



Soil fauna diversity is enhanced by vegetation complexity and no-till planting in regenerative agroecosystems

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ABSTRACT

Agricultural ecosystems are driven by the need to increase yield, due to increased food demands. Conventional, intensive practices are not sustainable as they disrupt the biodiversity in the soil which performs a range of ecosystem functions that sustain soil productivity and resilience. Conservation agriculture and crop-livestock integrated agriculture have been promoted as some of the most sustainable and biodiversity-conserving forms of agriculture. This study assesses how soil macro-and mesofauna in staple crops respond to different agricultural land uses, including conventional, integrated and conservation agriculture, and lastly, natural grassland ecosystems which were used as reference sites. We compared species richness, composition, and functional structure of soil fauna among the land uses and assessed environmental drivers of these patterns. Soil macro-and mesofauna species richness was generally lower in conventional management compared to other management practices, for overall arthropods and for the separate taxonomic groups, beetles, earthworms, spiders, and springtails. Different functional guilds varied in their responses to the farming systems. Vegetation cover and plant litter cover are the variables which benefited most fauna diversity. The practices of no-till plantings coupled with diversified crop rotations and cover crop mixtures under conservation and integrated agricultural management enhances the diversity of earthworms, collembola, beetles, and spiders. Low-disturbance soil management, crop diversification and within-crop habitat complexity preserves arthropod soil fauna diversity in staple crops.

1. Introduction

Agriculture is undoubtedly an integral part of human livelihoods, and at the same time the most significant contributor to natural resource degradation (Okolo et al., 2020). Frequent habitat destruction associated with agricultural land use intensification coupled with climate change have resulted in a considerable decline of farmland biodiversity (Cardoso et al., 2020). Cultivation practices such as soil tillage, agrochemical applications, and the removal or burning of crop residues degrades the soil and produces pollutants which subsequently diminishes biodiversity either through direct mortality or by altering habitat suitability (Plath et al., 2021). This consequently leads to the loss of agroecosystem functionality and stability as biodiversity is responsible for regulating important ecosystem processes (Didham et al., 2020). The major concern is whether it is possible to meet the ever-rising food demands without increasing the environmental footprint (Adenle et al., 2019; Tschardt et al., 2012). Consequently, several studies suggest that sustainable management of agricultural systems, such as

regenerative agricultural systems (RAS) holds the key to alleviate the impacts of intensive agriculture on crop production, environment, and the losses of important biodiversity (Adenle et al., 2019; Hassan et al., 2022). Regenerative agricultural systems are characterised into three major classes as (1) organic, (2) conservation and (3) livestock integrated agriculture, have been coined as sustainable alternatives to intensive systems (Adenle et al., 2019).

In South Africa, RAS has received major attention as a sustainable model, therefore, the Food and Agricultural Organisation of the United Nations (FAO et al., 2018; FAO and ITPS, 2015) has devised a national plan with local agricultural organisations to accelerate implementation. The Free State province is one of South Africa's major agricultural regions where important staple crops such as maize, wheat, oats, and barley are grown. Some farmers in this region have been responding well to calls for sustainable intensification and have gradually shifted towards RAS, with practices such as mulching, crop diversifications, residue maintenance, livestock rotations, and zero and/or reduced tillage being implemented into production systems (Palm et al., 2014;

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Swanepoel et al., 2018). This is encouraging, however the value of these systems in maintaining ecosystem services through soil biodiversity is still unknown. Therefore, there is a need to assess the effectiveness of RAS against conventional systems to provide more precise management recommendations and increase adoption in the farming communities.

Overall agricultural management is the main influential factor of agroecosystem stability, however various individual habitat elements may be responsible for shaping agroecosystem resilience and biodiversity responses. For instance, in a study conducted to explore predictors of predator diversity, Galloway et al. (2021) discovered that arthropod diversity is shaped by nearby natural land patches. Equally, other studies have linked habitat complexity (Diehl et al., 2013), grassy field margins (Steffan-Dewenter, 2003), zero soil disturbance (Sithole and Magwaza, 2019), vegetation cover (Birkhofer et al., 2019; Eckert et al., 2020), and semi-natural fragments (Plath et al., 2021) to the diversity of important fauna functional groups. Therefore, understanding how individual components of vegetation complexity and intensification influence soil fauna distribution holds important implications for the appropriate management of these components to build resilience and conservation measures. Specifically, the study seeks to (1) understand the responses of soil fauna species richness, composition, and functional

structure to different types of agricultural management (conventional, livestock integration and conservation), with natural grassland ecosystems as reference (2), establish whether the responses of soil fauna to management could be shaped by other factors associated with the intensity of land use i.e. soil management (tillage vs. no-till) and vegetation complexity, i.e., leaf litter, vegetation cover, bare soil, and plant species richness. To address these objectives, soil macro- and mesofauna (from here referred to as soil fauna), specifically, beetles, earthworms, collembolans, and spiders were used as model organisms for the study, owing to their ability to respond to land use disturbance and their important influence in many ecosystem processes. The selected fauna groups embody most feeding guilds and are relatively dominant in soils (Lavelle et al., 2022). Different arthropod species have been reported to respond differently to management in terms of diversity and functional guild structure, (Yekwayo et al., 2018). Therefore, their use as the study's focal taxa increases the range of environmental change responses and prevented any biases which might be associated with the analysis of a single organism group (Gerlach et al., 2013; Nascimbene et al., 2014). Understanding which of these management strategies best supports arthropod soil diversity will go a long way in determining the best strategies for sustainable agriculture in this region.

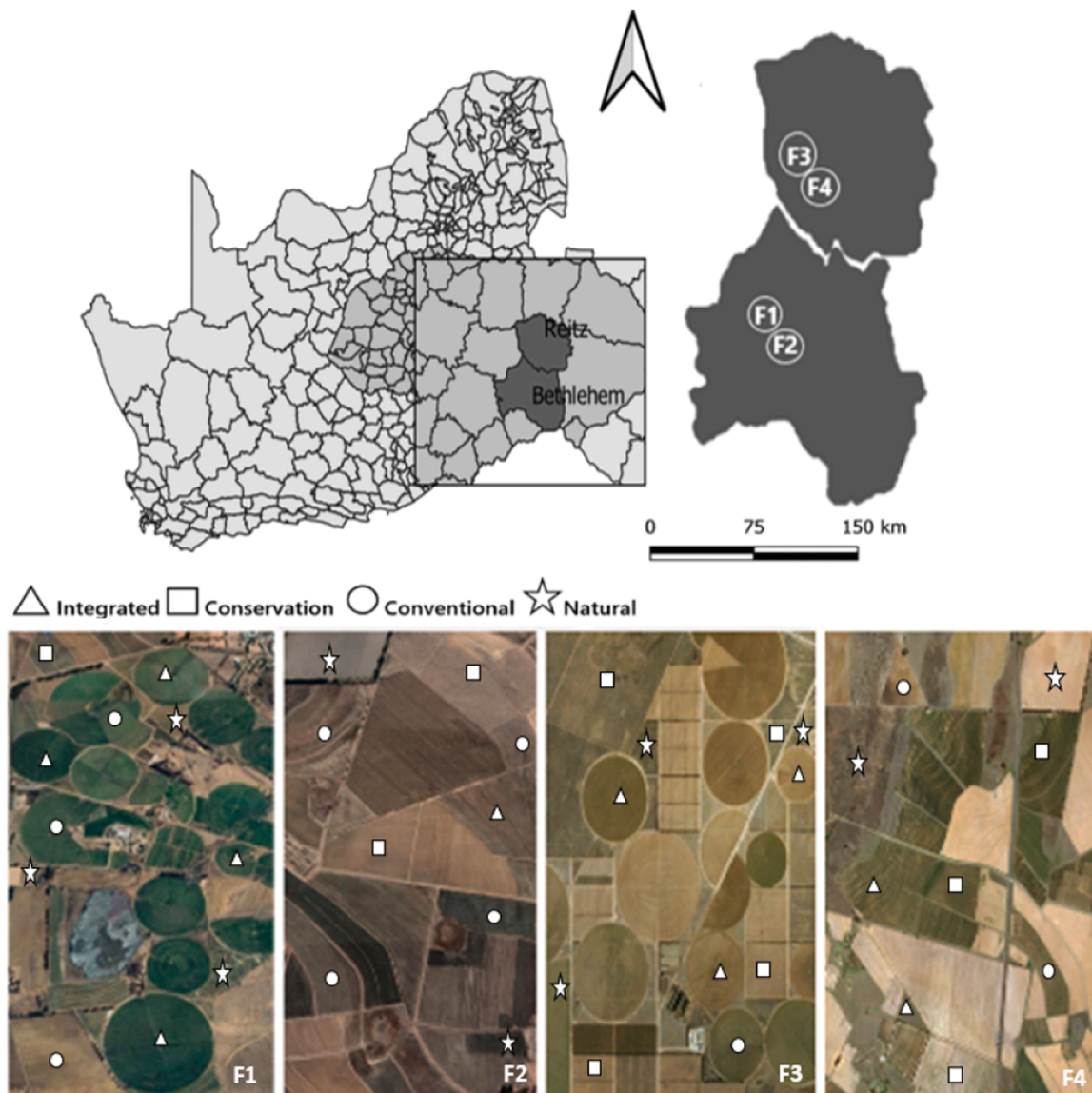


Fig. 1. Area map and design for the 40 study sites distributed across four farms (F1,F2,F3, F4) in the Free State.

2. Material and methods

2.1. Study area and site selection

The study was carried out in the Free State province of South Africa, in Thabo Mofutsanyane district at two key grain producing areas, Bethlehem (28°01'S; 28°18'E) and Reitz (27°58'S; 28°18'E) (Fig. 1). The annual precipitation in the area ranges from 200 mm to 600 mm with a semi-arid climate and monthly mean temperatures of 14 °C to 27 °C. Four management types typically used on commercial farms in the region were selected for sampling (1) Conventional agroecosystem: managed under tillage and monoculture cultivations with full chemical applications, (2) Conservation agroecosystem: managed under zero-tillage, crop diversification in the form of crop rotation and mixed cropping, and soil cover, (3) Integrated agroecosystem: livestock (cattle and sheep) is integrated into the cropping systems for grazing and (4) Natural ecosystem: undisturbed natural grassland to be studied as a reference system to get a more comprehensive picture of the native soil diversity (Appendix B).

A total of ten replicate sites distributed across four farms were sampled for each treatment, yielding an overall of 40 spatially heterogeneous sites. In a case where multiple sites of the same treatment occurred within the same farm, the sites were separated by a distance of at least 500 m to avoid pseudoreplication. The sampled agricultural sites were each at least 8 ha in size and managed with similar practices for more than 10 years before sampling. The natural sites (approximately 1.5 ha each) have been undisturbed and covered with natural vegetation for the past 40 years and characterised by the species *Chloris* sp., *Digitaria* sp., *Eragrotis* sp., *Andropogoneae* sp., and *Cymbopogon* sp. Some of the natural sites only had intermittent cattle grazing and trampling. Within the integrated agroecosystem, cattle and sheep were incorporated into the fields after harvesting crops to graze on cover crops, weeds, and crop residues. Since non-experimental agricultural fields were used, there were differences in crop rotations and species cultivated (both monoculture and mixed) within the agroecosystem treatments because farmers decisions influence crop history. Maize, soybean, oats, wheat, and sunflower were the main crops cultivated in the farmers' fields during the study, either in mono or mixed cultivation along with some combinations of summer and cool season crops i.e., legumes, grasses, brassicas. Atrazine and glyphosate (herbicides), tefluthrin and cyhalothrin (insecticides), phosphate, ammonium nitrate and urea (fertilisers) were the main agrochemicals applied in the study sites during the sampling period. Detailed management information (including cultivation history) of each agricultural field is presented in Appendix B.

2.2. Fauna sampling

Sampling was conducted over two seasons, from October to November 2020, and March to April 2021. Owing to their dynamic nature, soil fauna were sampled using three procedures. i.e., monoliths, pitfalls, and Berlese extractions. Monoliths sampling followed modified procedures developed by the Tropical Soil Biology and Fertility (TSBF) institute (Swift and Bignell, 2001) and Nxele et al. (2015). Four soil monoliths (25×25 ×30 cm) at 10 m apart were excavated from each sampling plot after clearing the litter layer and were hand sorted for visible fauna. Four pitfall traps were positioned 5 m away from each monolith sampling point at 10 m apart and filled with a mixture of ethylene glycol and 15% detergent to reduce surface tension (Souza et al., 2012) and left out open for seven days. The sampled individuals were preserved with 70% ethanol and taken to the laboratory for sorting and identification. For Berlese extractions, four soil samples were collected 5 m away from each corner of the monolith using a shovel at an approximate depth of ± 15 cm. The collected samples were appropriately tagged, sealed in brown paper bags and transported to the laboratory inside a thermally insulated container to avoid overheating and

desiccation. The fauna were extracted from the soil for a period of 72 hours using the Berlese funnel method modified by Espinaze et al. (2019). Identifications of fauna were made at genus and species level using appropriate taxonomic keys (Armstrong and Nxele, 2017; Dippenaar-Schoeman et al., 2010; Janion-Scheepers et al., 2015; Plisko, 2010, 2014; Plisko and Nxele, 2015; Schoeman et al., 2020). Individuals were sorted into morphospecies when species level identification was not possible (Oliver and Beattie, 1996). Feeding guilds (predators, herbivores, omnivores or detritivores) were also allocated to species based on the identity of family and morphological differences for beetles (Scholtz and Holm, 1985), Collembola (Malcicka et al., 2017), earthworms (Plisko and Nxele, 2015) and spiders (García et al., 2021).

2.3. Determination of environmental variables

To evaluate which environmental factors best explain variation in soil fauna diversity patterns, three 1 m² quadrats were used (5 m radius surrounding the pitfall traps and where monolith excavation took place) to record the percent leaf litter, vegetation cover, bare soil, and plant species richness (including non-crop/spontaneous spp.) (Gaigher et al., 2016; Joseph et al., 2018). Data from the three replicate quadrats per site were averaged for the analyses. Land use type (conservation, integrated, conventional, or natural) and tillage type (zero, deep, mulch) were included as categorical variables. Here, deep tillage is referred to as a cultivation method where soil is deeply inverted with mechanical implements such as mouldboard and disc ploughs (Kladivko, 2001), zero tillage as direct cultivation into undisturbed soil by means of a non-till planting implement (Roger-Estrade et al., 2010), and mulch tillage as a system where the intensity or frequency of soil disturbance is minimised and sufficient crop residues are retained to cover the soil surface by over 30% (Sithole and Magwaza, 2019).

2.4. Data analyses

2.4.1. Diversity and functional structure of soil fauna assemblages

Prior to analyses, assemblage catches for each sampling method and period were pooled and analysed together. Sample-based species rarefaction curves were conducted on each of the soil fauna groups using the R package *iNEXT* (Hsieh et al., 2020). To calculate the functional structure, species were categorised into four functional groups (predators, herbivores, detritivores, and omnivores) according to their known feeding habits and morphological characteristics. Species were given a binary score of 1 or 0 for whether they were predators, herbivores, omnivores, or detritivores. The scores were then used along with the matrix of species abundance at the different sites to measure the community weighted mean (CWM). The CWM values were calculated for each of the four feeding groups as a measure of species functional composition (de Bello et al., 2020), using the "functcomp" function of the *FD* package in R (Laliberté et al., 2015; Laliberté and Legendre, 2010) which computes the composition of functional communities as measured by the trait values of the community-level weighted means (Lavorel et al., 2008; Piano et al., 2020).

2.4.2. Generalized Linear Mixed Models on soil fauna species richness and functional CWM composition

The R package *lme4* was used to calculate Generalized Linear Mixed Models (GLMMs) (Bates et al., 2015) to test responses of the soil fauna richness and functional CWM against the four different land use types. Species richness assumed a Gaussian distribution while functional CWM assumed a gamma distribution when checked for probability distribution using Q-Q plots. Spatial autocorrelation was tested for using the *ape* package (Paradis et al., 2022) to calculate Moran's *I* on raw data matrix and model residuals (Piano et al., 2020). To account for the observed spatial autocorrelation, "site" was included as a random variable in all the models. Chi-square and *p*-values were calculated for each model and when significant differences were detected a Tukey post-hoc test was

calculated with the *multcomp* package (Hothorn et al., 2008) to highlight where the differences occur between the land use types.

To assess which variables best explained soil fauna species richness and functional CWM, a model selection and model averaging procedure was conducted with the Akaike's Information Criterion (AIC) using the "dredge" function within the *MumIn* package (Barton, 2022). Firstly, the *car* package (Fox et al., 2019) was used to test for multicollinearity with

the variance inflation factors (VIF) on rescaled variables, variables with VIF > 5 were removed from the model. Models with AICc values of $\leq \Delta 3$ from the top model were included in model averaging.

2.4.3. Determining differences in soil fauna assemblage composition

Differences in soil fauna assemblage composition between the land uses were assessed with a permutational multivariate analysis of

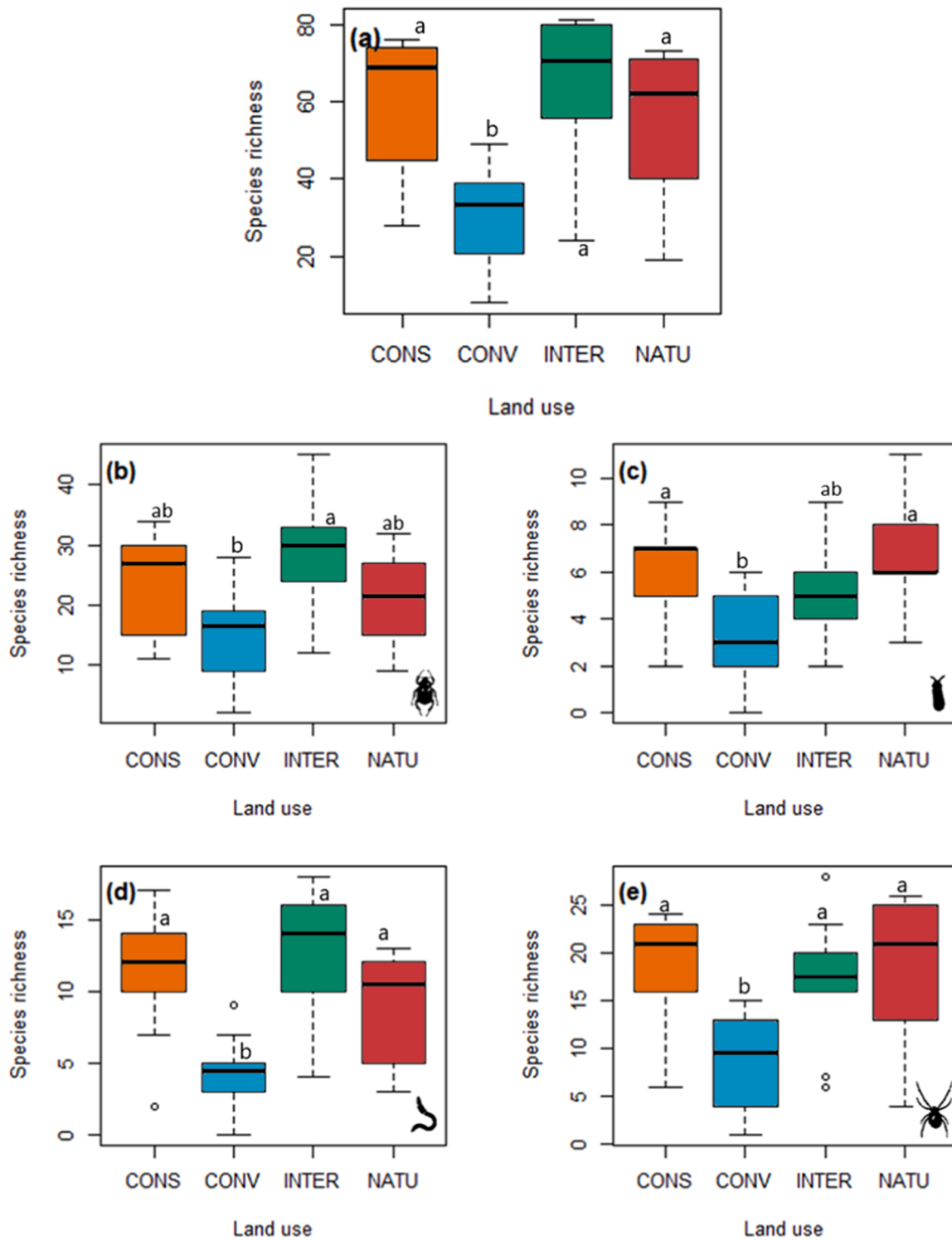


Fig. 2. Boxplots visualizing differences in soil fauna species richness between conservation (CONS) integrated (INTER), conventional (CONV) and natural systems (NATU). (a) Overall, (b) Beetle, (c) Collembola, (d) Earthworm, and (e) Spider. Means with letters in common are not significantly different (Tukey's post-hoc tests at $p < 0.05$).

variance (PERMANOVA) (Anderson, 2001), on the Bray-Curtis similarity matrix based on squared-root transformed abundance data with the “*adonis*” function in *vegan* (Oksanen et al., 2019). A pairwise test was also conducted at 999 random permutations to determine which management types differed significantly from each other (Legendre and Gallagher, 2001; Martinez Arbizu, 2020). To assess which variables best explained fauna assemblage composition a Bioenv analysis with a spearman correlation and Bray–Curtis similarity was conducted on the fauna presence-absence data using *vegan*. A Bioenv analysis identifies which particular variables within the different land uses best correlate with the observed assemblages. To visualize the relationship between the selected variables and assemblage composition sequential tests were conducted on the data and fitted with a distance-based redundancy analysis (dbRDA) (Anderson and Willis, 2003). All data analyses were performed with R statistical software version 3.6.3 (R Core Team, 2020).

3. Results

A total of 10 780 individuals representing 210 arthropod species or morphospecies were collected. These included 4098 beetles (91 species), 1614 collembolans (26 species), 2302 earthworms (44 species) and 2766 spiders (62 species). Species rarefaction curves displayed a near-asymptote for all land uses and arthropod groups (Appendix A), indicating that sampling effort was adequate.

3.1. Fauna species richness responses to land use

Overall species richness varied significantly across the different land uses ($\chi^2 = 19.82$; $p < 0.001$) (Fig. 2a). Pairwise test shows that the overall species richness did not differ between conservation, natural and integrated fields but it was significantly lower in conventional fields than in the other three land uses (Fig. 2a). The highest record of beetle

species was observed within the integrated land use ($\chi^2 = 15.81$; $p < 0.001$), which was significantly higher than the conventional land-use ($Z = 3.822$; $p < 0.001$), whereas conservation farming and natural grassland did not differ from integrated farming (Fig. 2b). Collembola species richness differed between land-uses ($\chi^2 = 15.71$; $p = 0.001$) (Fig. 2c), with conventional fields having significantly lower Collembola species richness than conservation fields and natural grassland, with no difference between conventional and integrated fields in species richness, nor between integrated fields, conservation fields or natural grassland. Earthworm species richness differed significantly between land uses ($\chi^2 = 30.60$; $p < 0.001$) (Fig. 2d) with no differences between conservation, natural and integrated land uses, and species richness was significantly lower in conventional fields than in the other land uses. Spiders from conventional land uses were significantly lower in species richness than those found in conservation, integrated and natural land uses ($\chi^2 = 19.49$; $p < 0.001$), with assemblages from the conservation and natural land uses displaying similar patterns (Fig. 2e).

3.2. Functional CWM responses to land use management

With regards to functional composition, different land uses affected fauna functional communities differently. Proportions of detritivore individuals significantly differed across the different land uses ($\chi^2 = 131.82$; $p < 0.001$) and the CWM for detritivores was significantly higher within the integrated land use than the other land-uses and was significantly higher within the conservation land use than the conventional and natural land-uses (Fig. 3a). Detritivores within the conventional land use did not differ from those found in natural system ($\chi^2 = 131.82$; $p = 0.954$). The CWM for the herbivore group was significantly higher within the conventional land use than the conservation and integrated land-uses ($\chi^2 = 13.79$; $p = 0.003$), although it did not differ from the natural land-use, and the other three land-uses were similar

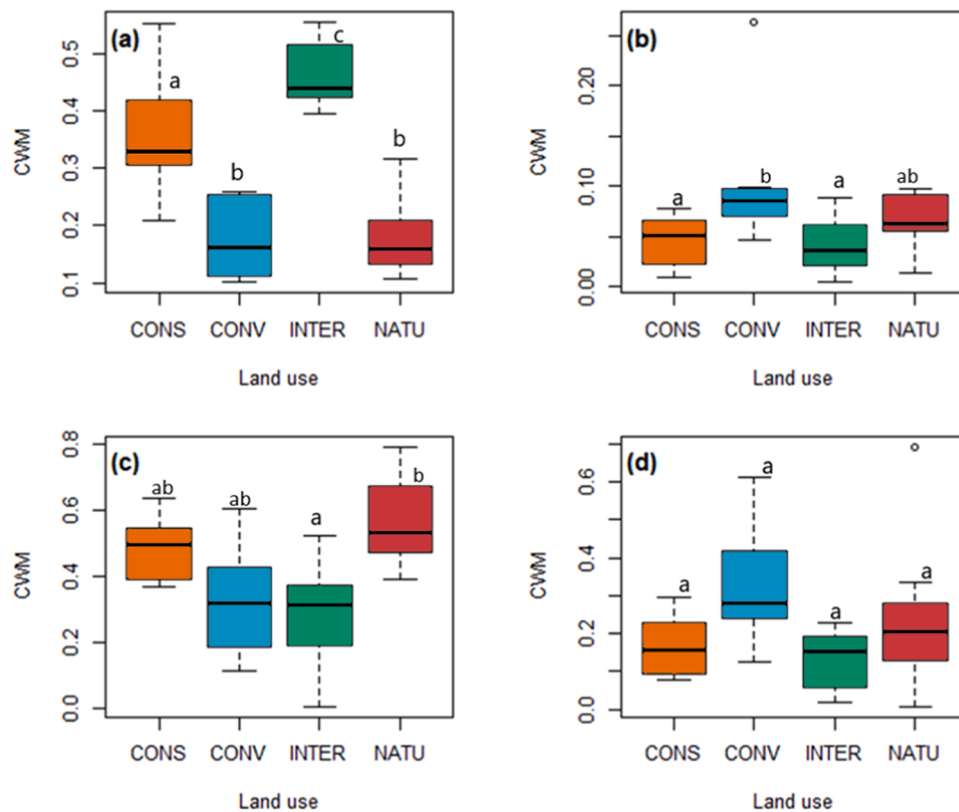


Fig. 3. Differences in proportions of the community-weighted mean (CWM) for (a) Detritivores, (b) Herbivores, (c) Predators, (d) and Omnivores across different land use types: CONS = Conservation, INTER = Integrated, CONV = Conventional and NATU = Natural. Means with letters in common are not significantly different (Tukey’s post-hoc tests at $p < 0.05$).

(Fig. 3b). The CWM for predators was significantly higher in natural compared to integrated fields, while neither natural grassland nor integrated fields differed from conservation and conventional fields (Fig. 3c). The main test revealed significant differences in omnivores groups across the different land uses ($\chi^2 = 8.73$; $p = 0.033$), but the pairwise test detected no differences between all the land uses (Fig. 3d).

3.3. Fauna community composition responses to land use

The PERMANOVA test results for soil fauna species composition are presented in Table 1. The overall species composition differed significantly across the different land uses ($F = 2.264$; $p < 0.05$), and significant differences were observed between conservation and integrated land uses ($F = 1.822$; $p < 0.01$) as well as between conventional and integrated land uses ($F = 1.809$; $p < 0.01$) as displayed by the pairwise test. Beetle species composition varied significantly across the different land use types ($F = 2.179$; $p < 0.01$) (Table 1). Pairwise test reveal that beetles from conventional, conservation and natural land uses are similar in species composition. Collembola main and pairwise tests reveal that, species composition is quite similar across the different land uses ($F = 2.230$; $p > 0.05$). Earthworm composition only differed between conventional and integrated land uses ($F = 1.725$; $p < 0.01$). Species composition of the spider group showed varying levels of differences between the land uses ($F = 2.199$; $p < 0.05$), with statistical differences observed between conservation versus integrated ($F = 1.738$; $p < 0.01$), conventional versus integrated ($F = 1.773$; $p < 0.01$) as well as between conventional versus natural ($F = 1.695$; $p < 0.01$). The overall results indicate that conventional and conservation land uses did not differ in assemblage composition for all the fauna groups ($p > 0.05$). The PERMANOVA results are supported by dbRDA results which showed clear separations between the different sites (Fig. 4).

3.4. Effects of soil management and vegetation complexity on soil fauna species richness, Functional CWM, and community composition

Model averaged estimates show that, overall species richness was positively and significantly influenced by percent leaf litter and vegetation cover (Table 2). Plant species richness is the only factor that significantly influenced beetle species richness with a positive relationship ($Z = 2.231$; $p = 0.026$). Collembolan species richness was influenced by percent bare ground ($Z = 2.943$; $p = 0.003$) with a significantly negative relationship. Percent leaf litter ($Z = 2.932$; $p = 0.003$) and vegetation cover ($Z = 3.081$; $p = 0.002$) were the main variables which positively influenced earthworm species richness, while deep tillage had a negative influence ($Z = 1.973$; $p = 0.049$) (Table 2). Spider species richness was positively influenced by plant species richness ($Z = 2.121$; $p = 0.034$), percent leaf litter ($Z = 2.065$; $p = 0.039$) and vegetation cover ($Z = 2.184$; $p = 0.029$). Zero tillage significantly exhibited a negative influence on spider richness ($Z = 0.485$; $p = 0.628$).

Table 1

PERMANOVA results for soil fauna community composition. Main (F-values) test statistics and pairwise (t-values) results between conservation (CONS) integrated (INTER), conventional (CONV) and natural systems (NATU) land uses. Significant p-values are indicated as: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

	Overall	Beetle	Collembola	Earthworm	Spider
Main (F)	2.264*	2.179**	2.230	2.093*	2.199*
df	3	3	3	3	3
Pairwise (t)					
CONS-INTER	1.822*	1.881	1.684	1.636	1.738*
CONS-CONV	1.738	1.686	1.757	1.739	1.829
CONS-NATU	1.718	1.908*	1.744	1.774	1.858
CONV-INTER	1.809*	1.714**	1.713	1.725**	1.773*
CONV-NATU	1.728	1.650	1.726	1.728	1.695*
INTER-NATU	1.667	1.791***	1.680	1.824	1.677

Effects of environmental variables on functional CWM composition, were not that distinct (Table 3). CWM for detritivores were significantly positively influenced by deep tillage ($Z = 3.384$; $p < 0.001$) and negatively influenced by percent leaf litter ($Z = 2.173$; $p = 0.030$). Deep tillage is the only factor which significantly and positively influenced the CWM of omnivores. Predator CWM was not significantly influenced by any of the variables ($p > 0.05$). Overall, tillage and leaf litter are the only two variables which significantly influenced the CWM of soil fauna functional groups (Table 3).

dbRDA results supported by distLM sequential tests show that soil fauna species composition responded differently to environmental variables. Overall species composition was influenced by percent vegetation cover and leaf litter (Fig. 4). Percent leaf litter is the only variable which influenced species composition of beetles (Fig. 4). Spider species composition was significantly influenced by percent leaf litter and vegetation cover (Fig. 4). Earthworm species composition was also significantly influenced by percent leaf litter and vegetation cover (Fig. 4). Collembola composition was influenced by plant species richness and percent vegetation cover (Fig. 4), while the effect of vegetation cover was however not significant ($p > 0.05$).

4. Discussion

4.1. Land use, soil management and vegetation complexity effects on soil fauna species richness and composition

The lowest diversity of taxa overall and within the different taxonomic groups was found in the conventionally managed crops compared to other land uses. Generally, conservation and livestock integrated land uses closely resembled natural grassland sites in soil faunal diversity, and this was consistent for most of the measured taxonomic groups and their responses to variables. This demonstrates that regenerative farming systems that use low-intensity practices and that increase structural and temporal complexity within crop fields through mixed cropping, crop rotation and increased soil cover greatly benefit soil biodiversity. This corresponds with trends from other regions on the benefits of diversified farming on soil biota (Bommarco et al., 2013; Tsiafouli et al., 2015). Our findings were supported by the fact that overall, there was a consistent positive influence of variables associated with increased plant litter and vegetation cover. Soil fauna species richness and composition patterns were affected differently by land use type, soil management and vegetation complexity. Earthworms were strongly linked to the integrated land use, which had more species compared to other land uses. Deep tillage resulted in significant decline of this group, whereas the presence of plant litter and vegetation cover as well as zero level of soil disturbance in the integrated management proved to be beneficial by providing suitable habitat conditions which supported this group. Most of the identified earthworm species in this study were predominantly characterised by deep burrowing and litter feeding species which are very sensitive to habitat destruction (Paoletti, 1999). Nuria et al. (2011) found higher numbers of earthworm species to be associated with undisturbed compared to intensively disturbed soils. Periodic soil disturbance via tillage and limited availability of food sources due to lack of litter cover or residues could possibly account for the low earthworm populations recorded in the conventional land use (Kladivko, 2001). Tillage significantly contributes to the reduction of earthworm's population by dislocating their biogenic structures and exposing them to adverse conditions which ultimately leads to injury or direct mortality (Briones, 2018; Chan, 2001). According to Coulibaly et al. (2022) less soil destruction diversifies micro-habitats with heterogeneous soil cover and structural complexity formed by the previous crop's remains. This promotes soil organic matter build-up, which subsequently promotes the accumulation and activities of earthworms (Stroud et al., 2016).

The natural, livestock integrated, and conservation land uses were rich in Collembola species, yet the results also revealed significant

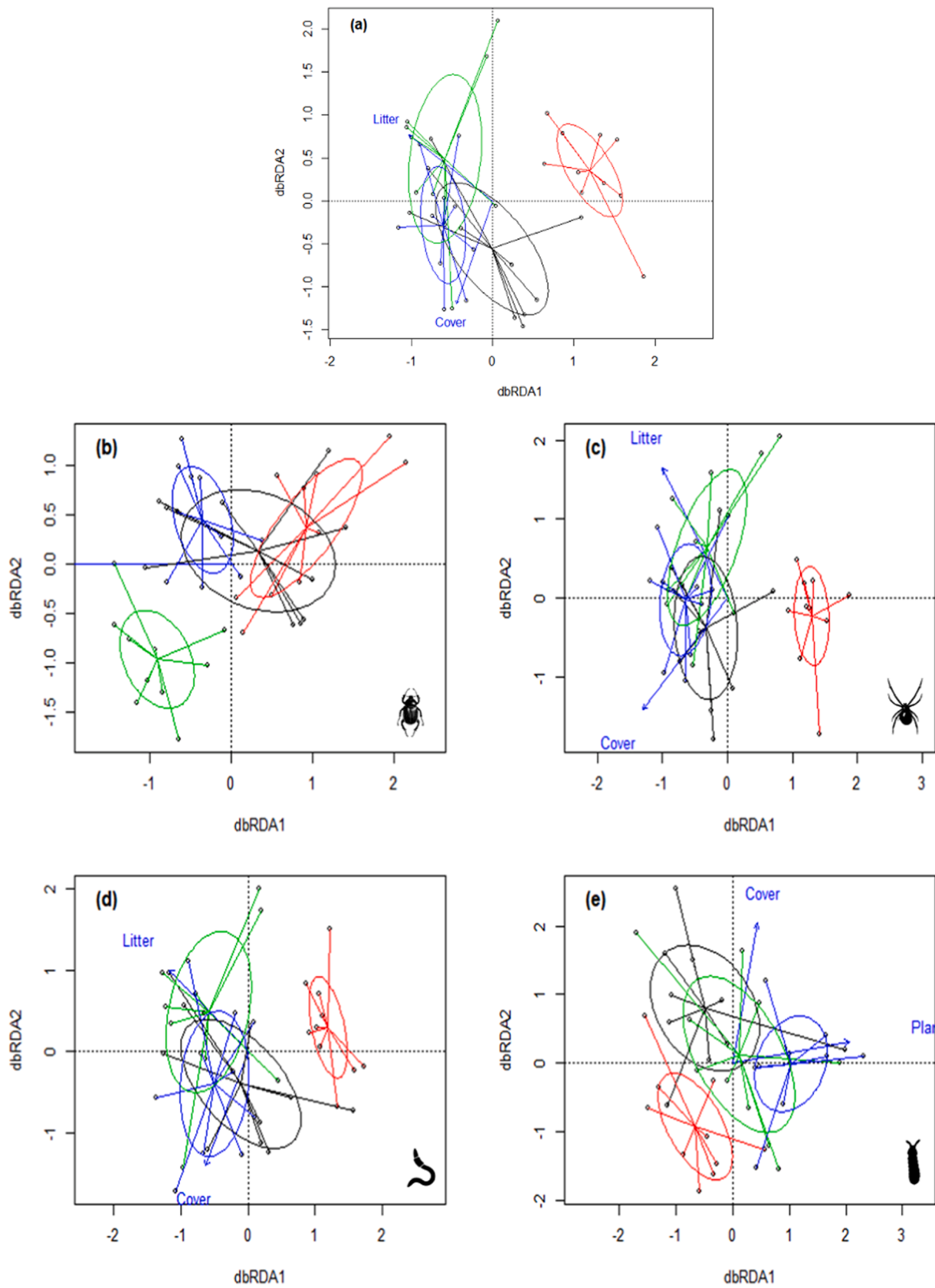


Fig. 4. Distance based redundancy analysis (dbRDA) visualizing differences in soil fauna community composition between conservation (grey) integrated (green), conventional (red) and natural systems (blue). (a) Overall, (b) Beetle, (c) Spider, (d) Earthworm and (e) Collembola.

Table 2

Summary of model averaging results for top model results for effects of tillage and habitat complexity on soil richness across all study sites based on model averaging estimated using Akaike's information criterion: AICc \geq 3. Significant bold p-values are indicated as: * $p < 0.05$, ** $p < 0.01$.

Responses	Predictors	Estimate	SE	Z	Pr(> z)
All	Deep tillage	-0.428	0.211	1.956	0.050
	Zero tillage	0.126	0.183	0.662	0.508
	Plant species richness	0.164	0.148	1.063	0.288
	Leaf litter (%)	0.385	0.142	2.623	0.009 **
	Vegetation cover (%)	0.450	0.152	2.856	0.004 **
Beetle	Plant species richness	0.320	0.139	2.231	0.026 *
	Leaf litter (%)	0.233	0.165	1.377	0.168
	Vegetation cover (%)	0.280	0.184	1.486	0.137
Collembola	Bare (%)	-0.475	0.156	2.943	0.003 **
	Plant species richness	-0.047	0.166	0.271	0.786
	Leaf litter (%)	0.197	0.272	0.715	0.475
	Vegetation cover (%)	0.189	0.236	0.788	0.431
Earthworm	Deep tillage	-0.437	0.214	1.973	0.049 *
	Zero tillage	0.161	0.193	0.804	0.421
	Plant species richness	0.051	0.160	0.307	0.759
	Leaf litter (%)	0.433	0.142	2.932	0.003 **
	Vegetation cover (%)	0.461	0.144	3.081	0.002 **
Spider	Deep tillage	-0.436	0.209	2.019	0.044
	Zero tillage	-0.097	0.192	0.485	0.628 *
	Plant species richness	0.360	0.165	2.121	0.034 *
	Leaf litter (%)	0.323	0.152	2.065	0.039 *
	Vegetation cover (%)	0.390	0.174	2.184	0.029 *

Table 3

Summary of model averaging results for top model results for effects of tillage and habitat complexity on soil fauna functional CWM across all study sites based on model averaging estimated using Akaike's information criterion: AICc \geq 3. Significant bold p-values are indicated as: * $p < 0.05$, *** $p < 0.001$.

Responses	Predictors	Estimate	SE	Z	Pr(> z)
Detritivores _{-CWM}	Deep tillage	3.09	0.883	3.384	<0.001 ***
	Zero tillage	0.607	0.605	0.971	0.332
	Plant species richness	1.893	1.057	1.775	0.076
	Leaf litter (%)	-3.807	1.742	2.173	0.030 *
	Vegetation cover (%)	-5.134	4.471	1.145	0.252
Herbivores _{-CWM}	Deep tillage	-10.09	5.642	1.731	0.083
	Zero tillage	1.117	5.753	0.188	0.851
	Plant species richness	-4.214	3.926	1.035	0.301
	Leaf litter (%)	7.315	4.060	1.750	0.080
Omnivores _{-CWM}	Vegetation cover (%)	-2.787	6.522	0.420	0.674
	Deep tillage	-6.086	2.468	2.388	0.017 *
	Zero tillage	-3.950	2.397	1.594	0.111
	Plant species richness	-1.462	1.139	1.240	0.215
Predators _{-CWM}	Leaf litter (%)	2.222	1.150	1.870	0.062
	Vegetation cover (%)	-2.366	1.391	1.647	0.100
	Plant species richness	-0.227	0.469	0.468	0.640
	Leaf litter (%)	-0.059	0.483	0.118	0.906
	Vegetation cover (%)	-0.745	0.437	1.649	0.099

degrees of similarities for Collembolan species composition across the different land uses. Moreover, the presence of bare ground was significantly negative to species richness, while plant species richness influenced assemblage composition. These observations may suggest that Collembola species are resilient to the conditions within the conventional land use. Alternatively, species assemblages may be homogenized across the different land use types as explained by the functional redundancy or homogenization hypothesis (Joimel et al., 2021; Piano et al., 2020), which implies that generalist species have greater

resistance to disturbance compared to specialist species, thereby resulting in homogenous species composition due to environmental filtering processes. Similar results were also reported in recent studies by Coulibaly et al. (2022), Fiera et al. (2020) and Sterzyńska et al. (2018) which showed that collembolans are not always affected by land use and thereby indicating better resistance of smaller fauna to land use effects. Wardle (1995) and Roger-Estrade et al. (2010) also found similar results and went on to suggest that larger fauna are more affected by management compared to smaller ones. Perhaps some underlying aspect which was not investigated in this study could explain the observed results, for example, epedaphic (living on the soil surface) and hemiedaphic (living partly on the litter layer and partly within the soil) collembolan species are reported to be more affected by intensive land use compared to other lifeforms (habitat position), e.g. euedaphic (living in the upper mineral layers of the soil) (Fiera et al., 2020).

The accessibility of adequate food sources and favourable habitat conditions (Fiera et al., 2020) are the most significant factors shaping agroecosystem biodiversity, and these factors are directly linked to different aspects of vegetation complexity (House and Brust, 1989). Unlike other taxonomic groups, the recorded beetle species in this study did not differ to a large extent across the measured land uses. Within this finding, plant species richness was the most influential factor affecting beetle species richness while leaf litter influenced composition. Most of the sampled beetle species were principally represented by carabid ground beetles. This observation may possibly be justified by Kromp (1999) who reported a limited number of ground beetle species to be associated with the vegetation layer while the majority is associated with the soil surface. Another possible explanation to this finding might be the sampling effects associated with pitfall trapping (Greenslade, 1964), which are reported to result in low catches of ground dwelling fauna in landscapes which are more complex in terms of vegetation structure compared to vegetation clear landscapes (Eckert et al., 2020). Vegetation complexity had a greater influence on spiders than on beetles and this may be attributed to the spider's ballooning and moving (cursorial) behaviours which enhance their dispersion (Wang et al., 2022) or the reliance of web-building spiders on structures for web construction. Several aspects of vegetation complexity, especially species richness of plants, leaf litter and vegetation cover, influenced spider communities in both species richness and composition. Unexpectedly, zero soil disturbance influenced spiders negatively, this may be explained by seasonal variations causing some species to show a delayed response to management effects. This result is contrary to other studies such as Domínguez and Bedano (2016) and Perner and Malt (2003), which reported spider community structure to be favoured by zero tillage cultivations than deep or conventional tillage. Overall, spider assemblages seem to be driven by features related to vegetation characteristics which not only differ with vegetation characteristics but also with management (Joseph et al., 2018; Lafage et al., 2019).

4.2. Land use, soil management and vegetation complexity effects on soil fauna Functional CWM

The functional guilds showed less consistent responses to the land uses than the taxonomic groups, and different functional groups were favoured by different land uses. High proportions of detritivores were associated with the integrated land use. This may be attributed to reduced chemical intensity and high organic modifications in this land use which is integrated with livestock (enriches organic matter), thereby providing suitable habitat conditions (Mata-Alvarez et al., 2000) and improving the detritus-based food web, which in turn stimulates the activities and population of detritivores (Scow et al., 1994).

Increased soil cover benefitted soil fauna functional groups, especially the detritivores and omnivores. Deep tillage positively influenced detritivores, while leaf litter exerted a negative influence. It is well established that deep tillage creates unstable environments for this functional group which ultimately discourages their establishment

(Nuria et al., 2011), therefore, the positive effect of deep cultivation on detritivores was not anticipated. Similar observations were also reported in a local study by Geldenhuys et al. (2021) who found that detritivores respond positively to tillage in vineyards. Other authors have argued that deep tillage is not systematically detrimental to all species, for example, Pelosi et al. (2009) found that soil fauna species are favoured by soil tillage. Nuutinen (1992) also observed that some species do not respond well to crop residues.

Omnivores were not significantly different amongst the land uses. Of all the measured variables, omnivores were negatively influenced only by deep tillage, which did not come as a surprise because intensive soil cultivation has previously been reported to prevent the proper establishment of omnivores (Aldebron et al., 2020).

Predators and herbivores are well known to influence each other through top-down and bottom-up forces (Crowl et al., 1997). For example, Forkner and Hunter (2000), showed that an increase in herbivore population density stimulates the density and prevalence of predators. In this study, predators were characterised by ground beetles and spiders which occurred in relatively large numbers within the natural land use and equally distributed between the conservation and integrated land use. Carabids and spiders are broadly accepted as predators of numerous insect pests, but various species are “generalists” and will feed on other insects, vegetation, and fungi (Birkhofer et al., 2008), which could possibly explain higher proportions in more structurally diverse land use types.

Herbivores also did not differ between land uses. Otieno et al. (2019) and Chaplin-Kramer et al. (2011) found that herbivores thrive well under conventionally managed landscapes which are less heterogeneous or more simplified in terms of vegetation complexity, which may explain why they were ubiquitous in all land uses in our study system. Although different functional groups responded differently to the different farming systems, habitat conditions within the conservation and integrated land uses proved to be beneficial to detritivore and predatory functional groups which are important for nutrient cycling and pest regulation.

5. Conclusion

The results here show that land use, soil management and vegetation complexity exert a significant influence on soil fauna species richness, taxonomic and functional composition. While some studies in grain agroecosystems focused on a single taxon to assess management effects, this study adapted a multitaxon approach. Through this approach, it was established that arthropod response is complex, depending on species, functional traits, micro-features of the landscape, soil management level as well as vegetation type and structure. The fact that the conservation agriculture and livestock-integrated farming resembled natural grasslands in species richness, composition and functional structure demonstrates the potential of these systems to safeguard ecosystem functions in staple crops in this understudied region. Here we show that sensitive soil management and crop diversification and crop habitat complexity preserves soil fauna within these agroecosystems. Overall, the findings support the idea that good soil management through e.g. reduced agrochemicals, minimal tillage and mimicking natural landscapes through habitat complexity or crop diversification goes a long way in preserving important soil fauna functional groups responsible for multi ecosystem functions.

CRedit authorship contribution statement

Emogine Mamabolo: Writing – original draft, Visualization, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **James Stephen Pryke:** Writing – review & editing, Validation, Supervision, Software, Methodology, Conceptualization. **René Gaigher:** Writing – review & editing, Validation, Supervision, Software, Methodology, Conceptualization.

Declaration of Competing Interest

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

Data availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2024.108973.

References

- Adenle, A.A., Wedig, K., Azadi, H., 2019. Sustainable agriculture and food security in Africa: The role of innovative technologies and international organizations. *Tech. Soc.* 58, 1–17. <https://doi.org/10.1016/j.techsoc.2019.05.007>.
- Aldebron, C., Jones, M.S., Snyder, W.E., Blubaugh, C.K., 2020. Soil organic matter links organic farming to enhanced predator evenness. *Biol. Control.* 146, 104278.
- Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. *Austr. Ecol.* 26, 32–46.
- Anderson, M.J., Willis, T.J., 2003. Canonical analysis of principal coordinates: A useful method of constrained ordination for ecology. *Ecology* 84 (2), 511–525.
- Armstrong, A.J., Nxele, T.C., 2017. English names of the megadrile earthworms (Oligochaeta) of KwaZulu-Natal. *Afr. Invertebr.* 58 (2), 11–20.
- Barton, K., 2022. *Multi-Model Inference* (R package, version 1.46.0). CRAN.
- Bates, D., Mächler, M., Bolker, B.M., Walker, S.C., 2015. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* 67 (1), 1–48. <https://doi.org/10.18637/jss.v067>.
- de Bello, F., Carmona, C.P., Diase, A.T.C., Götzenberger, L., Moretti, M., Berg, M.P., 2020. *Hand book of Trait-based ecology: from theory to R tools*. Cambridge University Press.
- Birkhofer, K., Fließbach, A., Wise, D.H., Scheu, S., 2008. Generalist predators in organically and conventionally managed grass-clover fields: Implications for conservation biological control. *Ann. Appl. Biol.* 153 (2), 271–280.
- Birkhofer, K., Addison, M., Arvidsson, F., Bazelet, C., Bengtsson, J., Booyse, R., Conlong, D., Haddad, C., Janion-Scheepers, C., Kapp, C., Lindborg, R., Louw, S., Malan, A.P., Storey, S., Swart, W.J., Addison, P., 2019. Effects of ground cover management on biotic communities, ecosystem services and disservices in organic deciduous fruit orchards in South Africa. *Front. Sustain. Food Syst.* 3 (107), 1–13.
- Bommarco, R., Kleijn, D., Potts, S.G., 2013. Ecological intensification: Harnessing ecosystem services for food security. *Trends Ecol. Evol.* 28, 230–238.
- Briones, M.J.I., 2018. The serendipitous value of soil fauna in ecosystem functioning: the unexplained explained. *Front. Environ. Sci.* 6, 1–11.
- Cardoso, P., Barton, P.S., Birkhofer, K., Chichorro, F., Deacon, C., Fartmann, T., Fukushima, C.S., Gaigher, R., Habel, J.C., Hallmann, C.A., Hill, M.J., Hochkirch, A., Kwak, M.L., Mammola, S., Ari, J., Or, A.B., Pedraza, F., Pryke, J.S., Roque, F.O., Samways, M.J., 2020. Scientists' warning to humanity on insect extinctions. *Biol. Conserv.* 242, 1–12. <https://doi.org/10.1016/j.biocon.2020.108426>.
- Chan, K.Y., 2001. An overview of some tillage impacts on earthworm population abundance and diversity - implications for functioning in soils. *Soil Res* 57, 179–191.
- Chaplin-Kramer, R., ÓRourke, M.E., Blitzer, E.J., Kremen, C., 2011. A meta-analysis of crop pest and natural enemy response to landscape complexity. *Ecol. Lett.* 14, 922–932.
- Coulibaly, F.M., Brunet, N., Bureau, F., Legras, M., Chauvat, M., 2022. Short-term dynamic responses of soil properties and soil fauna under contrasting tillage systems. *Soil Res* 215, 1–15. <https://doi.org/10.1016/j.still.2021.105191>.
- Crowl, T.A., Townsend, C.R., Bouwes, N., Thomas, H., 1997. Scales and Causes of Patchiness in Stream Invertebrate Assemblages: Top-down Predator Effects? *J. North Am. Benthol. Soc.* 16 (1), 277–285.
- Didham, R., Basset, Y., Collins, C.M., Leather, S.R., 2020. Interpreting insect declines: seven challenges and a way forward. *Insect Conserv. Divers.* 103–114.
- Diehl, E., Mader, V.L., Wolters, V., Birkhofer, K., 2013. Management intensity and vegetation complexity affect web-building spiders and their prey. *Oecologia* 173, 579–589. <https://doi.org/10.1007/s00442-013-2634-7>.

- Dippenaar-Schoeman, A.S., Haddad, C.R., Foord, S., Lyle, R., Lotz, L., Helberg, L., Mathebula, S., van den Berg, A., Marais, P., van den Berg, A.M., Van Niekerk, E., Jocke, R., 2010. First atlas of the spiders of South Africa (Arachnida: Araneae). Technical Report 2010 version 1.
- Domínguez, A., Bedano, J.C., 2016. The adoption of no-till instead of reduced tillage does not improve some soil quality parameters in Argentinean Pampas. *J. Appl. Ecol.* 98, 166–176. <https://doi.org/10.1016/j.apsoil.2015.10.014>.
- Eckert, M., Mathulwe, L.L., Gaigher, R., Joubert, L., James, V.D.M., 2020. Native cover crops enhance arthropod diversity in vineyards of the Cape Floristic Region. *J. Insect Conserv.* 24 (1), 133–149. <https://doi.org/10.1007/s10841-019-00196-0>.
- Espinaze, M.P., Hui, C., Waller, L., Matthee, S., 2019. The efficacy of a modified Berlese funnel method for the extraction of ectoparasites and their life stages from the nests of the African Penguin *Spheniscus demersus*. *Ostrich* 90 (3), 271–277.
- FAO, IFAD, UNICEF, WFP, WHO, 2018. The State of Food Security and Nutrition in the World 2018. Building climate resilience for food security and nutrition.
- Fiera, C., Ulrich, W., Popescu, D., Buchholz, J., Querner, P., Bunea, C., Strauss, P., Bauer, T., Kratschmer, S., Winter, S., Zaller, J.G., 2020. Tillage intensity and herbicide application influence surface-active springtail (Collembola) communities in Romanian vineyards. *Agric. Ecosyst. Environ.* 300, 1–8.
- Forkner, R.E., Hunter, M.D., 2000. What goes up must come down? Nutrient addition and predation pressure on oak herbivores. *Ecology* 81 (6), 1588–1600.
- FAO and ITPS, 2015. *Status of the World's Soil Resources (SWSR) – Main Report*.
- Fox, J., Weisberg, S., Price, B., Adler, D., Bates, D., Baud-ovy, G., Bolker, B., Ellison, S., Firth, D., Friendly, M., Graves, S., Heiberger, R., Laboissiere, R., Maechler, M., Monette, G., Murdoch, D., Ogle, D., Ripley, B., Venables, W., Walker, S., Winsemius, D., Zeile, A., 2019. Companion to Applied Regression (R package version 3.0-3). CRAN. (<https://cran.r-project.org/package=car>).
- Gaigher, R., Pryke, J.S., Samways, M.J., 2016. Old fields increase habitat heterogeneity for arthropod natural enemies in an agricultural mosaic. *Agric. Ecosyst. Environ.* 230, 242–250. <https://doi.org/10.1016/j.agee.2016.06.014>.
- Galloway, A.D., Seymour, C.L., Gaigher, R., Pryke, J.S., 2021. Organic farming promotes arthropod predators, but this depends on neighbouring patches of natural vegetation. *Agric. Ecosyst. Environ.* 310, 1–9.
- García, L.F., Núñez, E., Lacava, M., Silva, H., Martínez, S., Pétilion, J., 2021. Experimental assessment of trophic ecology in a generalist spider predator: Implications for biocontrol in Uruguayan crops. *J. Appl. Entomol.* 145, 82–91.
- Geldenhuys, M., Gaigher, R., Pryke, J.S., Samways, M.J., 2021. Diverse herbaceous cover crops promote vineyard arthropod diversity across different management regimes. *Agric. Ecosyst. Environ.* 307, 1–10.
- Gerlach, J., Samways, M.J., Pryke, J.S., 2013. Terrestrial invertebrates as bioindicators: an overview of available taxonomic groups. *J. Insect Conserv.* 17, 831–850.
- Greenslade, P.J.M., 1964. Pitfall trapping as a method for studying populations of Carabidae (Coleoptera). *J. Anim. Ecol.* 33 (2), 301–310.
- Hassan, W., Saba, T., Jabbi, F., Wang, B., Cai, A., Wu, J., 2022. Improved and sustainable agroecosystem, food security and environmental resilience through zero tillage with emphasis on soils of temperate and subtropical climate regions: A review. *Int. Soil. Water Conserv. Res.* 10, 530–545.
- Hothorn, T., Bretz, F., Westfall, P., 2008. Simultaneous inference in general parametric models. *Biom. J.* 50 (3), 346–363.
- House, G.J., Brust, G.E., 1989. Ecology of low-input, no-tillage agroecosystems. *Agric. Ecosyst. Environ.* 27, 331–345.
- Hsieh, T.C., Ma, K.H., Chao, A., 2020. iNEXT: Interpolation and extrapolation for species diversity (R package version 2.0.20). (http://chao.stat.nthu.edu.tw/wordpress/software_download/).
- Janion-Scheepers, C., Deharveng, L., Bedos, A., Chown, S.L., 2015. Updated list of Collembola species currently recorded from South Africa. *ZooKeys* 503, 55–88.
- Joimel, S., Schwartz, C., Bonfanti, J., Hedde, M., Krogh, P.H., Pérès, G., Permin, 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, 1–9. <https://doi.org/10.3389/fevo.2021.630919>.
- Joseph, G.S., Mauda, E.V., Seymour, C.L., Munyai, C., Dippenaar-schoeman, A., Foord, S. H., 2018. Land use change in savannas disproportionately reduces functional diversity of invertebrate predators at the highest trophic levels: spiders as an example. *Ecosystems* 21, 930–942. <https://doi.org/10.1007/s10021-017-0194-0>.
- Kladivko, E.J., 2001. Tillage systems and soil ecology. *Soil Res* 61, 61–76.
- Kromp, B., 1999. Carabid beetles in sustainable agriculture: a review on pest control efficacy, cultivation impacts and enhancement. *Agric. Ecosyst. Environ.* 74, 187–228.
- Lafage, D., Djoudi, E.A., Perrin, G., Gallet, S., Pétilion, J., 2019. Responses of ground-dwelling spider assemblages to changes in vegetation from wet oligotrophic habitats of Western France. *Arthro. Plant Inter.* 1–11.
- Laliberté, E., Legendre, P., 2010. A distance-based framework for measuring functional diversity from multiple traits. *Ecology* 91 (1), 299–305.
- Laliberté, E., Legendre, P., Shipley, B., 2015. Measuring functional diversity (FD) from multiple traits, and other tools for functional ecology (R package version 1.0-12). CRAN.
- Lavelle, P., Mathieu, J., Spain, A., Brown, G., Fragoso, C., Laped, E., De Aquino, A., Barois, I., Barrios, E., Barros, M.E., Bedano, J.C., Blanchart, E., Caulfield, M., Chagueza, Y., Dai, J., Decaëns, T., Dominguez, A., Dominguez, Y., Feijoo, A., Folgarait, P., Fonte, S.J., Gorosito, N., Huerta, E., Jimenez, J.J., Kelly, C., Loranger, G., Marchão, G., Marichal, R., Praxedes, C., Rodriguez, L., Rousseau, G., Rousseau, L., Ruiz, N., Sanabria, C., Suarez, J.C., Tondoh, J.E., De Valença, A., Vanek, S.J., Vasquez, J., Velasquez, E., Webster, E., Zhang, C., 2022. Soil macroinvertebrate communities: A world-wide assessment. *Glob. Change Biol.* 31, 1261–1276.
- Lavorel, S., Grigulis, K., McIntyre, S., Williams, N.S.G., Garden, D., Berman, S., Quéfier, F., Thébault, A., Bonis, A., 2008. Assessing functional diversity in the field – methodology matters! *Funct. Ecol.* 22, 134–147.
- Legendre, P., Gallagher, E.D., 2001. Ecologically meaningful transformations for ordination of species data. *Oecologia* 129, 271–280.
- Malcicka, M., Berg, M.P., Ellers, J., 2017. Ecomorphological adaptations in Collembola in relation to feeding strategies and microhabitat. *Eur. J. Soil Biol.* 78, 82–91. <https://doi.org/10.1016/j.ejsobi.2016.12.004>.
- Martinez Arbizu, P., 2020. Pairwise Adonis: Pairwise multilevel comparison using Adonis. R package version 0.4. (<https://github.com/pmartinezarbizu/pairwisAdonis>).
- Mata-Alvarez, J., Mace, S., Llabres, P., 2000. Anaerobic digestion of organic solid wastes. An overview of research achievements and perspectives. *Biores. Tech.* 74, 3–16.
- Nascimbene, J., Fontana, V., Spitale, D., 2014. A multi-taxon approach reveals the effect of management intensity on biodiversity in Alpine larch grasslands. *Sci. Total Environ.* 487 (626), 110–116.
- Nuria, R., Jérôme, M., Léonide, C., Christine, R., Gérard, H., Etienne, I., Patrick, L., 2011. IBQS: A synthetic index of soil quality based on soil macro-invertebrate communities. *Soil Biol. Biochem.* 43 (10), 2032–2045.
- Nuutinen, V., 1992. Earthworm community response to tillage and residue management on different soil types in southern Finland. *Soil Res* 23, 221–239.
- Nxele, T.C., Lamani, S., Measey, G.J., Armstrong, A.J., Plisko, J.D., Willows-Munro, S., Janion-Scheepers, C., Wilson, J.R.U., 2015. Studying Earthworms (Annelida: Oligochaeta) in South Africa. *Afr. Invertebr.* 56, 779–806.
- Okolo, C.C., Dippold, M.A., Gebresamuel, G., Zenebe, A., Haile, M., Bore, E., 2020. Assessing the sustainability of land use management of northern Ethiopian drylands by various indicators for soil health. *Ecol. Indic.* 112, 1–20.
- Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, H.H., Szoecs, E., Wagner, H., 2019. *Vegan: Community Ecology Package* (R package version:2.5-6). (<https://cran.r-project.org/package=vegan>).
- Oliver, I., Beattie, A.J., 1996. Invertebrate morphospecies as surrogates for species: a case study invertebrate morphospecies as surrogates for species: a case study. *Conserv. Biol.* 10 (1), 99–109.
- Otieno, N.E., Jacobs, S.M., Pryke, J.S., 2019. Maize-field complexity and farming system influence insectivorous birds' contribution to arthropod herbivore regulation. *Biotropica*.
- Palm, C., Blanco-canqui, H., Declerck, F., Gater, L., Grace, P., 2014. Conservation agriculture and ecosystem services: An overview. *Agric. Ecosyst. Environ.* 187, 87–105.
- Paoletti, M.G., 1999. Using bioindicators based on biodiversity to assess landscape sustainability. *Agric. Ecosyst. Environ.* 74, 1–18.
- Paradis, E., Blomberg, S., Bolker, B.M., Brown, J., Claramunt, S., Claude, J., 2022. *Analyses of Phylogenetics and Evolution (5.6-2)*. CRAN. (<http://ape-package.ird.fr/>).
- Pelosi, C., Bertrand, M., Roger-Estrade, J., 2009. Earthworm community in conventional, organic and direct seeding with living mulch cropping systems. *Agron. Sustain. Dev.* 29, 287–295.
- Perner, J., Malt, S., 2003. Assessment of changing agricultural land use: response of vegetation, ground-dwelling spiders and beetles to the conversion of arable land into grassland. *Agric. Ecosyst. Environ.* 98, 169–181.
- Piano, E., Giuliano, D., Isaia, M., 2020. Islands in cities: urbanization and fragmentation drive taxonomic and functional variation in ground arthropods. *Basic. Appl. Ecol.* 43, 86–98.
- Plath, E., Rischen, T., Mohr, T., Fischer, K., 2021. Biodiversity in agricultural landscapes: Grassy field margins and semi-natural fragments both foster spider diversity and body size. *Agric. Ecosyst. Environ.* 316, 1–8.
- Plisko, J.D., 2010. Megadrile earthworm taxa introduced to South African soils (Oligochaeta: Megadrile) earthworm taxa introduced to South African soils. *Afr. Invertebr.* 51 (2), 289–312. <https://doi.org/10.5733/afin.051.0204>.
- Plisko, J.D., 2014. New south african acanthodrilinae earthworm species, with new data for some earlier known members of the genus *Parachilota* (Oligochaeta: Acanthodrilidae). *Afr. Invertebr.* 49 (2), 21–36.
- Plisko, J.D., Nxele, T.C., 2015. An annotated key separating foreign earthworm species from the indigenous South African taxa (Oligochaeta: Acanthodrilidae, Eudrilidae, Glossoscolecidae, Lumbricidae, Megascolecidae, Microchaetidae, Ocnerothrididae and Tritogeniidae). *Afr. Invertebr.* 56 (3), 663–708.
- R Core Team, 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing. Version 3.6.3. (<https://www.R-project.org/>).
- Roger-Estrade, J., Anger, C., Bertrand, M., Richard, G., 2010. Tillage and soil ecology: Partners for sustainable agriculture. *Soil Res* 111 (1), 33–40.
- Schoeman, C.S., Toussaint, D.C., Tshililo, P., Foord, S.H., Hamer, M., 2020. Checklist of the pimeliine darkling beetles of the Vhembe Biosphere Reserve, South Africa (Coleoptera: Tenebrionidae: Pimeliinae). *Afr. Biodiv. Conserv.* 50 (1), 1–9.
- Scholtz, C.H., Holm, E., 1985. *Insects of Southern Africa*. Protea Book House, Pretoria, South Africa.
- Scow, K.M., Somasco, O., Ferris, H., Gunapala, N., Miller, R., Lau, S., Shennan, C., Venette, R., 1994. Agriculture changes soil fertility and biology. *Calif. Agric.* 48 (5), 20–26.
- Sithole, N.J., Magwaza, L.S., 2019. Long-term changes of soil chemical characteristics and maize yield in no-till conservation agriculture in a semi-arid environment of South Africa. *Soil Res* 194, 1–9. <https://doi.org/10.1016/j.still.2019.104317>.
- Souza, J.L.P., Baccaro, F.B., Landeirob, V.L., Franklin, E., Magnusson, E.W., 2012. Trade-offs between complementarity and redundancy in the use of different sampling techniques for ground-dwelling ant assemblages. *Appl. Soil Ecol.* 56, 63–73.

- Steffan-Dewenter, I., 2003. Importance of habitat area and landscape context fragmented orchard meadows. *Conserv. Biol.* 17 (4), 1036–1044.
- Sterzyńska, M., Nícia, P., Fiera, C., Shrubovych, J., Ulrich, W., 2018. Urban springtail species richness decreases with increasing air pollution. *Ecol. Indic.* 94, 328–335.
- Stroud, J.L., Irons, D.E., Watts, C.W., White, R.P., Mcgrath, S.P., Whitmore, A.P., 2016. Population collapse of *Lumbricus terrestris* in conventional arable cultivations and response to straw applications. *Appl. Soil Ecol.* 108, 72–75.
- Swanepoel, C.M., Swanepoel, L.H., Smith, H.J., 2018. A review of conservation agriculture research in South Africa. *S. Afr. J. Plant Soil.* 36 (4), 297–306. <https://doi.org/10.1080/02571862.2017.1390615>.
- Swift, M., Bignell, D., 2001. Standard methods for assessment of soil biodiversity and land use practice. International Centre for Research in Agroforestry. (<http://www.icraf.cgiar.org/sea>).
- Tscharntke, T., Clough, Y., Wanger, T.C., Jackson, L., Motzke, I., Perfecto, I., Vandermeer, J., Whitbread, A., 2012. Global food security, biodiversity conservation and the future of agricultural intensification. *Biol. Conserv.* 151, 53–59.
- Tsiafouli, M.A., Thébault, E., Sgardelis, S.P., de Ruiter, P.C., van der Putten, W.H., Birkhofer, K., Hemerik, L., de Vries, F.T., Bardgett, R.D., Brady, M.V., Bjornlund, L., Jørgensen, H.B., Christensen, S., Hertefeldt, T.D., Hotes, S., Gera Hol, W.H., Frouz, J., Liiri, M., Mortimer, S.R., Setälä, H., Tzanopoulos, J., Uteseny, K., Pižl, V., Stary, J., Wolters, V., Hedlund, K., 2015. Intensive agriculture reduces soil biodiversity across Europe. *Glob. Chang. Biol.* 21, 973–985. <https://doi.org/10.1111/gcb.12752>.
- Wang, M., Yu, Z., Liu, Y., Wu, P., Christoph, J., 2022. Taxon and functional group-specific responses of ground beetles and spiders to landscape complexity and management intensity in apple orchards of the North China Plain. *Agric. Ecosyst. Environ.* 323, 1–9.
- Wardle, D.A., 1995. Impacts of disturbance on detritus food webs in agro-ecosystems of contrasting tillage and weed management practices. In: Begon, M., Fitter, A.H. (Eds.), *Advances in Ecological Research*. Academic Press., New York, pp. 105–185.
- Yekwayo, I., Pryke, J.S., Gaigher, R., Samways, M.J., 2018. Only multi-taxon studies show the full range of arthropod responses to fire. *PLoS ONaE* 13 (4), e0195414.