



## RESEARCH PAPER

# Climate and land use primarily drive the diversity of multi-taxonomic communities in agroecosystems

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## ABSTRACT

To successfully conserve and restore agrobiodiversity, it is essential to understand the impact of multiple drivers and interlinkages across multiple taxa that occur above, across, and below the soil interface. Based on data from six agricultural landscapes in Central Germany, with 16 sampling plots per landscape, we used structural equation models to disentangle the impacts of climate, land-use, and soil factors on the diversity of multiple taxonomic groups. We expected belowground communities (soil bacteria and fungi) to be more driven by soil variables, mobile aboveground groups (wild bees, ground beetles) to be more driven by climate and land use, and vascular plants, that have an above- and belowground component, to respond to a combination of all factors.

According to our expectations, climate and land-use variables had an important role in shaping aboveground and plant communities. In contrast to our expectations, soil characteristics were of lesser importance for belowground organisms. Moreover, climatic factors had a strong impact on the soil microbiome, but this effect was indirect, modulated by soil pH. We also found indications for cascading effects of environmental factors via interlinkages within and among the above- and belowground communities. Our results highlight the importance of direct and indirect effects of multiple drivers on the diversity of multiple taxonomic groups and support recent calls for a multifunctional approach for sustainable landscape management and nature restoration, suggesting to focus on the promotion of semi-natural habitats but also considering the climatic context.

## Introduction

Agroecosystems are comprised of multiple taxonomic groups, covering the entire range from below, across, and above the soil surface, which are critically linked by complex interactions (Lefcheck et al., 2015; Soliveres et al., 2016). For instance, within the soil, competition and facilitation occur among bacterial and fungal communities (Barberán et al., 2012), which also apply to relationships between plants and soil biota (Chung et al., 2023). The biomass production and diversity of plants play also an important role in defining diversity and abundance of aboveground insects, such as pollinators and biocontrol agents (Tscharnkte et al., 2007; Ebeling et al., 2008). Given these trophic interlinkages, a high diversity of multiple taxonomic groups is required to sustain or increase relevant ecosystem functions and related services (e.g. regulating services such as pollination, pest suppression, nutrient cycling) (Soliveres et al., 2016). However, multiple pressures of global

change, such as habitat loss, climate change and changing soil conditions, threaten all groups, although to different extents (IPBES, 2019) and with potential cascading effects (Schuldt et al., 2017). The impact of certain pressures has become increasingly well-understood for certain taxa groups and their biological interactions. For example the negative impact of land use intensification on multiple taxa groups (IPBES, 2019), or climate change that threatens plant-pollinator community relationships (e.g. see Papanikolaou et al., 2017), while other interactions e.g. linking plant species richness to soil biota (Liliensiek et al., 2012) or fungal to bacterial communities (Emmett et al., 2021), or the impacts of environmental factors on multiple taxonomic groups still demand further research. To address this gap, detailed studies analyzing the response of multiple taxonomic groups that fill a broad range of functional roles within agroecosystems are essential (e.g. Billeter et al., 2008; Soliveres et al., 2016). These range from those related to soil processes, e.g. soil microbes (Schimel & Bennett, 2004); pollination and pest control, e.g.

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wild bees and ground beetles (Fusser et al., 2016; Senapathi et al., 2021); as well as taxa linking above- and belowground processes, e.g. plants (Hanisch et al., 2020).

Understanding how the different drivers of global change shape the diversity and interlinkages of multiple taxonomic groups is also relevant to set the efficiency of management options (e.g. decisions related to land use or soil management) into a wider environmental context. Drivers known to affect the diversity in agricultural landscapes include climatic and weather conditions (Evers et al., 2021; Slabbert et al., 2022), land use (Hedlund et al., 2004; Papanikolaou et al., 2016a), microclimatic, and soil conditions (Liliensiek et al., 2012; Vician et al., 2018). Climatic factors, such as mean annual temperature and precipitation, for example, are critical to physiological processes of both above- and belowground taxa, and important drivers across all groups (Teder-soo et al., 2014; Slabbert et al., 2022). Land use has also been shown to affect both above- and belowground diversity, however, the actual drivers can differ (Sirami et al., 2019; Le Provost et al., 2021). Papanikolaou et al. (2017), for example, found aboveground taxa (wild bees) to benefit from habitat richness at the landscape scale, while belowground diversity benefits from the local permanence of semi-natural habitats (Le Provost et al., 2021). Soil characteristics, such as fertility or pH, are particularly relevant for soil microbes (Glassman et al., 2017) and plants, but can also indirectly impact higher trophic levels (Carvalho et al., 2020).

Here, we investigate how climate, land use, and soil conditions impact local communities across the soil interface and how their trophic relationships might lead to cascading effects across the different taxonomic groups. We focus on five groups covering major functional roles across the soil interface, namely vascular plants (across), wild bees and ground beetles (aboveground), and free-living soil bacteria and fungi (belowground). We relate their species richness, diversity and abundance to weather conditions (mean annual temperature and precipitation), land use (proportion of semi-natural habitats and land cover diversity), microclimatic conditions (using variables based on local topography e.g. slope, hill shading during summer months), and soil conditions (soil nutrients, moisture, pH and texture).

Due to the pronounced ecological differences among the considered taxa, we expect above-, across, and belowground taxa to be affected differently by the factors considered in this study (e.g. Slabbert et al., 2020). Since insect populations and communities are highly responsive to climate or weather conditions (Papanikolaou et al., 2016b) and strongly depend on resource availability defined by different patterns of land use (Tscharrntke et al., 2012), we hypothesize that aboveground taxa are mostly affected by those factors (climate, land use), while the impacts of microclimatic and soil conditions are smaller and rather indirect, e.g. moderated by plants. We further expect that belowground communities will be mostly driven by soil properties and microclimatic conditions, and, given the enormous differences in the scale of activity compared to mobile aboveground taxa, less by larger-scale land-use patterns. Since soil can also buffer climate and weather fluctuations (Cruz et al., 2021), we also expect a smaller impact of temperature and precipitation. As plants straddle the above-belowground interface, we predict that a combination of all factors is important. We also consider feedback loops between certain taxonomic groups based on prior knowledge: these include a link between plant and soil microbial groups (Liliensiek et al., 2012), and plant and aboveground groups (Tscharrntke et al., 2007; Ebeling et al., 2008), and between soil bacteria and soil fungi (Landesman & Dighton, 2017). These relationships can be considered to be bi-directional as there is consistent evidence for strong feedback between plants and microbial communities as well as between soil fungi and bacteria (Barberán et al., 2012).

## Materials and methods

### Study sites

Data for this study were collected in six study sites as part of the Terrestrial Environmental Harz/Central German Lowland Observatory (TERENO) (Zacharias et al., 2011) biodiversity monitoring managed by the Helmholtz Centre for Environmental Research - UFZ. The sites are located in Saxony-Anhalt, Central Germany, and represent typical agricultural landscapes within this region. The cover of arable fields ranges from 71 to 97 %. Farmers are typically applying integrated pest management and the major crops grown in Saxony-Anhalt in 2023 are winter wheat (34 %), winter oilseed rape (17 %), maize (14 %) and winter barley (12 %). The cover of semi-natural elements ranges from 1.7 to 16.9 % and comprises field and road verges, hedgerows, mesic or semi-dry grasslands, and smaller patches of mixed or deciduous forests. The sites, located near Friedeburg (FBG), Schafstädt (SST), Greifenhagen (GFH), Wanzleben (WAN), Harsleben (HAR) and Siptenfelde (SIP), cover 16 km<sup>2</sup> each and have varying configurations of land use and abiotic conditions (see Appendix: Table 1). Sampling within these sites took place at edge habitats including field margins and road verges. These linear elements provide valuable habitat to agrobiodiversity that is complementary to adjacent semi-natural vegetation (Suárez-Esteban et al., 2016).

### Data collection

#### Wild bees and flying carabids

As part of the TERENO monitoring scheme, wild bees and flying carabids were sampled with flight traps which combine properties of window and yellow pan traps (see Duelli et al., 1999 and Papanikolaou et al., 2016b for details). Sixteen flight traps were installed per site (total of 96 sampling points; exact trap locations are available on the UFZ TERENO website under Biodiversity Platforms > Investigation areas). Traps were emptied biweekly and operational for six weeks in spring to early summer and six weeks in late summer. Wild bees and flying carabids of 2018 were selected and identified to species level in the laboratory. Due to in-field conditions and accessibility restrictions during 2018 only 92 of the 96 sampling points could be sampled (see Appendix: Table 1).

#### Vascular plants

In summer 2018, a vegetation survey was done at the base of each flight trap covering 1 m<sup>2</sup> to determine vascular plant species richness and percentage cover based on the nine-grade Braun-Blanquet scale (Braun-Blanquet, 1964). Recorded species names were cross checked against the Leipzig Catalogue of Vascular Plants (LCVP) using the *lcvplants* package (Freiberg et al., 2020) in R (R Core Team, 2021), seedlings were omitted from the dataset, and species complexes were pooled to species level. Due to the 3D-structure of the vegetation and respective overlaps, total cover of the plant community can reach values of more than 100 %. In cases of scarce cover and higher proportions of bare soil total plant cover can also be lower than 100 %.

#### Free-living soil fungi and bacteria

Soil microbial communities of free-living soil fungi and bacteria were sampled using standard composite sampling. Five soil cores (ca. 6 cm diameter) were taken at each flight trap to a depth of 10 cm (after removal of the organic litter layer), pooled and sieved (2 mm) in-field. From the pooled sample ten grams were flash-frozen on dry-ice for microbial analysis. Amplicon sequence variants (ASVs) were identified with next-generation sequencing as outlined in Singavarapu et al. (2021) which were considered to be the finest taxonomic units (i.e. species level). As an estimation of soil bacteria and fungi relative abundance we used the number of sequences reads per taxon ASV, a commonly applied approach which needs to be considered with care

(Catlett et al., 2020) but with powerful indicator value of community composition (Godhe et al., 2008). Only ASVs with a Phylum level identification were kept in the dataset. Hereafter, the data matrix was filtered using the *R phyloseq* package (McMurdie & Holmes, 2013) to only keep ASVs that occurred more than 5 times in at least 1 % of the dataset for further analysis. An additional 500 g soil sample was collected for standard soil analysis to determine soil moisture, soil texture, pH and soil nutrients.

#### Biodiversity metrics

Three biodiversity metrics were used as response variables for the respective taxa (wild bees and ground beetles, vascular plants, free-living soil fungi and bacteria): species richness, Shannon diversity, and abundance. These were assessed at the local-scale, measured at plot-level (1 m<sup>2</sup>) for the flight trap samples, floral survey plots and soil core samples, respectively. Species richness was used as a standard biodiversity measure to capture a change in number of species, while Shannon diversity was included to capture changes in both species richness and evenness of the species abundance distribution, as altered evenness had been found to be a dominant component driving biodiversity patterns (Slabbert et al., 2020). Additionally, we assessed the change in abundance of the respective taxon, using % cover as abundance proxy for plants, and ASV count for the soil microbes to investigate potential density-independent effects on species richness.

#### Explanatory variables

To assess the importance of climate, weather, land use, microclimate, and soil properties on biodiversity metrics of multiple taxonomic groups, and their potential direct and indirect effects on each other, we selected several explanatory variables based on our hypotheses. These included variables measured at the site-level (16 km<sup>2</sup>; climate and land use) and variables measured at plot-level (1 m<sup>2</sup>; microclimate and soil properties).

#### Climate and weather conditions

To quantify climatic and weather conditions that may be influencing the individual taxonomic groups, weather data for the mean daily temperature and total daily precipitation were obtained for the six study sites from weather stations managed by the UFZ (FBG, HAR, GFH and WAN) and the Deutscher Wetterdienst (DWD; SIP and SST) for the past 10 years (2009–2018). From this, we calculated mean annual temperature (MAT) and mean annual precipitation (MAP) per site for (1) the past 10 years, (2) the 12 months preceding field sampling (07.2017–06.2018), as it has potential impact on population growth and diversity in the following year, and (3) seasonal weather conditions of the fortnight prior to sampling, as this has a more direct impact on activity.

#### Land use

Land cover of semi-natural habitat and landscape heterogeneity of land-use types were calculated at site-level (16 km<sup>2</sup>) based on digitized habitat maps prepared from orthorectified aerial photos (see Frenzel et al., 2016 for more details). Habitat classification followed the 2012 revised European Nature Information System (EUNIS; <https://eunis.eea.europa.eu/habitats.jsp>) to the third level. The EUNIS classifications were aggregated to more general habitat categories relevant for, e.g. wild bees based on Frenzel et al. (2016). These included a category for arable land, managed grasslands, forest, semi-natural habitats, and urban. Based on these classifications, we calculated the proportion of semi-natural habitat per site and the Shannon diversity as a proxy for landscape heterogeneity.

#### Soil properties and microclimate

Soil parameters were determined from 500 g of the sieved soil collected in parallel to sampling soil microbes within the 1 m<sup>2</sup> plots. The

soil was under cooler storage in-field, and then stored at ca. 6 °C until standard soil parameters, soil moisture and soil acidity (pH) were measured following standard laboratory protocols (VDLUFU, 1991). Soil parameters measured (as grams per 100 g of dry soil) included soil carbon (C), nitrogen (N) and the carbon-nitrogen ratio (using a Vario EL III Element Analyzer), and plant-available soil phosphorus (P) and potassium (K), as well as soil pH (KCl method). The proportion of soil moisture content was determined using a drying oven after the removal of coarse organic matter. Additionally, soil texture was determined and calculated as the percentage of silt, clay and sand within a 10 g sample. As a proxy for microclimatic conditions at the plot-level, we used a digital elevation model with a resolution of 10 m, calculated aspect (geographical direction), slope, elevation and hill shading (for summer months) for each of the sites at the 10 m resolution, and extracted the respective values for each of the plots by intersection.

#### Statistical analysis

Initial variable selection was hypotheses driven, see Appendix Fig. S1A for a visual overview of the hypothesized links outlined in the introduction. As we aimed to characterize the micro-habitats at the plot-level, we compressed the topography variables (i.e. aspect, slope, elevation and hill shading), soil nutrient variables (soil C, N, C:N ratio, and plant available P and K), and soil texture variables (percentage silt, clay, and sand) into single variables by performing principle component analyses (PCA) per category (Table 1). For soil topography, the first PC axis explained 33.46 % and represented a gradient from high hill shading to steep slopes. The second axis explained 28.88 % with highest loadings of aspect and altitude. For soil nutrients, the first PC axis explained 44.58 % and predominantly reflected common gradients in soil N and C. The second axis explained 33.38 % with the highest loadings of soil P and K, while C:N ratio represented axis three (explaining 16.15 % of the variation). For soil texture, the first PC axis explained 63.34 % spanning a gradient from high proportions of silt to high proportions of sand, while proportion of clay loaded highest on the second axis (explaining 35.64 %). We used as standard only the PC loading per plot from the first axes for further analysis (Table 1). The soil variables for moisture and pH did not ecologically group well with the other soil variables, and thus were included in the analysis independently. As the remainder of the site- and plot-level variables were very different in their measurements, we standardized all variables by scaling (mean-centering and unit variance).

All the predictor variables were checked for correlation using the *Hmisc* package (*varclus* function, spearman method) (Harrell, 2023). For sets of variables that had a correlation of higher than 0.5 (transformed R<sup>2</sup>), we selected between them based on our assumptions of higher ecological interest. This led to the exclusion of the seasonal weather variables and long-term climatic variables, as these were correlated to MAP and MAT, respectively, of the preceding 12 months. We decided to rather include MAP and MAT from the preceding 12 months as these conditions would have a more direct impact on population dynamics, while also accounting for seasonal activity. Additionally, soil pH was also correlated to MAT, however, to ensure predictors remain scale-explicit, we retained both of these in the subsequent analysis while accounting for the direct link between predictors. Adding this link was

**Table 1**

Proportion of explained variation per 1st axis for PCAs done for soil nutrients, soil texture and local topography and the most prominent driver of variation per category.

Input variables	% Explained variation on 1st PC axis	Most prominent driver of variation
Soil nutrients	44.58	proportion of soil nitrogen (N)
Soil texture	64.34	proportion of sand vs. silt particles
Local topography	33.46	variation in hill shading

also supported by previous studies which found that soil pH can modulate the impact of other variables on local communities, such as the impact of climate on plants (e.g. see [Le Bagousse-Pinguet et al., 2017](#)).

Using the final set of explanatory variables, we checked for spatial autocorrelation using Moran's I but found none. The variables were used to construct three structural equation models (SEM), one per biodiversity metric using the *psem* function from the *piecewiseSEM* package ([Lefcheck, 2016](#)). The model structure was based on our hypotheses (see Appendix: Fig. 1A, Table 3), and was initially set as linear mixed-effects models (*lme4* package, [Bates et al., 2015](#)) with site as random factor. Since the model structure had singularity issues, due to several of the predictors being measured at site-level, we dropped the random factor which explained no or a negligible amount of variance. We evaluated the conditional independence claims arising from our model structure per response variable and added missing links (see Appendix: Fig. 1B) between response and predictor variables that were statistically significant ( $p < 0.05$ ) and considered ecologically relevant (e.g. a link between MAP and soil pH, several local-scale variables on carabids, and between soil fungi and wild bees). A link between soil fungi and wild bees was not initially considered, but seems plausible since many soil fungi, such as *Aspergillus* species, can either be directly pathogenic to bees ([Becchimanzi & Nicoletti, 2022](#)) or affect pollen provision during larval development ([Batra et al., 1973](#)), particularly for soil-nesting bees, which make up to two thirds of the bee species in the study region. We optimized the SEMs by performing step-wise backward selection based on Akaike Information Criterion (AIC) values ([Shipley, 2013](#)), starting with the least significant relationship. SEM models were visualized using the *DiagrammR* package ([Iannone, 2023](#)), with relative importance of the explanatory variables scaled to be proportional to the SEM standardized effect size per variable. General data management, statistical analysis and visualizations were done using R 4.0.5 ([R Core Team, 2021](#)).

## Results

### Data overview

We recorded 1033 vascular plants consisting of 227 species, representing 142 genera; 28 830 wild bees from 148 species and 15 genera; 5 830 ground beetles from 76 species and 32 genera. For the soil microbes, we recorded 1484 fungi ASVs from 327 genera, and 6121 bacteria ASVs from 464 genera (see Appendix: Table 2).

### Structural equation model overview

The three biodiversity metrics, species richness, diversity (Shannon index) and abundance, revealed complementary insights about the specific factors shaping the respective taxonomic groups (Fig. 1). All three final SEMs were robust (see Fischer's C and p-values in Table 2). For all three biodiversity metrics, there was a low importance of most microclimatic and soil characteristics with the exception of soil pH and generally a high importance of both weather and land-use variables.

When comparing the proportion of explained variation per taxonomic group ( $R^2$ ) for the respective models, we generally found similarity across metrics (Table 2). Comparing across taxonomic groups, explained variation was generally highest for soil microbes, followed by vascular plants and carabids (except for abundance), while explanatory power was lowest for wild bees, except for abundance which was lowest for carabids.

### Species richness

Land-use related variables were of particular importance for species richness of aboveground groups and vascular plants, with consistent positive effects of semi-natural area, while land cover diversity had negative effects on wild bees and carabid beetles (Fig. 1A). Mean annual

precipitation (MAP) was negatively related to the richness of aboveground groups, while vascular plant richness showed a positive relationship to mean annual temperature (MAT). Microclimatic and soil variables had little impact on both aboveground groups, except a small negative effect of proportion of sand in the soil on wild bees and a positive effect of hill shading on carabids. For belowground groups, only soil pH had a positively affected on species richness, in addition to a positive connection between species richness of soil bacteria and soil fungi.

### Diversity

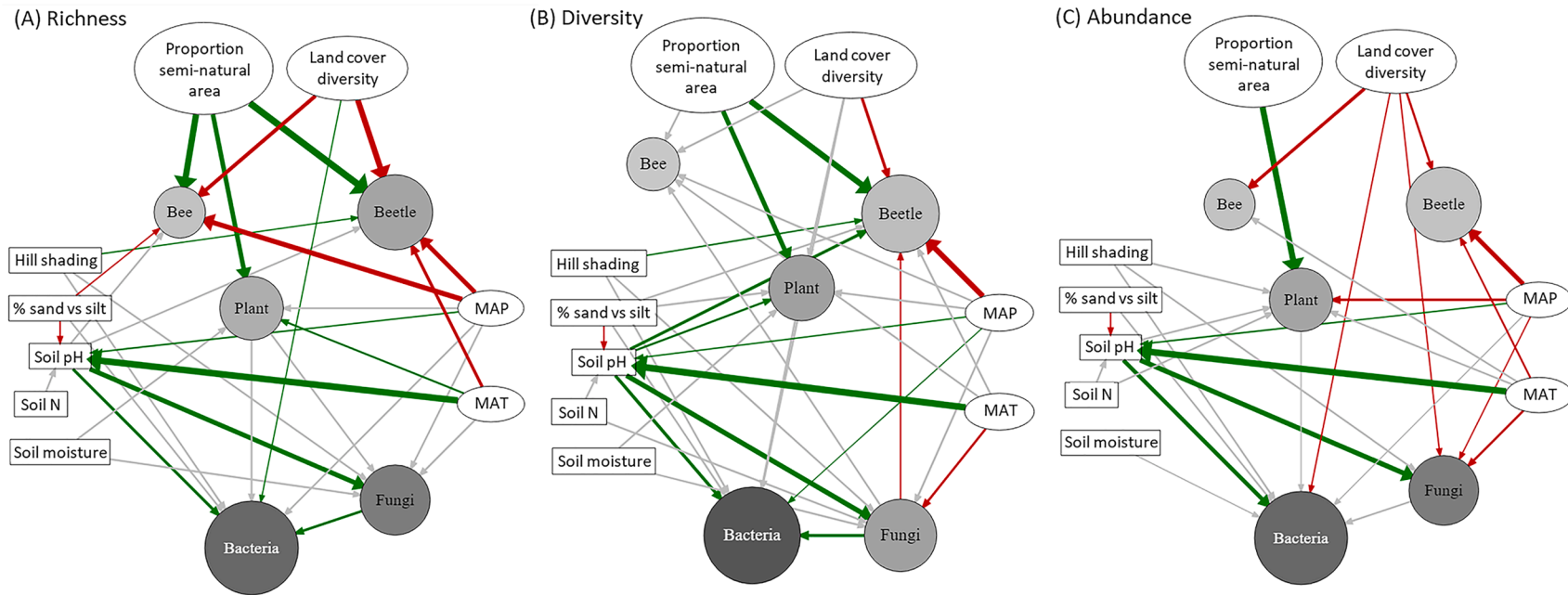
Results for diversity were similar to those of richness, however, a remarkable difference was found for wild bees (Fig. 1A). While wild bee richness was affected by MAP, land cover diversity, proportion of semi-natural habitat and soil texture, wild bee diversity was affected by none of the tested factors significantly. Factors that showed up as important for vascular plant diversity altered slightly in comparison to richness. Here, MAT no longer had a direct impact on vascular plant diversity, but acted indirectly via soil pH. Interestingly, we also found a direct effect of warmer conditions (MAT) reducing soil fungal diversity and a direct positive effect of MAP on soil bacterial diversity. Furthermore, we found an unexpected link between soil fungal diversity and carabid diversity, which indicates a network of linkage across weather and soil factors finally impacting two taxonomic groups. Carabid diversity was negatively associated with soil fungal diversity, which was impacted by soil pH which in turn was affected by MAT, MAP and soil texture.

### Abundance

Results for abundance were complementary to the results for richness and diversity (Fig. 1), and taken with the other metrics, provide a complete picture of biodiversity patterns. For wild bees, increases in richness with higher proportions of semi-natural area (Fig. 1A) was not caused by increased bee abundance (Fig. 1C) or evenness (Fig. 1B), and thus was due to increases in the number of rare bee species. Similarly, for the carabid beetles, increased species richness with higher proportions of semi-natural habitats (Fig. 1A) was not due to higher abundance of carabids (Fig. 1C), but accompanied by increases in evenness (Fig. 1B). In contrast to wild bees and carabids, plant increase in richness with higher proportions of semi-natural elements (Fig. 1A) were driven by increases in abundance (Fig. 1C) and evenness (Fig. 1B). Land cover diversity had a strikingly negative impact on the abundance of almost all taxonomic groups, with the exception of plants, with the largest effect size on the more mobile groups (wild bees and carabids). Interestingly, the positive relationship between the richness and diversity of fungi and bacteria was not observed for measures of abundance. The impacts of MAT and MAP on abundance of the taxonomic groups were similar as on richness and diversity, in particular with their indirect effect on fungal and bacterial abundance moderated by soil pH.

## Discussion

Our results revealed clear shifts in species richness, diversity and abundance of all taxonomic groups under specific environmental conditions that are especially linked to climate and land use, with the impact of climatic factors on soil microbes often being mediated via soil pH. These results support our hypothesis of the cross-cutting importance of annual climatic conditions for all groups and our expectation that mobile aboveground groups (wild bees and flying carabids) are predominantly impacted by climate and land use. However, the importance of microclimate and soil factors was lower than expected for vascular plants and soil microbes, with the exception of a strong effect of soil pH. We were surprised to find that higher diversity of land cover types had a positive effect on soil microbial richness (via soil bacterial richness), as well as having a negative direct effect on the abundance of both microbe



**Fig. 1.** Structural equation models with species richness (A), diversity (B) and abundance (C) as response variable per taxonomic group (circles) and how these are impacted by climate and land-use predictors (ellipses) and soil and microclimatic predictors (rectangles); see methods for more details. Arrows indicate modelled connections between taxa and predictors, and between taxonomic groups. Green and red arrows denote positive and negative effects, respectively, on richness, diversity or abundance. Arrow widths are adjusted to be proportional to the standardized effect sizes. Light grey lines are non-significant linkages. Taxa circles are shaded according to increasing proportion of explained variation ( $R^2$ ), see Table 1. MAP, MAT: mean annual precipitation and temperature of the preceding year.

**Table 2**

Overview of the goodness-of-fit of the structural equation models per response variable, and the proportion of explained variation per taxonomic group ( $R^2$ ).

Taxa	Richness	Shannon diversity	Abundance
Vascular plant	0.32	0.38	0.32
Wild bees	0.25	0.25	0.24
Carabid beetles	0.37	0.32	0.19
Soil bacteria	0.63	0.72	0.65
Soil fungi	0.46	0.38	0.48
Model details			
Goodness of fit (Fisher's C)	39.03	46.38	67.36
p-value	0.99	0.82	0.63
Degrees of freedom	62	56	72

groups. Likewise, we were surprised to find that soil texture, soil pH and the proportion of hill shading influenced biodiversity metrics of wild bees and carabids, as well as by the effects of soil fungi and soil pH on carabid diversity.

#### Importance of climatic and land-use factors in shaping biotic communities

Both climate and land-use variables had stronger effects on above-ground taxonomic groups (both insect groups and vascular plants) than on soil microbes. Wild bee and carabid richness were supported by higher proportions of semi-natural habitat, but their diversity was negatively affected by an increase of other land use types (e.g. urban or forested areas or managed grasslands). For carabids, this negative effect could be due to specific habitat requirements. Predominantly flying carabids, as captured in our flight traps, are usually adapted to open land, and higher proportions of, e.g. forested or urban areas can create an obstacle for their dispersal (Kotze et al., 2011).

Weather and landscape conditions impacted species richness, but not diversity of wild bees. The strong impact of semi-natural areas is likely related to the abundance of floral resources available in remnant patches within agroecosystems (Papanikolaou et al., 2017; St. Clair et al., 2022), and the availability of shelter and nesting sites (Harmon-Threatt, 2020; Tschanz et al., 2022). A closer look at the wild bee community supported this interpretation as we found a lower proportion of above-ground nesting families (e.g. Halictidae and Megachilidae) and higher dominance of ground nesting families (e.g. Andrenidae) in sites with a higher proportion of agricultural fields (e.g. in SST; see Appendix: Fig. 2A). The negative impact of land cover diversity on wild bee species richness and abundance might be a sampling artifact, as an increase in land cover diversity is often due to the presence of other habitats (e.g. forests and urban areas) with lower flower resource availability in addition to the agricultural dominated landscapes. Thus, the flight traps may have been more attractive to the pollinating insects that are present than otherwise expected (Baum & Wallen, 2011).

We also found both climatic and land-use conditions to be of importance in shaping local microbial communities. This is surprising since microbial communities are usually thought to be primarily impacted by soil conditions at very small scales (Herold et al., 2014; Glassman et al., 2017). However, there is also a growing body of literature reporting that global and local soil microbial communities are strongly driven by large-scale factors such as climate (Větrovský et al., 2019), which has an influence on decomposition conditions. Our results are thus in line with studies that have also used coarse-grained sampling for investigating the drivers shaping microbial communities (Tedesoo et al., 2014; Větrovský et al., 2019). However, our study is one of the first to also find these patterns to be present not only at global and continental scales, but also at landscape scales.

Our results show that the impact of landscape structure can also have direct impacts on belowground taxa. We found direct positive impacts of land cover diversity on soil bacterial richness, which is likely related to variation in the availability and diversity of suitable habitat niches and source pools spores can disperse from Amarasekare (2003); Ernakovich

et al. (2021). The positive impact on species richness was likely mainly an increase in rarer species having their specific habitat requirements met in more diverse landscapes (Le Provost et al., 2021). However, we also found negative impacts of land cover diversity on the abundance of both soil microbial groups which is likely due to a saturation point being reached in terms of resource availability (Ernakovich et al., 2021). It has been shown that the increase in species richness with higher land cover diversity increases inter- and intraspecific competition which has a plateauing and eventually negative effect on microbial abundance (Grime, 1973).

#### Importance of microclimatic and soil conditions in shaping biotic communities

Overall, microclimatic and soil conditions were less important than climatic and land-use factors at influencing biodiversity of both above- and belowground taxa. Only soil pH had a prominent influence across all three biodiversity metrics, however, it was strongly driven by the impact of temperature, and to a lesser extent precipitation. Thus, these climate variables had a strong impact at a local-scale via soil pH. This prominent link is in support of studies reporting climate, along with basal geology, to be dominant drivers of soil pH, mainly due to long-term impacts on weathering processes and influences on accumulation and decomposition of organic material (Fabian et al., 2014).

The lower significance of other soil variables and topography for plants was unexpected. The summer of the sampling year (2018) was particularly hot and dry, causing a severe drought, which might be one reason for the lack of effects. Such a diminishing effect of aridity has, for instance, been shown for the relationship of plant species richness and soil characteristics (Palpurina et al., 2017). Similarly, the lower significance of other soil variables and topography for soil microbes was also unexpected, as they are in contrast with other studies showing edaphic variables to be prominent in shaping microbial communities (Herold et al., 2014; Glassman et al., 2017). This could be due to local-scale heterogeneity being a more primary driver (Herold et al., 2014; Kaiser et al., 2016), which our sampling grain does not capture well. Cordero and Datta (2016), for instance, suggest a scale of investigation between 10 and 10<sup>3</sup> µm for determining local drivers and biological interactions of soil microbes. Alternatively, there might be a lagged microbial response to aboveground disturbances (e.g. from agricultural practices and road verge management) (Berga et al., 2012) or one missed due to fast turn over occurring at much shorter time intervals than sampling accounts for (e.g. an hourly-scale; Landesman & Dighton, 2017). Furthermore, the strong importance of soil pH may have proportionally outweighed the contribution of the other edaphic factors. The latter, would confirm the growing body of literature suggesting soil pH to play a central role in all soil-mediated processes (Glassman et al., 2017).

Several microclimatic and soil factors were of higher importance for the insect groups than predicted, suggesting they are representative of a larger spatial scale covering wild bee or carabid movement, particularly for small wild bees as central foragers with a limited foraging radius. More fine-textured soils, for example, had a negative impact on wild bee richness, as most ground-nesting bees prefer sandy or sandy-loamy soils (Harmon-Threatt, 2020). It is possible that finer textured soil could lead to wetter nesting conditions, which would increase the risk of pathogens (e.g. pathogenic fungi, bacteria or protists) and could hinder larval development due to lowered soil temperature (Harmon-Threatt, 2020). Soil texture also indirectly had an impact on carabid community composition via soil pH, which is a more obvious link for ground-dwelling organisms. Their larvae and imagoes are largely affected by microclimatic conditions that are mediated by soil composition in interaction with climate (Thiele, 1977). Carabid richness and diversity were also positively affected by hill shading, as is expected as many carabid species have a high preference for well sheltered habitats (Bennewicz & Barczak, 2020; Guseva & Koval, 2021). *Amara* species assemblages, for example, are known to be very sensitive to shading

(Guseva & Koval, 2021), corresponding with our results of higher species richness and diversity in shadier habitats, and supporting the interpretation of positive effects of semi-natural habitats, which also offer more shade, have on carabid diversity. Soil pH and texture further had an indirect impact on carabid diversity as mediated through the impact of soil fungi, as one might have expected since fungal infections of carabids are closely associated with host habitats and microhabitat conditions (Sugiura et al., 2010). Our results of soil fungal diversity being favored by basic soils under warmer temperatures and having a negative impact on carabid diversity could be due to these conditions favoring pathogenic or ectoparasitic fungi (Delgado-Baquerizo et al., 2020). This seems likely, considering that a large proportion of the top 10 most abundant soil fungi families in our sites were pathotrophic.

#### Links across trophic groups

We found a strong link between the soil fungi and bacteria as expected, while the link between plants and soil microbes was weaker than predicted. This could be because we have analyzed the plants and soil microbes at species level rather than functional group level. Gastine et al. (2003), for example, found that the functional role of species is more informative for understanding the relationship between plants and soil microbial communities than species richness and identity. Alternatively, it might be an issue of scale-mismatching (De Deyn & Van Der Putten, 2005; Cordero & Datta, 2016), since finding a suitable survey scale for studying aboveground–belowground diversity relationships is challenging and respective results might be interpreted with care (De Deyn & Van Der Putten, 2005). In particular, a higher sampling frequency for the soil microbiome might be beneficial to cover high temporal turnover.

However, understanding the strength of links among taxonomic groups allows for a better understanding of direct and indirect effects of environmental factors. Here, we show that there are complex networks of links across multiple environmental factors shaping different taxonomic groups across the soil interface. Specifically, we found a cascading impact of climatic factors (MAT and MAP) to soil pH that then affected belowground (soil fungi) and aboveground taxa (flying carabids). This highlights the importance of considering the entire system with both direct and indirect effects of environmental factors and the interlinkages among taxonomic groups for the maintenance of multi-taxa diversity within ecosystems (Schuldt et al., 2017; Meier et al., 2022). Several of the linkages that show up as significant in our study would need further investigation to better understand the mechanisms behind them, e.g. the link between carabids and the various soil variables.

#### Maintaining multi-taxonomic diversity within agroecosystems

Our work shows that the beneficial effects of semi-natural areas in the landscape do not only affect local aboveground and plant communities, but also lead to effects on soil microbial abundance and diversity. With this, managing semi-natural areas provides great potential to improve multi-taxonomic diversity across multiple trophic levels in the agricultural landscape and consequently multiple ecosystem functions and services. Beneficial impacts on the diversity of wild bees, for example, can increase the stability of pollination services for crops (Dainese et al., 2019; Senapathi et al., 2021) and wild plants (Potts et al., 2010). We also observed shifts in the diversity and composition of wild bees (see Appendix: Fig. 2A), already visible at the family level, indicating impacts on the functional structure and likely the provisioning of pollination services. The presence of semi-natural habitats within agroecosystems plays a vital role in facilitating ecosystem services including crop pollination, biological control and soil conservation (Holland et al., 2017). Bumblebees, for example, are important pollinators of crops (Fussell & Corbet, 1992) and their proportions increase with semi-natural area, suggesting that pollination quality can be

affected by the amount of semi-natural habitat (Ricketts et al., 2008). In the same way, supporting a higher diversity of carabids which serve as important natural enemies (Fusser et al., 2016) or weed control agents (Bohan et al., 2011), will increase and stabilize biocontrol services provided for agricultural production (Blubaugh & Kaplan, 2016; Snyder, 2019). Improving the diversity of plants, by increasing the proportion of semi-natural area, is also likely to increase plant functional trait diversity (Finney & Kaye, 2017), which in turn can increase ecosystem services linked to these traits, such as biomass production, fodder quality, water purification, or climate regulation (Hanisch et al., 2020).

Our results also indicate the importance of multiple drivers impacting species richness, diversity and abundance distributions and therefore aspects of rarity which could have implications on the functionality of agroecosystems. In the plant kingdom, different functional contributions are made by common and rare species to ecosystem multifunctionality (Soliveres et al., 2016). This is also the case for other aboveground (Senapathi et al., 2021) and likely also for belowground communities (Ramirez et al., 2018). The diversity of rare soil fungi and bacteria orders, for example, is especially important for belowground processes such as leaf litter decomposition, nutrient cycling, carbon sequestration and bioremediation (Wakelin et al., 2009; Burns et al., 2013).

The strong impacts of weather conditions observed are particularly relevant for potential land-based mitigation actions against climate change. It has been shown that the amount and diversity of semi-natural habitats can buffer the effects of climate change and weather extremes on pollinators (Oliver et al., 2015; Papanikolaou et al., 2016b). Given the beneficial effects of semi-natural habitats on multiple taxonomic groups such buffering effects might also stabilize the multi-taxonomic diversity and as a consequence also functionality within agroecosystems (Dainese et al., 2019; Tamburini et al., 2020).

#### Conclusions

Identifying relevant environmental factors and the interlinkages among taxa of different trophic levels has important implications for management and policy frameworks, which usually act at a diversity of spatial scales and often target specific taxonomic groups. Our results emphasize the importance of land use for ensuring multi-taxonomic diversity within agroecosystems. We found, for example across the soil surface, that more species-rich and diverse biotic communities are promoted by higher proportions of semi-natural habitats. With beneficial effects on multiple groups covering below-, across, and aboveground taxa, increasing semi-natural elements in agricultural landscapes are likely to also increase abundance of common service providers and occurrence of specialists, which in turn enhances the multifunctionality of agroecosystems (Soliveres et al., 2016).

In conclusion, our results emphasize the importance of proper management of agroecosystems and in particular the restoration of semi-natural habitats to promote multi-taxonomic diversity across multiple trophic groups. This is in line with recent calls for a strong sustainability transition during the coming decades (WWF, 2022) and for using a multifunctional approach for sustainable landscape management (IPBES, 2019), which is increasingly supported by policy regulations, such as the EU Nature Restoration Law. Our results also highlight the consideration of the climate context, with particular relevance under current climate change, since changing climates can impact soil conditions and in turn the soil microbiome, which provides a range of essential ecosystem functions and services.

#### Data availability

The datasets used for the current study have been archived by the UFZ and are available from the corresponding author on reasonable request.

## CRedit authorship contribution statement

**EL Slabbert:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing – original draft. **TM Knight:** Conceptualization, Supervision, Writing – review & editing. **T Wubet:** Data curation, Formal analysis, Funding acquisition, Methodology, Supervision, Writing – review & editing. **M Frenzel:** Data curation, Writing – review & editing. **B Singavarapu:** Data curation, Formal analysis, Methodology, Writing – review & editing. **O Schweiger:** Conceptualization, Funding acquisition, Methodology, Supervision, Writing – review & editing.

## 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.

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## Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.baae.2024.06.003](https://doi.org/10.1016/j.baae.2024.06.003).

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