Characterisation of soil macro- and mesofauna diversity and their contribution to soil health in grain agroecosystems

by

Emogine Mamabolo

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Department of Conservation Ecology and Entomology, Faculty of AgriSciences

Supervisor: Prof. James S. Pryke
Co-supervisor: Dr. René Gaigher

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DECLARATION

By submitting this thesis electronically, I declare that the entirety of the work contained therein is my own, original work, that I am the sole author thereof (save to the extent explicitly otherwise stated), that reproduction and publication thereof by Stellenbosch University will not infringe any third party rights and that I have not previously in its entirety or in part submitted it for obtaining any qualification.

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GENERAL SUMMARY

Agriculture is the most important source of food and critical to the South African economy, yet it is detrimental to the environment, including the soil. We need to find innovative ways to achieve agricultural sustainability. Sustainable models are increasingly being adopted, but the major challenge remains measuring their effectiveness. Soils are inextricably linked to sustainable agriculture, as good soils promote crop growth and yields, while sensitive to chemical inputs that farmers place on the croplands. Due to the importance and sensitivity of soil, the assessment of soil health and soil fauna biodiversity has been proposed as an indicator of sustainability yet rarely considered when making recommendation for sustainable agricultural intensification.

This dissertation explores the differences in diversity of soil macro-and mesofauna (from here on called soil fauna) under different agricultural land uses, namely conventional, conservation, integrated and natural grasslands, and how this affects the soil physicochemical environment and decomposition processes. The status of macrofauna as bioindicators of soil health was explored to provide a more direct tool in measuring soil function and sustainability. Biodiversity metrics revealed that cultivation under minimum soil disturbance coupled with complex vegetation and soil cover benefited soil fauna and allowed the establishment of most functional groups, which are crucial for pest control, nutrient cycling, and decomposition. Therefore, reduced tillage and increased structural complexity are recommended for preserving soil arthropod diversity and associated ecosystem services.

Litter decomposition was positively linked to soil fauna species richness and not abundance or diversity. Results also showed that, soil fauna significantly contributed to decomposition, but contributions are highly depended on temperature, soil moisture and land use intensity. These findings highlight the importance in understanding management effects on soil fauna functional roles in maintaining nutrient cycling and soil health. Soil characterisation showed that conventional land uses favoured some important soil properties, however the overall effects of the soil physicochemical environment on fauna were complex, implying that sustainable intensification will not only be beneficial for productivity but also for the promotion of soil fauna and ecosystem services. Multivariate analyses of soil health characterisation allowed for the development of a simple but robust soil health assessment tool using soil macrofauna as

indicators. The tool is important for assessing land use management and associated effects on soil health and ecosystem function. Overall, this dissertation shows that sustainable management, increased biodiversity, and increased soil health complement each other.

Compared to their conventional counterparts, the conservation and livestock integrated land uses optimised favourable and stable conditions for various soil fauna groups and were more like that of the natural grasslands. As some of the important soil variables are favoured by more intensive land uses, designing sustainable and functional schemes is a lengthy process which requires patience, as soil itself is an ever-evolving entity which needs time to generate and/or restore. Here it is shown that low intensity agriculture promotes health soil fauna, thus sustainable management of soils in agriculture has the potential to increase the overall soil health, biodiversity, and function, meaning they (ecosystem engineers) can restore degraded soils and ecosystem services.

ALGEMENE OPSOMMING

Landbou is die belangrikste bron van voedsel en krities vir die Suid-Afrikaanse ekonomie, tog is dit nadelig vir die omgewing, insluitend die grond. Ons moet innoverende maniere vind om landbouvolhoubaarheid te bereik. Volhoubare modelle word toenemend aangeneem, maar die groot uitdaging bly om hul doeltreffendheid te meet. Gronde is onlosmaaklik gekoppel aan volhoubare landbou, aangesien goeie gronde gewasgroei en opbrengste bevorder, terwyl dit sensitief is vir chemiese insette wat boere op die saailande plaas. As gevolg van die belangrikheid en sensitiwiteit van grond, is die assessering van grondgesondheid en grondfauna-biodiversiteit voorgestel as 'n aanduiding van volhoubaarheid, maar word selde oorweeg wanneer aanbevelings vir volhoubare intensivering gemaak word.

Hierdie proefskrif ondersoek die verskille in diversiteit van grondmakro- en mesofauna (van hier af, op grondfauna) onder verskillende landbougrondgebruike, naamlik konvensionele, bewaringsgeïntegreerde en natuurlike grasvelde, en hoe dit grondfisieschemiese omgewing en ontbindingsprosesse beïnvloed. Die status van makrofauna as bio-aanwysers van grondgesondheid is ondersoek om 'n meer direkte instrument te verskaf om grondfunksie en volhoubaarheid te meet. Biodiversiteitsmetrieke het aan die lig gebring dat bewerking onder minimum grondversteuring tesame met komplekse plantegroei en grondbedekking grondfauna bevoordeel het en die vestiging van die meeste funksionele groepe moontlik gemaak het, wat noodsaaklik is vir plaagbeheer, voedingstofsiklusse en ontbinding. Daarom word verminderde bewerking en verhoogde strukturele kompleksiteit aanbeveel vir die behoud van grondgeleedpotige diversiteit en gepaardgaande ekosisteemdienste.

Rommelontbinding was positief gekoppel aan grondfauna spesierykheid en nie volopheid of rykdom nie. Resultate het ook getoon dat grondfauna aansienlik bygedra het tot ontbinding, maar bydraes is hoogs afhanklik van temperatuur, grondvog en grondgebruikintensiteit. Hierdie bevindinge beklemtoon hoe belangrik dit is om bestuurseffekte op grondfauna-rolle in die handhawing van voedingstofsiklusse en grondgesondheid te verstaan. Grondkarakterisering het getoon dat konvensionele grondgebruike 'n paar belangrike grondeienskappe bevoordeel, maar die algehele uitwerking van die grond fisies-chemiese omgewing op fauna was kompleks, wat impliseer dat volhoubare intensivering nie net voordelig sal wees vir produktiwiteit nie, maar ook vir die bevordering van grondfauna en

ekosisteemdienste. Meerveranderlike ontledings van grondgesondheidskarakterisering het die ontwikkeling van 'n eenvoudige maar robuuste grondgesondheidsassesseringsinstrument moontlik gemaak deur grondmakrofauna as aanwysers te gebruik. Die instrument is belangrik vir die assessering van grondgebruikbestuur en gepaardgaande effekte op grondgesondheid en ekosisteemfunksie. Oor die algemeen toon hierdie proefskrif dat volhoubare bestuur, verhoogde biodiversiteit en verhoogde grondgesondheid mekaar aanvul.

In vergelyking met hul konvensionele eweknieë, het die bewarings- en vee-geïntegreerde grondgebruike gunstige en stabiele toestande vir verskeie grondfaunagroepe geoptimaliseer en was meer soos dié van die natuurlike grasvelde. Aangesien sommige van die belangrike grondveranderlikes deur meer intensiewe grondgebruike bevoordeel word, is die ontwerp van volhoubare en funksionele skemas 'n lang proses wat geduld verg, aangesien grond self 'n voortdurend ontwikkelende entiteit is wat tyd nodig het om te genereer en of te herstel. Hier word aangetoon dat lae intensiteit landbou gesondheid grondfauna bevorder, dus het volhoubare bestuur van gronde in landbou die potensiaal om die algehele grondgesondheid, biodiversiteit en funksie te verhoog, wat beteken dat hulle gedegradeerde gronde en ekosisteemdienste kan herstel.

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DEDICATION

Dedicated in Loving memory of my dear sister *Stephina "Stokie" Mamabolo*. Thank you for being my source of strength and for loving all of us unconditionally

"She sprouted love like flowers, grew a garden in her mind, and even on the darkest days, from her smile the sun still shined"

-Erin Hanson

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CHAPTER 1
General introduction

1.1.   Agricultural impacts on the soil ecosystem

The world is challenged by unprecedented issues of sustainability. Within the agricultural sector, the continued exponential increase of the global human population coupled with climate change and increased need for food production to meet vision 2050, have put vast pressure on agriculture and the environment (Okolo et al., 2020). The major constraints to sustainability are the widely adopted conventional agricultural practices characterised by monoculture cultivations, misuse of synthetic pesticide, mineral fertilisation, and tillage (Scherr & McNeely, 2008). These practices have been linked with several environmental and health concerns including pollution, the degradation of soil and water resources (Adenle et al., 2019; Giller et al., 1997; Lal et al., 1997), as well as the decline of biodiversity and their soil functions (Hanson et al., 2017).

Soils are regarded as important natural assets, which are key regulators of ecosystem services (Veum et al., 2017). Their ability to provide fundamental ecosystem services such as food production, water purification, climate regulation and habitat provision for flora and fauna is increasingly threatened by over-intensification and competing usages of soils for forestry, urbanization, pasture, and cropping (Chapin III et al., 1996). In South Africa, the issue of agricultural soil degradation has become a threat to food security and sustainability especially through the reduction in crop production (du Preez et al., 2011; Mills & Fey, 2003).

The extensive adoption of conventional agricultural practices such as tillage and the removal or burning of crop residues before planting subjects the soil to erosion and organic matter depletion due to the lack of soil cover and organic matter build-up (Njaimwe et al., 2018). Such circumstances will likely lead to the loss of soil resilience and significant crop yield declines due to poor soil health and loss of ecosystem services (Drobnik et al., 2018). As a result, agroecosystems will then have to be left uncultivated for prolonged periods to allow the soils to restore or regenerate (Kuria et al., 2018). According to Díaz et al. (2006), food production increase at the expense of ecosystem services can undermine agroecosystem sustainability and crop production, thereby affecting food security, which is already under threat. This means, agriculture must go through rigorous changes to achieve sustainability (FAO et al., 2018,

IPBES, 2019). It is evident from the plethora of existing literature that, the sustainability of the soil ecosystem is an important subject which is not only a growing concern to agriculturalists (Baker et al., 2007) but also to ecologists interested in soil biodiversity conservation and restoration (Eckert et al., 2019; Queiroz et al., 2014). And to social scientists dealing with policy development for sustainable development to meet demands for the growing human population (Garibaldi et al., 2019; Perrings & Lovett, 2010). This necessitates the deep rethinking of conventional agricultural models towards regenerative agroecosystem models that reduce carbon emissions, conserves natural resources while maintaining satisfactory crop yields to meet increasing food demands (FAO et al., 2018).

1.2.   A paradigm shift towards sustainable agricultural intensification

Efforts to mitigate the persistent global challenges, coupled with the adverse agricultural effects on biodiversity, soil and water resources and crop production, have called for urgent interventions to revise agricultural management principles (FAO et al., 2018; Millennium Ecosystem Assessment, 2005, IPBES, 2019). This has prompted a paradigm shift characterised by the adoption of practices and concepts such as organic agriculture (Pretty et al., 2018), conservation agriculture (Palm et al., 2014), agroecology (Gliessman, 2015), crop-livestock integration (Bansal et al., 2022) and functional agrobiodiversity to enhance ecosystem health and restore sustainability. In South Africa, crop-livestock integration (CLI) and conservation agriculture (CA) have gained momentum as sustainable concepts (Swanepoel et al., 2018).

The concept of CA is generally accepted as a regenerative technology which promotes soil restoration and conservation through crop diversity, soil cover and minimum disturbance (Sithole et al., 2016), while CLI leverages the interactions between several components of the agroecosystem and complexity through grazing livestock rather than depending on the high intensification of conventional inputs such as chemicals (Bansal et al., 2022). Developing sustainable agricultural production models is a complicated process which needs to consider several aspects including human needs, the efficacy of the model in terms of resources, and ability to maintain a stable environment that favours both humans and animal species (Wilson, 1997). The advancements of agricultural sustainable intensification models that balance the needs for environment and natural resource conservation with those for food and fibre production have already been proven to be a challenge (Doran & Zeiss, 2000). The adoption of the sustainable intensification models is encouraging, although ecological effectiveness through biodiversity conservation and ecosystem service provision is yet to be determined in the major regions of South Africa, more especially in grain agroecosystems which produce the

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most staple food crops (Sithole et al., 2017). To support successful implementation and longevity, there is a great need to provide discernible information about management stability and effectiveness (de Paul Obade & Lal, 2016). The assessment of soil health in agroecosystems has been proposed as a valuable tool for assessing the effectiveness of soil and crop management strategies (Purakayastha et al., 2019).

1.3. The soil health concept

Soil health is defined as "the soil's ability to function as a vital living structure, within land use and ecosystem boundaries, to maintain animal and plant production, uphold or increase the quality of air and water while promoting animal and crop health" (Doran & Zeiss, 2000). It generally embodies the nexus of various ecosystem services delivered by soil (Veum et al., 2017). The soil health concept was developed out of an increased concern over conserving soil resources in view of agricultural management practices and sustainable land use (Doran & Zeiss, 2000). There is a general understanding that soil is not only a medium for producing crops but serves as support for important ecosystem services, including the sequestration of carbon, water purification, nutrient cycling, and resource provision (Bünemann et al., 2018; Rinot et al., 2019).

Healthy soils are considered an economic and natural asset as they support sustainable crop production and the production of various minerals (Kibblewhite et al., 2008). Moreover, healthy soils have been found to stabilise the soil food web and energy flow through the maintenance of diverse soil biota which regulate plant diseases, pests and weed species (FAO & ITPS, 2015; Fiorini et al., 2020). There is a general understanding that, soil health is not only affected by aspects related to soil genesis or formation but also by complex factors related to land use-and or soil management (Muñoz-Rojas, 2018). This is why the assessment of soil health in agroecosystems is promoted as a valuable tool for assessing the sustainability of crop and soil management practices (Andrews & Carroll, 2001). The status of soil health in a given environment cannot be measured directly but can be inferred through the measure of the three broad categories of soil functions that inherently captures how well a soil is performing (Karlen et al., 2003; Muñoz-Rojas, 2018; Ritz et al., 2009). This includes soil chemical, physical, and biological characteristics which are commonly referred to as indicators of soil health (Andrews & Carroll, 2001). In definition, soil health indicators refer to the measurable characteristics of soil that affect its ability to function and provide ecosystem services (Rinot et al., 2019). Soil characteristics which show most sensitivity to changes in management are the most appropriate indicators (Karlen et al., 2003), as they can reveal fluctuations in soil functional properties and

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therefore can be utilised to measure the soil health status in agricultural landscapes (Congreves et al., 2015). The notions of "soil health" and "soil quality" are closely linked (Bünemann et al., 2018), the difference is that soil quality is used within the general scientific community and focuses more on the suitability of the soil for a particular purpose (Bai et al., 2018), while soil health is commonly used within the agricultural scientific community as they are most concerned by how agricultural practices influence the health of their soils and productivity (Wander et al., 2019). In essence, soil health is also more focused on the biological dynamics of the soil and their regulatory functions (Kibblewhite et al., 2008).

Many soil health measures have been proposed globally, including cards, indices, and molecular techniques amongst others (Nuria et al., 2011; Purakayastha et al., 2019; Raiesi, 2017; Yan et al., 2012). While most measures have focused on chemical and physical aspects (Mloza-Banda et al., 2016; Njaimwe et al., 2018), those which incorporate the biological aspects of the soil are still lacking (Lima et al., 2013; Rousseau et al., 2013). This then goes to question the reliability of these measures because an appropriate measure should include all the three aspects of soil function i.e chemical, physical and biological (Andrews & Carroll, 2001; Doran & Zeiss, 2000). Therefore, to capture the true essence of soil health, there is a need for assessments which include all the three aspects of soil function (Wander et al., 2019).

1.4.   Soil biodiversity and their status as bioindicators

Soil ecosystems not only contribute to the production of food and fibre, but also host megadiverse fauna and flora which facilitate important ecosystem processes (Kamau et al., 2017). Various soil fauna groups have been linked with nutrient cycling, decomposition, and maintenance of soil structure (Aldebron et al., 2020; Culliney, 2013). They are also involved in plant disease regulation, weed and pest control (Kleijn et al., 2019). Accordingly, increasing soil biodiversity in farmlands will not only provide ecological insurance against climatic pressures but can also reduce dependence on agrochemicals without reducing crop yields (Tamburini et al., 2020). As much as they influence important processes, soil fauna is not immune to disturbance and unfavourable conditions (Gaigher & Samways, 2010; Tsiafouli et al., 2014).

The soil macrofauna (2–20 mm) and mesofauna (0.2–2 mm) groups in particular, actively take part in processes that influence the soil properties and health (Lavelle & Spain, 2005). The macrofauna are the large components of the soil biodiversity accounting for almost 80% of the overall dry weight of organisms regulating soil ecosystem functioning (Culliney, 2013; Lavelle

& Spain, 2005; Lavelle et al., 2022). Through their burrowing and feeding activities (bioturbation), they are able to engineer their own living spaces, thereby contributing to the soil restructuring processes (Giller et al., 1997). Not only do they improve the soil physicochemical properties, but also improve the soil organic matter, therefore improving soil health (Kamau et al., 2017). The mesofauna group comprise of small fauna which inhabit in soil or litter (Lavelle & Spain, 2005). The group is characterised by Acari, Collembola and Diplura, which activate nutrient mineralisation through their feeding activities (Culliney, 2013). They also perform a vital role of linking primary decomposers such as microflora with larger macrofauna in the soil food-web (Bardgett & van der Putten, 2014; Janion-Scheepers *et al*., 2016). The macrofauna and mesofauna groups are both sensitive and most responsive to various ecological factors, therefore, unfavourable changes in their environment could disrupt their population dynamics and ecosystem services, thereby affecting energy flow and productivity (Gonçalves et al., 2020). For this reason, they are generally recognised as excellent bioindicator candidates for agroecosystem sustainability assessments (Lobry de Bruyn, 1997). Despite the significance of these two groups they are hardly considered in most recent agroecosystem assessments while microbial communities have received much attention (Nuria et al., 2011). One of the most important criteria for appropriate indicators of sustainability described by Doran and Zeiss (2000), is that an indictor must be easily measured and monitored even by non-experts in the case of agriculture "farmers". Therefore, building upon this notion, it is safe to suggest that the general use of microbial communities as indicators has limited applications in agriculture because they are not visible to the naked eye, so their identification requires advanced microscopes and genetic sequencing techniques, hence, it will be very difficult for farmers to measure these entities in their fields.

Therefore, there is a need for simple indicators of soil health that farmers can easily use as a decision support tool when it comes to managing their systems using ecosystem services provided by macro-and mesofauna groups which meet all the appropriate indicator criteria described by Doran and Zeiss (2000). There have been efforts in South Africa to explore this dynamic using soil macro-and mesofauna (Addison et al., 2013; Kapp et al., 2013; Louw et al., 2014; McGeoch, 1998), and the capacity of these assemblages to provide and maintain soil services required for sustainable production in different agricultural soils (Janion-Scheepers et al., 2016). The overall lack of empirical data on biological indicators of soil health is a significant knowledge barrier that prevents confidence about the viability of the currently adopted agroecosystems.

1.5.   Research aims and outline

The study aimed to provide a better understanding of how soil macro- and mesofauna assemblages are responding to different agricultural management systems under conservation, livestock integrated and conventional farming. I also explore their status as bioindicators of soil health to provide a more direct tool in measuring soil function and sustainability. The dissertation is composed of six different chapters. The chapters from two to five present the results of the research written as standalone papers with each chapter having its distinct introduction, materials and methods, results and discussion and reference sections. The contents and specific objectives of each chapter are summarised as follows:

Chapter 1: General introduction
The general introductory chapter which provides information about the background of the research study, motivation as well as the aim and objectives.

Chapter 2: Soil arthropod diversity is enhanced by vegetation complexity and no-till planting in regenerative agroecosystems
The aim was to understand the responses of soil fauna species richness, composition, and functional structure to different types of agricultural management and to determine whether the responses of soil fauna to management could be shaped by factors associated with soil management and vegetation complexity. Understanding which of the studied factors best supports arthropod soil diversity will go a long away in determining the best strategies for sustainable agriculture.

Chapter 3: Litter decomposition is positively related to soil fauna species richness especially in integrated agricultural fields
The aim was to understand the effects of agricultural land use intensity and environmental conditions as drivers of the decomposition process and how these factors influence soil fauna structure and contributions to the process. This will lead to a better understanding of the significant roles soil fauna in maintaining nutrient cycling and other processes as this knowledge is important for the sustainability of production landscapes

Chapter 4: The soil physicochemical status of contrasting agricultural land-uses have differential effects on the community structure of soil fauna groups
The aim was to explore how the distribution of soil fauna and physiochemical properties change within different agricultural land uses, and the association between soil physicochemical and soil fauna biodiversity across the different agricultural land uses. This

improved the general understanding of the important link between soil fauna and the physiochemical world (environment) which they inhibit.

Chapter 5: Soil macrofauna are important bioindicators of soil health in agroecosystems under different management

The aim was to use soil macrofauna as model a to understand the effects of agricultural management on soil health and function using biological, chemical, and physical indicators. Bioindicator species which could potentially assist farmers to measure the efficacy of their production systems were also identified.

Chapter 6: General discussion and conclusions

The chapter deliberates on the most important research findings, recommendations and concluding remarks.

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CHAPTER 2

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

Abstract

Agricultural ecosystems are driven by the need to increase yield, due to increased food demands. Some 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 has been centralised as one of the most sustainable and biodiversity-conserving forms of agriculture, functioning under the principles of crop diversification (e.g. crop rotation, mixed cropping and ground cover through residue retention) and reduced intensification of inputs such as chemical fertilisers, pesticides, and tillage. This study assesses how soil macrofauna and mesofauna respond to different intensities of agricultural management, including conventional, integrated and conservation agriculture, and lastly, natural ecosystems which were used as reference sites. Sampling was spatially and temporally replicated. Differences were examined between the management practices in terms of species richness, composition, and functional structure, and environmental drivers of these patterns were assessed. 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. Variables relating to vegetation and plant litter cover benefited most fauna diversity, however, different functional guilds varied in their responses to the farming systems. Although the responses differed for the various functional groups, I demonstrate here that no-till plantings coupled with diversified crop rotations and cover crop mixtures under conservation and integrated agricultural management stimulates soil macro-and mesofauna diversity. It also supports the establishment of functional groups, which are crucial for pest control, nutrient cycling, and decomposition. Proper soil management and crop diversification or habitat complexity preserves arthropod soil fauna diversity.

Keywords: soil biodiversity, agriculture, resilience, ecosystem functioning, conservation agriculture; arthropods

2.1. 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 considerable decline of farmland biodiversity (Cardoso et al., 2020). Cultivation practices such as soil tilling, agrochemical applications, and the removal or burning of crop residues degrades the soil and produces pollutants which subsequently diminishes biodiversity either through migration or direct mortality (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 evident drawbacks of intensive agriculture have led to concern from policy and the scientific community at large, with the future prospects of this model being critically probed (FAO et al., 2018). The major concern arising from every discussion surrounding intensive agriculture is whether one would meet the ever-rising food demands without increasing the environmental footprint (Adenle et al., 2019; Tscharntke et al., 2012). Consequently, several studies suggest that sustainable management of agricultural systems holds the key to alleviate the impacts of intensive agriculture on crop production, environment, and the losses of important biodiversity (Adenle et al., 2019; Govaerts et al., 2009; Hassan et al., 2022).

Agriculturalists, conservationists, and policymakers have joined forces in finding innovative measures to develop production methods which are alternatives of intensive models in a way that they not only increase ecosystem services and biodiversity but also provides satisfactory crop production and resilience to climate change and other environmental pressures (Garibaldi et al., 2019). Regenerative agricultural systems (RAS) are characterised into three major classes as (1) organic, (2) conservation and (3) livestock integrated agriculture, have since been coined as sustainable alternatives to intensive systems. In South Africa RAS has received major attention as a sustainable model, therefore, the Food and Agricultural Organisation of the United Nations (FAO, 2018; FAO & ITPS, 2015) has devised a national plan with local agricultural organisations to accelerate implementation.

The Free State region is one of South Africa's major agricultural producing provinces, with the cultivation of major staple crops including maize, wheat, oats, and barley. Some farmers in this region have been responding well to calls for sustainable intensification and have gradually shifted towards RAS, with concepts such as mulching, crop diversifications, residue

maintenance, livestock rotations, and zero and/or reduced tillage being implemented into production systems (Palm et al., 2014; Swanepoel et al., 2018). This is encouraging to a certain extent, however the value of these systems in maintaining ecosystem services through soil biodiversity is still in question. Therefore, there is a need to assess their effectiveness in order to provide a more precise management recommendation and increase confidence. To date the work done in these agroecosystems have largely focused on a single organism group to assess management effects, while this study adopts a multitaxon approach to assess the effectiveness of conservation and integrated systems against conventional systems with natural ecosystems as reference.

Different arthropod species have been reported to respond differently to management in terms of diversity and functional guild structure, (Yekwayo et al., 2018). This is because they have different resources preference, identities, and dispersal abilities. Yekwayo (2016), showed that the response of one taxa to landuse change does not necessarily provide a clear reflection of how the whole landscape biodiversity is affected. Therefore, in this study the multi-taxon approach was adopted to eliminate any biases which might be associated with the analysis of a single organism group (Gerlach et al., 2013; Kotze & Samways, 1999). Through this approach, the complete range of soil biodiversity responses to management effects will be fully captured (Yekwayo et al., 2018; Nascimbene et al., 2014).

Agricultural land use management is the main influential factor of ecosystem stability, however various 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 & Magwaza, 2019), vegetation cover (Birkhofer et al., 2019; Eckert et al., 2020), and semi-natural fragments (Plath et al., 2021) to proper establishment of important fauna functional groups. Therefore, understanding how components of vegetation complexity and land use intensification influence soil fauna distribution is of considerable interest as such information holds important implications for the proper 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), (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 influence in many ecosystem processes. The selected fauna groups embody the most feeding guilds and relatively dominant in soils (Dippenaar-Schoeman, 2013; García-Tejero et al.,2013; Lavelle et al., 2021; Nxele et al., 2021). Therefore, their use as the study's focal taxa increases the range of environmental change responses. Understanding which of these management strategies best supports arthropod soil diversity will go a long away in determining the best strategies for sustainable agriculture in this region.

2.2. Material and Methods

Study area and site selection

The study was carried out in the Free State province of South Africa, Thabo Mofutsanyane district at two key grain producing areas i.e. Bethlehem (28°01'S; 28°18'E) and Reitz (27°58'S; 28°18'E) (Figure S2). 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 non-experimental management types or treatments found within the farms were selected for sampling i.e. (1) Conventional agroecosystem: managed under tillage and monoculture cultivations with full chemical applications, (2) Conservation agroecosystem: managed under zero-tillage, crop diversification and soil cover, (3) Integrated agroecosystem: livestock (cattle & sheep) is integrated into the cropping systems for grazing and (4) Natural ecosystem: undisturbed natural land to be studied as a reference system to get a more comprehensive picture of the native soil diversity.

A total of ten replicate sites distributed across four farms were sampled for each treatment, yielding an overall of 40 spatially heterogenous 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 at least 8 ha in area each and were managed with similar practices for more than 10 years before sampling. The natural sites (approximately 1.5 ha) have been undisturbed and covered with natural vegetation for the past 40 years and largely characterised by the species *Chloris* sp., *Digitaria* sp., *Eragrotis* sp., *Andropogoneae* sp., and *Cymbopogon* sp. Some of the natural sites only had intermittent cattle

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grazing and trampling. 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 course of the study, either in mono or mixed cultivation setting 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 Table S1.

Fauna sampling

Sampling was conducted over two seasons, 26th October to 4th November 2020, and 22nd March to 6th April 2021. Owing to their dynamic nature, soil faunae 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 & 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 a litter layer and hand sorted for visible fauna. Following the same arrangement, 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 a small amount of detergent to reduce surface tension (Souza et al., 2012). The traps were left out open for seven days to reduce 'digging-in' effects described by Greenslade (1964). The sampled individuals were preserved with 70% ethanol and sent to the laboratory at Agricultural Research Council 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 and sealed in brown paper bags and transported to the laboratory inside a cooler box to avoid overheating and desiccation. The faunae 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 & Nxele, 2017; Dippenaar-Schoeman et al., 2010; Janion-Scheepers et al., 2015; Joseph et al., 2018; Plisko, 2010, 2014; Plisko & Nxele, 2015; Schoeman et al., 2020). Individuals were sorted into morphospecies when species level identification was not possible (Gaigher & Samways, 2010; Beattie & Oliver, 1996).

Feeding guilds were also allocated to species based on the identity of family and morphological differences for beetles (Scholtz & Holm, 1985), Collembola (Malcicka et al., 2017; Hopkin, 1997), earthworms (Plisko & Nxele, 2015) and spiders (García et al., 2021; Arias, 2012).

Determination of environmental variables

To evaluate which environmental/habitat factors best explain variation in soil fauna diversity patterns and function, 3 m^2 quadrats were used within each sampling site, to measure plant species richness (including spontaneous spp.), proportions of vegetation cover, leaf litter and bare ground (Gaigher et al., 2016; Joseph et al., 2018). Management (conservation, integrated, conventional, or natural) and tillage type (zero, deep, conservation) were included as categorical variables. The environmental measurements were collected across the two sampling seasons.

Data analyses

Diversity and functional structure of soil fauna assemblage community

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). In order 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 fall under a particular feeding group, with the categories being ''predator'', ''herbivore'', ''omnivore'', and ''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 & 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).

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 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 management 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 inflations factors (VIF) on rescaled variables, variables with VIF > 5 were removed from the model. Models with the lowest AICc value of ≤ 3 were included in model averaging.

Determining differences in soil fauna assemblage composition

Differences in soil fauna assemblage composition between management types were assessed with a permutational multivariate analysis of variance (PERMANOVA) (Anderson, 2001), on the squared-root transformed abundance data with the "*Adonis*" function in R (Martinez Arbizu , 2020). A pairwise test was also conducted at 999 random permutations to determine which management types differed significantly from each other (Legendre & Gallagher, 2001). 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* (Oksanen et al., 2019). 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 & Willis, 2003). All data analyses were performed with R statistical software version 3.6.3 (R Core Team, 2020).

2.3. Results

A total of 10780 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 use types and arthropod groups (Figure S2.1), indicating that sampling effort was adequate.

Fauna species richness responses to land use management

The overall species richness varied significantly across the different management systems (χ^2 = 19.82; $p < 0.001$), with the highest recorded within the integrated system (Figure 2.1a). Pairwise test shows that the overall species richness did not differ between conservation, natural and integrated fields ($p > 0.05$) but it was significantly lower in conventional fields than in the other three management systems. The highest record of beetle species was observed within the integrated land use ($\chi^2 = 15.81$; $p < 0.001$), with the pairwise test revealing significant differences only between, conventional and integrated ($Z = 3.822$; $p < 0.001$) while other land uses are relatively similar (Figure 2.1b). Collembola were more pronounced within the conservation land use ($\chi^2 = 15.71$; $p = 0.001$) (Figure 2.1c). According to Tukey test collembolans from conventional and integrated fields are not significantly different in species richness ($p > 0.05$). Earthworms were significantly richest within the integrated land use ($\chi^2 = 30.60$; $p < 0.001$) (Figure 2.1d) with similarities across 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 (Figure 2.1e).

Functional CWM responses to land use management

With regards to functional composition, different land use management, affected fauna functional communities differently. Detritivores significantly differed across the different land uses ($\chi^2 = 131.82$; $p < 0.001$) and were most pronounced within the integrated system and relatively high within the conservation land use (Figure 2.2a). Detritivores within the conventional land use did not differ from those found in natural system ($\chi^2 = 131.82$; $p = 0.954$) as indicated by the Tukey pairwise test with both these land uses being significantly lower than the other two. The herbivore group was significantly higher within the conventional land use ($\chi^2 = 13.79$; $p = 0.003$) and lowest within the integrated land use (Figure 2.2b). The conventional and integrated displayed relatively similar patterns in predator composition, while the highest record was observed in the natural land use (Figure 2.2c). Although the main test revealed significant differences in predator composition among the different land use types ($\chi^2 = 11.83$; $p = 0.008$), the pairwise test shows that the differences were really not that extreme, and only the natural and integrated land uses differed in predator composition ($Z = -2.830$; $p = 0.023$), while all the other land uses were rather similar. The omnivore group were more

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pronounced within the conventional land use and lowest within the integrated land use (Figure 2.2d). Like the predator group, the main test revealed slight 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 systems, suggesting that land use management has no effect on omnivore functional composition.

Fauna community composition responses to land use management

The PERMANOVA test results for soil fauna species composition are presented in Table 2.1. The overall species composition differed significantly across the different land use types ($F = 2.264$; $p < 0.05$), significant differences were observed between conservation and integrated ($F = 1.822$; $p < 0.01$) 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 2.1), pairwise test reveal that beetles from conventional, conservation and natural land use managements are similar in species composition. Collembola main and pairwise tests reveal that, species composition is quite similar across the different land use types ($F = 2.230$; $p > 0.05$). 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 use types $(F = 2.199$; $p < 0.05)$, 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 ($F = 1.695$; $p < 0.01$). Interestingly, 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 (Figure 2.3).

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

Model averaged estimate results show that, overall species richness was positively and significantly influenced by percentage leaf litter and vegetation cover (Table 2.2). 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 percentage bare ground ($Z = 2.943$; $p = 0.003$) with a significantly negative relationship. Percentage 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 2.2). Spider species richness was influenced by plant species richness (Z = 2.121; p = 0.034), percentage 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).

Effects of environmental variables on functional CWM composition, were not that distinct/significant (Table 2.3). Proportions of detritivores were to a larger extent, significantly influenced by deep tillage (Z = 3.384; p < 0.001) and percentage leaf litter (Z = 2.173; p = 0.030). Deep tillage is the only factor which significantly and positively influenced the distribution of omnivore functional group. Predator distribution was negatively affected by plant species richness, leaf litter and vegetation cover, the differences were, however, not statistically pronounced (p > 0.05). Overall, tillage and leaf litter are the only two variables which significantly influenced proportions of soil fauna functional groups (Table 2.3). dbRDA results backed up with distLM sequential tests show that soil fauna species composition responded differently to environmental variables. Overall species composition was influenced by percentage vegetation cover and leaf litter (Figure 2.3a). Percentage leaf litter is the only variable which influenced species composition of beetles (Figure 2.3b). Spiders were significantly influenced by percentage leaf litter and vegetation cover (Figure 2.3c). Earthworms were also significantly influenced by percentage leaf litter and vegetation cover (Figure 2.3d). Collembola composition was influenced by plant species richness and percentage vegetation cover (Figure 2.3e), while the effect of vegetation cover was however not significant (p > 0.05).
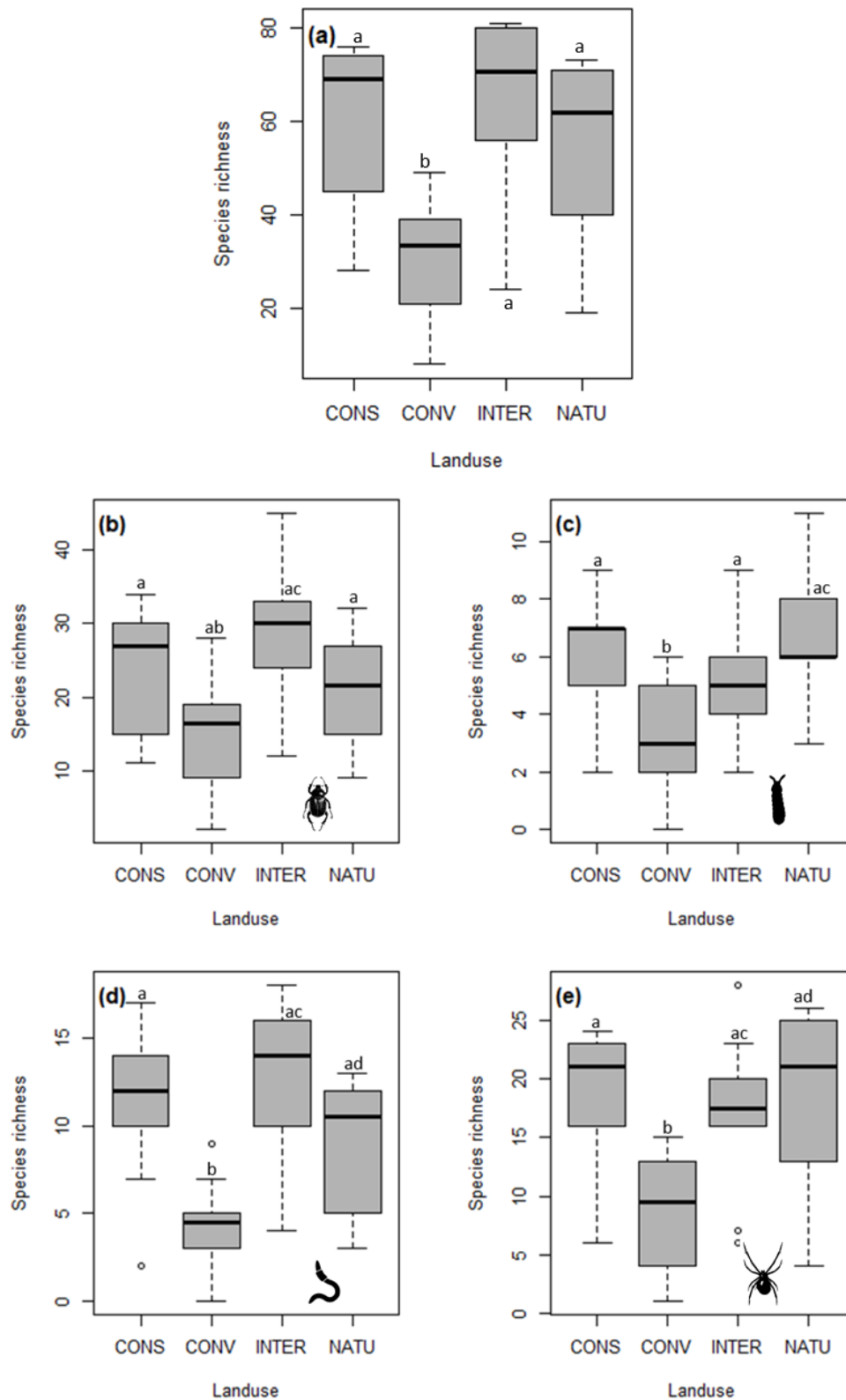
Figure 2.1. Boxplots visualizing differences in soil fauna species richness between conservation (CONS) integrated (INTER), conventional (CONV) and natural systems (NATU). (a) Overall, (b) Beetle, (c) Collembola, (d) Earthworm, and (e) Spider. Mean values with dissimilar letters are significantly different (Tukey's post-hoc tests at $p < 0.05$).

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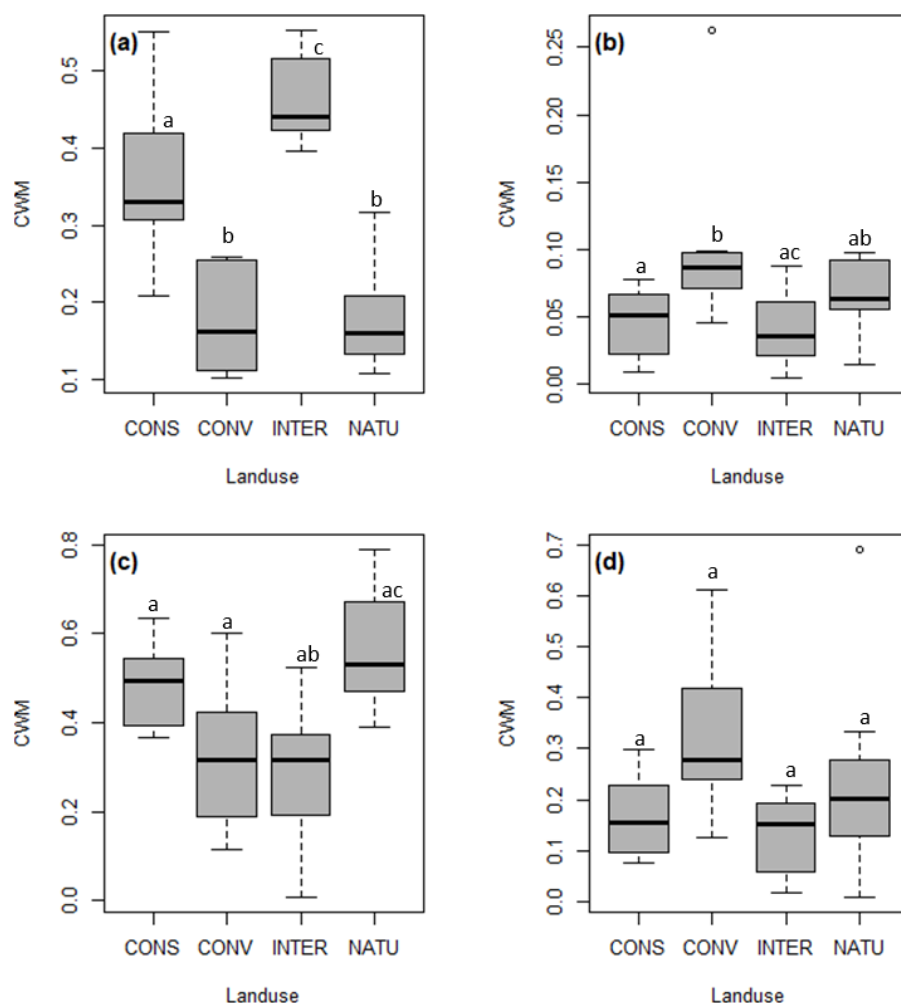
Figure 2.2. Differences in proportions of the community-weighted mean (CWM) for (a) Detritivores, (b) Herbivores, (c) Predators, (d) and Omnivores across different land use types: CONS = Conservation, INTER = Integrated, CONV = Conventional and NATU = Natural. Mean values with dissimilar letters are significantly different (Tukey's post-hoc tests at $p < 0.05$).

Table 2.1. PERMANOVA results for soil fauna community composition. Pairwise (t-values) and main (F-values) test statistics results between 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

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Table 2.2. 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.

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 *

Significant bold p-values are indicated as: * p < 0.05, ** p < 0.01

Table 2.3. 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.

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
	Vegetation cover (%)	-2.787	6.522	0.420	0.674
Omnivores-CWM	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
	Leaf litter (%)	2.222	1.150	1.870	0.062
	Vegetation cover (%)	-2.366	1.391	1.647	0.100
Predators-CWM	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

Significant bold p-values are indicated as: * p < 0.05, *** p < 0.001

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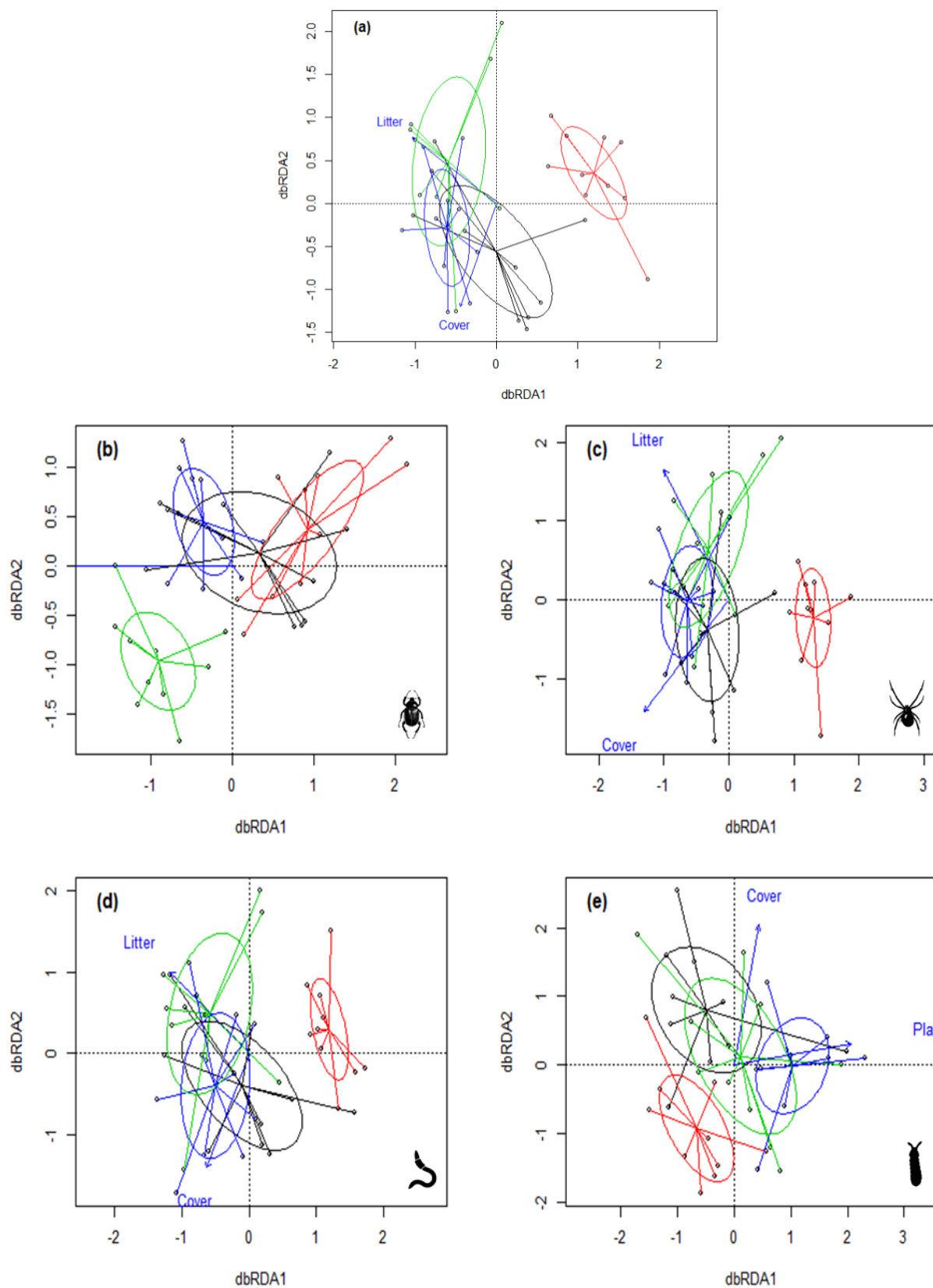
Figure 2.3. Distance based redundancy analysis (dbRDA) visualizing differences in soil fauna community composition between conservation (grey) integrated (green), conventional (red) and natural systems (blue). (a) Overall, (b) Beetle, (c) Spider, (d) Earthworm and (e) Collembola.

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2.4. Discussion

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

The lowest diversity of exclusive taxa and functional group composition were found within the conventional land use compared to other land uses. Generally, conservation and integrated sites were found to closely resembled natural sites, this observation was consistent for most of the measured taxonomic groups and variables. Overall, there seemed to be quite a consistent positive influence of variables associated with improved 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 considerably more species compared to other land uses. Deep tillage resulted in significant decline of this group, contrarily the presence of litter and vegetation cover as well as zero level of disturbance in the integrated management proved to be beneficial by providing suitable habitat conditions which supported proper establishment of 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) and Brown et al. (2001) also 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 heterogenous 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 integrated land use was species rich in Collembola, this result is consistent with previous studies (see; Wardle, 1995; Miyazawa et al., 2002). The results revealed significant degrees of similarities for Collembolan species composition across the different land use types. Moreover, the presence of bare ground was found to have a significantly negative effect on 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 or species proportions are 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 most recent studies by Coulibaly et al. (2022), Fiera et al. (2020) and Sterzyńska et al. (2018) which argued that collembolans are not always affected by land use management 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, epigaeic and hemiedaphic collembolan species are reported to be more affected by intensive land use management compared to other lifeforms (habitat position), e.g. euedaphic (Fiera et al., 2020). It is suggested that future work should focus on analysing collembolans in-depth according to their lifeforms or dispersal ability traits as this could reveal more clear and concrete evidence regarding the responses of these assemblages to land use management.

The accessibility of adequate food sources and favourable habitat conditions (Fiera et al., 2020) are the most significant factors shaping agroecosystem biodiversity (mostly, beetles and spiders), these factors are fundamental as they are directly linked to different aspects of vegetation complexity (House & Brust, 1989). The recorded beetle species in this study did not differ to a larger 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 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, this may be attributed to the spider's ballooning and moving (cursorial) behaviours which enhance their dispersion (Wang et al., 2022). Several aspects of vegetation complexity i.e species richness of plants, leaf litter and vegetation cover were found to be extremely influential to spider

communities in both species' richness and composition. Unexpectedly zero soil disturbance influenced spiders negatively, this can 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).

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

Ideally, increased soil cover benefitted soil fauna functional groups, more especially the detritivores and omnivores. High proportions of detritivores were found to be 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 improves the detritus-based food web, which in turn stimulates the activities and population of detritivores (Scow et al., 1994).

Deep tillage positively influenced detritivores within the conventional land use, 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 than soil fauna species are favoured by soil tillage. Nuutinen (1992) also observed that some species do not respond well to crop residues.

The omnivore were highly favoured within the conventional land use which had slightly more proportions compared to other land uses. However, statistical tests reveal otherwise, and show that there is a great degree of homogenisation in omnivores, as they are not significantly different amongst the land use. Of all the measured variables, omnivores were negatively influenced by deep tillage, of course this finding 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; Gaigher, 2008).

Predators and herbivores are the foremost important functional groups which are well known to influence each other through top-down and bottom-up forces (Crowl et al., 1997). For example, Forkner and Hunter (2000), found that an increase in herbivores population density stimulates the density and prevalence of predators. In this study, predators were predominantly 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 were higher within the conventional land use, preceding work by Otieno et al. (2019) and Chaplin-Kramer et al. (2011) also made similar observations and established that herbivores thrive well under conventionally managed landscapes which are less heterogeneous or more simplified in terms of vegetation complexity. Although some observations were not statistically significant, habitat conditions within the conservation and integrated managements proved to be beneficial to soil fauna structure and function by favouring the establishment of functional groups which are important for nutrient cycling and pest regulation.

2.5. Conclusion

The results here show that land use, soil management and vegetation complexity exert a significant influence on soil fauna species richness, composition, and function. While some studies in grain agroecosystems focused on a single taxon to assess managements 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 and integrated resembled natural systems in species richness, composition and functional structure holds promising ground for the potential of these systems to safeguard ecosystem functions. Here I highlight the significance of proper soil management and crop diversification or habitat complexity in preserving soil fauna community features.

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CHAPTER 3

Litter decomposition is positively related to soil fauna species richness especially in integrated agricultural fields

Abstract

Litter decomposition is an important ecosystem process for the maintenance of soil health and long-term sustainability of agricultural landscapes. Soil macro-and mesofauna facilitate decomposition and nutrient cycling ensuring nutrient availability for microbes and plants. Yet, information on how agricultural land-use intensity and environmental conditions influence the contribution of fauna to the process of litter decomposition remains poorly understood. To address this knowledge gap, a litter decomposition study was conducted in agricultural fields under conservation, conventional, and integrated agricultural management, with undisturbed natural grasslands as reference sites. Within each site, four pairs of litterbags of two mesh sizes containing fresh leaves of perennial *Lolium perenne* were used to permit (coarse mesh) and exclude (fine mesh) macro-and mesofauna effects on decomposition. The litterbags were collected at monthly intervals for a period of four months and analysed for fauna diversity and decomposition rates. The highest decomposition estimates were recorded within the integrated and conservation farming sites, and this was attributed to favourable habitat condition which supported a balance of diverse functional fauna communities found in these land-use treatments. Litter mass loss increased in the presence of soil fauna within the coarse mesh litterbags compared to fine mesh where fauna was completely absent. Litter mass loss was not significantly associated with arthropod diversity or abundance but was strongly linked to arthropod species richness. The contributions of fauna to decomposition were affected by temperature, soil moisture and land-use intensity. These results highlight that less intensive agricultural management maintains functional biodiversity structures which drive the process of litter decomposition and therefore nutrient cycling.

Keywords: biogeochemical cycling, decomposers, agriculture, resilience, ecosystem function

3.1. Introduction

In the midst of climate change and current sustainability uncertainties, understanding soil ecosystem functioning in agroecosystems has become vital for long-term food productivity and sustainability (Peña-Peña & Irmler, 2016). Litter decomposition is an important ecosystem process which not only supports ecosystem productivity and stability but also act as a response to climate fluctuation (Elias et al., 2020; Gessner et al., 2010). It is well-defined as the ecological process that alters plant litter into easily available mineral composites utilised by plants and soil consumers (heterotrophs) (Domínguez et al., 2014). During the process, litter enters the soil ecosystem, where it is then converted into nutrients due to biological, chemical, and physical processes e.g. nitrogen mineralisation (Frouz, 2018) thereby contributing to nutrient cycling.

Biodiversity performs important ecosystem functions in agroecosystems, beyond food production (Pant et al., 2017). This includes amongst others, detoxification of harmful chemicals (Greenslade et al., 2010), pest suppression (Birkhofer et al., 2008; Raderschall et al., 2022) and nutrient cycling to name a few (Chen et al., 2018; Pant et al., 2017). By maintaining these functions, biodiversity helps to maintain resilience against climate change and other pressures (e.g. drought and fire; Pryke et al., 2022). The significance of soil biodiversity on the process of litter decomposition has also been long recognised (David, 2014; González & Seastedt, 2001). Macro-and mesofauna groups in particular (from here on referred to as soil fauna) have been linked to the decomposition process directly (via litter ingestion) and indirectly (via fragmentation) (Wang et al., 2015; Xin et al., 2012; Petersen & Luxton, 1982).

Essentially, the functions of soil fauna accelerates litter decomposition and facilitates nutrient cycling as well as primary production (Meyer III et al., 2011) through the physical fragmentation of litter and by altering environmental conditions, thereby creating favourable and stable habitat conditions for decomposer microbes to thrive and drive the process (Schmidt et al., 2015). The ability of these assemblages to perform ecosystem functions is influenced by various factors in their environment which can either inhibit or support their functionality, these includes amongst others; climate variations, habitat quality and anthropogenic activities such as pollution, fire and agriculture (Geldenhuys et al., 2022; Janion-Scheepers et al., 2016). When considering agricultural effects, conventional models which are inherently driven by the intensification of inputs such as chemical applications, intensive tillage, residue removal and fertilisation can be detrimental to these groups by degrading their populations and functions in ecosystem service provision (Raderschall et al., 2022; Villanueva-López et al., 2019). In order

to lessen these effects and ameliorate soil fauna functions, sustainable management has become the key aspect of biodiversity-friendly agriculture. Within this narrative, integrated and conservation farming models, which are based on low-intensity management and farmland diversification, have been proposed as innovative measures to overcome detrimental effects associated with conventional farming models (Ke et al., 2005). Despite this, there is a limited knowledge of the mechanisms by which these farming models influence soil fauna contributions to ecosystem processes particularly litter decomposition which is important for soil fertility and health. While abiotic factors such as water, CO_2 levels, temperatures litter chemistry have received considerable attention within the decomposition literature (Aerts, 1997; Maisto et al., 2011; Zhang et al., 2016), soil fauna have remarkably received less research attention despite their established importance and recognised influences on key processes in various ecosystems. This is rather concerning, especially because research has shown that in order to accurately predict litter decomposition, ecosystem models must include and recognise soil fauna as important drivers of this process (González & Seastedt, 2001; Haanes & Gjelsvik, 2021).

Importantly, at a global scale some pioneering studies which included soil fauna in their decomposition models have been done in forestry ecosystems, post mining (Frouz, 2008; Frouz et al., 2015; González & Seastedt, 2001) and agroecosystems (Cassani et al., 2021; Domínguez et al., 2010, 2014; Pant et al., 2017). Likewise, in South African ecosystems, there is also notable published work specifically focused on forestry and fynbos ecosystems (Bengtsson et al., 2011, 2012; Swart et al., 2020, 2022). However, when considering agricultural ecosystems, research which deals with management and soil fauna contributions to litter decomposition is still lacking.

Here, I used the litterbag approach (two mesh sizes to exclude and include fauna) to understand the influence of soil fauna on leaf litter decomposition at four different land-use treatments under varying environmental conditions. The treatments included three agricultural management types (conservation, integrated, and conventional farming) and undisturbed natural grasslands as a reference. Specifically, the study sought to determine (1) differences in the diversity of soil fauna extracted from litterbags within different land-use types (2) if the rate of litter decomposition is influenced by the presence of soil fauna (3) the relationship between litter decomposition and soil fauna diversity estimates (i.e. abundance, species diversity and richness) and lastly (4) the extent to which agricultural management intensity influence soil fauna contributions to litter decomposition.

Decomposition is a multifaceted process affected by the interactions of complex factors (Peguero et al., 2019; Perez et al., 2013). So, even though soil fauna regulates this process, other factors such as soil characteristics, litter chemistry and climatic conditions, may control their functions or the process itself (Gessner et al., 2010; Kampichler & Bruckner, 2009). Therefore, effects of abiotic factors related to climate, soil and habitat characteristics were also investigated to obtain more insights into the causal factors that may influence soil fauna decomposition dynamics. Improved knowledge on how agricultural management, soil fauna, abiotic environment and their interactions influence litter decomposition is a fundamental aspect of soil ecology for understanding and predicting ecosystem functionality (Meyer III et al., 2011) as well as for safeguarding soil ecosystem health and productivity (Song et al., 2020).

3.2. Material and Methods

Study area and site selection

The study was conducted at non-experimental farms near Bethlehem (28°01'S; 28°18'E) and Reitz (27°58'S; 28°18'E) (Figure S2) within the Thabo Mofutsanyane district in the eastern Free State, South Africa. The region has a semi-arid climate with monthly mean temperatures of 14 °C to 27 °C and annual rainfalls of 200 mm to 600 mm. Treatments comprised of four different land-uses, i.e. (1) Conventional: intensively managed with agrochemical usage and deep tillage, (2) Conservation: under minimum intensification with crop diversification, zero-tillage and soil cover through mulching and cover crops, (3) Integrated: under minimum intensification with crop and livestock (cattle and sheep) grazing rotations and lastly (4) Natural: pristine grasslands with zero disturbance as reference sites. Non-experimental farmer's fields were specifically selected for this study to capture actual agricultural effects in real time. And since non-experimental fields were used, there were differences in crop rotations and species cultivated (both monoculture and mixed) within the agroecosystem treatments. Maize, soybean, oats, wheat, and sunflower were the main crops cultivated in the farmers' fields during the course of the study, either in mono or mixed cultivation setting along with some combinations of summer and cool season crops i.e., legumes, grasses, brassicas. A total of eight replicate sites distributed across four farms were selected for each land-use treatment, totalling an overall of 32 spatially heterogenous sites each of at least 8 ha (agricultural) and 1.5 ha (natural) in area. Where several sites of the same land-use type occurred within the same farm, the sites were segregated by at least 500 m distance to avoid pseudoreplication. Detailed management information (including cultivation history and agrochemicals) of each agricultural field is presented in Table S1.

Determination of decomposition

The litterbag method was used to evaluate soil fauna contributions to litter decomposition under field conditions from the 22nd of December 2021 to the 30th of April 2022. The "Home-Field Advantage" (HFA) hypothesis, which implies that litter species will decompose faster within its original environment (at home) than in an environment it does not originate from (away from home) (Sayer et al., 2006) has been supported in many studies (e.g. Perez et al., 2013; Wallenstein et al., 2013). Therefore, since all the study sites had different plant materials and/or mixtures, a single litter species of perennial grass *Lolium perenne* L. (*L. perenne*), which was absent or did not originate from any of the study sites was used to eliminate any bias or facilitation effects which might be associated with HFA (Tan et al., 2021). Fresh leaves of *L. perenne* were collected and air dried for a period of two weeks at room temperature (Wang et al., 2015). Approximately 15 g of the dried material was filled into the litterbags of 10 cm x 15 cm with two different mesh sizes (Xie, 2020), i.e. litterbags with a coarse mesh (5.2 mm) to permit soil macro-and mesofauna entry (Huang et al., 2020), and litterbags with fine mesh (0.02 mm) to restrict macro-and mesofauna (Swart et al., 2020). While used as a standard in several studies, I acknowledge that the size of the coarse mesh used here can restrict larger fauna groups which significantly influence the decomposition (Bush et al. 2019). The litter material in each bag was weighed with an analytical balance (Radwag, com.) to the nearest three decimals of accuracy. A study conducted by Bush et al. (2019), recorded that fine or small mesh size do not completely restrict the entry of all arthropods, therefore, to further reduce the entry of fauna, two naphthalene balls were inserted within the fine mesh litterbag traps as recommended by Cotrufo et al. (2014). The bottom part of all the litterbags was fitted with a double layer fine mesh to prevent material loss during handing (Bengtsson et al., 2012) and treated with a bixafen fungicide (containing prothioconazole as an active ingredient) to prevent fungal colonization (Sayer et al., 2006; Swart et al., 2020). A factorial trial with a total of eight replicates was established for each land-use. At each site, four pairs of litter bags were placed, resulting in a total of 256 litterbags (four land-use types x two mesh sizes x one litter species x eight replicates x four sampling occasions). A sampling grid (1.6 m x 6 m) with two columns and four rows was set out in each replicate field. Eight litterbags were anchored to the ground within the grid ensuring that the top is in level with the soil surface. The litterbags were placed as close to the shade (leaf canopy) as possible to reduce heat exposure from the sun (Bengtsson et al., 2012). To examine litter mass loss, the litterbags were sampled within each site at monthly intervals for four occasions: 30, 60, 90 and 120 days. During each sampling occasion,

two of litterbag types (coarse and fine mesh) were retrieved from each site, while the remaining were left for subsequent sampling occasions. The retrieved litterbags were carefully secured in plastic zip-lock bags to prevent litter loss and transported to the laboratory. Litter material from the zip lock bags were carefully removed and placed inside the Berlese-Tullgren funnels for 72 hours for faunal extraction (Espinaze et al., 2019). The obtained fauna were classified into morphospecies (Oliver, 1996), counted, and identified to family level by a taxonomic expert and appropriate keys (Armstrong & Nxele, 2017; Dippenaar-Schoeman et al., 2010; Hopkin, 1997; Janion-Scheepers et al., 2015; Picker et al., 2002; Plisko, 2010, 2014; Plisko & Nxele, 2015; Schoeman et al., 2020; Scholtz & Holm, 1985). After extracting the fauna, the litter material was cleaned from any organic particles with tap water in a plastic basin through a fine sieve to ensure that no litter material is lost during the washing process, thereafter, the water in the basin was thoroughly inspected for fragments. After cleaning, the litter was air-dried for 72 hours at room temperature, and weighed again to determine the mass loss (Song et al., 2020).

Environmental variables

Environmental variables were recorded during each sampling occasion. Climatic datasets were obtained from the nearby weather stations within the areas of Reitz and Bethlehem; these included mean monthly temperatures (MMT) and mean monthly precipitation (MMP). Soil and vegetation characteristics were estimated within each sampling grid, during every sampling occasion, including soil moisture (with a moisture meter: PMS-714, ManTech USA) , soil pH (with a pH meter: PH-220S, ManTech USA), richness of plant species as well as the percentages of leaf litter, bare ground, and vegetation cover.

Data analyses

R statistical software versions 3.6.3 and 4.1.2 were used to perform the analyses (R Core Team, 2020, 2021). The percentage mass loss resulting from decomposition was estimated as: $ML = Wr/Wi \times 100$; where Wr is the remaining litter mass, while Wi is the initial litter mass (Wang et al., 2015). The average of the mass loss per time period (30, 60, 90 days) was used to represent mean mass loss. The contributions of soil fauna to litter decomposition were estimated as the differences in mass loss between coarse and fine mesh litterbags. Arthropod species richness and diversity (Shannon) were estimated through hill numbers with the *hillR* package (Li, 2021). The *lme4* package (Bates et al., 2015) was used to generate linear mixed-effects models (LMMs) for gaussian distributed response variables (litter mass loss) and

generalized linear mixed-effects models (GLMMs) for gamma (arthropod diversity, and richness) as well as Poisson distributed variables (arthropod abundance). Moran's *I* test detected no spatial autocorrelation when tested for with the *ape* package (Paradis et al., 2022). Differences in species diversity measures and decomposition between the land-uses were tested, and significant probability (*p*) values were subjected to pairwise comparison using Tukey post-hoc with the *multcomp* package (Hothorn et al., 2008). To determine the most important set of predictor variables for each response variable, models were selected with the forward selection procedure and ranked with the second order Akaike's information criterion using the package *AICcmodavg* (Mazerolle, 2020) (models with AICc values that were ≤ 3 from that of the top model were included). Prior to model selection, the variance inflation factor was calculated using the *car* package to reduce collinearity (Fox et al., 2019), VIF values > 5 were excluded (Zuur et al., 2010). Patterns in soil fauna species composition between the land-use types were examined with multivariate generalised linear modelling with the function "*manyglm*" using *mvabund* package (Wang et al., 2012). Multivariate models were fitted with a negative binomial distribution, assuming quadratic mean-variance and estimated through the "PIT-trap" resampling approach at 999 permutations. Results were visualised with multivariate model-based ordinations of constrained and unconstrained latent variables using the *ecoCopula* package (Popovic et al., 2022).

3.3. Results

Soil fauna assemblages

A total of 13855 individuals from 167 morphospecies and nine orders (groups) were extracted from the litterbags. These included assemblages from Araneae (11 spp.), Diplopoda (21 spp.), Chilopoda (15 spp.), Coleoptera (32 spp.), Collembola (19 spp.), Dermaptera (9 spp.), Oligochaeta (14 spp.), Mesostigmata (20 spp.), and Oribatida (26 spp.). More information on how the assemblage groups differed across the studied land-uses is presented within the supplementary information section (Figure S3.1). Based on assumptions that arthropods could easily move in and out of the coarse mesh litterbags, the recorded number of individuals represents only a snapshot the actual fauna dynamic at the time of sampling. Abundance differed significantly across the different land-use types and was significantly higher within the integrated and conservation land-use management and lowest within the conventional (χ^2 = 109.85, p < 0.001) (Figure 3.1a). Species richness displayed similar patterns to abundance, with the integrated and conservation land-use management being the most taxonomically rich in soil fauna species and conventional being the lowest (χ^2 = 137.83, p < 0.001) (Figure 3.1b).

Species diversity also differed significantly between the land-use types with the conventional management having the lowest species diversity and conservation and integrated management having the highest diversity ($\chi^2 = 95.89$, p < 0.001) (Figure 3.1c). Arthropod abundance, species richness and diversity in natural grassland was higher than in conventional fields, but lower than in conservation or integrated fields (Figure 3.1a-c). Assemblage composition also varied significantly between the different land-use managements. The unconstrained latent biplot with the exclusion of predictors effects clearly shows a great degree of separation in the soil fauna composition (Figure 3.2a) compared to the residual biplot which did not show any observable separation (Figure 3.2b). Interestingly, the pairwise test from multivariate generalised linear modelling revealed no significant differences in assemblage composition between the conventional and natural grassland sites ($\chi^2 = 82$, p = 0.401) (Table S3.1), this observation is corroborated by the latent ordination which did not show any visible trend of separation between the two sites, even in the absence of predictor variables, thereby, suggesting similarities in a soil fauna composition between the two sites (Figure 3.2a).

Percentage mass loss

Leaf litter mass loss showed significant variations within the different land-use types (F = 8.80, p < 0.001) (Figure 3.1d). Mass loss in conventional sites were significantly lower than those within conservation (t-value = -4.02, p < 0.001) and integrated sites (t-value = 4.67, p < 0.001). Mass loss in the natural grassland sites was slightly lower than in the conservation and integrated sites, however, these differences were not significant. When compared with the integrated and conservation land-use sites, the percentage litter mass loss within the conventional land-use was lower by approximately 20-22%. Litterbags which included fauna (coarse mesh) lost the most leaf litter mass compared to those which excluded fauna (fine mesh) (Figure 3.3). Unexpectedly, coarse, and fine mesh litterbags within the conservation land-uses did not differ in mass loss, despite the relatively high leaf litter mass loss within the coarse mesh litterbags (F = 2.75, p = 0.10) (Figure 3.3a; Table S3.2). Coarse and fine mesh litterbags within the conventional sites were also not statistically different (F = 0.29, p = 0.59) (Figure 3.3c; Table S3.2), while differences were only observed between different litterbag types in the integrated (F = 15.00, p < 0.001) and natural land-uses (F = 13.31, p < 0.001) (Figure 3.3b,d). When analysing for correlations, leaf litter mass loss was positively linked with all biological estimates of soil fauna. As clearly visualised by the scatterplot, an increase in abundance, species richness and diversity, results in an increase in leaf litter mass loss (Figure 3.4a). However, a deeper look into the results shows that the visualised relationships are actually not

too extreme, species richness stands out as the only variable which is significantly linked with leaf litter percentage mass loss (t-value = 2.01, p = 0.04) (Table 3.1).

Factors driving soil fauna and leaf litter mass loss

Model averaged estimates for the effects of environmental variables on soil fauna and litter percentage mass loss are presented in Table 3.2. Abundance was significantly influenced by soil moisture, litter cover and vegetation cover. Interestingly, species richness and diversity were both influenced by temperature, soil moisture, litter cover and vegetation cover. Leaf litter mass loss was influenced by temperature, soil moisture and vegetation cover, surprisingly, litter cover did not influence percentage mass loss. Rainfall is the only variable which did not have an influence on soil fauna abundance, species richness, diversity, and leaf litter mass loss. Multivariate analyses revealed that soil fauna composition is significantly influenced by temperature, rainfall, and soil moisture (Table 3.3).
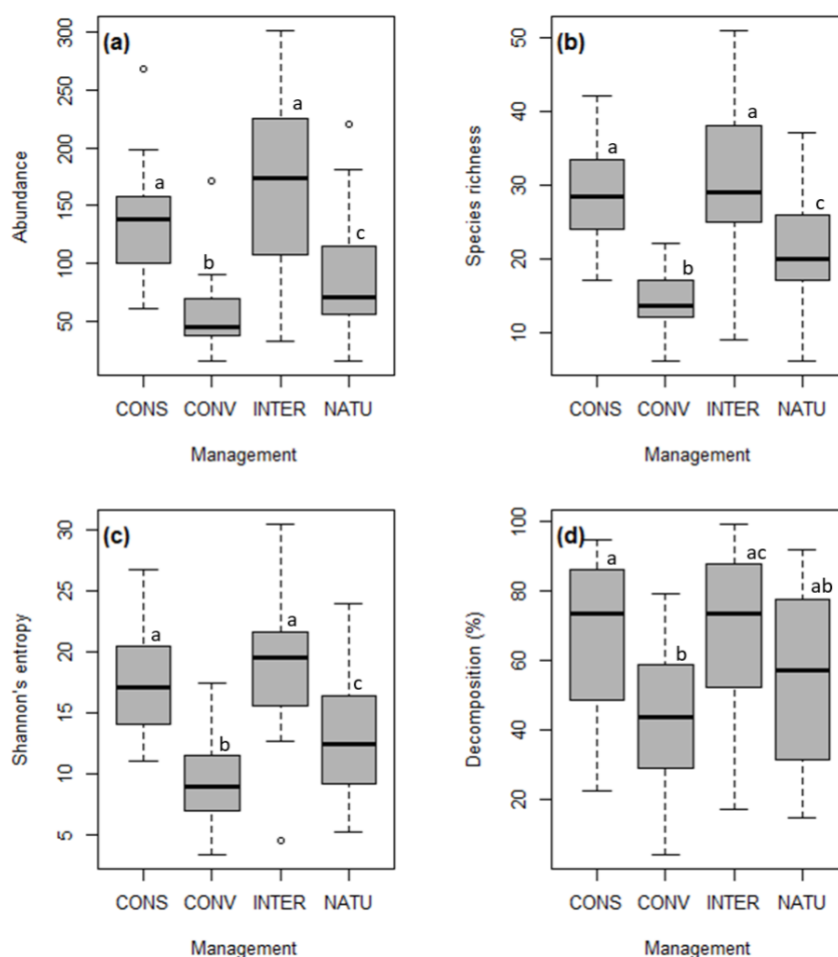
Figure 3.1. Comparison of soil fauna (a) abundance, (b) species richness, (c) Shannon's entropy (diversity), and (d) litter mass loss between the different land-use types. CONS = Conservation, INTER = Integrated, CONV = Conventional and NATU = Natural. Bars with dissimilar letters are significantly different (Tukey's post-hoc tests at p < 0.05).
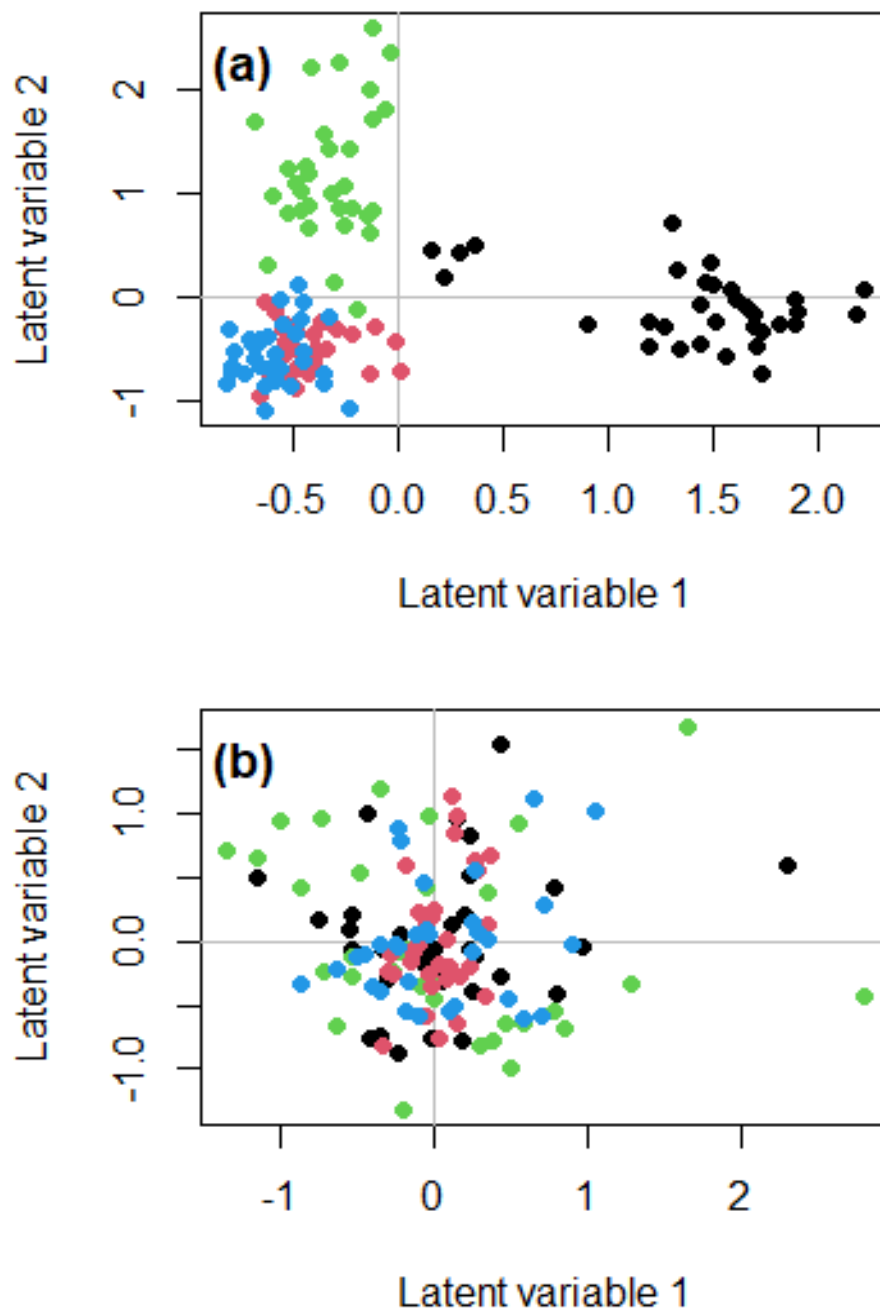
Figure 3.2. Model based latent ordination biplots displaying differences in soil fauna composition across different land-uses. The plots are presented as (a) an unconstrained biplot without predictors, and (b) residual biplot with predictors. Sites are represented by the coloured points as: Conservation = black; Integrated = green; Conventional = red; Natural = blue.
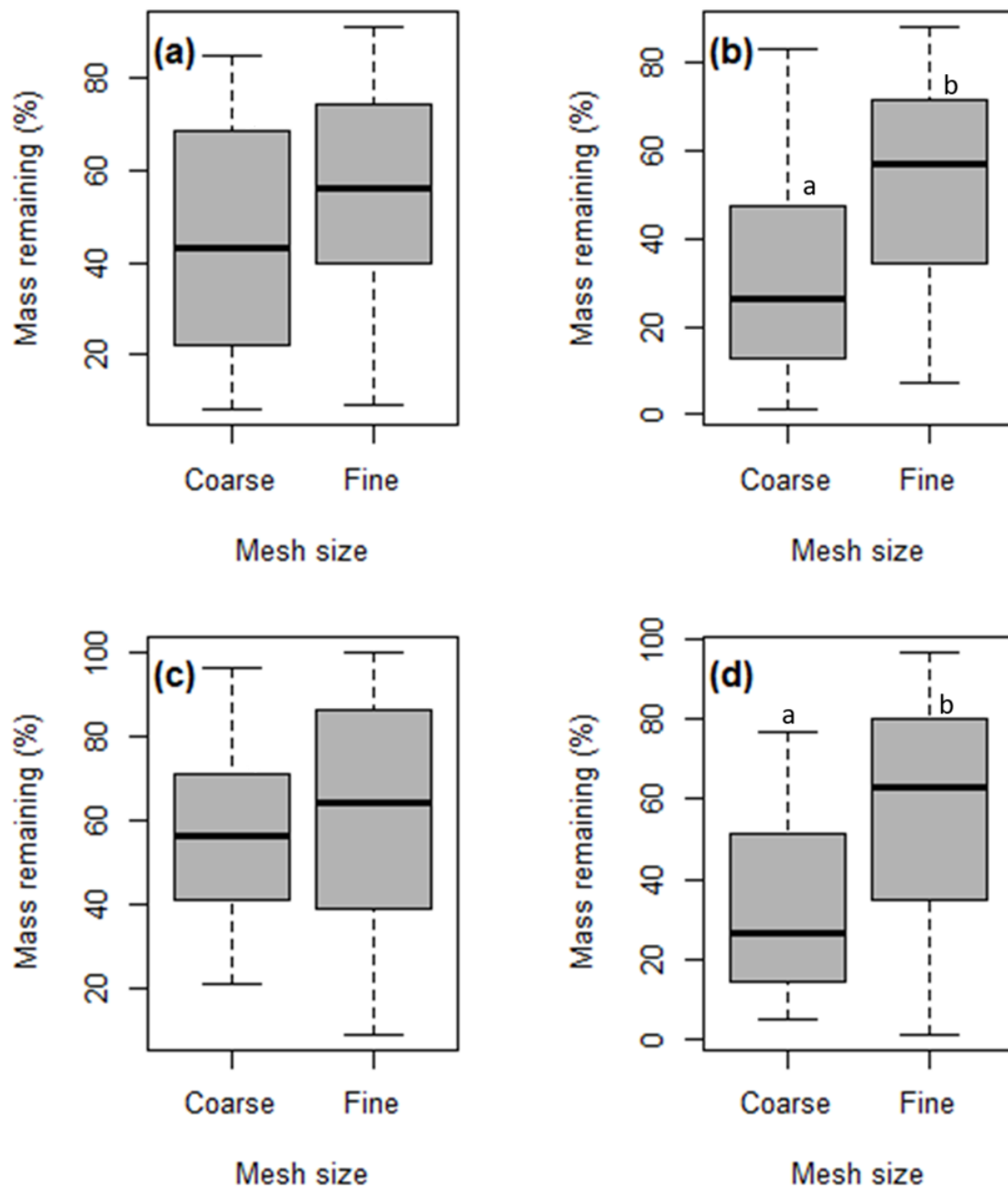
Figure 3.3. Comparison of the percentage remaining dry mass, between coarse mesh (fauna inclusion) and fine mesh (fauna exclusion) litterbags across the different treatments: (a) Conservation; (b) Integrated; (c) Conventional and (d) Natural. Bars with dissimilar letters are significantly different (Tukey's post-hoc tests at $p < 0.05$).
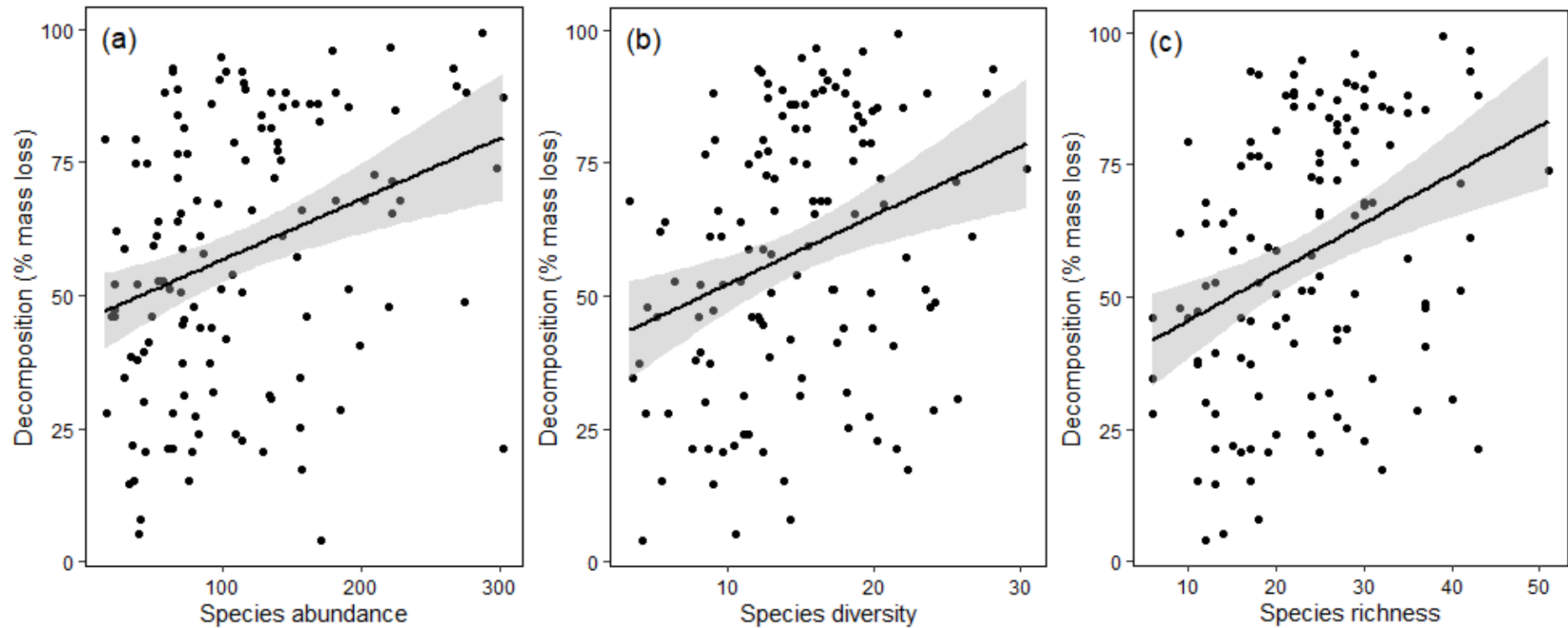
Figure 3.4. Model estimated relationship between litter percentage mass loss and detritivore species: (a) abundance, (b) diversity and (d) richness. The shaded grey area with a solid line represents the linear response at 95% confidence level.

Table 3.1. Effects of soil fauna species richness, abundance, and diversity on litter mass loss.

Factor (s)	Estimate	Std. Error	t-value	Pr(>|t|)
Abundance	0.05	0.04	1.47	0.14
Diversity	0.53	0.44	1.21	0.23
Richness	0.55	0.27	2.01	0.04*

* $p < 0.05$

Table 3.2. model-averaged estimates for the effects of environmental variables on soil fauna abundance, species richness, diversity, and percentage mass loss. Test statistics presented as z-values (abundance, species richness and diversity) and t-values (mass loss).

Factors	Abundance	Richness	Diversity	Mass loss
Temperature	-1.20	-2.18*	-2.38*	0.01**
Precipitation	-0.04	0.31	0.52	0.06
Soil moisture (%)	2.69**	2.30*	2.20*	0.04*
Litter cover (%)	2.99**	4.80***	5.29***	0.62
Vegetation cover (%)	4.39***	5.40 ***	5.22***	0.01**

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Table 3.3. Multivariate generalised linear modelling results, showing the effects of environmental factors on soil fauna assemblage composition.

Factor (s)	Wald χ^2 statistic	Pr(>wald)
Temperature	19.58	0.001 ***
Precipitation	16.84	0.001 ***
Soil moisture	20.78	0.001 ***
Litter cover (%)	21.32	0.157
Vegetation cover (%)	26.67	0.052

Test values were estimated assuming correlated response through ridge regularisation
P-values were estimated by means of 999 iterations through PIT-trap resampling.
*** $p < 0.001$

3.4. Discussion

Differences between land-use types were found in soil fauna species diversity, abundance, richness, and composition. The integrated and conservation land-use sites were considerably more abundant and diverse set of species, while the conventional was the lowest, which is not surprising considering the unfavourable conditions within this land-use i.e. chemicals, lack of soil cover, monoculture, and intense soil disturbance. The results corroborate findings from previous decomposition studies in agricultural landscapes, for example, Ke et al. (2005) found significantly low fauna in litterbags sampled from conventional land-use compared to less disturbed land-uses. In a related and most recent study, Cassani et al. (2021) also found similar results when they assessed the effects of agroecosystems on litter decomposition by soil fauna.

There was no significant difference between the abundance, richness, and diversity of assemblages from integrated and conservation land-uses. To provide a recap the examined land-uses, the conventional sites were managed under deep tillage and high applications of agrochemicals with little or no soil cover. On the other hand, the conservation and integrated sites were managed under zero or reduced tillage and organic fertilisation with complex habitat structuring and optimised soil cover. The key difference between sites of these two land-uses is that, the integrated sites had livestock (cattle) incorporated within the cropping systems. When considering the structuring of the obtained fauna, an interesting observation is that both the conservation and integrated land-uses had equally high fauna abundance and diversity, but very different species (see, Figure S3.1). Beetles (Coleoptera) showed sensitivity towards conventional sites, as shown by their high abundance within the integrated land-use. The sampled beetle species were predominantly generalist, meaning they are not diet specific and can therefore feed on whatever available food source e.g. dung, seeds, insects, organic matter, and plant material (Kalinkat et al., 2013; Kromp, 1999). So, it is not surprising that they were more abundant within the integrated land-use which is complex in vegetation, organic matter pathways and dung resulting from the integrated livestock. In the most recent study, Simba et al. (2022), also found dung beetles to be favoured by vegetation cover (including crops and spontaneous vegetation) in farmlands.

Low abundance of the soil fauna groups: Oribatida, Mesostigmata and Collembola, have been reported across intensively disturbed agricultural environments (see, Pollierer & Scheu, 2017). Likewise, in this study they were found to be lowest in conventional sites. Within this finding, Oribatida and Mesostigmata were more pronounced within the integrated land use, while Collembola was more pronounced within the conservation land use. All these assemblages

have life history characteristics which makes them sensitive or less adaptive to extremely disturbed conditions e.g. low dispersal, low fecundity, and long generational time (Behan-Pelletier, 2003; Laigle et al., 2021). Therefore, their relatively low abundance recorded within conventional sites can probably be attributed to the compaction of soil due to pesticide usage, tillage and lack of ground cover (George et al., 2017). The litter dwelling spiders (Araneae) were the only fauna group which was more abundant within the conventional land-use. This can be explained by their greater capacity to recolonize after a disturbance, primarily due to their high dispersal abilities, thereby making their populations to be less affected by practices such as tillage and agrochemicals (Teodorescu & Cogalniceanu, 2005). The fact that both the conservation and integrated land-uses were similar in species distributions highlights the significance of less intensive agricultural management for the protection of functional biodiversity and maintenance of their roles in ecosystem processes (i.e. nutrient cycling) (Domínguez et al., 2014; Huang et al., 2020).

Decomposition dynamics are likely to be affected by any change or loss of soil fauna species composition and diversity (Gessner et al., 2010). In this study this is reflected by the lowest decomposition rates coupled with significantly low abundance of important groups recorded within the conventional land-use sites compared to others. On the other hand, higher ecosystem function can be seen within the integrated land-use as reflected by high decomposition rates which are likely due to a good balance of diverse soil fauna observed in this land-use. The manipulation of litterbags with different mesh sizes is a typical practice for evaluating the influence of soil organisms to litter decomposition, assuming that changes in mass loss between the coarse and fine mesh litterbags are as a result of soil fauna activities (Wang et al., 2015).

Previous reports by García-Palacios et al. (2013) and Tan et al. (2021) found that the exclusion of soil fauna in litterbags considerably decreased the decomposition of litter by over 30%. Indeed, in this study significantly higher decomposition rates were also found in coarse mesh litterbags within the integrated and natural grassland sites, indicating that soil fauna contributed to the litter mass loss. No significant differences were observed in litter decomposition rates between the coarse and fine mesh litterbags in the conservation and conventional sites. Within conventional sites, the result is not surprising as it can be attributed to the significantly low soil fauna composition observed in this land-use. However, within the conservation land-use, this result is rather puzzling, considering the fact that the studied conservation sites incorporated practices such as increased crop diversity, reduced or no tillage, as well as low chemical

intensity which have been reported to improve soil detritivore communities (Domínguez & Bedano, 2016; Frouz et al., 2015).

Influences of soil fauna on ecosystem processes are complex, therefore understanding the relations between soil fauna diversity and decomposition has important implications for functional ecology, biogeochemical cycling, and soil health (Meyer III et al., 2011). Species richness appeared to be the main component of soil fauna significantly influencing leaf litter decomposition. In contrast, no significant correlations were observed between decomposition and abundance as well as decomposition and species diversity, despite the marked differences in these components between the different land-uses. A study conducted by Schmidt et al. (2015) also found no correlations between decomposition rate and soil fauna. The observed non-significant correlations can possibly be attributed to the soil fauna functional redundancy or the saturation of the decomposition process by detritivores' biomass as suggested by Patoine et al. (2017). Even though the activities and dynamics of microbes were not directly measured in this study, it can be possible that increased soil fauna diversity and decomposition within conservation and integrated sites was probably due to associations between microbes and detritivore arthropods (Carrillo et al., 2011). For instance, Peguero et al. (2019) found that the net soil fauna contributions to litter mass loss improved as the conditions for microbial decomposition were more optimised.

Effects of the abiotic environment have long been reported to regulate soil fauna populations and decomposition (García-Palacios et al., 2013). Through model selecting, factors which were most influential in soil fauna and decomposition dynamics were identified. Interestingly, when considering the effects of climatic variables on leaf litter decomposition, temperature was the most influential factor while precipitation had no effect whatsoever. Likewise, a meta-analysis of global decomposition predictors by Zhang et al. (2008) also found temperature to be more important than precipitation in litter decomposition process. Temperature was also found to be the driving factor for soil fauna species diversity, richness, and composition, of course this is somewhat not surprising because, favourable temperatures conditions have previously been reported to accelerate the activities of the decomposer groups and thereby resulting in increased litter decomposition rates (see, Aerts, 1997; García-Palacios et al., 2016; Peguero et al., 2019). With regards to habitat variables, vegetation cover seemed to be the most important factor influencing leaf litter decomposition compared to litter cover which did not have any influence. Although the results suggest that litter cover is not linked to decomposition, its relative importance to the process should not masked. This is, because it was found to be

strongly linked with both abundance, richness, and diversity, meaning, it contributed to the process indirectly by promoting important functional soil fauna species, which then resulted in increased decomposition rates. In light of these findings, García-Palacios et al. (2015) suggested that an increase in the biodiversity of soil fauna assemblages generally results in an increase in litter decomposition; this study therefore supports this notion and further reveals that climatic (temperature and moisture) and habitat variables (vegetation and litter cover) are important for facilitating the biodiversity increases and therefore, ecosystem function. It is interesting to note that soil moisture, plant cover and litter cover influenced all the fauna responses positively. The fact that soils within conventional sites were mostly bare while those within the conservation and integrated sites were covered with litter and complex vegetation, highlights the relative importance of more diversified management practices for creating suitable environmental conditions for the development and functioning of important soil fauna groups which will ultimately benefit agricultural productivity (Stroud et al., 2016).

The key difference between this study and preceding litter decomposition studies in agroecosystems is that a single litter species was used rather than multiple or mixed. Mixed litter has been reported to be more structurally complex than homogeneous litter as it has different breakdown stages therefore ensuring abundant resources and diverse niches for soil fauna (Huang et al., 2020). Even though, using the single litter species probably reduced the power of this study to detect complex effects associated with mixed litter species, confidence is drawn from Gessner et al. (2010), who confirmed that soil fauna diversity can influence decomposition rate and produce strong effects even when only a single litter type is present.

This study has shown how litter mass loss is affected by soil fauna and selected environmental factors. Although the temperatures and soil fauna proved to be beneficial for decomposition, other factors which were not incorporated in the study might mask the observed results. For instance, micro-climatic temperatures and humidity within the litter layer have the potential to lower or increase soil fauna diversity thereby influencing their roles in important ecosystem processes (Bradford et al., 2002). Additionally, litter quality has the potential to influence how soil fauna contributes to decomposition as some species have specific feeding preferences (Sauvadet et al., 2017; Leinaas et al., 2015), it will be interesting to see how the incorporation of these factors influence soil fauna decomposition dynamics.

3.5. Conclusion

The study assessed soil fauna contributions to litter decomposition in agricultural landscapes under different management and environmental conditions. Many studies have explored soil fauna decomposition dynamics under forest ecosystems, this is one of the very few studies which focused on agroecosystems, and the results seems to confirm assumptions that soil fauna exert an influence on litter decomposition. The rate of leaf litter mass loss increased in the presence of soil fauna within the coarse mesh litterbags compared to the fine mesh litterbags where soil fauna was absent. The results suggest that in addition to land-use intensity and local habitat conditions, soil fauna contributions to litter decomposition are to a large extent shaped by temperature and soil moisture. Generally, sites under conservation and integrated management proved to be beneficial and stable enough for soil fauna communities and the decomposition process itself through a good balance of diverse and functional fauna groups interacting throughout the decomposition process. Given that comparison of the results at a local scale was challenging, it is hoped that the study will encourage further decomposition dynamics research in agroecosystems of the studied region and possibly lead to better a understanding of the significant roles of soil fauna in maintaining nutrient cycling and other processes as this knowledge is important for the sustainability of production landscapes.

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CHAPTER 4

The soil physicochemical status of contrasting agricultural land-uses have differential effects on the community structure of soil fauna groups

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Abstract

The intensification of agricultural management practices has not only been linked to the degradation of important natural resources but also to the fluctuations in the soil environment, which plays an important role in regulating soil fauna biodiversity. Knowing how effects of soil physical and chemical properties associated with agricultural management effects on soil fauna functional groups is important for soil health and sustainability planning, however it has received limited research attention. Therefore, this study assessed the status of soil physical and chemical properties and their influence on soil fauna abundance and diversity in four contrasting land uses i.e. conventional, integrated, conservation and natural. The conventional land use favoured some nutrients, however both the integrated and conservation land uses integrated, and conservation soils had physical and chemical properties indicative of good soil quality e.g. low compaction, low C:N ratio and stable aggregates. Soil fauna abundance was more responsive to land use and the soil environment compared to species diversity which did not show significant responses as expected. Moreover, the physical status of soil had a greater influence on soil fauna than the chemical status. Overall, the analysed data provided an understanding that soil variables which regulate soil nutrient and water dynamics, mainly; the C:N ratio, calcium (Ca), magnesium (Mg), potassium (K), phosphorus (P), aggregate stability, clay, porosity, organic matter, and penetration are the main variables influencing soil fauna in agricultural soils. It is evident from the study that effects of the soil environment on fauna are complex, therefore, implementation of sustainable soil management practices which improves the physical and chemical status will not only be beneficial for productivity but also for the promotion of important soil fauna groups and ecosystem services they provide.

Keywords: fauna, soil health, environment, soil management, degradation

4.1. Introduction

Soil is an essential environmental interface which needs special attention to safeguard its functions for human wellbeing and ecosystem productivity (Janion-Scheepers et al., 2016; Silva-Olaya et al., 2022). It is defined as an active layer of unamalgamated material and biology covering the land surface fluctuating from the primary "parent" material with respect to morphological, biological, physical and chemical properties (Perkins et al., 2013). In agricultural landscapes, soils govern important ecosystem services and functions that are responsible for nutrient cycling, decomposition, plant production and resilience (Giller et al., 1997; Pant et al., 2017). The intensity of soil management practices have negative and positive influences on the soils and ecosystem services they provide (Ayuke et al., 2019).

The pursuits to feed an ever-increasing human population through intensive management has severely compromised the quality and productivity of agricultural soils, leaving them eroded and degraded with not much soil life (Sofo et al., 2020). Within this narrative, practices associated with tillage, residue burning and chemicals have been linked to reduced soil aggregate stability and organic matter due to soil erosion (Karlen et al., 2003). The destruction of soil and plant cover, through the application of conventional tillage has detrimental effects which not only affects the physical and chemical environment but also the biodiversity below and above ground (Domínguez et al., 2010). This affects functionality, because soil physical and chemical processes which significantly contributes to sustainable agricultural production greatly depend on the diversity and biological activities of soil fauna (Jiang et al., 2018). The goals of agro-ecological research have been centred on rethinking agriculture to achieve sustainable and cost-effective production (Coulibaly et al., 2022).

Conservation agricultural management practices can yield more food without exhausting and degrading natural resources at minimal costs (Nelson et al., 2009). Moreover, it can support water conservation and reverse the degradation of soil while improving its quality (Njaimwe et al., 2018). Over the past few decades, conservation management which is characterised by the reduction or absence of tillage, increased soil cover, and rotational cropping has gained widespread recognition for the maintenance of soil ecological stability and sustainable crop production (Kladivko, 2001). When compared with conventional tillage, these practices can minimize the erosion of soil, improve structure and organic matter as well as soil moisture (Hassan et al., 2022). It has also been shown to support nitrogen fixation by improving important soil physical and chemical properties such as temperature, humidity, permeability as

well as the maintenance soil biodiversity (Nuria et al., 2011; Rousseau et al., 2012; Zagatto et al., 2019).

The soil macro-and mesofauna (from here on referred to as soil fauna) forms a central part of the total soil biomass (Bitzer et al., 2018; Vincent et al., 2018). It contributes significantly to plant growth, leaf litter decomposition and overall biodiversity (Bottinelli et al., 2015; Jouquet et al., 2011). In agricultural soils, the functions of soil fauna groups have been extensively documented, especially its effects on soil physicochemical and structural properties such as soil aeration and formation, hydraulic characteristics, soil organic matter and bioturbation (Jouquet et al., 2011).

Several studies have shown that soil fauna biodiversity is not only influenced by land use but also by other factors related to habitat and environmental characteristics, including but not limited to the surrounding area, habitat connectivity, and complexity (Diehl et al., 2013; Plath et al., 2021). Importantly, the status of the soil physical and chemical (from here on physicochemical) environment also plays an important role in soil fauna biodiversity regulation in farmlands (George et al., 2017). Though soil biodiversity responds to the status of the soil physicochemical environment, they also have an impact on soil physical and chemical properties themselves, for example, burrowing activities of macrofauna such as earthworms construct macropores that are vital for hydraulic ecosystem services e.g. water retention, flow, and aeration (Hallam et al., 2021). This aids in the formation of soil aggregates as well as the mixing of organic particles into the soil (Kladivko, 2001).

There are many studies on agricultural soil physicochemical dynamics, which have drawn conclusions that intensive agricultural practices induce considerable changes in the soil physicochemical environment (de Tombeur et al., 2018; Mloza-banda et al., 2016; Njaimwe et al., 2018), however not much is known about the consequences and effects of these changes on soil fauna biodiversity in South Africa. Here I explore soil fauna and how it is related to soil physicochemical properties in four land uses. This study aims to explore: (1) how the distribution of soil fauna and physiochemical properties change within different agricultural land uses, and (2) the relationship between soil physicochemical properties and soil fauna biodiversity across the different agricultural land uses. This will allow us to determine the important link between soil fauna and the physiochemical world in which they live, because the soil can influence the fauna and vice versa.

4.2. Material and Methods

Study area and site selection

The study was carried out in the Free State province of South Africa, Thabo Mofutsanyane district at two key grain producing areas i.e. Bethlehem (28°01'S; 28°18'E) and Reitz (27°58'S; 28°18'E) (Figure S2). 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 non-experimental management types or treatments found within the farms were selected for sampling i.e. (1) Conventional agroecosystem: managed under tillage and monoculture cultivations with full chemical applications, (2) Conservation agroecosystem: managed under zero-tillage, crop diversification and soil cover, (3) Integrated agroecosystem: livestock (cattle & sheep) is integrated into the cropping systems for grazing and (4) Natural ecosystem: undisturbed natural land to be studied as a reference system to get a more comprehensive picture of the native soil diversity. A total of ten replicate sites distributed across four farms were sampled for each treatment, yielding an overall of 40 spatially heterogenous 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 at least 8 ha in area each and were managed with similar practices for more than 10 years before sampling.

The natural sites (approximately 1.5 ha) have been undisturbed and covered with natural vegetation for the past 40 years and largely characterised by the species *Chloris* sp., *Digitaria* sp., *Eragrotis* sp., *Andropogon* sp., and *Cymbopogon* sp. Some of the natural sites only had intermittent cattle grazing and trampling. 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 course of the study, either in mono or mixed cultivation setting 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 Table S1.

Soil fauna

Sampling was conducted over two seasons, 26th October to 4th November 2020, and 22nd March to 6th April 2021. Monoliths, pitfalls, and Berlese extractions methods were used to sample soil fauna. Monolith collections were conducted using procedures of the Tropical soil biology and fertility (TSBF) institute (Swift & Bignell, 2001). Four monoliths (25×25 ×30 cm) at 10 m apart were dug from each sampling plot after clearing a litter layer and hand sorted for fauna. Following the same procedure, four pitfall traps were placed 5 m away from each monolith sampling point at 10 m apart and filled with a mixture of ethylene glycol and a small amount of detergent to reduce surface tension (Souza et al., 2012). The traps were left out open for 7 days to reduce 'digging-in' effects (Greenslade, 1964). The sampled fauna were preserved with 70% ethanol and sent 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 ± 15 cm depth. The collected samples were marked and sealed in brown paper bags and extracted from the soil using the Berlese funnel technique at the laboratory for 72 hours (Espinaze et al., 2019). Arthropod identifications were made at genus and species level using appropriate published keys (Armstrong & Nxele, 2017; Dippenaar-Schoeman et al., 2010; Janion-scheepers et al., 2015; Joseph et al., 2018; Plisko, 2010, 2014; Plisko & Nxele, 2015; Schoeman et al., 2020). The morphospecies approach was adopted when species level identification was not possible (Beattie & Oliver, 1996).

Soil physico-chemical properties

Soils for physicochemical characterisation were collected from the 26th of October 2020 to the 4th November 2020 with the monoliths used to sample fauna using procedures adapted from Ayuke et al. (2019). Briefly after digging the monoliths, approximately 500 g of soil was collected from the 0-10 and 10-20 cm layers and mixed well and homogenized to attain composite samples. Soil sample was analysed for 19 variables, including: pH, available phosphorus (P), total nitrogen (Total N), total carbon (Total C), C:N ratio, calcium (Ca), sodium (Na), potassium (K), magnesium (Mg), soil organic matter (SOM), soil moisture (SM), water holding capacity (WHC), porosity (Poro), aggregate stability (AGS), bulk density (BD), penetration resistance (PR) (soil compaction), and soil texture (clay, sand, and silt). Total C and N were determined using the total combustion approach with an elemental analyser (Thermo Scientific, USA). pH was determined with KCL (Labcon pH meter), PR with a hand penetrometer, SM with a gravimetric method, SOM with the Walkley-Black method, P with Bray I method (AA3 Auto Analyser), soil texture with a hydrometer, while Ca, Na, K, and Mg

were determined with the 1M ammonium acetate extract (5300 Elmar Optima). AGS was measured using the wet sieving method Kandeler (1996). The analyses were conducted by the Natural Resources Institute and iThemba labs.

Data analysis

Soil fauna and physicochemical responses to land use management

Before conducting the analyses, arthropod samples for each collection method were pooled and analysed together. Beetles, earthworms, collembolans, and spiders were classed and used as the study's focal taxa, due to their abundance, complex functionally and links to many ecosystem processes (Coulibaly et al., 2022). R statistical software version 3.6.3 was used to complete all the analyses (R Core Team, 2020). Shannon species diversity was estimated using the *hillR* package of diversity (Li, 2021). Both the abundance and diversity data assumed a normal distribution when tested with Shapiro-Wilks tests. The *lme4* package (Bates et al., 2015) was used to generate linear mixed-effects models (LMMs) to determine the response of soil fauna abundance and diversity to different land uses. Spatial autocorrelation was detected when tested with the Moran test in the *ape* package (Paradis et al., 2022), therefore "site" was specified as a random variable in all the models. Chi-square (χ^2) and probability (*p*) values were estimated for each model, thereafter, Tukey post-hoc was used for pairwise comparisons with the *multcomp* package (Hothorn et al., 2008). LMMs and Tukey post-hoc were also used to determine whether soil variables differed between the land use sites, but, firstly, the *corpcor* package (Schafer et al., 2017) was used to test for collinearity between the soil variables with a spearman rank order correlation. Strongly correlated variables (r > 0.5 or r > 0.5) were carefully selected for either inclusion or exclusion from the analyses. Soil moisture, sand and silt were excluded due to significantly higher correlations with other variables. As a result, 16 out of 19 soil variables were included in the statistical models.

Effects of soil variables on soil fauna abundance, diversity, and composition

To determine the effect of soil variables on fauna abundance and diversity responses LMMs were calculated. To begin with, multicollinearity between soil variables was measured using the *car* package (Fox et al., 2019) by calculating the variance inflations factors (VIF) on rescaled variables, factors with VIF scores of < 3 were excluded from modelling (Zuur et al., 2010). Best models were identified and selected using the forward selection procedure based on AIC values within the *AICcmodavg* package (Mazerolle, 2020). Models with the lowest AICc value of ≤ 3 were used in model averaging. The distance based linear modelling and

canonical correspondence analysis (CCA) were used to test for effects between soil fauna composition and soil physicochemical variables (Ter Braak, 1986). A bioenv analysis with Spearman's correlation was conducted to select the group of variables that best explain variations in the datasets, this was done to prevent the probability of correlated variables giving false positive results. The tests were randomly permutated 999 times to standardise distribution and allow variables comparisons (Legendre & Gallagher, 2001). All the multivariate analyses and results visualisation were computed with the *vegan* package (Oksanen et al., 2019).

4.3. Results

Differences in physicochemical properties across land uses

Land use had a significant influence on soil physicochemical properties (Table 4.1). When considering the chemical properties, pH differed significantly across the land uses, with the highest levels recorded within the conventional land use and lowest within the conservation land use. Phosphorus displayed statistically similar patterns within the different land uses, though it was higher within integrated and lowest within the conventional land use. Total nitrogen and carbon were both higher within conservation land uses, but only total carbon differed significantly. The C:N ratio was significantly higher within the conventional land use. Of all the macronutrients, calcium, was high within the integrated soils, while sodium, potassium, and magnesium were highly concentrated within the conventional soils. Sodium was however relatively similar within the land uses due to the observed non-significance.

When considering physical properties, aggregate stability was significantly different and highest within the conservation land use. Bulk density on the other hand, was high within the conventional land use, but not significantly different across the land uses. Porosity was high within the integrated but not significantly different across the land uses. Percentage soil water holding capacity, moisture, clay content, and penetration resistance differed significantly across the different land uses. Water holding capacity, and clay content were higher within the conservation land use, while organic matter was highest within the integrated land use. Lastly, penetration resistance was found to be higher within the conventional land use.

Soil fauna abundance and diversity differences across land uses

Overall soil fauna abundance differed significantly across the land uses ($\chi^2 = 13.89$, p = 0.003) with the highest abundances recorded within the integrated land use (see, Figure S4.1a). Beetles were significantly different and higher within the integrated land use ($\chi^2 = 15.13$, p = 0.002) (Figure 4.1a). According to the post-hoc test beetle abundance did not differ between the

conservation and conventional land use (z-value = -2.45, p = 0.007). Collembola abundance was high within the natural land use but did not differ significantly within the land uses (χ^2 = 6.27, p = 0.10) (Figure 4.1c). Earthworms were significantly higher within the integrated land use and two times lower within the conventional (χ^2 = 15.16, p = 0.002) (Figure 4.1e). Spider abundance was high within the natural land use and significantly different across the land uses (χ^2 = 10.78, p = 0.01) (Figure 4.1g). Although the main test revealed significant differences, post-hoc test revealed that spider abundance only differed between the natural and conventional land uses (z-value = 3.40, p = 0.004) while the others are relatively similar.

The overall soil fauna species diversity was high within the conservation land use but did not differ between the land uses (χ^2 = 6.08, p = 0.11) (see, Figure S4.1b). Species diversity of beetles differed significantly and highest within the integrated land use (χ^2 = 8.07, p = 0.05) (Figure 4.1b), the differences were however not too extreme, as they were only detected between the integrated and conventional land uses (z-value = 2.89, p = 0.02). Collembola diversity was high within the natural land use and low within the conservation land use, but it was not significantly different between the land uses (χ^2 = 0.69, p = 0.87) (Figure 4.1d). The diversity of earthworms was also not significantly different, although highest within the conventional land use (χ^2 = 1.80, p = 0.62) (Figure 4.1f). Spider diversity also followed a similar trend with no detectable differences between the land uses (χ^2 = 4.75, p = 0.19) (Figure 4.1h).

Effects of soil physicochemical properties on soil fauna

Model averaging results revealed that soil physicochemical properties contributed much to the variation in soil fauna abundance and diversity (Table 4.2). Overall abundance was significantly affected by C:N ratio (F = 9.69, p = 0.004) and organic matter (F = 48.89, p = 0.033). Beetle abundance followed the same overall pattern, of also being significantly influenced by C:N ratio (F = 11.49, p = 0.002) and organic matter (F = 6.34, p = 0.017). Collembola abundance was affected by penetration resistance (F = 4.40, p = 0.043) and C:N ratio (F = 5.69, p = 0.022). Earthworm abundance was significantly influenced by calcium (F = 14.36, p = 0.001), magnesium (F = 3.25, p = 0.044) and C:N ratio (F = 5.71, p = 0.022), while spiders were only significantly influenced by the content of clay (F = 4.79, p = 0.034). An interesting trend observed in the overall results is that C:N ratio stands out as the most significant and influential variable for all soil fauna groups' abundance with the exception of spiders.

As shown in Table 4.2, soil physicochemical properties also contributed significantly to the variation in soil fauna species diversity. The overall soil fauna diversity was to a large extent influenced by aggregate stability ($F = 19.02$, $p < 0.001$) and organic matter ($F = 4.35$, $p = 0.05$). The species diversity of earthworms was significantly influenced by potassium ($F = 3.30$, $p = 0.002$), aggregate stability ($F = 4.13$, $p = 0.008$) and C:N ratio which exerted a negative influence ($F = 2.12$, $p = 0.04$). Interestingly, the species diversity of spiders was only influenced by aggregate stability ($F = 9.83$, $p = 0.003$). Another interesting observation shown in the results is that none of the measured soil physicochemical variables significantly influenced the species diversity of both beetles and Collembola ($p > 0.05$).

The distance based linear modelling results showing effects of soil physicochemical properties of soil fauna assemblage composition are illustrated in Table 4.3. The CCA biplots in Figure 2 illustrates the strength and direction of the effects. The results show that overall assemblage composition was significantly by clay (pseudo-$F = 1.37$, $p = 0.034$) and the C:N ratio (pseudo-$F = 1.77$, $p = 0.001$). Beetles were significantly and negatively influenced by C:N ratio (pseudo-$F = 1.80$, $p = 0.009$) (Figure 4.2a), Collembola was also significantly but positively influenced by the C:N ratio (pseudo-$F = 2.10$, $p = 0.026$) (Figure 4.2b). Earthworms were significantly and positively influenced by clay content (pseudo-$F = 1.48$, $p = 0.032$) (Figure 4.2c). Spiders were significantly and negatively influenced by aggregate stability (pseudo-$F = 1.81$, $p = 0.002$), C:N ratio (pseudo-$F = 1.76$, $p = 0.004$), and Clay (pseudo-$F = 1.47$, $p = 0.041$) (Figure 4.2d).

Table 4.1. Test statistics for the differences in soil physicochemical variables between the four studied land uses. Bold values and different letters denote significant differences between the land uses according to Tukey's post-hoc tests at $p < 0.05$.

Variables	Conservation	Integrated	Conventional	Natural	F-value	Pr(>F)
pH	5.71_a	6.2_{ab}	7.11_b	6.4_{ab}	3.018	**0.042**
Total N (%)	0.39	0.35	0.30	0.24	0.622	0.605
Total C (%)	4.30_a	2.65_b	2.80_b	2.14_b	9.610	**<0.001**
C:N ratio	12.6_b	10.5_b	16.1_a	15.7_a	13.80	**<0.001**
P (mg/kg)	1.78	1.92	0.70	1.34	2.071	0.121
Ca (mg/kg)	1.09_a	3.64_b	0.58_a	0.93_a	5.093	**0.005**
Na (mg/kg)	0.30	0.02	0.34	0.25	2.374	0.086
K (mg/kg)	0.66_a	0.24_{ab}	0.70_a	0.13_{bc}	3.886	**0.017**
Mg (mg/kg)	0.62_{ab}	0.40_{ab}	1.38_a	0.25_b	3.747	**0.019**
AGS (%)	85.5_a	70.3_b	83.1_{ac}	80.7_{ab}	4.699	**0.007**
BD (gcm−3)	1.24	1.09	1.63	1.251	2.314	0.092
Poro (%)	39.7	47.5	37.5	44.28	0.917	0.443
WHC (%)	84.3_a	78.2_{ac}	65.3_b	73.7_{bc}	12.16	**<0.001**
SOM (%)	15.8_a	28.40_b	8.50_a	14.2_a	12.22	**<0.001**
Clay (%)	45.2_a	33.8_{ab}	22.5_b	45.8_a	6.120	**0.002**
PR (%)	1.53_{ac}	1.07_a	2.02_b	1.87_{bc}	11.76	**<0.001**

BD: Bulk density; P: Phosphorus; Total C: Total Carbon; Total N:Total Nitrogen; SOM: Soil organic matter ; WHC: Water holding capacity; Poro: Porosity, AGS: Aggregate stability; PR: Penetration resistance; K: Potassium; Ca: Calcium; Mg: Magnesium; Na: Sodium
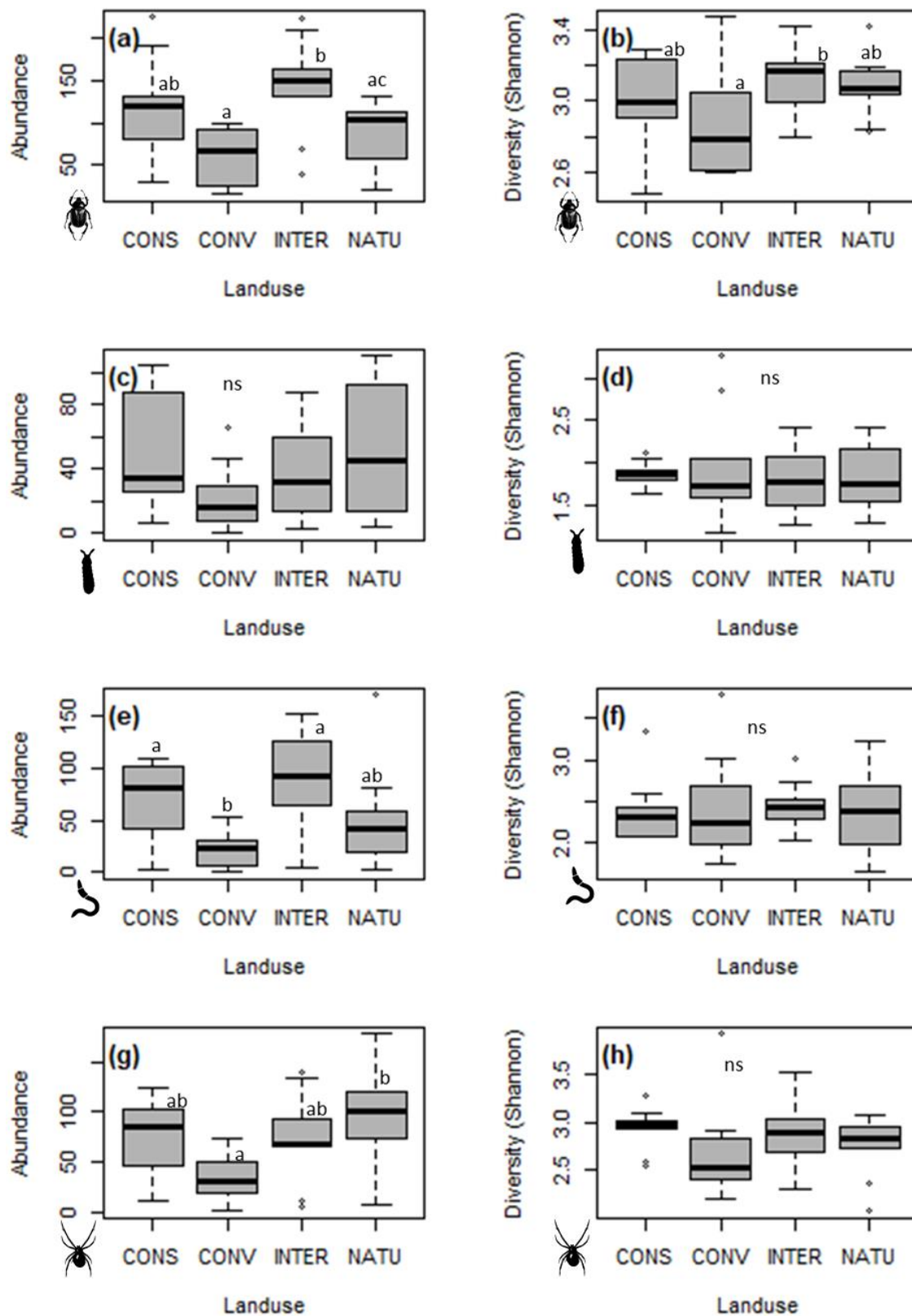
Figure 4.1. Differences in soil fauna abundance and diversity between conservation (CONS) integrated (INTER), conventional (CONV) and natural systems (NATU). Beetles (a and b), Collembola (c and d), Earthworm (e and f), and Spider (g and h). Mean values with dissimilar letters are significantly different (Tukey's post-hoc tests at p < 0.05), ns-non significance.

Table 4.2. Model-averaged estimates for the effects of soil variables on the abundance and species diversity (Shannon) of soil fauna assemblages.

	Abundance		Diversity	
Soil variables	F-value	Pr(>F)	F-value	Pr(>F)
ALL				
Phosphorus (mg/kg)	–	–	3.445	0.072
C:N ratio	9.689	0.004**(+)	–	–
Organic matter (%)	4.889	0.033* (+)	4.350	0.045*(+)
Aggregate stability (%)	–	–	19.021	0.000***(+)
Penetration resistance (MPa)	–	–	2.007	0.166
Porosity (%)	3.351	0.075	–	–
Bulk density (g cm^{-3})	–	–	1.784	0.191
BEETLE				
Phosphorus (mg/kg)	–	–	0.672	0.418
C:N ratio	11.490	0.002**(+)	–	–
Bulk density (g cm^{-3})	2.484	0.124	–	–
Magnesium (mg/kg)	–	–	3.662	0.064
Porosity (%)	2.121	0.154	–	–
Potassium (mg/kg)	–	–	0.001	0.972
Organic matter (%)	6.338	0.017*(+)	1.811	0.187
Clay (%)	–	–	0.924	0.343
COLLEMBOLA				
C:N ratio	5.692	0.022*(+)	–	–
Clay (%)	2.873	0.099	–	–
Penetration resistance (MPa)	4.400	0.043*(+)	–	–
Porosity (%)	–	–	3.443	0.071
EARTHWORM				
Calcium (mg/kg)	14.364	0.001***(+)	–	–
C:N ratio	5.705	0.022*(+)	2.118	0.042*(-)
Organic matter (%)	–	–	0.045	0.834
Aggregate Stability (%)	–	–	4.128	0.008*(+)
Potassium (mg/kg)	–	–	3.296	0.002**(+)
Magnesium (mg/kg)	–	–	3.251	0.044*(-)
Porosity (%)	2.720	0.108	–	–
SPIDER				
Clay (%)	4.787	0.035*(+)	–	–
Bulk density (g cm^{-3})	2.474	0.124	2.689	0.110
Water holding capacity (%)	–	–	1.870	0.180
Aggregate stability (%)	–	–	9.834	0.003**(+)

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Table 4.3. Distance-based linear modelling results of the effects of soil variables on soil fauna community composition. Test statistics are presented as F-values.

Soil variables	All	Beetle	Collembola	Earthworm	Spider
pH	–	–	1.697	–	–
Clay (%)	1.367*	1.234	–	1.478*	1.473*
Penetration resistance (MPa)	–	–	1.342	–	1.379
C:N ratio	1.772***	1.798**	2.101*	1.185	1.757**
Potassium (mg/kg)	1.141	1.262	1.110	–	0.982
Sodium (mg/kg)	–	–	0.831	–	–
Phosphorus (mg/kg)	–	1.374	–	–	–
Bulk density (g cm^{-3})	0.910	0.912	–	–	0.819
Organic matter (%)	–	–	1.246	–	–
Total Nitrogen (mg/kg)	–	–	1.395	–	–
Aggregate stability (%)	1.167	1.032	–	–	1.808**
Water holding capacity (%)	0.758	1.057	0.924	–	–

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$
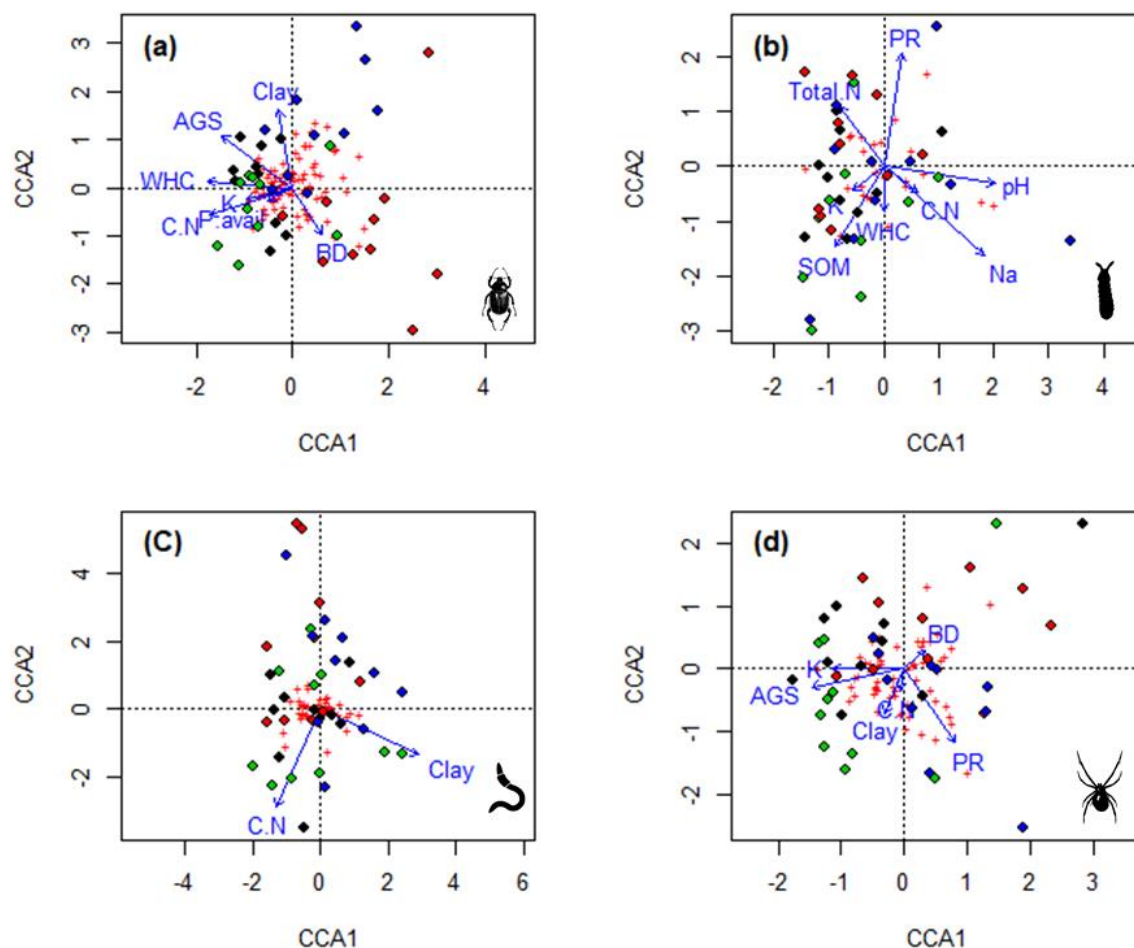
Figure 4.2. Canonical correspondence analysis ordination for soil variables that significantly influenced soil fauna assemblage composition, based on a distance based linear modelling. Sites are denoted by the coloured points as: Conservation = black; Integrated = green; Conventional = red; Natural = blue. (a) Beetle, (b) Collembola, (c) Earthworm and (d) Spider. The red crosses represent species scores. Refer to Table 4.1 for all abbreviations.

4.4. Discussion

Agricultural production and ecosystem functions are highly dependent on a good balance between soil biological and physicochemical resources (Garibaldi et al., 2019). The results reported here demonstrate that agricultural land use differentially affects the community structure and diversity of soil fauna by altering soil physicochemical properties which can either deter or promote soil fauna activities and functions. Soil fauna species diversity did not exhibit extreme significant differences across the land uses as expected, but abundance did show some very important variations. Modifications of the microclimate and the availability of food sources associated with agricultural management practices (agrochemicals, rotational cropping, tillage, inorganic fertilisation) can be attributed to these observations as they are known to have positive and negative influences on soil fauna biodiversity (Kamau et al., 2017; Vincent et al., 2018).

Generally, C:N ratio, calcium, magnesium, potassium, and phosphorus were found to be the most influential chemical variables affecting soil fauna, while aggregate stability, clay, porosity, soil organic matter, and penetration resistance were the most influential physical variables. The measured soil physicochemical properties did not contribute much to the variances in species diversity across the land uses, but they were quite important in regulating abundance and community composition. Soils within the integrated land use were less disturbed, enriched with soil organic matter, essential nutrients as well as low bulk density and resistance to penetration. While some important nutrients were favoured by conventional soils or did not differ significantly across the land uses, the integrated land use management essentially created suitable soil conditions e.g. water holding capacity, aeration which could serve as important features to reduce the negative effects of conventional agricultural management on soil fauna biodiversity while promoting their activities and functions.

The status of soil physical conditions can affect the hierarchical functions of soil biodiversity on soil ecosystems processes (Briones, 2014). For example, soil tillage alters soil aggregate stability, bulk density, and pore structure indirectly (Sithole et al., 2016), and this is primarily due to its influence on soil moisture, fauna, and organic matter redistribution (Gonçalves et al., 2020). Important differences were observed in the conventional land use soils, with higher soil penetration resistance "soil compaction" surpassing other land uses. Soil aggregate stability on the other hand was lower within the integrated land use and had significantly positive effects on the diversity of the overall soil fauna, earthworms, and spiders, while penetration resistance

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was found to only affect Collembola. It has been suggested that an increase in soil compaction and bulk density reduces aggregate stability and aeration, thereby having significantly negative effects on soil fauna (Duran-Bautista et al., 2020; Jouquet et al., 2011).

The clay content was considerably higher within the conservation land use and had a significant influence on earthworms, spiders, and the overall assemblage composition. An increase in soil fauna assemblages has been reported to increase in soils with high clay contents (Blanchart et al., 1999; Klok et al., 2007). The mechanism behind these effects is somewhat indirect and properly described by Baker et al. (1998), accordingly, clay contents influence soil properties such as cation exchange capacity (CEC) and soil water holding capacity which in turn influence soil fauna activities. The maintenance of organic matter through sustainable agricultural management is another interesting aspect of soil which is important for productivity and for the persistence of soil fauna functional groups. The levels of organic matter in this study were found to be low within conventional soils, exceeding the threshold amount of 20% within integrated land use, which is considered optimum for earthworms (Curry et al., 2002). Interestingly, soil organic matter did not have any effect on earthworms, this was not anticipated more especially because it is regarded as a good indicator of earthworm abundance, forming parts of their development, diet base and maintenance (Klok et al., 2007). Domínguez and Bedano (2016) also found similar results agricultural land uses under different levels of tillage and went on to suggest that maybe the most dominant species are less sensitive to lower contents of organic matter. Perhaps this could also be the case in this study, as different species are reported to be differently affected by soil organic matter (Li et al., 2009).

Although soil organic matter did not influence earthworms, it did have a significant influence on the abundance of the overall species diversity and abundance as well as the abundance of beetles. This finding was not unexpected because although most of the known beetle species are predators, some are coprophagous and saprophagous, meaning they depend on the decaying organic matter for nourishment (Aldebron et al., 2020; Culliney, 2013). Therefore, their population here was probably negatively affected by the non-significant organic matter within the conventional land use compared to the integrated land use which had a positive influence through rich organic matter resulting from dung deposited by the integrated livestock and residue retention practices (Bai et al., 2018; Coulis, 2021; Nependa et al., 2021).

When considering the soil chemical properties, the concentration of nutrients in agricultural soils holds key for estimating ecological functions and soil fertility (Jiao et al., 2019). The

stoichiometry of phosphorus, carbon, and nitrogen in particular can advance the understanding of nutrient cycling and ecosystem responses to disturbance and the changing climate (Bengtsson et al., 2011; Chen et al., 2018; Choudhary et al., 2018; Lou et al., 2012). In this study, the concentrations these three important nutrients exhibited inconsistent responses to land use management and soil fauna effects. The results show that both nitrogen and phosphorus were similar in concentrations across the different land uses and were not linked to any of the soil fauna. Interestingly, soil carbon was also not linked to any of the soil fauna groups, despite displaying significant differences across the different land uses. The non-significance between nitrogen and phosphorus is quite surprising because the land uses have different soil management practices and differed significantly in organic matter content which is known to increase nitrogen and phosphorus levels through the complex microbial activity (Bhat et al., 2017; Pant et al., 2017). Despite the recorded inconsistencies, the C:N ratio which is closely related to carbon and nitrogen did show some important results. It was lowest in the integrated and conservation sites and the most important variable significantly influencing the abundance and diversity of almost all the fauna groups with an exception of spiders. The lowest concentration of the C:N ratio recorded in the integrated and conservation land uses can possibly be attributed to the increased clay content compared to the other land uses as suggested by Lou et al. (2012). This is because, higher clay content has frequently been linked with lower C:N ratio and more decomposed organic matter (Lal, 1988; Ouédraogo et al., 2007).

Calcium, sodium, and magnesium are also important nutrients influencing soil fauna by driving the net primary production (NPP) of terrestrial dietary resources for fauna functional groups (Briones, 2018). They have also been linked to the development of body components such as exoskeletons (Ayuke et al., 2019). The higher concentrations of sodium and magnesium were recorded within the conventional land use which is not so surprising given the practice of chemical fertilisation in this land use. This observation is in line with Duiker and Beegle (2006), who previously reported that conventional management practices have no effect on magnesium and sodium. Unlike the other macronutrients, calcium concentration was high within the integrated soils. The exact cause for the low concentration of calcium in conventional soils compared to the other macronutrients is not completely clear, but the probable reason might be that it was less optimised in this land use, or it was simply lost during leaching (de Tombeur et al., 2018). Another interestingly observation detected here is that earthworms were the only fauna group which were significantly affected by calcium, sodium, and magnesium. The higher abundance of earthworms within the integrated land use can therefore be attributed to the

higher calcium concentration recorded in this land use. This is because this macronutrient has previously been reported to increase soil fauna abundance (Ohta et al., 2014; Springett & Syers, 1984). When looking at previous studies effects of both calcium, sodium, and magnesium on soil fauna are less clear with different studies reporting conflicting findings (Santana et al., 2021; Zechmeister-Boltenster et al., 1998), therefore further research is needed.

4.5. Conclusion

The quality of the soil physicochemical environment enriches conditions for the formation of the soil food web which functions to improve soil productivity and functionality. Land use intensification through conventional agriculture often leads to considerable losses of important soil nutrients which are most likely to affect soil fauna biodiversity adversely. However, in this study, soil physicochemical status showed certain degrees of differential responses to land use management with some considerable effects on soil fauna communities, more especially earthworms. Though in some instances conventional management favoured some beneficial soil properties more than the other land uses, the overall results highlight the complexity of the studied soil ecosystems and shows that good soil physicochemical environment and improved soil fauna biodiversity go hand in hand. Sustainable soil management is therefore important for conserving soil ecosystem function, productivity and diverse soil fauna groups which will ultimately improve soil health while mitigating agricultural soil degradation.

4.6. References

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CHAPTER 5

Soil macrofauna are important bioindicators of soil health in agroecosystems under different management

Abstract

Regenerative and resource conserving agriculture has gained recognition as a sustainable substitute to intensive agricultural models to reduce soil degradation and loss of ecosystem services. However, the major stumbling block to the successful implementation of these practices by farmers is the difficulty in measuring their sustainability and effectiveness. Understanding the status of soil health in agroecosystems has been proposed as a fundamental step towards agricultural productivity and sustainability. In this research, different indicators were used to evaluate soil health and function within differently managed land uses with special emphasis on soil macrofauna as biological indicators. Soil physical, chemical and biological samples were collected using soil monoliths within four land uses: (1) conservation management, (2) livestock integration within the cropping systems, (3) conventional management, and (4) natural grasslands used as reference sites. The obtained data allowed for the identification of soil macrofauna bioindicator species which represented important features of soil health (biodiversity, chemical fertility, and physical quality). The integrated land use demonstrated the uppermost values of soil health according to the biological, chemical, and physical indicators. Most of the indicator variables which indicated poor soil health were greatly associated with the conventional land use. The biodiversity indicator was found to be closely linked with the overall indicator, suggesting that soil macrofauna might be the major drivers of soil health but importantly can be used to assess overall soil health. Twenty-five species were identified as bioindicators of soil health. The soil macrofauna bioindicators could greatly simplify the assessments of land use management effects by farmers within the study area, thereby encouraging them to actively participate in decision-making concerning land use management. The overall results demonstrated that regenerative practices could restore degraded soils and ecosystem services.

Keywords: biodiversity, sustainability, agriculture, soil quality, indicators

5.1. Introduction

Soil is a multifunctional and central part of the ecological system producing fibre and food for human and animal consumption (Mulat et al., 2021). It is acknowledged as an important non-renewable natural resource because once degraded, it will take a lot of time and processes to regenerate (Lal et al., 1997). Given the significance of soil for livestock and crop production as well as for ecosystem services provision, soils of good health are important for sustainable and productive agriculture (Bai et al., 2018; Kibblewhite et al., 2008). Soil health (or quality) is essentially described as the ability of the soil ecosystem to provide satisfactory crop production for human sustenance, while upholding the environment's integrity and the biodiversity above and below ground (Doran & Zeiss, 2000).

Soil health has become a major research topic of interest more especially in developing countries because, as it rapidly addresses the challenges of sustainability and productivity (Okolo et al., 2020). According to Congreves et al. (2015) healthy soils will not only safeguard global food production through satisfactory crop yields under favourable climatic conditions, but will also endure adverse climatic scenarios and moderate the losses of nutrients. Over the past few decades, land use management associated with unsustainable agriculture has led to the destruction of natural plants and soil cover (Massaccesi et al., 2020; Perner & Malt, 2003), thereby resulting in the losses of soil structure, nutrient supply and the biodiversity performing important functions (Fiorini et al., 2020; Sanabria et al., 2014). This means loss of soil resilience and significant crop yield declines due to poor soil health and loss of ecosystem services (Foley et al., 2005).

To safeguard soils, ecosystem services, and food production, soil degradation has to be mitigated through the implementation of more sustainable agricultural practices. Regenerative practices such as crop diversification, rotations, reduced tillage as well as livestock integration within cropping systems, have been recommended as eco-friendly and sustainable alternatives of intensive practices (Goldman, 2019). Reduced soil tillage is frequently associated with less soil erosion, improved soil structure and nutrient distribution (Sithole & Magwaza, 2019), while livestock integration and crop diversity improves the biodiversity below and above ground as well as their vast ecosystem services (Bansal et al., 2022; Marja & Tscharntke, 2022). As farmers are gradually shifting towards more sustainable practices, they are challenged by the need to measure their effectiveness (Lobry de Bruyn, 1997), because successful implementation does not always mean the soil is productive or sustainable (Bünemann et al., 2018). This necessitates science based but cost effective and easy tools which can facilitate

farmers' decision making for managing their production systems effectively (Andrews & Carroll, 2001; Bai et al., 2018). The assessment of soil health under differently managed land uses can potentially identify the characteristics of unsustainable soils and the efficiency of production systems (Purakayastha et al., 2019). Soil health cannot be assessed directly but through a measure of biological, chemical, and physical properties, which are then used as indicators (Diack & Stott, 2001). Globally, relatively limited studies have been conducted to measure the appropriate indicators for assessing and monitoring soil health in agroecosystem (Bai et al., 2018; Nuria et al., 2011; Rinot et al., 2019; Rousseau et al., 2012; Sintim et al., 2019). In South Africa, some of the existing studies have largely focused on soil physical and chemical indicators (Sithole & Magwaza, 2019; Swanepoel et al., 2018) as well as the microbial communities such as nematodes and mycorrhizal fungi as biological indicators (Addison et al., 2013; du Preez et al., 2022; Kapp et al., 2013; Njaimwe et al., 2018).

This study focuses on soil macrofauna groups, which are the least considered in such assessments, to determine their status as bioindicators of soil health and function under different agricultural land uses. The specific objectives were to: (1) determine effects of agricultural management on soil health and function using biological (macrofauna), chemical and physical indicators, and (2) identify soil macrofauna bioindicator species using IndVal (indicator value index) and link them with different aspects of soil health, i.e biodiversity, chemical fertility, and physical quality

The soil macrofauna group were specifically used as model biological indicators because they are directly linked to soil health (Nuria et al., 2011; Lavelle et al., 2022; McGeoch, 1998) and perfectly fit into the criteria of reliable indicators of sustainability described by Doran and Zeiss (2000), in a way that they are (1) sensitive to environmental disturbance and therefore changes in their community assembly provides an integrative estimation of environmental quality (Vasconcellos et al., 2013), (2) their activities in the soil influence important ecosystem processes responsible for functionality and resilience (Giller et al., 1997) and, (3) they are relatively copious and visible to the naked eye, therefore, they can easily be monitored and measured by non-scientific expects such as farmers (Rousseau et al., 2013).

5.2. Material and Methods

Study area and site selection

The study was carried out in the Free State province of South Africa, Thabo Mofutsanyane district at two key grain producing areas i.e. Bethlehem (28°01'S; 28°18'E) and Reitz (27°58'S; 28°18'E) (Figure S2). 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 non-experimental management types or treatments found within the farms were selected for sampling i.e. (1) Conventional agroecosystem: managed under tillage and monoculture cultivations with full chemical applications, (2) Conservation agroecosystem: managed under zero-tillage, crop diversification and soil cover, (3) Integrated agroecosystem: livestock (cattle & sheep) is integrated into the cropping systems for grazing and (4) Natural ecosystem: undisturbed natural land to be studied as a reference system to get a more comprehensive picture of the native soil diversity. A total of ten replicate sites distributed across four farms were sampled for each treatment, yielding an overall of 40 spatially heterogenous 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 at least 8 ha in area each and were managed with similar practices for more than 10 years before sampling.

The natural sites (approximately 1.5 ha) have been undisturbed and covered with natural vegetation for the past 40 years and largely characterised by the species *Chloris* sp., *Digitaria* sp., Eragrotis sp., *Andropogon* sp., and Cymbopogon sp. Some of the natural sites only had intermittent cattle grazing and trampling. 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 course of the study, either in mono or mixed cultivation setting 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 Table S1.

Soil sampling and analysis

Biodiversity: soil macrofauna (2-20 mm) communities were used as an indicator of soil biodiversity and biodiversity processes (see, Lavelle & Spain, 2005). As ecosystem engineers, they ensure that microbial community composition and activities are regulated which justify their indicator status (Lavelle & Spain, 2005). Four soil monoliths (25×25×30 cm) at 10 m apart were dug from each sampling plot after clearing a litter layer and hand sorted for fauna, following standard methodologies of the Tropical soil biology and fertility (TSBF) institute (Swift & Bignell, 2001). Various methodologies exist for sampling soil fauna communities (Potapov et al., 2022; ISO, 2011) including the commonly used pitfall trapping. Pitfall traps were not used here so as to prevent redundancy in the biological properties of soil health (Rousseau et al., 2013) and to maintain consistency with the methodology application by Velasquez et al. (2007). Macrofauna species identifications were conducted using guides from published taxonomic keys (Armstrong & Nxele, 2017; Dippenaar-Schoeman et al., 2010; Janion-Scheepers et al., 2015; Joseph et al., 2018; Plisko, 2010, 2014; Plisko & Nxele, 2015; Schoeman et al., 2020). Fauna sampling was conducted over two seasons, 26th October to 4th November 2020, and 22nd March to 6th April 2021.

Chemical and physical: soils for physical and chemical analysis were sampled from the monoliths used to sample fauna using procedures adapted from Ayuke et al. (2019) from the 26th of October 2020 to the 4th November 2020. Briefly after the monolith excavations, 500 g of soil was collected from the 0-10 and 10-20 cm layers and mixed well to get composite samples. pH, available phosphorus (P), total nitrogen (Total N), total carbon (Total C), C:N ratio, calcium (Ca), sodium (Na), potassium (K), magnesium (Mg) and soil organic matter (SOM) were selected as indicators of chemical fertility. Aggregate stability (AGS), bulk density (BD), soil moisture (SM), porosity (Poro), penetration resistance (PR), and soil texture (clay, sand, and silt) were selected as indicators of physical quality. Total C and N were determined using the total combustion approach with an elemental analyser (Thermo Scientific, USA). pH was determined with KCL (Labcon pH meter), PR with a hand penetrometer, SM with a gravimetric method, SOM with the Walkley-Black method, P with Bray I method (AA3 Auto Analyser), soil texture with a hydrometer, while Ca, Na, K, and Mg were determined with the 1M ammonium acetate extract (5300 Elmar Optima). AGS was measured using the wet sieving method Kandeler (1996). The analyses were conducted by the Natural Resources Institute and iThemba labs.

Soil health indicators

To determine how different agricultural management systems influence soil health and function, multivariate procedures were implemented to obtain three sub-indicators, i.e., biodiversity (macrofauna order abundance), physical and chemical (ranging from 0.1 to 1) to be later summarized in one overall soil health indicator following procedures adapted from Velásquez et al. (2007). Firstly, principal component analysis (PCA) was conducted individually for each of the three sets of soil variables (chemical, physical and biodiversity) to identify minimum dataset that explains variation across different study sites. In addition, Co-inertia analyses were conducted on the PCA data to test for the relationships and similarities between the data sets (Dray et al., 2003). Variables with significant contributions to either of the two PCA axes (more than 50% of the maximum value) were selected and scaled to develop sub-indicators for each data set with values ranging from 0 to 1, this was done by subjecting the variables to homothetic transformation using the formulas (i) for variables with known positive soil health effects and variables with negative effects (ii) as follows:

$$(i)\,...\,Y = 0.1 + [(x - b)/(a - b)) \times 0.9)] \quad (ii)\,...\,Y = 1.1 - 0.1 + [(x - b)/(a - b)) \times 0.9)]$$

where Y = variable value after transformation; X = variable to transform; a = maximum value of variable and b = minimum value of variable. This procedure was done individually for each variable and resulted in three sets of sub-indicators i.e., biodiversity sub-indicator, chemical sub-indicator, and physical sub-indicator. The values of the three sub-indicators for each site were grouped in a data matrix and subjected to PCA. The contribution of each sub-indicator to the first two PCA axes and the total inertia explained were attained. The overall soil health indicator was obtained by combining the contributions of variables to factors 1 and 2 by the % inertia explained by factors. Sites with indicator values between 0.1–0.4 are considered of low health, 0.4–0.7 medium health, and 0.7–1.0 high health (Rousseau et al., 2013).

Characterisation of soil macrofauna indicator taxa

To identify specific soil macrofauna indicator species or taxa associated with sites of high soil health and function, the indicator value index (IndVal) method described by Dufrêne and Legendre (1997) was calculated as: $\text{IndVal}_{ij} = A_{ij} \times B_{ij}$. IndVal Index is the product of specificity (A_{ij} = presence of a species in a sample) and fidelity (B_{ij} = frequency of this species in that sample) and its value is between 0 and 100. A total of 108 species were analysed and each selected species was classified as bioindicator of low or high soil health relative to each sub-indicator and the overall indicator following methods by Rousseau et al. (2013).

Data analysis

All data analyses and visualisation were done using R statistical software version 3.6.3 (R Core Team, 2020). The Principal Component Analysis (PCA) and Co-inertia analyses (CoIA) were determined using the packages *ade4* (Dray & Dufour, 2007) and *FactoMineR* (Husson et al., 2020). The multivariate differences for the PCA and CoIA were estimated by means of the Monte-Carlo test at 9999 permutations using the "*randtest*" function within the *ade4* (Dray & Dufour, 2007) package. The packages *lme4* package (Bates et al., 2015) and *multcomp* (Hothorn et al., 2008) were used to compare the differences between the three soil health indicators (biodiversity, chemical and physical) and the overall indicator across the four land uses. IndVal was estimated with the multilevel pattern analysis using the *indicspecies* package (De Cáceres, 2022). The information presented in Tables S5.1 and S5.2 indicates a summary of soil macrofauna, chemical and physical variables used for the analyses.

5.3. Results

Soil health indicators

*Macrofauna***:** the first two axes of the soil macrofauna variables explained 38.66% of the overall variation (Figure 5.1). The PCA plot and the Monte-Carlo test displayed clear separations and significant variations (p < 0.001) amongst the different taxa (Figure 5.1a) and sites (Figure 5.1b). Araneae, Oligochaeta, Lepidoptera and Isoptera were most important groups positively correlated with axis 1 (21.39% variation) of the PCA. On the other hand, Dermaptera, Diplopoda and Hemiptera were negatively associated with axis 1. PC axis 2 (17.27%) was associated with the least abundant groups i.e., Hemiptera and Dermaptera.

*Chemical***:** the first two axes of the soil chemical variables explained 41.56% of the overall variation (Figure 5.2). The PCA plane shows a clear separation of sites within the first and second axes (Figure 5.2b), with the majority of variables being significantly (p < 0.001) associated with conservation and integrated land uses (Figure 5.2a,b). The first PC axis (26.64%) was highly associated with C:N ratio (negative), calcium (positive) and magnesium (positive), while the second axis (14.92%) was highly and positively associated with total nitrogen and carbon (Figure 5.2a).

*Physical***:** the total variation of 53.17% was explained by the first two axes of the soil physical variables PCA (Figure 5.3), with significant site separations (p < 0.001). The first PC axis (35.32%) positively associated with aggregate stability and negatively associated with variables of high soil compaction (bulk density and penetration resistance) (Figure 5.3a). These

variables seems to be driven by the conventional land use which is clearly separated from the other sites within the axes (Figure 5.3b). The second axis (17.85%) was significantly correlated with sand (negative) and clay (positive). The analyses of coinertia (CoIA) revealed significant covariation amongst all data sets (Table 5.1). Information of variables scores and contributions on each of the PCAs is presented in Table S5.3 and Figure S5.1. The sub-indicators for each soil conditions were developed based on the PCA, CoIA and Monte-Carlo test results. Seven out 10 variables were used for the biodiversity sub-indicator, eight out 10 variables for the chemical sub-indicator, while seven out eight variables were used for the physical sub-indicator. The overall soil health indicator was attained by totalling variable contributions to factors 1 and 2 of the PCA by the % inertia explained by the respective factors (Table 5.2).

Comparison of soil health across the land uses

The comparison of land uses according to the different soil health indicators revealed important and fairly consistent results (Figure 5.4). The biodiversity sub-indicator varied significantly between the land uses (F = 6.32, p = 0.001), with the highest values recorded within the conservation and integrated land uses. The conventional land use had intermediate biodiversity while the natural had the lowest, however, these two land uses did not differ significantly (t-value = -0.26, p = 0.99). The chemical sub-indicator also displayed significant differences (F = 6.56, p = 0.001), with the highest value observed within the integrated land use. The conventional and conservation land uses had contrasting chemical sub-indicator values, but they were not statistically different (t-value = -2.27, p = 0.13). When looking at the physical sub-indicator, none of the land uses reflected low value. Both the conservation and integrated land uses had high physical quality while the conventional and natural land uses were intermediate. Interestingly, the physical sub-indicator shows that the natural land use did not differ from the conservation (t-value = -2.61, p = 0.06) and conventional (t-value = 1.67, p = 0.35) land uses. The overall indicator also differed significantly between the land uses (F = 11.18, p < 0.001) and interestingly, it reflects the soil status which is quite consistent with the one observed for the biodiversity sub-indicator.

Characterisation of indicator taxa

Out of the taxa subjected to IndVal analysis, 25 were identified as significant bioindicators (p < 0.001) (Table 5.3). These included species from Araneae (3 spp.), Chilopoda (1 spp.), Coleoptera (4 spp.), Diplopoda (2 spp.), Hymenoptera (6 spp.), Blattodea (2 spp.), and Oligochaeta (7 spp.).

Biodiversity: nine taxa were found to be indicators of high biodiversity, including two termites *Trinervitermes dispar* and *Odontotermes* sp., two beetle species, *Phoberus* sp. and *Calosoma* sp., the spider *Trephopoda* sp., two earthworms *Dendrodrilus* sp. and *Lumbricus terrestris* as well as two ants *Trichomyrmex* sp. and *Camponotus* sp. The three ant species *Lepisiota* sp., *Pheidole* sp., and *Dorylus* sp., the beetle *Gymnoplerus leei* and the centipede *Paralamyctes* sp. were found to be indicators of low biodiversity.

Chemical fertility: the two earthworm species, *Eudrilus eugeniae* and *Pontodrilus* sp., as well as the ant *Camponotus* sp. were identified as indicators of high chemical fertility, while the diplopods *Brachyiulus* sp. and *Centrobolus* sp. were found to be indicators of low chemical fertility.

Physical quality: indicators of high soil physical quality were characterised by 17 species which are to a large extent dominated by seven earthworm species, including *Dendrodrilus* sp. *Lumbricus terrestris*, *Pontodrilus* sp., *Eudrilus eugeniae*, *Eisenia andrei*, *Microchaetus* sp. and *Lumbricus rubellus*. The termite species *Trinervitermes dispar* and *Odontotermes* sp. as well as the ant *Trichomyrmex* sp. were also found to be important indicators of soil physical quality. None of the identified indicator species were found to be associated with low physical quality.
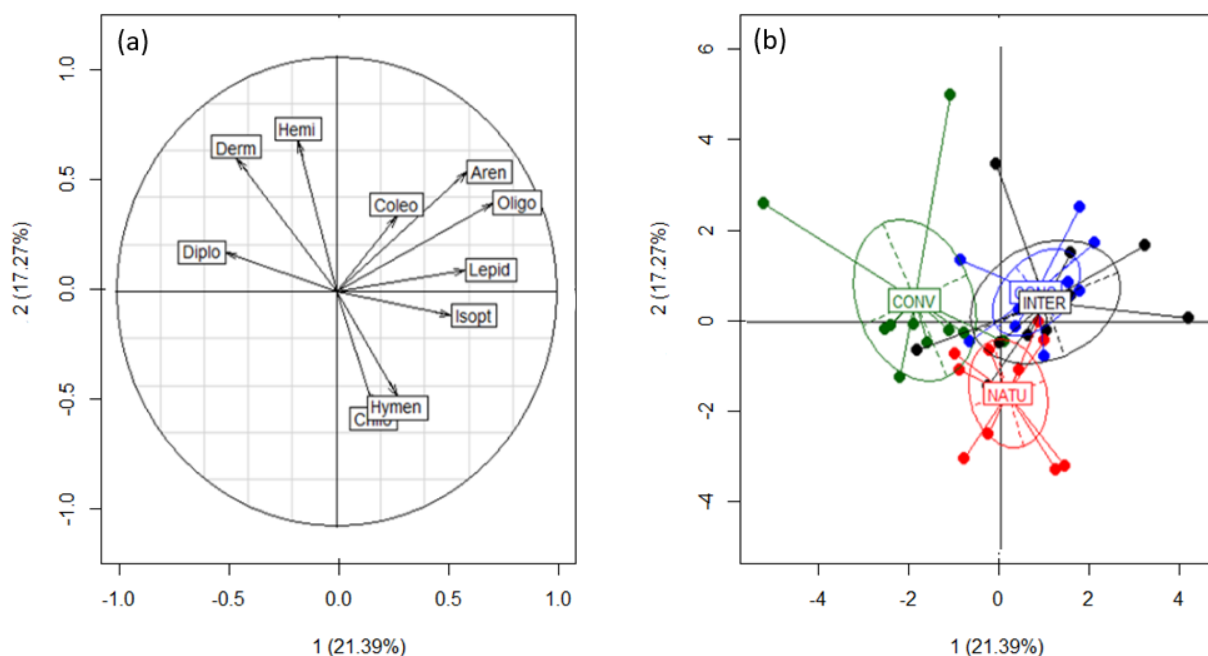
Figure 5.1. Principal components analysis (PCA) biplot of soil biodiversity showing (a) Correlation circle of soil macrofauna and (b) Projection of sites in the plane defined by factors 1 and 2. Conservation =CONS; Integrated =INTER; Conventional =CONV; Natural =NATU.
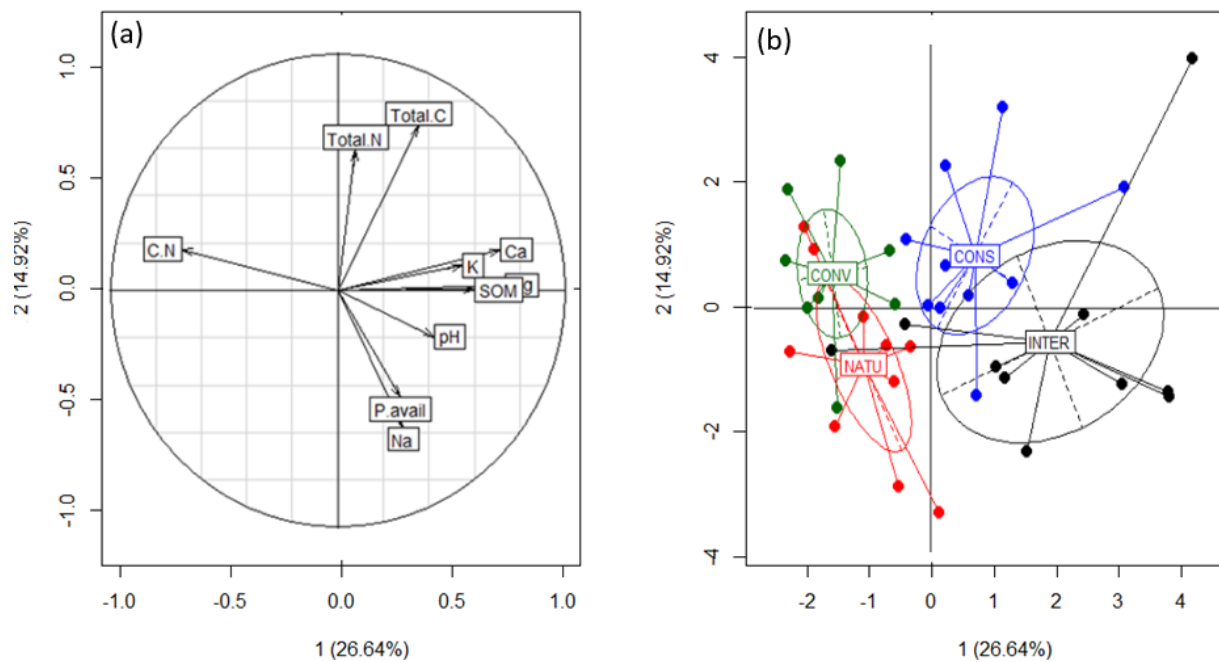
Figure 5.2. Principal components analysis (PCA) biplot of chemical soil variables showing (a) Correlation circle of variables and (b) Projection of sites in the plane defined by factors 1 and 2. Conservation =CONS; Integrated =INTER; Conventional =CONV; Natural =NATU.
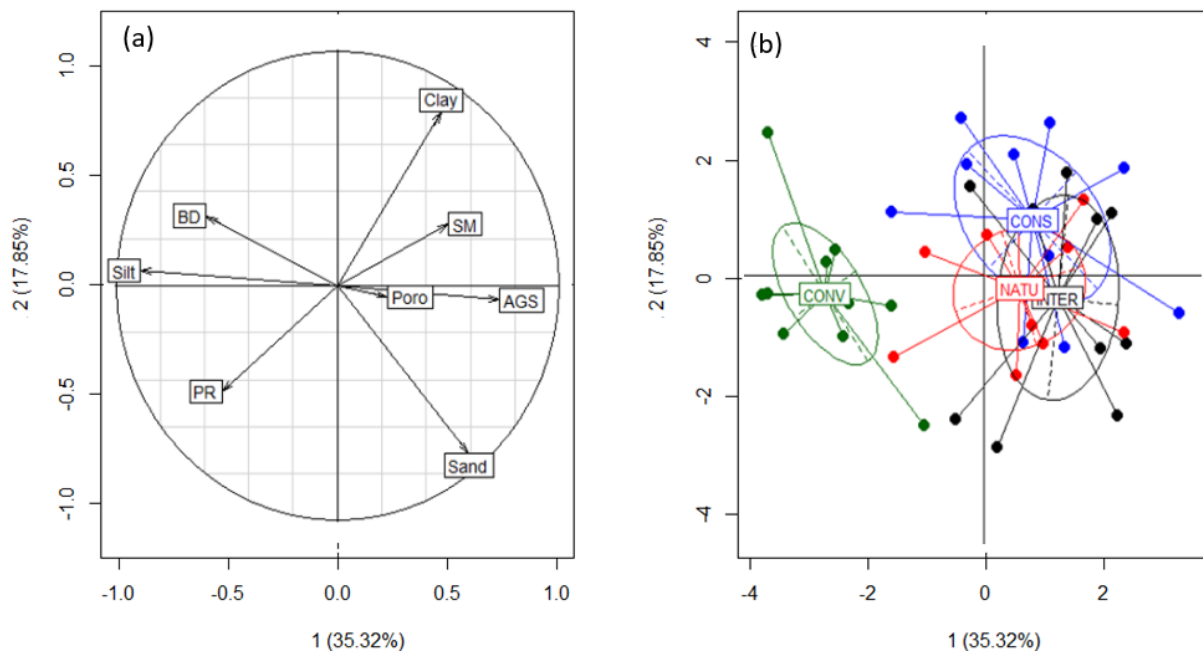
Figure 5.3. Principal components analysis (PCA) biplot of physical soil variables showing (a) Correlation circle of variables and (b) Projection of sites in the plane defined by factors 1 and 2. Conservation =CONS; Integrated =INTER; Conventional =CONV; Natural =NATU.

Table 5.1. Coinertia analyses matrix coefficient of covariation (RV) conducted on each pair of variable subsets. p-values estimated with Monte Carlo test (9999 permutations).

Variables	RV	p-value
Biodiversity and Chemical	0.36	0.001
Biodiversity and Physical	0.23	0.002
Chemical and Physical	0.24	0.002

Table 5.2. Contribution of each subindicator to Factors 1 and 2 of the PCA.

	Contributions		Factor inertia (%)		Contribution × Inertia		
	F1[a]	F 2[b]	F 1[a]	F 2[b]	a	b	Value
Biodiversity	0.917	-0.157	0.81	0.12	0.74	-0.02	0.72
Chemical	0.798	0.597	0.81	0.12	0.65	0.07	0.72
Physical	0.884	-0.347	0.81	0.12	0.72	-0.04	0.67
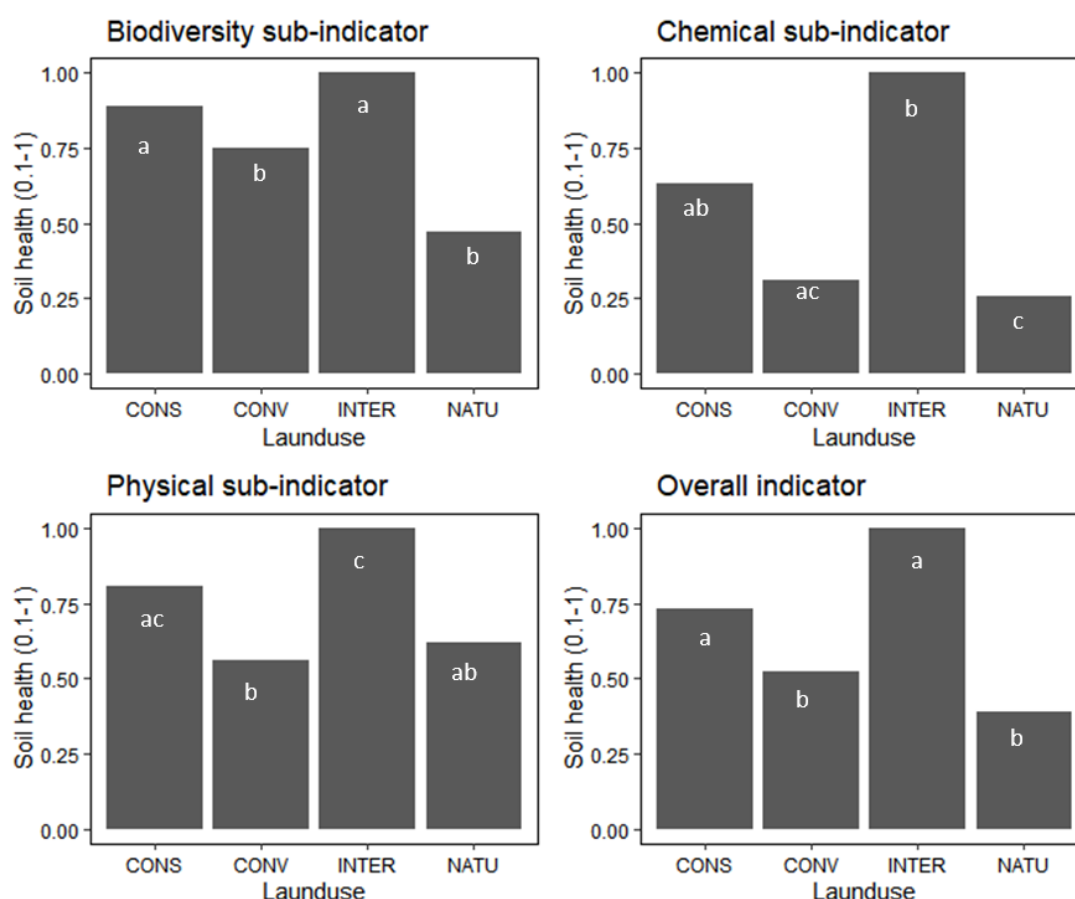
Figure 5.4. Comparison of soil health sub-indicators and the overall indicator under different land use managements. CONS = Conservation, INTER = Integrated, CONV = Conventional and NATU = Natural. Bars with different letters are significantly different (Tukey's post-hoc tests at $p < 0.05$).

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Table 5.3. Soil macrofauna indicator species determined with the IndVal method (p < 0.05), each species is classified as an indicator of high (↑) or low soil health (↓) according to the three indices.

Indicator species	Biodiversity			Chemical			Physical		
	IndVal	*p-value*	Class	IndVal	*p-value*	Class	IndVal	*p-value*	group
Odontotermes sp. (Blattodea)	65.00	0.023	↑				57.45	0.007	↑
Trephopoda sp. (Araneae)	44.36	0.009	↑				49.11	0.005	↑
Dendrodrilus sp. (Oligochaeta)	40.91	0.014	↑				42.86	0.004	↑
Trichomyrmex sp. (Hymenoptera)	40.00	0.018	↑				40.00	0.006	↑
Lumbricus terrestris (Oligochaeta)	35.53	0.045	↑				39.71	0.019	↑
Camponotus sp. (Hymenoptera)	33.65	0.046	↑				34.31	0.012	↑
Pontodrilus sp. (Oligochaeta)				59.46	0.001	↑	29.46	0.041	↑
Eudrilus eugeniae (Oligochaeta)				52.60	0.002	↑	30.51	0.032	↑
Tetramorium sp. (Hymenoptera)				41.25	0.015	↑			
Athia thoracica (Coleoptera)							43.25	0.025	↑
Gymnoplerus leei (Coleoptera)	30.00	0.029	↓						
Phoberus sp. (Coleoptera)	35.00	0.021	↑				35.00	0.008	↑
Trinervitermes dispar (Blattodea)	36.20	0.041	↑				42.00	0.015	↑
Rastellus sp. (Araneae)							39.13	0.030	↑
Eisenia andrei (Oligochaeta)							34.60	0.042	↑
Microchaetus sp. (Oligochaeta)							33.89	0.030	↑
Calosoma sp. (Coleoptera)	31.75	0.050	↑				33.29	0.024	↑
Lumbricus rubellus (Oligochaeta)							32.94	0.044	↑
Pardosa sp. (Araneae)							31.43	0.029	↑
Brachyiulus sp. (Diplopoda)				60.00	0.001	↓			
Centrobolus sp. (Diplopoda)				45.01	0.006	↓			
Paralamyctes sp. (Chilopoda)	46.60	0.012	↓						
Lepisiota sp. (Hymenoptera)	77.78	0.001	↓						
Pheidole sp. (Hymenoptera)	43.40	0.019	↓						
Dorylus sp. (Hymenoptera)	42.46	0.024	↓						

5.4. Discussion

The development of sustainable agroecosystems, while promoting biodiversity and ecosystem services provision, remains an important challenge for achieving conservation goals and food security (Andrews & Carroll, 2001; Velásquez et al., 2012). Here I assessed how different agricultural management systems influence soil health and functioning using different indicators. According to Doran and Zeiss (2000) the criteria for selecting soil health indicators is mainly based on their effectiveness in characterising ecosystem processes and integrating biological, chemical, and physical properties. To assess soil health, I adopted guidelines from Lavelle et al. (2021), to develop three soil health indicators which reflected soil function or its capacity to maintain: (1) biodiversity, (2) nutrient fertility, and (3) physical quality. The combination of the three indices allowed for the development of the general one which indicated the overall soil health. Soil macrofauna species which could serve as bioindicators of soil health and functioning were also identified. Overall, the studied agricultural management systems had significant effects on macrofauna, chemical and physical properties and therefore soil health. Though statistical differences were not observed in some instances, both the conservation and integrated land uses maintained quite consistent soil health values.

Land use management effects on soil health

The chemical sub-indicator which evaluates soil chemical fertility and its capacity to maintain crop production (Duran-Bautista et al., 2020) was fairly high within the integrated land use and showed intermediate values within the conservation land use. This sub-indicator displayed similarities between the conservation and conventional land uses. These two land uses were established differently and function under different principles and sources of inputs (Palm et al., 2014; Sithole et al., 2016), therefore, the observed result was not anticipated. The mechanism behind this observation might possibly be explained by factors associated with temporal and spatial variability (Lauber et al., 2013). For example, Chen et al. (2021) found that soil variables significantly changes with sampling depth and time. So, perhaps the comparison of chemical properties from soils sampled at different seasons and depth might yield clear or different results from those obtained here. Another possible explanation to the observed results could be that the synthetic inputs in the conventional system and the natural inputs in the conservation system have similar influences on the chemical composition of the soils, the physical sub-indicator reflected the soil hydrological status and physical conditions (Suárez et al., 2021). Although none of the land uses were found to have low soil physical quality, the multivariate analyses clearly separated bulk density, silt, and penetration resistance

from the conservation, natural and integrated land uses. These variables have frequently been associated with poor conditions which affect soil function and productivity e.g. soil compaction and the leaching of nutrients (Mulat et al., 2021; Okolo et al., 2020). The biological sub-indicator which evaluated soil biodiversity based on macrofauna (Sanabria et al., 2014), showed a trend which mirrors the soil health status displayed by the overall indicator. This observation is quite interesting and goes to show that better soil health is driven by the quality and quantity of the biological diversity. It is important to note that, the integrated land use maintained high soil health values regardless of the indicator type. This highlights the significance of practices such as soil cover, livestock integration and diverse crop rotations in providing stable conditions for the overall soil health maintenance and therefore, sustainability (Giller et al., 1997; Villanueva-López et al., 2019). This corroborates with the most recent study by Bansal et al. (2022), which also produced evidence that livestock integration within cropping increases diversifications and ecological benefits by improving energy flow and nutrient cycling, thereby increasing overall productivity.

Bioindicators of soil health

The soil macrofauna assemblages have been proposed as sustainability and soil health indicators due to their sensitivity and links with various ecosystem processes (Lobry de Bruyn, 1997; Rousseau et al., 2012). Although, the underlying mechanisms relating certain soil macrofauna species to soil processes might not always be clear, the identification of bioindicators provides important means of understanding land use effects on soil ecosystem function and stability. The IndVal results revealed that, biodiversity indicators were highly characterised by earthworms, termites, ants, and beetles most of which are composed of generalist feeders and taxa known to be sensitive to disturbance. The observed results can be explained by the fact that, reduced soil disturbance promotes micro-habitats diversification through structural complexity and the heterogeneous soil surface created by crop residues (Nuria et al., 2011). This subsequently leads to an increase in the diversity of weeds which provides refuge sites at the soil surface thereby enhancing herbivores availability for generalist feeders (Schmidt et al., 2005). Within this narrative, simple or less structurally complex landscapes, could experience drastic population decline of generalist arthropods due to low resource provision (Kromp, 1999; Marja & Tscharntke, 2022). The "ecosystem engineers" particularly termites and earthworms (anecic and epigeic) were the most important indicator taxa for soil physical quality. The activities of termites nest building significantly influence soil aggregation, porosity, air, and water flow (Kladivko, 2001). As the major ecosystem

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engineers, earthworm species have also been linked to functions which support crop production, including the formation of soil pores and water infiltration through their casting, burrowing, and feeding activities (Curry & Olaf, 2007; Stroud et al., 2016). The species, *Pontodrilus* sp., *Lumbricus terrestris*, *Lumbricus rubellus*, *Eudrilus eugeniae*, and *Eisenia andrei* were completely absent from the conventional land use (see, Table S2). The deep burrowing earthworms are highly sensitive to the occurrence of disturbance in their habitat; therefore, intense tillage activities significantly reduces their populations (Chan, 2001; Curry et al., 2002). The absence of some species within the conventional land use highlights the high intensification gradient existing within this land use. A single ant species was also found to be an indicator of chemical fertility, this observation is somewhat not surprising because ants have been illustrated to amend the soil chemical processes through pH modifications (Frouz & Jilková, 2008).

Farmers are slowly transitioning towards sustainable management practices in a quest to mitigate global challenges affecting crop production (Kuria et al., 2018). As these farmers are changing their production systems, they have a strong need to monitor or determine if the affected changes are actually beneficial (Lobry de Bruyn, 1997). Of course, various methodologies including the bioindicators have been used to assess the sustainability or effectiveness of agricultural land uses, environmental quality and restoration success (Nuria et al., 2011; Paoletti, 1999; Raiesi & Kabiri, 2016; Santorufo et al., 2012). While some studies have focused on characterising bioindicator taxa based on land use or habitat conditions (Curry, 2000; Shahabuddin et al., 2014), in this study, a different approach of relating the three sub-indicators of soil health to specific bioindicator taxa was adopted (Rousseau et al., 2013). This strategic approach provided robust but simple monitoring tools which reflect the status of soil health in a way that can persuade farmers within the studied region to affirm or change their management practices. For instance, the ants (*Tetramorium* sp.) of the family Myrmicinae were identified as bioindicators of good chemical fertility. Therefore, with appropriate training and identification guidelines, farmers who come across this taxon within their land uses will know that the area is enriched with important soil nutrients and organic matter. Similarly, farmers who come across the Scarabaeidae beetle *Gymnoplerus leei* will also know that the area's soil ecosystem is not biologically diverse. Indicating the need for corrective measures such as improved soil cover and vegetation complexity to attract more diverse arthropods below and above ground (Marja & Tscharntke, 2022; Theron et al., 2020). Although these

results are localised and likely only restricted to the sampling area here, this shows the value of understanding the local soil macrofauna for monitoring schemes.

5.5. Conclusion

The results from this study contribute to the important knowledge of understanding how intensive and regenerative agricultural practices shape soil function, stability, and production through soil health assessment. The status of soil health appeared to be affected by quite a few biological, chemical, and physical parameters within the different land uses, with different sub-indicators showing different responses. Notably, poor soil health was found to be associated with limiting parameters such as penetration resistance, bulk density, and silt, while good soil health was mostly reflected by total carbon, nitrogen, calcium, and sodium as well as the macrofauna groups, most importantly, earthworms, ants, and termites. In all the assessed sub-indicators, the land uses integrated with livestock consistently led to better soil health compared to the other land uses. This result highlighted the significance of farmland diversification for improving soil resilience and ecosystem services provision. Although only applicable to the studied region, the strategic application of IndVal allowed for the identification of important indicator species which could potentially assist farmers to measure the effectiveness of their production systems. Overall, the study demonstrates the potential of regenerative agricultural practices to maintain resilience and healthy soil.

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CHAPTER 6
General discussion and conclusions

Determining soil arthropod diversity responses to land use management

Responses of soil fauna diversity and functional group composition were compared between conventional, conservation and livestock integrated land uses to understand the ability of these land uses to sustain important biological functions. Variables relating to the complexity of vegetation and litter cover were the most important contributing factors to higher fauna populations in terms of species richness and functional groups distribution, therefore a well-balanced soil food-web (Marja & Tscharntke, 2022; Raderschall et al., 2022). Conservation and livestock integrated land uses were managed under different practices and principles with different habitat structures i.e., rotation, cover cropping, chemical inputs, vegetation complexity and soil management. However, they displayed almost similar patterns in arthropod diversity responses. There was a clear, consistent positive effect of conservation and integrated farming on arthropod species richness across different functional guilds. In some instances, they mirrored the reference natural sites which have no previous history of cultivation or anthropogenic disturbance. These findings confirm that proper soil management through e.g. minimal tillage, reduced agrochemicals and mimicking natural landscapes through crop diversification or habitat complexity goes a long way in preserving important soil fauna functional groups responsible for multi ecosystem functions.

Understanding soil fauna and land use effects on leaf litter decomposition

Litter decomposition is an important process that controls soil's biogeochemical cycles (Sauvadet et al., 2017). Its influence on the cycling of nitrogen and carbon is mainly associated with changes in soil fauna activities throughout the process (Verhoef & Brussaard, 1990). The findings from this chapter support those from chapter 2, confirming that sustainable farming practices not only benefit soil biodiversity compared to conventional farming, but also enhance ecological functioning in these agroecosystems. The results also showed that soil fauna contributions to litter decomposition were not only affected by land use factors but also by those related to climate and habitat structure. While the reported observations corroborate with previous studies (e.g. Bradford et al. 2002; Gessner et al. 2010; Tan et al. 2021), there is a need to look deeper into other possible contributing factors which were not explored here. For example, evidence about ecological traits of species is an interesting aspect which should be

considered in future studies as it can help predict the consequences of changes in community composition or biodiversity for focal ecosystem functions such as decomposition (Patoine et al., 2017). According to Gamez-Virues et al. (2015), species with different ecological features and requirements can differ in how they respond to land-use management and how they influence ecosystem processes. Likewise, a variability of ground-breaking functional diversity indices reflecting various aspects of biodiversity have been modelled based on trait information (Laliberté & Legendre, 2010; Lavorel et al., 2008; Paradis et al., 2022). While, other diversity measures can act as useful proxies of functional diversity in a community (e.g. evenness, richness and taxonomic diversity), direct classification of functional trait distribution effects is more likely to be a compelling predictor of soil fauna effects on the decomposition process (Fujii & Takeda, 2012). Body size has already been reported to be connected with decomposition rates in some studies (Briones, 2014; Gessner et al., 2010; Martins et al., 2020), however, other equally important traits (e.g. feeding habits, life forms, dispersal abilities) need to be thoroughly characterised in order to appropriately define ecosystem function dynamics.

Soil physicochemical characteristics and links with fauna

The characteristics of the soil physicochemical environment is important for quantifying important or limiting factors of soil productivity and function (Tresch et al., 2018). Here some important variables contributing to soil fertility were found to be more pronounced within the conventional land uses compared to the less intensive ones. While this may imply that the implementation of sustainable practices does not favour specific properties, confidence is drawn from the fact that integrated land use management created favourable soil conditions e.g., water holding capacity and aeration which could promote soil fauna functions while reducing effects associated with conventional agriculture. The quality or quantity of the assessed soil properties and fauna may to some extent change over time, however, the effects of management would most likely remain unchanged. Overall, the soil characterisation results highlighted the complexity of the conservation and integrated land uses in terms of soil characteristics distribution and fauna, comparable with Yu et al. (2022).

Soil macrofauna as bioindicators of soil health and function

Soil functioning is mainly regulated by biological activities; therefore, soil health should be in essence a measure of soil's capacity to host diverse fauna (Nuria et al., 2011). For the longest time, soil macrofauna have been known as good candidates for assessing land use management impacts on the environment (Santorufo et al., 2012). However, very few studies have so far managed to explore this dynamic more especially in soil health assessments (McGeoch, 1998).

Various studies have solely relied on chemical and physical variables as measures of soil health. For the first time at a local scale, this study identified and linked soil macrofauna bioindicator species with different aspects of soil health reflecting the capacity of soil to sustain: (1) functional biodiversity, (2) chemical fertility and (3) physical quality. The bioindicator strategy used here provided a robust technique of using soil macrofauna as tools which can potentially assist farmers measure the efficacy of their land management. This is particularly important for farmers who lack enough financial resources to access the usually expensive soil tests. Likewise, Doran and Zeiss (2000) and Andrews and Carroll (2001), also stressed that an appropriate indicator should not be costly to measure.

Management recommendations

The techniques which farmers and or land use managers use to manage their land can have significant influences on biodiversity, ecosystem services and productivity. This research revealed land use management as the main factor influencing soil fauna biodiversity, functioning, chemical fertility, and physical quality when compared to factors related to vegetation complexity. Overall, there was a clear benefit of integrated and conservation farming over conventional farming for increasing ecological integrity of these agroecosystems. This aligns with global patterns on the major biodiversity benefits of regenerative farming (Tamburini et al., 2020). Moreover, the research clearly showed that complex landscapes are important for enhancing important fauna and all-around ecosystem services which ensures resilience, soil health and productivity. Therefore, farmers who are interested in grasping the economic and ecological benefits of sustainable intensification are encouraged to:

- Incorporate soil conservation practices such as mulches, compost (through livestock), cover crops and residue retention as these practices have great potential for increasing soil health and functioning through optimising conditions for functional groups e.g., shelter and food.

- Limit soil destruction and agrochemical inputs as these practices were found to have detrimental effects on important soil biological groups which govern soil ecosystem functions. Deep tillage was found to be directly linked to the reduction of earthworm's populations as some species were completely absent in conventional fields. The loss of earthworms leads to losses of the soil's capacity to regulate many ecosystem processes and therefore soil health.

The reported results and methodology used here, more especially on the bioindicator tools are not only important for supporting the advancements of sustainable agriculture, but can also be applied for assessing the status of ecosystem health, restoration success, and ecological impacts (e.g. fire, drought, urbanization), in forests (Yekwayo et al., 2017), plantations (Eckert et al., 2019), floristic (Adedoja et al., 2019) and urban landscapes (Piano et al., 2020) which are equally important as agricultural landscapes.

Most farmers do not have enough resource to access the costly and complex soil health tests, they however have considerable knowledge of the various arthropods occurring in their fields (Rousseau et al., 2013). Linking soil macrofauna bioindicator species with various aspects of soil health is a strategic objective which will simplify soil assessments and management for farmers. With proper support, training and identification guidelines, the use of indicators can enable farmers to be more active participants agricultural land use assessments. The identified indicator species were to a larger extent dominated by beetles, earthworms, ants, spiders, and termites. These groups are not only important for regulating important ecosystem processes but are also familiar to farmers as they usually encounter them in their fields. A summary of the identified indicator taxa linked to different aspects of soil health is presented in Table 6.1. with recommendations for farmers.

Table 6. 1. Soil health recommendation based on indicator species.

Soil condition	Bioindicator species
Biodiversity	The species *Lepisiota* sp. (Hymenoptera: Formicinae), *Gymnoplerus* leei (Coleoptera: Scarabaeidae), and *Pheidole* sp. (Hymenoptera) are recommended as bioindicators of poor soil biodiversity. Farmers who encounter these species will know that the area's soil ecosystem is not biologically diverse. Highlighting the need for corrective measures such as improved soil cover and vegetation complexity to attract more diverse arthropods below and above ground.
Chemical fertility	The species *Pontodrilus* sp. (Oligochaeta), *Eudrilus eugeniae* (Oligochaeta) and *Tetramorium* sp. (Hymenoptera) are recommended as good indicators of chemical fertility. Farmers who come across this taxon within their land uses will know that the area is enriched with important soil macronutrients and organic matter.
Physical quality	The species *Trinervitermes dispar* (Blattodea), *Rastellus* sp. (Araneae), *Eisenia andrei* (Oligochaeta), *Microchaetus* sp. (Oligochaeta), *Pardosa* sp. (Araneae) *Lumbricus rubellus* (Oligochaeta) are recommended as bioindicators of good soil physical quality. Therefore, a farmer who encounter these taxa on particular plot of land will know that there is a low probability that the soil is compacted in this part of his/her farm.

Limitations and recommendations for future work

- The research design used here maximized the numbers of sites under actual agricultural management, this may increase confidence about the obtained results to a certain extent, however, some soil chemical variables are usually sensitive and more likely to be affected by temporal factors. Temporal factors were outside the scope of this study as this is often a trade off with spatial replication. However, temporal replication is an important consideration as it shows us how species turnover over time and how species will respond changes at the site level. The fact that only soil fauna was sampled for two season raises questions about the responses of some of the soil physicochemical variables to seasonal dynamics.

- The effectiveness and functioning of ecosystems can be examined with various existing methodologies, one being through species functional traits (Laliberté & Legendre, 2010). Which can predict the effects of management on important ecosystem functions through shifts in biodiversity structure (Patoine et al., 2017). In this study the analysis of fauna functional groups according to the community weighed means (CWM) provided important information about functional diversity, however this is complex, and some measures may only act as proxy.

- The fact that I was able to find indicators of soil health is a positive step towards local sustainable agriculture. The identified bioindicators proved to be robust and farmer friendly when analysing land use effects and soil health, however, they were not validated with local farmers. This farmer validation is in the realm of the social science and falls outside the scope of this study, but it is an important next step. Therefore, I encourage future work on the validation of indicator species with local farmers and analyse their knowledge and perceptions on different functions of soil macrofauna species occurring in their farms. This is will provide an important foundation for improving farmer understanding towards ecological interactions and processes which are some of the fundamental factors affecting land use management success (Pauli et al., 2012). Another important aspect which should be considered in future research is assessing how the conservation and or integrated farming are doing in terms of yield and yield stability over time (see, Kleijn et al., 2019). This is something that would greatly influence whether farmers would adopt these methods, more especially because they are yield driven.

Concluding remarks

The overall findings confirm that less intensive management systems have important benefits for soil properties, fauna, and important ecological processes. Increased biodiversity in a system increases the likelihood of increased ecosystem function, thereby increasing ecosystem productivity and resilience. This research has answered important questions related to agroecosystem sustainability, biodiversity, and soil health as well as the status of macrofauna as bioindicators, however, there is still much work and challenges remaining in this topic because it is as complex as the soils themselves. The findings provide the basis for assessing land use management effects on soil health. These results reveal the importance of soil organisms to soil health and illuminate the way forward for ecological monitoring of soil health in South African grain fields.

6.1. References

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APPENDICES

Appendix A: Supplementary material for chapter 2
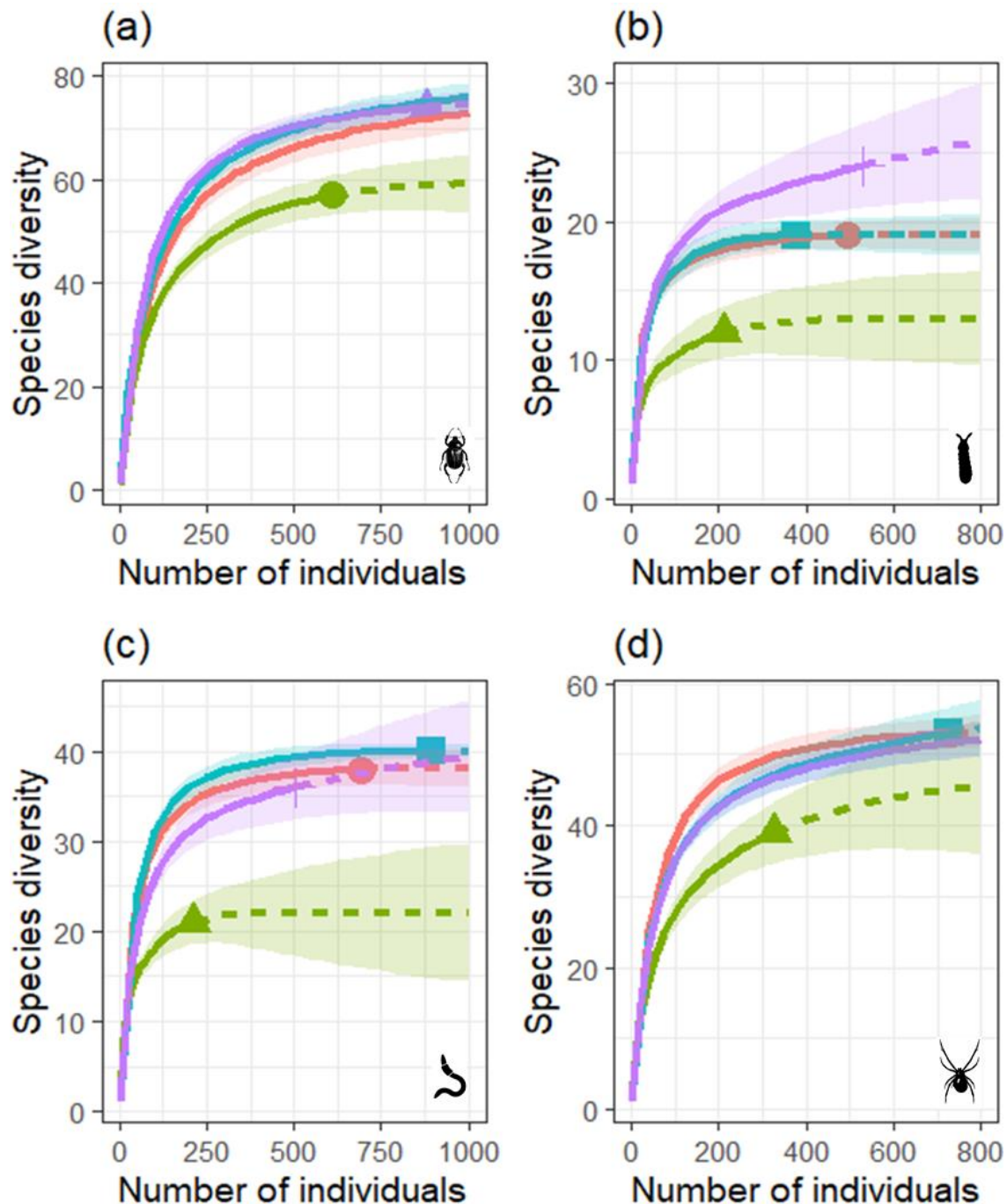
Figure S2.1. Species rarefaction curves for soil fauna groups: (A) Beetle, (B) Collembola, (C) Earthworm and (D) Spider. The curves represent observed interpolated (solid line) and extrapolated (dotted line) species richness in conservation(red), integrated(blue), conventional (green) and natural (purple) land use systems.

Appendix B: Supplementary material for chapter 3

Table S3.1. Multivariate generalised linear modelling results showing pairwise comparisons for the effects of land use management on detritivore assemblage composition.

	Observed test statistic	Adjusted P-value
CONS versus NATU	1432.4	< 0.001***
CONS versus CONV	1313.8	< 0.001***
CONS versus INTER	1290.5	0.01**
CONV versus INTER	1047.8	< 0.001***
INTER versus NATU	928.60	< 0.001***
CONV versus NATU	82.300	0.401

CONS = Conservation, INTER = Integrated, CONV = Conventional and NATU = Natural.
** p < 0.01, *** p < 0.001
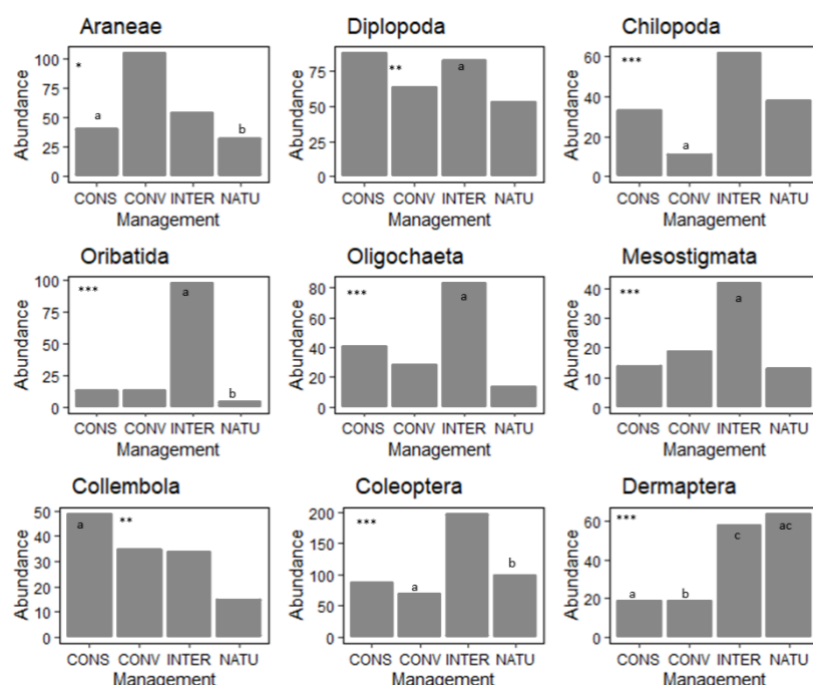
Figure S3.1. Total abundance of soil fauna groups sampled from litterbags across the different land-use types. CONS = Conservation, INTER = Integrated, CONV = Conventional and NATU = Natural. Bars with dissimilar letters are significantly different (Tukey's post-hoc tests at $p < 0.05$). * p < 0.05, ** p < 0.01, *** p < 0.001, ns- non-significant.

Table S3.2. Linear modelling results for the effects detritivore absence (fine mesh) and presence (coarse mesh) on litter mass loss measured as the percentage remaining dry mass.

	F-value	Pr(>F)
Conservation	2.7456	0.1026
Integrated	15.001	< 0.001***
Conventional	0.2942	0.5895
Natural	13.313	< 0.001***

*** p < 0.001

Appendix C: Supplementary material for chapter 4
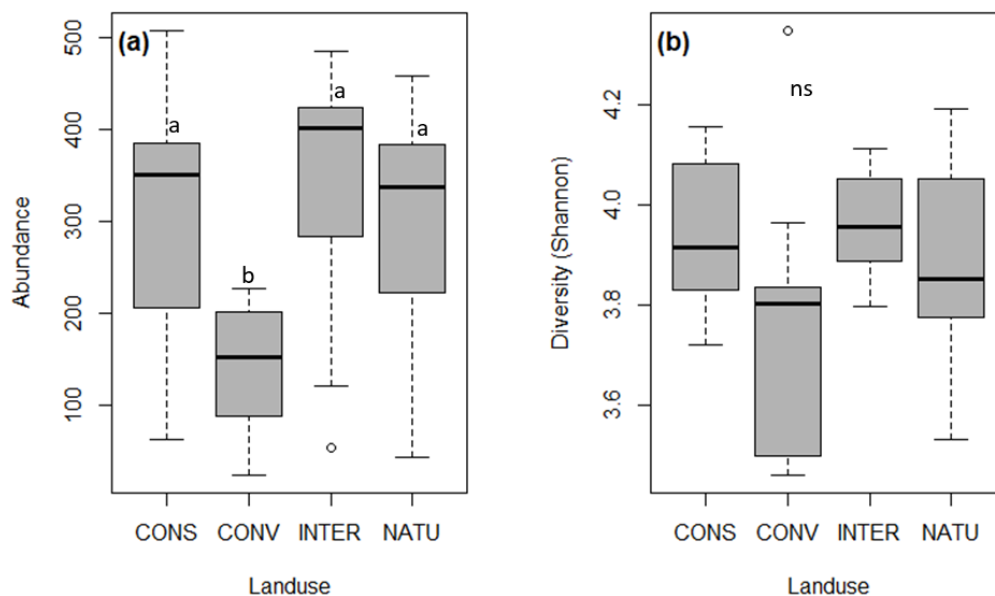
Figure S4.1. Differences in overall soil fauna abundance (a) and diversity (b) between conservation (CONS) integrated (INTER), conventional (CONV) and natural systems (NATU). Mean values with dissimilar letters are significantly different (Tukey's post-hoc tests at $p < 0.05$).
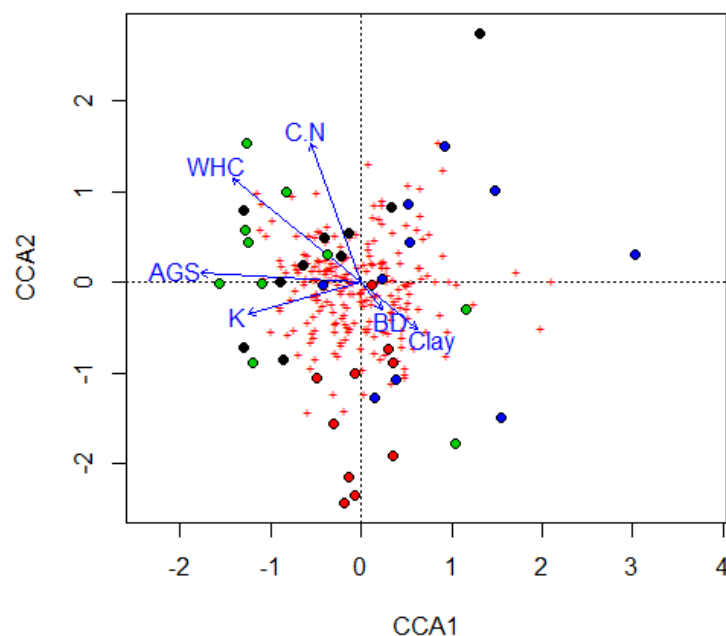
Figure S4.2. Canonical correspondence analysis ordination showing soil variables that significantly influenced the overall soil fauna assemblage composition, according to a distance based linear modelling and bioenv. Sites are represented by the coloured points as: Conservation = black; Integrated = green; Conventional = red; Natural = blue. BD: Bulk density; CN: Carbon and Nitrogen ; WHC: Water holding capacity; AGS: Aggregate stability; K: Potassium.

Appendix D: Supplementary material for chapter 5

Table S5.1. Mean and standard deviation (SD) of soil macrofauna abundance (individuals. m^{-2}) across the four studied management systems.

Taxa	Conservation		Integrated		Conventional		Natural	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Araneae	11.4 ±	5.04	9.90 ±	7.82	5.80 ±	6.75	4.20 ±	4.73
Chilopoda	1.40 ±	2.22	2.80 ±	4.05	1.90 ±	2.56	6.50 ±	9.30
Coleoptera	13.9 ±	13.4	10.0 ±	12.1	5.00 ±	5.40	10.9 ±	10.2
Dermaptera	2.50 ±	3.37	2.30 ±	3.40	5.30 ±	9.12	0.70 ±	1.06
Diplopoda	6.60 ±	4.25	3.80 ±	6.49	11.1 ±	8.32	7.60 ±	5.80
Hymenoptera	25.1 ±	23.4	17.3 ±	10.5	7.70 ±	5.58	52.7 ±	28.8
Hemiptera	2.40 ±	2.84	1.10 ±	2.47	4.10 ±	9.55	0.90 ±	1.45
Isoptera	7.30 ±	2.54	5.50 ±	3.10	2.30 ±	3.43	7.50 ±	5.70
Lepidoptera	13.3 ±	10.5	15.8 ±	15.7	5.20 ±	6.58	14.8 ±	15.3
Oligochaeta	36.2 ±	28.5	50.6 ±	31.1	2.20 ±	3.16	5.70 ±	5.14
Total abundance	1201 ±	43.1	1191 ±	61.5	506 ±	24.9	1115 ±	37.5

Table S5.2. Mean and standard deviation (SD) of soil chemical and physical properties across the four studied management systems.

Taxa	Conservation		Integrated		Conventional		Natural	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Chemical								
pH	5.71 ±	1.04	6.23 ±	0.87	7.11 ±	0.88	6.41 ±	1.33
Total C (%)	1.78 ±	1.26	1.92 ±	1.11	0.70 ±	1.44	1.34 ±	0.96
Total N (%)	0.39 ±	0.20	0.35 ±	0.35	0.29 ±	0.21	0.24 ±	0.26
C:N ratio	4.30 ±	1.31	2.64 ±	1.19	2.80 ±	0.44	2.14 ±	0.51
P (mg/kg)	1.78 ±	0.17	1.92 ±	0.60	1.34 ±	0.95	2.07 ±	0.39
Ca (mg/kg)	1.09 ±	1.30	3.64 ±	3.67	0.58 ±	0.39	0.93 ±	0.43
Na (mg/kg)	0.30 ±	0.28	0.02 ±	0.02	0.34 ±	0.41	0.25 ±	0.29
K (mg/kg)	0.66 ±	0.37	0.70 ±	0.36	0.35 ±	0.68	0.13 ±	0.12
Mg (mg/kg)	0.66 ±	0.89	0.44 ±	0.93	1.38 ±	0.95	0.25 ±	0.21
SOM (%)	1.07 ±	0.31	1.53 ±	0.45	2.02 ±	0.37	1.87 ±	0.41
Physical								
AGS (%)	85.5 ±	9.54	70.3 ±	10.3	83.6 ±	9.03	80.7 ±	10.8
BD (gcm−3)	1.24 ±	0.40	1.09 ±	0.45	1.62 ±	0.48	1.25 ±	0.55
Poro (%)	39.7 ±	21.8	47.5 ±	13.0	37.5 ±	9.05	44.3 ±	12.5
SM (%)	82.5 ±	11.1	72.4 ±	13.6	33.7 ±	17.9	61.1 ±	25.1
PR (%)	1.53 ±	0.72	1.07 ±	13.2	2.02 ±	2.64	1.87 ±	6.90
Sand (%)	32.2 ±	24.3	47.3 ±	15.7	21.7 ±	10.4	42.8 ±	14.9
Silt (%)	22.4 ±	19.9	18.8 ±	13.5	55.5 ±	7.64	11.4 ±	10.1
Clay (%)	45.2 ±	15.8	33.8 ±	16.3	22.5 ±	7.66	45.8 ±	14.8

BD: Bulk density; P: Phosphorus; Total C: Total Carbon; Total N:Total Nitrogen; SOM: Soil organic matter ;SM: Soil moisture; Poro: Porosity, AGS: Aggregate stability; PR: Penetration resistance; K: Potassium; Ca: Calcium; Mg: Magnesium; Na: Sodium.

Table S5.3. Results of principal component analysis of soil principal components analysis (PCA) of soil macrofauna, chemical and physical variables.

Variables	PC1	PC2
Biodiversity		
Eigenvalues	2.139	1.727
Variance %	21.40	17.28
Cumulative %	21.40	38.67
Araneae	**0.593**	0.510
Chilopoda	0.168	-0.491
Coleoptera	0.274	0.321
Dermaptera	-0.452	**0.567**
Diplopoda	**-0.505**	0.165
Hymenoptera	0.277	**-0.447**
Hemiptera	-0.175	0.644
Isoptera	**0.521**	-0.102
Lepidoptera	**0.586**	0.092
Oligochaeta	**0.710**	0.378
Chemical		
Eigenvalues	2.664	1.492
Variance %	26.64	14.92
Cumulative %	26.64	41.56
pH	0.425	-0.196
Total N (%)	0.079	**0.597**
Total C (%)	0.357	**0.697**
C:N ratio	**-0.686**	0.174
P (mg/kg)	0.274	-0.453
Ca (mg/kg)	**0.717**	0.171
Na (mg/kg)	0.286	**-0.579**
K (mg/kg)	**0.550**	0.105
Mg (mg/kg)	**0.736**	0.020
SOM (%)	**0.603**	0.004
Physical		
Eigenvalues	2.826	1.428
Variance %	35.32	17.85
Cumulative %	35.32	53.17
AGS (%)	**0.732**	-0.061
BD (gcm−3)	**-0.593**	0.297
Poro (%)	0.229	-0.047
SM (%)	**0.502**	0.262
PR (%)	**-0.520**	-0.449
Sand (%)	0.593	**-0.715**
Silt (%)	**-0.889**	0.065
Clay (%)	0.470	**0.740**

Total N:Total Nitrogen; SOM: Soil organic matter ;SM: Soil moisture; Poro: Porosity, AGS: Aggregate stability; PR: Penetration resistance; K: Potassium; Ca: Calcium; Mg: Magnesium; Na: Sodium
*Bold values are heavily weighed factors which were included for sub-indicator calculations.
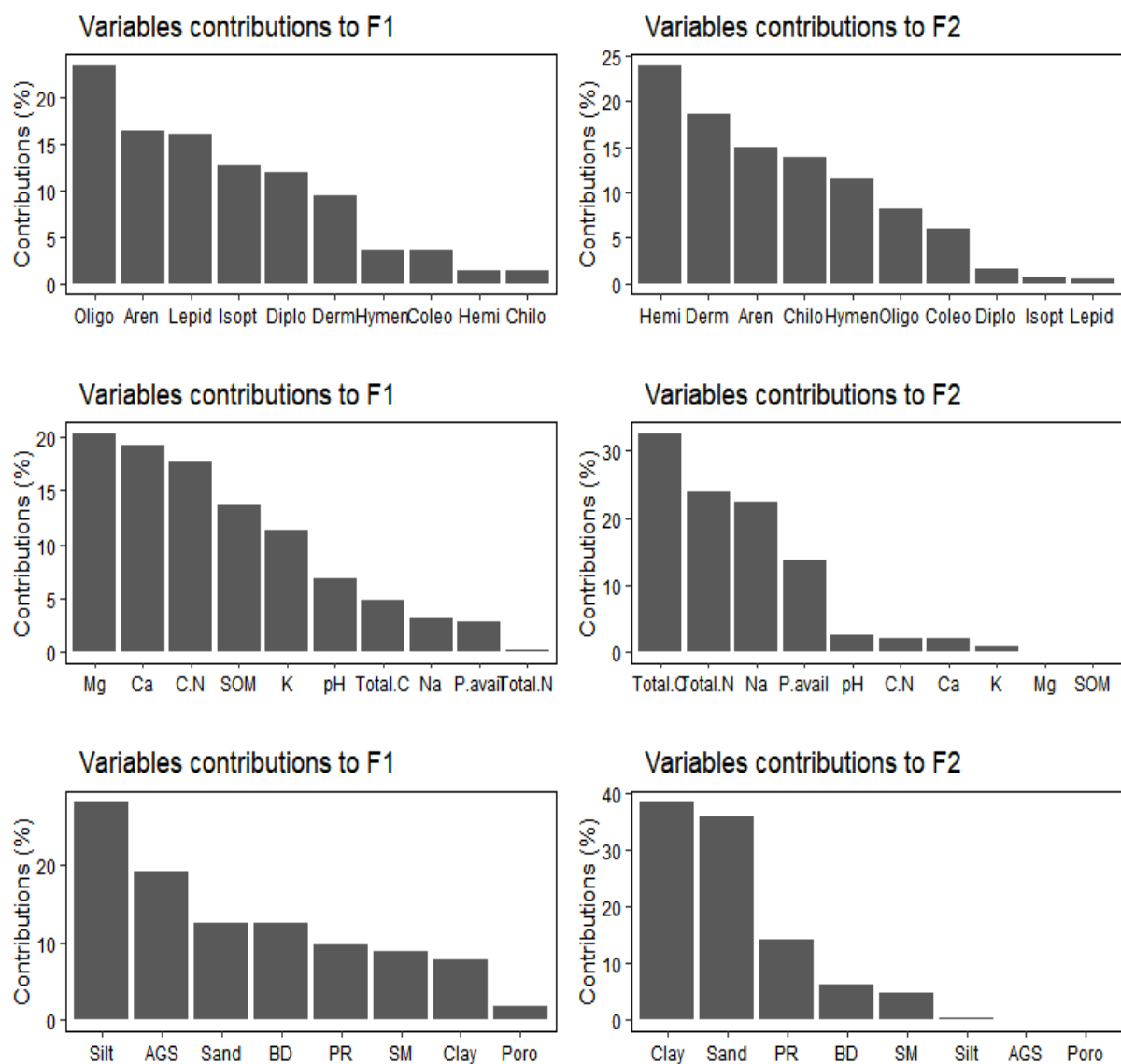
Figure S5.1: Contribution of biodiversity (a, b) chemical (b, c) and physical variables (d, e) to the formation of the F1/F2 of the PCA.

Table S5.4. Indicator species distribution under different land use managements. Conservation = CONS; Integrated = INTER; Conventional = CONV; Natural = NATU.

ID	Indicator species	CONS	INTE	CONV	NATU
sp052	*Odontotermes* sp. (Blattodea: Termitidae)	X	X		X
sp008	*Trephopoda* sp.(Araneae: Gnaphosidae)	X	X		X
sp039	*Dendrodrilus* sp. (Oligochaeta: Lumbricidae)	X	X	X	
sp043	*Trichomyrmex* sp. (Hymenoptera: Myrmicinae)	X	X		
sp040	*Lumbricus terrestris* (Oligochaeta: Lumbricidae)	X	X		X
sp016	*Phoberus* sp. (Coleoptera: Trogidae)	X	X		
sp047	*Camponotus* sp.(Hymenoptera: Formicinae)	X	X	X	
sp030	*Pontodrilus* sp. (Oligochaeta: Microchaetidae)		X		X
sp029	*Eudrilus eugeniae* (Oligochaeta: Eudrilidae)	X	X		X
sp044	*Tetramorium* sp. (Hymenoptera: Myrmicinae)	X	X		X
sp012	*Athia thoracica* (Coleoptera: Carabidae)	X	X	X	X
sp054	*Trinervitermes dispar* (Blattodea: Termitidae)	X	X	X	
sp002	*Rastellus* sp. (Araneae: Ammoxenidae)	X	X	X	X
sp037	*Eisenia andrei* (Oligochaeta: Lumbricidae)	X	X		X
sp036	*Microchaetus* sp. (Oligochaeta: Microchaetidae)	X	X	X	
sp015	*Calosoma* sp. (Coleoptera: Carabidae)	X	X	X	X
sp033	*Lumbricus rubellus* (Oligochaeta: Lumbricidae)	X	X		X
sp001	*Pardosa* sp. (Araneae: Licosidae)	X	X	X	
sp071	*Brachyiulus* sp. (Diplopoda: Julidae)			X	X
sp073	*Centrobolus* sp. (Diplopoda: Pachybolidae)			X	X
sp060	*Paralamyctes* sp. (Chilopoda: Henicopidae)	X		X	X
sp045	*Lepisiota* sp. (Hymenoptera: Formicinae)	X	X	X	X
sp048	*Pheidole* sp. (Hymenoptera: Myrmicinae)	X	X		X
sp041	*Dorylus* sp. (Hymenoptera: Dorylinae)		X		X
sp022	*Gymnoplerus leei* (Coleoptera: Scarabaeidae)				X
Total		**20**	**21**	**12**	**18**

Appendix E: General supplementary material

Table S1. Information on current and historic soil management of the of the conservation (CONS) integrated (INTER), conventional (CONV) and natural (NATU) sites.

Site	Landuse	Cropping	Tillage	Chemicals	Grazing	Years
S01	CONS	**MZ** – SB^{*RT}	Zero	None	None	From 2007
S02	CONS	MZ – SB^{*MC}	Deep	Lime	None	From 1998
S03	CONS	**MZ** – SB^{*MC}	Conserv	None	None	From 1998
S04	CONS	SB – **MZ**^{*RT}	Zero	None	None	From 2000
S05	CONS	SF – MZ^{*RT}	Zero	None	None	From 2006
S06	CONS	MZ – SB^{*RT}	Conserv	Lime	None	From 1999
S07	CONS	SB – SF^{*RT}	Zero	None	None	From 2000
S08	CONS	**MZ** – SB^{*MC}	Conserv	None	None	From 1999
S09	CONS	CP – MZ^{*MC}	Zero	None	None	From 2010
S10	CONS	BR – **MZ**^{*MC}	Conserv	None	None	From 2010
S11	INTER	LS – MZ^{*RT}	Zero	None	Continuous	From 1999
S12	INTER	RG – LS^{*RT}	Conserv	None	Rotational	From 2004
S13	INTER	MZ – LS^{*RT}	Zero	None	Continuous	From 2010
S14	INTER	LS – **MZ**^{*RT}	Zero	None	Rotational	From 1989
S15	INTER	RG – LS^{*RT}	Zero	None	Ultra-high	From 1999
S16	INTER	RG – LS^{*RT}	Zero	None	Rotational	From 1997
S17	INTER	RG – LS^{*RT}	Zero	None	Rotational	From 1993
S18	INTER	BR – RG^{*MC}	Conserv	None	Ultra-high	From 1983
S19	INTER	RG – LS^{*RT}	Zero	None	Continuous	From 1983
S20	INTER	RG – LS^{*RT}	Zero	None	Continuous	From 2000
S21	CONV	Mono-Wheat	Deep	NPK,UREA, cyhalothrin	None	From 1983
S22	CONV	Mono-Wheat	Deep	Glyphosate, tefluthrin	None	From 1983
S23	CONV	Mono-Oats	Deep	Paraquat, NPK	None	From 1983
S24	CONV	Mono-Wheat	Deep	LAN,Roundup	None	From 1970
S25	CONV	Mono-Oats	Deep	Glyphosate	None	From 1970
S26	CONV	Mono-Oats	Deep	Copper sulphate, UREA, tefluthrin	None	From 1970
S27	CONV	Mono-Oats	Deep	Glyphosate	None	From 1989
S28	CONV	Mono-Wheat	Deep	LAN, Potassium	None	From 1962
S29	CONV	Mono-Oats	Deep	LAN, Sulphur	None	From 1962
S30	CONV	Mono-Oats	Deep	Atrazine, cyhalothrin	None	From 1990
S31	NATU	Natural grass	Zero	None	Ultra-high	—
S32	NATU	Natural grass	Zero	None	Yes	—
S33	NATU	Natural grass	Zero	None	None	—
S34	NATU	Natural grass	Zero	None	Ultra-high	—
S35	NATU	Natural grass	Zero	None	None	—
S36	NATU	Natural grass	Zero	None	None	—
S37	NATU	Natural grass	Zero	None	None	—
S38	NATU	Natural grass	Zero	None	None	—
S39	NATU	Natural grass	Zero	None	Rotational	—
S40	NATU	Natural grass	Zero	None	Rotational	—

[1]RT=Rotational cropping; MC=Mixed cropping, BR= Brassica, MZ= Maize (genetically modified in bold), SF=Sunflower, SB= Soybean, CP=Cowpea, LS= Livestock, RG= Ryegrass.
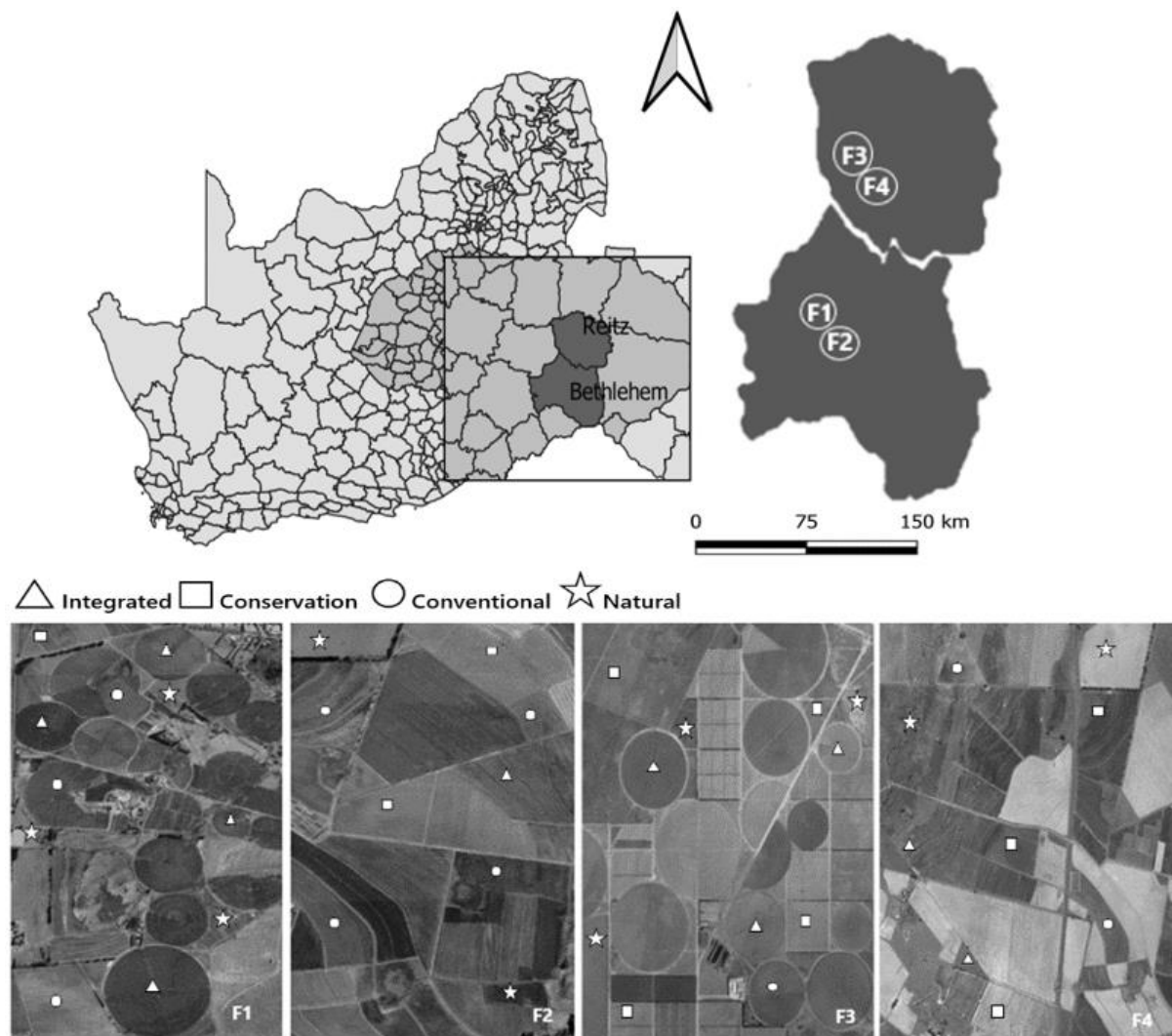
Figure S2. Area map and design for the 40 study sites distributed across four farms (F1 ,F2 ,F3, F4) in the Free State.

Table S2. Species checklist of morphospecies collected throughout the study. DETR = Detritivore; HERB = Herbivore; OMNI = Omnivore; PRED = Predator.

ORDER	FAMILY	SPECIES/MORPHOSPECIES	GUILD
Araneae	Ammoxenidae	*Amoxenus* sp.1	PRED
	Licosidae	Genus & species undetermined	PRED
	Ammoxenidae	*Rastellus* sp.	PRED
	Araneidae	*Cyclosa insulata*	PRED
	Araneidae	*Argiope australis*	PRED
	Araneidae	*Argiope cobata*	PRED
	Migidae	Genus & species undetermined	PRED
	Araneidae	*Neoscona* sp.1	PRED
	Araneidae	*Neoscona* sp.2	PRED
	Araneidae	*Neoscona* sp.3	PRED
	Araneidae	*Kilima* sp.	PRED
	Sicariidae	*Lexosceles reclusa*	PRED
	Theridiidae	*Latrodectus* sp.	PRED
	Atypidae	*Calommata merionalis*	PRED
	Thomisidae	Genus & species undetermined	PRED
	Trachelidae	Genus & species undetermined	PRED
	Eresidae	*Stegodyphus* sp.	PRED
	Corinnidae	Genus & species undetermined	PRED
	Corinnidae	Genus & species undetermined	PRED
	Corinnidae	*Fuchibotulus* sp.	PRED
	Araneidae	*Argiope* sp.	PRED
	Linyphiidae	Genus & species undetermined	PRED
	Linyphiidae	*Erigone* sp.	PRED
	Linyphiidae	*Meioneta* sp.	PRED
	Linyphiidae	*Tenuiphantes* sp.	PRED
	Licosidae	Genus & species undetermined	PRED
	Ammoxenidae	*Amoxenus* sp.2	PRED
	Licosidae	Genus & species undetermined	PRED
	Licosidae	Genus & species undetermined	PRED
	Araneidae	*Cyclosa insulata*	PRED
	Ammoxenidae	*Amoxenus* sp.2	PRED
	Licosidae	Genus & species undetermined	PRED
	Eresidae	*Dresserus* sp.	PRED
	Licosidae	*Pardosa* sp.	PRED
	Corinnidae	Genus & species undetermined	PRED
	Licosidae	Genus & species undetermined	PRED
	Migidae	Genus & species undetermined	PRED
	Linyphiidae	Genus & species undetermined	PRED
	Anapidae	Genus & species undetermined	PRED
	Anapidae	Genus & species undetermined	PRED
	Nemesiidae	*Lepthercus* sp.	PRED
	Licosidae	Genus & species undetermined	PRED

	Linyphiidae	*Acorigone* sp.	PRED
	Eresidae	Genus & species undetermined	PRED
	Eresidae	Genus & species undetermined	PRED
	Gnaphosidae	*Trephopoda* sp.	PRED
	Gnaphosidae	*Nomisia* sp.	PRED
	Ctenidae	Genus & species undetermined	PRED
	Theridiidae	Genus & species undetermined	PRED
	Corinnidae	Genus & species undetermined	PRED
	Theridiidae	*Theridion* sp.	PRED
	Sicariidae	Genus & species undetermined	PRED
	Sicariidae	Genus & species undetermined	PRED
	Salticidae	*Heliophanus* sp.	PRED
	Corinnidae	*Fuchibotulus kigelia*	PRED
	Zoropsidae	Genus & species undetermined	PRED
	Gnaphosidae	*Leptodrassus* sp.	PRED
	Zodariidae	*Diores* sp.	PRED
	Theridiidae	*Lasaeola* sp.	PRED
	Sicariidae	Genus & species undetermined	PRED
	Thomisidae	Genus & species undetermined	PRED
	Migidae	*Moggridgea* sp.	PRED
Blattodea	Termitidae	*Odontotermes* sp.	DETR
	Termitidae	Genus & species undetermined	DETR
	Termitidae	Genus & species undetermined	DETR
	Termitidae	*Fulleritermes* sp.	DETR
	Termitidae	*Trinervitermes dispar*	DETR
	Termitidae	Genus & species undetermined	DETR
Chilopoda	Henicopidae	*Paralamyctes* sp.	PRED
	Henicopidae	Genus & species undetermined	PRED
	Henicopidae	Genus & species undetermined	PRED
	Cryptopidae	*Crytops audax*	PRED
	Cryptopidae	Genus & species undetermined	PRED
	Cryptopidae	Genus & species undetermined	PRED
	Lithobiidae	Genus & species undetermined	PRED
	Scutigeridae	Genus & species undetermined	PRED
	Scutigeridae	Genus & species undetermined	PRED
	Scutigeridae	Genus & species undetermined	PRED
	Scolopendridae	Genus & species undetermined	PRED
	Scolopendridae	Genus & species undetermined	PRED
	Scolopendridae	Genus & species undetermined	PRED
	Geophilomorpha	*Geophilus* sp.1	PRED
	Geophilomorpha	*Schendyla* sp.1	PRED
Coleoptera	Carabidae	*Calosoma* sp.1	PRED
	Carabidae	*Calosoma* sp.2	PRED
	Carabidae	*Calosoma chlorostictum*	PRED
	Carabidae	*Athia thoracica*	PRED

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Carabidae	*Amara tibials*	PRED
Carabidae	*Amara fulva*	PRED
Carabidae	*Bembidion* sp.1	PRED
Carabidae	*Bembidion lampros*	PRED
Carabidae	*Lophyra flexuosa*	PRED
Carabidae	*Cylindera disjuncta*	PRED
Carabidae	*Geobaenus* sp.	PRED
Carabidae	*Carabus* sp1.	PRED
Carabidae	*Carabus* sp2.	PRED
Carabidae	*Thunatophilus* sp.	PRED
Carabidae	*Lachnothorax* sp.	PRED
Carabidae	*Thermophilum* sp.	PRED
Carabidae	*Graphipterus* sp.	PRED
Carabidae	*Passalidus fortipes*	PRED
Carabidae	*Praeugena* sp.	PRED
Anthicidae	*Anthicid* sp.1	DETR
Anthicidae	*Anthicid* sp.2	DETR
Bostrychidae	*Rhyzopertha* sp.1	HERB
Bostrychidae	*Rhyzopertha* sp.2	HERB
Scarabaeidae	*Gymnoplerus leei*	DETR
Scarabaeidae	*Gymnoplerus* sp.1	DETR
Scarabaeidae	*Gymnoplerus* sp.2	DETR
Scarabaeidae	*Phalops dregei*	HERB
Scarabaeidae	*Adoretus* sp.1	HERB
Scarabaeidae	*Adoretus* sp.2	HERB
Scarabaeidae	*Adoretus* sp.3	HERB
Scarabaeidae	*Adoretus* sp.4	HERB
Scarabaeidae	*Scarabeous* sp.1	DETR
Scarabaeidae	*Scarabeous* sp.2	DETR
Scarabaeidae	*Scarabeous* sp.3	DETR
Scarabaeidae	*Scarabeous* sp.4	DETR
Scarabaeidae	*Onthophagus taurus*	DETR
Scarabaeidae	*Onthophagus peringueyi*	DETR
Scarabaeidae	*Aphodius* sp.1	DETR
Scarabaeidae	*Aphodius* sp.2	DETR
Scarabaeidae	*Aphodius* sp.3	DETR
Scarabaeidae	*Aphodius* sp.4	DETR
Mycetophagidae	Genus & species undetermined	DETR
Staphylinidae	Genus & species undetermined	PRED
Staphylinidae	Genus & species undetermined	PRED
Staphylinidae	Genus & species undetermined	PRED
Staphylinidae	Genus & species undetermined	PRED
Staphylinidae	Genus & species undetermined	PRED
Silphidae	*Sipha* sp.1	DETR
Silphidae	*Sipha* sp.2	DETR
Silphidae	*Sipha* sp.3	DETR

Silphidae	*Sipha* sp.4	DETR
Silphidae	*Thunatophilus* sp.1	DETR
Silphidae	*Thunatophilus* sp.2	DETR
Silphidae	Genus & species undetermined	DETR
Silphidae	Genus & species undetermined	DETR
Ptiliidae	Genus & species undetermined	DETR
Elateridae	*Blapstinus* sp.	HERB
Elateridae	*Agriotes* sp.1	HERB
Elateridae	*Agriotes* sp.2	HERB
Elateridae	Genus & species undetermined	HERB
Elateridae	Genus & species undetermined	HERB
Elateridae	Genus & species undetermined	HERB
Cleridae	Genus & species undetermined	PRED
Clambidae	Genus & species undetermined	DETR
Curculionidae	Genus & species undetermined	HERB
Curculionidae	Genus & species undetermined	HERB
Cryptophagidae	Genus & species undetermined	DETR
Trogidae	*Phoberus* sp.1	DETR
Trogidae	*Phoberus* sp.2	DETR
Trogidae	*Trox* sp.	DETR
Trogidae	*Trox nasatus*	DETR
Melyridae	Genus & species undetermined	PRED
Melyridae	Genus & species undetermined	PRED
Lagriidae	Genus & species undetermined	PRED
Histeridae	*Saphrinus* sp.1	PRED
Histeridae	*Saphrinus* sp.2	PRED
Histeridae	*Saphrinus* sp.3	PRED
Tenebrionidae	Genus & species undetermined	OMNI
Tenebrionidae	Genus & species undetermined	OMNI
Tenebrionidae	Genus & species undetermined	OMNI
Tenebrionidae	Genus & species undetermined	OMNI
Nitidulidae	Genus & species undetermined	OMNI
Histeridae	Genus & species undetermined	PRED
Histeridae	Genus & species undetermined	PRED
Histeridae	Genus & species undetermined	PRED
Hydrophilidae	Genus & species undetermined	DETR
Aphodiinae	*Aphodiinae sp.1*	DETR
Aphodiinae	*Aphodiinae sp.2*	DETR
Aphodiinae	*Aphodiinae sp.3*	DETR
Chrysomelidae	*Chrysomelid sp.1*	HERB
Chrysomelidae	*Chrysomelid sp.2*	HERB
Collembola Isotomidae	Genus & species undetermined	DETR
Isotomidae	Genus & species undetermined	DETR
Isotomidae	Genus & species undetermined	DETR
Isotomidae	Genus & species undetermined	DETR
Neelidae	Genus & species undetermined	DETR

	Isotomidae	Genus & species undetermined	DETR
	Entomobryidae	Genus & species undetermined	DETR
	Entomobryidae	Genus & species undetermined	DETR
	Entomobryidae	Genus & species undetermined	DETR
	Entomobryidae	Genus & species undetermined	DETR
	Cyphoderidae	Genus & species undetermined	DETR
	Cyphoderidae	Genus & species undetermined	DETR
	Sminthurididae	Genus & species undetermined	DETR
	Isotomidae	Genus & species undetermined	DETR
	Isotomidae	Genus & species undetermined	DETR
	Brachystomellidae	Genus & species undetermined	DETR
	Isotomidae	Genus & species undetermined	DETR
	Isotomidae	Genus & species undetermined	DETR
	Isotomidae	Genus & species undetermined	DETR
	Tullbergiidae	Genus & species undetermined	DETR
	Tullbergiidae	Genus & species undetermined	DETR
	Isotomidae	Genus & species undetermined	DETR
	Entomobryidae	Genus & species undetermined	DETR
	Entomobryidae	Genus & species undetermined	DETR
	Onychiuridae	Genus & species undetermined	DETR
	Hypogastruridae	Genus & species undetermined	DETR
Dermaptera	Labiduridae	*Nala* sp.1	PRED
	Labiduridae	*Nala* sp.2	PRED
	Labiduridae	Genus & species undetermined	PRED
	Labiduridae	Genus & species undetermined	PRED
	Labiduridae	Genus & species undetermined	PRED
	Labiduridae	Genus & species undetermined	PRED
	Labiduridae	*Nala* sp.3	PRED
	Labiduridae	*Labidura riparia*	PRED
	Labiduridae	*Labidura* sp.1	PRED
Diplopod	Pachybolidae	*Centrobolus* sp.	DETR
	Pachybolidae	Genus & species undetermined	DETR
	Pachybolidae	Genus & species undetermined	DETR
	Pachybolidae	Genus & species undetermined	DETR
	Julidae	*Brachyiulus* sp.	DETR
	Julidae	Genus & species undetermined	DETR
	Julidae	Genus & species undetermined	DETR
	Julidae	Genus & species undetermined	DETR
	Julidae	Genus & species undetermined	DETR
	Julidae	Genus & species undetermined	DETR
	Julidae	Genus & species undetermined	DETR
	Julidae	Genus & species undetermined	DETR
	Julidae	*Ommatoiulus* sp.	DETR
	Dalodesmidae	*Gonokollesis* sp.	DETR
	Dalodesmidae	Genus & species undetermined	DETR
	Dalodesmidae	Genus & species undetermined	DETR

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	Dalodesmidae	Genus & species undetermined	DETR
	Julomorphidae	Genus & species undetermined	DETR
	Julomorphidae	Genus & species undetermined	DETR
	Julomorphidae	Genus & species undetermined	DETR
Hymenoptera	Formicidae	*Tetramorium* sp.1	OMNI
	Formicidae	*Tetramorium* sp.2	OMNI
	Formicidae	*Tetramorium* sp.3	OMNI
	Formicidae	*Dorylus* sp.1	OMNI
	Formicidae	*Camponotus* sp.	OMNI
	Formicidae	*Dorylus* sp.2	OMNI
	Formicidae	*Anoplolepis* sp.	OMNI
	Formicidae	*Lepisiota* sp.1	OMNI
	Formicidae	*Lepisiota* sp.2	OMNI
	Formicidae	*Lepisiota* sp.3	OMNI
	Formicidae	*Pheidole* sp.1	OMNI
	Formicidae	*Pheidole* sp.2	OMNI
	Formicidae	*Technomyrmex* sp.1	OMNI
	Formicidae	*Technomyrmex* sp.2	OMNI
	Formicidae	*Solenopsis* sp.1	OMNI
	Formicidae	*Solenopsis* sp.2	OMNI
	Formicidae	*Solenopsis* sp.3	OMNI
	Formicidae	*Solenopsis* sp.4	OMNI
Lumbricina	Lumbricidae	*Eisenia andrei*	DETR
	Lumbricidae	*Eodriloides* sp.	DETR
	Lumbricidae	*Amythas* sp.1	DETR
	Lumbricidae	*Amythas* sp.2	DETR
	Lumbricidae	*Amythas* sp.3	DETR
	Lumbricidae	*Lumbricus terrestris*	DETR
	Lumbricidae	*Lumbricus* sp.1	DETR
	Lumbricidae	*Lumbricus* sp.2	DETR
	Lumbricidae	*Lumbricus rubellus*	DETR
	Lumbricidae	*Eisenia rosea*	DETR
	Acanthodrilinae	*Eodriloides* sp.	DETR
	Megascolecidae	*Perionyx* sp.1	DETR
	Megascolecidae	*Perionyx* sp.2	DETR
	Megascolecidae	*Pontodrilus litoralis*	DETR
	Megascolecidae	*Metaphire* sp.	DETR
	Microchaetidae	Genus & species undetermined	DETR
	Microchaetidae	Genus & species undetermined	DETR
	Microchaetidae	*Pontodrilus oresbiosus*	DETR
	Microchaetidae	*Pontodrilus lesothoensis*	DETR
	Lumbricidae	*Aporrectodea trapezoides*	DETR
	Lumbricidae	*Aporrectodea* sp.	DETR
	Lumbricidae	*Eiseniella* sp.	DETR
	Lumbricidae	*Aporrectodea* sp.3	DETR
	Lumbricidae	*Eiseniella* sp.	DETR

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	Lumbricidae	*Eiseniella* sp.	DETR
	Eudrilidae	*Eudrilus eugeniae*	DETR
	Eudrilidae	Genus & species undetermined	DETR
	Eudrilidae	Genus & species undetermined	DETR
	Eudrilidae	Genus & species undetermined	DETR
	Eudrilidae	Genus & species undetermined	DETR
	Lumbricidae	*Octolasion* sp.	DETR
	Microchaetidae	*Microchaetus papillatus*	DETR
	Microchaetidae	*Proandricus* sp.	DETR
	Tritogeniidae	*Tritogenia* sp.1	DETR
	Tritogeniidae	*Tritogenia* sp.2	DETR
	Tritogeniidae	*Tritogenia* sp.3	DETR
	Tritogeniidae	*Michalakus* sp.1	DETR
	Tritogeniidae	*Michalakus* sp.2	DETR
	Microchaetidae	*Microchaetus vernoni*	DETR
	Lumbricidae	*Dendrodrilus* sp.	DETR
	Lumbricidae	*Lumbricus rubellus*	DETR
	Acanthodrilinae	*Microscolex* sp.	DETR
	Microchaetidae	*Proandricus sestosus*	DETR
	Lumbricidae	*Allolobophoridella* sp.	DETR
Mesostigmata	Parasitidae	Genus & species undetermined	PRED
	Parasitidae	Genus & species undetermined	PRED
	Parasitidae	Genus & species undetermined	PRED
	Parasitidae	Genus & species undetermined	PRED
	Parasitidae	Genus & species undetermined	PRED
	Parasitidae	Genus & species undetermined	PRED
	Parasitidae	Genus & species undetermined	PRED
	Parasitidae	Genus & species undetermined	PRED
	Parasitidae	Genus & species undetermined	PRED
	Parasitidae	Genus & species undetermined	PRED
	Parasitidae	Genus & species undetermined	PRED
	Parasitidae	Genus & species undetermined	PRED
Oribatida	Ceratozetidae	Genus & species undetermined	DETR
	Ceratozetidae	Genus & species undetermined	DETR
	Ceratozetidae	Genus & species undetermined	DETR
	Ceratozetidae	Genus & species undetermined	DETR
	Ceratozetidae	Genus & species undetermined	DETR
	Phthiracaridae	Genus & species undetermined	DETR
	Phthiracaridae	Genus & species undetermined	DETR
	Phthiracaridae	Genus & species undetermined	DETR
	Phthiracaridae	Genus & species undetermined	DETR
	Nothridae	Genus & species undetermined	DETR
	Nothridae	Genus & species undetermined	DETR
	Nothridae	Genus & species undetermined	DETR