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RESEARCH ARTICLE

Grassland extensification enhances nest densities of ground-nesting wild bees

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Abstract

1. Ground-nesting wild bees provide essential pollination services in agroecosystems, but they are jeopardized by intensive agricultural management. To mitigate such negative impacts, agri-environment schemes have been implemented. While the success of enhancing floral food resources is relatively well studied, the role of agri-environmental schemes in providing suitable nesting habitat remains underexplored.
2. We studied the effectiveness of meadow extensification according to the Swiss agri-environment scheme in promoting nesting of ground-nesting bees. Using a paired design, we quantified their nests during four rounds (March–June) in pairs of nine randomly selected extensively (i.e. no fertilizer input, postponed first mowing) and nine intensively managed meadows with similar soil properties, slope, exposure and landscape context. Nest numbers and vegetation characteristics were surveyed in areas of 250 m^2. Vegetation properties were also assessed in 0.5×0.5 m plots around nest locations and randomly selected locations without nests within each meadow to assess their role as drivers of nesting incidence (nest presence/absence) at this plot scale.
3. We found substantially higher nest numbers of ground-nesting bees in extensively (mean $\pm$ SE per sampling round $= 46.8 \pm 14.2$) compared to intensively managed meadows (0.8 ± 0.3; no nests in three of nine intensively managed meadows). Extensively managed meadows harboured nests of several dominant crop pollinator species, including aggregations of, for example, *Lasioglossum malachurum* contributing to high nest densities in some of them. Number of nests was negatively related to grass cover and vegetation height, which were lower in extensively compared to intensively managed meadows. Plot-level nesting incidence increased with bare ground and moss cover, and decreased with grass cover.
4. *Synthesis and applications.* Our study shows that extensively managed meadows are better nesting habitats for ground-nesting bees than intensively managed meadows, if reduced management intensity is associated with altered vegetation

characteristics such as reduced grass cover and vegetation height, and small-scale availability of bare ground, driving these effects. This highlights that maintaining and promoting extensive management of meadows can promote ground-nesting wild bees, including dominant crop pollinators, not only by enhancing floral resources but also by improving nesting opportunities in agroecosystems.

KEYWORDS
agri-environment schemes, extensive grassland management, farmland biodiversity, grassland restoration, land-use intensity, mowing regime, nitrogen input, pollinator conservation

1 | INTRODUCTION

Wild bees play a crucial role as pollinators of wild flowering plants and crops (IPBES, 2016; Kleijn et al., 2015; Ollerton et al., 2011). However, declines of wild bee abundance and diversity in several regions of Europe and North America have been reported during the last decades (Biesmeijer et al., 2006; IPBES, 2016). Land-use intensification and associated loss, degradation and fragmentation of habitats offering suitable floral food resources and nesting opportunities are considered primary drivers of wild bee decline (Ekroos et al., 2020; IPBES, 2016). Concerns over the loss of wild bee pollinators have triggered incentives to promote wild bees, for example through agri-environment schemes and other conservation and restoration measures in particular in agroecosystems (Albrecht et al., 2007, 2020; Kovács-Hostyánszki et al., 2017). Most of these measures focus on enhancing floral food resource availability for pollinators, for example, through wildflower strips or flower-rich hedgerows (e.g. Albrecht et al., 2020; Blaauw & Isaacs, 2014; Ganser et al., 2021; Kremen et al., 2019). However, wild bees rely not only on suitable floral food resources, but also on suitable nesting habitats within their foraging ranges, which can be an important driver of their population persistence and diversity in agricultural landscapes (Cane, 1991; Grundel et al., 2010; Harmon-Threatt, 2020; Potts et al., 2005; Roulston & Goodell, 2011; Williams et al., 2010).

Of the non-parasitic wild bees of Europe and many other regions of the world for which data are available, the vast majority of species nest in the soil (i.e. ground-nesting bees; Michener, 2007). Hence, ground-nesting bees represent a particularly important guild of wild bees, both from a biodiversity conservation perspective and regarding their functional role as pollinators of wild plants and crops (e.g. Kleijn et al., 2015; Sardiñas et al., 2016). Alarmingly, a high percentage of ground-nesting bee species are listed as threatened or endangered species on Red Lists and are therefore of high conservation concern (e.g. Nieto et al., 2014; Westrich et al., 2011). Despite their key role for conservation and pollination, knowledge on the nesting requirements of ground-nesting wild bees in agroecosystems remains scarce (Antoine & Forrest, 2021; Harmon-Threatt, 2020; Ullmann et al., 2020). Particularly little is known about how agricultural management practices affect nesting opportunities of ground-nesting wild bees, and how the quality of nesting habitats could be promoted through adequate management and agri-environmental measures (Buckles & Harmon-Threatt, 2019; Ullmann et al., 2016; Venturini et al., 2017).

We hypothesize that less intensive management of grasslands promotes ground-nesting wild bees in agroecosystems, beyond their acknowledged role in providing diverse floral food resources to bee pollinators (e.g. Albrecht et al., 2007; Ekroos et al., 2020; Maurer et al., 2022; Sutter et al., 2017). Grasslands, in contrast to tilled arable crops (Ullmann et al., 2016), are relatively less disturbed and may offer nesting opportunities close to floral food resources. However, as most ground-nesting bee species are considered to prefer relative sparsely vegetated areas (Antoine & Forrest, 2021; Gardein et al., 2022; Harmon-Threatt, 2020; Potts et al., 2005; Potts & Willmer, 1997; Sardiñas & Kremen, 2014; Tschanz et al., 2023), the vegetation of intensively managed and fertilized grasslands may be too dense to serve as suitable nesting habitat. We therefore hypothesize that less intensive grassland management, as promoted though agri-environmental schemes, which is expected to reduce overall vegetation cover and increase vegetation patchiness and heterogeneity (Knop et al., 2006), promotes adequate nesting habitats for ground-nesting wild bee in agroecosystems. However, this hypothesis and the role of improved quality of grasslands as nesting habitat for ground-nesting bees through grassland extensification schemes remains, to our knowledge, largely unexplored.

We address the following main research questions: (1) Is nesting of ground-nesting wild bees enhanced in extensively managed meadows compared to intensively managed meadows? (2) What are the nest densities of ground-nesting bees in differently managed meadows, and which species nest in these meadows? (3) What is the role of different vegetation properties potentially driving the number of nests of ground-nesting bees across differently managed meadows and plot-level presence/absence of nests (i.e. nesting incidence) within meadows?

2 | MATERIALS AND METHODS

2.1 | Study design

The study was conducted in 2019 in agricultural landscapes of the cantons of Zurich and Aargau in the Swiss Plateau dominated by grasslands, arable crops and forest patches. Within the study region, nine pairs of meadows (hereafter sites) were randomly selected, with each pair consisting of an intensively and an extensively managed meadow adjacent to each other (directly adjacent (0 m) or up to 32 m distance between meadows within a pair; mean ± SE = 6.2 ± 3.7 m). This 'choice' design ensured similar soil conditions, slope and exposure (as confirmed by the absence of statistically significant differences; Table S1) of the intensively and extensively managed meadow within a pair, and minimal potential confounding influences of the surrounding landscape composition, which was almost identical for the two adjacent meadows. Moreover, the floral resources offered by both meadows within a pair were readily accessible for nesting bees even for species with very small observed foraging ranges (e.g. Zurbuchen et al., 2010). This allowed us to assess nesting preferences of locally present ground-nesting bees (i.e. preference or choice of nesting location within one of the two adjacent meadows), minimizing the potential influence of local floral resource availability (e.g. Albrecht et al., 2007). The selected intensively managed meadows represent permanent conventionally managed meadows which were all fertilized, typically receiving generally 150–200 kg ha^{-1} nitrogen each year of the study region and mown up to five or six times per year if weather conditions allow it, the first cut mostly taking place in May (Huguenin-Elie et al., 2017; Knop et al., 2006). The selected extensively managed meadows were all managed according to the requirements of the Swiss agri-environment scheme for extensively managed meadows (as confirmed by farmers; postponed mowing [no mowing before 15 June]) and prohibition of any fertilizer applications are the major management prescriptions of the scheme (Bundesrat, 2013). Extensively managed meadows are also mown less frequently than intensively (conventionally) managed ones, generally twice a year or rarely less (Huguenin-Elie et al., 2017; Knop et al., 2006). All studied extensively managed meadows have been managed according to these prescriptions for at least 6 years. All meadows were managed as mown hay meadows, but we cannot exclude the possibility that an intensively or extensively managed meadow may have been grazed for a short time period in autumn in the past, as we lack detailed historical management records. Sites were at least 1.0 km apart from each other (mean ± SE distance to the next site: 6.0 ± 1.3 km; range: 1.0–13.2 km). The size of meadows was in the typical range of meadows in the study region and ranged from 0.12 to 4.5 ha, with an average size of 1.0 ± 0.25 ha.

2.2 | Quantifying ground-nesting bee nests

We assessed nest density of ground-nesting bees 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; Pereira et al., 2021; Potts & Willmer, 1997; Tschanz et al., 2023; Venturini et al., 2017; Wuellner, 1999). Nest numbers of the few largest and most dense nest aggregations were approximated, as for example, separation of some nests with merged tumuli was not unambiguously possible. For a detailed description of the methodology and a discussion of advantages and potential limitations compared to alternative methods such as the use of emergence traps see Tschanz et al. (2023). The majority of ground-nesting bee species build characteristic tumuli (i.e. mounds of excavated soil material around the nest entrance, sometimes also covering the (closed) nest entrance; Figure 1). We focused on nests of tumuli-building ground-nesting bees because they are distinctive (e.g. round hole marking the nest entrance, round and smooth nest tunnel, characteristic soil tumuli) and are generally well identifiable by a trained person (Tschanz et al., 2023; Ullmann et al., 2020), but the possibility of misclassification cannot be completely ruled out. In each meadow, nests

FIGURE 1 Nest of a ground-nesting wild bee. Left: Marked nest of *Colletes cunicularius* (Apoidea: Colletidae) with visible excavated soil material ('tumulus') around nest entrance in an extensively managed meadow; right: 0.5 × 0.5 m plot in which vegetation properties were assessed around a marked nest (see Section 2).

of tumuli-building bees were quantified in a randomly chosen area of 250 m^2 in the meadow interior (excluding a 3 m wide edge zone at the border of the meadow to minimize potential edge effects) during four sampling rounds from mid-March to the end of June 2019 (the 250 m^2 sampling area was newly randomly selected for each round). This period represents the main nesting period of most ground-nesting bees in the study region (Scheuchl & Willner, 2016), but some species are partly or entirely active later in the year. Located nests were marked in each sampling round by a small pink waterproof colour point sprayed onto the ground a few centimetres away from the nest entrance (Figure 1) to avoid double counting of nests within and across sampling rounds. Since heavy rainfall can erode tumuli and therefore the detectability of bee nests, sampling was only done during dry and sunny weather conditions and at least 2 days after the last rainfall. Sampling of the two differently managed meadows within a pair was always carried out on the same day during each sampling round, and the order of sampling of a meadow type within a pair was randomized. Visual detection of nests is typically easier and takes less time until a plot is thoroughly surveyed in sparsely compared to densely vegetated areas (Antoine & Forrest, 2021). To avoid introducing any systematic bias in nest detection probability in our study, it was ensured that the necessary time for nest searching was invested until each square metre of the searching area was systematically and thoroughly surveyed, which resulted in disproportionally more time invested to search for nests in denser vegetation, thereby minimizing the risk to overlook any nests (see discussion section and Tschanz et al., 2023). Moreover, comparisons of the proportion of bare ground and vegetation height in plots around detected nests with plots at randomly selected locations without nests within each meadow that were meticulously searched for nests (see 'Vegetation characteristics' below), corroborated that ground-nesting bees prefer to nest in less densely vegetated patches, which was not due to different detection rates.

To gain additional insights into the composition of the nesting bee species, female bees leaving or returning to nests or males hovering around nests were captured when encountered during nest sampling with a butterfly net (males were only captured if no flowers were present to rule out the possibility of collecting foraging bees). Due to the very low number of nests in intensively managed meadows, all bees that could be sampled and identified were from extensively managed meadows. Captured bees were stored at −20°C in a freezer, pinned and identified by a bee taxonomic expert (Dr. Mike Herrmann) and are curated at Agroscope in Zürich, Switzerland.

2.3 | Vegetation characteristics

To determine the influence of different components of vegetation cover and structure on small-scale nest location preference (i.e. nesting incidence) of ground-nesting bees across different locations within meadows, the percentage of cover of bare ground, grasses, herbaceous plants, mosses, as well as the vegetation height were assessed within 0.5 × 0.5 m plots within the 250 m^2 sampling area of each meadow centred on newly located nests (nest plots) as well as in plots of identical size at randomly selected locations in the same meadow without nests (control plots) in each meadow (newly randomly selected in each sampling round). Vegetation was assessed in nest plots for all new nests detected in each sampling round, but in meadows with more than nine nests, vegetation was assessed in plots around nine randomly selected nests. An identical number of control plots were recorded (up to nine if up to nine nests were recorded), but if fewer than nine nests were available, assessment of nest plots were substituted with assessment of control plots to achieve identical numbers of vegetation plots for the two differently managed meadows within a pair.

We obtained permission from all land owners for accessing their land and for data collection. No ethical approval or other permissions were required for this research.

2.4 | Soil sampling and analysis

To assess soil properties as a potential factor influencing nesting across the two differently managed meadows within a pair, a total of six cylindrical soil core samples were taken (100 mL; 5.0 cm height, 5.1 cm diameter) from randomly chosen locations within the nest-searching area of each meadow. Bulk density (dry soil weight per volume [g cm^{-3}]) was quantified for each sample after they had been dried for 48 h at 105°C. Average soil texture (i.e. percentage of clay, silt and sand), and organic carbon (C_{org}) content were determined from composite samples per meadow. For the determination of soil texture, silt and clay were assessed by sedimentation in an aqueous suspension, while sand was summed up to 100%. Soil organic matter (SOM) was obtained by multiplying C_{org} by 1.725. All analyses followed standard reference methods (Agroscope, 2012).

2.5 | Statistical analyses

To test the effect of the management intensity (i.e. factor with two levels: extensive or intensive meadow management) on the response variable number of nests (total number of nests per 250 m^2 sampling area and sampling round) a GLMM assuming a Poisson error distribution with log-link function including meadow pair and sampling round as crossed random effects was run using the package *lme4* (Bates et al., 2015). We tested for potential zero-inflation using *DHARMa::testZeroInflation* (Hartig, 2022), which showed that there was no significant zero-inflation.

To analyse the effects of vegetation characteristics (bare ground cover, grass cover, vegetation height) on number of nests at this sampling plot level (250 m^2) across meadows as potential drivers behind observed differences in nest numbers across the differently managed meadows, nest density was analysed using a GLMM with a Poisson error distribution and log-link function fitted with proportion of bare ground, grass cover and vegetation height (using averaged data from all vegetation survey plots per meadow and sampling round) as explanatory variables, and meadow pair and sampling round as random effects.

Furthermore, to investigate how the presence or absence of nests at certain locations within a meadow is driven by small plot-scale variation in these vegetation characteristics (0.5 × 0.5 m plots), that is, how nesting incidence (plot-level presence/absence) is related to this small-scale variation in vegetation characteristics within meadows, a GLMM was fitted with binomial error distribution and logit-link function with meadow ID nested in meadow pair and sampling round as random effects. For this and all other models, potential correlation among explanatory variables was assessed, and only explanatory variables that were not strongly correlated were included in the models ($|r| < 0.5$; Zuur et al., 2009). Therefore, cover by herbaceous plants was excluded as explanatory variable from these models due to high negative correlation with grass cover.

Finally, to test for the effect of meadow management on vegetation characteristics, GLMMs with meadow management intensity (extensively or intensively managed) as explanatory variable were fitted for each vegetation response variable (bare ground cover, grass cover, moss cover, vegetation height) including meadow pair and sampling round as random effects in all models. GLMMs were used to analyse variation of soil properties (SOM content, sand content, silt content, clay content, soil dry bulk density) across differently managed meadows (extensive vs. intensive management) of pooled samples of each meadow. Non-normally distributed response variables were modelled using a beta distribution (for proportion data derived from continuous numbers) with the package *betareg* (Cribari-Neto & Zeileis, 2010) or gamma distribution (for continuous count data) with the package *lme4* (Bates et al., 2015). The circular response variable slope was modelled using a Watson's two-sample test of homogeneity from the package *circular* (Agostinelli & Lund, 2022). Test statistics and *p*-values are based on likelihood ratio tests comparing the model with and without meadow management intensity.

In case of overdispersion, an observation-level random effect was included into each GLMM as an additional random factor (Zuur et al., 2009). All statistical analyses were conducted in R 4.3.1 (R Core Team, 2023). For mixed-effect models, confidence bands were computed using a Bayesian framework with samples drawn from the joint posterior distribution using *arm::sim* (Gelman & Su, 2020). Continuous explanatory variables were standardized (mean = 0, SD = 1).

3 | RESULTS

3.1 | Impact of grassland management intensity on nesting

A total of 1714 nests of ground-nesting bees were found in the 18 studied meadows. The number of nests per sampling round was significantly higher in extensively managed (estimated mean [95% CIs] = 6.88 [2.18, 21.75] nests per meadow and sampling round) than in intensively managed meadows (0.13 [0.03, 0.52] nests; Figure 2; $\chi^2(1) = 51.84$, $p < 0.001$). Overall, variable numbers of nests were

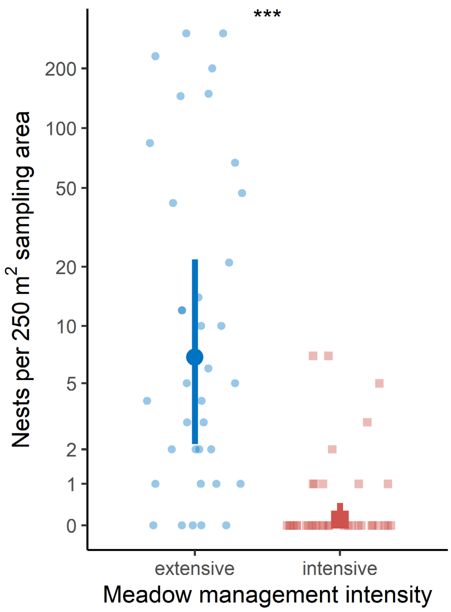

FIGURE 2 Predicted mean nest density (number of nests per 250 m^2 sampling area and sampling round) with 95% confidence intervals of ground-nesting bees in extensively and intensively managed meadows. Raw data points are plotted in the background. Note that values on the *y*-axis are on a $\log_{10}$ scale that transitions to a linear scale for values close to zero. Significance: ***$p < 0.001$.

found in all nine extensively managed meadows, with ≥78 nests (totals from all four sampling rounds) found in five extensively managed meadows (mean ± SE per sampling round = 46.8 ± 14.2; range of totals from all four sampling rounds 2 to 875), while the number of nests was consistently low in all intensively managed meadows with totals from all four sampling rounds (eight of nine intensively managed meadows with three or less nests) ranging from 0 (three of nine meadows) to 22 (mean ± SE per sampling round = 0.8 ± 0.3); but also in two extensively managed meadows relatively few nests were found (seven and two nests respectively). The high nest numbers in some extensively managed meadows were due to larger nest aggregations of, for example, *Colletes cunicularius*, *Lasioglossum malachurum* or *Lasioglossum politum*, and they harboured nests of several dominant wild crop pollinator species (e.g. *Andrena flavipes*, *L. malachurum*). A total of 42 bees (31 females and 11 males) of 16 different ground-nesting bee species could be sampled (all in extensively managed meadows) and identified. They were of the genera *Andrena* (nine species), *Lasioglossum* (five species), *Halictus* (*H. scabiosae*) and *Colletes* (*C. cunicularius*) (Appendix S1, Table S1). According to Nieto et al. (2014) none of the sampled species is threatened in Europe; *Andrena ovatula* is classified as near threatened, all other species are of least concern (11 species) or data deficient (four species).

3.2 | Vegetation characteristics as drivers of nesting

Soil properties (and as ensured by our design, also exposure and slope) did not significantly differ between extensively and

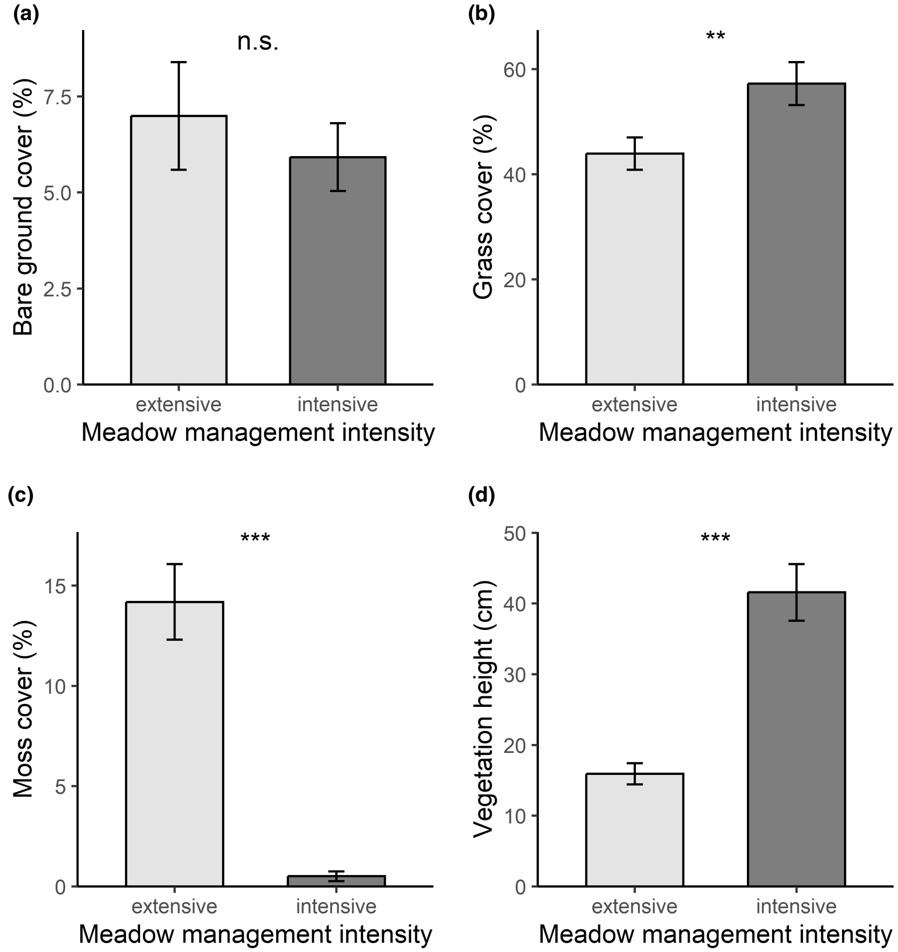

FIGURE 3 Mean (average per sampling round; ±1 SE) cover of (a) bare ground, (b) grasses, (c) moss and (d) vegetation height of the sampled extensively and intensively managed meadows. Significance: **>0.001, $p<0.01$; ***$p<0.001$; n.s., not significant.

intensively managed meadows (all $\chi^2 \leq 0.44$, $p \geq 0.505$; Appendix S1, Table S2, Figure S1). However, vegetation height and grass cover were lower and moss cover higher in extensively managed compared to intensively managed meadows (vegetation height: $\chi^2=51.58$, $p<0.001$; grass cover: $\chi^2=7.14$, $p=0.008$; moss cover: $\chi^2=46.96$, $p<0.001$), whereas bare ground cover did not significantly differ between meadow management intensity ($\chi^2=0.06$, $p=0.807$; Figure 3; Appendix S1, Table S2). Number of nests at the 250 m^2 sampling area scale was negatively related to vegetation height and grass cover (Figure 4; Table 1). Nesting incidence (nests presence/absence) within meadows at the small plot scale (0.5 × 0.5 m) increased with the percentage of bare ground and moss cover, and decreased with grass cover, while vegetation height did not significantly affect nesting incidence (Figure 5, Table 1).

4 | DISCUSSION

Our study demonstrates that meadows with reduced management intensity, that is, abandonment of fertilizer input and postponed first cut of meadows according to the Swiss meadow extensification scheme, are valuable nesting habitats for ground-nesting wild bees with strongly enhanced numbers of nests compared to intensively managed meadows. Our findings indicate that vegetation characteristics are significant underlying drivers of these differences in nesting habitat suitability for ground-nesting bees, also accounting for the large variation of nesting incidence within extensively managed meadows. They further suggest that at the meadow (250 m^2 sampling area) scale, mainly reduced vegetation height and grass cover, associated with extensive meadow management, contributed to increased numbers of nests, while at the smaller plot scale (0.5 × 0.5 m) increased bare ground and moss cover, and decreased grass cover enhanced nesting incidence.

While number of nests were consistently low in intensively managed meadows, number of nests were highly variable in extensively managed meadows, including meadows with particularly high numbers of nests, partly due to nest aggregations of gregariously nesting species such as *C. cunicularius*, *L. malachurum* or *L. politum* found in three of the nine extensively managed meadows. Nevertheless, in all extensively managed meadows (typically numerous) nests were found, while only in two thirds of the intensively managed

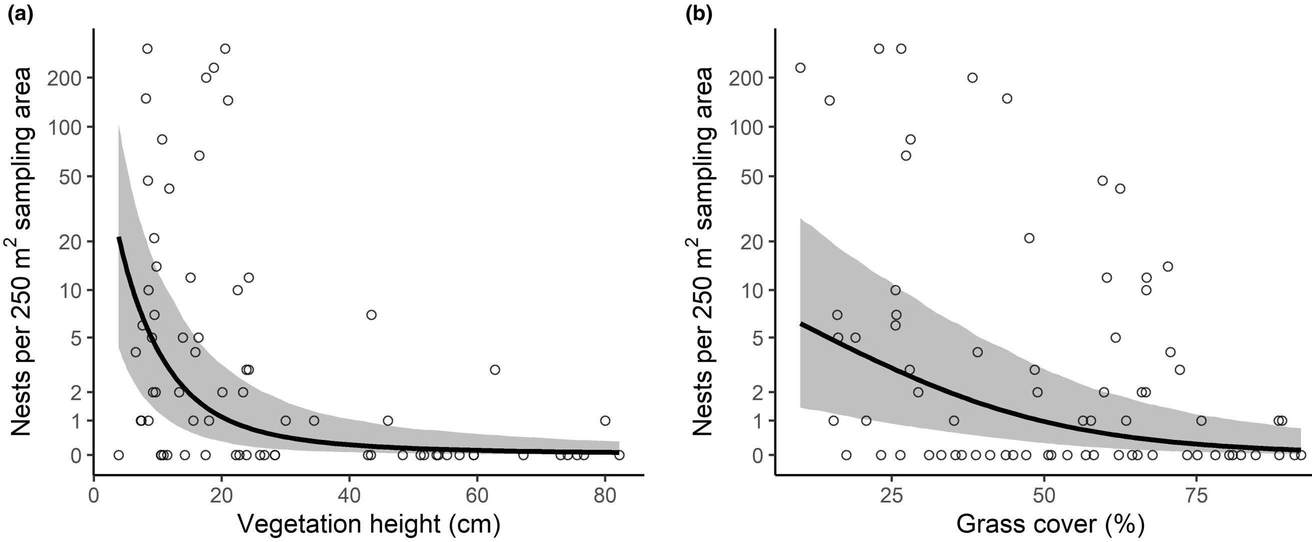

FIGURE 4 Predicted nest density, that is, the number of nests per 250 m^2 sampling area of ground-nesting bee nests per sampling round, as function of (a) vegetation height and (b) grass cover. Regression lines show predicted significantly negative relationships with 95% credible intervals (shaded areas) with covariates fixed at their mean values (vegetation height: $p<0.001$; grass cover: $p=0.002$). Circles show the raw data. Note that values on the *y*-axis are on a $\log_{10}$ scale that transitions to a linear scale for values close to zero.

TABLE 1 Summary of the generalized linear mixed-effect model analysis testing the effect of vegetation characteristics on nesting incidence (i.e. the presence/absence of nests) of ground-nesting wild bees at the 0.5×0.5 m plot scale (top rows) and on nest density (i.e. number of nests per 250 m^2 sampling area) (bottom rows) in extensively and intensively managed meadows. Significant effects with *p*-value ≤0.05 are shown in bold.

Explanatory variables	Estimate	SE	χ^2	*p*-value
Effects on nesting incidence at the 0.5×0.5 m plot scale				
Bare ground cover (%)	1.78	0.23	98.14	**<0.001**
Grass cover (%)	−0.45	0.17	7.14	**0.008**
Moss cover (%)	0.59	0.13	20.69	**<0.001**
Vegetation height (cm)	−0.42	0.28	2.20	0.138
Effects on nest density at the 250 m^2 sampling scale				
Bare ground cover (%)	0.27	0.35	0.60	0.438
Grass cover (%)	−1.05	0.32	9.73	**0.002**
Vegetation height (cm)	−1.49	0.40	17.20	**<0.001**

meadows nests were present (with typically only one or only very few nests found in the 250 m^2 sampling area). This highlights that the pronounced increase in nest numbers in extensively compared to intensively managed meadows was not only driven by the very high nest numbers of large aggregations in few extensively managed meadows, but rather the high nesting habitat quality also for bee species not typically nesting in larger aggregations (Appendix S1, Tables S1 and S2), while at the same time evidencing the poor potential of the studied intensively managed meadows as nesting habitat for ground-nesting bees.

A total of 16 different species of ground-nesting bees of several different genera could be sampled and identified in extensively managed meadows. The sampled species are relatively common in the study region and in Central Europe, and include species considered as dominant wild crop pollinators in Europe (according to Kleijn et al., 2015), such as *A. flavipes* or *L. malachurum* (Nelson et al., 2022). The identified species are classified as least concern or data deficient, except for *A. ovatula*, which is categorized as near threatened according to the Red List of bees of Europe (Nieto et al., 2014). However, it was beyond the scope of our study to perform a comprehensive assessment of all nesting bee species, and since only a fraction of the nesting bees could be sampled, it is likely that more species nested in the meadows studied. Thus, it remains to be explored in future studies which ground-nesting bee species regularly nest in extensively and/or intensively managed meadows, and how important extensively managed meadows are as nesting habitat for species of high conservation concern. One reason not to sample nesting bees more intensively was to avoid a strong influence this could have had on the number of nests, as females could possibly build multiple nests. Nevertheless, given the fact that large nesting aggregations of important crop-pollinating species were found in extensively managed meadows, future studies should examine the role of meadow management extensification for the contribution to crop pollination services provided by ground-nesting bees to bee-pollinated crops in the surrounding agricultural landscape. Furthermore, pollination service models rely on quantitative data where and at what densities wild bee pollinators nest in agroecosystems (Häussler et al., 2017; Lonsdorf et al., 2009). Due to a lack of empirical data, such models are currently largely based on expert opinion (e.g. Brosi et al., 2008; Keitt, 2009). Our findings should therefore help to improve modelling and predictions of pollination services in agroecosystems (Tschanz et al., 2023).

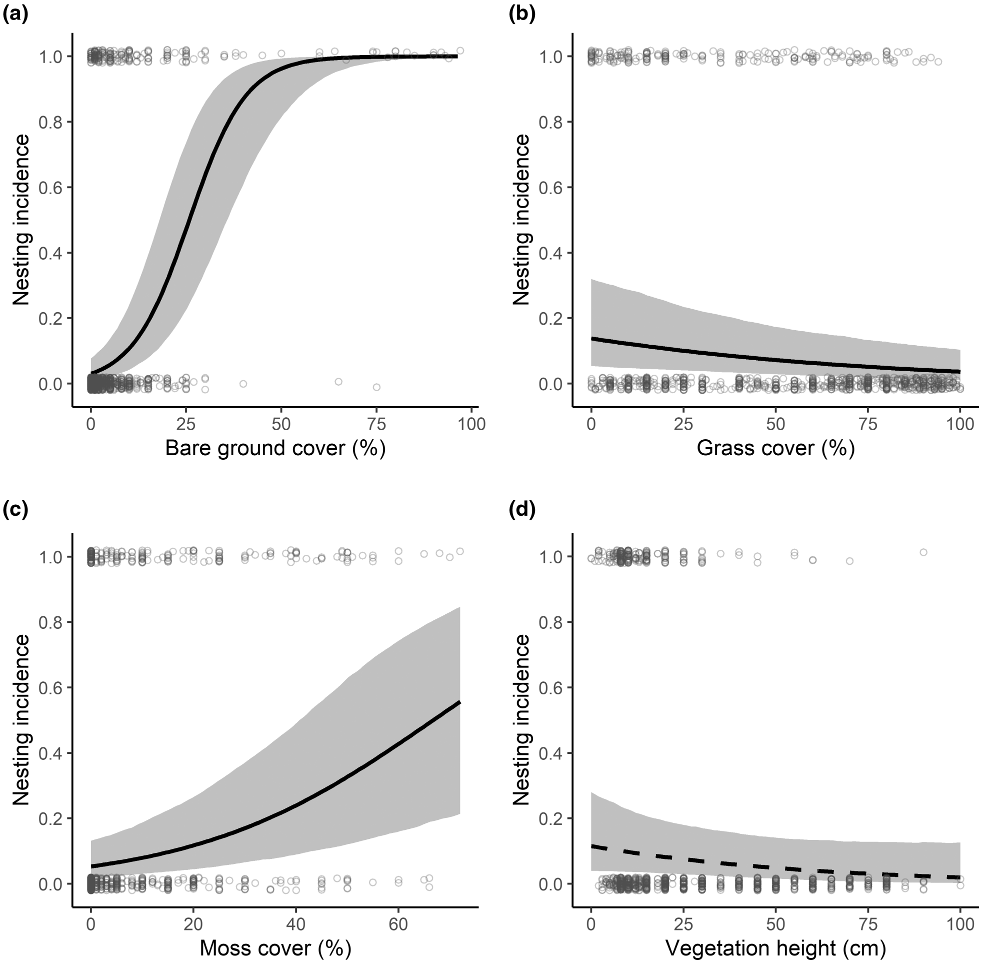

FIGURE 5 Predicted nesting incidence, that is, probability of nest occurrence of ground-nesting bees at the 0.5 × 0.5 m plot scale, as function of percentage cover by (a) bare ground, (b) grass and (c) moss, as well as (d) vegetation height. Regression lines show significant (solid lines; bare ground: $p < 0.001$; grass cover: $p = 0.008$; moss cover: $p < 0.001$) and non-significant (dashed line: vegetation height: $p = 0.138$) relationships with 95% credible intervals (shaded areas) with covariates fixed at their mean values. Circles show the raw data.

4.1 | Vegetation characteristics driving nesting in grasslands

Our results indicate that altered vegetation characteristics were important underlying drivers of differences in nesting habitat suitability for ground-nesting bees between extensively and intensively managed meadows, as well as within managed meadows on a smaller spatial scale. Nest numbers at the meadow scale decreased with grass cover and vegetation height, and nesting incidence (nest presence/absence) at the smaller plot scale similarly decreased with grass cover and increased with bare soil and moss cover. Although nesting preferences can be species specific (Antoine & Forrest, 2021; Harmon-Threatt, 2020), this largely corroborates evidence that most ground-nesting bees prefer less densely vegetated soil or smaller patches with bare ground for nesting (e.g. Gardein et al., 2022; Harmon-Threatt, 2020; Potts et al., 2005; Potts & Willmer, 1997; Sardiñas & Kremen, 2014; Wuellner, 1999). Consequently, small-scale active removal of vegetation in patches of up to a few square metres to create bare soil patches has been proposed as conservation measures to promote ground-nesting bees, for example in urban areas, vehicle routes in field margins or calcareous grasslands (Fortel et al., 2016; Gardein et al., 2022; Nichols et al., 2020). It might be expected that also grazing could positively affect habitat quality of ground-nesting bees in grasslands, for example, by keeping vegetation short and increasing heterogeneity in vegetation cover and creating small patches of bare soil (Kimoto et al., 2012; but see Buckles & Harmon-Threatt, 2019). Reduced grass cover and vegetation height associated with extensive meadow management, as it is typically observed along with reduced plant biomass growth after grassland extensification (e.g. Marriott et al., 2004), strongly promoted number of nests in our study. Soils covered by less dense vegetation of lower height are less shaded and better insolated, and should thus, at least at the surface, be warmer during sunshine, which may be beneficial for offspring development and earlier emergence, which in turn can increase parental fitness of ground-nesting bees (Forrest & Chisholm, 2017; Weissel et al., 2006). Shorter and sparser vegetation may also facilitate nest finding and thus reduce time and energy costs for female bees to find their nests after foraging (Wuellner, 1999). Furthermore, soil moisture could be lower due to increased sun exposure and thus desiccation; wet soils may negatively affect offspring survival due to higher rates of mould infestation, and they might therefore be less preferred for nesting than drier soils (Antoine & Forrest, 2021), but vegetation cover could also contribute to increased transpiration, which could reduce soil moisture. Moreover, intensively managed meadows are probably characterized by a more continuous and possibly denser root system, and, depending on the plant species composition, may also be shallower, and this dense root network close to the surface could prevent nesting (Wuellner, 1999). This could also partly explain the observed positive relationship between moss cover and nesting incidence, as shallow rooting mosses might prevent the establishment of grasses and the typically denser vegetation and root network associated with grass dominance.

Extensively managed meadows typically offer a more diverse and continuous (but not necessarily more abundant) availability of floral resources (e.g. Albrecht et al., 2007; Humbert et al., 2012; Johansen et al., 2019). Enhanced floral resource diversity has been shown to increase abundance and species richness of wild bees in grasslands (Albrecht et al., 2007; Buckles & Harmon-Threatt, 2019; Ekroos et al., 2020; Gardein et al., 2022; Sutter et al., 2017). Thus, floral resource availability may represent a further factor associated with extensive meadow management positively affecting nest site preference of ground-nesting wild bees. However, as the extensively and intensively managed meadows within a local meadow pair where directly adjacent or up to 32 m to each other, the floral resources offered by both meadows within a pair should have been accessible within the foraging ranges of the locally nesting bees, even for the species with the shortest foraging ranges (e.g. Zurbuchen et al., 2010), and likely played a less important role in the present study. Besides vegetation characteristics, soil properties can influence nesting of ground-nesting bees (Antoine & Forrest, 2021; Buckles & Harmon-Threatt, 2019; Harmon-Threatt, 2020; Tschanz et al., 2023). The measured soil properties that may affect nesting habitat quality, that is, soil texture, bulk density and soil organic carbon content, did not differ between intensively and extensively management meadows, and can therefore not explain the higher nest numbers associated with meadow management extensification. Finally, the surrounding landscape composition and the availability of landscape-level floral resource and nesting habitat availability can determine local bee populations (e.g. Ganser et al., 2021; Tschanz et al., 2023). Owing to our design of adjacent extensively and intensively managed meadows within a local site pair, these landscape factors were almost identical for the two differently managed meadows at a site, and thus rule out potential confounding of local management effects.

4.2 | Conclusions and policy and management implications

Our results show that reduced vegetation height and grass cover and thus reduced vegetation density associated with extensive meadow management associated with abandonment of fertilizer input and postponed and less frequent mowing, and at a smaller plot scale within meadows also higher proportion of bare ground, were primary drivers of the observed enhanced nest quality of extensively compared to intensively managed meadows in our study. Intensively managed meadows were largely unsuitable nesting habitat for most ground-nesting bees in our study. Thus, the studied grassland extensification scheme is not only important for diverse and relatively stable provisioning of floral food resources, but also for suitable nesting habitats for sustaining ground-nesting wild bee populations in agroecosystems. Our findings suggest that important crop-pollinating wild bees can strongly benefit from stopping further meadow intensification and improved nesting opportunities through meadow extensification, which should further encourage the promotion of grassland extensification measures through agricultural policies such as agri-environment schemes.

AUTHOR CONTRIBUTIONS

Matthias Albrecht, Louis Sutter and Thomas Keller designed the study with contributions from Stefanie Bossart; Stefanie Bossart collected the data; Philippe Tschanz analysed the data with contributions of Stefanie Bossart, Matthias Albrecht and Louis Sutter; Thomas Keller contributed to the sampling design and analysis of soil samples. Matthias Albrecht wrote the manuscript with substantial contributions from Stefanie Bossart and Philippe Tschanz; all authors contributed to writing, revised it critically for important intellectual content, gave final approval for publication and agreed to be accountable for the aspects of the work that they conducted and ensured that questions related to the accuracy or integrity of any part of their work are appropriately investigated and resolved.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.9ghx3ffpn (Albrecht et al., 2023).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Ground-nesting bees sampled (all from extensively managed meadows) and their conservation status according to the European Red List of bees (Nieto et al., 2014). Please note that this list of bee species should not be considered as a comprehensive list of all species that nested in the studied meadows, and the number of captured specimens of a bee species should not be considered as representative of the number of nests constructed by a species across the studied meadows (see Sections 2 and 4 of the main text).

Table S2. Summary of the (generalized) linear (mixed)-effect models testing for differences between extensively and intensively managed meadows in vegetation and soil properties. Mean ± SE with range (minimum to maximum) are given separately for extensively (ext) and intensively (int) managed meadow systems. Significant effects (p-value ≤ 0.05) are shown in bold. Mean slopes for each sampling area in each meadow were extracted from the extremely precise digital elevation model ("swissALTI3D") for Switzerland available through the federal GIS geoportal www.geo.admin.ch.

Figure S1. Mean (±1 SE) (a) soil dry bulk density, (b) soil organic matter content, (c) sand content, (d) silt content, and (e) clay content of the sampled extensively and intensively managed meadows. No significant differences between extensively and intensively managed meadows were found for any of these measured soil variables (see Table S2).

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