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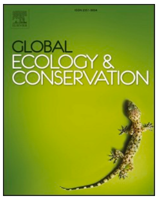

Ground-nesting bees prefer bare ground areas on calcareous grasslands

Hanna Gardein [a,b,*], Yvonne Fabian [c,d], Catrin Westphal [a], Teja Tscharntke [c], Annika Hass [a]

[a] *Functional Agrobiodiversity, Department of Crop Sciences, University of Göttingen, Grisebachstraße 6, Göttingen, Germany*
[b] *Julius Kühn-Institute, Institute for Bee Protection, Messeweg 11/12, Braunschweig, Germany*
[c] *Agroecology, Department of Crop Sciences, University of Göttingen, Grisebachstraße 6, Göttingen, Germany*
[d] *Agricultural Landscapes and Biodiversity, Agroscope, Reckenholzstrasse 191, 8046 Zurich, Switzerland*

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ABSTRACT

Although most of the wild bee species are ground-nesting, little is known about their nesting requirements and the conservation measures to promote ground-nesting bees. Calcareous grasslands are one of the most species-rich habitats in Central Europe and therefore essential for protecting bee diversity. The management practices of calcareous grasslands are so far often focused on plant populations, but in order to support declining insect populations, additional measures have to be considered for nature conservation. As wild bees depend on the availability of nesting sites, we studied the effects of locally increased bare ground availability on ground-nesting bees on four large and four small calcareous grasslands in Central Germany. Vegetation cover of 24 experimental plots (1 m^2) was removed. The number of bee nests as well as the presence of bees on these plots (here: nesting activity) were compared to 24 control plots during six sampling runs. Results showed that the number of bee nests on experimental plots was fourteen times higher compared to control plots, positively related to the surrounding flower cover and higher on steeper slopes, independent of grassland area. Moreover, the observed nesting activity on experimental plots was 2.5 times higher compared to the control and positively related to the currently prevailing soil surface temperature. Bee abundance quantified during transect walks increased on grasslands with a generally higher bare ground availability and a higher flower cover. In conclusion, our study emphasizes the need to consider the availability of nesting resources to promote the vast majority of wild bees, which are ground-nesting. They benefited from bare ground availability as well as adjacent floral resources, and experimental removal of the vegetation cover appeared to be a major, so far underestimated conservation practice.

1. Introduction

The abundance and species richness of most wild bee families are strongly decreasing globally (Potts et al., 2016; Powney et al., 2019; Zattara and Aizen, 2021). The main drivers are the loss and degradation of habitats, invasive species, pathogens, climate change

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[*] Corresponding author at: Julius Kühn-Institute, Institute for Bee Protection, Messeweg 11/12, Braunschweig, Germany.
E-mail address: hanna.gardein@julius-kuehn.de (H. Gardein).

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and pesticides (Cardoso et al., 2020). The decline of bee species has not only important ecological but also economic consequences: Pollinators like wild bees provide critical pollination services for natural ecosystems (Ollerton et al., 2011; Rodger et al., 2021) and cultivated crops (Kleijn et al., 2015).

The vast majority of all wild bee species nest below ground (Cane and Neff, 2011; Westrich, 2018; Danforth et al., 2019; Harmon-Threatt, 2020). Despite the dominance of this functional trait, ground-nesting bees are less studied than cavity-nesting bees (Winfree, 2010; Orr et al., 2022), which built their nests in wood or use pre-existing cavities e.g., in pithy or hollow stems (Cane et al., 2007). Many ground-nesting bees build their nests in bare ground (Antoine and Forrest, 2020), which develops naturally through dynamic processes such as droughts and erosion (Westrich, 2018), flooding of rivers (Exeler et al., 2009) or fire (Campos et al., 2021). As these processes are anthropogenically suppressed, bees can benefit from disruptive activities like mowing or grazing (Tonietto and Larkin, 2018) or even quarrying (Heneberg et al., 2013). However, excessive disturbance due to agricultural practices such as tillage can destroy nests and reduces the number of offspring (Williams et al., 2010; Ullmann et al., 2016). Hence, ground-nesting bees are threatened by the conversion of natural habitat to arable land (Westrich, 2018).

Local habitat quality is essential for habitat colonization (Franzén and Nilsson, 2010) and species persistence (Pöyry et al., 2009). For bees, the habitat suitability depends mainly upon two characteristics: floral and nesting resources. The importance of floral resource availability on bees has been studied extensively, whereas findings about their nesting requirements are often restricted to cavity-nesting bees (Potts et al., 2005; Antoine and Forrest, 2020). For ground-nesting bees, the availability of bare ground as a nesting resource is one of the most important factors for reproduction (Potts et al., 2005; Sardiñas and Kremen, 2014; Twerd et al., 2021). More knowledge is needed regarding specific soil characteristics ground-nesting bees depend on (Antoine and Forrest, 2020), including soil temperature (Buckles and Harmon-Threatt, 2019) and slope (Sardiñas and Kremen, 2014; Hopfenmüller et al., 2014) among others. Bare ground availability can increase both bee species richness and abundance (Murray et al., 2012) and the proportion of ground-nesting bees within the community (Sardiñas and Kremen, 2014; Quistberg et al., 2016). Removing vegetation to create bare ground may promote ground-nesting bees, because they often prefer sparsely vegetated patches (Potts et al., 2005). Several studies examined conservation practices like vegetation removal or artificially heaped up structures to create nesting sites, mainly for urban surroundings (Wesserling and Tscharntke, 1995; Severns, 2004; Gregory and Wright, 2005; Fortel et al., 2016; Martin et al., 2017; Widenfalk et al., 2018; Nichols et al., 2020). However, management practices for natural habitats to promote ground-nesting bees have rarely been investigated.

In Germany, about half of the 557 wild bee species are endangered (Westrich et al., 2011). An important habitat for wild bees is calcareous grassland (Westrich, 2018), one of the most species-rich habitats in Central Europe (Poschlod and WallisDeVries, 2002; Murray et al., 2012). These dry grasslands provide a high diversity of plants including important pollen resources for generalist and specialist bees (Steffan-Dewenter and Tscharntke, 2002). Further, they are often characterised by south facing slopes and a warm microclimate, which is beneficial for thermophilic bees (Ellenberg and Leuschner, 2010). Due to nutrient-poor conditions, the vegetation is sparse and spots of bare ground provide excellent nesting resources for ground-nesting bees (Westrich, 2018).

Calcareous grasslands are endangered by the cessation of traditional use, mainly sheep grazing (Poschlod and WallisDeVries, 2002). As it is not profitable anymore, many of these grasslands are nowadays unmanaged leading to conversion into scrubland through succession (Bauer and Albrecht, 2020). Moreover, grassland management for biodiversity conservation is usually optimized for promoting (rare) plant species (Wallis DeVries et al., 2002; Tonietto and Larkin, 2018), which allows the use of time-saving and low-cost practices, like mowing and mulching (Kahmen et al., 2002). These cheaper alternatives do not affect the plant species composition (Kahmen et al., 2002), while possible negative effects on other taxa are often not perceived (Wallis DeVries et al., 2002). For example, these management changes can lead to a loss of nesting sites for ground-nesting bees due to increasing litter-cover and therefore a lower availability of bare ground compared to extensive grazing, which can be detrimental for some ground-nesting bee species (Grundel et al., 2010; Kormann et al., 2015; Quistberg et al., 2016). In addition, the deposition of atmospheric nutrients leads to eutrophication resulting in a denser vegetation cover (Bauer and Albrecht, 2020). Creating bare ground in valuable habitat types like calcareous grasslands might therefore be a highly efficient strategy to promote wild bee diversity and abundance (Gregory and Wright, 2005).

In addition to food and nesting resource availability, habitat size can be an important factor for bee occurrence. Within the study area, around 70% of calcareous grassland fragments are smaller than one hectare (Rösch et al., 2015). Many studies found a higher diversity and abundance of bees in larger habitats (e.g., Steffan-Dewenter, 2003; Krauss et al., 2009; Quistberg et al., 2016), which can even spill over across habitat borders leading to a higher floral visitation rate in the surrounding landscape (Klaus et al., 2021). Due to a higher heterogeneity, large habitats are more likely to provide all food and nesting requirements simultaneously (Hopfenmüller et al., 2014).

Therefore, conservation strategies commonly concentrate on the protection of large habitats (Tscharntke et al., 2012). Nevertheless, small fragments might also play a crucial role for conservation (Rösch et al., 2015). They can either provide (partial) habitat for species with broad resource requirements or act as stepping stones for mobile species. Thus, several studies could not find a correlation between habitat size, bee abundance and species richness or found even an inverse relationship, probably because many species are not sensitive to habitat area and benefit from the greater heterogeneity of small habitat patches spread across landscapes and regions (Tscharntke et al., 2002; Franzén and Nilsson, 2010; Murray et al., 2012; Rösch et al., 2015). However, habitat size may be important for the effectiveness of management practices for ground nesting bees.

The aim of this study was to investigate vegetation removal as a potential management option for enhancing ground-nesting bees in calcareous grasslands with different habitat sizes and qualities, including the availability of bare ground and floral resources. We studied the nesting activity and number of bee nests on plots with experimentally removed vegetation. In addition, we assessed wild bee abundance and species richness and the proportion of ground-nesting bees within the communities.

The following hypotheses were tested:

1. The nesting activity and the number of bee nests on experimental plots, where the herbaceous vegetation has been experimentally removed, are higher compared to control plots with natural vegetation.
2. The nesting activity and number of bee nests on experimental and control plots increase with a higher surface temperature and a steeper slope.
3. Habitat size and quality, represented by the availability of bare ground and floral resources, have positive effects on nesting activity and number of bee nests as well as species richness, the abundance of all bees and of ground-nesting bees.

2. Material and methods

2.1. Study region and study sites

The investigation took place in rural landscapes around the city of Göttingen (Germany, Lower Saxony, Fig. A.1). Eight calcareous grassland study sites of two size classes were selected: Four small (mean 0.42 ha ± 0.22 SE; range 0.05–1.18 ha) and four large grasslands (mean 6.17 ha ± 1.23 SE; range 3.44–9.88 ha; Table A.1). The size of the study sites was measured with the help of satellite images and the geographical information system QGIS version 2.18 (QGIS Development Team, 2016). Four study sites were grazed and four were mown (Table A.1). Distances between study sites were more than 4 km. They are all protected areas and managed under supervision of the local nature conservation authority. Neighbouring habitats, like cropland and forests, can influence grassland communities, e.g., due to spill-over of species (Madeira et al., 2016), the provision of nesting sites (Bailey et al., 2014) or due to impacts on microclimate leading to different rates of nectar production (Bennett et al., 2014). Therefore, we only selected study sites that were located adjacent to both, cropland and forest, to control for these factors.

2.2. Experimental plots

In March 2019, we selected three experimental plots of 1 m^2 each (minimum distance of 30 m between the plots) on each study site,

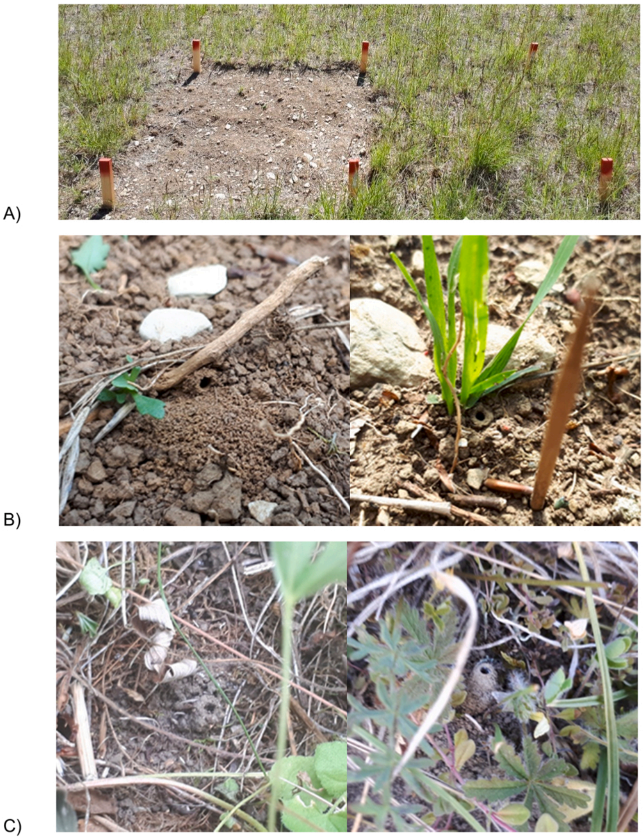

Fig. 1. A) Experimental set-up of the plots: On the left side the experimental plot and on the right side the control plot. Picture taken on site one in mid-June 2019. B) Nest entrances (diameter of ~ 3 mm) on control plots and C) exposed on experimental plots, constructed under plant parts to screen from view.

representing the prevailing conditions on the calcareous grassland. Within the experimental plots, we removed at least 5 cm of the upper soil cover. Next to each experimental plot, we marked control plots of the same size with undisturbed nesting conditions and vegetation cover (Fig. 1A). The control plots represented different conditions of the study site: from sparse up to denser vegetation (range 64.17–99.7% vegetation cover).

2.3. *Sampling period*

As solitary bees greatly differ in their emerging time and lifespan and usually occur only for four to five weeks (Danforth et al., 2019), sampling was conducted between April and July 2019 to account for seasonality of different bee species. All study sites were visited during six sampling runs ("run"), i.e., every 2–3 weeks. Each study site was visited three times in the mornings and in the afternoons (Table A.2) if day temperatures were over 12 °C and there was no heavy wind or rain. To avoid an observation bias, the whole sampling was conducted by the same person.

2.4. *Number of bee nests*

The number of bee nests on the plots was visually determined by carefully searching for bee nests, until no further nest was found (approx. 10 min). On the control plots, the vegetation was pushed aside to see the ground. Most of the nests are identifiable by volcano-like tumuli or turrets (Danforth et al., 2019), which are missing at the perfectly circular nesting tubes of tiger beetles, and can be distinguished from burrows of other ground-dwelling species like earthworms or ants by the texture of the excavated soil (Eiseman et al., 2010). Even on the experimental plots it was difficult to find all nests because they can be very small (small *Lasioglossum* species in Germany have a body length of 3.5 mm; Westrich, 2018) and are often built under visual shelters like stones (Fig. 1B; Potts and Willmer, 1997). Because of the dense vegetation on the control plots, the number of bee nests was even more difficult to count (Fig. 1C), but we intended to minimize a potential observation bias by intensively searching for nests within the vegetation. As significantly fewer nests were recognized even on the control plots of study sites with sparse vegetation this potential observation bias did presumably not influence our results.

2.5. *Nesting activity*

We chose nest activity as a metric complementing the number of nests to achieve comprehensive recordings of the ground-nesting bees. The nesting site choice of females depends on the perfect conditions for the development of the offspring, as well as for their own activity. Further, using only nest counts, we might miss hidden or buried nests of some species. The Observation of nesting activity is less influenced by vegetation density since flying bees were more obvious than their nests. However, using only observations of bees that were actively constructing or provisioning their nests, might overrate bees' activities, for instance due to social bee species sharing one entrance (Danforth et al., 2019).

Nesting activity was measured as number of nest-searching or provisioning bees observed during ten minutes. A bee was categorised as "nest searching" when the bee flew back and forth and close to the ground. As parasitic cuckoo bees do not build nests on their own, but use the provisioned brood cells of other bees (Danforth et al., 2019), they depend on a vital host population and therefore indirectly on the availability of nesting sites. Hence, they were included in nesting activity when searching for host nests. The nesting activity on the plots was recorded before counting nests to avoid disturbances and to identify hidden nest entrances. After the observations, the experimental plots were carefully weeded without destroying nest structures in every run to keep the soil vegetation free during the whole sampling period.

2.6. *Bee abundance and species richness*

To quantify species richness and abundance of wild bees on the eight study sites, we conducted two transect walks per site in every run. The transects had a length of 50 m and all bees found within ten minutes (without handling time) per transect were caught with a net in a 4 m corridor. The position of the transects was recorded with GPS points to walk the same paths in every run. When identification was not possible in the field, the caught bees were killed with ethyl acetate to identify the bee species in the laboratory. Bee species were identified using several identification keys (Amiet et al., 1999, 2001, 2004; Scheuchl, 1995, 2006; Schmid-Egger and Scheuchl, 1997; Von Hagen et al., 2003). Uncertain and rare species were verified by a bee expert (F. Creutzburg, Jena).

2.7. *Proportion of ground-nesting bees*

As we focus on ground-nesting bees, we used the nesting type to analyse a potential shift of this functional trait within the bee community depending on habitat characteristics. Based on the transect walk data, we assigned the nesting type "ground-nesting" to actively ground-burrowing bees and their cuckoo bees (Andrena, Anthophora, Colletes, Eucera, Halictus, Lasioglossum, Nomada, Sphecodes (Westrich, 2018)). The proportion of ground-nesting bees within the communities was then calculated based on binary encodings, i.e. ground-nesting bees versus all other nesting types (above ground-nesting solitary bees and bumblebees; see Antoine and Forrest, 2020). Nesting types were assigned based on Westrich (2018) (Table A.3).

2.8. Availability of bare ground

The availability of bare ground was used as an indicator for the nest site availability for ground-nesting bees and was measured at two spatial scales, the plot and the grassland scale. First, in every run, the percentage of bare ground on the control plots was estimated (means over all runs in Table A.4). Second, once in the last run, the total availability of bare ground on the whole study site was estimated during a survey walk over the whole site (in percent; Table A.1).

2.9. Soil surface temperature and slope

On both plots, the soil surface temperature was measured every run with an infrared thermometer (model RAY 31.1136, TFA Dostmann/Wertheim) to record the current conditions on the plots during the observation. If there was no bare soil surface accessible on the control plot, the measurement was done very close to the ground level. Furthermore, between 11th July 2019 and 5th September 2019 one Thermochron iButton® (model DS1921G-F5#, Maxim Integrated, San Jose, USA) was installed on the surface of each experimental plot to measure the daytime temperature between 9 am and 6 pm once per hour. This was done to record the surface temperature more consistently and to monitor the variation of sun exposure during the course of the day. Unfortunately, five out of the 24 iButtons® were lost and could not be analysed. The slope of the experimental plots was measured with the help of a spirit level and a gradient triangle. The steepest plot had a slope of 33.33% (Table A.4).

2.10. Floral resources

On the control plots, the cover of flowering plants (in %) was estimated every run. All blooming plant species within transects were identified and the number of blossoms per inflorescence was counted once per plant species. In every transect walk, the number of inflorescences was estimated for each species. Later, the number of inflorescences of every plant per run was multiplied with the average number of blossoms per inflorescence. This was multiplied with the average size of a single blossom to calculate the whole flower cover in square decimeter (dm^2) for each transect (Table A.1).

2.11. Data analyses

All statistical analyses were performed in R version 3.6.2 (R Core Team, 2019). Figures were created with the package ggplot2 (Wickham, 2016) and the function *ggpredict* from the package ggeffects (Johnson and O'Hara, 2014). Variables, for which a correlation was expected, were tested using cor.test and Pearson coefficient (Best and Roberts, 1975; Table A.5). Because of a significant correlation ($r = 0.67$, $p < 0.001$) between flower cover and plant species richness within transects, only flower cover was used. The bare ground availability on the sites and habitat size were correlated ($r = 0.58$; $p < 0.001$; Fig. A.2) and thus could not be used in the same model. In all models we first used bare ground availability on the sites as an explanatory variable and then reran the models replacing this bare ground availability by habitat size.

We applied generalized linear mixed effects models, which were fitted using Template Model Builder (TMB) implemented by the glmmTMB package (Brooks et al., 2017). First, models with count data were fitted using the Poisson error distribution. If under- or overdispersion was detected, models were re-calculated using a negative binomial distribution (family = nbinom2; Hardin and Hilbe, 2007). We tested the models for zero inflation with the function *testZeroInflation* from the package DHARMa (Hartig, 2020) and, if necessary, re-fitted them with the zero inflation term (ziformula=~1). Variables were removed stepwise to simplify the models with the help of the function *stepAIC* (Venables and Ripley, 2002). To assess the model fit the function *simulateResiduals* from the package DHARMa was implemented (Hartig, 2020). Additionally, the conditional R^2 values were calculated for the best fitting model with the function *r2_nakagawa* (tolerance=0.00) from the performance package (Lüdecke et al., 2021).

2.11.1. Number of bee nests and nesting activity

In a first set of models, we analysed the effects of experimental ground removal and local habitat characteristics on the number of bee nests and the nesting activity per plot and run. Explanatory variables were availability of bare ground and flower cover on the control plot (%; values per run), plot type (experimental or control plot), slope of the experimental plot (%) and soil surface temperature (°C). For the number of bee nests, the surface temperature measured with iButtons® on the experimental plots was used as explanatory variable for both plot types, as bees prefer to nest on sunlit sites with generally higher temperatures (e.g. Potts and Willmer, 1997). For the model with nesting activity as response variable, we used the surface temperature measured with an infrared thermometer every run on the experimental and control plots as explanatory variable, since the activity of ectothermic bees depend on the current temperature conditions (Cameron et al., 1996; Danforth et al., 2019). We used crossed random effects with run as a first and study site as a second random factor, with plot ID nested in study site. As the residual test for the nesting activity showed better results after fitting the model against zero inflation, *ziformula* was implemented.

2.11.2. Bee abundance and species richness

In a second set of models, we tested the effects of local habitat characteristics on bee abundance and species richness within transects. Therefore, bee abundance and bee species richness from the two transects were summed per study site and run. Explanatory variables were availability of bare ground (%) at the grassland scale and flower cover within transects (dm^2; values per run). The run and the study site were included as crossed random factors.

2.11.3. *Proportion of ground-nesting bees*

To analyse the proportion of ground-nesting bees, the functional composition of nesting types (ground-nesting vs. cavity-nesting) was used. The proportion of ground-nesting bees from all bees sampled during the transect walks per study site and per run is reflected in the community weighted mean (CWM). For the estimation of CWMs, the function *functcomp* from the package FD was applied (Lavorel et al., 2008). Because the data was normally distributed, the effects of habitat characteristics on estimated CWMs of nesting type were tested in models with a Gaussian error distribution. Explanatory variables were the availability of bare ground (%) at the grassland scale and flower cover within transects (dm^2; values per run). The run and the study site were included as crossed random factors.

3. Results

Although the plots were created in March, only four to six weeks before the first sampling run, bees were already nesting on them in April. Overall, 846 bee nests were counted, 785 bee nests on the experimental and 61 on the control plots (Table A.4). In total, 168 bees

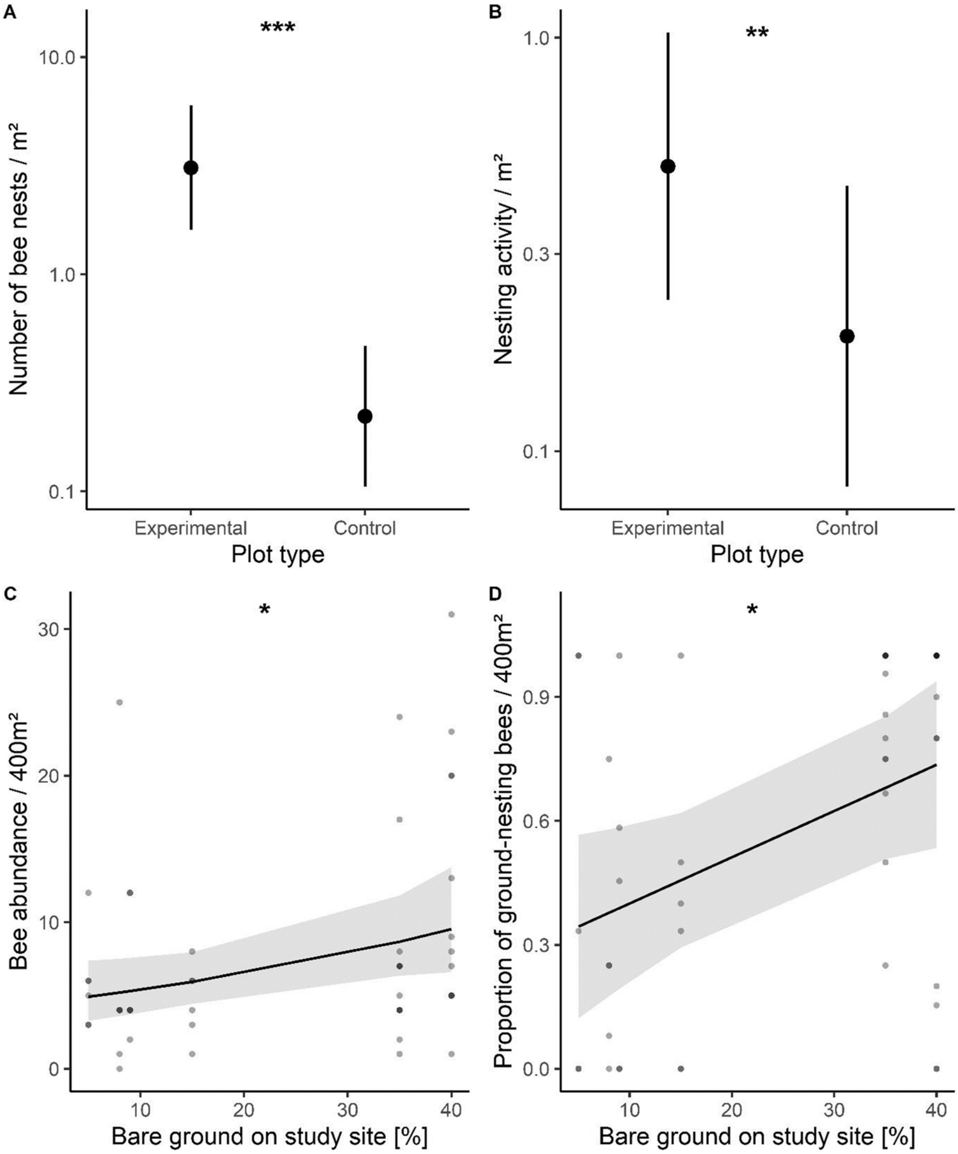

Fig. 2. Effect of plot type (experimental vs. control plots) on A) number of bee nests per m^2 and run ($p < 0.001$,R^2=0.77); B) nesting activity per m^2 and run ($p = 0.001$, R^2=0.4); Effect of bare ground availability on C) bee abundance within transects ($p = 0.029$, R^2=0.39) and D) proportion of ground-nesting bees within transects (CWM per study site, 1 =ground-nesting, 0 =above ground-nesting; $p = 0.015$, R^2=0.3). Estimates and 95% confidence intervals are shown, darker points show overlaying data points. Significance codes: $p < 0.001$ '* ** ', $p < 0.01$ '* *', $p < 0.05$ '* ', $p < 0.1$ '. '. For scatterplots showing the data points see Fig. A.7.

with nesting activity were observed, 135 on the experimental and 33 on the control plots (Table A.4). 92 non-parasitic bees were observed during searching flights on the plots, 37 bees while entering their nests for nest building or provisioning and 39 cuckoo bees searching for host nests. In total, 373 wild bees were caught during the transect walks. We identified 65 species belonging to 15 genera and five families (Westrich, 2018) (Table A.1). The most dominant genus was *Lasioglossum* with 155 individuals, representing 42% of all bees collected during transect walks, followed by the genus *Bombus* with 94 individuals representing 25% of all collected bees during transect walks. 26 of the 45 recorded non-parasitic bee species build their brood cells below ground (Table A.3).

3.1. *Number of bee nests and nesting activity*

The number of bee nests and the nesting activity were both enhanced on experimental compared to control plots and while the number of bee nests was impacted by steeper slopes and higher flower cover, nesting activity increased with soil temperatures.

We recorded fourteen times more nests on the experimental plots (mean 3.09 nests/plot & run) compared to the control plots (mean 0.22 nests/plot & run; Fig. 2A, Table 1). The number of bee nests increased with steeper slopes of the plots (Fig. A.3, Table 1). Furthermore, the flower cover on the control plots significantly increased the number of bee nests on both the experimental and control plots (Fig. A.4, Table 1). No effect of habitat size, the availability of bare ground on the control plots and the soil surface temperature on the number of bee nests could be detected (Table 1). 77% of the variance of the number of bee nests was explained by the explanatory variables in our model (R^2=0.77).

The nesting activity was more than 2.5 times higher on experimental plots (mean 0.43 bees/plot & run) compared to the control plots (mean 0.16 bees/plot & run; Fig. 2B, Table 1). The nesting activity increased significantly with higher soil surface temperatures (Fig. A.5, Table 1). No effect of habitat size, flower cover on the control plots and the slope of the plots on the nesting activity could be found (Table 1).

3.2. *Bee abundance and species richness*

Availability of bare ground and flower cover were important predictors of bee abundance, but not species richness within transects, while no effect of habitat size could be detected (Table 2). Bee abundance increased with a higher bare ground availability (Fig. 2C, Table 2) and with a higher flower cover within transects (Fig. A.6, Table 2). For none of the local habitat characteristics (habitat size, flower cover and availability of bare ground) an effect on bee species richness could be found (Table 2).

3.3. *Proportion of ground-nesting bees*

In habitats with a higher availability of bare ground more ground-nesting bees were found (Fig. 2D, Table 3). Neither for habitat size nor flower cover an effect on the proportion of ground-nesting bees could be detected (Table 3).

Table 1

Effect of explanatory variables: bare ground on the control plot (%) in the first model and habitat size (small) in the second model, else flower cover on the control plot (%), plot type (control), slope (%) and temperature (°C) for number of bee nests and nesting activity in generalized linear mixed models. Full models can be seen in Table A.6 in the Appendix.

Number of bee nests	*Full model = best model*		
Predictors	*Estimate*	*Conf. Int. (95%)*	*p-Value*
Model 1			
Bare ground on plot [%]	1.02	0.99 – 1.05	0.297
Flower cover on plot [%]	1.12	1.03 – 1.22	**0.006**
Type (control)	0.07	0.05 – 0.11	**< 0.001**
Slope [%]	1.03	1.01 – 1.06	**0.011**
Temperature [°C]	1.04	0.96 – 1.14	0.340
Model 1a			
Habitat size [small]	1.01	0.91 – 1.13	0.832
Flower cover on plot [%]	1.11	1.02 – 1.21	**0.012**
Type [control]	0.07	0.05 – 0.11	**< 0.001**
Slope [%]	1.04	1.01 – 1.06	**0.002**
Temperature [°C]	1.04	0.95 – 1.14	0.353
Nesting activity	*Full model = best model*		
Predictors	*Estimate*	*Conf. Int. (95%)*	*p-Value*
Bare ground on plot [%]	0.99	0.95 – 1.02	0.474
Flower cover on plot [%]	1.00	0.90 – 1.13	0.888
Type (control)	0.38	0.21 – 0.68	**0.001**
Slope [%]	1.03	0.99 – 1.07	0.138
Temperature [°C]	1.06	1.03 – 1.10	**< 0.001**
Habitat size [small]	0.55	0.21 – 1.47	0.233
Flower cover on plot [%]	0.98	0.87 – 1.10	0.720
Type [control]	0.36	0.20 – 0.65	**0.001**
Slope [%]	1.03	0.99 – 1.08	0.130
Temperature [°C]	1.05	1.02 – 1.09	**0.001**

Table 2

Effect of explanatory variables: bare ground on the study sites (%) in the first model and habitat size (small) in the second model, else flower cover within transects (%) for bee abundance and species richness in generalized linear mixed models. Full models can be seen in Table A.6.

Bee abundance	*Full model = best model*					
Predictors	*Estimate*	*Conf. Int. (95%)*	*p-Value*			
Model 3						
Bare ground on study site [%]	1.02	1.00 – 1.04	**0.029**			
Flower cover transects [dm^2]	1.13	1.05 – 1.21	**< 0.001**			
Model 3a						
Habitat size [small]	0.71	0.4 – 1.24	0.228			
Flower cover transects [dm^2]	1.13	1.05–1.21	**0.001**			
Bee species richness	*Full model*			*Best model*		
Predictors	*Estimate*	*Conf. Int. (95%)*	*p-Value*	*Estimate*	*Conf. Int. (95%)*	*p-Value*
Model 4						
Bare ground on study site [%]	1.00	0.99 – 1.01	0.779			
Flower cover transects [dm^2]	1.04	0.99 – 1.09	0.128	1.04	0.99 – 1.09	0.130
Model 4a						
Habitat size [small]	0.99	0.74 – 1.32	0.942			
Flower cover transects [dm^2]	1.04	0.99 – 1.09	0.131	1.04	0.99 – 1.09	0.130

4. Discussion

In contrast to floral foraging resources of bees, the availability of their nesting resources and particularly bare ground availability is rarely assessed in ecological bee studies. Here, we demonstrate that bare ground was of vital importance for ground-nesting bee species. Our experimental patches on calcareous grasslands provided bare ground, due to the removed vegetation cover, and these new nesting opportunities attracted more bees to build their nests than vegetated control plots. This effect was independent of habitat size. Further, across all calcareous grasslands studied, a generally high availability of bare ground on the whole grassland increased the bee abundance and proportion of ground-nesting bees in the bee communities.

4.1. Ground-nesting bees prefer bare ground patches

Knowledge about the biology and ecology of ground-nesting bees is urgently needed, as the drivers of nest building remain largely unknown for many species (Harmon-Threatt, 2020). We demonstrate that experimental bare ground patches with vegetation removal in calcareous grasslands result in a higher number of bee nests and also increase bee nesting activity compared to control plots.

As shown in previous studies, bees nested on experimental plots already a few weeks after the establishment (Gregory and Wright, 2005; Martin et al., 2017; Nichols et al., 2020), confirming that vegetation free areas represent strongly demanded nesting habitats (Potts et al., 2005) that are accepted over short time periods. Therefore, the provision of preferred nesting conditions through vegetation removal appeared to be an important factor for viable populations of some ground-nesting bee species. The limited visibility of the nest entrances on the control plots might have influenced our results due to an observation bias (Harmon-Threatt, 2020). Within the denser vegetation, it was more difficult to find the nests despite intense searching. Furthermore, it could not be controlled for counting nests of other animals, e.g. wasps. However, we assume that this potential bias can be neglected, as the nesting activity, which was easier to record, was also significantly higher on experimental plots, i.e. showing the same patterns. Although it was not always possible to classify the observed behaviour to nest building or provisioning activity, we found that bees were clearly attracted to the experimental plots.

Other studies support our findings as areas without vegetation are often chosen for nesting (Potts et al., 2005; Sardiñas and Kremen, 2014; Harmon-Threatt, 2020). The excavation and locating of nests is facilitated and the microclimatic conditions are improved on nesting sites with bare ground (Stephen and Evans, 1960; Wuellner, 1999). Bare ground is not shaded by vegetation and no roots can absorb soil moisture necessary for brood development (Stephen and Evans, 1960; Packer and Knerer, 1986). Further, growing roots may destroy the nests and vegetation perches can be beneficial for natural enemies like parasitic flies (Wuellner, 1999). Many bee

Table 3

Effect of explanatory variables: bare ground on the study sites (%) in the first model and habitat size (small) in the second model, else flower cover within transects (%) for the proportion of ground-nesting bees in generalized linear mixed models. Full models can be seen in Table A.6.

Proportion of ground-nesting bees	*Full model*			*Best model*		
Predictors	*Estimate*	*Conf. Int. (95%)*	*p-Value*	*Estimate*	*Conf. Int. (95%)*	*p-Value*
Model 5						
Bare ground on study site [%]	0.01	0.00– 0.02	**0.024**	0.01	0.00 – 0.02	**0.015**
Flower cover transects [dm^2]	-0.03	-0.06–0.01	0.113			
	Full model = best model					
Model 5a						
Habitat size [small]	-0.03	-0.07–0.00	0.079			
Flower cover transects [dm^2]	-0.17	-0.49–0.15	0.307			

species have specific requirements regarding the nesting location and invest considerable time to assess site conditions before nest building (Danforth et al., 2019). The transect walks revealed that species like *Lasioglossum laticeps* and *L. pauxillum* (Westrich, 2018) were common in the study sites and were therefore also, most probably, the main nesting species on the experimental plots. These species prefer nesting sites without or with sparse vegetation (Westrich, 2018).

There are a few bee species that prefer areas with vegetation cover, why other studies recommend rather vegetated areas to promote ground-nesting bees (Cane, 2015; Maher et al., 2019; Twerd and Banaszak-Cibicka, 2019). Vegetation and litter can protect nests against parasitism (Stephen and Evans, 1960; Packer and Knerer, 1986). Further, some bee species prefer nesting sites with visual landmarks like plants or stones that facilitate the retrieval of their nests (Potts and Willmer, 1997). Bee nests on the experimental plots were partly constructed under plants that grew between two sampling rounds (Fig. 1B). Therefore, first successional stages and a medium level of bare ground cover might be better than a complete vegetation removal as they provide heterogeneous conditions, which match better the different requirements of several species. The amount of bare ground at the study sites had a positive effect on wild bee abundance and, specifically, on ground-nesting bees recorded within transect walks. When ground-nesting bees are promoted by conservation measures, the general bee abundance might increase, as they constitute the bulk of wild bee species (Cane and Neff, 2011; Harmon-Threatt, 2020). This supports the findings of the few previous studies that the availability of bare ground is one of the most important factors determining abundance and colonization of wild bees (Potts et al., 2005; Murray et al., 2012; Sardiñas and Kremen, 2014).

The enhancement of bare ground availability is particularly important, as natural and anthropogenic causes of bare ground have often been lost in modern landscapes (Exeler et al., 2009; Heneberg et al., 2013; Campos et al., 2021). Moreover, ruderal areas with a formerly low vegetation cover are often overgrown rapidly due to over-fertilization and nutrition deposition (Bauer and Albrecht, 2020) or are sown with seed mixtures for aesthetic or conservation reasons (Anderson and Harmon-Threatt, 2016). Further, the management of essential bee habitats like calcareous grasslands is often neglected to save money and time (Bauer and Albrecht, 2020). Thus, future management of grasslands needs to consider our findings and target at creation of bare ground patches, which is particularly recommended on mulched sites providing a very low proportion of bare ground. Extensive grazing can also improve the availability of nesting sites as grazing animals create bare ground by trampling (Wesserling and Tscharntke, 1995) and may therefore complement or replace experimental bare ground patches. Creating bare ground can promote the general flying insect abundance (Theodorou et al., 2017) and vegetation free patches can be used by other thermophilic species like beetles (Simon-Reising et al., 1996; Widenfalk et al., 2018), reptiles or wasps (Gregory and Wright, 2005).

The creation of experimental bare ground patches can also be done by the banking of sand (Fortel et al., 2016; Martin et al., 2017). This might be an appropriate measure in urban or agricultural areas, especially in combination with flower strips (Nichols et al., 2020), but in protected areas like calcareous grasslands there could be a risk of introducing undesired plant seeds and of changing soil type and habitat features. The preparation of the bare ground through vegetation removal is an easy and cheap method to monitor ground-nesting bee populations with the advantage that it can indicate nesting and offspring production on the study site. In contrast to transect walks or pan traps, it does not only record transitory foragers (“food tourists”). However, studies on artificial bare ground patches entail regular time-consuming observations that are necessary to detect all nests and the bee nest dynamics. Further, bee species identification by nest observation needs expert knowledge, thus an identification key for nest characteristics would be helpful, similar to the identification keys for nest features in cavity-nesting bees (Gathmann and Tscharntke, 2002). In future studies, later successional stages of the experimental plots should be monitored in the following years (Gregory and Wright, 2005; Fortel et al., 2016), as plots might become less attractive to some species when vegetation starts to regrow (Nichols et al., 2020), or more attractive for others that prefer slightly hidden nesting places (Cane, 2015).

Our results indicate that this measure of vegetation removal is appropriate to promote ground-nesting bees as it increases the availability of preferred nesting sites. Due to philopatry (Yanega, 1990), the artificially made nesting areas were probably colonized by a vital source population from the calcareous grasslands or near surroundings in the first year of sampling (Tscharntke et al., 2012; Franzén and Nilsson, 2013). Since we did not monitor the change of the community composition of the wild bee population over several years and compared it to study sites without this measure, we cannot make any statements about whether ground-nesting wild bees were promoted by the measure. To see whether the population size is enhanced and thereby the extinction risk is reduced by this measure, further studies are needed. However, the transect walks confirmed that areas with a higher bare ground availability resulted in a higher proportion of ground-nesting bees and an increased general abundance of wild bees. This supports our conclusion that a higher bare ground availability, as induced artificially on a small scale in our experiment, can lead to a general promotion of wild bees. Stephen and Evans (1960) found a 300% increased population size of the alkali bee (*Nomia melanderi*) after removing vegetation cover on existing bee nesting sites.

Trapping the hatching bees with emergence traps (Sardiñas and Kremen, 2014) may provide additional information through species identification. A beta-diversity comparison between experimental and control plots could indicate which species prefer vegetation free areas and which prefer vegetated nesting sites. Further, this additional approach could answer the question, whether the observed increased nesting activity is due to a larger colony size of socially living wild bee species, as we expected mainly *Lasioglossum* species nesting on the patches.

4.2. Abiotic factors and floral resources

Several studies have highlighted missing information about abiotic factors influencing nest site selection (e.g., Harmon-Threatt, 2020; Antoine and Forrest, 2020). For ground-nesting bees, soil temperature is an important factor for successful nest building and larval development (Forrest and Chisholm, 2017). With higher surface temperatures, the ectothermic bees can warm up earlier and forage longer leading to accelerated nest construction and provisioning (Cameron et al., 1996; Weissel et al., 2006; Barbosa et al., 2013). In our study, soil temperature was a key factor predicting the nesting site activity on the plots (see also Forrest and Chisholm, 2017). With an increase of the soil temperature by 1 °C, five percent more bees were counted. Additionally, a steeper slope had a positive influence on the number of bee nests on the plots (Martin et al., 2017; Nichols et al., 2020), as it facilitates water drainage and increases solar irradiation (Potts and Willmer, 1997). Therefore, both factors - soil temperature and slope - need to be considered when new plots are established, and southern exposition without shading vegetation at steeper slopes should generally be preferred (Hopfenmüller, 2014; Sardiñas and Kremen, 2014). However, single bee species often have specific preferences regarding factors like texture or inclination (Antoine and Forrest, 2020; Harmon-Threatt, 2020). If certain rare species are targeted, the experimental nesting areas should meet the requirements of these species.

The strong positive influence of flower cover on the bee abundance recorded with transect walks in our study is not surprising, as high availability of food resources attracts foraging bees (e.g. Hegland and Boeke, 2006; Bennett et al., 2014; Quistberg et al., 2016). Moreover, the flower cover from the surrounding area partly explained the number of bee nests on the experimental plots, indicating that the small distances between nesting and foraging sites have beneficial effects on the nesting activity of wild bees. As bees are central place foragers, a reduced foraging distance can have benefits for the provision of the brood cells and therefore increases the reproductive success (Zurbuchen et al., 2010; Ganser et al., 2021).

4.3. Habitat size

Contrary to our expectations, based on previous studies (e.g. Krauss et al., 2009; Quistberg et al., 2016), we could not find an positive effect of habitat size on the number of nests, nesting activity, abundance, species richness and proportion of ground-nesting bee species within transects. However, we were also unable to prove any negative effect or lack of influence in our analysis. One reason for the missing effect could be that our sample size (eight study sites) was not large enough to allow for its detection in our statistical models. We suppose that habitat size per se is not an important factor determining nesting activity and the occurrence of ground-nesting bee species within the communities. Our results show that rather the habitat quality, which is indicated by the availability of bare ground and floral resources, is the driving factor (Sections 4.1 and 4.2), which is often enhanced in larger habitats. For specialized bees, the abundance of their host plants is more important than habitat size and therefore they can occur even in very small habitats (Franzén and Nilsson, 2010), explaining why species richness is not necessarily related to habitat size. Similar to Quistberg et al. (2016), habitat size was positively correlated with bare ground availability. Additionally, the missing effect of habitat size on nest building and nesting activity on experimental bare ground plots indicates that this measure works for both, small and large study sites.

5. Conclusions

This study demonstrated that the availability of bare ground determines bee abundance and the proportion of ground-nesting bees within the communities and thus should be considered in management plans for nature conservation and statutory guidelines. Experimental removal of vegetation to create bare ground plots featured more nests and nesting activity and could therefore be used as a management tool to promote ground-nesting bees. To make the establishment of these plots more effective, we identified a set of variables that play a crucial role for bee nesting: First, abiotic factors like slope and soil temperature influenced this conservation measure, as we found more nests and a higher nesting activity when soil temperature and inclination increased. Second, a high coverage of floral resources adjacent to the experimental plots had a positive effect on the nest number. In this study, no influence of the habitat size was found indicating that the measure of experimental bare ground plots is effective in habitats of all sizes. However, further studies are necessary to investigate whether experimental plots can really enhance population growth and how they can be used to achieve specific conservation aims or increase ecosystem services. Plots with removed vegetation could be used as a standardized method to monitor populations and to gain a better understanding of their biology, which is missing so far (Antoine and Forrest, 2020).

Overall, providing artificial bare ground patches in calcareous grasslands, a valuable bee habitat, seems to be an appropriate method to promote and study ground-nesting bees. This is particularly important when the grasslands are mulched, leading to low bare ground availability. The management practices of calcareous grasslands are so far often focused on plant populations, but in order to support declining insect populations, additional measures have to be considered for nature conservation. To ensure the availability of bare ground in natural habitats as calcareous grasslands is a key factor for the preservation of wild bee populations.

Declaration of Competing Interest

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

Data availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2022.e02289.

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