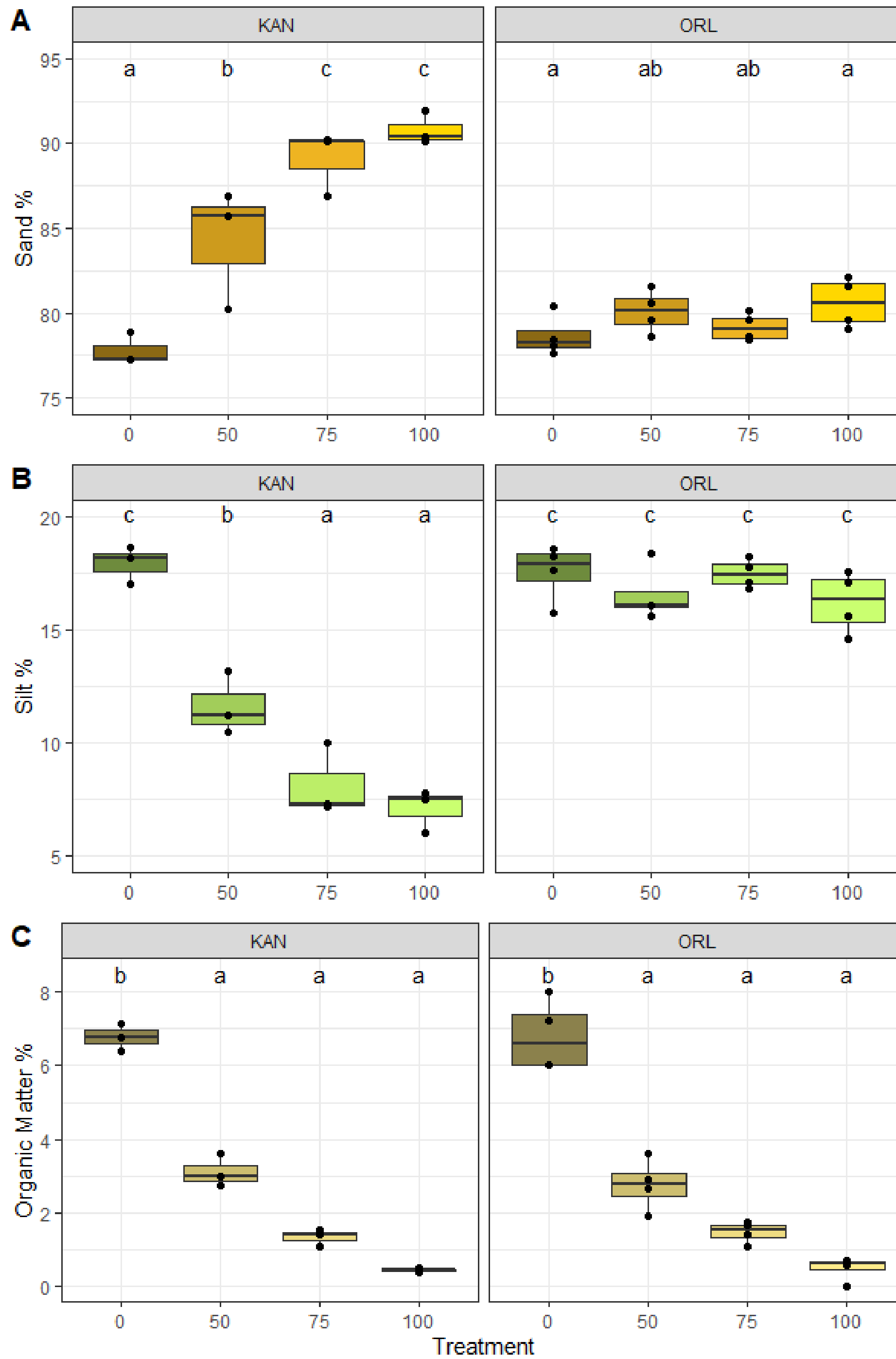

Figure 4‒S2: Boxplots of the percent sand, silt and organic matter in the four treatments (0: topsoil; 50: equal mix of sand and topsoil; 75: ¾ sand and ¼ topsoil; 100: sand) from the soil texture analysis using the hydrometer method. Tukey HSD test significance ($p < 0.05$) is indicated by letters. $N_{ORL} = 4$, $N_{KAN} = 3$.

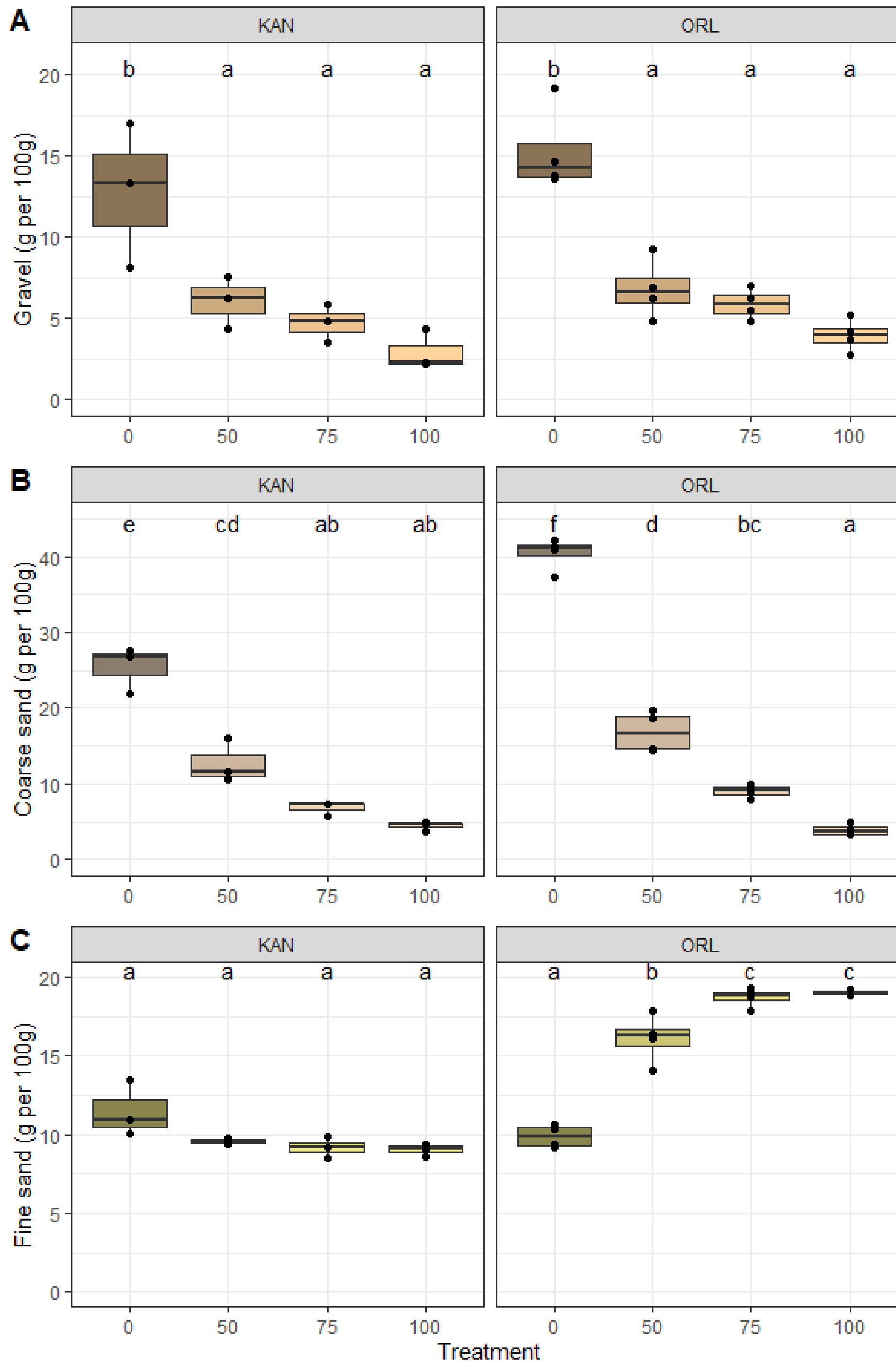

Figure 4‒S3: Boxplots of the amounts of gravel, coarse sand and fine sand in the four treatments (0: topsoil; 50: equal mix of sand and topsoil; 75: ¾ sand and ¼ topsoil; 100: sand) from the sieving method. Tukey HSD test significance ($p < 0.05$) is indicated by letters. $N_{ORL} = 4$, $N_{KAN} = 3$.

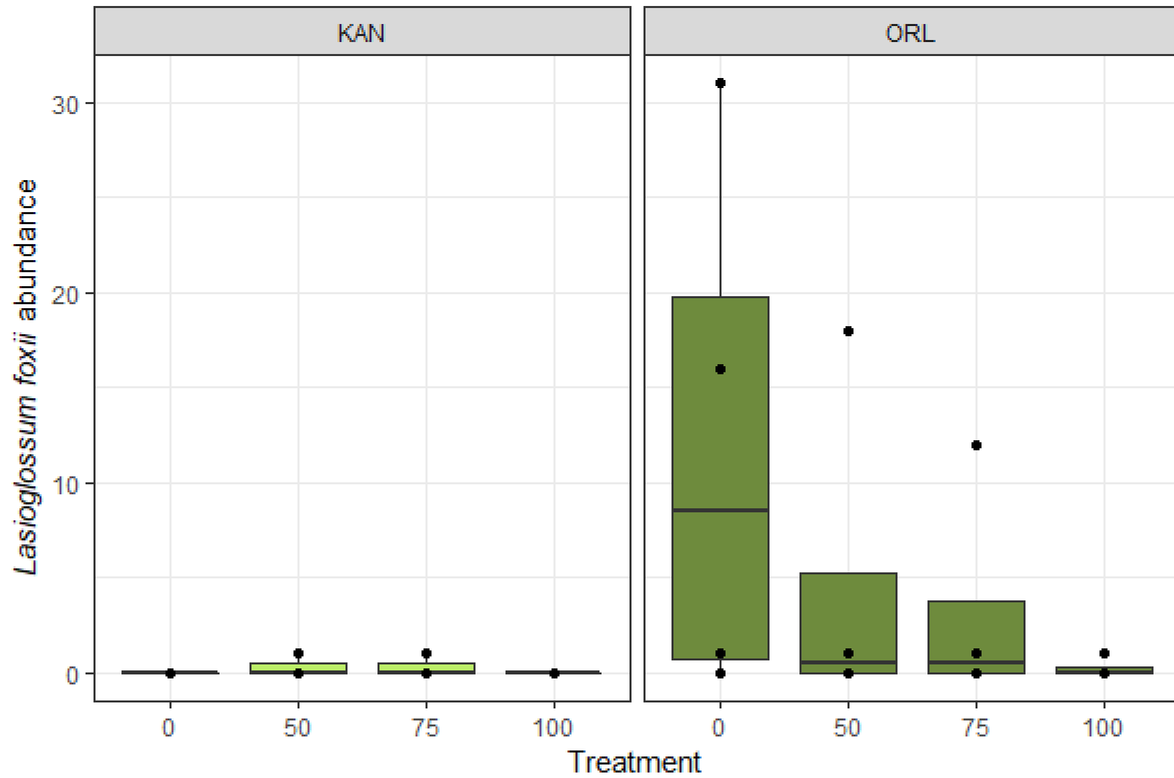

Figure 4−S4: Graphs showing the numbers of *Lasioglossum foxii* caught per soilbox for each treatment at the two sites (KAN: Kanata and ORL: Orleans). Treatments are: 0 = topsoil only, 50 = equal mix of topsoil and sand, 75 = ¾ sand and 100 = only sand. N_{KAN} = 3, N_{ORL} = 4 soilboxes per treatment.

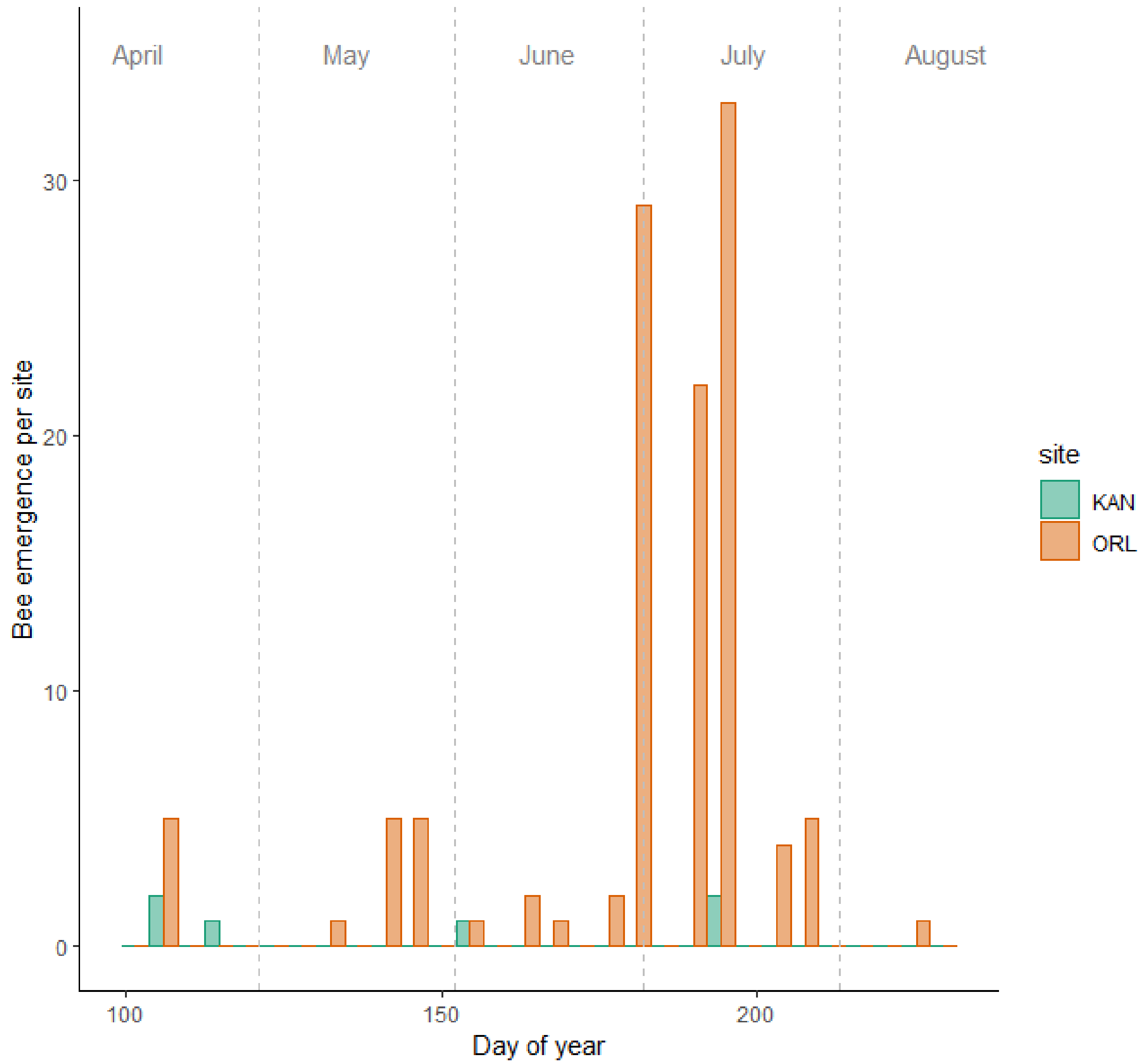

Figure 4−S5: Phenology of bee emergence throughout the 2021 season in the two experimental sites (ORL: Orleans, KAN: Kanata).

Chapter 5: General discussion

Ground-nesting bees and their nesting habitat have long been overlooked. This lack of research mainly stems from the difficulty of finding their underground nests in the field. Existing scientific articles regarding nesting sites are generally from opportunistic observations. Moreover, there is a bias towards studying ground-nesting bees with obvious nest entrances (e.g., those with large, circular openings, or with turrets or chimneys) or nesting behaviours (e.g., gregariousness, nest guarding in social species). However, nests of most ground-nesting bee species are inconspicuous—especially those of smaller, solitary species—and thus remain undescribed. In studying nest-site selection, finding actual nests is imperative as well as finding a large enough number to have a robust sample size. I believe the difficulty of finding nest locations is a major limitation to studying nest-site selection by ground-nesting bees, which has been one of the challenges I have faced in my PhD. This issue in locating nest-sites did not allow me to study nest-site selection per se, but I tackled this obstacle by documenting associations between ground-nesting bees and soil characteristics at the site of capture, while being inclusive of all ground-nesting bee species.

There is little quantitative data on the effects of abiotic factors on ground-nesting bees, and only a handful of papers that have measured soil characteristics. Despite this, I determined soil characteristics that may be critical for nest-site selection in Chapter 2 and reviewed possible explanations for how these characteristics may affect bee fitness. Important soil characteristics for ground-nesting bees are soil texture, compaction, temperature, moisture, slope, and surface features such as ground cover, cracks, and stones. Because ground-nesting bees spend most of their lives underground, from the mother's nest initiation and excavation through offspring development and overwintering, soil characteristics might play a key role in bee fitness. More research is needed to answer questions related to bee nesting habitat, especially research focusing

on bee fitness or using nest-site selection methods. Nonetheless, my review in Chapter 2 lays the groundwork for such future research.

In my thesis, I demonstrated the importance of soil texture, ground cover, soil compaction, and slope for ground-nesting bee communities on farms in eastern Canada (Chapter 3). As in Cane (1991), I showed that some species were positively associated with higher sand content. However, I also found that some species were negatively or not associated with sandier soils, despite the general belief that ground-nesting bees prefer to nest in sandy areas. Species-specific associations were not only found with sand content but also with other soil factors that I measured (e.g., ground cover, slope, and compaction). Overall, this is the first time that associations have been shown between the whole ground-nesting bee community, while looking both at species-level and at the community-level, and soil characteristics. My thesis complements studies focused on ground-nesting bees at the species-level (Potts and Willmer 1997), and at the community-level focused only on ground-nesting bee abundance, richness and diversity (Sardiñas and Kremen 2014, Sardiñas et al. 2016). My results show the importance of providing different nesting resources (e.g., sandy vs less sandy) in a given environment to maintain a more diverse ground-nesting bee community. These results also provide insight on the nesting requirements of ground-nesting bees in agroecosystems where pollination needs are high and fulfilled, in part, by this diverse group of bees.

Moreover, the project from Chapter 3 yielded a large database that can be used in future efforts to study bee habitat. The database includes 8,661 ground-nesting bees from 102 species (11,723 total bees, but not all of them identified to species level) sampled on 131 plots from 35 farms around Ottawa. This database will be published and shared with the scientific community so that it can be used to answer other questions related to bee habitat, which includes edaphic

factors previously discussed along with other variables not explored in this thesis. Abundance and diversity of flower species were sampled in each plot with repeated measurements throughout the 2019 season. By integrating floral resources and possibly landscape data, it would be interesting to test the importance of nesting resources compared to other resources for ground-nesting bees (as suggested by Roulston and Goodell 2011). It is now well known that bees in general are limited by the presence of food (pollen and nectar) and therefore by the presence and abundance of floral resources. Floral resource scarcity is evident when looking at seasonal foraging success, community-level health, and species-level success (Rundlöf et al. 2008, 2022, Mandelik et al. 2012, Crone and Williams 2016, Mallinger et al. 2016, Martins et al. 2018b, Guezen and Forrest 2021). Combining abiotic (e.g., edaphic factors) and biotic factors (e.g., floral resources, landscape features) would be valuable in assessing ground-nesting bees' habitat needs at a larger scale. Furthermore, I have argued in my thesis that bee traits may have an impact on nest-site choice (e.g., social or gregarious species could prefer more compact soils, as in Potts and Willmer (1998)). Future efforts could also go into analysing bee traits in relation to soil factors in order to answer questions such as: do smaller bees prefer softer ground? Are bigger bees associated with more clayey soils (as in Cane (1991))? Overall, this dataset will be useful to future research to ameliorate our understanding of ground-nesting bee associations with specific habitat resources.

The novel experimental design used in Chapter 4 has proven successful in attracting ground-nesting bees. This ongoing project can shed light on species' preferences for sand or topsoil, but more research can be achieved using this design to answer further questions related to ground-nesting preferences. Additional bees collected in summer 2022 have yet to be identified and incorporated in the analysis. Furthermore, in the spring of 2022, I set up a new

experimental site at Fletcher Wildlife Garden in Ottawa. I used the same experimental design—randomized block design with four planters—but this time, I also tested the effect of ground cover on ground-nesting bees' nesting preferences by leaving half of the planters bare and half with dead vegetation on the soil surface. An undergraduate student in the lab (Lori Fernandez) managed the bee sampling this summer and will use this new experimental site for her Honours project this year. In the future, this experimental design can be used to study other untested factors (e.g., shading), or the design could be modified to test the effect of management practices (e.g., irrigation, pesticide application) in a controlled experiment. To do the latter, more planters and treatment replicates are needed. Indeed, in Chapter 4, I was not able to detect effects of treatments on bee nesting preferences, probably because the sampling area was small. Increasing the number of planters and using larger emergence tents would be critical in detecting effects.

There is growing interest in ground-nesting bee nesting habitat and related threats, with many research papers published this year on the topic. For example, researchers have tested the effects of pesticides in the soil on ground-nesting bees (Willis Chan and Raine 2021, Gaudreault et al. 2022), artificial nesting hills on bee communities (Neumüller et al. 2022), and bare ground on nesting activity (Gardein et al. 2022). This non-exhaustive list includes papers showing more examples of associations between nesting resources and ground-nesting bees or highlighting the risks posed to their nesting habitat. Future studies testing the effect of soil characteristics on ground-nesting bees should also include natural and urbanized habitats, and examine different locations, to have a better sense of how soil factors affect ground-nesting bees' presence and abundance at broader scales. Further research should also assess the importance of both abiotic and biotic factors on ground-nesting bees (as discussed previously), to better understand where bees nest and what factors may limit their populations. A better understanding of habitat

requirements will help conserve ground-nesting bee populations in agricultural and natural habitats. My thesis is one of many steps toward providing and protecting suitable habitat for ground-nesting bees.

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