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The impact of grazing and fertilization intensity on functional trait diversity and assembly processes of soil mesofauna in grasslands

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ABSTRACT

Assessing the impact of land-use intensification on soil communities is important for developing conservation strategies to maintain grassland ecosystem functioning. We aimed to establish a trait-based mechanistic understanding of how soil community composition responds to varying grazing and fertilization intensity, and whether this alters assembly processes of soil microarthropod metacommunities (Collembola and Oribatida). Microarthropods were sampled at 150 grassland plots of the German DFG Biodiversity Exploratories, covering gradients in three regions (north, centre, south).

First, functional community responses (functional richness, functional dispersion) to grazing and fertilization gradients were analysed using a trait-based approach. Hierarchical assembly models then estimated contributions of stochastic (dispersal-driven) vs. niche-based (environmental filtering, limiting similarity) processes. We compared low- vs. high-intensity plots to test whether trait-based responses shifted assembly processes. Trait–environment relationships were assessed using RLQ analyses.

Increased grazing reduced functional diversity and increased similarity in collembolan communities. Environmental filtering dominated Collembola assembly in intensively grazed grasslands in north and central Germany, but not in the south. Grazing had no effect on oribatid assembly processes. The strength of environmental filtering was region-specific. Fertilizer input was positively correlated with functional richness in Collembola but not Oribatida. Environmental filtering contributed less to Collembola assembly in intensively fertilized than unfertilized sites, suggesting low nutrient availability limits community structure.

Oribatida appeared more resistant to land-use change than Collembola. We conclude that grazing intensification reduces soil microarthropod functional diversity. Under high-intensity use, this promotes environmental filtering (especially for Collembola), altering assembly processes. Medium-intensity grazing reduced some functional groups but communities remained more resilient than at high-intensity sites, where filtering excluded entire groups. We recommend reducing high-intensity grazing to conserve soil biodiversity and ecosystem functioning.

1. Introduction

The study presented here addresses the influence of selected management practices on the functional composition of invertebrate communities in temperate grassland soils. Grassland is an important landscape element for ensuring essential ecosystem services, including food and feed production, and biodiversity conservation (Bengtsson et al., 2019). Management intensity depends on various factors such as the number of livestock, the amount of fertilizer applied, the frequency of mowing, and local land use patterns. It affects aboveground and belowground communities (Birkhofer et al., 2017), with the response of edaphic biota greatly varying among taxa and functional groups (le Provost et al., 2021). The actual mechanisms of soil community assembly and relation to land use intensity in grasslands soil have recently been in the focus of soil ecological research (Gao et al., 2025), but are still not completely understood, especially at the functional trait level.

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As an essential component of terrestrial communities, soil fauna affects numerous ecosystem functions (Delgado-Baquerizo et al., 2020). The extent and nature of this multifunctionality, however, strongly depends on the functional composition of belowground communities (Bradford et al., 2014). Trait-based approaches are highly promising in this respect as they allow for the quantification of the functional implications of community composition and the influence of environmental conditions on assembly processes (Fry et al., 2019), if traits are linked to ecosystem functions (Violle et al., 2007). These approaches should therefore provide a deeper understanding of how trait responses of soil fauna to anthropogenic stressors, such as fertilization (Betancur Corredor et al., 2020) and livestock density (Qi et al., 2011; Andrés et al., 2016), can drive shifts in community assembly and thereby alter the trait structure of the belowground community, ultimately affecting grassland functioning (Yin et al., 2020). Emerging evidence indicates that land-use intensification can shift whole-community trait expression along a slow–fast continuum, and that soil microarthropods such as Oribatid mites and Collembola may respond not only differently from above-ground organisms but in fundamentally distinct ways within this slow–fast ecosystem axis (Neyret et al. 2024). However, trait-based rules for the assembly of soil organisms have so far received little attention.

Recent developments in coexistence theory recognize that assembly of communities is simultaneously driven by different subsequent filtering processes that are niche-based (environmental filtering or biotic interaction) and stochastic (dispersal and random birth–death events). These filters are difficult to quantify and are often applied in a loose sense, which is particularly true for the environmental filter (Cadotte and Tucker, 2017). Since different processes can result in the same pattern in community composition, it is demanding to disentangle the relative contribution of each process based on community pattern alone (Kraft et al., 2015). However, emerging methodologies make it possible to analyse of the relative contribution of subsequent filtering processes to community assembly (Van Der Plas et al., 2015). Concerning soil communities, stochastic dispersal is assumed to be the dominant filter at regional scales, while environmental filtering appears to be more important at local scales (Guo et al., 2019). However, environmental filtering may extend to larger spatial scales when concerning metacommunities through soil community response to environmental gradients (Gao et al., 2016; Andriuzzi et al., 2020). An important consideration is that regional environmental conditions shape regional species pools, which in turn influence the structure and assembly of local soil fauna, yet this relationship remains only partially understood. (Thakur et al., 2020). Analyzing the functional responses of metacommunities to environmental filtering can help address this gap by linking regional species exchanges to local assembly patterns of functionally similar species sets (Leibold et al., 2004).

We focussed on the response of soil microarthropods to two of the most important types of disturbances affecting agricultural grasslands in temperate regions: soil compaction and disruption associated with grazing and heavy machinery (Nawaz et al., 2012; Mueller et al., 2014), and changes of chemical soil conditions and plant growth through fertilization (Blüthgen et al., 2012). We therefore selected Collembola and oribatid mites because they are among the most abundant and functionally important soil microarthropods in grasslands, and they differ strongly in life histories, feeding strategies and mobility (Wolters, 2000, Orgiazzi et al., 2016). Collembola typically have short generation times and respond rapidly to changes in soil structure and plant litter (Hopkin, 1997), whereas oribatid mites are longer-lived, often more strongly linked to organic matter quality and slower in their responses (Behan-Pelletier, 1999; Pfingstl and Schatz, 2021). These contrasts make them particularly suitable for detecting how physical disturbance and fertilization differentially shape the functional structure and assembly processes of soil animal communities at the metacommunity scale (Menta and Remelli, 2020; Joimel et al., 2021).

We analysed a) local belowground community trait-based assembly pattern along regional land use intensity gradients, and b) regional level assembly processes in high vs low intensity grassland-metacommunities. Grasslands were selected in three contrasting regions in northern, central, and southern Germany that exhibit region-specific variability in landscape conditions, land use type, and intensity of use. We tested the following hypotheses:

A) Increasing grazing and fertilization intensity reduces functional diversity of the soil mesofauna.
B) High intensity grazing changes assembly processes by increasing the role of niche-based processes as environmental filtering.
C) Assembly processes and functional response of soil mesofauna are based on the region-specific species-trait-environment relationships.

2. Methods

2.1. Sampling design, setup and material collection

Sampling was conducted at 150 permanent grassland plots in Germany that are part of the DFG Biodiversity-Exploratories (Fischer et al., 2010), with 50 plots per region across three regions: in the south (Schwäbische Alb, Federal State of Bavaria), centre (Hainich-Dün, Federal State of Thuringia), and north (Schorfheide-Chorin, Federal State of Brandenburg). Based on a standardized annual questionnaire for farmers including information about the mowing frequency, livestock density and the amount of nitrogen fertilization sampling plot were selected along a gradient of land-use intensities (Vogt et al., 2017). We used the 3-year averages from 2016 to 2018 of the livestock density (livestock unit days of grazing ha^{-1} $year^{-1}$) and N fertilizer input amount (kg nitrogen ha^{-1} $year^{-1}$) per grassland plot which were standardized across the three study regions as predictor variables (Blüthgen et al., 2012). The need in a multiple-year monitoring of land management was required due to high soil buffering capacity for all kinds of impacts and possible related delay in soil biota response to disturbances (Zaitsev et al., 2002). Detailed data information on livestock density and fertilization input can be obtained from Biodiversity Exploratories Information System (https://www.bexis.uni-jena.de). To ensure comparable timing of spring sampling across the three regions in Germany, we initiated collection of oribatid mites and Collembola when Forsythia started to bloom, using flowering as a phenological cue.

Nine soil cores with a diameter of 5 cm and a depth of 10 cm were collected from each plot. Soil cores were transported and stored in cool boxes at + 5°C until extraction in the laboratory. Extraction was performed in the high gradient Kempson Extractor (Kempson et al., 1963) for seven days (temperature in the above heated area gradually increased from + 20 to + 60°C, temperature in the cooled basin was constant at + 12°C). Nine soil cores (5 cm in diameter each) were combined into a composite sample and placed in a container (20 × 20 cm) filled with 70% ethylene glycol, with a drop of liquid soap added to reduce surface tension. To obtain a representative subsample, we followed the method described by Bruckner et al. (2000): a plastic ring with the inner diameter of 5 cm was placed in the centre of the container, and after evenly distributing the extracted animals across the container bottom, all individuals within the ring area (equivalent to 8.7 cm^2 of soil surface based on the 9 Soil cores in the 20x20 cm container) were collected using a pipette. The extracted fauna was then transferred to 75% ethanol and later sorted into major taxonomic groups (Collembola, Acari, and others) for further identification.

2.2. Microarthropod identification and allocation to traits

Oribatida were identified to the species level except for a few larvae and nymphs, where species allocation was problematic. Identification was conducted using light microscopy with magnification up to x200 following Weigmann (2006) and Ghilarov and Krivolutskiy (1975) using a stereomicroscope. When necessary, individual specimens were slide

mounted and fixed and then identified with magnification up to x2000 using a light microscope. Astigmata, Prostigmata, and Mesostigmata were counted but not further identified. Springtails were identified to the species level following keys suitable for European species: Bretfeld (1999), Fjellberg (1998; 2007), Potapov (2001) and Thibaut et al. (2004).

Trait data for oribatid mites and collembolans were compiled based on the available literature (mainly from Zaitsev et al., 2013, 2014) and best expert knowledge (Supplementary Material Appendix 2 Table 1 & 2 respectively). For both groups, body size (mean for Collembola and size categories for oribatids) and soil vertical strata preferences (soil, surface or litter) were included in the dataset. For Oribatida the trophic guild (herbivorous, omnivorous, herbifungivorous or fungivorous) was used (following Zaitsev et al., 2014). For Collembola such a detailed distinction was not possible. Further for oribatid mites the developmental time was included as continuous variable and sexual vs parthenogenetic reproduction mode as a categorical variable (Supplementary Material Appendix 2 Table 1). For Collembola as categorical variables the presence or absence of a furca, pigmentation, anal spines (ASP), pseudocelli (PSO), number of ocelli and post antennal organ (PAO) were included in the dataset (Supplementary Material Appendix 2 Table 2).

2.3. Data analyses

2.3.1. Functional diversity measures and environmental gradients

To understand how grassland management shaped edaphic microarthropod communities, we followed a hierarchical approach combining three complementary procedures (Fig. 1). First, two functional diversity indices were used to reveal how grazing and fertilization intensity affect the functional response of microarthropod communities along the intensity gradient over 150 grasslands: We used functional richness (FRic) from the R package FD (Laliberte and Legendre, 2010; Mason et al., 2013; Laliberté E *et al.*, 2014, Villéger et al. 2008) to explain the amount of traits in a community as a measure for general functional diversity (convex hull of all traits in a community). Furthermore, we applied the abundance-based index functional dispersion (FDis) which is the mean distance from the centroid in two-dimensional trait-space (Laliberte and Legendre, 2010; Laliberté et al., 2014). Functional dispersion decreases if functional similar species increase in abundance. Moreover, FDis is independent of species richness (Laliberte and Legendre, 2010). To statistically evaluate the effects of grazing and fertilization intensity, we fitted generalized additive models (GAMs) using the R package mgcv (Wood, 2001) and piecewise linear regression models with estimated breaking points using the R package segmented (Muggeo, 2008). These models allowed us to account for low sampling density at the high-intensity end of the gradients. Analyses were implemented in R (R Development Core Team, 2019).

2.3.2. Relative contribution of assembly processes

Second, to determine whether modified functional diversity may lead to changes in assembly processes, we compared the relative contribution of assembly processes in local metacommunities from high versus low intensity grassland management. This qualitative separation was necessary since an analysis of gradients might reveal correlations

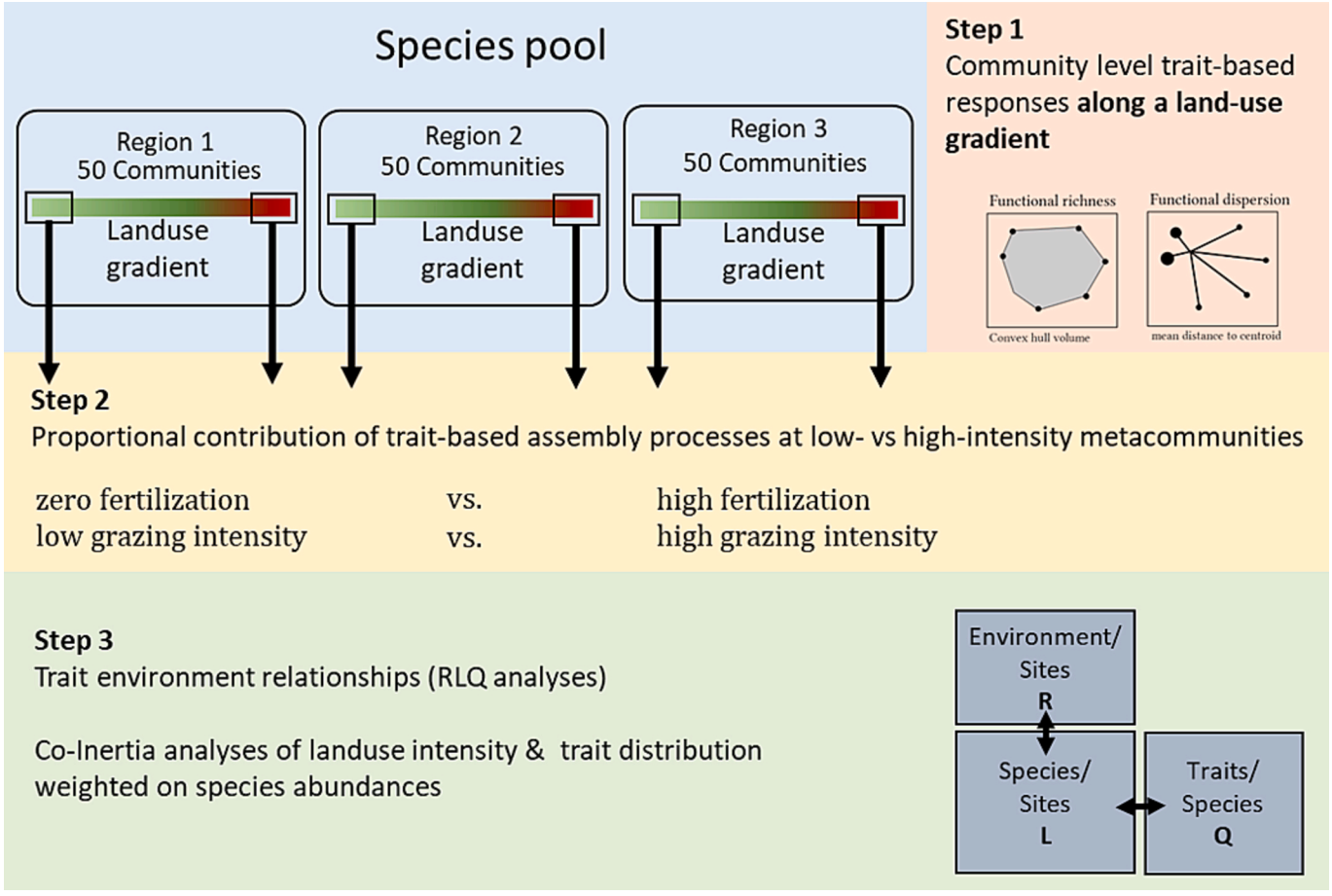

Fig. 1. Hierarchical approach to analyse the different levels of community assembly. Step 1: regression of functional diversity indices along a land use gradient over 150 plots from 3 regions. Step 2: randomized sampled Metacommunities from the datasets for high vs low intensity managed grasslands are compared to simulated communities to calculate relative importance of assembly processes. Step 3: Trait matrices, species abundances and land-use are combined in a RLQ analyses to show the trait- land use relationships.

but not filtering processes. The metacommunities were constructed by randomly selecting data from previously sampled grasslands. Specifically, we performed 100 rounds of resampling, where in each round, we randomly selected five community samples from either all extensive or all intensively managed grasslands within a region and pooled them to form one metacommunity. This resampling was done on the existing dataset, not through additional field sampling. The approach was used to minimize sampling bias and account for the unequal number of extensive and intensive grasslands across regions. The assembly analyses at the regional level were based on the overall species pool from all three regions thus supposing a central Europe dispersal potential of soil fauna based on their known distribution. Hence, we explicitly analysed the dispersal between metacommunities from three distinct regions in Germany and between and within extensive and intensive grassland metacommunities. Process importance was assessed based on a stepwise reduction model from the R package "STEPCAM" (Van Der Plas et al., 2015) which is based on ABC-SMC inference and approximates generated communities linked to assembly processes within observed communities and calculates relative process contribution. We used an adapted STEPCAM model for categorical and continuous traits (Hauffe et al., 2016). Stochastic processes (dispersal limitation) were calculated in a first step by the removal of species inversely proportional to their occurrence frequency from the full species pool. In the next step the contribution of environmental filtering was quantified by the removal of species with greatest distance from the respective functional mean and by fitting functional diversity patterns between observed and simulated communities. These patterns were based on the indices for functional richness, evenness, divergence and the mean distance to centroid from the R package FD using the dbFD function (Laliberte and Legendre, 2010; Laliberté et al., 2014). At the final step, interaction based on limiting similarity is calculated by the removal of one member of a pair of functionally similar species (van der Plas et al., 2015).

2.3.3. *Trait-environment-relationship: RLQ analyses*

To understand the underlying trait-based response of collembolan and oribatid communities to grazing and fertilization intensity we analysed trait-environment relationships for 50 grasslands per region. We used RLQ analyses, a co-inertia method that couples individual species traits (Q) to species distribution (L) and environmental factors (R) to identify co-relationships between them (Dufrêne and Legendre, 1997; Dray et al., 2014). RLQ analyses are performed using the ad4 package (Dray and Dufour, 2007). R, version 4.1 (R Development Core Team, 2013) was used for all analyses. Means and standard errors are reported further.

3. Results

A total of 1536 Collembola and 1850 oribatid mite individuals were found, belonging to 63 and 54 species, respectively. We observed 38, 29, and 35 Collembola and 20, 26, and 40 Oribatida species from the 50 grasslands within the south, central and north region respectively.

Across the grazing intensity gradient of the 150 grassland plots, grazing negatively affected functional dispersion (FDis) but not functional richness in both Collembola (Fig. 2a, Fig 4a) and Oribatida (Fig. 2b, Fig 4b), as indicated by GAM models (Supplementary Material Appendix 3 Table 1 & Supplementary Material Appendix 4 Table 1). FDis decreased sharply at higher grazing intensities above 2.8 in Collembola (Fig. 2a) and remained stable at grazing intensities above 2.1 in Oribatida (Fig. 2b). In Collembola, environmental filtering contributed significantly to metacommunity assembly in highly grazed grasslands, particularly in the central and, to a lesser extent, northern regions, whereas stochastic processes dominated at low grazing intensity (>80%; Fig. 6). In Oribatida, metacommunity assembly was largely stochastic in the south and central regions, with a larger contribution of niche-based processes in the northern region (Fig. 7). Along the fertilization gradient, functional richness (FRic) increased in Collembola across all grasslands and regions (Fig. 5a), while Oribatida FRic showed little response except in the northern region (Fig. 5b) (Supplementary Material Appendix 3 Table 4 & Supplementary Material Appendix 4 Table 4).

This strong impact of intensive grazing on the functional structure of microarthropod population was further reflected in a modulation of metacommunity assembly processes in Collembola, but not in Oribatida (Figs. 6 & 7). The relative contribution of environmental filtering to collembolan metacommunity assembly increased dramatically compared to grasslands with low grazing intensity across all regions on average but remained region-specific (Fig. 6). It was significant only in the central and to a smaller extent in the northern region (Fig. 6). At the same time, the assembly of collembolan metacommunities in grasslands with low intensity of grazing was strongly dominated by stochastic processes across all three regions (> 80%; Fig. 6). Concerning Oribatida metacommunities, the relative proportion of assembly processes in the northern region differed from those in the south and centre of Germany (Fig. 7). In the latter two regions oribatid metacommunity assembly was dominated by stochastic processes, similar to collembolan metacommunity assembly (Fig. 6). However, the contribution of niche-based processes, especially environmental filtering, to community assembly

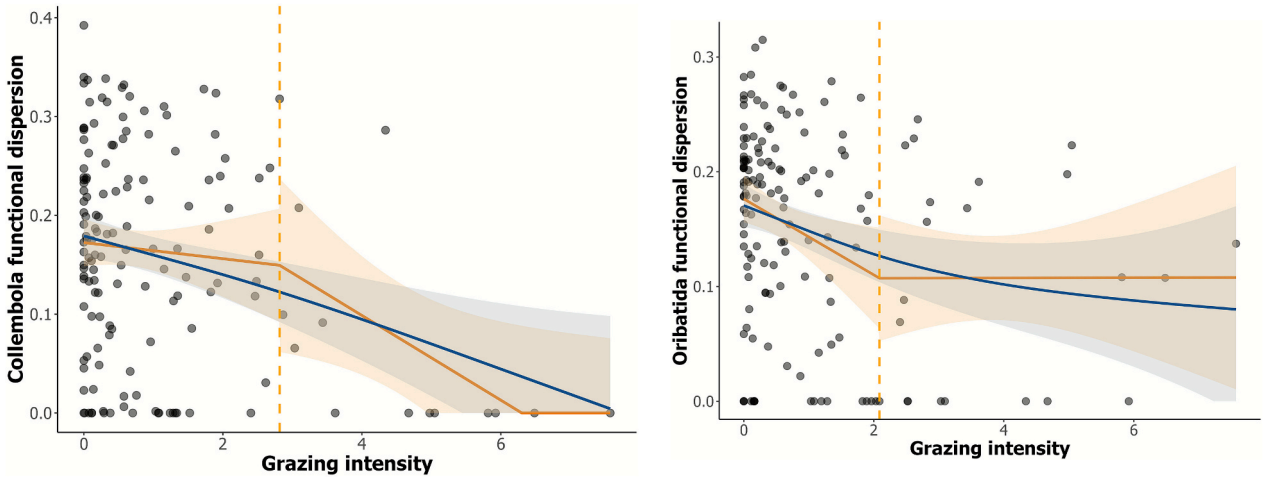

Fig. 2. Functional dispersion (FDis) of Collembola (a) and Oribatida (b) in response to grazing intensity. Collembola FDis decreased significantly with increasing grazing intensity (GAM: $p < 0.005$; Supplementary Material Appendix 3 Table 1). Piecewise modeling showed that this decline was driven by high-intensity sites above a breakpoint of 2.8 (Table 1), indicating that functionally similar Collembola became more abundant under strong grazing. This pattern was region-specific for AEG and HEG (Supplementary Material Appendix 1, Fig. 3). Oribatida showed no significant response to grazing intensity.

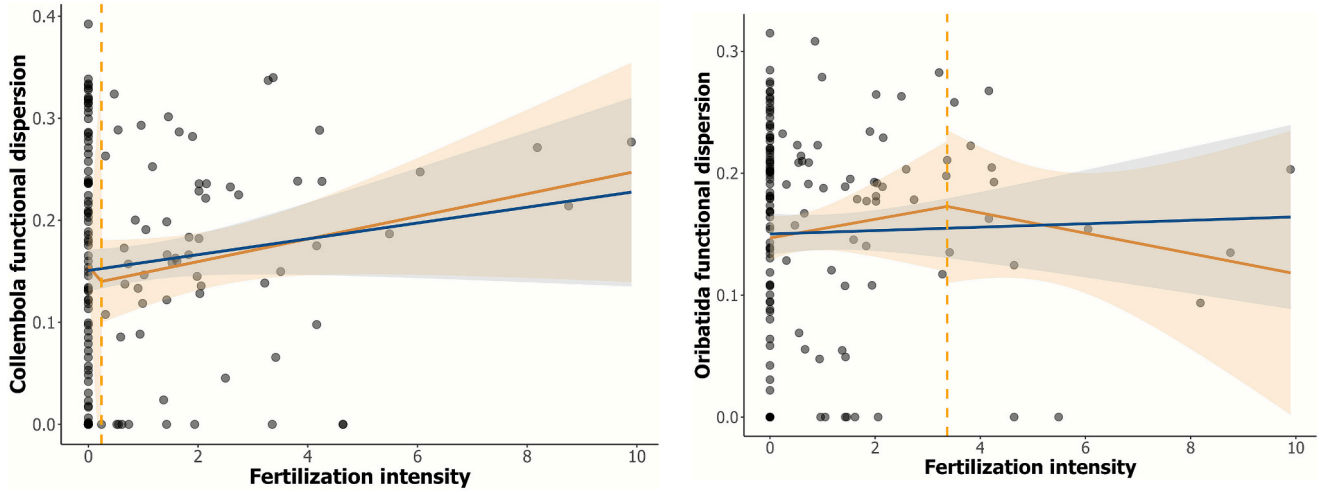

Fig. 3. Functional dispersion (FDis) of Collembola (a) and Oribatida (b) in response to fertilization intensity. Neither Collembola nor Oribatida showed significant responses to fertilization (Collembola: GAM $p = 0.13$; Oribatida: GAM $p = 0.65$; Supplementary Material Appendix 3 Table 2). Segmented models indicated no significant breakpoints or slope changes (Supplementary Material Appendix 4 Table 2).

was greater in the northern than in the other two regions (Fig. 6 & 7).

Intensive fertilization increased functional richness but not functional dispersion of Collembola across the gradient of all 150 grasslands and regions (Fig 3 a, Fig. 5a & Supplementary Material Appendix 3 Table 4), and for Oribatida assemblages in the northern region (Fig 3b, Fig. 5b & Supplementary Material Appendix 4 Table 4). The functional response of Collembola communities to land use was further reflected in changes in the relative contributions of processes shaping metacommunity assembly, although overall levels remained low (Fig. 6). Intensive fertilizer application reduced the influence of environmental filtering and slightly increased the contribution of biotic interactions to Collembola metacommunity assembly (Fig. 6). Stochastic processes remained predominant, but their contribution decreased to 50–60% (Fig. 6). In contrast, high fertilizer input did not alter the relative contributions of assembly processes in Oribatida metacommunities (Fig. 7). Species richness of Collembola declined in highly fertilized metacommunities (Supplementary Material Appendix 1 Figs. 1 & 7), a pattern also observed for Oribatida (Supplementary Material Appendix 1 Figs. 2 & 7).

Region-specific differences in microarthropod metacommunity assembly were found to be reflected in region-specific trait-based responses to land use as identified by RLQ analyses (Fig. 8). Soil-dwelling Collembola were negatively associated with grazing intensity but positively correlated with the amount of fertilizer application in the southern region. In the other two regions, however, soil-dwelling collembolans were positively related with grazing intensity and rather negative with fertilization in the central region (Fig. 8). Litter-dwelling Collembola, in contrast, were negatively related to grazing, while larger surface-dwelling springtail species were positively related to grazing in each of the three regions (Fig. 8). The response of Oribatida to grazing significantly differed between northern and the other two regions (Fig. 8). The negative effect on large surface-dwelling oribatids was comparable to the effect on Collembola, but most detectable in the north (Fig. 8). Additionally, grazing had a strong negative impact on herbivorous Oribatida across all regions, but omnivorous species were strongly negatively associated with grazing intensity in the northern region, but not the other two (Fig. 8).

Intensive grazing reduced Collembola species richness in metacommunities in two (south and centre) out of three regions (Supplementary Material Appendix 1 Fig. 1). Therefore, the environmental filter shaping metacommunities in intensively grazed grasslands can be associated with a loss in species richness (in the central region) or

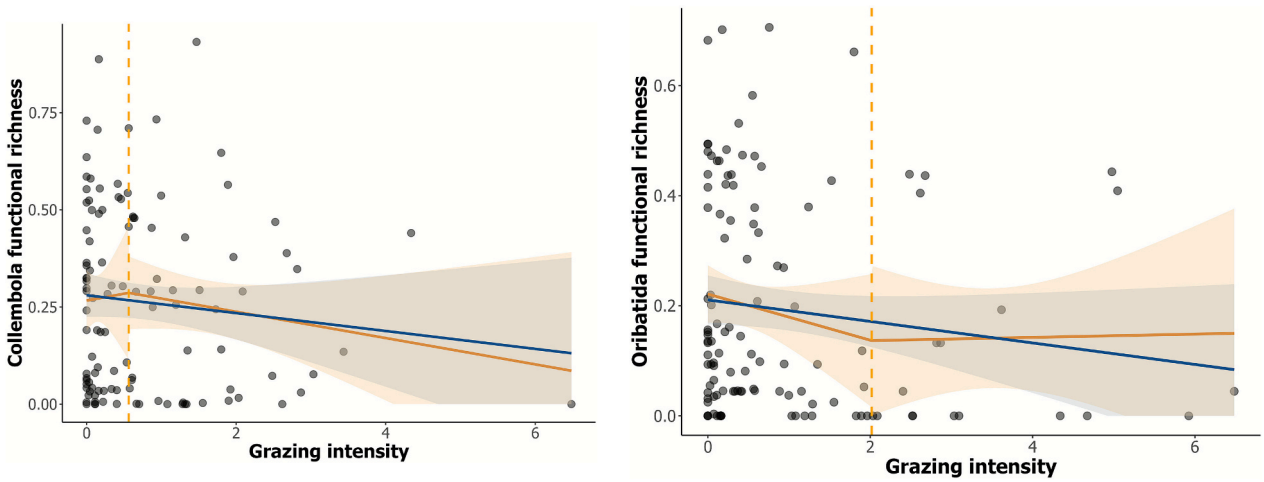

Fig. 4. Functional richness of Collembola (a) and Oribatida (b) in response to grazing intensity. Neither Collembola nor Oribatida showed significant responses to grazing (Collembola: GAM $p = 0.28$; Oribatida: GAM $p = 0.16$; Supplementary Material Appendix 3 & 4 Table 3). Segmented slopes and breakpoints were non-significant (Table 3), indicating no effect of grazing on functional richness.

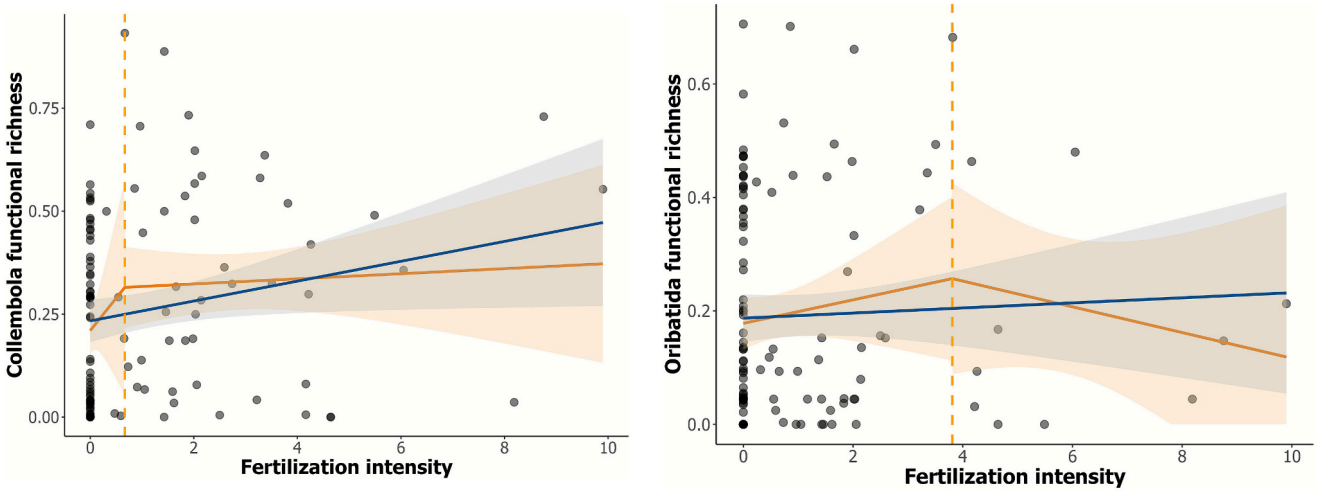

Fig. 5. Functional richness of Collembola (a) and Oribatida (b) in response to fertilization intensity. Collembola functional richness increased significantly with fertilization (GAM: $p = 0.036$; Supplementary Material Appendix 3 Table 4), although segmented slopes were not significant. Oribatida functional richness decreased at low fertilization intensities (segmented slope before breakpoint: -0.0331, $p < 0.05$; GAM smooth term: $p = 0.006$; Supplementary Material Appendix 4 Table 4), while high-intensity sites showed no significant change, indicating a nonlinear, intensity-dependent response.

with species turnover (in the northern region), depending on the region (Supplementary Material Appendix 1 Figs. 1 & 2). However, in the southern region intensive grazing reduced collembolan species richness which was in this case not reflected in a detectable environmental filter (Supplementary Material Appendix 1 Fig. 1).

4. Discussion

The gradual decrease in functional diversity in soil microarthropods with increasing grazing intensity was clearly demonstrated. Moreover, the relative contribution of community assembly processes for Collembola changed under high grazing intensity but remained stable in Oribatida metacommunities in the central and the southern regions. In the northern region Oribatida metacommunities experienced a increase of dispersal effects in more intensively grazed grasslands. At the highest level of grazing intensity, grazing appears to act as an environmental filter, excluding many functional similar species. In contrast, in grasslands with low-intensity land use, assembly processes in Collembola

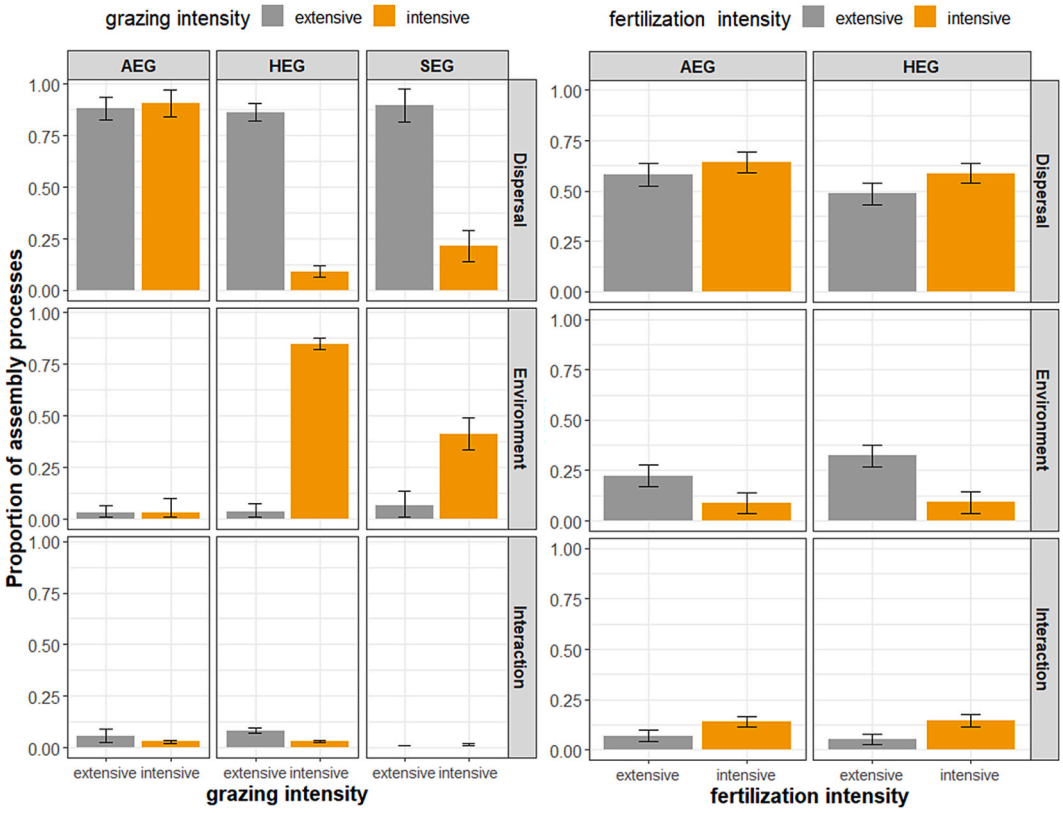

Fig. 6. Proportional contribution of the three assembly processes to Collembola metacommunities under extensive and intensive grassland management (left grazing, right fertilization). Columns represent the median; error bars show the 95 % confidence interval of all modelled metacommunities. AEG = South region, HEG = Central Region, SEG = northern Region

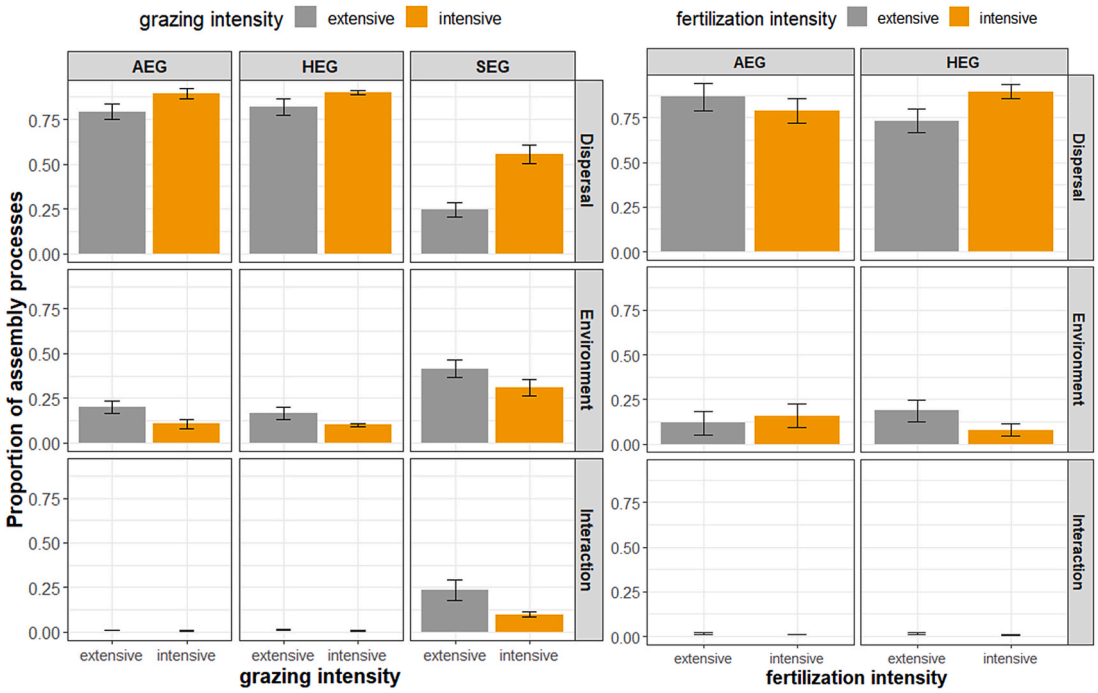

Fig. 7. Proportional contribution of the three assembly processes to Oribatida metacommunities under extensive and intensive grassland management (left grazing, right fertilization). Columns represent the median, error bars - the 95% confidence interval of all modelled metacommunities.

metacommunities were mostly driven by stochastic processes. Fertilization had a positive effect on Collembola functional diversity but not on Acari and did not substantially alter assembly processes. The effect of grazing and fertilization, however, differed between regions and between Collembola and Acari. This was also true for the relationship between single traits and land-use components.

4.1. *Different trait responses of Collembola and Oribatida*

Collembola turned out to be a far more responsive component of the soil microarthropod metacommunity than oribatit mites, especially with regards to fertilization what may be at least partially explained by the diet of the group. There is a clear separation of smaller and more abundant species consuming microbes and larger surface-dwellers – that are relatively rare in grasslands – due to their dependence on leaf litter (Potapov et al., 2022). Oribatid mites, tend to be trophically more dependent on fungi and other resources that are not directly linked to nitrogen input with fertilization (Potapov et al., 2022). Smaller soil-dwelling oribatid mites, which are dominant in the studied grasslands, appear to be more resistant to trampling (Battigelli et al., 2004). In oribatid mites the abundance weighted functional dispersion decreases with grazing intensity. The RLQ analyses also showed that grazing had an opposing effect on large oribatid mites. This is concordant with other studies which showed that large oribatids decreased in abundance due to smaller soil pore volume (Schon et al., 2011). However, contrary to Collembola, at the metacommunity level, the decrease in abundance of many functional groups did not result in an environmental filtering for Oribatida. This also highlights a fundamental difference of the role of oribatid mites and collembolans in agroecosystems as conservative and dynamic compartments of a soil microarthropod metacommunity, respectively.

4.2. *Regional differences*

Regional differences are most likely expressed via soil type and texture but seem to be highly important in determining assembly processes of soil microarthropod communities as they are defined by species level trait responses to land use. This points at the important role of spatial patterns independent of land-use variables, especially in the sandy soils typical for the northern region in our study (Caruso et al., 2012). Grazing seems to be an important factor modifying edaphic conditions crucial for certain collembolan traits and consequently strongly modifying functional dispersion (Fdis) for springtail metacommunities. Intensive grazing can result in soil compaction which reduces pore space and changes physical properties of soil and might therefore be the leading cause to a decrease in soil mesofauna (Larsen et al., 2004; Schon et al., 2011). The intensification of grazing gradually reduces the functional diversity of soil microarthropods, particularly in Collembola. The metacommunities in the latter group exhibit significant spatial structuring due to their evolutionary conservatism (Minor, 2011). Therefore, regional variations in the overall negative impact of intensive grazing can be attributed to differences in regional species pools with different resistance to soil compaction but also regional specific soil properties. But our understanding of resilience following this disruption is limited. Future studies could provide insights into the long-term effects of changes in management practices focusing on changes in soil properties after disturbance, e.g., soil specific recovering of soil pore volume after compaction.

4.3. *Community assembly*

Our results demonstrate that different community assembly processes dominate at the extreme ends of an environmental gradient. The underlying mechanism appears to be an increasing negative impact on the abundance of specific functional groups along the gradient, ultimately leading to genuine environmental filtering at the most intensive end. It is therefore crucial to distinguish between environmental effects that reduce the abundance of functional groups and those that result in species exclusion through true environmental filtering to better understand community assembly processes (Cadotte and Tucker, 2017). We were able to show that the increased impact of grazing can reach a threshold where functional diversity dropped to a low. Even though, this gives hints to an environmental filter, without the application of complex hierarchical models the detection of relative importance of

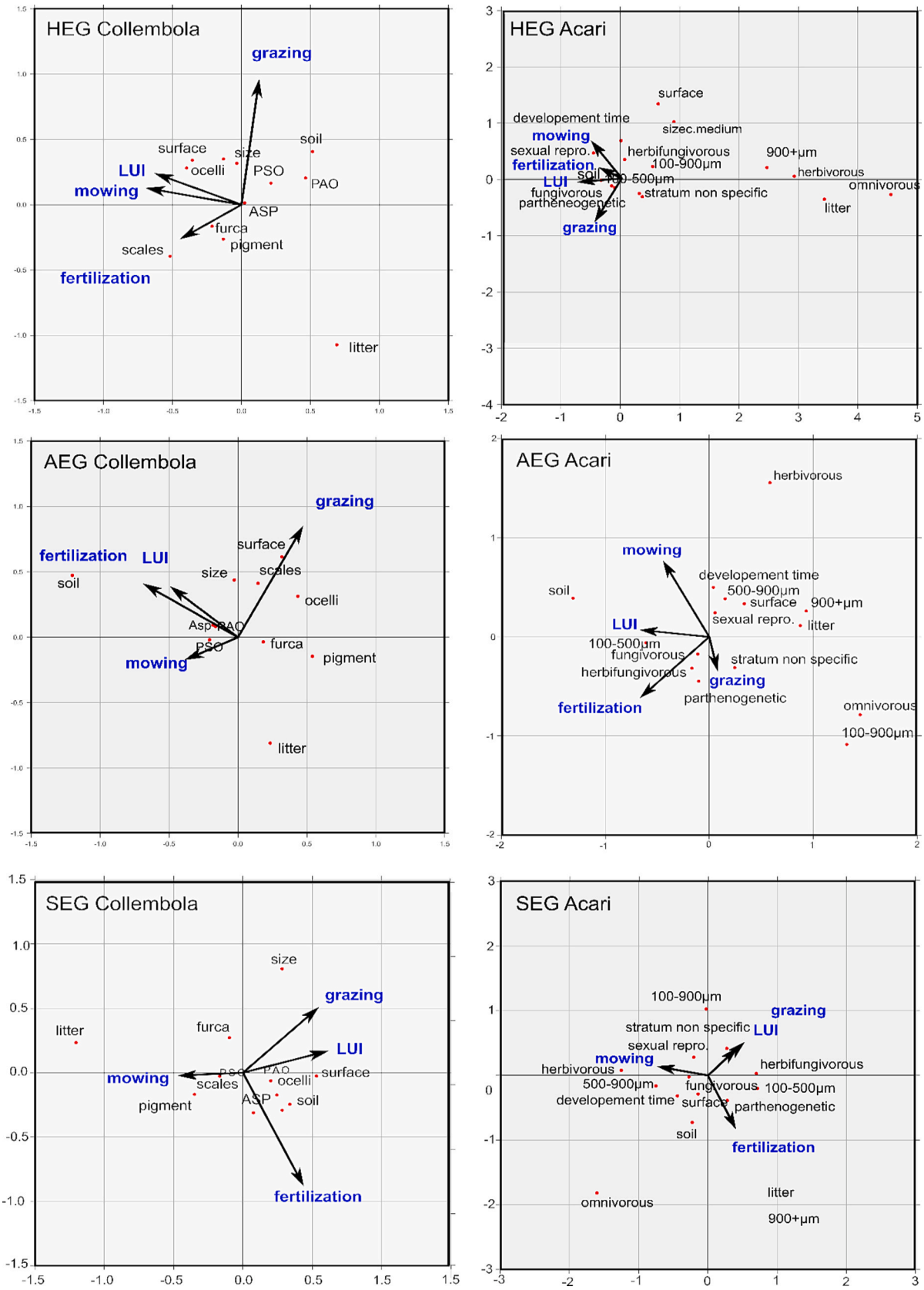

Fig. 8. RLQ analyses for each region and taxa. Land use and trait relationships are depicted based on community composition. LUI corresponds to the land use index.

assembly processes would not be possible. Thus, we were able to discover that the major driver behind Collembola species-loss in intensively used grasslands is a genuine environmental filtering process. Threshold analyses can help to identify grazing intensities below which assembly processes remain unchanged, which potentially can lead to irreversible changes and promote more sustainable land-use management.

Limited research has focused on the functional diversity and assembly processes of edaphic arthropod communities in grassland (Solascasas et al., 2022). This paucity is partly due to the scarcity of well resolved functional traits and to the challenge of assigning species to these traits: for example, feeding type assignments are complicated by intraspecific variation in resource use (Potapov et al., 2022). Such variation may bias our estimation of niche based competitive assembly processes, and hence the role of competition in grassland soil communities may be underestimated in plot based sampling designs.

Importantly, facilitation may also shape community structure, particularly under stressful conditions. According to the Stress Gradient Hypothesis (SGH) (Bertness and Callaway, 1994), species interactions can shift along environmental stress gradients, with facilitation becoming more important under high stress and competition dominating under more benign conditions. Empirical and modelling work has shown that this framework can apply not only to plants but also to belowground systems, and that the balance of facilitation versus competition depends strongly on context (e.g., type of resource limiting, interaction types). For instance, recent mechanistic modeling work demonstrates that the intensity and importance of facilitation do not necessarily increase monotonically along stress gradients but rather depend on interaction type and stress axis (Díaz-Sierra et al., 2024a,b).

The Intermediate Disturbance Hypothesis (IDH) provides a complementary lens, predicting that species diversity peaks at intermediate levels of disturbance because moderate disturbance can prevent competitive exclusion while not excluding sensitive species (Connell, 1978; Fox, 2013; Guo et al., 2021). For example, in grassland systems, a two-year survey in an alpine meadow found that moderate grazing maximised arthropod species richness and diversity, consistent with the IDH (Guan et al., 2023). However, in our study, we did not detect a pattern consistent with IDH, suggesting that either the disturbance gradient in our plots did not span a sufficient range or that other factors such as facilitation, microhabitat heterogeneity, or non equilibrium processes override the disturbance effect in structuring soil microarthropod communities. Comparable trait-based shifts have also been reported from other intensively used habitat types. In agricultural systems, increasing management intensity—through tillage, fertilization, or pesticide application—often favours small-bodied, disturbance-tolerant soil fauna and reduces the occurrence of larger, litter-dependent taxa (Chassain et al., 2024). Urbanization similarly filters soil fauna toward stress-tolerant and generalist trait profiles (Yao et al., 2022). Although the nature of disturbance differs strongly between grazing, cropping, and urban development, functional trait responses often converge along intensification gradients: communities increasingly consist of taxa with traits conferring tolerance to habitat disturbance, reduced resource stability, and fragmentation. This broader cross-system consistency provides an additional context for interpreting the trait-based filtering observed in our study. At the level of the functional trait community composition, more general analysis might help understanding the importance of the land use intensity with regards to such important processes as organic matter turnover (Bonfanti et al., 2024). This is particularly so in the light of grassland habitat fragmentation by land use gradients (Pedley et al., 2020). Taken together, these findings indicate that while SGH and IDH provide useful theoretical frameworks, edaphic communities may respond differently than aboveground assemblages, with facilitation and context dependency playing particularly important roles.

4.4. Conclusion

Intensive land-use has a severe impact on functional diversity of microarthropods. High intensity livestock management results in a real change of environmental filters, which is probably not easily reversable when functional groups are lost. However, at low to medium intensities, livestock farming on grasslands and even fertilization are not necessarily acting negatively on microarthropod metacommunities and under certain environmental conditions may be even positive for microarthropods. Thus, livestock farming at low intensities can be a soil biodiversity-friendly measure which is important to maintain and conserve open grassland ecosystems with still maintaining human livelihoods.

CRediT authorship contribution statement

Dennis Baulechner: Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Katharina John:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Data curation, Conceptualization. **Andrey Zaitsev:** Writing – review & editing, Supervision, Project administration, Methodology, Investigation, Conceptualization. **Ruslan Saifutdinov:** Writing – review & editing, Validation, Resources, Formal analysis, Data curation. **Volkmar Wolters:** Writing – review & editing, Validation, Supervision, Methodology, Funding acquisition, Conceptualization.

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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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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.geoderma.2026.117715.

Data availability

Data will be made available on request.

References

Andrés, P., Moore, J.C., Simpson, R.T., Selby, G., Cotrufo, F., Denef, K., Haddix, M.L., Shaw, E.A., de Tomasel, C.M., Molowny-Horas, R., Wall, D.H., 2016. Soil food web stability in response to grazing in a semi-arid prairie: the importance of soil textural heterogeneity. Soil Biol. Biochem. 97, 131–143. https://doi.org/10.1016/j.soilbio.2016.02.014.

Andriuzzi, W.S., Franco, A.L.C., Ankrom, K.E., Cui, S., de Tomasel, C.M., Guan, P., Gherardi, L.A., Sala, O.E., Wall, D.H., 2020. Body size structure of soil fauna along geographic and temporal gradients of precipitation in grasslands. Soil Biol. Biochem. 140, 107638. https://doi.org/10.1016/j.soilbio.2019.107638.

Battigelli, J.P., Spence, J.R., Langor, D.W., Berch, S.M., 2004. Short-term impact of forest soil compaction and organic matter removal on soil mesofauna density and oribatid mite diversity. Can. J. For. Res. 34, 1136–1149. https://doi.org/10.1139/x03-267.
Behan-Pelletier, V.M., 1999. Oribatid mite biodiversity in agroecosystems: role for bioindication. Agr Ecosyst Environ 74 (1–3), 411–423. https://doi.org/10.1016/S0167-8809(99)00046-8.
Bengtsson, J., Bullock, J.M., Egoh, B., Everson, C., Everson, T., O'Connor, T., O'Farrell, P. J., Smith, H.G., Lindborg, R., 2019. Grasslands—more important for ecosystem services than you might think. Ecosphere 10, e02582. https://doi.org/10.1002/ecs2.2582.
Bertness, M.D., Callaway, R., 1994. Positive interactions in communities. Trends Ecol. Evol. 9, 191–193. https://doi.org/10.1016/0169-5347(94)90088-4.
Betancur Corredor, B., Lang, B., Russell, D., 2020. Effects of nitrogen fertilization on soil fauna - a meta-analysis. EGUGA 7779. https://doi.org/10.5194/egusphere-egu2020-7779.
Birkhofer, K., Gossner, M.M., Diekoetter, T., Drees, C., Ferlian, O., Maraun, M., Scheu, S., Weisser, W.W., Wolters, V., Wurst, S., Zaitsev, A.S., Smith, H.G., 2017. Land-use type and intensity differentially filter traits in above- and below-ground arthropod communities. J. Anim. Ecol. 86, 511–520. https://doi.org/10.1111/1365-2656.12641.
Blüthgen, N., Dormann, C.F., Prati, D., Klaus, V.H., Hölzel, N., Alt, F., Boch, S., Gockel, S., Hemp, A., Müller, J., Nieschulze, J., Renner, S.C., Schöning, I., Schumacher, U., Socher, S.A., Wells, K., Birkhofer, K., Buscot, F., Oelmann, Y., Rothenwöhrer, C., Scherber, C., Tscharntke, T., Weiner, C.N., Fischer, M., Kalko, E.K.V., Linsenmair, K. E., Schulze, E.-D., Weisser, W.W., 2012. A quantitative index of land-use intensity in grasslands: Integrating mowing, grazing and fertilization. Basic Appl. Ecol. 13, 207–220. https://doi.org/10.1016/j.baae.2012.04.001.
Bretfeld, G., 1999. Synopses on Palaearctic Collembola, Vol. 2: Symphypleona. Abh. Ber. Naturkundemus. Görlitz 71(1), 1–318.
Bonfanti, J., Potapov, A.M., Angst, G., et al., 2024. Linking effect traits of soil fauna to processes of organic matter transformation. Funct. Ecol. https://doi.org/10.1111/1365-2435.14720.
Bradford, M.A., Wood, S.A., Bardgett, R.D., Black, H.I.J., Bonkowski, M., Eggers, T., Grayston, S.J., Kandeler, E., Manning, P., Setälä, H., Jones, T.H., 2014. Discontinuity in the responses of ecosystem processes and multifunctionality to altered soil community composition. PNAS 111, 14478–14483. https://doi.org/10.1073/pnas.1413707111.
Bruckner, A., Barth, G., Scheibengraf, M., 2000. Composite sampling enhances the confidence of soil microarthropod abundance and species richness estimates. Pedobiologia 44, 63–74. https://doi.org/10.1078/s0031-4056(04)70028-1.
Cadotte, M.W., Tucker, C.M., 2017. Should environmental filtering be abandoned? Trends Ecol. Evol. 32, 429–437. https://doi.org/10.1016/j.tree.2017.03.004.
Caruso, T., Taormina, M., Migliorini, M., 2012. Relative role of deterministic and stochastic determinants of soil animal community: a spatially explicit analysis of oribatid mites. J. Anim. Ecol. 81, 214–221. https://doi.org/10.1111/j.1365-2656.2011.01886.x.
Chassain, J., Joimel, S., Gardarin, A., Vieublé Gonod, L., 2024. Indicators of practice intensity unearth the effects of cropping systems on soil mesofauna. Agric. Ecosyst. Environ. 362, 108854. https://doi.org/10.1016/j.agee.2023.108854.
Connell, J.H., 1978. Diversity in tropical rain forests and coral reefs. Science 199, 1302–1310. https://doi.org/10.1126/science.199.4335.1302.
Delgado-Baquerizo, M., Reich, P.B., Trivedi, C., Eldridge, D.J., Abades, S., Alfaro, F.D., Bastida, F., Berhe, A.A., Cutler, N.A., Gallardo, A., García-Velázquez, L., Hart, S.C., Hayes, P.E., He, J.Z., Hseu, Z.Y., Hu, H.W., Kirchmair, M., Neuhauser, S., Pérez, C.A., Reed, S.C., Santos, F., Sullivan, B.W., Trivedi, P., Wang, J.T., Weber-Grullon, L., Williams, M.A., Singh, B.K., 2020. Multiple elements of soil biodiversity drive ecosystem functions across biomes. Nat. Ecol. Evolut. https://doi.org/10.1038/s41559-019-1084-y.
Díaz-Sierra, R., Rietkerk, M., Verwijmeren, M., Baudena, M., 2024a. Facilitation and competition deconstructed: a mechanistic modelling approach to the stress gradient hypothesis applied to drylands. Sci. Rep. 14, 2205.
Díaz Sierra, R., Rietkerk, M., Verwijmeren, M., Baudena, M., 2024b. Facilitation and competition deconstructed: a mechanistic modelling approach to the stress gradient hypothesis applied to drylands. Sci. Rep. 14, 2205. https://doi.org/10.1038/s41598-024-22209-8.
Dray, S., Choler, P., Dolédec, S., Peres-Neto, P.R., Thuiller, W., Pavoine, S., ter Braak, C.J. F., 2014. Combining the fourth-corner and the RLQ methods for assessing trait responses to environmental variation. Ecology 95, 14–21. https://doi.org/10.1890/13-0196.1.
Dray, S., Dufour, A.B., 2007. The ade4 package: Implementing the duality diagram for ecologists. J. Stat. Softw. 22, 1–20. https://doi.org/10.18637/jss.v022.i04.
Dufrêne, M., Legendre, P., 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecol. Monogr. 67, 345–366. https://doi.org/10.2307/2963459.
Fischer, M., Kalko, E.K.V., Linsenmair, K.E., Pfeiffer, S., Prati, D., Schulze, E.D., Weisser, W.W., 2010. Exploratories for large-scale and long-term functional biodiversity research, in: Long-Term Ecological Research: Between Theory and Application. doi: 10.1007/978-90-481-8782-9_29.
Fjellberg, A., 1998. The Collembola of Fennoscandia and Denmark, Part I: Poduromorpha. Brill, Leiden.
Fjellberg, A., 2007. The Collembola of Fennoscandia and Denmark, Part II: Entomobryomorpha and Symphypleona. Brill, Leiden.
Fox, J.W., 2013. The intermediate disturbance hypothesis should be abandoned. Trends Ecol. Evol. 28, 86–92. https://doi.org/10.1016/j.tree.2012.08.014.
Fry, E.L., De Long, J.R., Álvarez Garrido, L., Alvarez, N., Carrillo, Y., Castañeda-Gómez, L., Chomel, M., Dondini, M., Drake, J.E., Hasegawa, S., Hortal, S., Jackson, B.G., Jiang, M., Lavallee, J.M., Medlyn, B.E., Rhymes, J., Singh, B.K., Smith, P., Anderson, I.C., Bardgett, R.D., Baggs, E.M., Johnson, D., 2019. Using plant, microbe, and soil fauna traits to improve the predictive power of biogeochemical models. Methods Ecol. Evol. 10, 146–157. https://doi.org/10.1111/2041-210X.13092.
Gao, M., Liu, D., Lin, L., Wu, D., 2016. The small-scale structure of a soil mite metacommunity. Eur. J. Soil Biol. 74, 69–75. https://doi.org/10.1016/j.ejsobi.2016.03.004.
Gao, Ch., Schild, J.E.M., Moinet, G.Y.K., Bezemer, T.M., de Vries, F.T., Hassink, J., van Eekeren, N., Beentjes, K., van Bodegom, P.M., 2025. Land use intensity differently influences soil communities across a range of arable fields and grasslands. Geoderma 454, 117201. https://doi.org/10.1016/j.geoderma.2025.117201.
Ghilarov, M.S., Krivolutskiy, D.A., 1975. Opredelitel Obitayushikh v Pochve Kleschei (Soil-Dwelling Mites Identification Key). Nauka Publishers, Moscow (in Russian).
Guo, Y., Gao, M., Liu, J., Zaitsev, A.S., Wu, D., 2019. Disentangling the drivers of ground-dwelling macro-arthropod metacommunity structure at two different spatial scales. Soil Biol. Biochem. 130, 55–62. https://doi.org/10.1016/j.soilbio.2018.12.002.
Guo, C., Zhao, D., Zheng, D., Zhu, Y., 2021. Effects of grazing on the grassland vegetation community characteristics in Inner Mongolia. J. Resour. Ecol. 12, 319–331. https://doi.org/10.5814/j.issn.1674-764x.2021.03.002.
Guan, Y., Li, X., Zhang, T., Wang, L., 2023. Moderate grazing increases arthropod species richness and diversity in alpine meadows. Grassl. Sci. 69, 105–116. https://doi.org/10.1111/grs.12345.
Hauffe, T., Albrecht, C., Wilke, T., 2016. Assembly processes of gastropod community change with horizontal and vertical zonation in ancient Lake Ohrid: a metacommunity speciation perspective. Biogeosciences 13, 2901–2911. https://doi.org/10.5194/bg-13-2901-2016.
Hopkin, S.P., 1997. Biology of the springtails:(Insecta: Collembola). OUP Oxford.
Joimel, S., Schwartz, C., Bonfanti, J., Hedde, M., Krogh, P.H., Pérès, G., Pernin, C., Rakoto, A., Salmon, S., Santorufo, L., Cortet, J., 2021. Functional and taxonomic diversity of Collembola as complementary tools to assess land use effects on soils biodiversity. Front. Ecol. Evol. 9, 630919. https://doi.org/10.3389/fevo.2021.630919.
Kempson, D., Lloyd, M., Ghelardi, R., 1963. A new extractor for woodland litter. Pedobiologia.
Kraft, N.J.B., Adler, P.B., Godoy, O., James, E.C., Fuller, S., Levine, J.M., 2015. Community assembly, coexistence and the environmental filtering metaphor. Funct. Ecol. 29, 592–599. https://doi.org/10.1111/1365-2435.12345.
Laliberte, E., Legendre, P., 2010. A distance-based framework for measuring functional diversity from multiple traits. Ecology 91, 299–305. https://doi.org/10.1890/08-2244.1.
Laliberté, E., Legendre, P., Shipley, B., 2014. FD: Measuring functional diversity from multiple traits, and other tools for functional ecology. URL https://www.researchgate.net/publication/312463190_FD_Measuring_functional_diversity_from_multiple_traits_and_other_tools_for_functional_ecology (accessed 11.9.22).
Larsen, T., Schjønning, P., Axelsen, J., 2004. The impact of soil compaction on euedaphic Collembola. Appl. Soil Ecol. 26, 273–281. https://doi.org/10.1016/j.apsoil.2003.12.006.
le Provost, G., Thiele, J., Westphal, C., Penone, C., Allan, E., Neyret, M., van der Plas, F., Ayasse, M., Bardgett, R.D., Birkhofer, K., Boch, S., Bonkowski, M., Buscot, F., Feldhaar, H., Gaulton, R., Goldmann, K., Gossner, M.M., Klaus, V.H., Kleinebecker, T., Krauss, J., Renner, S., Scherreiks, P., Sikorski, J., Baulechner, D., Blüthgen, N., Bolliger, R., Börschig, C., Busch, V., Chisté, M., Fiore-Donno, A.M., Fischer, M., Arndt, H., Hoelzel, N., John, K., Jung, K., Lange, M., Marzini, C., Overmann, J., Pašalić, E., Perović, D.J., Prati, D., Schäfer, D., Schöning, I., Schrumpf, M., Sonnemann, I., Steffan-Dewenter, I., Tschapka, M., Türke, M., Vogt; , J., Wehner, K., Weiner, C., Weisser, W., Wells, K., Werner, M., Wolters, V., Wubet, T., Wurst, S., Zaitsev, A.S., Manning, P., 2021. Contrasting responses of above- and belowground diversity to multiple components of land-use intensity. Nat. Commun. 12, 1–13. https://doi.org/10.1038/s41467-021-23931-1.
Leibold, M.A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J.M., Hoopes, M.F., Holt, R.D., Shurin, J.B., Law, R., Tilman, D., Loreau, M., Gonzalez, A., 2004. The metacommunity concept: a framework for multi-scale community ecology. Ecol. Lett. 7, 601–613. https://doi.org/10.1111/j.1461-0248.2004.00608.x.
Mason, N.W.H., De Bello, F., Mouillot, D., Pavoine, S., Dray, S., 2013. A guide for using functional diversity indices to reveal changes in assembly processes along ecological gradients. J. Veg. Sci. 24, 794–806. https://doi.org/10.1111/jvs.12013.
Menta, C., Remelli, S., 2020. Soil health and arthropods: from complex system to worthwhile investigation. Insects 11 (1), 54. https://doi.org/10.3390/insects11010054.
Minor, M.A., 2011. Spatial patterns and local diversity in soil oribatid mites (Acari: Oribatida) in three pine plantation forests. Eur. J. Soil Biol. 47, 122–128. https://doi.org/10.1016/j.ejsobi.2011.01.003.
Mueller, L., Behrendt, A., Graham Shepherd, T., Schindler, U., Ball, B.C., Khudyaev, S., Kaiser, T., Dannowski, R., Eulenstein, F., 2014. Simple field methods for measurement and evaluation of grassland quality. Environ. Sci. Eng. 199–222. https://doi.org/10.1007/978-3-319-01017-5_11.
Muggeo, V.M.R., 2008. Segmented: an R package to fit regression models with broken-line relationships. R News 8 (1), 20–25.
Nawaz, M.F., Bourrié, G., Trolard, F., 2012. Soil compaction impact and modelling. A review. Agron. Sustain. Develop. 33, 291–309. https://doi.org/10.1007/s13593-011-0071-8.
Neyret, M., Le Provost, G., Boesing, A.L., Schneider, F.D., Baulechner, D., Bergmann, J., de Vries, F.T., Fiore-Donno, A.M., Geisen, S., Goldmann, K., Merges, A., Saifutdinov, R.A., Simons, N.K., Tobias, J.A., Zaitsev, A.S., Gossner, M.M., Jung, K., Kandeler, E., Krauss, J., Penone, C., Schloter, M., Schulz, S., Staab, M., Wolters, V.,

Apostolakis, A., Birkhofer, K., Boch, S., Boeddinghaus, R.S., Bolliger, R., Bonkowski, M., Buscot, F., Dumack, K., Fischer, M., Gan, H.Y., Heinze, J., Hölzel, N., John, K., Klaus, V.H., Kleinebecker, T., Marhan, S., Müller, J., Renner, S.C., Rillig, M. C., Schenk, N.V., Schöning, I., Schrumpf, M., Seibold, S., Socher, S.A., Solly, E.F., Teuscher, M., van Kleunen, M., Wubet, T., Manning, P., 2024. A slow-fast trait continuum at the whole community level in relation to land-use intensification. Nat. Commun. 15, 1251. https://doi.org/10.1038/s41467-024-45113-5.

Potapov, A.M., Beaulieu, F., Birkhofer, K., Bluhm, S.L., Degtyarev, M.I., Devetter, M., Goncharov, A.A., Gongalsky, K.B., Klarner, B., Korobushkin, D.I., Liebke, D.F., Maraun, M., McDonnell, R.J., Pollierer, M.M., Schaefer, I., Shrubovych, J., Semenyuk, I.I., Sendra, A., Tuma, J., Tůmová, M., Vassilieva, A.B., Chen, T.W., Geisen, S., Schmidt, O., Tiunov, A.V., Scheu, S., 2022. Feeding habits and multifunctional classification of soil-associated consumers from protists to vertebrates. Biol. Rev. 97, 1057–1117. https://doi.org/10.1111/brv.12832.

Potapov, M., 2001. Synopses on Palaearctic Collembola, Volume 3: Isotomidae. Abh. Ber. NaturkMus., Görlitz.

Qi, S., Zheng, H., Lin, Q., Li, G., Xi, Z., Zhao, X., 2011. Effects of livestock grazing intensity on soil biota in a semiarid steppe of Inner Mongolia. Plant and Soil 340, 117–126. https://doi.org/10.1007/s11104-010-0463-6.

R Development Core Team, 2013. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

R Development Core Team, 2019. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria https://www.r-project.org/.

Schon, N.L., Mackay, A.D., Minor, M.A., 2011. Soil fauna in sheep-grazed hill pastures under organic and conventional livestock management and in an adjacent ungrazed pasture. Pedobiologia 54, 161–168. https://doi.org/10.1016/j.pedobi.2011.01.001.

Solascasas, P., Azcárate, F.M., Hevia, V., 2022. Edaphic arthropods as indicators of the ecological condition of temperate grassland ecosystems: a systematic review. Ecol. Ind. 142, 109277. https://doi.org/10.1016/j.ecolind.2022.109277.

STEPCAM R Package — the University of Groningen research portal, n.d. URL https://research.rug.nl/en/publications/stepcam-r-package (accessed 11.8.22).

Thakur, M.P., Phillips, H.R.P., Brose, U., De Vries, F.T., Lavelle, P., Loreau, M., Mathieu, J., Mulder, C., Van der Putten, W.H., Rillig, M.C., Wardle, D.A., Bach, E.M., Bartz, M.L.C., Bennett, J.M., Briones, M.J.I., Brown, G., Decaëns, T., Eisenhauer, N., Ferlian, O., Guerra, C.A., König-Ries, B., Orgiazzi, A., Ramirez, K.S., Russell, D.J., Rutgers, M., Wall, D.H., Cameron, E.K., 2020. Towards an integrative understanding of soil biodiversity. Biol. Rev. 95, 350–364. https://doi.org/10.1111/brv.12567.

Thibaut, J.-M., Schulz, H.-J., Assalino, M.M.da.G., 2004. Synopsis on Palaearctic Collembola, 4: Hypogastruridae. Senckenberg Naturkunde Museum, Görlitz.

van der Plas, F., Janzen, T., Ordonez, A., Fokkema, W., Reinders, J., Etienne, R.S., Olff, H., 2015. A new modeling approach estimates the relative importance of different community assembly processes. Ecology 96, 1502–1515. https://doi.org/10.1890/14-0454.1.

Villéger, S., Mason, N.W.H., Mouillot, D., 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. Ecology 89 (8), 2290–2301. https://doi.org/10.1890/07-1206.1.

Vogt, J., Klaus, V., Both, S., Fürstenau, C., Gockel, S., Gossner, M., Heinze, J., Hemp, A., Hölzel, N., Jung, K., Kleinebecker, T., Lauterbach, R., Lorenzen, K., Ostrowski, A., Otto, N., Prati, D., Renner, S., Schumacher, U., Seibold, S., Simons, N., Steitz, I., Teuscher, M., Thiele, J., Weithmann, S., 2017. A quantitative index of land-use intensity in grasslands: Integrating mowing, grazing and fertilization. This appears to be an incorrect entry. The authors and title match the Blüthgen et al. (2012) paper. I have removed it and kept the correct Blüthgen citation.

Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., Garnier, E., 2007. Let the concept of trait be functional! Oikos 116, 882–892. https://doi.org/10.1111/j.0030-1299.2007.15559.x.

Weigmann, G., Miko, L., 2006. Hornmilben (Oribatida): Acari, Actinochaetida. Die Tierwelt Deutschlands und der angrenzenden Meeresteile, 76. Teil. Goecke & Evers, Keltern, pp. 520–pp.

Wolters, V., 2000. Invertebrate control of soil organic matter stability. Biol. Fertil. Soils 31 (1), 1–19. https://doi.org/10.1007/s003740050618.

Wood, S.N., 2001. mgcv: GAMs and generalized ridge regression for R. R News 1 (2), 20–25.

Yin, R., Siebert, J., Eisenhauer, N., Schädler, M., 2020. Climate change and intensive land use reduce soil animal biomass via dissimilar pathways. eLife 9, e54749. https://doi.org/10.7554/eLife.54749.

Zaitsev, A.S., Berg, M.P., van Straalen, N.M., 2013. Landscape geological age explains large scale spatial trends in oribatid mite diversity. Landsc. Ecol. 28, P.285-296.

Zaitsev, A.S., Chauvat, M., Pflug, A., Wolters, V., 2002. Oribatid mite diversity and community dynamics in a spruce chronosequence. Soil Biol. Biochem. 34, 1919–1927. https://doi.org/10.1016/S0038-0717(02)00208-0.

Zaitsev, A.S., Chauvat, M., Wolters, V., 2014. Spruce forest conversion to a mixed beech-coniferous stand modifies oribatid community structure. Appl. Soil Ecol. 76, 60–67. https://doi.org/10.1016/j.apsoil.2013.12.009.

Orgiazzi, A., Panagos, P., Yigini, Y., Dunbar, M.B., Gardi, C., Montanarella, L., Ballabio, C., 2016. A knowledge-based approach to estimating the magnitude and spatial patterns of potential threats to soil biodiversity. Sci. Total Environ. 545–546, 11–20. https://doi.org/10.1016/j.scitotenv.2015.12.092.

Pedley, S.M., Dolman, P.M., 2020. Arthropod traits and assemblages differ between core patches, transient stepping-stones and landscape corridors. Landsc. Ecol. 35, 937–952. https://doi.org/10.1007/s10980-020-00991-0.

Pfingstl, T., Schatz, H., 2021. A survey of lifespans in Oribatida excluding Astigmata (Acari). Zoosymposia 20, 7–27. https://doi.org/10.11646/zoosymposia.20.1.4.