Global Ecology and Conservation 64 (2025) e03977

Contents lists available at ScienceDirect

Global Ecology and Conservation

journal homepage: www.elsevier.com/locate/gecco

Original research article

Restoration of abandoned calcareous grasslands promotes habitat diversity and overall wild bee beta diversity

Marcel Kettermann [a,1,*], Thomas Fartmann [a,b,2], Dominik Poniatowski [a,3]

[a] Department of Biodiversity and Landscape Ecology, Faculty of Biology and Chemistry, Osnabrück University, Osnabrück, Germany
[b] Institute of Biodiversity and Landscape Ecology (IBL), Münster, Germany

ARTICLE INFO

Keywords:
Biodiversity conservation
Flower resource
Habitat heterogeneity
Land-use change
Microclimate
Nesting site
Pollinator
Vegetation structure

ABSTRACT

Land-use change has led to a widespread loss of biodiversity across Central Europe, with calcareous grasslands being particularly affected, mainly due to the shift from traditional management to intensive agriculture or complete abandonment. To counteract the negative impacts of management cessation, shrub removal followed by grazing can serve as an effective restoration measure. In this study, we used wild bees as bioindicators to assess the ecological value of restored calcareous grasslands for biodiversity conservation. Across 21 restored grasslands (RestGras) and 21 regularly managed calcareous grasslands (Control) within the largest connected calcareous grassland area in northern Germany, we investigated environmental conditions and wild bee communities for all, threatened, belowground-nesting and snail shell-nesting species. Despite differences in habitat structure between the two grassland types, wild bee species richness and abundance did not differ. However, species composition varied to a certain extent, with some species, particularly those reliant on specific nesting structures like deadwood, plant stems and snail shells, favoring restored grasslands. Both direct incident radiation (DIR) and flower cover were found to have a positive impact on species richness and abundance of all and belowground-nesting wild bees. However, threatened species were positively influenced only by DIR. Furthermore, a higher cover of shrubs proved to be a crucial factor positively influencing snail shell-nesting wild bees. Our results show that restoration measures create structures that are not present in the control plots, thereby increasing heterogeneity at the regional scale. This, in turn, supports diverse pollinator communities in grassland ecosystems, highlighting the importance of restoration efforts for biodiversity conservation.

1. Introduction

Land-use change is a major cause of biodiversity loss, leading to dramatic declines in species richness across various ecosystems (Foley et al., 2005; Cardoso et al., 2020; Díaz and Malhi, 2022). The transition from traditional land-use practices to industrial agriculture—particularly since the mid-20th century—has caused the large-scale disappearance of semi-natural habitats (Poschlod et al., 2005; Henle et al., 2008; Veen et al., 2014). Among the most severely affected habitats are calcareous grasslands, which are

* Corresponding author.
E-mail address: makettermann@uni-osnabrueck.de (M. Kettermann).
[1] 0000–0002-2523–2989
[2] 0000–0002-2050–9221
[3] 0000–0002-9955–688X

https://doi.org/10.1016/j.gecco.2025.e03977
Received 24 June 2025; Received in revised form 11 November 2025; Accepted 15 November 2025
Available online 17 November 2025

biodiversity hotspots in Central Europe (Poschlod and WallisDeVries, 2002; Wilson et al., 2012; Feurdean et al., 2018; Fartmann, 2024). As a result of land-use change, over 90 % of this habitat type has been lost, primarily due to abandonment, land-use intensification or afforestation (WallisDeVries et al., 2002; Veen et al., 2014). In combination with fragmentation and inadequate management, biodiversity decline in grasslands is further exacerbated by habitat degradation, such as microclimatic cooling caused by atmospheric nitrogen deposition or grass encroachment driven by climate change (WallisDeVries and van Swaay, 2006; Poniatowski et al., 2018a; Fartmann et al., 2025).

A key concept in understanding the drivers of biodiversity loss is the *Habitat Heterogeneity Hypothesis*, which suggests that a greater variety of resources within a habitat can better meet the specific requirements of many species, leading to higher biodiversity (Speight et al., 1999; Benton et al., 2003; Diacon-Bolli et al., 2012). For insects, especially pollinators, structural diversity is crucial, as multiple resources are needed for their life cycle (Winfree, 2010; Westrich, 2018). However, afforestation, extensive encroachment of shrubs, and land-use intensification often lead to structural homogenization and ultimately a decrease in biodiversity (Proesmans et al., 2019; Ekroos et al., 2020). By contrast, conservation measures such as shrub removal on former calcareous grasslands with subsequent grazing can restore habitat heterogeneity, which in turn benefits specialized species that depend on different microhabitats and certain key structures (Tonietto and Larkin, 2018; Drossart and Gérard, 2020; Albrecht et al., 2023).

In grassland ecosystems, wild bees have an essential function as pollinators, contributing to plant reproduction and overall ecological stability (Klaus et al., 2021; Gardein et al., 2022; Albrecht et al., 2023). Their strong dependence on certain flowering plants and on specific key structures like bare soil, deadwood, snail shells or hollow stems for reproduction and nesting makes them highly sensitive to changes in their habitat (Potts et al., 2010; Roulston and Goodell, 2011; Fartmann et al., 2021; Eckerter et al., 2021). As such, wild bees serve as excellent bioindicators for assessing habitat quality (Roulston and Goodell, 2011; Abrol, 2012). Their populations decline if crucial resources are absent, even if floral diversity increases.

Most studies that have used wild bees to evaluate the success of grassland restoration have focused on the North American prairie (e.g. Purvis et al., 2020; Stein et al., 2020; Griffin et al., 2021; Lane et al., 2022). These studies offer valuable insights into factors influencing pollinator communities, particularly the role of plant species composition. For example, Purvis et al. (2020) suggest that the time since restoration is less critical than the establishment of suitable plant communities, which can support pollinator

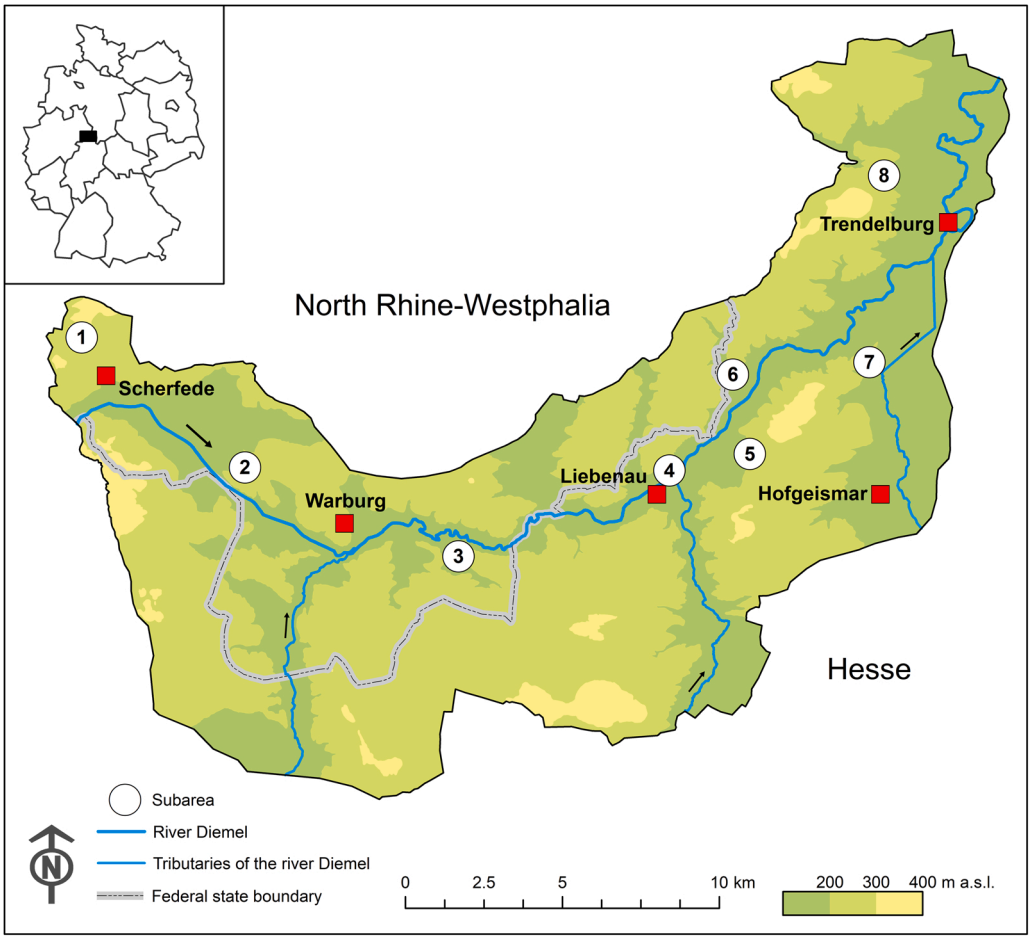

Fig. 1. The study area, the middle and lower Diemel Valley in central Germany (inlay) and the location of the eight subareas.

assemblages closely resembling reference conditions.

However, the transferability of these findings to Central Europe remains limited due to differences in landscape history, habitat configuration, and land-use intensity. In this part of Europe, wild bees have so far rarely been used as indicators to assess restoration outcomes.

A notable exception is the study by Exeler et al. (2009), which investigated the restoration of inland sand dunes in northwestern Germany. While establishing the full target community proved challenging, the implemented measures nonetheless promoted species-rich and abundant wild bee communities. This suggests that the functional role of pollinator communities may be restored even when full species turnover is not achieved.

Building on this, Öckinger et al. (2018) emphasized the importance of landscape structure and habitat connectivity. In their study on the restoration of semi-natural grasslands in Sweden, they found that nearby source populations are crucial for the successful reestablishment of pollinator communities. Their findings highlight that local habitat quality alone is insufficient; landscape-scale connectivity plays a decisive role in determining restoration success.

Taken together, these studies demonstrate the potential of wild bees as indicators for grassland restoration success. At the same time, they underscore a significant research gap in Central Europe, where comprehensive assessments of pollinator responses to restoration remain scarce. Further research is needed to evaluate how well wild bee communities can reflect restoration outcomes across diverse grassland types.

This study aims to address this knowledge gap by investigating the role of wild bees as bioindicators for assessing the conservation value of restored calcareous grasslands, particularly on sites formerly abandoned and overgrown with shrubs. While previous research has shown that shrub removal combined with grazing can enhance species richness of plants and insect primary consumers (Poniatowski et al., 2020; Helbing et al., 2021), its impact on wild bees, as surrogates of pollinators, still remains unclear. To examine this, we compare species richness and abundance of all wild bees, including threatened species and both belowground and snail shell nesters, in restored versus long-established calcareous grasslands. Specifically, we aim to answer the following questions:

(i) Can restored calcareous grasslands match long-term managed grasslands in wild bee species richness and abundance?
(ii) Are there differences in wild bee communities between these two grassland types?
(iii) Which environmental conditions determine wild bee species richness and abundance within both grassland types?

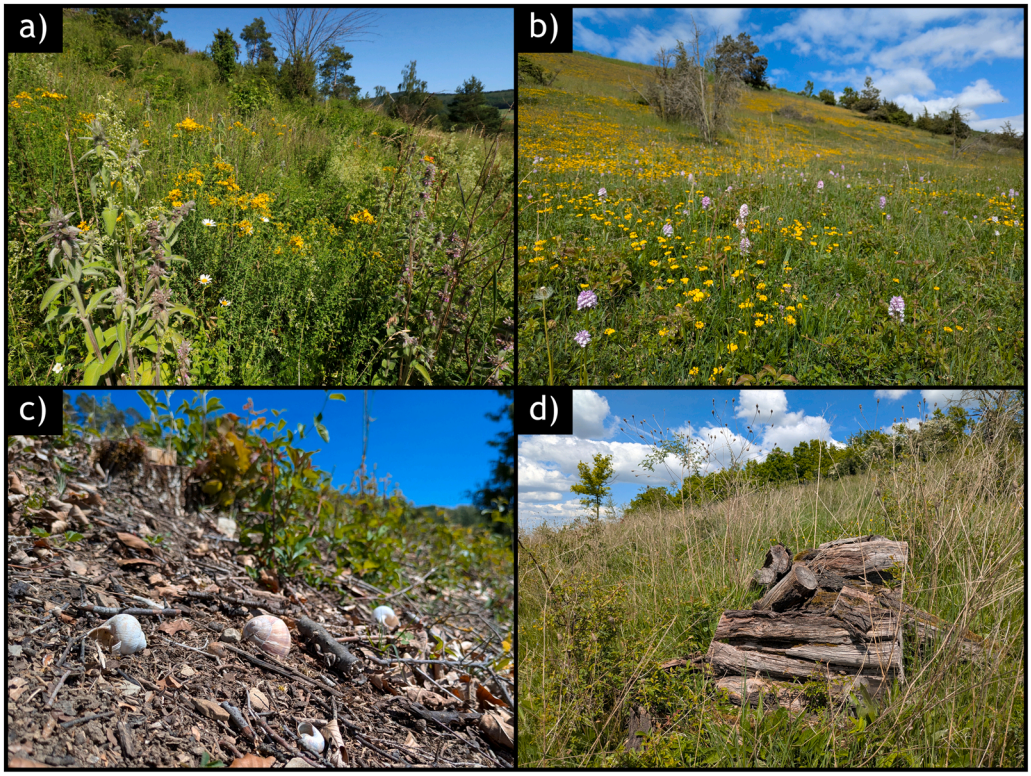

Fig. 2. Examples of (a) restored grassland, (b) extant calcareous grassland with a long history of low-intensity grazing (Control), (c) exposed snail shells following shrub removal and (d) deadwood as nesting structure within a restored grassland (Photo credits: a – Dominik Poniatowski; b to d – Marcel Kettermann).

2. Material and methods

2.1. Study area

The research was conducted in the middle and lower sections of the Diemel Valley, located at the northern edge of the central German uplands (51°32′N, 9°00′E and 51°36′N, 9°24′E; North Rhine-Westphalia and Hesse). The study area lies at an elevation of 160–280 m a.s.l. (Fig. 1) and is characterized by mean annual temperatures ranging from 9.0 to 9.6 °C, with an average annual precipitation of 630–795 mm, based on the reference period 1991–2020 (LANUK.,2022). In the study year 2020, the mean annual temperature was 10.3 °C, and the total annual precipitation measured 646 mm (Station 5347 – Warburg). The landscape features a dense network of calcareous grasslands (approx. 400 ha), interspersed with arable land, improved grassland and woodland. As part of the Diemel Valley, this region represents one of the largest semi-dry calcareous grassland areas in northern Germany (Fartmann, 2004) and is a hotspot of plant (Streitberger et al., 2017; Poniatowski et al., 2020) and animal diversity (Poniatowski and Fartmann, 2008; Stuhldreher and Fartmann, 2018; Helbing et al., 2021; Fartmann et al., 2022).

2.2. Subareas and plots

In our study, we investigated calcareous grasslands where restoration measures had been implemented within a period of eleven years prior to our study. These measures were carried out by regional stakeholders on behalf of the federal states of North Rhine-Westphalia and Hesse to comply with the requirements of the EU Habitats Directive (92/43/EEC), with the aim of improving the conservation status of calcareous grasslands (habitat type 6210). The restored grasslands were always located within remaining calcareous grasslands, and their size ranged from 1.7 to 20.5 ha (mean: 8.6 ha; total restored area: 35 ha). To avoid issues with spatial autocorrelation, closely adjacent calcareous grasslands were grouped into a total of eight subareas (see also Section 2.5: GLMM with random effects) (Fig. 1), where we examined wild bee diversity in 42 randomly selected plots. The number of plots per subarea varied depending on the size and habitat configuration, ranging from two to six. The study focuses on two distinct habitat types, both of which were consistently present across all subareas:

(i) former calcareous grasslands that had become overgrown with shrubs due to abandonment and which were restored by shrub removal and suppressing the resprouting woody plants by mulching. After these restoration measures, the grasslands have been seasonally grazed at low intensity (RestGras, 21 plots, Fig. 2a).
(ii) extant calcareous grasslands with a long history of low-intensity grazing. These grasslands were characterized by high phytodiversity and represent the target state for calcareous grassland restoration in the study area (Control, 21 plots, Fig. 2b).

All plots had an area of 16 m^2 (4 m × 4 m) and were permanently marked. For this purpose, magnets were fixed at each corner of the plot with tent pegs. Using a magnet detector, the plots were precisely relocated during subsequent visits.

2.3. Plot characteristics

In June 2020, we assessed habitat structure across all 42 plots, estimating the percentage cover of shrubs, the field layer (herbs and grasses), bare ground and litter using 5 % increments (with finer 2.5 % steps for values below 5 % and above 95 %). Additionally, during each survey, we estimated flower cover as a proxy for nectar and pollen abundance as well as the number of flowering plant species within the entire 16 m^2 plot, following the same percentage-based approach. The vegetation height of the field layer was measured with an accuracy of 1 cm at five representative locations, and the mean value was calculated. Sunshine duration in June was measured in the center of each plot using a horizontoscope (Table 1). To approximate the local climate, we calculated the amount of direct incident radiation (in MJ $cm^2 \times yr^{-1}$) based on the latitude, aspect and slope of each plot (McCune and Keon, 2002).

During the first survey, the number of empty snail shells from species found in the study area (*Arianta arbustorum, Bradybaena similaris, Cepaea* spp., *Fruticicola fruticum, Helicella itala, Helix pomatia, Xerolenta obvia*), which are relevant for helicophilous (snail shell-dwelling) wild bee species according to Westrich (2018) and Heneberg et al. (2020), was counted, provided that the vegetation had not yet covered them.

The age of the restored plots, i.e. the time since shrub-cutting had been carried out, varied from six to eleven years. However, this variable could not be used in the analyses because precise information on the date of the restoration measures was not available for all plots. Instead, we used the variables height of the shrub layer and total cover of vegetation as an indicator for the time period since the application of the restoration measures (Table 1; cf. Poniatowski et al., 2020; Helbing et al., 2021).

2.4. Bee sampling

Wild bee assemblages were sampled from late March to late August 2020 in the same 16 m^2 plots as described above. Each plot was visited seven times, with an interval of three weeks between each survey. During a standardized sampling period of 20 min, we collected wild bees under favorable weather conditions (dry, sunny and windless days with a minimum air temperature of 15 °C) from 10 am to 5 pm. Detected bees were collected using an insect net (e.g., Kettermann et al., 2022). Species that could be identified in the field were released after identification. All other individuals were killed with ethyl acetate and identified in the lab using binoculars. All bees were identified to species level according to the identification keys provided in Appendix A. For the statistical analysis, species

Table 1
Overview of environmental parameters in the two grassland types (mean ± SE, minimum and maximum). Differences in parameters between restored grassland (RestGras, $N = 21$) and calcareous grasslands (Control, $N = 21$) were analyzed using Generalized Linear Mixed-effects Models (negative binomial error structure) with 'subarea' as a random intercept. Statistical significance is indicated as follows: n.s. = not significant, $^{*}P < 0.05$; $^{***}P < 0.001$.

Parameter	RestGras						Control								
	Mean (± SE)			Min.–Max.			Mean (± SE)			Min.–Max.			Estimate	*Z*	*P*
Local climate															
DIR (MJ cm^{-2} × yr^{-1})[a]	0.86	±	0.03	0.48	–	0.95	0.84	±	0.02	0.52	–	0.94	0.013	0.028	n.s.
Sunshine June (h/day)[b]	12.7	±	0.7	4.0	–	16.0	14.4	±	0.3	11.0	–	16.0	-0.127	-0.395	n.s.
Habitat structure (%)															
Shrub layer	18.7	±	3.1	2.5	–	56.3	5.6	±	2.0	0.0	–	42.5	1.309	3.753	***
Field layer	56.9	±	3.1	25	–	81.3	71.6	±	2.8	30.0	–	85.0	-0.229	-0.737	n.s.
Bare ground	11.3	±	1.4	2.5	–	23.8	8.7	±	1.6	0.0	–	21.3	0.255	0.786	n.s.
Litter layer	14.4	±	1.3	7.5	–	32.5	15.0	±	1.0	8.8	–	29.0	-0.038	-0.119	n.s.
Vegetation height (cm)	22.6	±	1.7	10.3	–	41.9	10.8	±	0.8	5.9	–	21.4	0.738	2.314	*
No. snail shells	5.0	±	0.9	0.0	–	13.0	2.2	±	0.9	0.0	–	7.0	0.819	2.214	*
Nectar and pollen sources															
No. flower species	21.6	±	1.3	13	–	34	21.0	±	1.0	9	–	26	0.009	0.029	n.s.
Flower cover (%)[c]	101	±	11	42	–	209	99	±	10	27	–	211	0.016	0.050	n.s.

[a] Direct incident radiation (DIR) was calculated according to McCune and Keon (2002).
[b] Measured by using a horizontoscope; mean of four measures at N, E, S, W (Holtmann et al., 2018).
[c] The maximum flower cover in % for each species was recorded during the seven survey dates for each plot. The highest value per species was used, and the total flower cover for each plot was calculated by summing the values for all species.

richness per plot was used, referring to the total number of species recorded across all seven surveys. Another response variable was abundance per plot, calculated by summing the maximum number of individuals observed per species across the seven visits (cf. Fartmann et al., 2013; Holtmann et al., 2018). This approach ensures that the highest observed count of each species is accounted for, minimizing the risk of underestimating abundance due to temporal variability in observations. Species richness and abundance were then categorized according to the following four groups: all, threatened, belowground-nesting and snail shell-nesting species. The threat status was based on Esser et al. (2010) for North Rhine-Westphalia and Tischendorf et al. (2009) for Hesse. Species listed as near-threatened, vulnerable, endangered or threatened with unknown extent in either of the two federal states were classified as 'threatened species'. Belowground-nesting and snail shell-nesting species were classified according to Westrich (2018). Parasites whose hosts belong to belowground nesters were also assigned to the corresponding category.

2.5. Statistical analysis

All statistical analyses were performed using R 4.4.2 (R Development Core Team, 2024). We applied Generalized Linear Mixed-effects Models (GLMMs), incorporating 'subarea' (see Section 2.2) as a random intercept (lme4 package; Bates et al., 2025). Univariable GLMMs were used to compare environmental parameters and the number of all, threatened, belowground-nesting and snail shell-nesting bee species between the two grassland types. Depending on the distribution of the response variable, GLMMs with either a negative binomial or Poisson error structure were applied. The significance of the predictor variable was assessed with likelihood-ratio tests (Type III tests). Model assumptions were assessed by visually inspecting residual plots and quantile-quantile (Q-Q) plots. No violations of these assumptions were detected.

Species composition of restored grasslands and control plots were compared via non-metric multidimensional scaling (NMDS; R package vegan, metaMDS function; (Oksanen et al., 2022) with the Kulczynski distance as a distance measure and a maximum number of 200 random starts in search of a stable solution. The four studied species groups were analyzed separately. We included only those species in the analyses that were sampled on at least three plots. For each species group, we performed a Permutational Multivariate Analysis of Variance with 999 permutations (PERMANOVA; Bray-Curtis distance; R package vegan, adonis2 function; (Oksanen et al., 2022) to test for significant differences between restored grasslands and control plots.

We conducted multivariable GLMMs to determine which environmental parameters (see Section 2.3) influenced the species richness and abundance of all, threatened, belowground-nesting and snail shell-nesting bees (see Section 2.4) within both habitat types (RestGras and control, $N = 42$). Prior to the analyses, all predictor variables were tested for multicollinearity. When two or more variables were strongly intercorrelated (Pearson correlation [r], $|r| > 0.6$, $P < 0.05$), only one—the ecologically most comprehensible variable—was included in the statistical models (e.g. Kettermann et al., 2022; Tables B1 and B2). Intercorrelation occurred in only two cases: between shrub layer and field layer ($|r| = 0.90$), and between vegetation height and shrub cover ($|r| = 0.72$). In the multivariate model where these correlations were relevant, shrub layer was selected as the ecologically most meaningful variable, whereas field layer cover and vegetation height were excluded from the model.

To prevent model overfitting, the construction of the multivariable GLMMs was conducted in two steps. First, univariable GLMMs were applied to all possible combinations of response and predictor variables to identify predictors significantly associated with the response variable (likelihood ratio tests, $P < 0.05$) (Tables B1 and B2). In the second step, multivariable models were developed for all bee species, threatened species, belowground-nesting and snail shell-nesting bee species using the significant predictor variables identified in the first stage.

In order to identify the most relevant environmental parameters and their relative importance (RI) within our multivariable models, we used model averaging based on an information-theoretic approach (Grueber et al., 2011). This was performed using the 'dredge' function (MuMIn package; Bartoń, 2024) considering only top-ranked models with $\Delta AIC_C < 3$ (cf. Grueber et al., 2011).

To investigate how environmental conditions shape community-level functional composition, we performed an RLQ analysis (Dolédec et al., 1996), which integrates three data tables:

R: a site-by-variable table of environmental conditions,

L: a site-by-species table of species abundances, and

Q: a species-by-trait table containing categorical functional traits.

The trait nesting type comprised the modalities belowground-nesting, snail shell-nesting, and other aboveground-nesting strategies. Given the ecological specificity of snail shell-nesting, this modality was emphasized in subsequent analyses. To exclude rare and randomly distributed species and to identify robust patterns, only species with a constancy of at least 10 % were included in the analysis.

First, we conducted a correspondence analysis (CA) on the L-table to identify the major gradients in species composition based on abundance data. Then, we applied a principal component analysis (PCA) to the environmental variables in the R-table. Since the functional trait data consisted exclusively of categorical variables, a Hill–Smith analysis was applied to the Q-table to account for their nominal nature.

The RLQ analysis integrates the results of these three ordinations to assess the joint structure between environmental conditions and species traits, mediated by species abundances. The resulting RLQ axes represent combinations of traits and environmental gradients that are most strongly associated across sites.

The statistical significance of the trait–environment associations was tested using a Monte Carlo permutation procedure with 49,999 iterations, as implemented in the ade4 package in R (Dray and Dufour, 2007).

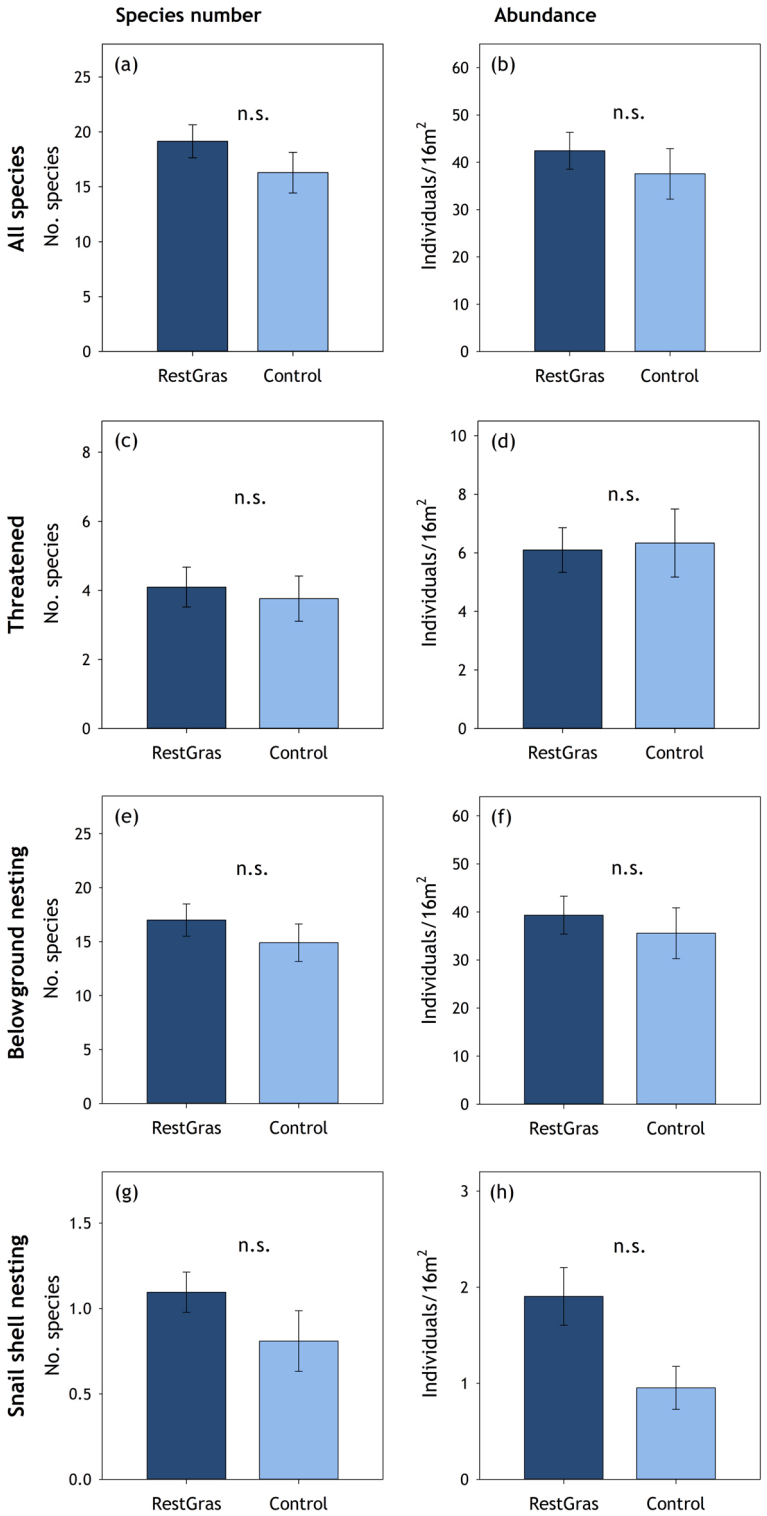

Fig. 3. Mean values (±SE) of all (a), threatened (b), belowground-nesting (c) and snail shell-nesting bee species (d) in restored grasslands (RestGras, $N = 21$) and calcareous grasslands (Control, $N = 21$). Species number was pooled for each plot across all visits, while abundance was determined by summing the maximum number of individuals observed per species across all visits. Differences between the habitat types were analyzed using Generalized Linear Mixed-effects Models (GLMMs) with a Poisson error structure and 'subarea' as a random intercept. Statistical significance is indicated as follows: n.s. = not significant.

3. Results

3.1. Environmental conditions

Local climatic conditions as well as nectar and pollen sources did not differ between restored grassland (RestGras) and extant calcareous grassland (Control) (Table 1). By contrast, our analyses showed differences in structural parameters. RestGras plots were characterized by significantly higher cover of shrubs, taller vegetation and higher number of snail shells compared to the control plots.

3.2. Bee species assemblages

In total, we detected 127 bee species across the 42 plots (Table B3). Among them, 39 species (31 %) were classified as threatened, 109 (86 %) as belowground-nesting. The latter group comprises three species that construct their nests within snail shells. Species richness and abundance of bees (including all, threatened, belowground-nesting and snail shell-nesting species) did not differ between the two habitat types (Fig. 3; Table B4). However, differences between RestGras and Control in terms of species composition were detected using NMDS (Fig. 4). Although bees exhibited some overlap between the two habitat types, several plots of RestGras and Control were dominated by distinct species assemblages, highlighting habitat-specific community composition.

Direct incident radiation was the the most important predictor of species richness and abundance across all, threatened and belowground-nesting bee species (Fig. 5 and Fig. B1; Table B5). Additionally, a higher flower cover correlated positively with both the number and abundance of all species, as well as belowground-nesting species. Among snail shell-nesting bees, a higher shrub layer was the only factor positively affecting species richness and abundance.

The RLQ analysis revealed strong associations between key environmental variables (e.g. vegetation height, shrub layer and field layer) and specific functional traits (e.g. belowground-nesting, snail shell-nesting, and other aboveground-nesting strategies) (Table 2). The first RLQ axis explained 78 % of the total covariation between environmental variables and functional traits and was highly significant ($P < 0.001$). These results suggest that variation in species composition across sites is not random but linked to underlying environmental gradients.

4. Discussion

4.1. Differences between the two grassland types

In our comparison of RestGras and Control, we observed notable differences in habitat structure. RestGras were characterized by higher cover of shrubs, taller vegetation and higher number of snail shells than Control. Despite these structural differences, species richness and abundance remained similar across all studied groups (all, threatened, belowground-nesting and snail shell-nesting species). However, species composition varied to a certain extent between the two habitat types.

Accordingly, RestGras contributes to a higher overall bee beta diversity of the entire calcareous grassland ecosystem (cf. Rivers-Moore et al., 2020). Structurally, the restored grasslands were comparable to fringes or forest edges on calcareous soils, which serve as habitats for some species. For instance, *Anthophora furcata* and *Ceratina cyanea* were found exclusively in restored grasslands. Both species prefer edge structures, with *Anthophora furcata* nesting in deadwood and *Ceratina cyanea* using plant stems (e.g. *Carduus nutans* and *Rubus* spp.) (Westrich, 2018)—resources that are scarce in open calcareous grasslands. Moreover, the high frequency of *Osmia bicolor* in RestGras plots can be attributed to the large number of snail shells in the restored grasslands, which the species needs for nesting (Westrich, 2018, see also Section 3.2 below). Other species occur mainly in the RestGras plots due to the availability of their specific pollen sources there. *Andrena florea*, for example, is an oligolectic species that collects pollen exclusively from *Bryonia* species (Westrich, 2018). The pollen source in the region is the fringe species *Bryonia dioica*, which exclusively occurred in RestGras plots (own observation). The herb *Stachys germanica* was also restricted to restored grasslands (own observation), as previously noted by

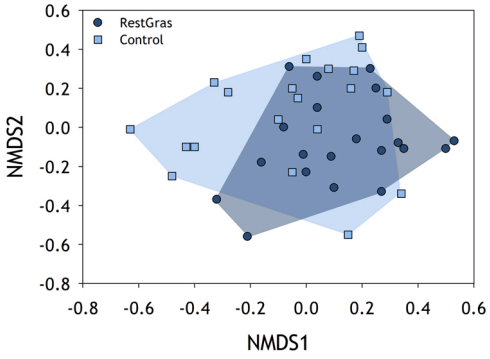

Fig. 4. NMDS ordinations (Kulczynski distance, four dimensions) for assemblages of wild bees (based on 127 species and 1680 individuals, stress= 0.15) across restored grasslands ($N = 21$) and calcareous grasslands (Control, $N = 21$).

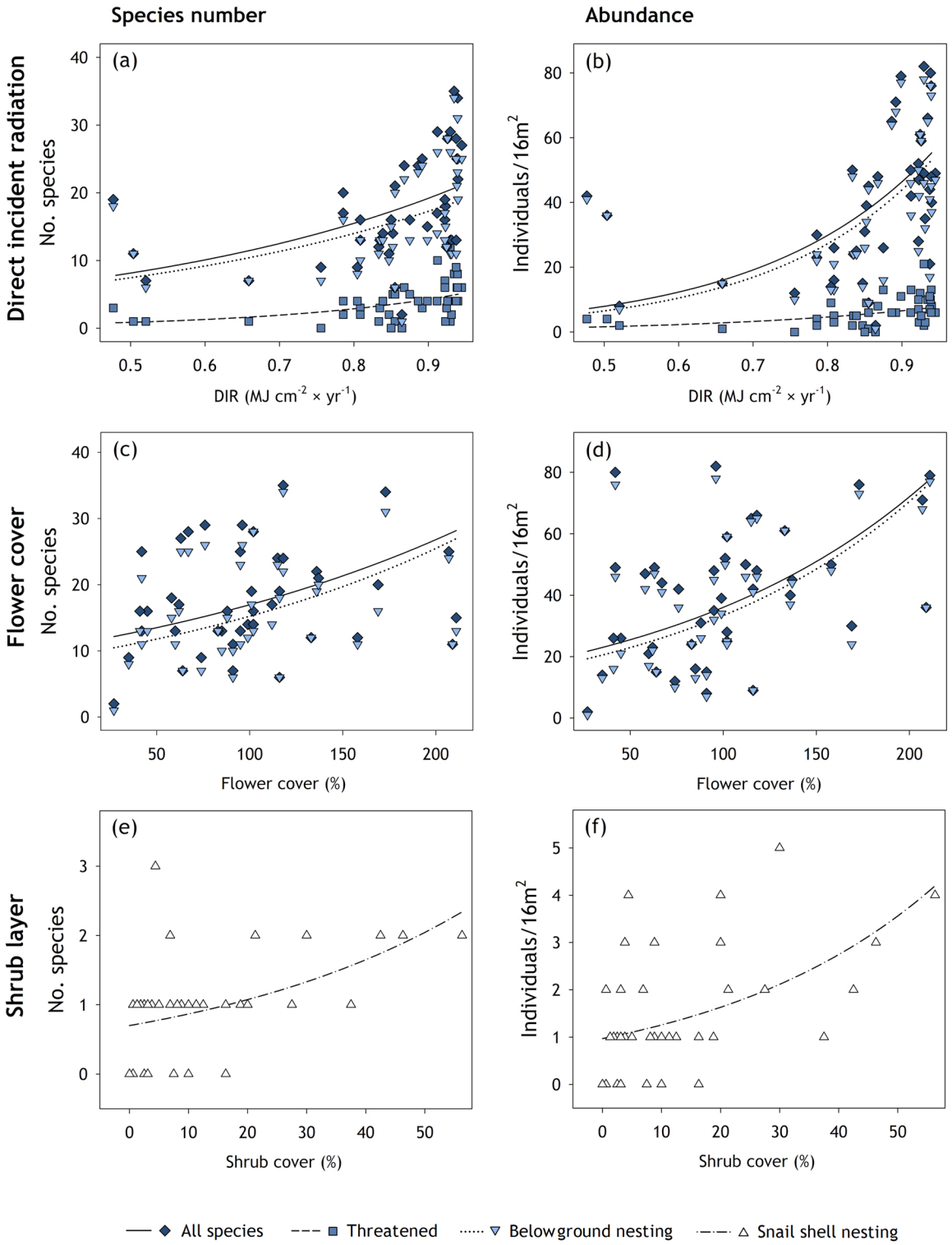

Fig. 5. Relationship between significant environmental parameters and species number (a, c, e), as well as abundance (b, d, f) of wild bees based on multivariable models (Poisson error structure, $N = 42$). The regression slopes were fitted using univariable Generalized Linear Mixed-effects Models with 'subarea' as a random intercept.

Table 2
Results of the RLQ analysis linking environmental variables (R), species composition (L), and functional traits (Q). For each axis, the percentage of explained variance is reported, along with the three environmental variables showing the strongest correlations with the RLQ axes and the three traits with the highest loadings. The significance of the global RLQ relationship was assessed by permutation tests (49,999 iterations). Statistical significance is indicated as follows: n.s. = not significant; ***$P < 0.001$.

Axis	% var. explained	Environmental correlations	Functional traits (loadings)	*P*
1	78	Vegetation height (0.314) Shrub layer (0.287) Field layer (0.265)	Belowground nesting (−0.225) Snail shell nesting (0.216) Other aboveground nesting (0.058)	***
2	21	Direct incident radiation (0.274) No. Flower species (0.243) Field layer (0.201)	Belowground nesting (0.010) Snail shell nesting (−0.083) Other aboveground nesting (0.184)	n.s.

Poniatowski et al. (2020). Along with *S. recta* and *S. sylvatica* (which were also only found in RestGras plots; own observation), it represents an essential pollen source for *Anthophora furcata* (Westrich, 2018) and was also highly attractive to other Megachilidae and Apinae species (own observation). In addition, exclusive plant species in RestGras plots with high relevance for wild bees included *Carduus nutans*, *Cirsium vulgare* and *Veronica chamaedrys* (own observation, Kuppler et al., 2023).

By contrast, there were also some bee species that could only be observed in the control plots (e.g. *Andrena polita*, *Eucera nigrescens* and *Lasioglossum costulatum*) or which showed a clear preference for this habitat type (e.g. *Anthidium punctatum*, *Halictus rubicundus* and *Sphecodes gibbus*). This pattern is primarily attributable to the species-specific preferences for particular pollen sources. For instance, *Andrena polita* predominantly forages on *Hieracium pilosella* and *Leontodon hispidus* within the study area—both plant species that occur regularly in the control plots but are largely absent from the RestGras plots. A comparable pattern is observed for *Eucera nigrescens* and *Lasioglossum costulatum*, which also exhibit a high degree of specialization on pollen sources that are mainly associated with the control plots.

Nevertheless, there were many bee species, which regularly occurred in both grassland types. This can at least partly be explained by the relatively high mobility of bees and their complex habitat requirements (cf. Westrich, 2018). In contrast to other insects such as leafhoppers, which usually exhibit a high philopatry (Poniatowski et al., 2018b; Helbing et al., 2021), bees have to collect pollen and transport it over more or less long distances to their nesting sites to supply their brood. Depending on the species and its body size, documented foraging distances range from 100 to over 1000 m (Greenleaf et al., 2007; Westrich, 2018). However, only a few individuals are capable of foraging over such long distances (Zurbuchen et al., 2010). Our results indicate that the RestGras and control plots in the calcareous grassland ecosystem are well connected for wild bees, allowing for continuous exchange in terms of foraging resources and nesting sites. Considering this, the high mobility of bees can additionally explain the absence of significant differences in species richness and abundance between both habitat types.

4.2. Environmental drivers of species richness and abundance of wild bees

Wild bees, like many other insects, depend strongly on a warm microclimate that promotes their activity and larval development (Roulston and Goodell, 2011; Banaszak and Twerd, 2018; Proesmans et al., 2019). Direct Incident Radiation (DIR), which measures sunlight exposure and surface warming, thus positively influences species richness and abundance across wild bee communities, including threatened species and those nesting below ground. Belowground-nesting bees, in particular, rely heavily on dry and warm microclimatic conditions, as high humidity can destabilize their nests and increase the risk of fungal contamination of their brood (Antoine and Forrest, 2021). In contrast, aboveground-nesting sites—such as empty snail shells—typically offer more buffered and thermally stable conditions with respect to moisture fluctuations, but due to their direct exposure to sunlight, they face a higher risk of overheating. Accordingly, the significance of DIR is less pronounced for bees nesting in snail shells.

A high cover and diversity of flowers promoted both the species richness and abundance of wild bees (all and belowground nesting), which is consistent with numerous previous studies (Lozada-Gobilard et al., 2021; Kettermann et al., 2022; Streitberger et al., 2025). Flowering plants not only serve as a source of pollen and nectar, but parts of them are also needed for nest building (Requier and Leonhardt, 2020). However, a high flower density and richness alone is insufficient to sustain a diverse and abundant wild bee community (Grass et al., 2016). Instead, it is essential that there are adequate nesting structures such as bare ground available in the surroundings to support wild bee populations in the long term (Klaus et al., 2021; Gardein et al., 2022; Schubert et al., 2022; Kettermann et al., 2022).

The availability of empty snail shells is an essential prerequisite for the occurrence of snail shell-nesting bee species such as *Osmia aurulenta*, *O. bicolor*, and *O. spinulosa* (Heneberg et al., 2020). However, shell availability alone is often insufficient; additional resources such as pollen sources or a special microclimate must also be met for these species to establish (cf. Bogusch et al., 2019).

Our multivariable analysis identified a single significant environmental factor influencing snail shell-nesting bees: increased shrub cover was positively associated with both species richness and abundance. We propose that shrub cover exerts several indirect effects on shell-nesting species, offering a more comprehensive explanation for their occurrence than snail shell availability alone.

4.3. Effects of shrubs on shell availability

Prior to the implementation of restoration measures, the abandoned RestGras plots were characterized by a cooler and more humid microclimate due to the presence of shrubs and taller herbaceous vegetation—conditions generally favorable for snail populations (Moreno-Rueda, 2014; Kirchenbaur et al., 2017). This led to the gradual accumulation of empty snail shells over time.

Following shrub removal as part of the restoration, the microclimate shifted to conditions more suitable for wild bees, while the previously accumulated snail shells—especially from species rare in open dry grasslands (e.g. *Arianta arbustorum*, *Cepaea* spp., *Helix pomatia*)—became available as nesting structures. This shift was particularly reflected in increased densities and frequencies of *O. bicolor*, and to a lesser but still notable extent *O. spinolosa*, in the restored grasslands, as this species utilizes medium-sized shells of *A. arbustorum* and/or *Cepaea* spp. for nesting (Westrich, 2018).

Snail shell-nesting bees are generally considered disturbance-sensitive, as their fragile nesting structures are vulnerable to destruction from intensive grazing or mowing. Accordingly, significantly fewer snail shells were found in the open control plots, likely due to both a drier microclimate and mechanical disturbances caused by livestock grazing (Boschi and Baur, 2007; Hopfenmüller et al., 2020). In contrast, the higher proportion of shrubs in the restored grasslands created protected microsites, where snail shells were better preserved and remained available to helicophilous wild bees (Bogusch et al., 2020).

4.4. Effects of shrubs on microclimate

The snail shell-nesting species recorded in the study area are characteristic of ecotones—structurally diverse transitional habitats. Accordingly, they showed a clear preference for the RestGras plots. In particular, *O. bicolor* and *O. spinulosa* were predominantly found in these areas (cf. Tab. B3).

Compared to control plots, the RestGras plots featured taller vegetation and greater shrub cover, which may help buffer temperature and humidity fluctuations. Such moderated microclimatic conditions are known to promote successful brood development in cavity-nesting bees in general (Kierat et al., 2017), although this has not yet been demonstrated specifically for snail shell-nesting bees. However, it is noteworthy that vegetation height in the RestGras plots averaged only 23 cm, and mean shrub cover was approximately 20 %. These habitats were thus neither tall-growing nor heavily shaded. On the contrary, a higher DIR, as a proxy for solar exposure and surface warming (see above), may also have had a positive effect, although the result narrowly missed statistical significance.

5. Conclusions

Although restored calcareous grasslands (RestGras) do not, in isolation, reach the ecological quality of traditionally managed sites, they nonetheless constitute a meaningful contribution to the broader calcareous grassland ecosystem (Poniatowski et al., 2020; Helbing et al., 2021). Structurally, they exhibit increased shrub cover and taller vegetation, rendering them more similar to ecotone habitats in both structure and floristic composition.

Importantly, these sites provide a range of critical resources for wild bees, including deadwood, plant stems, and specific flowering plants. Additionally, RestGras offer further key nesting materials such as snail shells, which are utilized by helicophilous wild bee species.

As a result, species assemblages in the RestGras plots diverge—at least partially—from those found in the control plots. Furthermore, our analyses demonstrate distinct functional differences between these habitat types. This highlights the role of structural heterogeneity in facilitating diverse nesting strategies and in supporting the persistence of specialist species.

Rather than being regarded as ecologically inferior transitional stages, restored calcareous grasslands should be acknowledged as valuable, complementary components within the calcareous grassland mosaic. At the regional scale, these areas increase wild bee beta diversity by enhancing habitat heterogeneity and expanding the range of available ecological requisites.

These findings underscore the necessity of targeted restoration strategies. Priority should be given to sites characterized by low nutrient content, shallow topsoil and warm microclimates (high Direct Incident Radiation), as these conditions favor the establishment of unique plant communities and the insect assemblages adapted to them (Poniatowski et al., 2020; Helbing et al., 2021; this study). Additionally, maintaining a mosaic of different successional stages within calcareous grasslands can increase diversity of pollinators such as wild bees while contributing to higher ecosystem services in the surrounding landscapes.

CRediT authorship contribution statement

Marcel Kettermann: Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Conceptualization. **Thomas Fartmann:** Writing – review & editing, Project administration, Funding acquisition. **Dominik Poniatowski:** Writing – review & editing, Validation, Methodology, Conceptualization.

Funding

This study was funded by the German Federal Agency for Nature Conservation (Bundesamt für Naturschutz) (Grant number 3516892017).

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.

Acknowledgements

We would like to thank Jürgen Düster and Henny Hartmann-Dinges (both from Fachdienst Landschaftspflege, Landkreis Kassel), Burkhard Beinlich, Frank Grawe and Sven Mindermann (all from Landschaftsstation im Kreis Höxter e. V.) as well as Wilfried Bettenhausen and Reinhard Vollmer (both from HessenForst) for providing background information on the study area. Permits to catch wild bees within nature reserves were issued by the Landscape Authority Höxter (Untere Naturschutzbehörde Höxter) and the Regional Council of Kassel (Regierungspräsidium Kassel). We are grateful to three anonymous reviewers for their valuable comments on the manuscript.

Appendix

Identification literature for bees

Amiet, F., 1996. Hymenoptera Apidae, 1. Teil. Allgemeiner Teil, Gattungsschlüssel, Die Gattungen *Apis*, *Bombus* und *Psithyrus*. Insecta Helvetica 12, 98 pp.

Amiet, F., Herrmann, M., Müller, A., Neumeyer, R., 2001. Apidae 3 — *Halictus*, *Lasioglossum*. Fauna Helvetica 6, 208 pp.

Amiet, F., Herrmann, M., Müller, A., Neumeyer, R., 2004. Apidae 4 — *Anthidium*, *Chelostoma*, *Coelioxys*, *Dioxys*, *Heriades*, *Lithurgus*, *Megachile, Osmia*, *Stelis*. Fauna Helvetica 9, 274 pp.

Amiet, F., Herrmann, M., Müller, A., Neumeyer, R., 2007. Apidae 5 — *Ammobates*, *Ammobatoides*, *Anthophora*, *Biastes*, *Ceratina*, *Dasypoda*, *Epeoloides*, *Epeolus*, *Eucera*, *Macropis*, *Melecta*, *Melitta*, *Nomada*, *Pasites*, *Tetralonia*, *Thyreus*, *Xylocopa*. Fauna Helvetica 20, 356 pp.

Amiet, F., Herrmann, M., Müller, A., Neumeyer, R., 2010. Apidae 6 — *Andrena*, *Melitturga*, *Panurginus*, *Panurgus*. Fauna Helvetica 26, 317 pp.

Amiet, F., Müller, A., Neumeyer, R., 1999. Apidae 2 — *Colletes*, *Dufourea*, *Hylaeus*, *Nomia*, *Nomioides*, *Rhophitoides*, *Rophites*, *Sphecodes*, *Systropha*. Fauna Helvetica 4, 239 pp.

Bogusch, P., Straka, J., 2012. Review and identification of the cuckoo bees of central Europe (Hymenoptera: Halictidae: *Sphecodes*). Zootaxa 3311: 1—41. https://doi.org/10.11646/zootaxa.3311.1.1.

Dathe, H. H., Scheuchl, E., Ockermüller, E., 2016. Illustrierte Bestimmungstabelle für die Arten der Gattung *Hylaeus* F. (Maskenbienen) in Deutschland, Österreich und der Schweiz. Entomologica Austriaca, Supplement 1, 51 pp.

Praz, C., Genoud, D., Vaucher, K., Bénon, D., Monks, J., Wood, T. J., 2022. Unexpected levels of cryptic diversity in European bees of the genus *Andrena* subgenus *Taeniandrena* (Hymenoptera, Andrenidae): implications for conservation. J. Hymenopt. Res. 91, 375–428. https://doi.org/10.3897/jhr.91.82761.

Scheuchl, E., 2000. Illustrierte Bestimmungstabellen der Wildbienen Deutschlands und Österreichs. Band I: Anthophoridae, second ed. Eigenverlag, Velden.

Scheuchl, E., 2006. Illustrierte Bestimmungstabellen der Wildbienen Deutschlands und Osterreichs. Band II: Schlüssel der Arten der Familien Megachilidae und Melittidae. Apollo Books, Stenstrup.

Scheuchl, E., Schwenninger, H. R., Burger, R., Diestelhorst, O., Kuhlmann, M., Saure, C., Schmid-Egger, C. & Silló, N. (2023) Die Wildbienenarten Deutschlands–Kritisches Verzeichnis und aktualisierte Checkliste der Wildbienen Deutschlands (Hymenoptera, Anthophila). Anthophila, 1(1), 25–138.

Schmid-Egger, C., Scheuchl, E., 1997. Illustrierte Bestimmungstabellen der Wildbienen Deutschlands und Österreichs unter Berücksichtigung der Arten der Schweiz. Band III: Andrenidae. Eigenverlag, Velden.

Straka, J., Bogusch, P., 2011. Contribution to the taxonomy of the *Hylaeus gibbus* species group in Europe (Hymenoptera, Apoidea and Colletidae). Zootaxa, 2932, 51—67. https://doi.org/10.11646/zootaxa.2932.1.6.

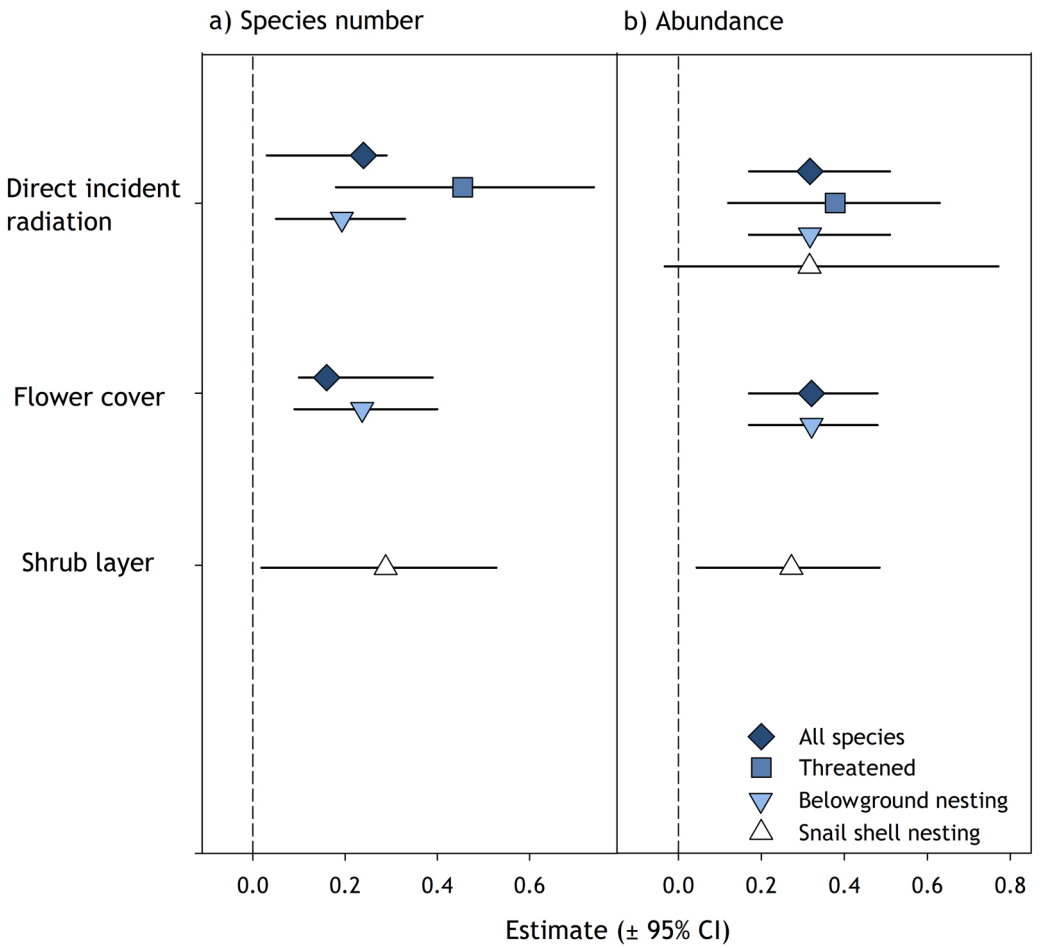

Figure B1. Parameter estimates for the relationship between species number (a) and abundance (b) of wild bees and environmental parameters (Poisson error structure) using multivariable GLMMs, including 'subarea' as a random intercept. Model-averaged coefficients (standardized estimates ± 95 % confidence intervals CI) derived from the top-ranked models ($\Delta AIC_C < 3$) are shown. Confidence intervals of significant predictors ($P < 0.05$) do not cross x = 0

Table B1 (Species number)

Table B1
Univariable models (GLMMs, Poisson error structure): Influence of environmental parameters (predictor variables) on the species number of all (a), threatened (b), belowground-nesting (c) and snail shell-nesting species (d) across all plots ($N = 42$). DIR = Direct incident radiation, Veg. height = Vegetation height. Statistical significance is indicated as follows: n.s. = not significant, $P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$

Parameter	All species			Threatened			Belowground nesting			Snail shell nesting		
	Estimate	SE	*P*	Estimate	SE	*P*	Estimate	SE	*P*	Estimate	SE	*P*
DIR	0.219	0.066	***	0.455	0.139	**	0.207	0.071	**	0.436	0.246	n.s.
Sunshine	–0.076	0.074	n.s.	0.013	0.115	n.s.	–0.007	0.079	n.s.	0.032	0.182	n.s.
Shrub layer	0.135	0.067	*	0.168	0.100	n.s.	0.127	0.071	n.s.	0.288	0.129	*
Field layer	–0.105	0.071	n.s.	–0.132	0.097	n.s.	–0.097	0.075	n.s.	–0.270	0.146	n.s.
Bare ground	0.108	0.070	n.s.	0.136	0.095	n.s.	0.110	0.074	n.s.	0.058	0.162	n.s.
Litter layer	–0.137	0.070	*	–0.174	0.100	n.s.	–0.164	0.071	*	–0.111	0.174	n.s.
Vegetation height	0.080	0.076	n.s.	0.034	0.101	n.s.	0.068	0.073	n.s.	0.230	0.144	n.s.
Snail shells	0.112	0.070	n.s.	0.150	0.101	n.s.	0.101	0.072	n.s.	0.267	0.140	n.s.
Flower species	0.112	0.079	n.s.	0.082	0.110	n.s.	0.116	0.081	n.s.	–0.088	0.164	n.s.
Flower cover	0.0178	0.073	*	0.200	0.108	n.s.	0.202	0.077	**	–0.001	0.166	n.s.

Table B2 (Abundance)

Table B2
Univariable models (GLMMs, Poisson error structure): Influence of environmental parameters (predictor variables) on the abundance of all (a), threatened (b), belowground-nesting (c) and snail shell-nesting species (d) across all plots ($N = 42$). DIR = Direct incident radiation. Statistical significance is indicated as follows: n.s. = not significant, $P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$

Parameter	All species			Threatened			Belowground nesting			Snail shell nesting		
	Estimate	SE	*P*	Estimate	SE	*P*	Estimate	SE	*P*	Estimate	SE	*P*
DIR	0.276	0.092	**	0.378	0.124	**	0.272	0.099	**	0.472	0.220	*
Sunshine	–0.123	0.103	n.s.	0.059	0.123	n.s.	–0.137	0.105	n.s.	0.041	0.153	n.s.
Shrub layer	0.102	0.100	n.s.	0.209	0.110	n.s.	0.093	0.107	n.s.	0.350	0.101	***
Field layer	–0.153	0.099	n.s.	–0.185	0.110	n.s.	–0.146	0.107	n.s.	–0.331	0.130	*
Bare ground	0.215	0.095	*	0.106	0.113	n.s.	0.242	0.101	*	–0.068	0.137	n.s.
Litter layer	–0.106	0.099	n.s.	–0.053	0.109	n.s.	–0.152	0.105	n.s.	0.185	0.128	n.s.
Vegetation height	0.065	0.100	n.s.	0.129	0.124	n.s.	0.434	0.107	n.s.	0.317	0.127	*
Snail shells	0.119	0.099	n.s.	0.161	0.117	n.s.	0.101	0.072	n.s.	0.283	0.124	*
Flower species	0.131	0.103	n.s.	–0.002	0.121	n.s.	0.160	0.104	n.s.	–0.241	0.145	n.s.
Flower cover	0.0315	0.099	**	0.221	0.120	n.s.	0.344	0.104	***	–0.091	0.150	n.s.

Table B3
Frequencies (%) of all bee species in restored grasslands (RestGras, $N = 21$) and calcareous grasslands (Control, $N = 21$). Nomenclature: (Scheuchl et al., 2023). Threatened species: Tischendorf et al. (2009), Esser et al. (2010); see Section 2 for details

Species	Threatened	RestGras (%)	Control (%)
Andrena afzeliella	.	.	4.8
Andrena alfkenella	x	9.5	4.8
Andrena bicolor	.	9.5	14.3
Andrena cineraria	.	28.6	.
Andrena dorsata	.	4.8	4.8
Andrena falsifica	x	9.5	4.8
Andrena flavipes	.	52.4	38.1
Andrena florea	.	4.8	.
Andrena fulva	.	9.5	.
Andrena gravida	.	23.8	4.8
Andrena haemorrhoa	.	4.8	.
Andrena labiata	.	4.8	.
Andrena minutula	.	42.9	42.9
Andrena minutuloides	.	42.9	28.6
Andrena nigroaenea	.	4.8	4.8
Andrena nitida	.	4.8	.
Andrena ovatula	.	23.8	38.1
Andrena polita	x	.	9.5
Andrena proxima	.	4.8	.
Andrena strohmella	.	.	4.8
Andrena subopaca	.	9.5	.
Andrena vaga	.	.	4.8
Andrena viridescens	x	.	4.8
Andrena wilkella	.	4.8	9.5
Anthidiellum strigatum	.	.	4.8
Anthidium manicatum	.	23.8	4.8
Anthidium punctatum	x	4.8	19.0
Anthophora aestivalis	x	14.3	33.3
Anthophora furcata	x	19.0	.
Anthophora plumipes	.	19.0	4.8
Bombus bohemicus	.	19.0	9.5
Bombus hortorum	.	9.5	4.8
Bombus hypnorum	.	9.5	.
Bombus lapidarius	.	95.2	95.2
Bombus lucorum Komplex	.	71.4	61.9
Bombus pascuorum	.	52.4	42.9
Bombus pratorum	.	9.5	9.5
Bombus rupestris	.	19.0	9.5
Bombus sylvarum	x	23.8	23.8
Bombus sylvestris	.	14.3	4.8

(*continued on next page*)

Table B3 (*continued*)

Species	Threatened	RestGras (%)	Control (%)
Bombus vestalis	.	4.8	.
Ceratina cyanea	.	9.5	.
Chelostoma campanularum	.	4.8	4.8
Chelostoma rapunculi	.	.	4.8
Coelioxys afra	x	4.8	4.8
Coelioxys mandibularis	.	4.8	4.8
Coelioxys rufescens	x	4.8	.
Colletes cunicularius	.	33.3	42.9
Colletes similis	x	9.5	4.8
Epeolus variegatus	.	4.8	9.5
Eucera longicornis	x	.	4.8
Eucera nigrescens	x	.	28.6
Halictus maculatus	x	.	4.8
Halictus quadricinctus	x	19.0	4.8
Halictus rubicundus	.	4.8	38.1
Halictus scabiosae	.	23.8	9.5
Halictus simplex	x	42.9	28.6
Halictus tumolorum	.	71.4	47.6
Heriades truncorum	.	4.8	.
Hylaeus brevicornis	.	.	4.8
Hylaeus communis	.	4.8	.
Hylaeus confusus	.	9.5	.
Hylaeus difformis	.	9.5	.
Hylaeus dilatatus	.	19.0	14.3
Hylaeus gredleri	.	4.8	.
Hylaeus nigritus	x	4.8	4.8
Hylaeus styriacus	.	.	4.8
Lasiglossum laticeps	.	9.5	.
Lasioglossum albipes	.	9.5	.
Lasioglossum calceatum	.	33.3	14.3
Lasioglossum costulatum	x	.	19.0
Lasioglossum fulvicorne	.	28.6	28.6
Lasioglossum interruptum	x	.	4.8
Lasioglossum laevigatum	x	4.8	.
Lasioglossum laticeps	.	23.8	38.1
Lasioglossum lativentre	x	14.3	.
Lasioglossum leucozonium	.	9.5	23.8
Lasioglossum lineare	x	9.5	9.5
Lasioglossum malachurum	x	4.8	.
Lasioglossum minutissimum	.	14.3	.
Lasioglossum minutulum	x	4.8	4.8
Lasioglossum morio	.	95.2	66.7
Lasioglossum nitidiusculum	x	4.8	.
Lasioglossum parvulum	x	.	9.5
Lasioglossum pauxillum	.	95.2	71.4
Lasioglossum pygmaeum	x	19.0	23.8
Lasioglossum villosulum	.	23.8	23.8
Megachile ericetorum	x	14.3	9.5
Megachile nigriventris	.	.	4.8
Megachile pillidens	x	19.0	19.0
Megachile versicolor	.	14.3	4.8
Megachile willughbiella	.	.	9.5
Melitta haemorrhoidalis	.	4.8	14.3
Melitta leporina	x	4.8	.
Nomada bifasciata	.	9.5	4.8
Nomada fabriciana	.	23.8	9.5
Nomada flava	.	4.8	.
Nomada flavoguttata	.	38.1	19.0
Nomada fucata	.	33.3	23.8
Nomada goodeniana	.	4.8	.
Nomada guttulata	x	4.8	.
Nomada lathburiana	.	4.8	.
Nomada sexfasciata	x	9.5	.
Nomada sheppardana	.	42.9	38.1
Nomada succincta	.	4.8	14.3
Osmia aurulenta	x	9.5	23.8
Osmia bicolor	x	85.7	52.4
Osmia bicornis	.	4.8	9.5
Osmia brevicornis	x	.	4.8
Osmia spinulosa	x	14.3	4.8

(*continued on next page*)

Table B3 (*continued*)

Species	Threatened	RestGras (%)	Control (%)
Panurgus calcaratus	.	4.8	.
Sphecodes albilabris	.	9.5	.
Sphecodes crassus	.	23.8	57.1
Sphecodes ephippius	.	33.3	52.4
Sphecodes ferruginatus	.	4.8	4.8
Sphecodes geofrellus	.	19.0	4.8
Sphecodes gibbus	.	9.5	33.3
Sphecodes hyalinatus	.	4.8	14.3
Sphecodes miniatus	.	4.8	4.8
Sphecodes monilicornis	.	4.8	9.5
Sphecodes niger	.	4.8	14.3
Sphecodes puncticeps	.	4.8	.
Sphecodes rufiventris	x	4.8	.
Stelis ornatula	.	4.8	.
Trachusa byssina	x	4.8	.
Xylocopa violacea	x	9.5	4.8

Table B4
Overview of all, threatened, belowground-nesting and snail shell-nesting species (mean ± SE, minimum and maximum). Differences in parameters between restored grassland (RestGras, $N = 21$) and calcareous grasslands (Control, $N = 21$) were analyzed using Generalized Linear Mixed-effects Models (negative binomial error structure) with 'subarea' as a random intercept. Statistical significance is indicated as follows: n.s. = not significant

Parameter	**RestGras**			**Control**			
	Mean (± SE)	Min.–Max.		Mean (± SE)	Min.–Max.		*P*
All species							
Species number	19.1 ± 1.5	9 – 35		16.3 ± 1.9	2 – 34		n.s.
Abundance	42.4 ± 3.9	12 – 80		37.6 ± 5.3	2 – 82		n.s.
Threatened							
Species number	4.1 ± 0.6	0 – 10		3.8 ± 0.7	0 – 12		n.s.
Abundance	6.1 ± 0.8	0 – 13		6.3 ± 1.2	0 – 21		n.s.
Belowground nesting							
Species number	17.0 ± 1.5	7 – 34		15.1 ± 1.8	1 – 31		n.s.
Abundance	39.3 ± 3.9	10 – 76		35.6 ± 5.3	1 – 78		n.s.
Snail shell nesting							
Species number	1.1 ± 0.1	0 – 2		0.8 ± 0.2	0 – 3		n.s.
Abundance	1.9 ± 0.3	0 – 5		1.0 ± 0.2	0 – 4		n.s.

Table B5
Influence of environmental parameters (predictor variables) on species number and abundance of all (a), threatened (b), belowground-nesting (c) and snail shell-nesting species (d) across all plots ($N = 42$). Effects were analyzed using Generalized Linear Mixed-effects Models (GLMMs) with a Poisson error structure and 'subarea' as a random intercept. Model-averaged coefficients (conditional averages) were derived from the top-ranked GLMMs ($\Delta AIC_C < 3$). R^2_m represents the variance explained by fixed effects, and R^2_c represents the variance explained by both fixed and random effects (Nakagawa et al., 2017). Statistical significance is indicated as follows: n.s. = not significant, $^*P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$

Parameter	Estimate	SE	Z	*P*
a) All species				
Species number ($R^2_m = 0.24–0.38$, $R^2_c = 0.71–0.73$, AIC= 286.0)				
(Intercept)	2.812	0.073	38.649	***
Direct incident radiation	0.240	0.069	3.494	***
Flower cover	0.162	0.066	2.466	*

(*continued on next page*)

Table B5 (*continued*)

Parameter	Estimate	SE	Z	*P*
Abundance (R^2_m = 0.44–0.45, R^2_c = 0.94, AIC= 368.2)				
(Intercept)	3.530	0.075	47.300	***
Direct incident radiation	0.321	0.077	4.151	***
Flower cover	0.317	0.076	4.198	***
b) Threatened				
Species number (R^2_m = 0.35, R^2_c = 0.51, AIC= 189.0)				
(Intercept)	1.249	0.137	9.177	***
Direct incident radiation	0.455	0.139	3.265	**
Abundance (R^2_m = 0.26, R^2_c = 0.68, AIC= 235.3)				
(Intercept)	1.647	0.120	13.779	***
Direct incident radiation	0.378	0.124	3.046	**
c) Belowground nesting				
Species number (R^2_m = 0.28–0.37, R^2_c =0.70–0.73, AIC= 281.4)				
(Intercept)	2.702	0.080	33.776	***
Direct incident radiation	0.237	0.074	3.217	**
Flower cover	0.193	0.069	2.800	**
Abundance (R^2_m = 0.44–0.45, R^2_c = 0.94, AIC= 366.8)				
(Intercept)	3.442	0.080	42.958	***
Direct incident radiation	0.323	0.083	3.909	***
Flower cover	0.354	0.081	3.355	***
d) Snail shell nesting				
Species number (R^2_m = 0.07, R^2_c =0.07, AIC= 99.4)				
(Intercept)	-0.096	0.165	-0.585	n.s.
Shrub layer	0.288	0.129	2.236	*
Abundance (R^2_m = 0.03–0.28, R^2_c = 0.72, AIC=126.5)				
(Intercept)	0.247	0.144	1.720	n.s.
Shrub layer	0.273	0.111	2.465	*
Direct incident radiation	0.426	0.203	1.557	n.s.

Data availability

Data are stored in the osnaData repository (DOI: https://doi.org/10.26249/FK2/GGCH0Z) and will be made publicly available upon article publication

References

Abrol, D.P., 2012. Pollination biology: biodiversity conservation and agricultural production, 792. Springer, New York.

Albrecht, M., Bossart, S., Tschanz, P., Keller, T., Sutter, L., 2023. Grassland extensification enhances nest densities of ground-nesting wild bees. J. Appl. Ecol. 60 (12), 2550–2560. https://doi.org/10.1111/1365-2664.14527.

Antoine, C.M., Forrest, J.R., 2021. Nesting habitat of ground-nesting bees: a review. Ecol. Entomol. 46 (2), 143–159. https://doi.org/10.1111/een.12986.

Banaszak, J., Twerd, L., 2018. Importance of thermophilous habitats for protection of wild bees (Apiformes). Community Ecol. 19 (3), 239–247. https://doi.org/10.1556/168.2018.19.3.5.

Bartoń, K. 2024. Package 'MuMIn'Version 1.48.4. Retrieved 10.1.2025 from ⟨https://CRAN.R-project.org/package=MuMIn⟩.

Bates, D., Maechler, M., Bolker, B., & Walker, S. 2025. Linear mixed-effects models using 'Eigen' and S4 (package lme4, version 1.1-36). Retrieved 15.1.2025 from ⟨https://cran.r-project.org/web/packages/lme4/lme4.pdf⟩.

Benton, T.G., Vickery, J.A., Wilson, J.D., 2003. Farmland biodiversity: is habitat heterogeneity the key? Trends Ecol. Evol. 18 (4), 182–188. https://doi.org/10.1016/S0169-5347(03)00011-9.

Bogusch, P., Roháček, J., Bañař, P., Astapenková, A., Kouklík, O., Pech, P., Janšta, P., Heller, K., Hlaváčková, L., Heneberg, P., 2019. The presence of high numbers of empty shells in anthropogenic habitats is insufficient to attract shell adopters among the insects. Insect Conserv. Divers. 12, 193–205. https://doi.org/10.1111/icad.12335.

Bogusch, P., Hlaváčková, L., Šilhán, K., Horsák, M., 2020. Long-term changes of steppe-associated wild bees differ between shell-nesting and ground-nesting species. J. Insect Conserv. 24, 513–523. ⟨https://link.springer.com/article/10.1007/s10841-020-00232-4⟩.

Boschi, C., Baur, B., 2007. The effect of horse, cattle and sheep grazing on the diversity and abundance of land snails in nutrient-poor calcareous grasslands. Basic Appl. Ecol. 8 (1), 55–65. https://doi.org/10.1016/j.baae.2006.02.003.

Cardoso, P., Barton, P.S., Birkhofer, K., Chichorro, F., Deacon, C., Fartmann, T., Fukushima, C.S., Gaigher, R., Habel, J.C., Hallmann, C.A., 2020. Scientists' warning to humanity on insect extinctions. Biol. Conserv. 242, 108426. https://doi.org/10.1016/j.biocon.2020.108426.

Diacon-Bolli, J., Dalang, T., Holderegger, R., Bürgi, M., 2012. Heterogeneity fosters biodiversity: linking history and ecology of dry calcareous grasslands. Basic Appl. Ecol. 13 (8), 641–653. https://doi.org/10.1016/j.baae.2012.10.004.

Díaz, S., Malhi, Y., 2022. Biodiversity: Concepts, patterns, trends, and perspectives. Annu. Rev. Environ. Resour. 47 (1), 31–63. https://doi.org/10.1146/annurev-environ-120120-054300.

Dolédec, S., Chessel, D., ter Braak, C.J.F., Champely, S., 1996. Matching species traits to environmental variables: a new three-table ordination method. Environ. Ecol. Stat. 3, 143–166. https://doi.org/10.1007/BF02427859.

Dray, S., Dufour, A.B., 2007. The ade4 package: implementing the duality diagram for ecologists. J. Stat. Softw. 22, 1–20. https://doi.org/10.18637/jss.v022.i04.

Drossart, M., Gérard, M., 2020. Beyond the decline of wild bees: optimizing conservation measures and bringing together the actors. Insects 11 (9), 649. https://doi.org/10.3390/insects11090649.

Eckerter, T., Buse, J., Bauhus, J., Förschler, M.I., Klein, A.M., 2021. Wild bees benefit from structural complexity enhancement in a forest restoration experiment. For. Ecol. Manag. 496, 119412. https://doi.org/10.1016/j.foreco.2021.119412.

Ekroos, J., Kleijn, D., Batáry, P., Albrecht, M., Báldi, A., Blüthgen, N., Knop, E., Kovács-Hostyánszki, A., Smith, H.G., 2020. High land-use intensity in grasslands constrains wild bee species richness in Europe. Biol. Conserv. 241, 108255. https://doi.org/10.1016/j.biocon.2019.108255.

Esser, J., Fuhrmann, M., Venne, C., 2010. Rote Liste und Gesamtartenliste der Wildbienen und Wespen (Hymenoptera: Apidae, Crabronidae, Sphecidae, Ampulicidae, Pompilidae, Vespidae, Tiphiidae, Sapygidae, Mutillidae, Chrysididae) Nordrhein-Westfalens.1. Fass. Stand Novemb. 2009. Ampulex 2, 5–60.

Exeler, N., Kratochwil, A., Hochkirch, A., 2009. Restoration of riverine inland sand dune complexes: implications for the conservation of wild bees. J. Appl. Ecol. 46, 1097–1105. https://doi.org/10.1111/j.1365-2664.2009.01701.x.

Fartmann, T., 2004. Die Schmetterlingsgemeinschaften der Halbtrockenrasen-Komplexe des Diemeltales; Biozönologie von Tagfaltern und Widderchen in einer alten Hudelandschaft. West. älisches Mus. F. üR. Nat. Münster.

Fartmann, T., 2024. Insect Conservation in Grasslands. In: Pryke, J., Samways, M.J., New, T., Cardoso, P., Gaigher, R. (Eds.), Routledge Handbook of Insect Conservation. Routledge, London, pp. 263–274. https://doi.org/10.4324/9781003285793-24.

Fartmann, T., Müller, C., Poniatowski, D., 2013. Effects of coppicing on butterfly communities of woodlands. Biol. Conserv. 159, 396–404. https://doi.org/10.1016/j.biocon.2012.11.024.

Fartmann, T., Jedicke, E., Streitberger, M., & Stuhldreher, G. 2021. Insektensterben in Mitteleuropa. Eugen Ulmer KG, Stuttgart.

Fartmann, T., Drung, M., Henning, O., Löffler, F., Brüggeshemke, J., 2022. Breeding-bird assemblages of calcareous grasslands and heathlands provide evidence for Common juniper (Juniperus communis) as a keystone species. Glob. Ecol. Conserv. 40, e02315. https://doi.org/10.1016/j.gecco.2022.e02315.

Fartmann, T., Streitberger, M., Poniatowski, D., Kettermann, M., Schmidt, C., Holtmann, L., 2025. Encroachment of the Upright brome (Bromus erectus) in calcareous grasslands — Assessment of the drivers and effects on plant species assemblages. J. Environ. Manag. 380, 125068. https://doi.org/10.1016/j.jenvman.2025.125068.

Feurdean, A., Ruprecht, E., Molnár, Z., Hutchinson, S.M., Hickler, T., 2018. Biodiversity-rich European grasslands: Ancient, forgotten ecosystems. Biol. Conserv. 228, 224–232. https://doi.org/10.1016/j.biocon.2018.09.022.

Foley, J.A., DeFries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C., Gibbs, H.K., 2005. Global consequences of land use. Science 309 (5734), 570–574. https://doi.org/10.1126/science.1111772.

Gardein, H., Fabian, Y., Westphal, C., Tscharntke, T., Hass, A., 2022. Ground-nesting bees prefer bare ground areas on calcareous grasslands. Glob. Ecol. Conserv. 39, e02289. https://doi.org/10.1016/j.gecco.2022.e02289.

Grass, I., Albrecht, J., Jauker, F., Diekötter, T., Warzecha, D., Wolters, V., Farwig, N., 2016. Much more than bees—Wildflower plantings support highly diverse flower-visitor communities from complex to structurally simple agricultural landscapes. Agric. Ecosyst. Environ. 225, 45–53. https://doi.org/10.1016/j.agee.2016.04.001.

Greenleaf, S.S., Williams, N.M., Winfree, R., Kremen, C., 2007. Bee foraging ranges and their relationship to body size. Oecologia 153, 589–596. https://doi.org/10.1007/s00442-007-0752-9.

Griffin, S.R., Bruninga-Socolar, B., Gibbs, J., 2021. Bee communities in restored prairies are structured by landscape and management, not local floral resources. Basic Appl. Ecol. 50, 144–154. https://doi.org/10.1016/j.baae.2020.12.004.

Grueber, C.E., Nakagawa, S., Laws, R.J., Jamieson, I.G., 2011. Multimodel inference in ecology and evolution: challenges and solutions. J. Evolut. Biol. 24 (4), 699–711. https://doi.org/10.1111/j.1420-9101.2010.02210.x.

Helbing, F., Fartmann, T., Poniatowski, D., 2021. Restoration measures foster biodiversity of important primary consumers within calcareous grasslands. Biol. Conserv. 256, 109058. https://doi.org/10.1016/j.biocon.2021.109058.

Heneberg, P., Bogusch, P., Hlaváčková, L., 2020. Experimental confirmation of empty snail shells as limiting resources for specialized bees and wasps. Ecol. Eng. 142, 105640. https://doi.org/10.1016/j.ecoleng.2019.105640.

Henle, K., Alard, D., Clitherow, J., Cobb, P., Firbank, L., Kull, T., McCracken, D., Moritz, R.F., Niemelä, J., Rebane, M., 2008. Identifying and managing the conflicts between agriculture and biodiversity conservation in Europe–A review. Agric. Ecosyst. Environ. 124, 60–71. https://doi.org/10.1016/j.agee.2007.09.005.

Holtmann, L., Juchem, M., Brüggeshemke, J., Möhlmeyer, A., Fartmann, T., 2018. Stormwater ponds promote dragonfly (Odonata) species richness and density in urban areas. Ecol. Eng. 118, 1–11. https://doi.org/10.1016/j.ecoleng.2017.12.028.

Hopfenmüller, S., Holzschuh, A., Steffan-Dewenter, I., 2020. Effects of grazing intensity, habitat area and connectivity on snail-shell nesting bees. Biol. Conserv. 242, 108406. https://doi.org/10.1016/j.biocon.2020.108406.

Kettermann, M., Poniatowski, D., Fartmann, T., 2022. Active management fosters species richness of wild bees in limestone quarries. Ecol. Eng. 182, 106733. https://doi.org/10.1016/j.ecoleng.2022.106733.

Kierat, J., Szentgyörgyi, H., Czarnoleski, M., Woyciechowski, M., 2017. The thermal environment of the nest affects body and cell size in the solitary red mason bee (Osmia bicornis L.). J. Therm. Biol. 68, 39–44. https://doi.org/10.1016/j.jtherbio.2016.11.008.

Kirchenbaur, T., Fartmann, T., Bässler, C., Löffler, F., Müller, J., Strätz, C., Seibold, S., 2017. Small-scale positive response of terrestrial gastropods to dead-wood addition is mediated by canopy openness. For. Ecol. Manag. 396, 85–90. https://doi.org/10.1016/j.foreco.2017.03.034.

Klaus, F., Tscharntke, T., Uhler, J., Grass, I., 2021. Calcareous grassland fragments as sources of bee pollinators for the surrounding agricultural landscape. Glob. Ecol. Conserv. 26, e01474. https://doi.org/10.1016/j.gecco.2021.e01474.

Kuppler, J., Neumüller, U., Mayr, A.V., Hopfenmüller, S., Weiss, K., Prosi, R., Schanowski, A., Schwenninger, H.-R., Ayasse, M., Burger, H., 2023. Favourite plants of wild bees. Agric. Ecosyst. Environ. 342, 108266. https://doi.org/10.1016/j.agee.2022.108266.

Lane, I.G., Portman, Z.M., Herron-Sweet, C.H., Pardee, G.L., Cariveau, D.P., 2022. Differences in bee community composition between restored and remnant prairies are more strongly linked to forb community differences than landscape differences. J. Appl. Ecol. 59, 129–140. https://doi.org/10.1111/1365-2664.14035.

LANUK N.R.W. (State Agency for Nature, Environment and Climate Protection of North Rhine-Westphalia) 2022. Climate Atlas North Rhine-Westphalia – Interactive map portal. Version of November 2022. Retrieved 18.09.2025 from ⟨https://www.klimaatlas.nrw.de⟩.

Lozada-Gobilard, S., Albis, C.M.L., Rupik, K.B., Pätzig, M., Hausmann, S., Tiedemann, R., Joshi, J., 2021. Habitat quality and connectivity in kettle holes enhance bee diversity in agricultural landscapes. Agric. Ecosyst. Environ. 319, 107525. https://doi.org/10.1016/j.agee.2021.107525.

McCune, B., Keon, D., 2002. Equations for potential annual direct incident radiation and heat load. J. Veg. Sci. 13 (4), 603–606. https://doi.org/10.1111/j.1654-1103.2002.tb02087.x.

Moreno-Rueda, G., 2014. Distribution of arid-dwelling land snails according to dryness. J. Arid Environ. 103, 80–84. https://doi.org/10.1016/j.jaridenv.2014.01.006.

Nakagawa, S., Johnson, P.C., Schielzeth, H., 2017. The coefficient of determination R 2 and intra-class correlation coefficient from generalized linear mixed-effects models revisited and expanded. J. R. Soc. Interface 14 (134), 20170213. https://doi.org/10.1098/rsif.2017.0213.

Öckinger, E., Winsa, M., Stuart, P.M.R., Bommarco, R., 2018. Mobility and resource use influence the occurrence of pollinating insects in restored seminatural grassland fragments. Restor. Ecol. 26, 873–881. https://doi.org/10.1111/rec.12646.

Poniatowski, D., Fartmann, T., 2008. The classification of insect communities: lssons from orthopteran assemblages of semi-dry calcareous grasslands in central Germany. Eur. J. Entomol. 105 (4), 659–671. https://doi.org/10.14411/eje.2008.090.

Poniatowski, D., Hertenstein, F., Raude, N., Gottbehüt, K., Nickel, H., Fartmann, T., 2018b. The invasion of Bromus erectus alters species diversity of vascular plants and leafhoppers in calcareous grasslands. Insect Conserv. Divers. 11, 578–586. https://doi.org/10.1111/icad.12302.

Poniatowski, D., Stuhldreher, G., Löffler, F., Fartmann, T., 2018a. Patch occupancy of grassland specialists: Habitat quality matters more than habitat connectivity. Biol. Conserv. 225, 237–244. https://doi.org/10.1016/j.biocon.2018.07.018.

Poniatowski, D., Stuhldreher, G., Helbing, F., Hamer, U., Fartmann, T., 2020. Restoration of calcareous grasslands: The early successional stage promotes biodiversity. Ecol. Eng. 151, 105858. https://doi.org/10.1016/j.ecoleng.2020.105858.

Poschlod, P., WallisDeVries, M.F., 2002. The historical and socioeconomic perspective of calcareous grasslands—lessons from the distant and recent past. Biol. Conserv. 104 (3), 361–376. https://doi.org/10.1016/S0006-3207(01)00201-4.

Poschlod, P., Bakker, J.P., Kahmen, S., 2005. Changing land use and its impact on biodiversity. Basic Appl. Ecol. 6 (2), 93–98. https://doi.org/10.1016/j.baae.2004.12.001.

Potts, S.G., Biesmeijer, J.C., Kremen, C., Neumann, P., Schweiger, O., Kunin, W.E., 2010. Global pollinator declines: trends, impacts and drivers. Trends Ecol. Evol. 25 (6), 345–353. https://doi.org/10.1016/j.tree.2010.01.007.

Proesmans, W., Bonte, D., Smagghe, G., Meeus, I., Decocq, G., Spicher, F., Kolb, A., Lemke, I., Diekmann, M., Bruun, H.H., 2019. Small forest patches as pollinator habitat: oases in an agricultural desert? Landsc. Ecol. 34, 487–501. https://doi.org/10.1007/s10980-019-00782-2.

Purvis, E.E.N., Vickruck, J.L., Best, L.R., Devries, J.H., Galpern, P., 2020. Wild bee community recovery in restored grassland-wetland complexes of prairie North America. Biol. Conserv. 252, 108829. https://doi.org/10.1016/j.biocon.2020.108829.

Oksanen, J., Simpson, G.L., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., et al. 2022. Community ecology package (package "vegan," version 2.6–8). Available at: ⟨https://cran.r-project.org/web/packages/vegan/vegan.pdf⟩ (Accessed 21 October 2024).

R Development Core Team 2024. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. ⟨https://www.R-project.org/⟩.

Requier, F., Leonhardt, S.D., 2020. Beyond flowers: including non-floral resources in bee conservation schemes. J. Insect Conserv. 24 (1), 5–16. ⟨https://link.springer.com/article/10.1007/s10841-019-00206-1⟩.

Rivers-Moore, J., Andrieu, E., Vialatte, A., Ouin, A., 2020. Wooded semi-natural habitats complement permanent grasslands in supporting wild bee diversity in agricultural landscapes. Insects 11 (11), 812. https://doi.org/10.3390/insects11110812.

Roulston, T. a H., Goodell, K., 2011. The role of resources and risks in regulating wild bee populations. Annu. Rev. Entomol. 56 (1), 293–312. https://doi.org/10.1146/annurev-ento-120709-144802.

Scheuchl, E., Schwenninger, H.R., Burger, R., Diestelhorst, O., Kuhlmann, M., Saure, C., Schmid-Egger, C., Silló, N., 2023. Die Wildbienenarten Deutschlands–Kritisches Verzeichnis und aktualisierte Checkliste der Wildbienen Deutschlands (Hymenoptera, Anthophila). Anthophila 1 (1), 25–138.

Schubert, L.F., Hellwig, N., Kirmer, A., Schmid-Egger, C., Schmidt, A., Dieker, P., Tischew, S., 2022. Habitat quality and surrounding landscape structures influence wild bee occurrence in perennial wildflower strips. Basic Appl. Ecol. 60, 76–86. https://doi.org/10.1016/j.baae.2021.12.007.

Speight, M.R., Hunter, M.D., Watt, A.D., 1999. Ecology of insects: concepts and applications, Second Edition. Wiley-Blackwell, Chichester.

Stein, D.S., Debinski, D.M., Pleasants, J.M., Toth, A.L., 2020. Evaluating native nee communities and nutrition in managed grasslands. Environ. Entomol. 49, 717–725. https://doi.org/10.1093/ee/nvaa009.

Streitberger, M., Schmidt, C., Fartmann, T., 2017. Contrasting response of vascular plant and bryophyte species assemblages to a soil-disturbing ecosystem engineer in calcareous grasslands. Ecol. Eng. 99, 391–399. https://doi.org/10.1016/j.ecoleng.2016.11.037.

Streitberger, M., Fartmann, T., Kettermann, M., Drung, M., Poniatowski, D., 2025. Disturbance fosters vascular plant and bee species richness in sand quarries. J. Environ. Manag. 392, 126628. https://doi.org/10.1016/j.jenvman.2025.126628.

Stuhldreher, G., Fartmann, T., 2018. Threatened grassland butterflies as indicators of microclimatic niches along an elevational gradient–Implications for conservation in times of climate change. Ecol. Indic. 94, 83–98. https://doi.org/10.1016/j.ecolind.2018.06.043.

Tischendorf, S., Frommer, U., Flügel, H.-J., Schmalz, K.-H., & Dorow, W.H. 2009. Kommentierte Rote Liste der Bienen Hessens–Artenliste, Verbreitung, Gefährdung. Hessen Ministerium für Umwelt, Energie, Landwirtschaft und Verbraucherschutz, Wiesbaden.

Tonietto, R.K., Larkin, D.J., 2018. Habitat restoration benefits wild bees: A meta-analysis. J. Appl. Ecol. 55 (2), 582–590. https://doi.org/10.1111/1365-2664.13012.

Veen, P., Jefferson, R., De Smidt, J., Van der Straaten, J., 2014. Grasslands in Europe: Of high nature value. KNNV Uitgeverij, Zeist.

WallisDeVries, M.F., van Swaay, C.A.M., 2006. Global warming and excess nitrogen may induce butterfly decline by microclimatic cooling. Glob. Change Biol. 12, 1620–1626. https://doi.org/10.1111/j.1365-2486.2006.01202.x.

WallisDeVries, M.F., Poschlod, P., Willems, J.H., 2002. Challenges for the conservation of calcareous grasslands in northwestern Europe: integrating the requirements of flora and fauna. Biol. Conserv. 104, 265–273. https://doi.org/10.1016/S0006-3207(01)00191-4.

Westrich, P., 2018. Die Wildbienen Deutschlands. Eugen Ulmer Verlag, Stuttgart.

Wilson, J.B., Peet, R.K., Dengler, J., Pärtel, M., 2012. Plant species richness: the world records. J. Veg. Sci. 23 (4), 796–802. https://doi.org/10.1111/j.1654-1103.2012.01400.x.

Winfree, R., 2010. The conservation and restoration of wild bees. Ann. N. Y. Acad. Sci. 1195 (1), 169–197. https://doi.org/10.1111/j.1749-6632.2010.05449.x.

Zurbuchen, A., Landert, L., Klaiber, J., Müller, A., Hein, S., Dorn, S., 2010. Maximum foraging ranges in solitary bees: only few individuals have the capability to cover long foraging distances. Biol. Conserv. 143 (3), 669–676. https://doi.org/10.1016/j.biocon.2009.12.003.