Received: 15 February 2022 | Accepted: 4 October 2022

DOI: 10.1111/1365-2664.14317

Journal of Applied Ecology BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

Nesting of ground-nesting bees in arable fields is not associated with tillage system per se, but with distance to field edge, crop cover, soil and landscape context

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Funding information
Schweizerischer Nationalfonds zur Förderung der Wissenschaftlichen Forschung, Grant/Award Number: 185273

Handling Editor: Erik Öckinger

Abstract

1. Ground-nesting wild bees are crucial for the pollination of wild plants and crops and thus human wellbeing. Arable land currently covers 14 million km^2 globally, but little is known about the role of arable fields as potential nesting habitats and how agricultural management, such as tillage system, affects nesting.
2. We quantified nest density and nesting incidence (plot-level nest presence/absence) of ground-nesting bees in 12 conventionally tilled and 13 no-till winter cereal fields in southwestern Switzerland. In each field, nests were quantified in eight belt transects at increasing distances from field edges within an area of 400 m^2, and vegetation cover and soil properties were measured at nest sites and sites without nests.
3. Nest density ranged from 0 (32% of fields) to 16 nests (mean: 4.0 nests) per 400 m^2, corresponding to 0 to 400 nests ha^{-1} (mean: 101 nests ha^{-1}). Fifteen nesting species were captured.
4. Nest density was not significantly different between tillage systems. Nest density declined exponentially with distance from the field edge. Nest density and incidence were positively related to proportion of bare ground. Nests occurred across a wide range of soil textures and tended to increase with soil bulk density and sand content. Moreover, nest density tended to increase with the proportion of and proximity to areas under agri-environment scheme in the surrounding landscape.
5. *Synthesis and applications*. Our study shows that arable fields, irrespective of tillage system, are used as nesting sites by various ground-nesting bee species, including important crop pollinators. The concentration of nests along field edges suggests that incentives to maintain small field sizes and to increase edge density have a great potential to support nesting of ground-nesting bees in agricultural landscapes. Moreover, measures to reduce crop cover, for example, through increased row spacing, offer a promising way to promote nesting opportunities in arable fields, in particular, if floral-rich agri-environment scheme

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areas are locally available. Further studies are needed to better understand to what extent tilled arable fields are suitable nesting habitats for ground-nesting bees or whether they act as ecological traps due to the adverse effects of tillage on bee offspring.

KEYWORDS
agri-environment schemes, biodiversity, habitat requirements, nesting ecology, pollinator conservation, soil disturbance, soil-nesting bees, tillage

1 | INTRODUCTION

Animal pollination plays a crucial role in the functioning of both natural and managed ecosystems. Globally, nearly 90% of wild flowering plant species and approximately 75% of the worldwide most important crops depend on or profit from the transfer of pollen by animals for pollination (Klein et al., 2007; Ollerton et al., 2011). In most ecosystems, bees are usually by far the most important pollinators (Garibaldi et al., 2013; IPBES, 2016; Michener, 2007), but the contribution of wild bees to crop pollination has long been underestimated (Garibaldi et al., 2013). However, a recent global synthesis estimated their worldwide economic contribution to crop pollination at about half that of managed bees (Kleijn et al., 2015).

Wild bee species nesting below-ground in the soil, that is, ground-nesting bees, dominate the wild bee fauna of most regions of the world (e.g. Cane, 1997; Michener, 2007) and are considered key pollinators not only for wild plants but also for crops (Kleijn et al., 2015). Hence, ground-nesting bees represent a functionally particularly important guild of pollinators (Kleijn et al., 2015). However, many ground-nesting bees are of particular conservation concern, with high percentages of them listed on Red Lists as threatened or endangered (e.g. Müller & Praz, in press; Nieto et al., 2014).

Because bees are central-place foragers, the availability and location of suitable nesting habitats and floral food resources within the agricultural landscape are key determinants of the distribution and density of ground-nesting bees and associated pollination services (Lonsdorf et al., 2009; Sardiñas et al., 2016). Despite the important role of nesting habitat as a driver of bee community structure and dynamics (e.g. Potts et al., 2005; Roulston & Goodell, 2011), surprisingly little is known about the nesting habitat requirements of most ground-nesting bee species in agroecosystems (e.g. Antoine & Forrest, 2021), and in particular about the role of arable cropland as potential nesting habitat (e.g. Brosi et al., 2008; Sardiñas et al., 2016). Furthermore, knowledge about the impacts of agricultural practices on nesting and reproductive success is largely lacking (Ullmann et al., 2020). Thus, to better protect and promote pollination services provided by ground-nesting bees in agroecosystems, it is important to improve our understanding of the role of different agricultural management practices driving nesting of ground-nesting bees.

Soil management may have particularly profound impacts on ground-nesting bees in arable crop-dominated agroecosystems. These impacts may occur both directly through soil disturbance, such as tillage (Ullmann et al., 2016), and indirectly through changes in soil properties (e.g. bulk density) and vegetation cover (e.g. litter cover) (Soane et al., 2012), which are considered important drivers of nesting (Antoine & Forrest, 2021). Soil management systems with minimal soil disturbance, such as no-till systems, may therefore offer tremendous potential to promote nesting opportunites for ground-nesting bees, thereby fostering their populations and pollination services in agroecosystems. Moreover, it is important to quantify the spatial distribution of nesting within fields (Sardiñas et al., 2016), as this has important applied implications for landscape management (e.g. with respect to size and configuration of fields, and thus edge density), to promote ground-nesting bee pollinators and their pollination services and to adequately assess the nesting potential of an arable field in pollination service models (Lonsdorf et al., 2009). Finally, as arable crops, such as cereals, generally do not provide adequate floral resources for nesting bees, potentially beneficial effects of no-till systems on nesting may be reinforced when combined with measures that promote adequate floral food resources within foraging distances of bees in the surrounding landscape, for example, through the establishment of floral-rich agri-environment scheme areas such as flower strips, hedgerows or extensified grasslands (Albrecht et al., 2007, 2020; Ganser et al., 2021). Thus, integratively studying the impacts of tillage system in combination with these within-field and landscape-level drivers should not only improve our mechanistic understanding of the direct and indirect pathways by which tillage system affects nesting of ground-nesting bees in different local and landscape contexts, but also has potentially strong applied implications for bee pollinator conservation, pollination services management and agri-environmental policy (Ullmann et al., 2020). However, surprisingly few studies have investigated the effects of arable soil management practices on ground-nesting bees, and reported results are not unanimous (Ullmann et al., 2020). Furthermore, most studies have (i) focused on a single species (e.g. the squash bee, *Peponapis pruinosa*; Skidmore et al., 2019; Ullmann et al., 2016), (ii) assessed impacts of soil management on ground-nesting bee abundance only indirectly (e.g. by measuring their local flower visitation rates, Appenfeller et al., 2020; Shuler et al., 2005) or (iii) represented descriptive single-site case studies (Mathewson, 1968; Wuellner, 1999). We lack replicated field studies that directly examined the impacts of tillage system along with associated local crop and soil properties on nesting of ground-nesting bees in arable crops. Such studies would be particularly valuable if linked to landscape-scale measures to increase floral resource availability.

Here, we studied the potential of arable cropland as nesting habitat for ground-nesting bees in 25 arable crop fields in southwestern

Switzerland, focusing on winter cereals as a model crop system, by directly quantifying nests constructed by bees and capturing nesting females. We assessed how tillage system (i.e. no-till and conventional tillage), and potentially important drivers of nesting linked to the tillage system (i.e. soil properties and vegetation cover), are related to nesting of ground-nesting bees. To determine whether the entire field was used as nesting habitat or mainly the edge areas and whether this depended on tillage system, we quantified nest densities at various within-field distances. Lastly, we investigated whether the proportion of and proximity to floral-rich agri-environment scheme areas in the surrounding agricultural landscape are positively related to nest density in arable fields.

2 | MATERIALS AND METHODS

2.1 | Study design and region

The study was conducted in spring 2020 in agricultural landscapes of the southwestern part of the Swiss lowland in a region characterized by a small-scale agricultural landscape mosaic dominated by arable crops, interspersed with intensively managed grasslands, vineyards and semi-natural habitats, which are (with the exception of forest fragments) typically biodiversity promotion areas (BPAs; see Section 2.5). We studied 26 winter cereal fields, with 13 fields cultivated following conventional tillage (i.e. moldboard ploughing to approx. 20 cm depth) and 13 fields following no-till practices. Winter wheat as a model crop was selected because of its local and global importance as an arable crop, and because there were several months between sowing (autumn 2019) and sampling campaign (spring 2020), reducing effects of small variations in sowing dates. However, one conventionally tilled field was excluded from analyses because it was sown much later than the other fields (January compared with October/November) and was almost completely bare at the beginning of the sampling campaign. Therefore, we report data from 25 fields throughout this study.

Fields were on average similar between tillage systems with respect to size, slope, exposure and surrounding landscape composition but had individual differences in landscape context (Table S1). All fields were at least 900 m apart from each other. All fields were cultivated with winter wheat (*Triticum aestivum* L.) except for two fields (one no-till and one tilled), which were cultivated with winter barley (*Hordeum vulgare* L.). These two fields were included because of difficulties in finding suitable winter wheat fields in the region. Fields were managed according to Swiss ‘extenso’ guidelines, that is, applications of fertilizer and herbicides are allowed, but use of insecticides, growth regulators and chemical-synthetic stimulators of natural defences are prohibited (FOAG, 2020). All no-till fields have been managed with continuous no-till practices during the entire crop rotation for at least 5 years before our study. To minimize soil disturbance in no-till fields, only fields with neither a root nor a tuber crop as preceding crop were selected, whereas two tilled fields with a root or tuber crop as a previous crop were included.

2.2 | Quantifying nest density and sampling of nesting bees

Nest density of ground-nesting bees was assessed by visually locating and quantifying nests of tumuli-building ground-nesting bees following the methodology proposed by Ullmann et al. (2020) (see also Cane, 2003; Michener et al., 1958; Pereira et al., 2021; Potts & Willmer, 1997; Venturini et al., 2017; Wuellner, 1999). Bee nests with tumuli (i.e. excavated soil material; see Figure S1) were quantified within a total sampling area of 400 m^2, divided into eight belt transects of 50 m length and 1 m width that were running in parallel to one of the field edges at 0, 1, 2, 5, 10, 15, 20 and 30 m into the field (Figure S2). Two sampling rounds (21 March–9 April and 22 April–20 May), during which each field was searched once, were conducted within the main nesting period of most ground-nesting bee species in the study region (SwissBeeTeam, 2021). See Supporting Information for a more detailed description of the applied method and a discussion of advantages and limitations of different methods.

Nesting bees were sampled for identification using mini emergence traps installed over all nests found during nest sampling rounds (see Figure S3 for trap design). Traps were installed in the morning (between 7 and 9 a.m., when air temperature was typically <10°C) following nest counts, when bees were likely still in their nests, and traps were left in the field for at least 1 day with weather conditions suitable for foraging activity. Bees were collected from traps and stored in 70% ethanol until they were pinned and identified to species level. No fieldwork permit or ethical approval for wild bee sampling was required. See Supporting Information for details.

2.3 | Assessing vegetation characteristics

Vegetation characteristics were assessed at two spatial scales in each sampling campaign: within 1 m^2 plots and in 10 cm^2 subplots within the larger 1 m^2 plots. These scales were chosen to determine whether potential effects, such as a positive influence of the proportion of bare ground, occur only at a scale smaller or (also) larger than typical row spacing, as the latter would indicate that increasing row spacing should promote nesting in arable fields, while this may not be the case if effects are observed only at the smaller scale. Plots were centered on up to 10 nests per field (nest plots) in the belt transects at varying distances from the field edge and at 10 locations without nests (control plots) within the same 50 m × 30 m area containing the belt transects according to a stratified random sampling approach, ensuring that control plots were also selected at varying distances from the field edge. All 1 m^2 control plots from a field were averaged to obtain mean vegetation characteristics per field for the field-level analysis. Within each plot, the proportion of ground covered by crop vegetation, other vegetation (weeds), moss, litter and crop residues (dead plant material) were visually estimated. All estimates were conducted by the same person to avoid potential observer bias. Proportion of bare ground was defined as the remainder to 100%. Due to high co-linearity of estimated vegetation properties, only the proportion of bare ground was included in statistical analysis.

2.4 | Soil sampling and analysis

Five soil samples per field were taken at randomly selected locations within the belt transects where no nest was found and the nearest nest was at least 5 m away (control samples), and up to five samples per field were taken directly at the nest entrance (nest samples) from nests found during nest sampling rounds. Undisturbed cylindrical soil cores (100 ml, 50 mm diameter, 51 mm height) were taken from the surface layer (approx. 1–6 cm depth) after the last nest sampling campaign between 8–12 June for determination of soil bulk density, texture, organic matter content and pH. To compare soil compactness across different soil textures, the relative soil bulk density was estimated (see Supporting Information for details). Due to high co-linearity of some soil properties, only sand content, relative soil bulk density, and pH were included in statistical analyses. All control samples from a field were averaged to obtain mean soil properties per field for the field-level analysis.

2.5 | Quantifying landscape context

The proportion of the different land-use categories in the landscapes surrounding the study fields was quantified within a 500 m radius around the center of the bee sampling. This radius was selected because mainly small-bodied ground-nesting bees were caught, which are considered to have maximum foraging distances of a few hundred meters (Gathmann & Tscharntke, 2002; Greenleaf et al., 2007) and even shorter average foraging distances (e.g. Westrich, 2018; Zurbuchen et al., 2010). Based on detailed land-use maps available as GIS data from the cantons of Geneva (Système d'information du territoire à Genève SITG) and Vaud (Géodonnées Etat de Vaud), complemented by satellite images, land use was classified into five main classes: forest, grassland, cropland (both permanent and arable crops), urban and BPAs (Figures S4 and S5). BPAs are a major component of the Swiss agri-environment schemes policy. In the studied landscapes, BPAs were mainly extensively used meadows and pastures, vineyards with high natural biodiversity and hedgerows. In addition to the proportion of BPA, the distance to the nearest BPA was also computed. All spatial data analysis was done in R version 4.2.0 (R Core Team, 2022) using the package SF (Pebesma, 2018).

2.6 | Statistical analysis

Statistical analyses were performed in R version 4.2.0 (R Core Team, 2022). For regression analyses, collinearity of predictor variables was checked ($|r| < 0.6$) and continuous variables were standardized (mean = 0, SD = 1). For mixed models, confidence bands were computed using a Bayesian framework, with samples drawn from the joint posterior distribution using the function *arm::sim* (Gelman & Su, 2020).

To analyse the overall effect of the tillage system on nesting incidence (binary response variable: presence/absence of nests within 400 m^2 sampling area) and nest density (count data: number of detected nests within 400 m^2 sampling area), generalized linear models (GLMs) were fitted with binomial (nesting incidence) and negative binomial (nest density) error distributions using the functions *glm* and *MASS::glm.nb* (Venables & Ripley, 2010), respectively. Nesting data from both sampling rounds were pooled, because neither the interaction between sampling round and tillage system nor the sampling round significantly improved model fit (Table S2).

To examine the effects of distance from the field edge on nesting, nest density (pooled per transect and field across sampling rounds) was analysed using a generalized linear mixed model (GLMM) with negative binomial error distribution, fitted using the function *lme4::glmm.nb* (Bates et al., 2015). Tests were performed for both linear and exponential decline relationships, respectively, using distance and $\log_{10}$ (distance) as explanatory variables, and field was included as a random effect. Furthermore, whether the relationship differed between tillage systems was tested by including an interaction of tillage system and distance from field edge.

To examine the effects of soil properties and vegetation cover on nesting at the plot level, nesting incidence (binary response: presence/absence of nests within the plot) was analysed using GLMMs with binomial error distribution. Since soil properties and vegetation cover were assessed at different locations, separate GLMMs were fitted for the soil and vegetation data. A full soil model with sand content, relative soil bulk density and pH as explanatory variables was fitted, and a set of best models (ΔAICc <2) was selected using the function *MuMIn::dredge* (Bartoń, 2022). Inference was then drawn from model-averaged parameter estimates based on their weighted support from the set of best models. For the vegetation model, the proportion of bare ground was used as the only explanatory variable, and a separate model was fitted for each spatial scale (1 m^2 plot and 10 cm^2 subplot). Field was included as a random effect in all models.

To examine the effects of landscape composition on nest density at the field level, nest density (pooled across sampling rounds) was analysed by fitting a GLM with negative binomial error distribution using the function *MASS::glm.nb* (Venables & Ripley, 2010). A full model was fitted with the landscape variables %Grassland, %Crop, %BPA, and distance to the nearest BPA, and sand content, relative soil bulk density and the proportion of bare ground were included as covariates because the plot-level analysis (see above) showed that they were associated with nesting incidence. Inference was then drawn from model-averaged parameter estimates based on their weighted support from the set of best models (ΔAICc <1.5) identified using *MuMIn::dredge* (Bartoń, 2022).

3 | RESULTS

3.1 | Nest density and species diversity in winter cereal fields

Nests were found within the 400 m^2 sampling area in 17 of the 25 analysed fields (Figure 1). Nest density, summed over both sampling rounds, was on average 4.0 (SD 4.8) nests per 400 m^2 sampling area and ranged from 0 to 16 nests per 400 m^2, corresponding to 101 (SD 119) nests ha^{-1} and a range of 0 to 400 nests ha^{-1}.

The nesting female bee could be captured from 28 of the total 101 nests found within 400 m^2 sampling areas across all fields, corresponding to a capture success rate of 29%. These individuals belonged to 12 species (15 when including captures from incidentally found nests outside the 400 m^2 sampling areas) from three families (Andrenidae, Halictidae, Colletidae) (Table 1). None of the species are listed as threatened in the IUCN Red List for Europe (Nieto et al., 2014) or Switzerland (Müller & Praz, in press). Nests were found in soils classified as sandy loam, sandy clay loam, loam and clay loam (Figure S6).

3.2 | Effects of tillage system on nesting

The mean number of nests per 400 m^2 sampling area of each field, summed over both sampling rounds, was 5.2 (95% CI 2.5–10.9) in conventionally tilled and 3.0 (1.4–6.3) in no-till fields, corresponding to 129 and 75 nests ha^{-1}, respectively (Figure 1). Tillage system was not significantly associated with nesting incidence, that is, the presence or absence of nests in the 400 m^2 sampling area of a field (df = 1, $\chi^2 = 0.52$, $p = 0.469$) or nest density (df = 1, $\chi^2 = 1.03$, $p = 0.310$).

3.3 | Effects of distance from field edge on nest density

Nests were strongly concentrated within the first two meters from the field edge, declined sharply within the first approximately five meters from the field edge and then levelled off (Figure 2, Table 2). Hence, decline of nest density with increasing distance from the field edge was better described by an exponential than a linear relationship, and the exponential decay function did not significantly differ between tillage systems (Table S3).

3.4 | Effects of vegetation cover, soil properties and landscape context on nesting

Proportion of bare ground was strongly positively related to nesting incidence at the plot level, with stronger effects at the 10 cm^2 compared with the 1 m^2 plot scale (Figure 3a, Table 2). Nesting incidence at the plot level increased with relative soil bulk density and tended to increase with sand content but was not affected by soil pH (Figure 3b–d, Table 2).

The set of best models predicting nest density at the field level included the variables mean proportion of bare ground, mean relative soil bulk density, mean sand content, %BPA within 500 m and distance to nearest BPA. Nest density at the field level increased with mean proportion of bare ground and tended to increase with mean relative soil bulk density, mean sand content, %BPA within 500 m, and proximity to nearest BPA (Figure 4, Table 2).

4 | DISCUSSION

4.1 | Arable fields are neglected nesting sites

Arable fields have received surprisingly little attention as potential nesting sites for ground-nesting bees, despite being the predominant component of many agricultural landscapes and the availability

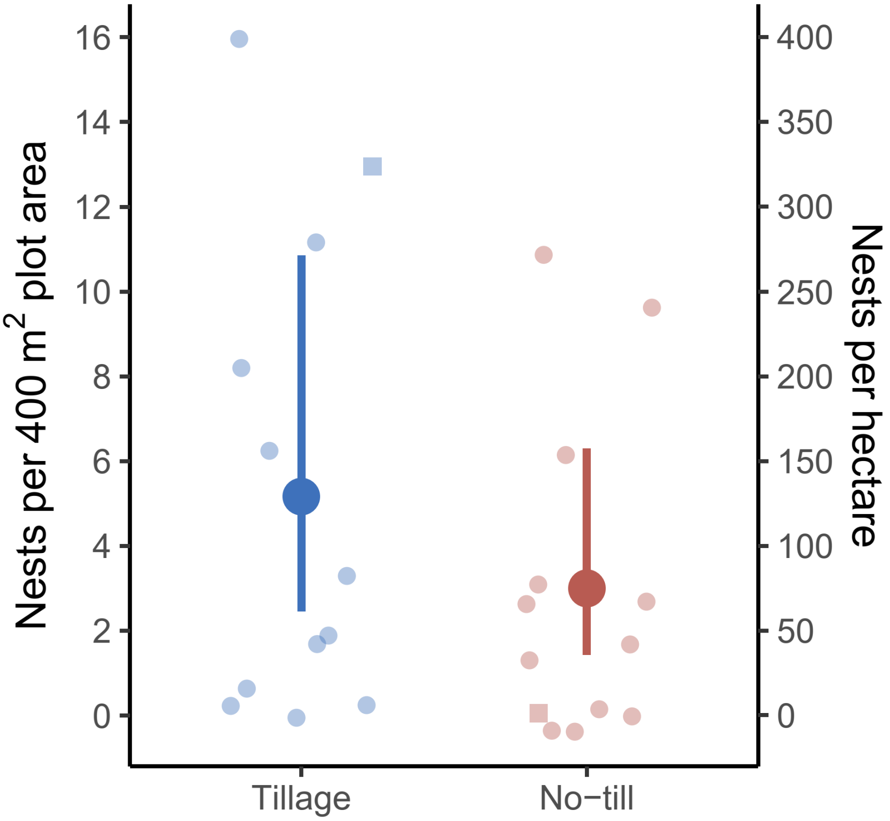

FIGURE 1 Number of nests per 400 m^2 plot area (left axis) or per hectare (right axis) with 95% confidence intervals, summed over both sampling rounds, for conventionally tilled and no-till fields. Symbols show raw data for tilled (blue, $n = 12$) and no-till (red, $n = 13$) winter wheat (circles, $n = 23$) and winter barley (squares, $n = 2$) fields.

TABLE 1 Number of individuals and species of ground-nesting bees caught nesting within conventionally tilled and no-till winter cereal fields. Numbers in round brackets include captures from incidentally found nests within fields but outside the 400 m^2 study plots, and numbers in square brackets include captures from one field that was excluded from analysis (see Section 2). Only captures from within the 400 m^2 study plots were used for analysis. For five conventionally tilled fields, the plough furrow between the field and the adjacent grassland strip was searched for nests.

	Status		400 m^2 study plot		
Species	EU[a]	CH[b]	Tillage	No-till	Plough furrow[d]
Andrena carantonica	DD	LC	1	0	0
Andrena dorsata	DD	LC	1	0	0
Andrena flavipes	LC	LC	3	0	1
Andrena lagopus[c]	LC	LC	0	0 (2)	0
Andrena minutula	DD	LC	1	0	0
Andrena tibialis	LC	LC	1	0	0
Andrena ventralis[c]	DD	LC	0	0 (1)	0
Colletes cunicularius	LC	LC	1	1	0
Lasioglossum calceatum	LC	LC	2	1	2
Lasioglossum leucozonium	LC	LC	0	1	0
Lasioglossum lineare	DD	NT	1	0	0
Lasioglossum malachurum	LC	LC	5 (7) [9]	0	0
Lasioglossum pauxillum	LC	LC	0 [13]	3	0
Lasioglossum subhirtum	LC	DD	4	2	2
Lasioglossum villosulum[c]	LC	LC	0	0	1

Abbreviations: DD, data deficient; LC, least concern; NT, near threatened.

[a] European Red List status (Nieto et al., 2014).

[b] Swiss Red List status (Müller & Praz, in press).

[c] Species captured exclusively outside the 400 m^2 sampling areas.

[d] Captures from unsystematic searches in plough furrows of five conventionally tilled fields.

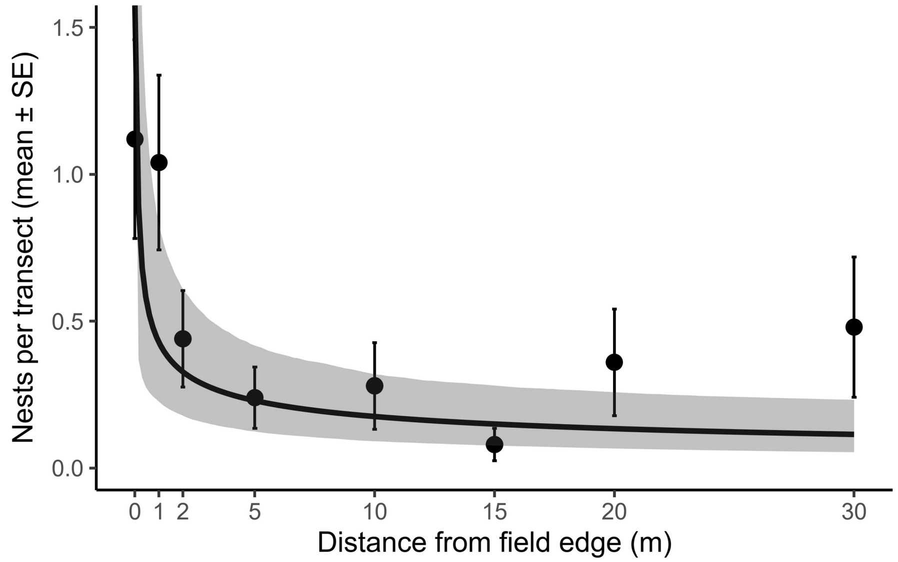

FIGURE 2 Mean ± 1 standard error (SE) number of nests per belt transect (50 m × 1 m; parallel to field edge) as a function of distance from field edge. The line and grey area show the predicted exponential decline relationship between nest density per transect and the decimal logarithm of distance from the field edge with 95% credible interval.

of nesting sites being critical to the distribution and density of wild bees and associated pollination services (Lonsdorf et al., 2009). The findings of this field study show that both conventionally tilled and no-till winter cereal fields are used as nesting sites by various ground-nesting bee species, reaching nest densities as high as 400 nests ha^{-1}. These observed nest densities in cereal fields should prompt a reexamination of the assumption of current models for predicting wild bee distribution and pollination services in agroecosystems, which are largely based on expert opinion on nesting site suitability rather than empirical evidence, according to which tilled arable fields are typically neglected as nesting sites for ground-nesting bees (e.g. Brosi et al., 2008; Lonsdorf et al., 2009). In addition, comparable nest density data from other habitats are needed to assess the relevance of the densities observed in this study. However, we found 15 species of ground-nesting bees belonging to three families (Halictidae, Andrenidae, Colletidae), including food plant generalist (e.g. *Andrena flavipes*) and food plant specialist species (e.g. the Brassicaceae specialist *Andrena lagopus*), and common species considered dominant crop-pollinating wild bees in Europe, such as *Andrena flavipes* or *Andrena carantonica* (Kleijn et al., 2015). Given the fact that we focused on tumuli-building species during only two sampling rounds and that we could only identify nesting species of

TABLE 2 Summary results from generalized linear and generalized linear mixed models testing the effects of soil, vegetation and landscape variables on nesting incidence and nest density at different spatial scales. Standardized effect sizes with 95% confidence intervals (CI) and p-values ($p < 0.05$ in bold, $0.05 \le p \le 0.10$ in bold italic) are shown. For models with more than two candidate variables, model averaged standardized regression coefficients and the variable's relative importance (RI) are reported.

Response variable	Scale	Explanatory variable	Est	95% CI	*p*-value	RI
Effects of distance from field edge						
Nest density	transect	Log$_{10}$(distance)	−0.52	[−0.78, −0.26]	**<0.001**	–
Effects of soil properties at the plot level						
Nesting incidence	10 cm^2	Relative soil bulk density	0.53	[0.11, 0.95]	**0.014**	1.00
		Sand (%)	0.34	[−0.02, 0.71]	***0.067***	0.70
		pH	0.12	[−0.24, 0.48]	0.511	0.21
Effects of vegetation at the plot level						
Nesting incidence	10 cm^2	Bare ground (%)	1.78	[1.37, 2.24]	**<0.001**	–
	1 m^2	Bare ground (%)	1.23	[0.86, 1.65]	**<0.001**	–
Drivers at the field level						
Nest density	field	Bare ground (%)	0.73	[0.23, 1.23]	**0.004**	1.00
		Distance to nearest BPA (m)	−0.50	[−1.04, 0.04]	***0.069***	0.31
		Relative soil bulk density	0.45	[−0.04, 0.93]	***0.071***	0.51
		Sand (%)	0.38	[−0.07, 0.83]	***0.097***	0.21
		%BPA in 500 m radius	0.38	[−0.06, 0.82]	***0.092***	0.20

Abbreviation: BPA, biodiversity promotion area.

roughly one third of the nests found in the fields (see also Figure S7), it is likely that more species nest in cereal fields in the study region.

Nest density declined exponentially with increasing distance from the field edge. The slightly higher average nest densities at distances between 20 and 30 m from the field edge (Figure 2) were mainly due to tramlines used for vehicular field traffic, creating patches of bare soil: 11%–42% of nests between 20 m and 30 m distance from the field edge were located on tramlines. A noteworthy observation was the relatively high nest density in the plough furrow of one field (30 nests per 72 m plough furrow length). To our knowledge, few other studies have quantified nests in arable fields. Generalist and specialist bee species have also been found to nest within conventionally tilled sunflower fields, with a similar exponential decline of nest density from field edges (Kim et al., 2006; Sardiñas et al., 2016). Some species of ground-nesting bees, such as the specialist squash bee *Peponapis pruinosa*, have even been reported to nest at higher densities in squash fields (*Cucurbita* spp.) compared with adjacent field margins (Julier & Roulston, 2009).

4.2 | Effects of tillage systems on nesting

While some ground-nesting bee species change their nesting sites every year (e.g. Rozen & Buchmann, 1990), others remain loyal to their nesting site for years or even decades (e.g. Cane, 2008; Potts & Willmer, 1997) and may grow to enormous local population sizes (Cane, 2008). Since tillage was observed to reduce the number of emerged *P. pruinosa* offspring (Ullmann et al., 2016) and no-till minimizes soil disturbance (Soane et al., 2012) during the phase when most ground-nesting bees remain in a vulnerable state below-ground (Ullmann et al., 2020), we hypothesized that no-till would allow populations of ground-nesting bees to persist and accumulate over time, resulting in higher nest densities in no-till compared with tilled fields. However, contrary to our expectations, we did not find a significant difference in nest density between tillage systems. To our knowledge, no other field study has so far directly quantified nest densities of ground-nesting bees in tilled compared with no-till fields. Results from studies on flower visitation rates by the ground-nesting bee species *P. pruinosa* in North American squash and pumpkin (*Cucurbita* spp.) fields are mixed: Julier and Roulston (2009) found no difference in flower visitation rates between tilled and no-till fields, but two other studies reported approximately three times higher flower visitation rates in no-till compared with tilled fields (Appenfeller et al., 2020; Shuler et al., 2005).

Arable fields managed under different tillage systems may be associated with distinctly different community assemblages of nesting bees due to tillage system-specific effects on soil properties and vegetation characteristics critical for nest site selection (Antoine & Forrest, 2021). While some species prefer to nest in more compacted soils (e.g. Wuellner, 1999), others prefer softer soils (e.g. Potts & Willmer, 1997; Sardiñas & Kremen, 2014). Similarly, some species have been found to prefer bare ground (e.g. Potts et al., 2005; Sardiñas & Kremen, 2014), whereas others also nest in more vegetated areas (e.g. Kim et al., 2006). No-till management generally leads to firmer topsoils and higher vegetation cover, since crop residuals are not incorporated into the soil (Soane et al., 2012). Therefore, which tillage system is more attractive as a nesting site for ground-nesting bees likely depends on the species. Furthermore,

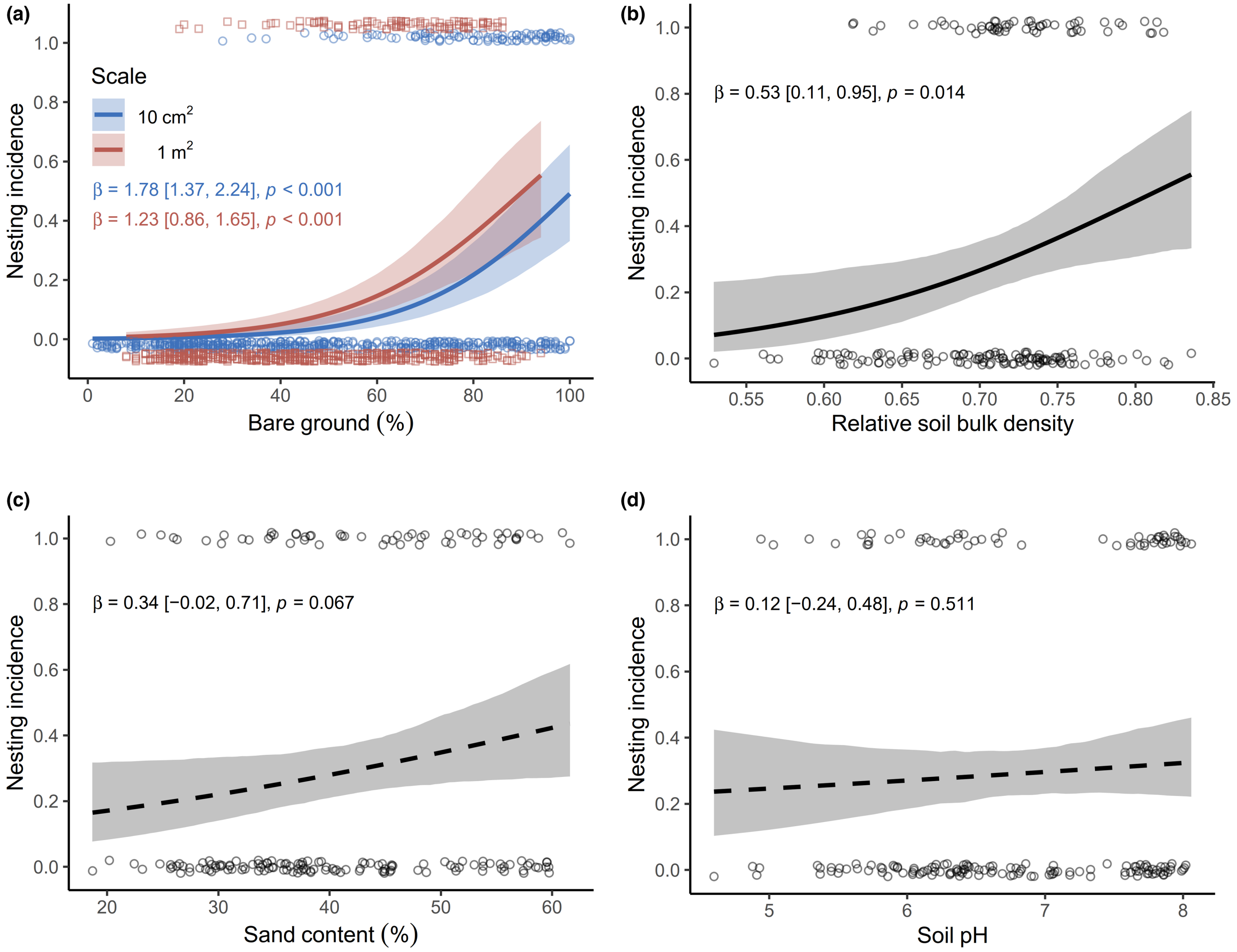

FIGURE 3 Relationships of proportion of bare ground (a) and soil properties (b–d) with nesting incidence at the plot level. Regression lines show significant (solid lines, $p < 0.05$) and non-significant (dashed lines, $p \geq 0.05$) predicted relationships with 95% credible intervals (shaded areas) with covariates fixed at their mean values. Model averaged standardized regression coefficients (β) with 95% confidence intervals and p-values are shown. Circles show the raw data.

only species that are able to withstand mechanical disturbance, for example, because they nest below tillage depths, may be able to establish in tilled fields (Harmon-Threatt, 2020; Ullmann et al., 2016). This has not yet been studied in ground-nesting bees to our knowledge, but research on ground beetles indicates that community composition can differ between tillage systems (Cárcamo, 1995) and that tillage can lead to species assemblages that are more tolerant of mechanical soil disturbance (Kromp, 1999). Since only four of the 15 species were collected in both tilled and no-till fields, our data suggest that similar impacts of tillage on community composition may also occur in ground-nesting bees, but this requires more scrutiny in future studies.

4.3 | Key drivers of nesting

Irrespective of tillage system, vegetation cover was a key variable associated with nesting. Nesting incidence increased substantially with increasing proportion of bare soil, at spatial scales both smaller and larger than typical row spacing. In addition, nesting incidence increased with increasing relative soil bulk density and tended to increase with sand content, but nests occurred across a wide range of textural classes. Increased numbers of nests of ground-nesting bees has often been linked to bare ground, but it has been debated whether this relationship reflects a genuine nesting preference of bees, is a product of observation bias towards bare areas or reflects the difficulty of finding nests in vegetation (Antoine & Forrest, 2021; Harmon-Threatt, 2020). By comparing the proportion of bare ground at the nest with randomly selected locations without nests within fields, our results demonstrate that at least some species of ground-nesting bees prefer patches with sparse or no vegetation cover to establish their nests over more densely vegetated patches (see also Supporting Analysis 2.2).

Soil properties are generally considered key factors influencing nest-site selection by ground-nesting bees (Antoine & Forrest, 2021; Harmon-Threatt, 2020), but some studies have found no effects of

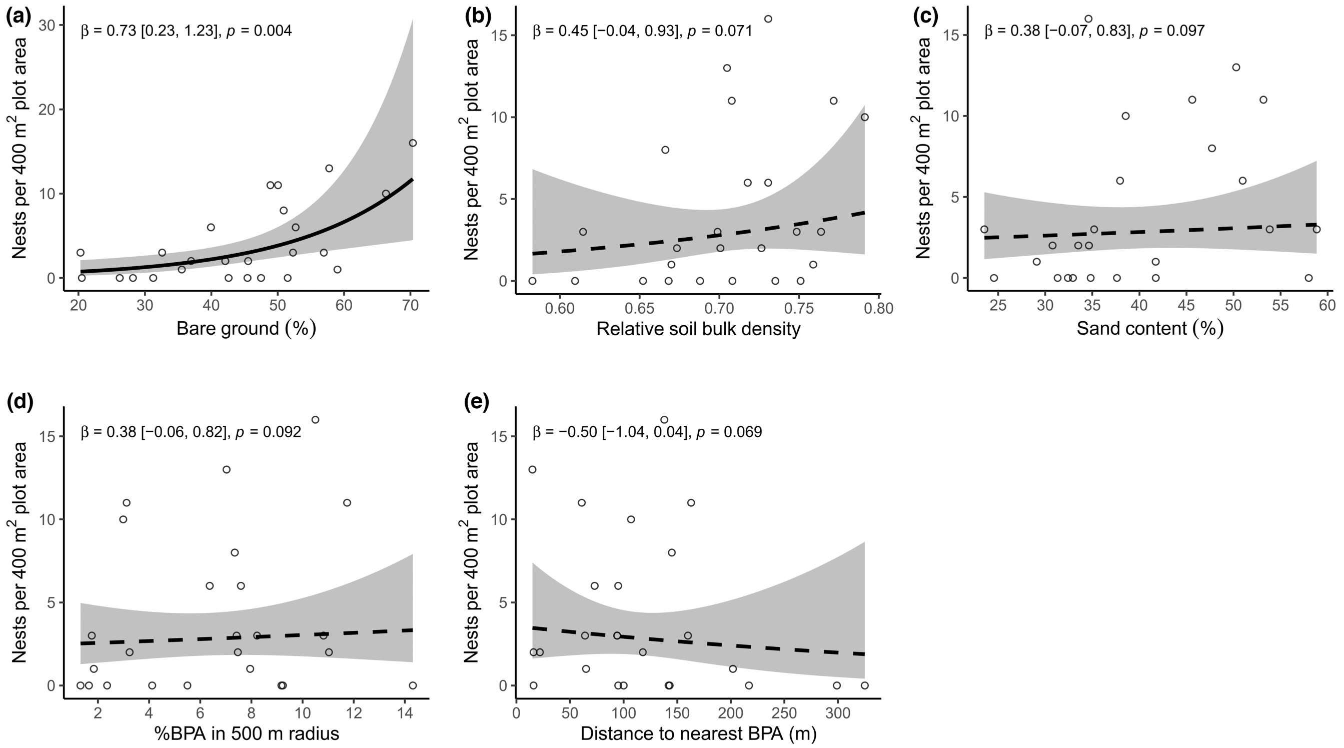

FIGURE 4 Relationships of proportion of bare ground (a), soil properties (b, c) and biodiversity promotion area (BPA; d, e) with the number of nests per 400 m^2 plot area. Regression lines show significant (solid lines, $p < 0.05$) and non-significant (dashed lines, $p \geq 0.05$) predicted relationships with 95% confidence intervals (shaded areas) conditional on all covariates. Model averaged standardized regression coefficients (β) with 95% confidence intervals and p-values are shown. Circles show the raw data.

soil properties on nesting (Fortel et al., 2016). Although soil preferences differ between species, nesting has often been associated with soils classified as sands or loams for most species (Cane, 1991; Harmon-Threatt, 2020). While there was some evidence in our study that sand content was positively related to nesting, nests of identified species occurred across a wide range of textural classes within soils classified as loams (sandy loam, sandy clay loam, clay loam and loam). For example, *Lasioglossum pauxillum* nested in soils with a sand content of 23%–61%, and a clay content of 18%–31%, respectively. The observed positive association of soil density with nesting may rather reflect avoidance of soft soils than preference for compacted soils, as indicated by the complete absence of nests in soft soils, which may provide poor structural (mechanical) stability for nests. However, similar to texture, soil hardness preference can differ across taxonomic groups of ground-nesting bees (Antoine & Forrest, 2021).

At the field level, nest density tended to increase with the proportion of and proximity to BPAs, after accounting for local field-level drivers (i.e. proportion of bare ground, sand content and relative soil bulk density). As central-place foragers, bees require adequate floral food resources within their foraging range (Westrich, 1996), which is on average typically a few hundred meters for the mostly small to medium-sized bee taxa we captured (Greenleaf et al., 2007; Zurbuchen et al., 2010). In fact, the most commonly implemented BPA types under the Swiss agri-environment scheme, such as extensively managed meadows (Albrecht et al., 2007), flower strips (Albrecht et al., 2020; Ganser et al., 2021) or hedgerows (Kremen et al., 2019), have been shown to promote wild bee pollinators through enhanced availability and diversity of floral resources. Indeed, we found no nests in fields where the distance to the closest BPA was more than about 200 m from the center of our sampling area.

4.4 | Conclusions and implications for management and conservation

Here we show that arable fields, irrespective of tillage system, are used as nesting sites by both specialist and generalist ground-nesting bee species—including important crop pollinators. Considering the tremendous area and typically dominant role of arable land in agro-ecosystems, our results highlight that the role of arable croplands as nesting habitat deserves more attention in pollinator conservation planning and management, as well as in future research to better inform such management.

The finding that nest densities were on average even slightly higher in tilled compared with no-till fields has important implications for the key open question of whether and to what extent ground-nesting bee offspring can survive tillage, or to what extent tilled fields act as ecological traps. This result underpins the need to gain more insights to quantify and identify key factors affecting the survival probability of ground-nesting bees in arable fields.

Our observation that most of the species were collected only in either no-till or tilled fields provides some evidence that no-till and tilled fields may be used by relatively distinct and thus complementary assemblages of ground-nesting bee species. Further insights into how different tillage systems affect community composition could be gained by monitoring community composition dynamics over multiple years to identify key species-specific traits associated with the ability to persist in no-till and especially tilled fields.

The strong concentration of nests along field edges underscores the crucial role of field edges for nesting of ground-nesting bees and implies that incentives to increase landscape configurational heterogeneity and edge density (i.e. as a result of maintaining small fields or reducing field sizes) have a great potential to promote nest density in agricultural landscapes. Future studies could further examine the role of arable field edges as nesting sites for ground-nesting bees and the potentially important role of high edge density on the population dynamics of ground-nesting bees and its consequences for pollination services in agroecosystems. They could gain additional insights into the processes driving increased nesting along field edges, such as field edge features and spillover effects from adjacent habitats, and how management interventions may enhance their quality as nesting habitat. Furthermore, our findings suggest that measures that involve reducing crop cover, such as reducing crop density by increasing row spacing or creating patches of bare soil, may be promising management options to promote nesting opportunities for ground-nesting bees in arable fields. However, such measures should take into account potential trade-offs, for example, reduced floral resource availability or lower yields (but see Abichou et al., 2019). As ground-nesting bees were found across a wide range of soil textural classes and soil density, many soils may offer suitable nesting sites. Finally, our study highlights the important role of proximity and local availability of areas providing adequate quantity and diversity of floral resources, such as suitable agri-environmental scheme areas, to protect and promote ground-nesting bees and their pollination services in agricultural landscapes.

AUTHOR CONTRIBUTIONS

Philippe Tschanz, Matthias Albrecht and Thomas Keller designed the study with contributions from Achim Walter; Philippe Tschanz and Stefan Vogel collected the data; Philippe Tschanz analysed the data with contributions from Thomas Keller and Matthias Albrecht; Philippe Tschanz wrote a first draft of the manuscript with substantial contributions from Matthias Albrecht, Thomas Keller and Achim Walter. Thomas Keller and Matthias Albrecht acquired funding. All authors gave final approval for publication.

ACKNOWLEDGEMENTS

We thank Stephan Bosshart, Lucca Andreoli, Valerio Volpe, Jonas Winizki and Beatrice Schüpbach (Agroscope, Zurich, Switzerland) for their support in the preparation of field work equipment; Marlies Sommer, Diane Bürge, Johanna Keita and Inge Stockinger (Agroscope, Zurich, Switzerland) for support and soil laboratory analyses; Mike Herrmann (Büro für angewandte Tierökologie & Botanik, Konstanz, Germany) for bee identification; Ariane Stöckli (University of Bern, Switzerland) for fruitful discussions on the study design; Romina Rader, Erik Öckinger, and two anonymous reviewers for their valuable comments on an earlier version of the manuscript; and finally, all involved farmers for their interest to participate in this study and their permission to work on their fields. This study was funded by the Swiss National Science Foundation (SNSF, grant number 185273).

CONFLICT OF INTEREST

The authors declare that they have no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code are available on GitHub (https://github.com/ptschanz/Tschanz_et_al_2022_JApplEcol) and archived on Zenodo under: https://doi.org/10.5281/zenodo.7034869 (Tschanz et al., 2022).

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How to cite this article: Tschanz, P., Vogel, S., Walter, A., Keller, T., & Albrecht, M. (2023). Nesting of ground-nesting bees in arable fields is not associated with tillage system per se, but with distance to field edge, crop cover, soil and landscape context. *Journal of Applied Ecology*, *60*, 158–169. https://doi.org/10.1111/1365-2664.14317