



Landscape heterogeneity correlates with bee and pollen diversity while size and specialization degree explain species-specific responses of wild bees to the environment

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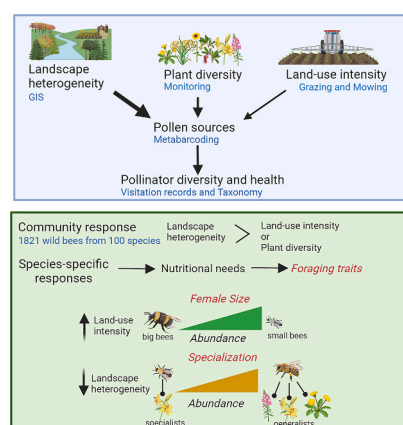
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HIGHLIGHTS

- Landscape heterogeneity enhances bee species richness and functional diversity.
- Pollen diversity collected by bees correlates with landscape heterogeneity.
- Larger bees show negative responses to increased land-use intensity.
- Diet specialization in bees is positively correlated with landscape heterogeneity.
- Effective conservation measures require detailed knowledge of pollinator resource use.

GRAPHICAL ABSTRACT



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ABSTRACT

Access to adequate pollen sources in agricultural landscapes is critical for the nutrition and development of bees. The type and quantity of pollen available to bees and may be determined by local plant diversity, land-use

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Dataset link: [Visitation records of bees in 56 plots in 2020 and 61 plots in 2021 across the 3 Exploratories \(Original data\)](#)

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intensity and landscape structure but different bee species likely respond differently to these parameters. Identifying community and specific responses is therefore imperative to understand pollinator population dynamics in agricultural landscapes. We sampled bees in 36 plots along a land-use gradient at 4 sites in Belgium and Germany over two years. We collected 1821 bees from 100 bee species and constructed a pollen foraging network with 36 common wild bee species based on pollen metabarcoding. We investigated differences in community responses and species-specific responses to environmental variables.

Landscape heterogeneity positively correlated with bee species richness, diversity and functional richness, and significantly explained bee community composition per plot. Bee collected pollen diversity correlated with bee species diversity. Furthermore, landscape heterogeneity positively correlated with bee collected pollen diversity when pooling abundant bee species, while it did not correlate with pollen diversity of the most abundant generalists. Land-use intensity and local plant diversity had no significant effect on bee diversity. Larger bees showed negative responses to increasing land-use intensity and bees with more specialized diets showed positive correlations with landscape heterogeneity. Our study goes beyond mere floral diversity and provides new insight into the responses of wild bee communities to landscape structure and regional pollen availability, as well as the interplay between bee abundance and pollen foraging traits. Our results highlight the importance of determining species-specific nutritional needs and considering landscape level structure in pollinator conservation programs.

1. Introduction/background

Biodiversity supports the stability and functioning of ecosystems and also the well-being of humans (Duffy, 2009). The abundance, diversity and composition of plant-animal communities shapes the structure of ecosystems through directly or indirectly affecting resource dynamics and ecological interactions (Bascompte and Jordano, 2007). Individual species appear to benefit from increasing resource diversity in their habitat as a consequence of multiple factors, e.g. a prolonged phenology of resources, enhanced resource quality or toxin dilution, or facilitated resource provision (Ganser et al., 2021; Kaluza et al., 2017), suggesting that resource diversity may be a major driver of their population dynamics.

Bees are key species for ecosystem functioning as pollinators or as ecosystem engineers, as well as part of food webs and nutrient cycles (Cardoso et al., 2023; Filipiak et al., 2023; Memmott, 1999; Ollerton, 2021). Furthermore, they provide numerous ecosystem services of importance to humans, such as crop pollination, medicines and soil formation (Klein et al., 2018; Requier et al., 2023). Declines in bee diversity, as observed in recent decades, have been linked to multiple factors primarily related to land-use change and intensification for agriculture and forestry (e.g., monocultures, pesticide use) and landscape fragmentation (Requier et al., 2023). All these factors typically lead to the loss of floral and nesting resources at the local and landscape level (Bartual et al., 2019; Potts et al., 2010). Plant diversity and availability are directly affected by land-use and landscape fragmentation; and the direction and magnitude of this effect depends on the type of ecosystem, the species involved and on the temporal and spatial scales considered (Gerstner et al., 2014; Priyadarshana et al., 2024).

Pollen is the main diet component of the larvae of bees, as it provides crucial micro- and macro-nutrients for the developing organism (Danforth et al., 2019). Pollen composition can differ significantly in the type, amount and ratios of nutrients and plant secondary metabolites and its elemental composition between plants (Filipiak, 2019; Leonhardt et al., 2024). Hence, variation in the composition and diversity of plant communities results in context-specific floral and nutritional offerings, that bees from different species need to navigate in search of the ones that best fulfill their nutritional niche requirements (Parreno et al., 2022). The composition, diversity and population dynamics of bee communities are in turn strongly determined by floral and nesting resources available within foraging range, as bees are central place foragers and thus limited by the resources available around their nesting sites (Klein et al., 2017). The availability of suitable host plants providing pollen within foraging distance is therefore a major factor of bee population dynamics. Flexible pollen generalists like *Apis mellifera*, some *Bombus* species or *Osmia bicornis* are more likely to adapt their foraging spectrum or range to changes in landscape configurations and seasons. This is not possible for all wild bees due to (nutritional) niche

and/or morphological limitations (Danner et al., 2017; Jha and Kremen, 2013; Peters et al., 2022). The general consensus is that small species with comparatively shorter foraging ranges and species with specialist diets show stronger declines in flower-poor landscapes (E. Benjamin et al., 2014; Palma et al., 2015).

In their remarkable diversity, wild bees differ not only in their foraging range, but also in other traits like lecty, pollen load carrying mode and capacity, length of flying season, phenology, sociality or body size (Greenleaf et al., 2007; Westrich, 2019). Many of these traits likely shape the pollen foraging behavior and preferences. The trait and functional diversity of bee communities has furthermore been shown to affect bee responses to variation in floral resources. The functional diversity of bee communities in agricultural landscapes was found to be in decline even in areas with land-use practices traditionally thought to support biodiversity (e.g. organic agriculture) when compared to natural habitats (Forrest et al., 2015), with no clear winners and losers based on single traits (e.g., size). This suggests that species' responses are driven by a combination of traits interacting with the landscape structure over time (Bartomeus et al., 2018). Identifying how bee foraging traits or trait combinations respond to variation in local and regional pollen availability and diversity may help to, for example, predict how bee communities respond to environmental changes (Minckley et al., 2013), and to more accurately tailor flora enhancing interventions matching targeted species needs (Schleuning et al., 2015).

Agricultural intensification is characterized on one hand by the higher input of external chemicals (e.g., fertilizer) and on the other hand by higher fragmentation and "homogenization" of the landscape composition (e.g., low crop diversity) (Palma et al., 2015). Land use in the form of increased mowing, grazing pressure and fertilizer input affects the plant community in complex ways, directly by exposure to chemicals and indirectly by reducing the local availability of pollen sources for the pollinator community (Blüthgen et al., 2012; Kovács-Hostyánszki et al., 2011; Peters et al., 2022). The loss of semi-natural habitats and connectivity is linked to detrimental effects on abundance and shifts in community composition of pollinators (Maurer et al., 2022). However the effects of agricultural intensification on wild bee populations have been studied in detail for only few of the almost 20.000 known wild bee species worldwide (Tonietto and Larkin, 2018). Furthermore, most previous studies relating changes in the composition and diversity of floral resources to wild bee communities and diversity have primarily recorded bee-plant interactions based on visitation data (e.g. Fründ et al., 2013; Hülsmann et al., 2015; Seitz et al., 2020; Sutter et al., 2017), while much fewer studies have tried to disentangle the differential contribution of pollen and nectar providing plants (Lowe et al., 2022). In fact, several studies pointed out the shortcomings of studying visitation networks without knowledge on which plants are actually used as pollen hosts, particularly for deriving conclusions on dietary choice (King et al., 2013; Popic et al., 2013). More recently,

pollen metabarcoding has become a valuable tool for inferring pollen hosts in pollination studies (Baksay et al., 2022; Encinas-Viso et al., 2022; Keller et al., 2015; Pornon et al., 2016) and may prove useful in filling this gap. In our study, we investigated pollen foraging of a diverse bee community in relation to local land-use intensity and plant diversity as well as landscape heterogeneity, and we explored species-specific responses based on bee foraging traits.

Specifically, we hypothesized:

- Species diversity and functional diversity of wild bee communities will positively correlate with increasing plant diversity and with increasing landscape heterogeneity and with decreasing land-use intensity, because plant diversity at local and landscape scale offers more pollen providing plants in an agricultural landscape matrix.
- At within-species level, the strength and direction of the bees' responses to changes in local plant diversity and landscape heterogeneity will depend on species-specific combinations of pollen foraging traits. Specifically, larger female size (directly related to pollen carrying capacity), a broader foraging range (directly related to the distance that can be covered to search for suitable resources) and a more generalist diet specialization will strongly determine the species' responses (i.e. variation in abundance) to changes in local plant diversity and landscape heterogeneity.

2. Methods

2.1. Sample collection

2.1.1. Study sites and plots

We observed bee-plant visitations and sampled bees between April and July 2021 and between April and July 2022, at three sites in Germany and one site in Belgium, sampling each plot 4 times over the period of both years. The three sites in Germany are managed within the Biodiversity Exploratories (BE), a long-term research program that has carried biodiversity analyses since its foundation in 2008 when already existing managed grasslands and forests were adhered to the scientific network that started studying them (Fischer et al., 2010). It comprises the Schwäbische Alb, Hainich-Dünn and Schorfheide Chorin, each with approximately 50 plots in grasslands ecosystems, from which we used a subset of 58 plots over the three sites. The grasslands differ spatially (size, shape, distance to roads and forest) as well as in their plant composition. Farmers may have different land use management practices (e.g., crops, seedling time, mowing time, etc.) and that management is reported to the BE. The BE does not provide specific seeds mixtures or management recommendations – but notes down what the farmers do and also provides a weather station surrounded with subplots for specific analysis (e.g., soil). The site in Belgium consisted of nine plots which are managed by the nature conservation organization Natuurpunt vzw, collaborating with local farmers for grazing/mowing services. Just like in the BE, the plots are managed independently by local farmers who report the activities to the nature conservation organization. All plots were managed by farmers for cattle (cows/sheep) and/or mowing (cutting of grass regularly for cattle fed); none of the plots were managed for commercial crops (coordinates in Protocol 1, more information is available in the Protocol 1, Suppl. Material).

We chose low, intermediate and high intensity land-use plots to obtain a gradient of plant diversity, because land-use intensity (LUI – as described below) is directly and negatively correlated with plant diversity (Dainese et al., 2019; Weiner et al., 2011, 2014).

2.1.2. Bee sampling

During each visit, we performed two types of sampling: transect and targeted. For *transect sampling*, we established five transects of 50 m × 2 m (length per width) in Germany and ten transects of 25 m × 2 m (length per width) in Belgium (which gives the same total amount of area

covered in plots of both countries). We walked each of them once within overall 1 h (standardized over 250 m/500 m²) and collected bees found resting or foraging on flowers using an entomological net and 1.5 ml microcentrifuge tubes (Eppendorf™) or 15 ml falcon tubes for bigger species. Both bee and plant species were recorded. The transect sampling was performed to obtain normalized data for bee and plant diversity comparable between plots and years. For *targeted sampling*, we additionally walked in every direction and up to 150 m away from the managed plot (still staying within the same grassland management) during at least 1 h, and caught all bees found on flowers or flying. For bees on flowers, we again recorded the respective plant species. The targeted sampling was performed to obtain sufficient bees carrying pollen in order to capture the pollen diversity available within the bees' foraging area in and outside of the plot. For both sampling types, the identity of 99 % of the flowering plant species visited by bees could be determined using field guides (Eggelte, 2007; Schauer et al., 2020; Spohn and Spohn, 2021). Likewise, the identity of several bee species, i. e. *Apis mellifera*, *Andrena haemorrhoa* and *Dasypoda hirtipes*, was obtained directly in the field. The rest of the bee species as well as a few unidentified plants were identified using DNA barcoding. As the focus of our study was on wild bees, we limited the collection of honeybees (*Apis mellifera*) to 10 individuals per plot.

2.1.3. Bee, plant and pollen sample processing

Unidentified plants from the plant assessment in the plots were DNA barcoded to determine the species using the ITS2 marker using the NucleoSpin 96 Plant II kit (Macherey-Nagel GmbH & Co. KG) for DNA extraction and utilizing the ITS2 markers S2F and S3R for amplification (Chen et al., 2010). All bees were stored in dry ice immediately after capture. They were sexed and weighted in the evening of the day of collection. Their hind legs were then carefully removed using clean scissors and forceps (cleaned with 10 % bleach between samples) and then placed in a separate 1.5 ml microcentrifuge tube (Eppendorf™) with a PBS solution (PBS; VWR Chemicals, Ohio, USA) for removing pollen from legs (in bees with scopa the pollen was removed carefully with forceps). Samples were stored at –20 °C until processing. The legs with pollen were shook in a high-speed vortex for 1 min and subsequently centrifuged to bring the pollen down in a cold centrifuge for 3 min at –4 °C (7000 rcf). One of the legs was used for DNA barcoding and species identification (i.e. several legs in the case of small species, like some Halictidae) using the COI marker following (Leray et al., 2013). The second hind leg was used if repetitions were necessary or it was stored. All pollen carried by bees of the same species was pooled per plot and month (up to 14 bees per pool). Pollen metabarcoding followed an existing protocol (Sickel et al., 2015) with more details provided in Campos et al. (Campos et al., 2021; Keller et al., 2015). DNA extraction and sequencing was performed by Advance Informatics Methods (AIM) for bees caught in 2020; and in the Canadian Center for DNA barcoding (University of Guelph) for bees and in the house (Germany) for pollen, in 2021. For bioinformatics we followed the strategy of Leonhardt et al. (Leonhardt et al., 2022).

2.2. Environmental variables and bee foraging traits

We considered plant diversity, landscape heterogeneity index (LHI) and land use intensity (LUI) as environmental variables to be used to explain the patterns observed in bee diversity. The study assessed plant diversity in Germany and Belgium. In Germany, plant diversity was measured as the percentage cover of all flowering plant species within 16 m² per plot during the flowering season of 2020 and 2021. In Belgium, measurements involved placing 30 quadrats of 1 m² along transect lines to count flowering stems available for bees. Shannon diversity and Hill index were calculated for plant diversity (Chao et al., 2014; Roswell et al., 2021). Land-use intensity (LUI) was measured based on mowing frequency, grazing intensity, and fertilizer use and it is a standardized index used within the Biodiversity Exploratories to

compare between studies and sites (Blüthgen et al., 2012). In the fields used in our study, high intensity land-use was mainly driven by high fertilization and strong grazing activity in the study plots (Suppl. Material Protocol 3). The Landscape Heterogeneity Index (LHI) was calculated to capture diversity of habitats and land-uses in the surrounding landscape up to 500 m². We defined land-use classes based on ATKIS classifications and subtypes, using existing satellite image databases from 2020 to 2023 to quantify the area of each land-use, and calculating the Shannon diversity index per plot. The index considers both the number of classes and their abundance. In Belgium, the Biological Valuation Map was used, while in Germany, a remote sensing open access platform from the Biodiversity Exploratories was utilized (Magdon et al., 2023; Wöllauer et al., 2021). Analysis was conducted using ArcGIS Software and Python. More information about the definition and calculation of environmental variables is found in the supplementary material (Suppl. Material Protocol 3).

We considered size and diet specialization level as bee traits related to foraging in order to disentangle patterns observed in bees' responses to environmental variables. Bee species' traits important for pollen foraging were identified and quantified using a database developed and curated by Stuart Roberts at the University of Reading. The average female size and foraging range was extrapolated from intertegular distance (ITD) measurements. Weight measurements of sampled species were also taken in the field. Since the body of the bees was meant to be used in physiological analyses for another study, we could not dry the bees and wet weight was used instead. We provide evidence of correlation between the wet weight in our bees with size traits reported for species in the literature in the supplementary material Fig. S2. Diet-related foraging traits were assessed using the specialization index (*d'*), which indicates the level of specialization of each bee species in terms of visited pollen plants (Blüthgen et al., 2006). The index ranges from 0 to 1, with 0 representing generalist bees and 1 representing specialist bees. The *d'* index was calculated based on bee-pollen interactions obtained from pollen metabarcoding for a subset of bee species.

2.3. Statistical analyses

2.3.1. Environmental effects on bee community composition, bee diversity and bee-collected pollen diversity

In order to account for unequal sampling efforts, we reduced our full dataset to data from plots which were sampled at least 4 times across both years (36 plots). From our standardized transect dataset, we calculated bee species richness and bee diversity (Shannon index) per plot across all seasons of sampling, as well as abundances of all species present. From both transect and targeted datasets, we also calculated bee-collected pollen diversity, as a Shannon diversity index of plants, for all species of bees found with pollen. Pools of pollen for metabarcoding included pollen from 4 to 10 bees per species, plot and season. All diversity measures were performed with the *vegan* package (Oksanen et al., 2022). We then explored the relationship between these parameters and the environmental variables: land-use heterogeneity (LHI), local plant diversity and land-use intensity (LUI). These environmental variables were not correlated with each other (calculated using package *corrplot* (Wei and Simko, 2021)) (Suppl. Material Fig. S2a). We explored spatial autocorrelation between our plots for all variables of interest (plant diversity, land use intensity and land use heterogeneity). We found significant spatial autocorrelation (Moran's test, Protocol 1, Suppl. Material) and hence we accounted for it in our statistical models (correlation = spatial autocorrelation). To evaluate the effect of environmental variables on pollen and bee diversity we performed linear mixed models (using site as a random variable), performed with the package *nlme* (Pinheiro et al., 2023), for which we report estimated effect size, *F*/*Chi*²-values and significances for all explanatory variables. We define significance level at $\alpha = 0.05$, but we take a Fisherian approach to null-hypothesis testing, in which *p*-values serve as a graded

evidence against the null hypothesis, for which we also report on marginal significances around 0.05 (Amrhein et al., 2017). Consequently, for the interpretation of results we focus not only on the *p*-values but also on the size of effects and the trends observable. To visualize differences in bee community composition between plots and along our diversity gradient, we performed a non-metric multidimensional scaling (NMDS). In order to evaluate underlying trends affecting community composition, we overlay the environmental variables plant diversity, LUI and LHI using an environmental fitting provided by the package *vegan* (*envfit*), that allows one to determine weak from strong predictors of the ordination (Oksanen et al., 2022).

2.3.2. Environmental effects on bee species abundances and as a function of pollen foraging traits

To explore how the abundances of different bee species were related to the different environmental variables we used a subset of 36 bee species that were found in 4 or more plots to ensure meaningful correlations along our diversity gradient. The list of species in the main dataset and the subset can be found in the Suppl. Material (Table S2). We investigated the response of each species by calculating Spearman correlations between their absolute abundance, plant diversity, LUI and LHI.

To subsequently determine how species-specific responses in abundances were related to species' traits we performed generalized linear models using diet-related traits as explanatory variables and the Spearman correlation coefficients ρ (*p*) obtained for correlations between species' abundances and environmental variables as response variables. Before, we constructed a correlation matrix with the traits (Suppl. Material, Fig. S2b) and only used traits that were not highly correlated in our models: average female size and average specialization (*d'*). Note that the average wet weight for species that we calculated from field samples correlated with other size related foraging measures obtained from various literature sources, indicating that our dataset is representative of average species' traits.

2.3.3. Functional diversity analysis

To determine how the functional diversity of bee communities changed along our landscape gradient we used 32 species of the core set of the 36 most abundant bee species where *d'* could be calculated. Based on the pollen foraging traits (average female size and *d'* index) we calculated functional richness (FRic) and functional evenness (FEve) for each plot (Villéger et al., 2008). We performed linear mixed models to test for covariations between the environmental variables and variation in these functional trait indices across plots. All analyses were performed in R Software (R Core Team (2024), n.d.), in R Studio 2023.06.1, using the mentioned packages, plus tidyverse packages from data wrangling and visualization (i.e., particularly *ggplot2*, *pheatmap*, *gplots* and *ggpmisc* (Wickham et al., 2019)).

3. Results

3.1. Environmental effects on bee community composition, richness and diversity and bee collected pollen diversity

In 36 plots which were visited 4 or more times across the two years of sampling, we recorded 1821 bee-plant interactions (visitation observations) in the transect sampling comprising 100 bee species and 99 plant species, excluding cuckoo bees and those we could not identify to species level (abundances and richness per plot in Suppl. Material Table S1). Of those bees caught in transects, 1075 carried pollen. In addition, 1599 bees with pollen were caught in the targeted sampling to ensure sufficient pollen for the metabarcoding analysis (2674 bees in total). Transect and targeted bees with pollen were pooled by plot, season and species together to perform the metabarcoding analyses.

Bee species richness and diversity per plot were positively correlated with landscape heterogeneity, but not with local land-use intensity or

plant diversity on plots. Bee-collected pollen diversity from all species pooled correlated with bee species richness and was significantly positively correlated with landscape heterogeneity and local plant diversity (Table 1; Fig. 1; Suppl. Material Fig. S2). For the most abundant species, we also tested for correlations of environmental variables with pollen diversity in pools of individual species: Pollen diversity collected by *Bombus lapidarius* correlated with plant diversity, and pollen diversity collected by *Bombus pascuorum* correlated with landscape heterogeneity, while pollen diversity collected by the rest of the most abundant species (all generalists) did not correlate with any environmental variable (Suppl. Material Table S3). Landscape heterogeneity was the strongest predictor of bee community composition (Table 2 – r2 and significance, Fig. 2 – longest arrow).

3.2. Environmental effects on bee species abundances and as a function of pollen foraging traits

When calculating Spearman correlations (ρ) between the absolute abundance of each species and each environmental variable for the species found on 4 or more plots, we found variable responses, even within genera (visualized in a heatmap in Suppl. Material Fig. S4). Twenty-four species showed a strong positive correlation with landscape heterogeneity, 4 showed negative correlations and the rest showed no correlation. Abundances of approximately half of the species showed strong negative correlations with land-use intensity, but 5 showed strong positive correlations (*Lasioglossum malachurum*, *Andrena gravena*, *Andrena cineraria*, *Chelostoma florissomne*, *Halictus tumulorum*) and 7 showed weak or no correlation, such as *Osmia bicornis*. Surprisingly, abundances of 12 species showed strong negative correlations with local plant diversity (calculated for all sampling plots), but abundances of 7 species, including many *Bombus* and *Andrena* species, showed a strong positive correlation, and the rest were weak.

In the next step we tried to disentangle these patterns in abundance-environment correlations using generalized linear models including species traits related to pollen foraging as explanatory variables. Table 3 and Fig. 3a show the Spearman correlations identified above, as explained by the average female size and specialization level. Average

Table 1
Linear mixed effects model between bee species richness, bee diversity, pollen diversity (response variables) and environmental variables (explanatory - plant diversity (Shannon), land-use intensity (LUI) and landscape heterogeneity (LHI)). Significance (sign.) codes of p-values: ***<0.001; **<0.01; *<0.05; ns >0.05, marg. sign.: Marginally significant (0.055).

Bee Richness	Estimate	St. Error	F	Pr(>F)	sign.
Plant Diversity	0.008	0.194	0.043	0.837	Ns
Land-use intensity (LUI)	−0.887	0.743	2.234	0.146	Ns
Landscape heterogeneity (LHI)	7.865	0.969	65.812	<0.0001	***

Bee Diversity	Estimate	St. Error	F	Pr(>F)	sign.
Plant Diversity	0.019	0.016	0.978	0.331	Ns
Land-use index (LUI)	−0.030	0.063	0.435	0.515	Ns
Landscape heterogeneity (LHI)	0.397	0.082	23.528	<0.0001	***

Pollen Diversity	Estimate	St. Error	F	Pr(>F)	sign.
Plant Diversity	0.538	0.231	4.626	0.04	*
Land-use index (LUI)	−0.627	0.887	0.849	0.364	Ns
Landscape heterogeneity (LHI)	6.682	1.157	33.351	<0.0001	***

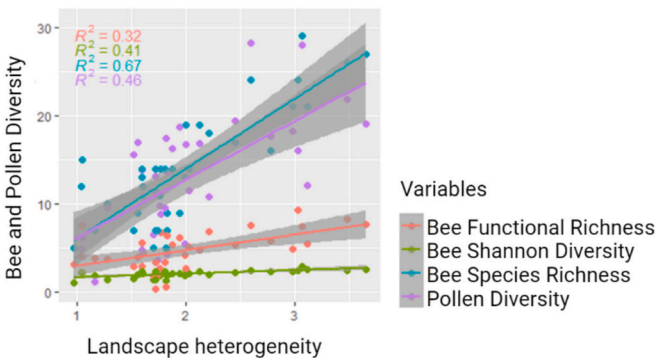


Fig. 1. Functional richness, species richness and diversity (Shannon) of bees collected at 36 grassland plots in three regions in Germany and one region in Belgium in 2020 and 2021, and bee-collected pollen diversity (Shannon Index from pollen metabarcoding) in relation to landscape heterogeneity (LHI).

Table 2
Environmental fitting of environmental variables plant diversity (Shannon), land-use intensity (LUI) and landscape heterogeneity (LHI) onto the community composition of bees based on abundances per bee species. Axes positions in non-metric multidimensional scaling (NMDS). r2- and p-values. Significance (sign.) codes of p-values: ***<0.001; **<0.01; *<0.05; ns >0.05, marg. sign.: Marginally significant (0.055).

Environmental variable	NMDS1	NMDS2	r2	p	sign.
Plant Diversity	0.606	0.796	0.028	0.649	ns
Land-use index (LUI)	0.987	0.163	0.114	0.156	ns
Landscape heterogeneity (LHI)	−0.900	0.436	0.326	0.002	**

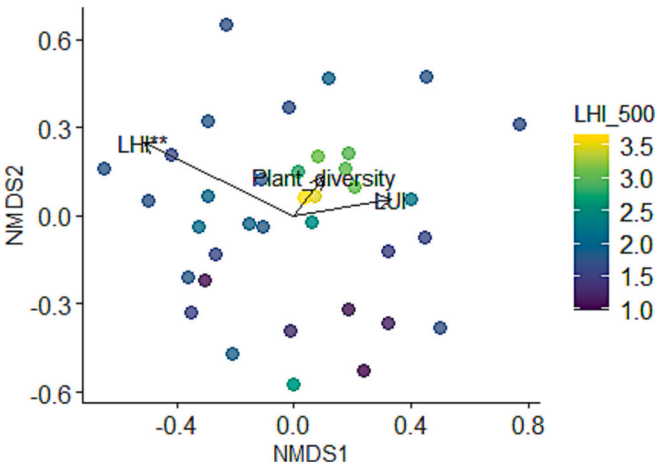


Fig. 2. Bee species community composition displayed by non-metric multidimensional scaling (NMDS) using Bray-Curtis dissimilarities based on bee abundances. Arrows show direction of effect of the environmental variables landscape heterogeneity (LHI) plant diversity and land-use intensity (LUI) (left to right), based on environmental fitting (see Table 2). Plots are colored according to the LHI gradient (low in blue and high in yellow).

female size was found to significantly correlate with the bees' responses to LUI - in particular, larger bees showed stronger negative correlations with land-use intensity ($\rho = -0.4$ to -0.2), indicating that their abundances decreased with LUI more than abundances of smaller bees. Many species with smaller and intermediate average female sizes showed no correlation with LUI or tended to show a positive, albeit weak correlation ($\rho = 0$ to 0.2), indicating that their abundances were less affected by LUI (Table 3 and Fig. 3a). Pollen specialization d' (average d' for all plots on which the species was present) was found to be marginally significantly correlated with the bees' responses to pollen diversity and LHI.

Table 3

Results of generalized linear models (model estimates, F- and p-values) testing for effects of bee traits related to pollen foraging, i.e. average female size and pollen specialization d' from pollen metabarcoding correlations, on Spearman correlation coefficients (obtained for correlations between absolute bee abundances of each species and environmental variables). Significance (sign.) codes of p-values: ***<0.001; **<0.01; *<0.05; ns >0.05, marg. sign.: Marginally significant (0.055).

Spearman correlations abundance to LUI	Estimate	St. Error	F	Pr (>F)	sign.
Bee Female Size	−0.021	0.007	9.665	0.004	**
Specialization d'	0.007	0.226	0.001	0.975	ns

Spearman correlations abundance to Plant diversity	Estimate	St. Error	F	Pr (>F)	sign.
Bee Female Size	0.010	0.007	1.818	0.188	ns
Specialization d'	0.214	0.226	0.898	0.351	ns

Spearman correlations abundance to LHI	Estimate	St. Error	F	Pr (>F)	sign.
Bee Female Size	−0.011	0.010	1.852	0.184	ns
Specialization d'	0.671	0.335	4.014	0.055	marg. sign.

Even though the p -value of this correlation was marginally significant ($p = 0.055$), the effect size was large and the trend clear: most bees with high levels of pollen specialization in our dataset (up to $d' = 0.6$) showed stronger positive correlations with LHI ($\rho = 0.2$ to 0.7), whereas bees considered as the most generalist in our dataset showed no consistent correlation or even a negative one ($\rho = 0$ to -0.2). Average female size and diet specialization were not correlated, meaning both large bees and pollen specialist bees were “independently” affected. We found no significant correlations between the tested foraging traits and bee responses to plant diversity on plots (Table 3).

3.3. Functional diversity analysis

A hierarchical clustering of the species based on their functional traits split them into 2 main groups (Suppl. Material Fig. S5). Generally, species from *Bombus* clustered with some *Andrena* into one group and species from *Lasioglossum* clustered with the rest of the *Andrena* and *Osmia* into a second group (Suppl. Material Fig. S5). Functional richness was significantly positively correlated with LHI while functional evenness showed no significant correlation (Table 4).

4. Discussion

We aimed to explore how variation in local land-use intensity and plant diversity as well as landscape heterogeneity affected the composition, species and functional diversity of wild bee communities, and the pollen they collect. At the community level, we hypothesized to find a higher species and functional diversity of bees with increasing plant diversity and landscape heterogeneity, and lower land-use intensity. This was partially confirmed: we found bee communities to be richer and more diverse, in terms of both species and functional groups, in landscapes with higher heterogeneity. However, this was not the case on plots with higher plant diversity, which we speculate might be related to the lack of resources (abundance) directly in the plot which leads to the surroundings being determinant of the pollinator community. Higher landscape heterogeneity typically comprises a more diverse range of habitats, which provide a higher resource diversity, i.e. different pollen providing plants or a higher number of rare valuable plant species that bees search outside the grassland plots, which in turn appears to be crucial for maintaining a high bee diversity. More diverse habitats

provide overall more plants and thus an overall larger number of potential resources. Alternatively, they provide more nesting opportunities sustaining a more diverse bee community which in turn forage on a larger spectrum of pollen host plants.

Several studies found bee diversity to increase with plant diversity (Ebeling et al., 2008; Isbell et al., 2017). Moreover, land-use intensification and decreasing local plant diversity were found to be negatively affect bee richness on farms (Hyjazie and Sargent, 2022; Tommasi et al., 2021). At least one meta-analysis found effects of landscape fragmentation and habitat loss to be minor when considering bee/plant richness at larger scales, provided there are still natural habitat patches (Winfree et al., 2009). In contrast, our study found significant negative effects of reduced landscape heterogeneity on the bee community, while, contrary to our predictions, local effects of land-use intensity and plant diversity were less pronounced or entirely absent.

We additionally aimed to identify patterns in bee traits related to pollen foraging that correlated with species-specific responses to environmental change. We found that larger bees responded negatively and more strongly to land-use intensity than smaller bees (which showed no or a weak correlation). A priori, this finding seems counter-intuitive to what is expected based on the bees' foraging range and carrying capacity. In fact, Benjamin et al. (2014) found larger bees to respond negatively to increasing agricultural cover (mostly) at landscape scale, while smaller bees responded negatively (mostly) at local farm scale, which corresponded to their foraging ranges (Benjamin et al., 2014). Abundances of small wild bees also correlated negatively with open farmland and roadsides and positively with scattered trees and nectar-bearing crops (Hall et al., 2019), suggesting that smaller species are more limited by local resource availability, while larger species increased their foraging ranges in the search for suitable resources when local flowering plant species richness was low (Jha and Kremen, 2013). Our results may consequently suggest that larger bee species are more likely to avoid low local plant diversity and specific (likely non-attractive) plant communities typically associated with high land-use intensity grasslands. Instead, they move on to better foraging patches, while smaller bees cannot avoid these plots as easily as larger bees and therefore have to forage on the available plant spectrum. This hypothesis also agrees with the fact that our study landscapes were still comparatively heterogeneous and may provide suitable nesting sites for a variety of different bee species.

Regarding diet traits, we found that the most specialist bees in our dataset, i.e. bees with high d' values, showed strong positive and significant responses to landscape heterogeneity, indicating that their abundance depended more strongly either on specific nesting habitats available in the surrounding landscape or on the presence of specific (rare) plants that are not present in comparatively more homogeneous landscapes. In fact, specialist bees collected pollen from few and/or the rarest plants of the spectrum of pollen plants revealed by pollen metabarcoding. Thus, specialist bees (in terms of high d' values) may have a more restricted plant niche in terms of species which might be related to the plants' pollen nutritional profiles (Parreno et al., 2022; Vaudo et al., 2024). Alternatively, such low flexibility may be explained by sensory or physiological limitations (van der Kooi et al., 2021). If some of the bees' pollen host plants are missing within the foraging range specialist bees will have more difficulties to find a replacement than generalist bees. A landscape that is poor in pollen host plants increases search efforts, which may result in more specialist bees having comparatively smaller populations in pollen host-poor landscapes (Peters et al., 2022). Notably, only a few studies (Hass et al., 2018; Machado et al., 2020; Malagnini et al., 2022), linked their results to pollen resources at local or regional scale, because identifying and quantifying pollen supplies in the landscape is challenging.

Our approach of using d' based on a bee-pollen network as a proxy for specialization to test for responses to landscape heterogeneity or local land-use intensity and plant diversity is novel, especially for so many wild bee species. Most studies using the d' index derived it from bee-

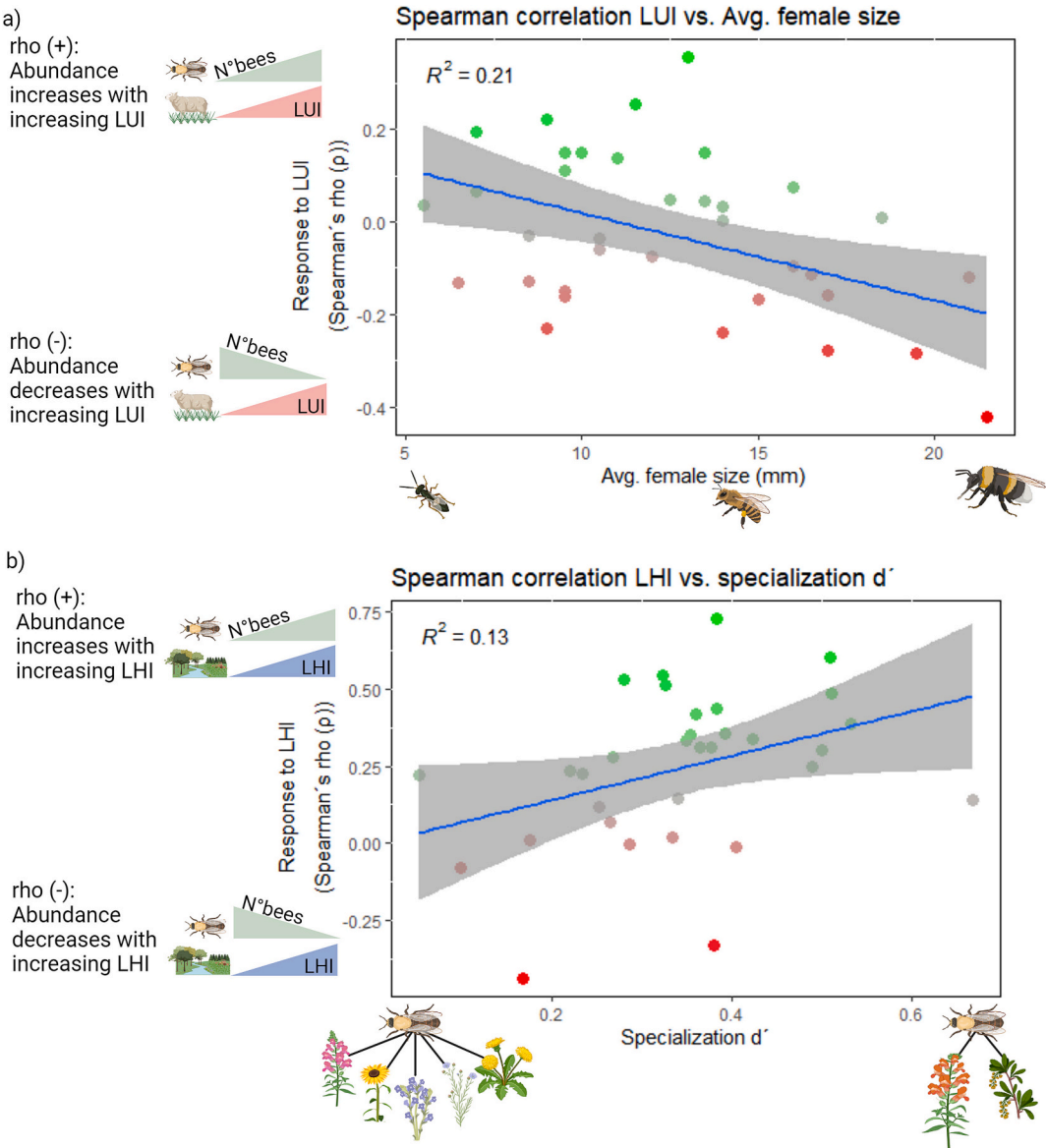


Fig. 3. Spearman correlation responses in relation to pollen foraging traits ($p < 0.05$). Shaded area is the 95 % confidence level interval. Each dot represents a bee species' correlation coefficient for correlating its abundance with the respective environmental variable. For a size reference, smaller bees include *Lasioglossum* sp., intermediate *Apis mellifera* and large *Bombus* sp. are shown. Generalist bees: $d' = 0$ (share all pollen with other bee species), specialist bees: $d' = 1$ (collect exclusive pollen not shared with other bee species).

Table 4
Results of linear models analyzing effects of environmental variables on bee functional indices. Significance (sign.) codes of p-values: ***<0.001; **<0.01; *<0.05; ns >0.05, marg. sign.: Marginally significant (0.055).

Functional Richness (Fric)	Estimate	St. Error	F	Pr (>F)	sign.
Plant Diversity	-0.042	0.086	0.043	0.837	ns
Land-use index (LUI)	-0.246	0.327	0.107	0.746	ns
Land heterogeneity index (LHI)	1.627	0.656	6.146	0.019	*

Functional Evenness (FEve0)	Estimate	St. Error	F	Pr (>F)	sign.
Plant Diversity	0.002	0.004	0.181	0.674	ns
Land-use index (LUI)	-0.027	0.016	3.165	0.086	ns
Land heterogeneity index (LHI)	-0.031	0.031	1.002	0.325	ns

plant visitation networks based on observational records in the field, which includes plants that are visited for nectar foraging (King et al., 2013). Other studies referring to pollen diet specialization use the classical categories provided in the literature along the monoleptic-polylectic spectrum (Cane and Sipes, 2006; Müller and Kuhlmann, 2008). This classification however, does not take into account community-specific exclusiveness, i.e. bees with broader but restricted pollen diets (including e.g. primarily rare plant species), or host plant availability, i.e. bees foraging on a restricted spectrum of few but common pollen hosts. However, this approach also needs to be interpreted with caution as it always depends and thus varies with the respective bee community. It may therefore not be representative for other communities or seasons and for the same species in a different environmental context. In fact, d' represents mostly a snapshot of commonness and exclusiveness in partitioning of those resources that were available to the bees at a certain time. In this light, our results support existing scattered evidence that there is a higher specialization of bees with higher plant diversity in the landscape regardless of their

ideal niche (Ebeling et al., 2011; Guzman et al., 2019).

Our dataset with numerous species shows a large diversity in terms of richness but only low numbers in terms of abundance of most species, which may explain why we did not find significant effects of our environmental parameters on functional evenness (Geppert et al., 2023). Also, other life history traits, such as colony size, sociality and nesting traits, all of which have been found at least once in the literature to affect bee community composition and/or bee species responses to landscape heterogeneity changes, may have affected our species' distribution (Hall et al., 2019).

5. Conclusion

Our study places a strong emphasis on the role of food resource diversity and restricted our trait analysis to those traits actually related to pollen collection, which complements the manifold studies demonstrating positive correlations between plant diversity and pollinator diversity. Our results reveal a strong effect of landscape and highlights a link between landscape heterogeneity, the diversity of bee communities and the pollen diversity collected by and thus likely available to these communities in an agricultural landscape. We also show that landscape heterogeneity may play an important role in structuring the richness, functional trait diversity and composition of wild bee communities. Traits related to pollen foraging (e.g. diet specialization/exclusiveness and body size) mediate the bees' responses to environmental parameters (plant diversity and land-use) at local and landscape scales. Our findings highlight the need for taking into account more detailed information on the actual resource use by pollinators (e.g. pollen plants in wild bees) which goes beyond mere overall floral diversity and may be a prerequisite for effective conservation measures targeting wild bee communities in agricultural areas. Future research into wild bee responses to human interventions should consider additional factors, such as nesting resources, intraspecific trait variation, differences in foraging flexibility among pollinator species or the role of pollen nutritional profiles.

CRediT authorship contribution statement

M.A. Parreno: Writing – review & editing, Writing – original draft, Project administration, Investigation, Formal analysis, Data curation, Conceptualization. **S. Werle:** Investigation, Data curation. **L. Buydens:** Investigation, Data curation. **C. Leroy:** Investigation. **S. Roberts:** Investigation, Data curation. **S. Koirala:** Formal analysis. **M. Filipiak:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization. **M. Kuhlmann:** Writing – review & editing, Funding acquisition, Data curation, Conceptualization. **J.-L. Brunet:** Supervision, Project administration, Investigation, Conceptualization. **M. Henry:** Writing – review & editing, Supervision, Conceptualization. **C. Alaux:** Supervision, Project administration, Funding acquisition, Conceptualization. **F. Requier:** Writing – review & editing, Investigation, Conceptualization. **N. Piot:** Writing – review & editing, Supervision, Investigation. **I. Meeus:** Writing – review & editing, Supervision, Project administration, Funding acquisition, Conceptualization. **A.-M. Klein:** Writing – review & editing, Project administration, Conceptualization. **A. Keller:** Supervision, Project administration, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **S.D. Leonhardt:** Writing – review & editing, Supervision, Project administration, Investigation, Funding acquisition, Formal analysis.

Declaration of competing interest

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

Data availability

Raw datasets for the different environmental and trait variables are available at the Biodiversity Exploratories data management central database (Bexis), with the following codes: visitation records (311331), metabarcoding (31545), foraging traits (31731), basic plot data (20826), land-use management values (31514), land-use heterogeneity classification (31557) and plant diversity from the core botany group (31175). A Data in Brief manuscript with the visitation records and basic plot data combined has been submitted as a supporting article.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2024.176595>.

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