Do bare soil landscapes encourage ground nesting bees?

by

Konstantinos Tsiolis

Canterbury Christ Church University

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Contents

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Abstract

Most bee species are ground-nesters, yet knowledge on this vast group remains sparse when compared to their better-known cousins, honeybees and bumblebees. Whilst evidence on the effectiveness of ground-nesting bee species as crop pollinators is growing, limited information exists regarding their nesting habits and preferences. In this study, artificially prepared plots of bare soil were used where nine different soil properties were investigated to determine the preferred soil properties of the attracted species. Eleven ground-nesting bee species (7 Andrena, 3 Lasioglossum and 1 Halictus) were recorded from the study plots. The findings of this study suggest that compaction, hydraulic conductivity and the soil textures, sandy loam and sandy clay loam, being the soil properties that play a significant role in the nesting of the recorded species. Building a greater understanding of their nesting ecology will allow better management of their populations, resulting in enhancement of pollination services in agriculture.

Introduction

Insect pollination is not only an essential ecosystem function but it also contributes greatly to agricultural productivity. Pollination is the transfer of pollen within and between flowers by pollinator insect species and has a vital ecological function in the reproduction of 78% of temperate flowering plants (Ollerton et al. 2011). Animal pollination supports more than 75% of the 115 leading crop species globally which depend on or benefit from it (Klein et al. 2007). The annual market value of animal pollination has been estimated at $235-$577 billion worldwide (Potts et al. 2016b) which demonstrates its importance economically and for the viability of agricultural production. Both managed and wild pollinators are not only highly beneficial to society by contributing towards the maintenance of biodiversity, ecosystem stability and food security but they also play significant role towards farmer and beekeeper livelihoods and social and cultural values (Potts et al. 2016a).

Yields of insect pollinated crops are managed globally via the addition of honeybees (*Apis mellifera* L.) (Goodwin et al. 2011; Morse 1991; Rucker et al. 2012). However, there is evidence that honeybee hive

numbers have been declining in many developed nations (Potts et al. 2010b; vanEngelsdorp & Meixner 2010) and might not be capable of supplying the pollination service demands. Also, UK honeybee populations were able to supply just 34% of pollination demands in 2011 falling from 70% in 1984 and the fact that insect pollinated crop yields have increased by an average of 54% from 1984 to 2011, it is doubtful whether honeybees provide the majority of pollination services (Breeze et al. 2011). Furthermore, the extreme dependency of European crops on a single pollinator species carries numerous risks if this pollinator were to fail. Current literature suggest that pollinator-dependent crops are increasing (Aizen et al. 2008; Calderone 2012) but pollinators have declined in several parts of the world (Biesmeijer et al. 2006; Bommarco et al. 2012; Cameron et al. 2011; Potts et al. 2010a; Winfree et al. 2009). The causes of this decline are believed to be invasive species (Schweiger et al. 2010), climate change (Hegland et al. 2009), introduced pathogens (Cameron et al. 2011), the extensive use of pesticides (Brittain & Potts 2011; Johansen 1977) and human disturbances to the environment (Brosi et al. 2008; Quintero et al. 2009). Therefore, it would be highly beneficial to investigate on other valuable bee pollinators to provide security to pollination services. According to Kleijn et al. (2015) only a small number of species is needed for the provision of ecosystem services as 2% of all known bee species are capable of providing almost 80% of crop pollination. Growing evidence suggest that wild bees could provide beneficial pollination services which may not be replicable by honeybees (Garibaldi et al. 2013; Mallinger & Gratton 2015).

Though no extensive research has been done on the agricultural benefits of solitary ground-nesting bees, there is evidence suggesting that their value may be significant, and possibly underestimated. Holzschuh et al. (2012) found that the most common wild bee family visiting sweet cherry crops was *Andrenidae*, making up 92% of bees sampled. A study from Javorek et al. (2002) indicated that the pollen-harvesting *Andrenidae* species pollinated over 85% of the visited flowers compared to nectar-foraging *Apis* and *Megachile* species which pollinated less than 25% of visited flowers on lowbush blueberry (*Vaccinium angustifolium*). Furthermore, Kendall (1973) studied the visitation of insect-pollinators on apple blossom and found that the species *Andrena haemorrhoa* F. and *Andrena jacobi* P. pollinated a significantly higher proportion of ovules and produced better fruit set (seed content) than honeybees. This could be because species such as *A. haemorrhoa* are able to carry large quantities of pollen grains

(up to 15,000) to apple blossom, compared to honeybee workers which carry a much smaller amount (4000 on average) (Kendall & Solomon 1973). Garratt et al. (2014) has studied the visitation of various insect species such as honeybees, bumblebees, hoverflies and solitary bees on apple flowers with solitary bees having the highest visitation activity. In another study Garratt et al. (2016) has estimated the economical contribution of solitary bees on UK apple pollination at £51.4 million. A study on pollination of melon (*Cucumis melo*) found *Apis mellifera* L. to be a nectar-forager and *Lasioglossum malachurum* K. a pollen-forager, resulting in the latter being a more effective pollen depositor on stigma. Also, *L. malachurum* visited the melon flowers one week earlier and it was overall a more frequent visitor than *A. mellifera* (Rodrigo et al. 2016). Moreover, studies indicate that pollination services of *Lasioglossum* species could be important for agriculture too. A study by Adamson et al. (2012) showed that the genus *Lasioglossum* Curtis was one of the most abundant in caneberry fields. Also, it suggested that watermelon and cantaloupe may be benefitted by *Lasioglossum* which comprised most non-*Apis* visitors. Another study that investigated the potential of small sweat bees as pollinators of melon (*Cucumis melo*) reported that *Lasioglossum* species accounted for more than 70% of species visiting the flowers of the plant, with *L. marginatum* B. and *L. malachurum* the most abundant visitors (Rodrigo et al. 2016). Morandin et al. (2007) have assessed the wild bee populations of canola crops and found 42.5% of the visitors to be from the genus *Lasioglossum*. There may be enough evidence to persuade us of the importance of ground-nesting bee populations, but a crucial element of their presence in crops is the appropriate nesting habitat.

There are 25,000 known bee species which differ significantly in their ecology, habits and size, diverging according to their plants of interest (FAO 2004). More than 85% percent of existing bee species are not perennially social (Honeybees) but solitary. Solitary bee females mate independently, create their own nests of an average of ten brood cells (depending on species), provide enough food for each offspring (pollen and nectar), lay an egg in each cell and finally die before the emergence of the next generation (Batra 1984). Solitary bee species are divided into six families: *Megachilidae* (Long-tongued, leafcutter and mason bees) and *Halictidae* (Short-tongued, sweat bees) with worldwide distribution; *Andrenidae* (Short-tongued, digger bees) mainly present in the Northern Hemisphere; *Colletidae* (Short-tongued, membrane bees), mostly diverse and numerous in the Southern Hemisphere;

Melittidae (Short-tongued), a small diverse group; and finally *Apidae* (Long-tongued, carpenter bees, orchid bees, stingless bees, honeybees, bumblebees), the largest family within the superfamily *Apoidea* (Batra 1984; Falk 2015; Else et al. 2016).

There are bee species which are not solitary throughout their lifetime. Sweat bees (*Halictidae*) can be divided into three different categories: solitary, obligately social and facultatively social (Richards 1994; Packer 1997). Obligatory social sweat bees have some sort of cooperation between adult females in the nest to raise the next reproductive brood. Eusocial species have at least two phases in their colony cycle with the females of the first brood (workers) helping with the raising of reproductive or final brood (Richards 2000). Facultative social species comprise both social and solitary populations and even social and solitary colonies within a single population. This eusocial habit has been reported in *Halictus rubicundus* C. (Eickwort et al. 1996) and *Lasioglossum calceatum* S. (Sakagami & Munakata 1972). An example of a kin-selected eusocial sweat bee could be described as one where a mother queen has complete control of the oviposition of eggs and her altruistic daughter workers, which neither mate nor lay eggs, are assisting with the raising of her brood (Eickwort 1985). *Lasioglossum malachurum* is often seen as a classic example of a eusocial sweat bee (Richards 2000).

Ground-nesting bees have a number of well-known predators and parasites. There are two recognised parasitic strategies: parasitoidism, which includes free-living mothers that lay eggs on or in the host; and kleptoparasitism, which encompasses stealing the host's food resources via the laying of eggs inside the nest of other species, avoiding the cost of brood care (O'Neill 2001). It is believed that around thirteen families of *Aculeata* contain parasitoids, while around eight families contain obligate kleptoparasites (Bohart 1970; O'Neill 2001). Depending on the species, some attack just one, others several more bee hosts and they have a variety of strategies for getting into the host's nest (Bogusch et al. 2006). The *Sphecodes* genus (Family: *Halictidae*), commonly known as cuckoo bees, are one of the main enemies of solitary bees as its females are mainly kleptoparasitic on species of *Halictic* genera (*Halictus* and *Lasioglossum*) but also attack other bee families such as *Melittidae*, *Andrenidae*, *Anthophoridae* and *Colletidae* (reviewed by Michener 1978). Seventeen species of this genus have been recorded in the British Isles (Falk 2015). Nests of solitary species remain unguarded during foraging. The same is true during the first reproductive cycle of facultatively social species but once the first

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worker brood emerges, a guard bee usually blocks the entrance of each nest to prevent any conspecific females and parasites entering the nest (Knerer, 1969). Bogusch et al. (2006) have observed that *Sphecodes* parasitic females can enter the host's nest during absence but also during presence of the host. Another interesting observation by the authors is that when the host female is present it does not prevent the kleptoparasite's entry, and even during the contact of the two females, no fighting occurs. Someone could argue that from an ecological and practical point of view, no parasite remains effective if it kills the host. However, the presence of parasites and kleptoparasites should be considered as high level of parasitism could have negative effects on bee populations (Antonini et al. 2003).

The nesting ecology and soil properties preferred by ground-nesting bee species are also relatively under-researched. The ground-nesting bee *Nomia melanderi* C. (Hymenoptera: Halictidae) is reported to prefer nesting beds without surface vegetation, silty soils with good hydraulic conductivity and moist subsoils (Johansen et al. 1978). Osgood (1972) found species of *Halictine*, *Colletes* and *Andrena* nesting frequently in thinner organic layers compared to soils present nearby. A study from Cane (1991) showed that ground-nesting bees had not been found nesting in silt or clay soils and all examined soils were from 33% to 94% sand. Furthermore, Potts & Willmer (1997) attempted to study a range of edaphic and microclimatic parameters possibly involved in nesting of the ground-nesting halictine bee *Halictus rubicundus* C., providing important findings. They observed that bees initially nested in soft soils, but, despite the availability of soft soils, as nest aggregations were growing, bees moved to hard soils which is believed to provide strong nest structure, avoiding collapsing of nests. Nest temperature is also considered a significant component of nest productivity of hymenoptera as it determines the rates of development in eggs and larva (Miyano 1981) and influences emergence timing of broods which can be closely related to survivorship (Jeanne & Morgan 1992). Potts & Willmer (1997) reported that *H. rubicundus* preferred to nest in warm soils and favoured south facing steep slopes, a factor that is believed to be closely related to high absorption of sunlight. The authors also suggested that the ground nesting bee *H. rubicundus* tends to nest near or under stones which may have a thermal role to play by absorbing solar radiation and keeping the entrance of a nest at a relative warm temperature. Soil surface temperature is considered a good indicator of the thermal properties of substrate area and it is believed

to be the reason why females spend some time basking at different points on the substrate's surface during the nest founding period (Potts & Willmer 1997).

Nesting is a crucial component of the life cycle of ground-nesting bee species, and it is particularly important to understand in order to provide pollination resources in crop systems. The aim of this study was to examine how various soil properties affect nest site preference and nesting success in an agricultural environment, using artificially prepared plots of bare soil to mimic a natural nesting habitats. A greater understanding of the preferred nesting habitat of *Lasioglossum* and *Andrena* species could be used to encourage them to nest near crops and gain their pollination services.

Methods and Materials

Study site

Fruit orchards at the National Institute of Agricultural Botany-East Malling Research (NIAB EMR) (51°17'16.1"N 0°26'17.9"E) were used for the study. Ten South/South East facing bare soil plots (Fig. 1) were created by herbicide treatment to reduce plant growth followed by top soil being mechanically removed with a 0.91 m bucket digger in mid-February 2018. Each study plot (except plot 7) was 10 m x 2 m with a 1 m slope (10 °) (Fig 2). The vegetation of the 10 x 2 m area was removed by scraping off with a digger and then 0.88 m^3 soil was removed from an adjacent area to create the slope. Plot 7 was the only study plot that was not man-made as it was created on a landscape which was mostly on slope angle (around 30 °) and no soil from off-site was used, just scraped its surface to remove the existed vegetation.
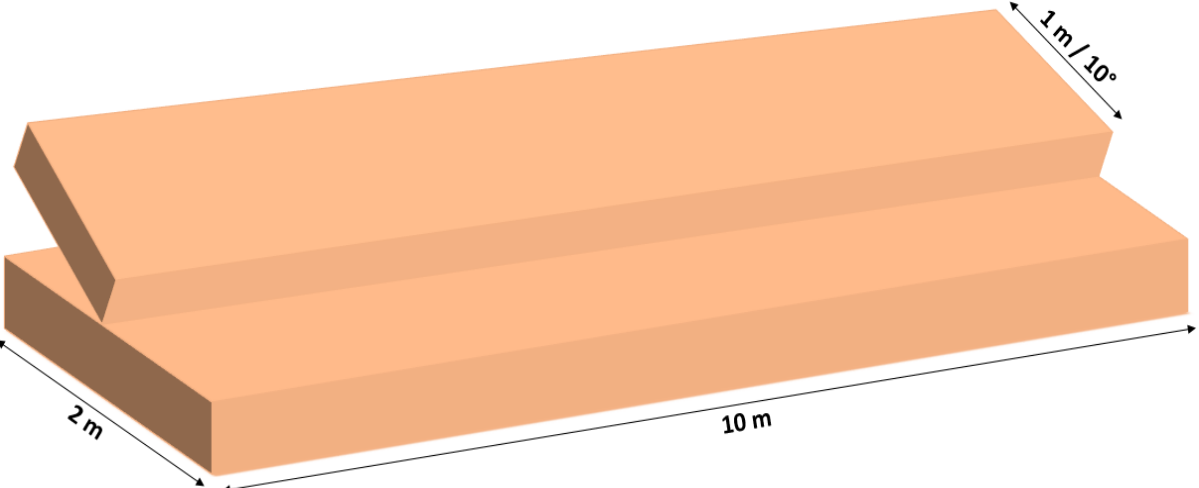
Figure 1. Locations of bare soil plots at NIAB EMR farm.

Figure 2. Experimental design and dimensions of bare soil plots.

Bee nesting surveys

The bee and nest surveys were undertaken during sunny and/or mild weather with temperatures above 10°C, provided that cloud cover did not exceed 4 oktas. On cloudier days, (5-8 oktas), surveys were conducted if the temperature was above 14°C. Also, wind speeds were below Beaufort scale 5, or 29 km/h (Pywell et al. 2005). The surveys took place between mid-April and May. These months are within the active flight period of many of *Andrena*, *Halictus* and *Lasioglossum* mining-bee species. The majority of *Andrena* species (67 species in Britain and Ireland) are univoltine (one brood of adults per year) such as *A. haemorrhoa* and *A. nitida*. The flight period of particular species is species-dependent and can be from early spring to late summer. The small group of bivoltine (two adult broods per year) *Andrena* species such as *A. dorsata* and *A. minutula* have a longer flight period between April-July (Provisional atlas of the aculeate Hymenoptera of Britain and Ireland 1997-2016; Falk 2015). The flight period of *Lasioglossum* (34 species in the British Isles) and *Halictus* (8 species in the British Isles) species is season-dependent too and it can vary from early spring to the end of summer and some species can fly into mid-Autumn. Mated females of the eusocial species, such as *L. albipes, L. malachurum, L. pauxillum* and *Halictus tumulorum* appear in March and can fly into October. By mid-summer these species have produced a brood of workers and the second generation of males and females flies at the end of summer. Such species maybe present from July to October (Provisional atlas of the aculeate Hymenoptera of Britain and Ireland 1997-2016; Falk 2015).

The purpose of the behavioural study was to record the ground-nesting bee species' visitation to study plots. The bee visitation study was performed twice a week where possible and plots were sampled in randomized order. This enabled the study plots to be visited several times, both in the morning and afternoon, by the end of the field study and gives a representative view of bees' activity on the study plots. Ten surveys took place overall. Thirty minutes were spent observing each study plot, walking slowly around the perimeter. Once a bee visited the plot, it was collected using a 60 cm x 46 cm entomological sweep net (Watkins & Doncaster, Leominster, UK) and it was placed carefully into a 5 ml, 41 mm x 15 mm clear plastic tube (NHBS Ltd., Totnes, UK). Each plastic tube was placed into an ice bucket where bees were kept inactive until the end of the observation period (Grixti et al. 2009). Subsequently, various photographs of individual bees were taken for later identification and

confirmation by Mr. Mike Edwards. Bees were then released at the site. Destructive sampling is thought to be inappropriate when considering the ecology of solitary ground-nesting bees, as the removal of individuals (most likely females) from the site could have a significant negative impact on the populations at the study site. Parasitic species were not destructively sampled due to their potential ecological value and significant negative impact.

Furthermore, nests of ground nesting-bee species were counted individually as total number for the flat and slope sections of each plot prior to each 30-minute observation period of bee visitation. The same method was applied at all study sites. Identification of nests is a complicated and challenging procedure as a number of other insects create holes on the ground too such as ants and earthworms. The identification took place having in mind characteristics of solitary bees' nests such tumuli (volcano-shaped, mound of earth) that are made by females in the nest excavation phase. Ants could create soils structures similar to solitary bee tumuli but usually ant's tumuli are made out of scattered soil particles compared to solitary bee tumuli which have a more organised and firm structure (K. Tsiolis, personal observation). If it was not clear whether a nest belonged to an ant or bee, a very small amount of soil was thrown into the nest and if ants came out, it was counted as ant nest otherwise it was assumed to be a solitary bee nest.

Soil analyses

Eight soil samples of 10 cm depth were taken from each site using a Buerkle soil sampler (Fisher Scientific International Inc., Hampton, US). The first sample was taken from the flat section of the plot, 30 cm away from edges of the plot and the second was taken from the slope 120 cm horizontally away from sample one and 30 cm from edge. The same pattern was followed until eight soil samples were taken (see Fig. 3). The soil samples were analysed individually in the soil laboratory of Canterbury Christ Church University to determine the soil properties of each plot. Firstly, each sample was placed in aluminium foil, weighed and dried in an oven (Genlab MINO/6, Genlab Ltd, Cheshire, UK) at 80 °C for 5 days. Then, soil samples were re-weighed to establish their gravimetric water content (Martin-Vertedor & Dodd 2011). At this stage, each sample had a number of lumps of various sizes which were broken down using a 500 ml mortar and pestle (Cole-Parmer Instrument Co Ltd., Cambridgeshire, UK). Afterwards, each sample was placed in a 312 mm x 427 mm x 75 mm plastic tray (Gratnells Shallow

trays) and using a pair of forceps (non-toothed 15 cm) all visible roots were removed and weighed to

determine the root biomass. Subsequently, a 2 mm aperture sieve (Fieldmaster Ltd., Pukekohe, New

Zealand) was used where each sample was hand sieved for 30 seconds to separate the gravel fraction
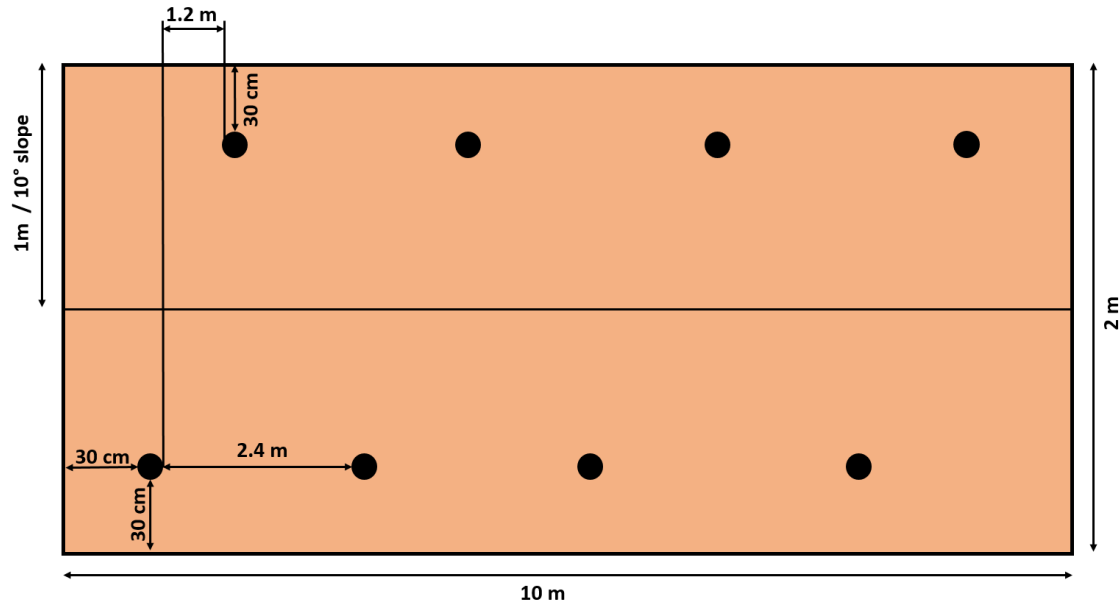

Figure 3. Soil sampling method showing the arrangement of soil sampling points (black dots) as arranged across the 10x2m plot.

and determine the stoniness of each sample (Potts & Willmer 1997). Weight of stones was measured as

a percentage of total soil weight. Two grams of the remaining non-gravel fraction of each sample was

weighed in a 50 ml porcelain crucible (Cole-Parmer Instrument Co Ltd., Cambridgeshire, UK) and

placed in a muffle furnace (ELF 11/14B, Carbolite Gero Ltd, Derbyshire, UK) for seven hours at 550

°C (Goldin 1987). Then, the samples were left to cool in the muffle furnace overnight and the

subsequent weight loss was recorded in order to calculate the weight of organic matter as percentage

loss on ignition. The infiltration rate of soils was also measured as the mean of three positions using

three mini disc infiltrometers (METER Group Inc., Washington, U.S.) (METER Group Inc. 2018). Soil

texture was determined using the Bouyoucos hydrometer method (Lesikar et al. 2005) by calculating

percentage of sand, silt and clay of each sample. Particulate fractions and size classes used were in

accordance with U.S Department of Agriculture: gravel (> 2.0 mm), sand (0.05 – 2.0 mm), silt (0.002

– 0.05 mm) and clay (> 0.002 mm) (Lesikar et al. 2005). This was to ensure compatibility with the data

processing software for the infiltrometers. Soil compaction (unconfined compression strength) recorded

as the mean of three positions per slope/flat sections was measured using an electronic penetrometer

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(Solutions for Research Ltd, Bedfordshire, UK) and a soil moisture meter MO750 (Extech Instruments Corp., New Hampshire, U.S.). The cone index corrected for soil moisture content was calculated according to Busscher et al. (1997). Atwell (1993) reported that root growth is reduced significantly where MPa values are greater than 2, thus compaction was measured as % of compaction greater than 2 MPa.

Statistical analyses

All statistical analysis was performed using Minitab 18. The data from soil analyses of each slope/flat area were combined per plot. The Anderson-Darling normality test was used to determine whether the data of study variables was normally distributed. The data failed to pass the assumption of normality and as a result the Box-Cox Transformation ($\lambda = 0$ (natural log)) was used. A Principal Components Analysis (PCA) was used (Correlation Matrix), inserting all study variables (Organic matter, root biomass, soil water content, stoniness, soil compaction, hydraulic conductivity, sand, clay and silt) in the model to determine the variability between study plots. Each nest count was treated as a replicate for each plot in the model. Also, the Mahalanobis distance was used to determine which factors play significant role to some plots being outliers which were still included in the analysis. Subsequently, the Analysis of variance (ANOVA) Mixed Effects Model was used where numbers of bees set as response, date as random effects, plot and flat/slope as fixed factors and all soil variables as covariates. Furthermore, a regression analysis was performed to test for collinearity which it is known to exist between various soil properties (Dormann et al. 2013). A pairwise t test was also used to determine whether there was a significant difference between the number of nests on flat and slope sections of study plots.

Results

The ANOVA Mixed Effects Model was used to determine whether there was a significant relationship (positive or negative) between each soil characteristic and number of tumuli (Tab. 1). The model shows soil compaction, hydraulic conductivity, sand and clay soil textures being statistically significant positively correlated with number of bee nests (see Tab. 1). The Regression Analysis test suggests collinearity (VIF values) for sand and silt soil texture as their VIF values is 10 > (Hair et al. 1995; Tab.

1). The pairwise t test demonstrated significant difference between nest density on the flat and slope sections of study plots (t = 2.55, p = 0.012).

Table 1. Results of ANOVA Mixed Effects Model and Regression Analysis.

Variable	β values	DF	p values	VIF
Organic matter	2.682047	171.17	0.073	1.79
Root biomass	0.007663	171.17	0.909	1.21
Soil water content	-0.041065	172.48	0.985	2.84
Stoniness	0.090142	171.76	0.717	1.77
Compaction	0.183811	171.17	0.013	1.28
Hydraulic conductivity	3.924604	171.17	0.022	3.72
Soil texture (Sand)	23.349115	171.17	0.022	13.97
Soil texture (Clay)	9.490848	171.17	0.005	5.01
Soil texture (Silt)	-1.525082	171.17	0.555	10.49

The PCA employed Mahalanobis distance to determine the outliers which are indicated to be plot 1-slope, plot 5-flat and plot 10-flat (Fig. 4). Hence, the sections of these three plots varied significantly to the rest. It was decided to investigate these outliers to determine the cause of this variance. Table 2 shows that comparing the outlier plots with all other plots, plot 10-flat had the highest percentage of organic matter and root biomass. Plot 5-flat had the highest percentage of sand and as a result the highest hydraulic conductivity rate. Despite that it is not clearly evident why plot 1-slope is outlier, it was found to suffer from surface water flooding which could be due to combination of variables. At the same time, plots 1 and 5 have attracted 5 and 0 solitary ground-nesting species to nest respectively (Fig. 5).
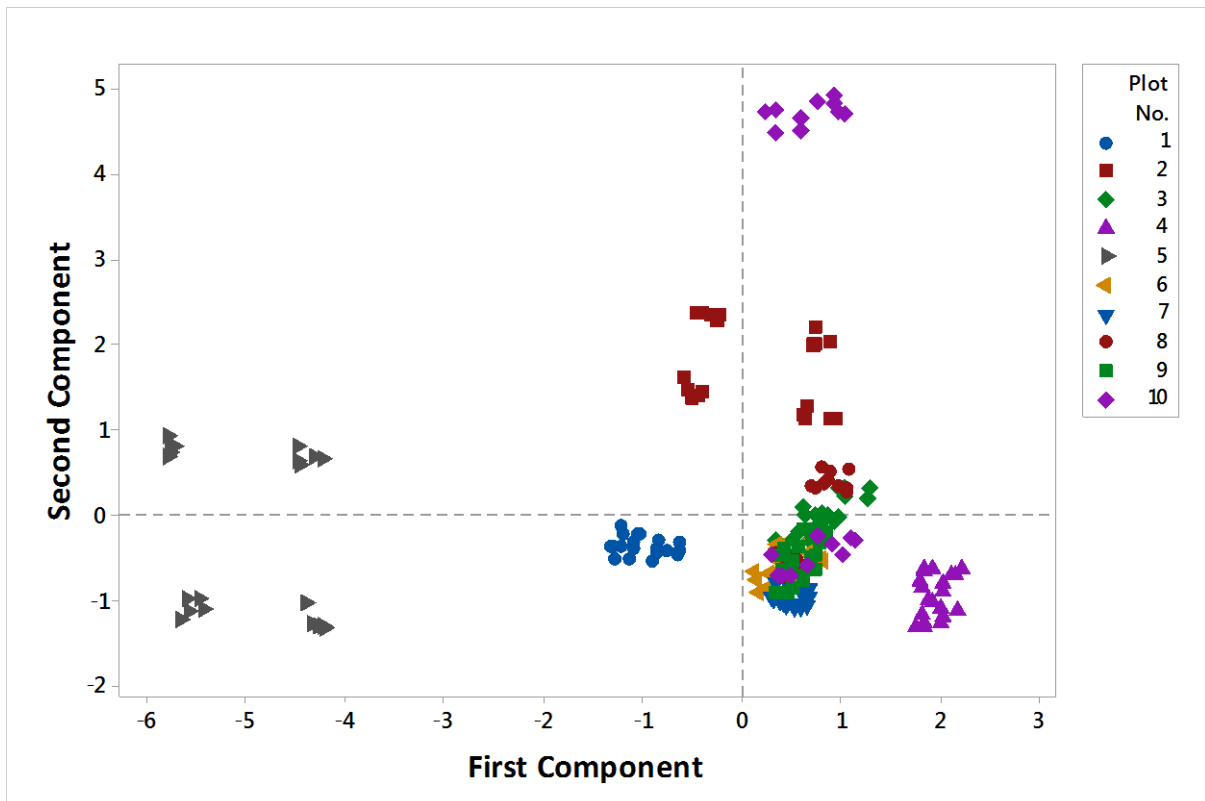
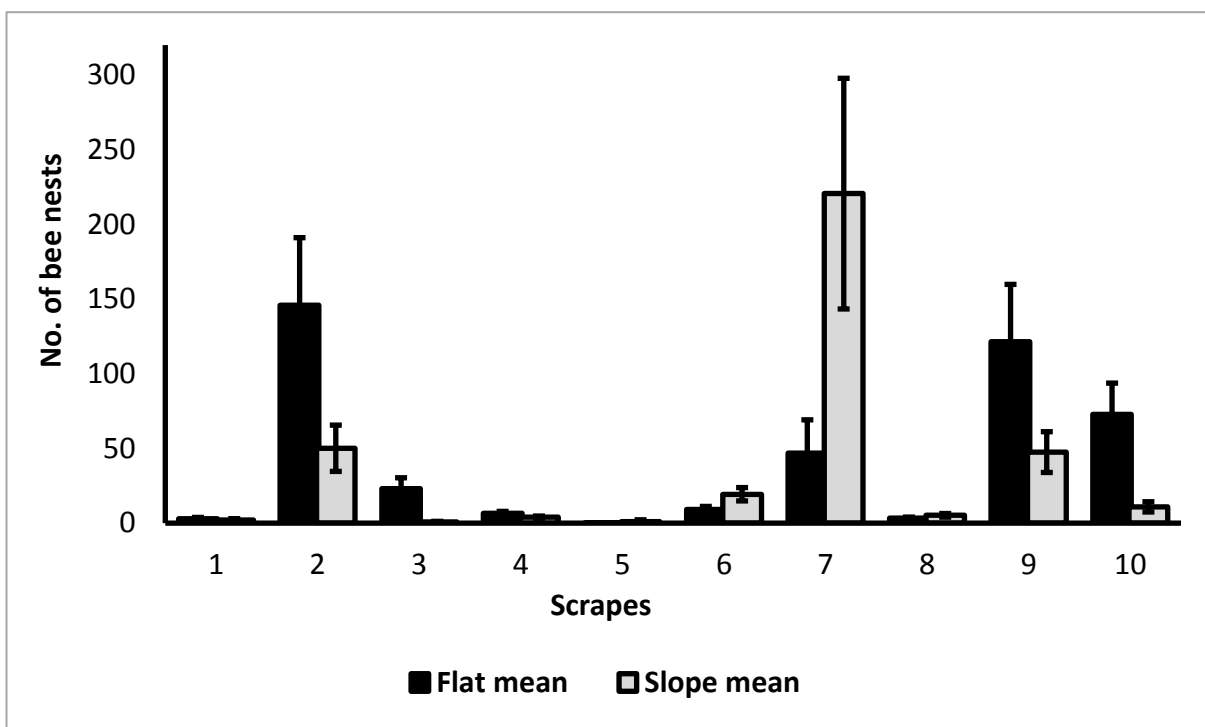Figure 4. Score plot showing the variance between plots.

Figure 5. Mean number of nests in flat and slope area of each plot. Error bars represent standard error based on ten different time points (n =10).

Table 2. Values of variables for flat and slope sections of plots.

Plots	Variables								
	Organic matter - %	Root biomass - %	Soil water content - %	Stoniness - %	Sand - %	Clay - %	Silt - %	Compaction (> 2 MPa) - %	Hydraulic conductivity (cm s^{-1})
1 – Flat	3.57	0.0024	11.25	24.00	67.80	22.80	9.40	37.50	0.000143
1 – Slope	3.69	0.0178	11.43	20.00	70.00	18.00	14.00	62.50	0.000211
2 – Flat	9.70	0.0097	23.16	19.84	70.90	12.82	16.28	62.50	0.000245
2 – Slope	10.02	0.0722	23.23	17.15	56.96	16.12	26.92	50.00	0.000461
3 – Flat	5.98	0.0159	20.64	5.97	58.80	23.60	17.60	37.50	0.000515
3 – Slope	6.94	0.0110	24.13	3.34	59.80	16.60	23.60	0	0.000525
4 – Flat	3.90	0.0143	16.95	1.04	49.40	17.20	33.40	0	0.000122
4 – Slope	3.80	0.0449	17.93	2.71	48.40	17.20	34.40	12.50	0.000120
5 – Flat	2.89	0.0156	9.79	16.22	95.00	3.20	1.80	25.00	0.002175
5 – Slope	6.65	0.0244	17.43	24.21	92.90	4.00	3.10	12.50	0.001099
6 – Flat	4.89	0.0039	19.02	1.11	59.20	10.80	30.00	75.00	0.000366
6 – Slope	4.43	0.0040	18.35	6.55	59.20	11.80	29.00	25.00	0.000563
7 – Flat	4.08	0.0047	16.02	5.08	60.40	16.40	23.20	25.00	0.000222
7 – Slope	4.05	0.0044	16.48	4.34	60.40	15.20	24.40	25.00	0.000223
8 – Flat	5.01	0.0000	16.43	2.81	60.00	14.00	26.00	62.50	0.000332
8 – Slope	7.86	0.0115	21.48	2.63	62.00	15.00	23.00	50.00	0.000170
9 – Flat	4.53	0.0000	15.24	7.77	60.60	22.80	16.60	62.50	0.000172
9 – Slope	4.85	0.0123	18.08	6.23	60.60	19.80	19.60	25.00	0.000189
10 – Flat	15.92	0.2252	14.04	4.93	60.40	17.40	22.20	50.00	0.000180
10 – Slope	4.96	0.0111	20.42	2.72	63.40	16.20	20.40	12.50	0.000255

Table 3. Ground-nesting bee species and parasitic species sampled from study plots. Species that were not identifiable were grouped as small medium and large to the nearest conjecture. Small *Andrena* (*A. minutula* Kirby, *A. semilaevis* Pérez and *A. subopaca* Nylander), medium *Andrena* (*A. dorsata* Kirby and *A. bicolor* Fabricius), large *Andrena* (*A. flavipes* Panzer). Medium *Lasioglossum* (*L. malachurum* Kirby, *L. calceatum* Scopoli, *L. albipes* Fabricius), large Lasioglossum (*L. zonulum* Smith). *Specodes* that were not identifiable were grouped together too.

Plots	Andrena	Andrena haemorrhoa Fabricius	Andrena nitida Müller	Andrena scotica Perkins	Andrena dorsata Kirby	Andrena flavipes Panzer	Andrena bicolor Fabricius	Andrena (Micrandrena) - Small	Andrena - Medium	Andrena - Large	Lasioglossum	Lasioglossum malachurum Kirby	Lasioglossum pauxillum Schenck	Lasioglossum villosulum Kirby	Lasioglossum - Medium	Lasioglossum - Large	Halictus	Halictus tumulorum Linnaeus	Parasitic	Sphecodes	Sphecodes monilicornis Kirby	Bombylius major Linnaeus	Nomada fucata Panzer	Nomada flavogutata Kirby
1		1						1		1				2										
2			1	1	1				1			10	3		9	5				2		1		
3		1					1		1			4			1			1		4				
4									2											4		3	1	
5																								
6			1			2	1		2											1				3
7						6	1					8		1	3					9	6			
8			1	2					2						6					2				
9						2			3			6			8					6	3		1	
10				1		3			2			4			7					3				

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The plots attracted several species mainly from the families *Halictidae* and *Andrenidae* (see tab. 3). Among all non-parasitic bees sampled from study plots, the most abundant was the genus *Lasioglossum* 65%, second most abundant the genus *Andrena* 34% and the least common the genus *Halictus* 1%. Three species from the genus *Lasioglossum* were recorded (*L. malachurum, L. villosulum* and *L. pauxillum*), seven species from the genus *Andrena* (*Andrena-Micrandrena, A. haemorrhoa, A. albipes, A. nitida, A. scotica, A. flavipes* and *A. bicolor*) and one species from the genus *Halictus* (*H. tumulorum*). Bees from the genus *Lasioglossum* were found at plots 2, 3, 7, 8, 9 and 10. *L. malachurum* was the most common visitor of its genus (42%). *Andrena* species were found mostly at plots 6, 7, 8 and 9. The parasitic *Sphecodes monilicornis* was mainly common on plots 7 and 9 and it was the most abundant visitor of its genus (29%).

Table 4. Textural class of flat and slope sections of each study plot.

Plot	Flat	Slope
1	Sandy clay loam	Sandy loam
2	Sandy loam	Sandy loam
3	Sandy clay loam	Sandy loam
4	Loam	Loam
5	Sand	Sand
6	Sandy loam	Sandy loam
7	Sandy loam	Sandy loam
8	Sandy loam	Sandy loam
9	Sandy clay loam	Sandy loam
10	Sandy loam	Sandy loam

Discussion

Species richness and nesting preferences

The 11 identifiable ground-nesting bee species (7 *Andrena*, 3 *Lasioglossum* and 1 *Halictus*) recorded (Tab. 3) and their density at the study plots provided important information on their preferred soil properties. The data suggests that double-brooded *Andrena* (*A. dorsata, A. bicolor* and *A. flavipes*) and obligately social *Lasioglossum* (*L. pauxillum* and *L. malachurum*) are nesting in bare soil areas. This is possibly because they are more warmth dependant than univoltine species. Single-brooded *Andrena*

species (*A. scotica*, *A. nitida* and *A. haemorrhoa*) may not require the rapid development time needed of bivoltine and eusocial species and it might be the reason that were not observed utilising the bare ground plots created in this study. A few single-brooded species were sampled too but in small numbers.

Soil variables and nesting preferences
Compaction
The model (Tab. 1) suggests a positive relationship between compaction and number of bee nests. The excavation process of a nest is a significant investment for most ground-nesting *Hymenoptera* carrying both energy and time costs (McCorquodale 1989; Michener & Rettenmeyer 1956). Nevertheless, harder soils have their own benefits. Potts & Wilmer (1997) noted that soft soils are initially selected but as the aggregation gets bigger, ground-nesting *Hymenoptera* favour harder soils which can support the architecture of their nests. The findings of this study show that the flat sections of study plots were mostly more compacted than the slope sections (Tab. 2) and they also attracted more bees to nest (Fig. 5). It could be assumed that as the density of nests is increasing, the likelihood of losing structural integrity is also increasing, unless the soil is compacted enough. Ground-nesting bee species may consider compaction of soils as a crucial element during the process of selecting their nesting location. Female *Halictus rubicundus* have nest selection behaviour; visually searching an area for other nest entrances (Potts & Wilmer 1997) and they could even bite the soil surface and carry out a digging test to determine the soil hardness of a specific soil landscape (S. G. Potts personal observation, cited in Potts & Wilmer 1997).

Hydraulic conductivity
This variable displayed a positive relationship with the number of bee nests (Tab. 1). Hydraulic conductivity can be defined as the rate of water that can be absorbed by soil. A higher rate of hydraulic conductivity allows a higher rate of drainage which could result in soils with limited water content. In theory, soils with higher rate of hydraulic conductivity could be considered favourable by ground-nesting bees as their nests will have less risk of waterlogging. Johansen et al. (1978) reported that hydraulic conductivity is one of the soil properties favoured by alkali bees for nesting. Higher rates of hydraulic conductivity could be also linked to soils with a greater percentage of stoniness which could

have beneficial elements towards the structural support of a nest such as the case of *Forficula auricularia* L. (*Dermaptera*: *Forficulidae*) (Lamb 1976). On the other hand, high absorbance rates could be linked to sandy or very soft soils which could be disadvantageous for ground-nesting bees and unsafe for their nests. Table 2 shows that the plot with the highest rate of hydraulic conductivity was plot 5 which has been classified as sandy (Tab. 4) and attracted no bees for nesting (Fig. 5). This variable could often be influenced by compaction of soils as the shape, size and connectivity of microscale pores controls water flow in soils (Ebina et al. 2004).

Soil texture

A positive relationship between sand and number of bee nests was shown by the model (Tab. 1). Sand is a soil property that might be assumed as highly preferred for ground-nesting bees as it requires less energy and time to dig. However, it should be taken into account that extremely sandy soils could be disadvantageous and unattractive for ground-nesting bees. Plot 5 contained a high percentage of sand (95% at flat and 92.9% at slope section). No nesting took place at this plot, possibly because it would not be able to support the structure of a nest. The model shows a positive relationship between clay and number of bee nests and negative relationship between silt and number of bee nests (Tab. 1). Cane (1991) found ground-nesting bees including *Halictus*, *Lassioglossum* and *Andrena* species nesting in clay loam, sandy loam and silt loam but found no bees nesting in silt or clay soils. Potts & Wilmer (1997) reported that soils where the ground-nesting bee *Halictus rubicundus* nested were all in sand/loamy sand/sandy loam category but none of the soil texture variables were correlated with the number of bee nests. This study agrees with both previous studies as plots 2, 7 and 9 (the plots with highest nest density) (Fig. 5) had soils in the categories sandy loam and sandy clay loam (Tab. 4).

Stoniness

A high density of stones in soils could be considered an obstacle for bee digging; increasing digging effort but possibly lower stoniness's density could be beneficial for some nesting elements. It was noticed that a number of nests were placed next to stones but at first instance was not considered as a possible significant factor. However, according to Potts & Wilmer (1997), 57% of nests of the ground-nesting bee *Halictus rubicundus* were created under or next to stones and nests with stone's association

had significantly greater temperature than nest without stone's association. There are a few possible explanations to this assumption which might be difficult to disentangle. It could be due to the high absorption of solar radiation by stones but at the same time, this preference could be also a defensive act against parasitism and the positive temperature correlation is a pure coincidence (Potts & Wilmer 1997). Furthermore, stoniness may also have an important structural role in the case of large ground-nesting bee aggregations, preventing nests from collapsing. Preference for nesting under stones was observed in the ground-nesting *Forficula auricularia* (Beall 1932). Lamb (1976) suggested this could be due to heat regulation of its nests as soil temperature near the surface is not as stable as in deeper levels; *F. auricularia* by moving her eggs against the stone or near surface, could regulate egg temperature and speed of hatching. Ground-nesting bee species are not known to move their eggs near the surface but they may use stones in the upper level of their nests for the same reason as *F. auricularia*. Effects of stoniness on bee colonisation were not observed in this study.

Organic matter

Organic matter may be considered advantageous for ground-nesting bee species as it could soften the soils, enabling bees to dig their nest much easier than in soils without or with very low percentage of organic matter. However, a low percentage of organic matter could increase soil compaction (Hamza & Anderson 2005) which could also be advantageous according to the findings of this study. Another beneficial element of organic matter is that it darkens the colour of a soil (Jackson 2014), which could have an impact towards a better absorbance of solar radiation, resulting in a quicker and better heated soil substrate. On the other hand, thick layers of organic matter could absorb large amounts of water (Bescansa et al. 2006), creating a waterlogged environment that can be disadvantageous for their nests. Osgood (1972) found that *Halictine*, *Andrena* and *Colletes* species showed nesting preference in soils where their organic layers were thinner than other soils in the same area. This variable was not considered statistically significant by the model.

Root biomass

Root biomass was presented by the model as not statistically significant. However, the actual percentage of root biomass recorded from plots should be taken into account. The average percentage of root

biomass (excluding plot 1 and 5) is 0.034% for flat and 0.021% for slope. This consideration may support the claim that ground nesting bee species do not prefer a high density of roots. It was also observed (different location) that *Colletes* species in grass heavy landscapes with a vertical bare soil area, seem to nest horizontally in the bare soil area, around 10-15 cm below the first soil layer (K. Tsiolis, personal observation) where there is a low density of roots. In soil landscapes with a high percentage of root biomass, it could be assumed that it would be much harder for these bee species to create their nest, much harder for the next brood to emerge and the likelihood of a nest getting damaged by roots would be high.

Gravimetric soil water content

This variable was shown by the model as not statistically significant for bee nesting. However, there are several possible reasons why water content would be important to ground-nesting bees. Firstly, soils that are capable of absorbing water could be easier to dig. Secondly, soil moisture is an important element for several ground-nesting species including *Lasioglossum albipes*, *Andrena haemorrhoa and Andrena marginata*, which create water-insoluble substances on pollen balls or interior walls which polymerase or solidify their subterranean nest cells and it seems crucial for the maintenance of cell moisture homeostasis in the nest (Cane 1981; Shinn 1967; May 1972). Soils considered good for nesting are soils that are neither waterlogged nor too dry. Soils that are capable of moderating moisture levels are of a great importance for healthy nests, contributing to successful larva development and minimizing the risk of brood cells' desiccation (Potts & Wilmer 1997).

Flat vs. Slope

Slope was assumed to be one of the factors that could play a significant role in the attraction of ground-nesting bee species as it was hypothesised that it would increase absorption of solar radiation and decrease the likelihood of waterlogging compared to flat landscapes (Potts & Wilmer 1997; Michener 2000). This study shows that flat sections of plots with the highest nest densities have attracted more ground-nesting bees than slope sections, except plot 7 (Fig. 5). Also, the flat sections of those plots were more compacted than the slope sections (Tab. 2). The findings of this study show that there is significant statistical difference between nest density of flat and a 10º gradient slope sections of study

plots. Someone could argue that the comparison between flat and slope sections is not entirely representative as the slope was created with off-site soil and it is not as compacted as flat section (Tab. 2). This argument is supported by the fact that the non-manmade slope section of plot 7 attracted a large number of bees. Furthermore, it is important to take into consideration that the landscape where plot 7 was created is fundamentally different from the rest in age of establishment even though was previously covered with vegetation. Soil water content and soil moisture are two of the most important factors that influence soil compaction (Soane & Ouwerkerk 1994; Turnbull et al. 1949). Gradually the compaction of slope could increase and then it may be significantly selected by ground-nesting bees. Furthermore, the gradient of the slope should be considered; increasing it could result in increasing of nesting preference.

Parasitism

The parasitic bees found in the study plots were mostly from the genus *Sphecodes* (86% of sampled parasitic bees) and the rest from the genus *Nomada* (Family: *Apidae*) (14% of sampled parasitic bees). The two *Nomada* species seen were, *Nomada fucata*; a kleptoparasite of *Andrena flavipes* and *Nomada flavogutata* whose hosts are the *Andrena minutula* group (Falk 2015). The most abundant species was *Sphecodes monilicornis*, a well know kleptoparasite of *L. malachurum* (Knerer G 1973; Legewie 1925; Sick et al. 1994) which was one of the most abundant ground-nesting bee species present on study plots. The literature suggests that *S. monilicornis* is more active during peak foraging activity of their host, they decrease following the decrease of foraging activity, and they are not active once foraging activity stops. This is believed to be related to optimal foraging theory as during periods of full provisioning, the kleptoparasite has a better chance of finding fresh pollen in a ground-nesting bee nest (Polidori et al. 2009). *S. monilicornis* has also been observed as a kleptoparasite of *L. pauxillum* (Bogusch et al. 2006) (found on study plot 2) and of the two medium-sized *Lasioglossum* species (possibly present on study plots), *L. calceatum* (Stöckhert 1933; Vegter 1993) and *L. albipes* (Alfken 1912; Blüthgen 1934). The presence of these ground-nesting bee species at study plots (Tab. 3) explains the abundance of *S. monilicornis* but it should be also taken into account that *S. monilicornis* is the most readily

distinguished *Sphecodes* species from a photo (K. Tsiolis, personal observation; M. Edwards, personal communication), which may have played its own role in the recorded abundance.

The impact of *S. monilicornis* on its host's population has not been extensively studied. However, a study by Strohm & Bordon-Hauser (2003) shows parasitism of approximately 20% on a *L. malachurum* population but parasitism of entire nests or colonies has also been recorded (Sick et al. 1994). During the surveys in this study, five bees were found dead next to the entrance of five different nests. Strohm & Bordon-Hauser (2003) have observed this phenomenon; *S. monilicornis* killed several *L. malachurum* workers (up to 19) inside the nest, extracting them out of the nest one by one. More sampling seasons and detailed observations will be needed to determine whether density-dependent mortality exists at study plots such as is the case of *Halictus rubicundus* attacked by a *Leucophora* sp. Fly (Eickwort et al. 1996). Potts & Wilmer (1997) argue that the existence of gregarious nesting is an indication that specific factor(s) is/are present which outweigh(s) the cost of parasitism.

Management of ground-nesting bee populations

This study has identified key variables which need to be controlled in the process of creating attractive soil nesting substrates for the recorded *Lasioglossum* and *Andrena* species. Compaction, hydraulic conductivity and texture of soils are shown to be the variables that play a critical role towards bee nesting. The other variables tested in this study may have importance too but lacking sufficient data to be proven. Furthermore, other variables not included in this study may play a significant role towards nesting of these bee species, such as soil temperature and soil humidity. The preferred nesting habitat of single brooded spring *Andrena* species (*A. nitida* and *A. haemorrhoa*) requires further investigation too.

The availability of nesting resources as well as adequate food resources are vital elements for the effective management of ground-nesting bee populations. Mass-flowering crops are in bloom for a few weeks (Martins et al. 2018) and the provision of additional food resources is required to encourage bee populations to remain at the location of interest. Literature suggests that the increase of density and diversity of flower strips (Haaland et al. 2011, Wratten et al. 2012), field margins (Rands & Whitney 2010), hedgerows (Schulp et al. 2014) and semi-natural land near farms (Martins et al. 2015) could

have a significant effect on bee abundance and diversity (Garibaldi et al. 2014, Venturini et al. 2016). At the locations where both appropriate food resources and nesting habitat exist, ground-nesting bees could remain and multiply for many years. Examples of long-lived aggregations are the *Panurginus polytrichus* C. for 20 years (Neff, 2003) and *L. malachurum* for 37 years (Stöckhert cited in Michener, 1974). A study by Cane (2008) shows that populations of alkali bee (*Nomia melanderi* C.), which is the world's only managed (intensively) ground-nesting bee due to its efficiency to pollinate alfalfa (*Medicago sativa* L.) crops, have grown nine-fold (16.7 million females) over the period of eight years. The author also reports that the successful management of these populations is a result of farmers' awareness of species' ecological needs, providing subsurface water using buried perforated pipes in many cases to sustain moisture levels and also avoiding spraying of pesticides during bloom. A critical component of successful and sustainable ground-nesting bee populations in an agricultural environment is the understanding of their nesting needs. This study has attempted to build a better understanding of those needs.

Conclusion

This study has provided evidence of specific soil characteristics that could encourage and support bee nesting. Soil compaction and hydraulic conductivity of soils are shown to be the variables that play a positive role in the nesting of recorded *Lasioglossum* and *Andrena* species. Also, sandy loam and sandy clay loam are shown to be the preferred soil textures of these species. Further research is needed to enrich the current limited knowledge of these important ground-nesting bee pollinators, which will allow the improvement and productive sustainability of those population in agricultural environments. The sustainability and increase of populations of interest would play a crucial role in the effectiveness of pollination services.

Acknowledgments

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