



Seasonality and crop type override the effects of long-term agricultural management on collembolan communities and traits



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ABSTRACT

Current agricultural practices, dominated by monocultures and chemical inputs, challenge soil-dwelling mesofauna to adapt to dynamic conditions. We conducted a two-year study within a long-term (50 year) experiment to investigate how monocultures, crop rotations (winter wheat and maize), and fertilisation (organic and mineral) types affect collembolan communities. Based on 360 soil samples, we examined functional and life form traits, as well as taxonomic and functional diversity across seasons. We hypothesised that disturbance-resistant traits would be prevalent in open habitats such as maize fields, while soil-adapted traits would dominate in more closed habitats such as wheat fields and meadows. Our results confirmed these predictions. Maize fields supported dispersal and disturbance-resistant traits but had lower Collembola diversity, whereas wheat fields supported higher diversity and soil-adapted traits, demonstrating that agroecosystems filter functional traits according to crop type and management. Compared to the cropped fields, the control meadow exhibited higher values of traits connected to adaptation to the soil environment and higher species richness. Grouping functional traits into life forms offered clearer ecological insights than examining individual traits alone. Interestingly, soil-adapted traits were more abundant in autumn, following disturbances, rather than during the growing season. This suggests that disturbance-resistant species had already been filtered out, with remaining species primarily inhabiting soil layers under the surface in disturbed areas. Crop rotation, as a form of temporal diversification, favoured dispersal traits, with specific trait patterns influenced by crop type, while fertilisation type had minor effects. Despite long-term exposure to consistent agricultural treatments, plant type and seasonality exerted the strongest influence on Collembola traits and diversity, underscoring the adaptability of these communities to environmental change in agroecosystems.

1. Introduction

Although many alternatives exist, the vast majority of current agricultural practices rely on a narrow range of plant species, often grown in monocultures (Foley et al., 2011). Today, it is widely acknowledged that increasing biodiversity in agricultural landscapes is essential for both sustainable and profitable management (Mouratiadou et al., 2024). Arable land typically exhibits reduced biodiversity due to frequent chemical and physical disturbances, loss of habitat diversity, and vegetation simplification (Attwood et al., 2008; Tsiafouli et al., 2015). Agricultural areas undergo sudden environmental changes, such as increased soil desiccation and frequent mechanical disruption. While agricultural practices favour crop species, many fauna species inhabiting these fields must adapt to the altered environmental conditions.

Soil macro- and mesofauna are increasingly used to monitor agro-

environments due to their sensitivity to environmental changes (Domínguez et al., 2024; Nicolay et al., 2021; Pauli et al., 2016). Among soil mesofauna, Collembola is one of the most abundant and diverse group (George et al., 2017) occupying different soil layers (mainly between 0 and 20 cm depth) and serving as effective bioindicators due to their high densities, limited mobility, and rapid reproduction (Coller et al., 2022; Joimel et al., 2021; Menta et al., 2020). Beyond bio-indication, they contribute to soil quality and vitality by decomposing organic matter, enhancing microbial activity, and influencing nutrient uptake of plants (Filser, 2002; Hedde et al., 2007; Kreuzer et al., 2004; Neher and Barbercheck, 2019). Despite their ecological importance, the factors that shape collembolan communities, distributions and traits in agroecosystems remain poorly understood (Potapov et al., 2022). This knowledge gap is particularly evident in agroecosystems, where communities and species traits must withstand a high level of perturbation.

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Understanding the drivers of potential collembolan community decline in agro-environments is essential, as maintaining their functional diversity supports key ecosystem services, such as nutrient cycling and crop productivity, contributing directly to sustainable agricultural outcomes (Brussaard et al., 2007).

Collembola exhibit a broad range of traits. Traits refer to morphological, physical, phenological, or behavioural characteristics measurable at the individual level (Joimel et al., 2024; Pey et al., 2014). Functional traits reflect organisms' adaptations to their environments and their effects on ecosystem properties (Moretti et al., 2017). An emerging trend in soil ecology emphasises functional trait-based approaches, moving beyond traditional species abundance and taxonomic classifications (Martins da Silva et al., 2016; Salmon et al., 2014; Vandewalle et al., 2010). The functional trait-based approach has proven more effective in assessing the impacts of environmental factors on Collembola communities, monitoring and identifying key drivers of land-use change, and uncovering underlying ecological processes (Brousseau et al., 2018; Salmon et al., 2014; Vandewalle et al., 2010). Collembola represent a highly diverse group with many species coexisting in soil (Rusek, 1998), employing various strategies to cope with unfavourable conditions, especially in agricultural systems. Using traits instead of different taxonomic resolutions provides more information can be gained, considering the effects of agricultural management on soil biota. However, only a few studies have assessed the effects of agricultural management and crop type on collembolan traits (Chassain et al., 2023; Joimel et al., 2021). Moreover, rather than examining traits in isolation, grouping them provides a clearer and more comprehensive perspective. This is achieved by counting different life form (LF) traits (Vandewalle et al., 2010; de Filho et al., 2016; Joimel et al., 2021). LF traits represent a set of selected functional traits, each reflecting a specific ecological aspect of the organism, such as adaptation to the soil environment, resistance to disturbance, or dispersal ability.

In agro-environments, species must adapt to disturbances due to tillage, pesticides and fertilisers. Agricultural practices, crop types and consequently crop rotation play a fundamental role in shaping Collembola communities (Bokova et al., 2023; Chassain et al., 2023; Gergócs et al., 2022; Rieff et al., 2020). Crop plants indirectly influence soil mesofauna communities, such as Collembola, by shaping the soil environment through their biological traits, growth dynamics, and interactions with microbiota. Different crop species create distinct microhabitats and alter soil properties having bottom-up effects, via root architecture, exudates, and the quality and quantity of crop residues left after harvest. All these factors affect microbiota such as fungi and bacteria (Bais et al., 2006; Sasse et al., 2018), the main food source of Collembola (Hopkin, 1997). Consequently, Collembola must adapt to the unique characteristics (chemical, physical and life history traits) of each crop species, which can shape the soil communities (Menta et al., 2020). In agroecosystems, agronomic practices associated with the current crop—such as sowing and harvesting time, sowing rates, fertilisers, herbicides, and pesticides—act as a combined disturbance regime (Jagger et al., 1988; Meyer et al., 2019). Vegetation cover, which varies with crop types and their seasonal growth patterns, is one of the most critical factors regulating the activity of soil arthropods in arable lands (Filser, 1995; Menta et al., 2020; Moos et al., 2020; Tóth et al., 2025). In soil mesofauna studies, habitats are typically classified as either open or closed (Martins da Silva et al., 2016; Salmon et al., 2014). Open habitats are generally associated with higher disturbance levels, while closed habitats provide more stable conditions. Agricultural areas are generally classified as open habitats; however, distinctions can be made within this category as well, based on their management intensity. For example, Ponge et al., (2013) and Tsiafouli et al., (2015), describe a gradient of increasing habitat openness from meadows to crop fields. Within this continuum, mowed lawns can be considered more closed habitats compared to crop fields. Ponge et al. (2013) further demonstrated that increasing openness negatively affects most microarthropods, with the exception of epigeic Collembola.

In agriculture, enhancing both plant and fauna diversity is a key objective. A greater variety of plant species is advantageous, as different species exploit distinct resources and support more diverse communities both above and below ground, thereby strengthening the resilience of agroecosystems (Cappelli et al., 2022). In addition to intercropping diversity, temporal diversity has long been recognised as an effective strategy for improving nutrient availability and plant uptake, while also providing protection against specialist pests (Bennett et al., 2012; Tiedemann et al., 2015). As a result, crop rotation is expected to reduce the prevalence of specialist species while promoting an increase in generalist groups, such as Collembola.

Fertilisers also play a crucial role in influencing soil communities, often through indirect bottom-up effects. As a result, an increase in both species size and population density is typically expected. However, studies on the density and diversity of Collembola have yielded mixed results, highlighting the complex and sometimes contradictory impacts of fertiliser inputs on soil fauna (Betancur-Corredor et al., 2023; Bokova et al., 2023; Tabaglio et al., 2009; Zhu et al., 2023), an area where trait-based analyses can offer deeper insight. The positive bottom-up effect of manure was demonstrated by Ponge et al., (2013) who found that it had a beneficial impact on saprophagous macrofauna and bacterivorous nematodes. A similar effect was observed in a study on Collembola, where increased organic matter input led to higher population densities (Miyazawa et al., 2002).

In agro-environments, intensive management practices and low plant diversity may amplify seasonal effects compared to natural habitats. These seasonal effects may be driven more by management practices than by natural variables such as temperature and humidity, or management may enhance the effects of these natural factors. Seasonal effects have been reported to be more important than yearly ones (Berg and Bengtsson, 2007). Additionally, the temporal dynamics of surface-dwelling arthropod activity-density (the number of caught individuals derived from their abundance and activity (Lensing et al., 2005)) have been found to be influenced by crop species as well as the legacy effects of previous years (Meyer et al., 2019).

Short-term experiments are insufficient for fully assessing the effects of different management practices on soil fauna (Pollierer and Scheu, 2017; Tabaglio et al., 2009). While long-term monoculture management is increasingly rare, long-established systems provide valuable insights into how various agricultural practices influence soil-dwelling animal communities. In a long-term fertilisation and monoculture experiment, we sampled mesofauna communities for two years. Our previous species-based study revealed significant effects of crop plants and year-to-year variation (Gergócs et al., 2022), but no significant impact of fertilisation. In this study, using a trait-based approach, and also considering seasonality, we aimed to complement our earlier findings and gain a deeper understanding of the processes and factors driving Collembola trait selection under different agricultural management practices. Our goal was to identify which Collembola traits are favoured in agro-environments and how key agricultural factors (crop type, cropping system, fertilisation) affect both community structure and functional composition. We hypothesised that distinct Collembola functional traits would vary between different crop types. Specifically, we expected traits adapted to soil environments to be more prevalent in more closed habitats, such as wheat fields and especially in the meadow, whereas traits associated with dispersal and disturbance resistance would be more dominant in open habitats, such as maize fields. Based on plant cover, we hypothesised the following gradient of increasing habitat openness: meadow → wheat fields → maize fields, which we expected to correspond with a decreasing trend in species and functional diversity. Additionally, we expected seasonal variations in trait dominance and diversity. Since crop rotation introduces temporal plant diversity, we expected Collembola diversity to be higher in rotation systems than in monocultures. Given the significant nutrient supply, we also predicted an increase in species size in all fertilised treatments.

2. Materials and methods

2.1. Study site and design

The current study was conducted on a long-term experimental site, in Martonvásár, Central Hungary ($N 47^{\circ}19'53.25''$, $E 18^{\circ}47'22.06''$) on Chernic Phaeozem soil (Loamic, Aric, WRB, 2015). Since 1962, various treatments have been applied to examine the effects of different crop types, fertilisation regimes, and agricultural management strategies, including crop rotations with varying numbers of plant (crop) species. Prior to the long-term experiment, the area was managed uniformly under conventional agricultural management practices, with crop rotation. Since then, the same treatments have been maintained for over 50 years. The site is characterized by 529 mm mean annual precipitation and 10.5 °C mean annual temperature (means of 50 years, Hungarian Meteorological Service). At the time of the present study, which was conducted in 2018 and 2019, the mean yearly temperature was higher (Table 1). We selected three cropping systems for our study: wheat (*Triticum aestivum* (Linnaeus 1753)) monoculture, maize (*Zea mays* (Linnaeus 1753)) monoculture, and biennial crop rotation alternating between the two crop species (with winter wheat in 2018 and maize in 2019 in the time of the present study). Each cropping field employed three different fertilisation treatments: control (without fertilisation, C), mineral fertiliser (nitrogen-phosphorus-potassium, NPK), and a combination of mineral and organic fertiliser (NPK + farmyard manure), referred to as organic treatment throughout the article. Manure is applied every four years, with the most recent application in 2017, one year prior to the start of this study (Table S1). Each treatment was replicated four times in 30×50 m blocks, with plot sizes of 5×7 m (Fig. 1). As a control, a nearby meadow located 70 m from the experimental area was used (Fig. 1). A detailed description of the study site and treatments is available in Gergócs et al., (2022) and Table S1.

2.2. Environmental variables

Daily precipitation and air temperature were recorded using a nearby meteorological station in Martonvásár. From these data, we calculated the total precipitation and average daily temperature for the 10 days preceding each sampling event (Table 1). Soil samples were collected at the time of mesofaunal sampling to measure soil humidity (W/W%). Summer 2018 was characterized by extreme heatwaves, with maximum temperatures exceeding 30 °C for several days prior to the sampling date, accompanied by high precipitation. In contrast, spring 2019 was dry, with lower average temperatures and wheat fields showed the lowest soil moisture levels (Table 1). Although summer 2019 was cooler than summer 2018, it still experienced significant rainfall (Table 1). Throughout both summers, soil moisture was higher in maize fields, with particularly elevated levels observed in 2018. Soil moisture in autumn 2019 was notably higher in wheat fields (Table 1). Although we collected data on various soil chemical and physical variables, no significant differences were found between treatments relevant to the current research. Therefore, these parameters were not included in this

study (see Gergócs et al., 2022 and Table S2).

Substrate-induced respiration (SIR) was used to estimate microbial biomass (Anderson and Domsch, 1978; Holden and Treseder, 2013; Kaiser et al., 1992). Three soil subsamples (totaling 500 g) were collected from the top 10 cm of soil during the same period as soil faunal sampling. For a detailed description of the analysis, see Gergócs et al. (2022).

2.3. Fauna sampling

For soil faunal sampling, 400 cm³ soil cores (8 cm diameter, 8 cm deep) were taken with a metal soil corer, two times in 2018, in summer (4th June) and autumn (10th October) and 3 times in 2019, in spring (23rd April), summer (4th June) and autumn (10th October). From each plot, two subsamples (pseudo-replicates) were collected and processed separately (Fig. 1), however, as they originated from the same experimental unit, they were not treated as independent replicates in statistical analysis. Considering four blocks, three cropping practices, and three fertilisation treatments, a total of 72 samples were collected per sampling occasion. We also took four samples at each sampling occasion from different parts of the nearby meadow (Fig. 1). Samples were immediately taken to the laboratory and extracted for one week into 70 % ethyl-alcohol with Berlese extractors. Animals were sorted and identified into main groups with a stereomicroscope. Collembola were identified at the species level with a Leica MZ755 microscope, and using identification keys (Bretfeld, 1999; Fjellberg, 1998; Hopkin, 2007; Jordana, 2012; Potapov, 2001; Stach, 1960; Thibaud et al., 2004).

2.4. Traits and indices

For the basic dataset, we assessed the mean Collembola abundance for each plot (calculated from the pseudo-replicates, $N = 2$ for the treatment plot, $N = 4$ for the meadow). For each Collembola taxa, we collected species-level traits (not individual-level traits). The traits considered are related to the agricultural landscape, focusing on adaptation to the soil environment (e.g., vertical distribution in the soil profile), resistance to disturbance, recolonisation potential, and dispersal ability (Vandewalle et al., 2010). A total of eight morphological traits (presence of furca, number of ocelli, presence of scales or dense macrosetae (e.g. clavate or ciliate setae), presence of post antennal organ (PAO), body, antenna, and leg length), and one life history trait (reproduction: sexual, parthenogenetic) were considered, as detailed in Table S3. These functional traits were sourced from various literature references (Table S3). In cases where data for a specific species were unavailable, we used the traits of the closest related species, or checked on the specimens in the sample (e.g. dense seata, scales, pigmentation, size) which is noted in Table S3.

In addition to individual traits, we identified three life form traits (LF) (Vandewalle et al., 2010): adaptation to the soil environment, dispersal ability, and disturbance resistance. Each functional trait was assigned a score ranging from 0 to 4, where 0 indicates a weak association with the given LF, and 4 represents a strong association. Different

Table 1

Yearly average soil moisture (W/W%) and temperature, total precipitation and the number of heat days (>30 °C) in the three most relevant years of the study. For seasonal interpretations, data represent averages from the two weeks preceding each sampling.

Year/Sampling time	Soil moisture			Precipitation (mm)	Temperature (°C)	Number of heat days
	Wheat monoculture	Crop rotation	Maize monoculture			
2017	-	-	-	509.8	11.2	37
2018	-	-	-	672	12	38
June	13.8	14.8	20.6	20.1	20.9	2
October	17.3	18.8	18.2	1	12.1	0
2019	-	-	-	555.7	12.1	44
April	12.5	21.1	20.6	2.2	10.7	0
June	22.3	23.9	23.0	41.8	16	0
October	18.4	15.9	15.6	14.7	11.3	0

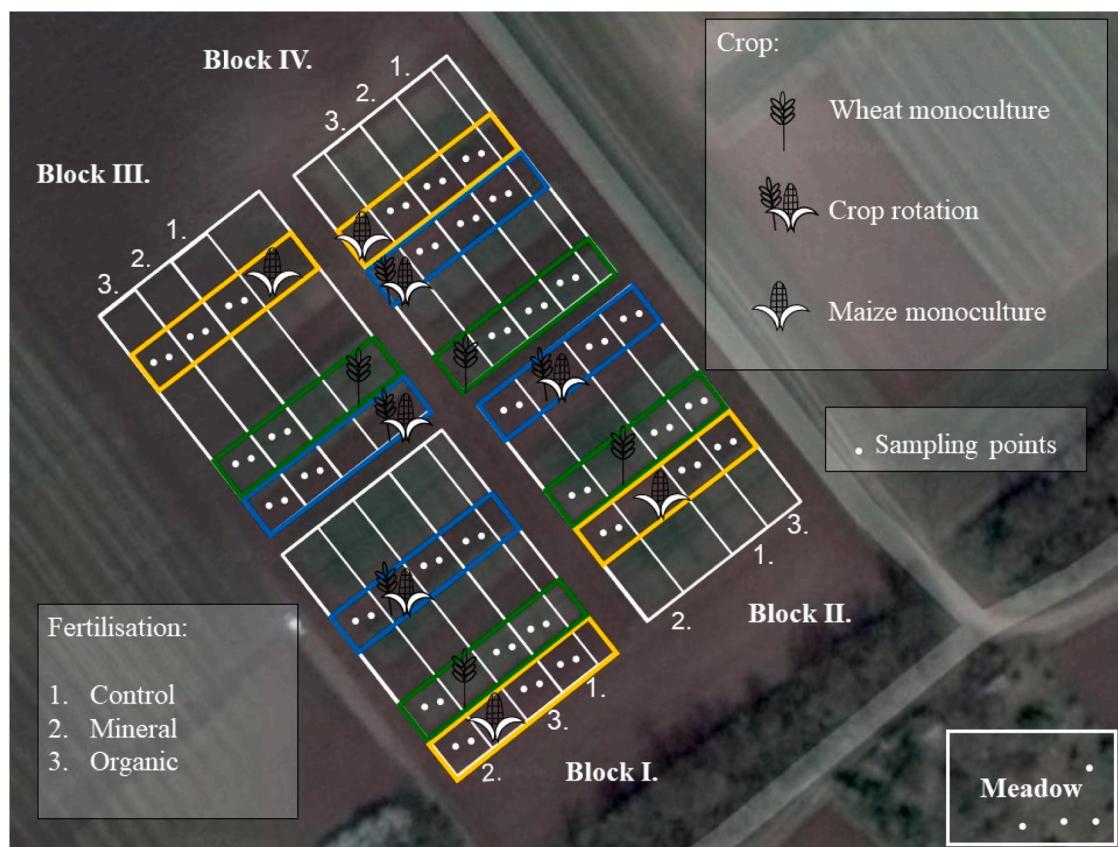


Fig. 1. The experimental field setup, consisting of four blocks and three fertilisation treatments: Control (no fertilisation), mineral (mineral fertiliser containing nitrogen, phosphorus, and potassium), and organic (mineral fertiliser combined with farmyard manure). Three cropping treatments were applied: winter wheat monoculture (green frame), maize monoculture (orange frame), and crop rotation (winter wheat in 2018, maize in 2019; blue frame). A nearby meadow served as a control area. White dots indicate the sampling points.

functional traits, with varying scores, were used to calculate the different LFs (Table 2). We followed scoring systems used in the literature (de Filho et al., 2016; Joimel et al., 2021; Pollet et al., 2022; Vandewalle et al., 2010; Yin et al., 2020) to provide more comparable and consistent data.

To calculate the LF index, trait scores were summed for each species, based on the functional traits presented in Table S2. The score for adaptation to the soil environment was obtained by adding the trait scores for furca, number of ocelli, pigmentation, presence of scales or dense macrosetae, and antenna length, resulting in a value between 0 and 20. Dispersal ability was determined by summing the scores for the number of ocelli, furca- and leg length, yielding a value between 0 and 12. Disturbance resistance was calculated by adding the scores for body length, presence of dense macrosetae or scales, and pigmentation, resulting in a score from 0 to 12. Higher values correspond to greater adaptation to the soil environment, greater resistance to disturbance, and higher dispersal ability, respectively (Table S2).

Each species was categorised as either parthenogenetic or sexual, as their life history traits. Species exhibiting both traits were classified in the parthenogenetic group. For reproductive traits, various indices were calculated. The number of parthenogenetic and sexual species was counted per sample. Based on that data, we calculated the percentage of parthenogenetic species (number of parthenogenetic species / total species * 100) within each plot. Body size data were obtained from the literature (see Table S3). For traits presented on a fuzzy scale, we used the average value.

For each plot and each functional and LF trait, community weighted mean (CWM) values were calculated (Ricotta and Moretti, 2011). First, we determined the relative abundance of each species by dividing the abundance of the species by the total abundance of all species present in

the plot. Next, the relative abundance of each species was multiplied by the score of the corresponding trait. Finally, the weighted trait values for each species in the plot were summed. These CWM values were then used for subsequent statistical analyses.

Species richness and the Shannon–Wiener diversity index were calculated using the PAST program (Hammer and Harper, 2001). In addition, functional diversity indices were computed to assess the effects of the treatments on community structure. Functional diversity indices complement classical diversity measures, by providing insight into the ecological processes shaping biological communities (Mouchet et al., 2010). These indices are based on the functional traits of species. Villéger et al. (2008) suggested that three complementary indices are essential for describing the facets of functional diversity: functional richness (Fric), functional evenness (Feve), and functional divergence (Fdiv). Fric estimates the volume of a T-dimensional space (where T represents the number of traits) occupied by the community under investigation (Villéger et al., 2008). Feve describes the evenness of abundance distribution within this T-dimensional space, while Fdiv indicates how abundance is distributed within the volume of the T-dimensional space occupied by the species (Mason et al., 2005).

To calculate the functional diversity indices, we prepared two matrices: 1. the functional trait values of species (including adaptation to the soil environment, dispersal ability, and disturbance resistance), and 2. the species abundances in the plots. Following Villéger et al. (2008), we considered species abundance rather than merely their presence or absence. We calculated the functional diversity indices using the fundiv package in R (Grenié and Gruson, 2023) with the functions fd_fdiv, fd_feve, and fd_fdis. These values formed the basis of further diversity investigations.

Table 2

Various functional traits and their corresponding score values were used to calculate the life form (LF) traits: adaptation to the soil environment, dispersal ability, and disturbance resistance. Traits and their scores, which contributed to the calculation of different LF values, are highlighted in bold.

Traits	Adaptation to the soil environment	Dispersal ability	Disturbance resistance
Furca			
Absent	4	0	0
Reduced/short	2	2	2
Fully developed	0	4	4
Ocelli			
Absent	4	0	0
1 + 1 – 2 + 2 ocelli	3	1	1
3 + 3 – 4 + 4 ocelli	2	2	2
5 + 5 – 6 + 6 ocelli	1	3	3
7 + 7 – 8 + 8 ocelli	0	4	4
Pigmentation			
Absent (white colour)	4	1	1
Coloured but no patterns	2	2	2
Coloured with patterns	1	4	4
Presence of scales or dense setae			
Present	0	4	4
Absent	4	0	0
Body length			
X > 3 mm	1	4	4
2 < X ≤ 3 mm	2	3	3
1 < X ≤ 2 mm	3	2	2
X ≤ 1 mm	4	1	1
Antenna length			
X ≤ 0.5 x body length	4	0	0
0.5 x body length	2	2	2
< X ≤ 1 x body length			
X > 1 body length	0	4	4
Leg length			
X ≤ 0.2 x body length	4	0	0
0.2 x body length	2	2	2
< X ≤ 0.5 x body length			
X > 0.5 body length	0	4	4
Post antennal organ (PAO)			
Complex	4	0	0
Simple	1	1	1
Absent	0	4	4
Reproduction			
Sexual	0	1	1
Parthenogenetic	1	0	0

2.5. Statistical analyses

All statistical tests were performed by using R version 4.2.1 (R Core Team, 2020). RLQ analysis was conducted to uncover the co-inertia relationships among species abundance (L-table), species functional (nine individual traits) or life form traits (Q-table), and environmental factors (R-table) (Dolédec et al., 1996; Kleyer et al., 2012). Environmental factors (plant type, cropping system, season, and fertilisation type) were transformed into Dummy variables (fastDummies package; (Kaplan, 2020)). This analysis reveals a maximal covariance between environmental factors and traits, which are weighted by species densities. Models for the two years and the two types of traits (functional and LF traits) were calculated separately. For the RLQ analysis, first, a correspondence analysis (CA) was performed on the species abundance table. The CA species weights were then utilized in a principal component analysis (PCA) with the trait table, while the CA site weights were used in a PCA with the environmental factors. These two PCAs, along with the CA, were incorporated into the RLQ analysis (rlq() function in ade4 package; (Dray and Dufour, 2007)). Correlations between levels of environmental factors and traits were subsequently calculated, and results were plotted for nine functional traits.

We examined the effects of agricultural practices (factors: crop type,

crop rotation, fertilisation, season, and block) on two ecologically most relevant collembolan traits (size, reproduction), LF traits (soil adaptation, disturbance resistance, dispersal ability) and community parameters (species richness, Shannon diversity, and functional diversity indices) according to the methods in Zuur et al. (2009). As fertilisation and block effects were minimal across the response variables, the models contained only the factors crop plant (maize, wheat) and cropping system (monoculture, crop rotation) together as a combined factor. Specifically, this comprised five categories: wheat monoculture, maize monoculture, wheat in crop rotation, maize in crop rotation, and meadow. Season was also included as a separate factor in the models. The years 2018 and 2019 were analysed separately. Linear models were used with lm() function (package stats). If heteroscedasticity and non-normality occurred, generalised least squares models (gls) were used with variance structure allowing different variances for the factor levels. Decisions for better models were made based on AIC values using anova() function. For species richness and proportion of parthenogenetic species, generalized linear models with glm() function were used with Poisson and binomial distributions, respectively. Significant differences between factor levels were calculated with pairwise Tukey-tests using emmeans() and contrast() functions (packages emmeans (Lenth, 2022) and stats). For visualisation of statistical results, we used ggplots generated by the ggplot() function (Wickham, 2016). Data from the nearby meadow (average of four samples) were not included in the statistical analyses due to the inappropriate sampling design, but were used as reference points in the visual presentations.

3. Results

3.1. Microbial biomass

Microbial biomass, based on SIR values, was not affected by plant type or cropping system. However, it tended to be (p value is lower than 0.10, p = 0.097) or was significantly higher in the manure treatment for both years, particularly in June, compared to other fertilisation treatments (Table S4). Seasonal differences were observed only in 2018, when samples collected in June exhibited lower SIR values than those collected in October across all culture types.

3.2. Functional traits

In the RLQ analysis, axis 1 accounted for the majority of the co-inertia in both years, explaining 91.90 % of the inertia in 2018 and 47.86 % in 2019. In contrast, axis 2 contributed less to the explained inertia, with 7.52 % in 2018 and 25.28 % in 2019.

In 2018, samples showed distinct structuring of functional traits (Fig. 2A). Summer communities were characterised by species with longer antennae (correlation = 0.35) and legs (0.37), larger body size (0.53), and greater pigmentation (+0.44), and increased presence of dense macrosetae or scales (0.55) (Fig. 2A, Table 3). These traits are commonly associated with surface activity: enhanced mobility, and resistance to desiccation or UV exposure. By contrast, autumn communities were dominated by species with a well developed post antennal organ (PAO; 0.31), while surface-associated traits such as pigmentation (-0.44), dense setae or presence of scales (-0.55), and body size (-0.53) declined, suggesting adaptations to the deeper soil microhabitats.

Clear trait-based differentiation was also observed among cropping systems. Maize and wheat monocultures were positively associated with pigmentation (0.21, 0.16), dense macrosetae or scales (both 0.22), antenna length (0.12, 0.16), and body size (0.20, 0.30), suggesting dominance by surface-active, disturbance-tolerant species. Conversely, wheat crop rotation plots were negatively associated with pigmentation (-0.26) and dense macrosetae or scales (-0.31), reflecting a shift towards species adapted to more stable and deeper soil environments, but showed positive correlations with furca length (0.23), which is a

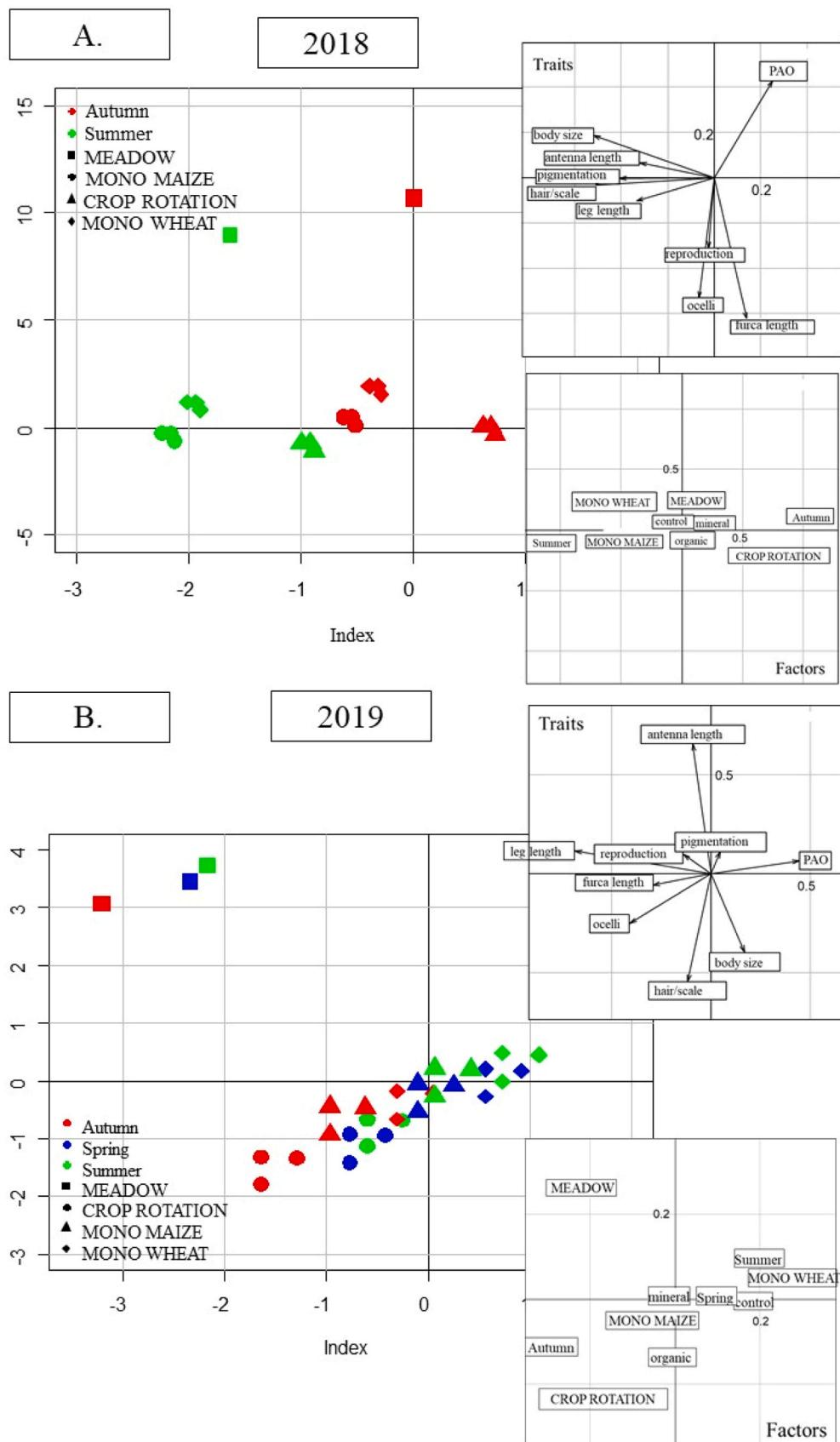


Fig. 2. Results of the RLQ analyses for 2018 (A) and 2019 (B). The sites, traits (furca length, pigmentation, presence of dense setae or scales (hairs/scales), antenna length, leg length, post antennal organ (PAO), sexual reproduction, body size, number of ocelli), and environmental scores (factors: MONO WHEAT = wheat monoculture, CROP ROTATION = winter wheat in 2018 and maize in 2018, MONO MAIZE = maize monoculture, control = no fertiliser, mineral: NPK fertiliser, organic = NPK + farmyard manure) are displayed separately for better visibility. Co-inertia of the axes: 2018: 91.90 %, 7.52 %; 2019: 47.86 %, 25.28 %.

Table 3

Correlations between the environmental factors (agricultural practices, seasons; for fertilisation: control = no fertiliser, mineral = NPK fertiliser, organic = NPK + farmyard manure) and the traits (functional/life history traits: furca length, pigmentation, hairiness and/or presence of scales, antenna length, leg length, post antennal organ (PAO), sexual reproduction, body size, number of ocelli; life form traits: adaptation to the soil environment, dispersal ability, disturbance resistance), according to the RLQ models. I. indicates the RLQ model for functional traits, and II. indicates the RLQ model for life form traits. Asterisks indicate the significant correlation between the model axes and the variables, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

2018	I.	II.	furca length	pigmentation	dense setae/ scales	antenna length	leg length	PAO	reproduction	size	ocelli	soil	disper-	distur-
significance			***	***	***	***	***	***	***	***	***	***	***	***
maize monoculture	***	***	-0.02	0.21	0.22	0.12	0.16	-0.16	-0.06	0.20	0.07	-0.19	0.08	0.22
wheat in crop	***	***	0.23	-0.26	-0.31	-0.21	-0.19	0.08	0.07	-0.38	0.07	0.18	0.05	-0.27
rotation														
wheat monoculture	***	***	-0.22	0.16	0.22	0.16	0.12	-0.01	-0.02	0.30	-0.09	-0.10	-0.08	0.17
meadow	***	***	-0.14	0.02	0.01	0.03	-0.02	0.10	-0.09	0.03	-0.14	0.06	-0.13	0.00
fertilisation_control			-0.03	0.02	0.04	0.01	0.03	-0.02	0.00	0.07	-0.01	-0.02	0.00	0.03
fertilisation_mineral			-0.02	0.01	-0.02	-0.01	-0.02	0.02	-0.02	0.00	0.01	0.01	-0.01	-0.01
fertilisation_organic			0.07	-0.03	-0.02	0.00	-0.01	-0.02	0.03	-0.07	0.03	0.00	0.03	-0.01
season_summer	***	***	-0.08	0.44	0.55	0.35	0.37	-0.31	0.07	0.53	0.12	-0.44	0.17	0.51
season_autumn	***	***	0.08	-0.44	-0.55	-0.35	-0.37	0.31	-0.07	-0.53	-0.12	0.44	-0.17	-0.51
2019	I.	II.	furca length	pigmentation	dense setae/ scales	antenna length	leg length	PAO	reproduction	size	ocelli	soil	disper-	distur-
significance			***		***	**	***	***	**	***	***	***	***	***
maize monoculture			0.02	-0.07	0.01	-0.06	0.02	0.01	0.01	-0.05	-0.07	0.04	-0.02	-0.01
maize in crop	***	***	0.09	0.00	0.21	-0.09	0.17	-0.15	0.03	0.11	0.09	-0.10	0.14	0.11
rotation														
wheat monoculture	***	***	-0.11	0.03	-0.12	0.01	-0.25	0.16	-0.06	0.01	-0.04	0.07	-0.16	-0.07
meadow	**	***	0.05	0.03	-0.11	0.20	0.20	-0.10	0.05	-0.14	0.05	-0.03	0.12	-0.02
fertilisation_control			-0.04	-0.14	-0.07	-0.11	-0.05	0.10	0.01	-0.03	-0.13	0.12	-0.10	-0.11
fertilisation_mineral			0.03	0.04	0.06	0.03	-0.03	0.00	0.07	-0.02	0.00	-0.04	0.00	0.07
fertilisation_organic	*	***	-0.02	0.09	0.07	-0.03	-0.02	-0.05	-0.10	0.12	0.11	-0.07	0.04	0.06
season_spring	***	***	-0.05	-0.04	0.00	0.00	-0.11	0.07	-0.04	-0.08	0.05	0.01	-0.04	0.01
season_summer	***	***	-0.04	0.12	-0.02	0.10	-0.07	0.03	0.00	0.12	-0.24	0.04	-0.16	0.01
season_autumn	***	***	0.09	-0.10	0.02	-0.11	0.18	-0.10	0.04	-0.06	0.21	-0.04	0.20	-0.02

dispersal trait. Meadow plots differed from crop fields, showing lower values for sexual reproduction (-0.09), ocelli number and furca length (both -0.14), while displaying higher PAO values (0.10) (Fig. 2A, Table 3).

In 2019, trait-environment relationships remained seasonally structured. Summer and spring samples exhibited differences from autumn samples along axis 1 for each plant type driven by the number of ocelli, PAO, furca- and leg length (Fig. 2B). Autumn samples exhibited higher number of ocelli (0.21) and longer legs (0.18), indicating communities dominated by more mobile, and light-sensitive surface dwellers. By contrast, summer communities again showed greater body size and pigmentation (both 0.12) as in 2018 (Fig. 2B, Table 3). Across all plant types, there was a noticeable shift from dominance by a higher number of ocelli and increased leg- and furca lengths (in crop rotation and meadow) to a dominance of the presence of PAO (in wheat plots). Samples from maize monoculture were positioned between those from maize crop rotation and wheat monoculture along axis 1 (Fig. 2B). Additionally, the meadow samples were distinctly separated from the treated plots, characterized by species with longer antennae and smaller body sizes with fewer macrosetae or scales.

In both years, the body sizes in wheat plots were consistently smaller in autumn compared to spring or summer, regardless of the cultivation type (Fig. 3). In contrast, maize plots exhibited reduced body sizes only in autumn 2018 compared to summer, whereas in 2019, no significant differences among the seasons were observed (Fig. 3, Table S4). Body sizes in the meadow were comparable to those in the treated plots, except in autumn 2019, when values were lower than those from the treated plots. When considering crop types, body sizes did not differ significantly from one another, except during the autumn seasons. A significant difference in body sizes was observed between crops, particularly when the crop was part of a rotation (wheat in rotation in 2018 and maize in rotation in 2019) (Fig. 3).

According to the binomial generalised model, the proportion of

parthenogenetic species tended to be higher in the autumn of 2018 across all plot types (binomial glm, $p = 0.1507$) (Fig. 3). In 2019, only minor effects of the examined factors were observed. However, in the autumn, wheat monoculture exhibited a higher proportion of parthenogenetic species compared to maize crop rotation, although the standard deviations were high (Fig. 3, Table S4).

The only notable effect of the fertilisation treatment was seen in the body size trait of Collembola. In 2018, individuals tended to be the smallest in summer, whereas, in 2019, they were larger in both summer and autumn within the organic treatment, compared to the other treatments (Table S4). For other functional and LF traits, we did not observe any effects of fertilisation.

3.3. Life form traits

For the adaptation to the soil environment LF trait, wheat exhibited significantly higher values in autumn compared to maize in both years (Fig. 3). In 2018, models indicated that autumn values were significantly higher than those in summer, regardless of the cropping system. Maize plots recorded higher values in summer than in autumn in both years. The nearby meadow displayed the highest adaptation to the soil environment in both years and seasons, except for autumn 2019, when the values were comparable to those in cultivated fields throughout the year. Dispersal ability and disturbance resistance LF traits exhibited an opposite pattern to that of adaptation to the soil environment LF trait (Fig. 3, Table S4), with higher values observed primarily in maize plots during autumn compared to other crop plots. In contrast, these variables displayed similar values across crop plants during both summer and spring.

For disturbance resistance LF traits, clear differences emerged between crop types. In both years, wheat plots consistently exhibited significantly lower disturbance resistance than maize plots, particularly in autumn and in the summer of 2019, regardless of the cultivation type

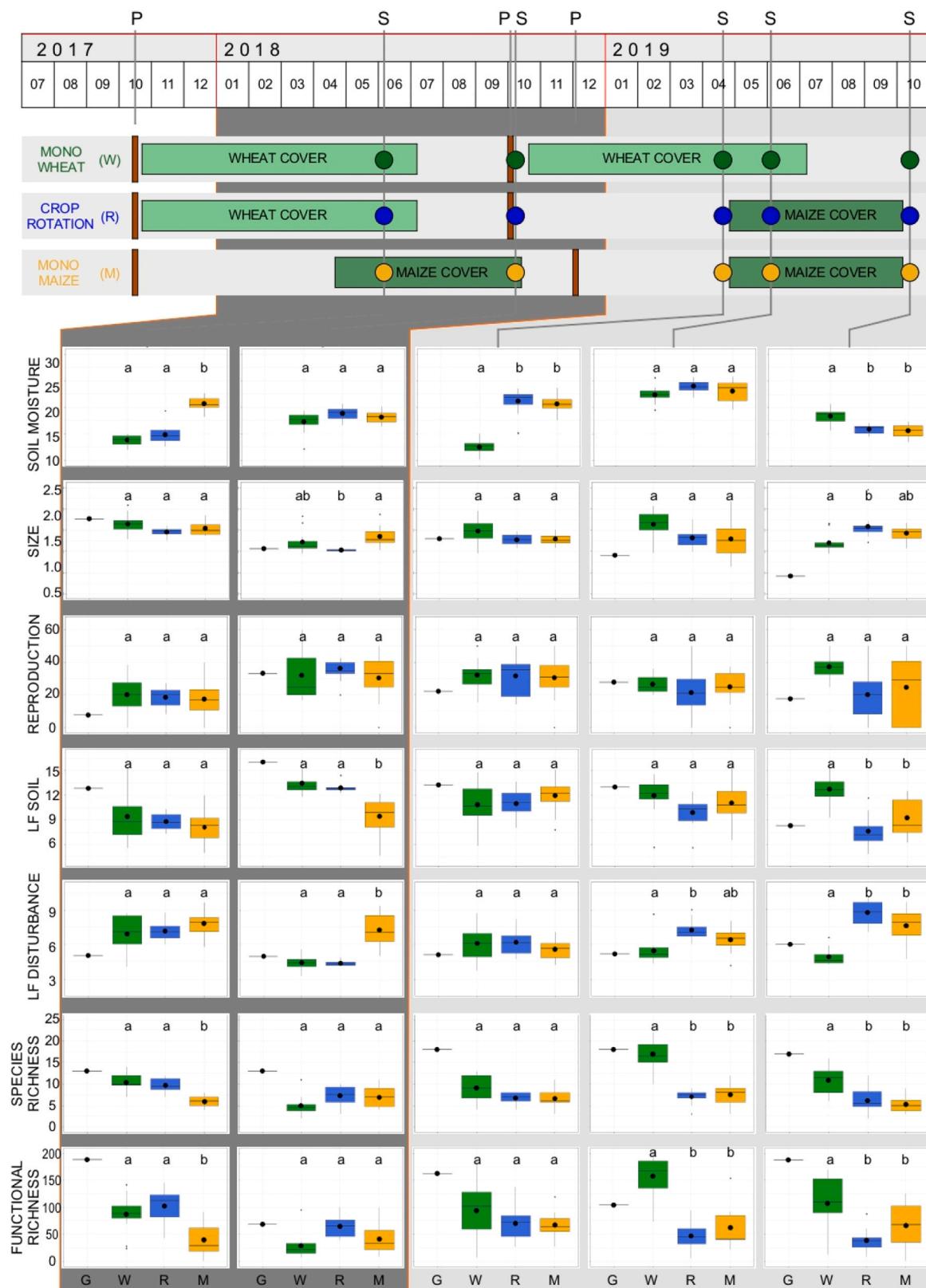


Fig. 3. Timeline of the sampling (S) and ploughing (P) dates and the vegetation cover in the three agricultural practices: winter wheat monoculture (W), maize (M) monoculture, and crop rotation (R) (winter wheat in 2018 and maize in 2019). A meadow (G) served as a control site. Green shading represents vegetation cover. Boxplots display soil moisture and functional trait: body size (SIZE), life history trait: percentage of parthenogenetic species (REPRODUCTION) and life form traits: adaptation to the soil environment (LF SOIL), disturbance resistance (LF DISTURBANCE), and species- and functional richness values for 2018 and 2019. Black points indicate the average values. Different letters indicate significant differences between groups ($p < 0.05$), separately for each season, based on Tukey's HSD. Data points from the meadow were only used for demonstration and were not included in the statistical tests.

(Fig. 3). In wheat, disturbance resistance declined from summer to autumn in 2018, across all cultivation types. A similar decline was observed in 2019, where wheat plots again showed reduced values in autumn compared to earlier seasons. By contrast, maize values remained similar in the summer and autumn of 2018. However, in 2019, maize plots showed an increase in disturbance resistance during autumn compared to spring and summer, indicating a seasonal shift. Meadow plots exhibited minimal seasonal variation, with consistently moderate disturbance resistance values. An exception occurred in autumn 2019, when values peaked, suggesting increased dominance of disturbance-resistant species during that period. Results for dispersal ability LF traits were nearly similar to those for disturbance resistance to disturbance resistance, reinforcing the close ecological linkage between these traits (Table S4).

3.4. Community parameters

Collembola species richness was highest in the meadow compared to the treated crop plots, except in the summer of 2019, when species richness was close to the values recorded in wheat plots. In addition, species richness was significantly lower in maize plots in the summers and in autumn of 2019 (Fig. 3). Functional richness was also predominantly higher in the meadow than in other plots, with the exception of autumn 2018 and summer 2019. In autumn of 2018 and in spring of 2019, functional richness values across all plots were similar, while in both summers and in autumn of 2019, wheat plots exhibited the highest functional richness. In both years during summer, wheat plots demonstrated higher richness values (both species and functional) than maize plots, irrespective of cultivation type. Richness values in maize plots remained consistently low across seasons and cultivation types. In wheat plots, richness values declined in autumn for both years and remained low in spring (Fig. 3). The only significant difference for other parameters was observed in Shannon-Wiener diversity, which showed lower values in the autumn of both years (significant only in 2018) (Table S4).

4. Discussion

Our results largely support the hypotheses proposed, revealing clear patterns in how *Collembola* functional and life form traits and community structure respond to different crop types, seasonal variation and management practices. We hypothesised that traits related to disturbance resistance and surface activity, such as increased pigmentation, larger body size, and the presence of dense setae or scales, would be more prevalent in maize fields, due to their open vegetation structure and associated environmental fluctuations. Conversely, we expected traits linked to adaptation to the soil environment, such as a well-developed post-antennal organ (PAO) and reduced pigmentation, to dominate in wheat fields and natural meadows, reflecting more stable and buffered conditions. Our findings confirmed this pattern. *Collembola* in maize fields commonly exhibited surface-adapted traits, while communities in wheat fields and meadows were characterised by traits associated with living in the soil. In particular, PAO presence and complexity were a defining trait in wheat fields. Larger species could be expected in the meadow compared to agricultural areas, as larger representatives of the soil biota are reported to be more sensitive to agricultural intensity than smaller ones (Postma-Blaauw et al., 2010). In both autumns, we found smaller, fast-reproducing (parthenogenetic) species, which reflects an r-selection strategy, exploiting available resources rapidly, primarily in wheat fields and especially in the meadow. However, within the size range of *Collembola*, larger body size could confer an advantage as a disturbance resistance trait (Salmon et al., 2014). The emergence of smaller species may also be linked to the seasonal decline in vegetation during autumn, which likely favours soil-dwelling species. This seasonal shift in vegetation cover coincided with drier and cooler conditions, which may have further promoted soil-adapted traits due to moisture sensitivity and limited aboveground

microhabitats. For these animals, a smaller body size offers an advantage in moving between soil pores. Additionally, we observed distinct traits in the meadow compared to the treated plots, notably longer antennae (associated with dispersal) and a reduction in hairiness and the absence of scales (traits adapted to soil environments). These functionally different traits likely reflect the diversity of microhabitats found in more natural, untreated areas.

Parthenogenesis and sexual reproduction represent distinct adaptive strategies. The proportion of parthenogenetic species within a community may reflect its capacity to cope with environmental disturbance (Wehner et al., 2021). Although there are different interpretations of the sexual-parthenogenetic concept (e.g., Lindberg and Bengtsson, 2005), both Ponge (2020) and Salmon et al. (2014) noted that sexual reproduction can occur in a stressed environment, whereas true euedaphic species are often parthenogenetic. Given the openness and environmental stress of maize fields, we expected a higher proportion of sexual species, but no significant differences were found in this number. Additionally, maize fields also favoured larger species, which tend to be more resilient to environmental fluctuations, and size can serve as a dispersive trait (Ponge, 2020; Ponge et al., 2006). Although some yearly differences were present, species exhibiting sexual reproduction, longer legs, and more ocelli, dense macrosetae and the presence of scales, and larger furca were observed in maize fields. Species with these traits are considered more effective colonisers and are better able to withstand small-scale temporary disturbances (Ponge, 2020).

We had assumed that the meadow would act as a functionally stable baseline or control. However, our results challenge this assumption. In 2018, the meadow community was dominated by dispersal-related traits such as sexual reproduction and longer legs and antennae. In contrast, in 2019, traits reflecting stronger adaptation to the soil environment became more prominent. These inter-annual differences may be influenced by climatic variation, such as precipitation and temperature patterns (e.g., 2019 was drier in autumn), which affect soil moisture and subsequently shape trait selection in *Collembola* communities. These year-to-year shifts in functional composition, despite constant vegetation cover and the absence of management (e.g., mowing), suggest that natural grasslands may exhibit internal ecological dynamics and cannot always be treated as stable references. These findings suggest that natural grasslands, though often used as reference systems, may experience internal dynamics that complicate their role as fixed ecological baselines.

Although the specific traits varied between years, the life form trait analyses showed that traits related to dispersal and disturbance resistance were more common in maize fields across both years. Traits indicating adaptation to the soil environment were more prevalent in wheat fields and especially in the meadow. Parisi (2001) found that a higher occurrence of euedaphic species—indicated in our case by higher values of the adaptation to soil environment LF trait—suggests a stable, closed habitat with higher soil quality. In the context of *Collembola*, Salmon et al. (2014) noted that traits like developed locomotory and sensory organs, larger body size, and strong pigmentation are typical of open habitats, while traits such as a higher number of defensive organs, the presence of PAO, and parthenogenesis are more common in closed (woodland) habitats. In terms of plant effects, the functional and LF traits associated with different crop species were consistent with our hypothesis. In our study, meadows were considered the most closed and least disturbed habitats, while wheat and maize fields were more open and disturbed, with winter wheat regarded as a more closed habitat than maize. The effects of the management practice and biological traits of the given crop species cannot be separated. Wheat has dense vegetation, narrow row spacing, and a complex root system, which provide a suitable environment for *Collembola*. In contrast, maize, with its wider sowing distance, does not form dense ground cover during its growing season. Our results align with those of Postma-Blaauw et al. (2010), who found that, compared to maize, soil biota increased under barley, a crop with similar traits to wheat.

Similar to findings on aboveground arthropods (Meyer et al., 2019), our research on Collembola showed that community parameters varied by plant species and were season-dependent. In both years, species and functional richness were significantly higher in wheat fields compared to maize, particularly in summer, when dense vegetation was present. Species richness also mirrored our hypothesised habitat openness gradient. Since functional richness tends to be higher in more diverse and heterogeneous habitats (Winck et al., 2017), it was not surprising that the meadow reached the highest values. In autumn, the termination of wheat created a much more open habitat, which could potentially lead to a loss in diversity. In contrast, species richness in maize fields remained stable over time, as major vegetation changes occurred only a day before the autumn sampling, likely not allowing enough time for the communities to be affected. This highlights the importance of timing in ecological sampling, and we suggest that future studies aim to standardise the timing of sampling relative to harvest or disturbance events across treatments, to enable clearer interpretation of community responses.

Our findings differ from those of Twardowski et al. (2016), who reported higher collembolan diversity in monoculture fields during autumn compared to spring. However, their focus was on a different crop, the potato, which also lacks ground cover in spring. Potatoes are typically planted later and harvested earlier than cereal crops, resulting in reduced ground cover and soil organic inputs during key parts of the growing season. This timing may limit habitat availability and food resources for soil fauna in spring, influencing the seasonal diversity pattern they observed. Previous studies have shown that spring-sown crops tend to have lower Collembola diversity than winter-sown crops (Frampton and Van den Brink, 2002), consistent with our results. This also aligns with the previous findings that Collembola diversity in agro-environments is more closely linked to plant cover than other factors (Gergócs et al., 2022).

Grasslands, compared to agricultural fields, offer greater plant diversity, which in turn provides more microhabitat variety and food source heterogeneity, along with continuous plant cover (Gruss et al., 2023; Salomon et al., 2004). Although not statistically confirmed, the meadow consistently emerged as a better habitat for Collembola communities, with species richness and Shannon diversity remaining high or the highest in this environment. It is worth noting that we found only minor differences in Shannon diversity between the agricultural treatments. This may reflect environmental filtering, where communities are already resilient to change, or it may indicate functional redundancy, a situation in which Shannon diversity fails to detect underlying functional shifts.

Previous studies (Parisi, 2001; Salmon et al., 2014) suggested that collembolan traits should indicate a more undisturbed, closed habitat, with euedaphic dominance during periods of dense vegetation. Surprisingly, our findings contradict this assumption. During vegetation peak, we observed only minor differences in life form traits, and the RLQ analysis did not identify clear distinctions. Instead, notable differences primarily emerged once vegetation was terminated, with soil-adapted traits becoming more dominant in plots without vegetation. The environmental effects on Collembola communities vary across life forms (Gruss et al., 2023; Pollierer and Scheu, 2017). Considering epigeic species, which are more closely associated with the vegetation (Filser, 1995), our findings are not surprising. In autumn, environmental conditions on bare soil (even with plant residues remaining) were not suitable for these species. Larger epigeic species react sensitively to disturbances (Malmström, 2012; Rousseau et al., 2018) and this sensitivity is likely even more pronounced in tilled agricultural areas. After vegetation termination these species are either eliminated or more likely, become inactivated (dormant or emigrated) (Frampton et al., 2001; Ponge, 2020). Migration could occur, as our plot size was smaller than the distance, over which epigeic Collembola can migrate in search of a more suitable habitat (Ponge and Salmon, 2013). In contrast, euedaphic or hemiedaphic species are less exposed to small-scale

environmental variability. Gruss et al. (2023) also found that land-use treatments influenced the biomass of epigeic Collembola, while no significant effects were observed for euedaphic or hemiedaphic forms. Moreover, Yin et al. (2020) reported that from grassland to cropland, increasing disturbance led to a higher dominance of soil-dwelling species, indicating that croplands favour euedaphic species. By feeding on microorganisms, these species may influence nutrient availability to plant roots, shape the microbial composition of the rhizosphere, and contribute to the breakdown of soil organic matter, ultimately benefiting plant growth (Potapov et al., 2016). Species on the surface can survive or remain active when vegetation is present, provided they possess higher dispersal and disturbance resistance traits. The observed unexpected pattern highlights the complexity of trait–environment relationships and the importance of direct field observation in testing ecological assumptions.

It is important to note that, contrary to the results presented above, Martins da Silva et al. (2016) discovered a higher proportion of soil-dwelling species in natural sites compared to arable sites, where epigeic species were dominant. In the RLQ analysis, meadows exhibited the same pattern of seasonal separation (autumn vs. vegetated seasons) as observed in the crop plant groups. This indicates that not only vegetation but also seasonality has a significant effect on traits.

The statement by Parisi (2001), which forms the basis of QBS studies, may not be directly applicable for examining collembolan species or forms within agro-environments. However, it remains useful for comparing broader management practices, such as arable fields versus grasslands, or farming systems that aim to mimic natural processes (e.g., regenerative vs. conventional agriculture). We propose that Collembola species in agro-environments, particularly those subjected to long-term treatments, where predictable cyclic events occur, have already been selected by environmental constraints. Therefore, to effectively evaluate agricultural practices based on collembolan groups, it is more informative to consider the balanced representation of all three ecomorphological groups (euedaphic, hemiedaphic, and epigeic), rather than focusing solely on the presence of soil-dwelling species. This also suggests that monitoring tools should assess community structure and the relative abundance of life forms, rather than species richness alone. Our results also indicate that outcomes depend on the type of vegetation, which should be considered in the evaluation of agricultural management practices. For evaluations based on Collembola, it is essential to conduct seasonal sampling that aligns with the phenological stages of the actual crop plant.

While the effect of plant species was the most significant in our study, other factors also played an important role. In contrast to Meyer et al. (2019), who found no significant effects of temporal diversity of crop plants (i.e. different crop species in rotation over time) on soil microarthropods, our results indicated that crop rotation influenced community indices and some traits. RLQ analysis consistently separated monocultures from crop rotations in each season. In 2018, wheat in rotation showed more soil-adapted traits, such as smaller body size, shorter antennae, and reduced pigmentation, while dispersal traits (such as longer furca and more ocelli) were also more dominant there. In 2019, these dispersal traits remained significant in crop rotations (maize), and differences in LF traits persisted between crops. However, we could not compare different plants in crop rotations within the same year, complicating the distinction between crop and yearly effects. Temporal and spatial crop diversification can enhance biodiversity and support decomposer species (Meyer et al., 2019). Initially aimed at improving nutrient efficiency and reducing specialist pests (Bennett et al., 2012; Bullock, 1992), crop rotation also affected generalist Collembola traits, which appeared to diminish over time. In 2018, species and functional richness were higher in wheat rotations than in monocultures, but Shannon diversity was lower. This suggests that while some species from the previous maize crop persisted, only a fraction of the species pool achieved higher abundances. In 2019, no significant differences were observed between crop rotations and monocultures, indicating that

species from maize can adapt to wheat, while wheat-adapted species struggle in maize plots. Overall, the impact of temporal diversification depends on the plant species involved. Long-term rotation of only two crops is insufficient to significantly boost species- or functional diversity. A broader rotation with varied crop traits would likely enhance diversity (Meyer et al., 2019).

Fertilisation effects on soil fauna vary geographically and are influenced by the dosage, chemical composition, and application frequency (Bokova et al., 2023; Zhu et al., 2023). Interestingly, our previous study found no significant differences in species abundance as a result of long-term fertilisation (Gergócs et al., 2022). We hypothesised that fertilisation might affect species traits more than species abundances. However, we did not observe any significant effects of mineral fertiliser (NPK) on collembolan traits or community indices. In contrast, organic fertilisation did affect collembolan species size. While in the first year, the effects of fertilisation were minor and insignificant, in the second year, three years after the current application, species in the organic (farmyard) manure treatment were significantly larger in summer and autumn compared to other treatments. This delayed response may reflect a time lag in belowground ecological processes, highlighting the importance of multi-year studies for capturing long-term trait dynamics. The increase in microbial biomass (SIR) observed in manure-treated plots supports a bottom-up effect, as organic fertilisers stimulate microbial communities, particularly fungi, which are a key food source for Collembola (Hopkin, 1997; Jørgensen et al., 2005). The dominance of larger species in 2019 may thus be linked to improved resource availability. Interestingly, we had expected stronger effects of organic fertilisation in 2018, the second year after manure application, but these became evident only in 2019. It is possible that drier conditions in 2018 suppressed microbial activity, delaying the trophic cascade to Collembola until the following year. This suggests that trait responses to organic inputs may be context-dependent and temporally lagged, again reinforcing the need for long-term, multi-seasonal monitoring.

Our study applied farmyard manure, but other organic materials, such as composts, could yield different results. Furthermore, fertilisation is often combined with tillage to incorporate organic matter into the soil, and Collembola may be more sensitive to mechanical disturbance than to itself (Chassain et al., 2024). Therefore, disentangling the effects of fertilisation from associated practices like tillage remains a challenge and warrants further study. Although individual traits (e.g., size differences within species) were not investigated in the present study, our findings suggest that even 50 years of fertilisation may not be sufficient to induce long-term changes in collembolan species traits and community composition.

This study offers valuable insights into collembolan communities under long-term agricultural management, but several limitations should be noted. As the research was conducted at a single site with only three crop types (wheat, maize, and meadow), the generalisability of the findings to other cropping systems, climates, or soil types may be limited. Future studies across multiple sites and broader crop rotations would help validate and extend these results. Additionally, while we evaluated the effects of crop type and rotation, our dataset lacked within-year rotation contrasts (e.g., split-plot or side-by-side comparisons within the same season). This limits the ability to capture short-term responses to rotational changes, which could be addressed in future experimental designs. Our trait-based approach relied on literature-derived life-form classifications, focusing on traits commonly reported in collembolan ecology. Other relevant traits may have been overlooked, and trait categorisation involves assumptions that could affect resolution. Collembola were identified at the species level, enabling trait assignment, but individual-level trait variation was not captured. While such data could offer greater ecological precision, collecting it would require substantially more effort.

Despite these limitations, the study offers a valuable basis for understanding how long-term agricultural practices influence collembolan community structure and function. Addressing these constraints in

future research will enhance the robustness and applicability of trait-based soil ecological assessments.

5. Conclusion

We asked how over 50 years of consistent agricultural practices influence Collembola functional traits and community structure. Our findings show that long-term crop management, particularly crop type, acts as a powerful filter on trait composition, favouring species with different resistance and dispersal strategies depending on habitat openness. In agroecosystems, a high degree of biotic and functional homogenization is present. This may reduce resilience by limiting the range of ecological strategies present in the community. Despite that, in our case distinct patterns in trait composition were still apparent. Agroecosystems filter functional traits through crop management and plant types. Maize, characterised as an open habitat, promoted traits linked to dispersal and disturbance resistance but was associated with lower diversity. In contrast, wheat, as a more closed habitat, favoured soil-adapted traits and supported higher diversity, a pattern particularly evident in the meadow. These findings align with previous research, which highlights a strong link between plant cover and Collembola diversity in agroecosystems.

Importantly, our seasonal analysis yielded some unexpected shifts in trait dominance. Disturbance-resistant traits appeared in closed, vegetated habitats, while soil-adapted traits were observed in disturbed ones. These findings suggest that disturbance-resistant species have already been filtered out by the agro-environment, and in highly disturbed areas, species tend to survive or remain active primarily below the surface. Despite long-term exposure to the same agricultural conditions, the dominance of certain traits varied seasonally, indicating that traits can shift rapidly in response to environmental changes. This highlights a key conclusion: temporal fluctuations, linked to season and inter-annual variation, can have a greater influence on trait composition than five decades of consistent land use.

From a methodological perspective, aggregating individual functional traits into life form trait groups provided clearer ecological insights than analysing traits separately. We recommend this approach for future studies to better capture community-level responses to management and environmental filters. Practically, our findings highlight the importance of considering not just crop type and land-use history, but also seasonal timing, as trait dominance shifts throughout the year. Maintaining continuous plant cover and enhancing crop diversity, e.g., through rotation, can promote both taxonomic and functional diversity, boosting the resilience and ecological function of soil mesofauna.

CRediT authorship contribution statement

Veronika Gergócs-Winkler: Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis. **Norbert Flórián:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Miklós Dombos:** Writing – review & editing, Visualization, Supervision, Methodology, Investigation, Funding acquisition, Conceptualization. **Tibor Szili-Kovács:** Writing – review & editing, Funding acquisition, Formal analysis, Data curation.

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 data

The Supplement includes four tables. **Table S1:** Dates of different treatments relevant to the two years (2018, 2019) of the mesofaunal study. **Table S2:** Soil variables under different agricultural management (crop plant, fertilisation). **Table S3:** The summary of different traits of collembolan species found in the experiment. **Table S4:** The summary of different models and their data used to evaluate response variables.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.agee.2025.109810](https://doi.org/10.1016/j.agee.2025.109810).

Data availability

Data will be made available on request.

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