FUNCTIONAL INTERACTIONS BETWEEN MANAGEMENT OF ARABLE FIELD MARGINS AND SOIL MESOFAUNA

By

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A thesis submitted to the University of Nottingham

School of Biosciences

In Collaboration with

Rothamsted Research, North Wyke

August 2018

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Abstract

LEA CARLESSO

The damage to soils caused by agricultural intensification greatly affects belowground faunal communities, typically via a reduction in population size and diversity in comparison with those in semi-natural habitats. This can cause an imbalance in associated soil functions. The soil mesofauna, including *Acari* (mites) and *Collembola* (springtails), fulfil a wide range of these functions and our understanding of soil processes is closely linked to our knowledge of the dynamics of invertebrate communities. In the context of current global change, sustainable food production is a significant challenge that can potentially be better met by improved understanding of the abundance and composition of the soil mesofaunal populations, in order to optimize ecosystem services delivered by agricultural soils.

This PhD project addressed this issue by investigating the changes induced by sown grass field margins on the abundance of populations and community structure of soil mesofauna in the context of arable fields. It aimed to understand to what extent field margins affect soil mesofauna communities and whether these effects extend into the adjacent crop. To do so, the project investigated: (i) the nature of the ecological succession of the mesofaunal populations in relation to time since establishment of the margin; (ii) the impact of field operations on the abundance and structure of the invertebrate communities, regarding the effects of the margin; (iii) whether faunal-driven soil processes, such as decomposition, are affected by field management (establishment of field margins) and field operations (traffic; restitution of crop residues); (iv) the impact of historical landscape management on current biodiversity markers. To answer these questions, field margins, on two UK farms which work with BASF to demonstrate sustainability in Agriculture, that had been established for different durations (1, 6 and

10 years) were investigated and changes in structure and population sizes of invertebrate communities associated with these field margins and their adjacent crop areas were studied over two years. Soil mesofauna were sampled, counted and identified from the various field margins of different ages, with differing orientations regarding the field traffic, and their adjacent crop.

It was found that population abundances and complexity of the community structures were generally enhanced in the field margins: more invertebrates and complex communities were found in the margins than in the adjacent crops. Likewise, community composition in the margins changed over time toward larger organisms and specialist species. Although it was hypothesised that mesofaunal populations in the crop would be influenced by the presence of the margin (the closer to the margin, the more similar the composition), it was found that field management was also an important driver of the soil mesofaunal communities. In the cropped areas, the heterogenous distribution of species abundances and the differences in community structure reflected the degree of disturbance caused by the different agricultural activities, such as tillage practices, management of crop residues or wheeling from field traffic. The ability of certain groups of soil invertebrates to disperse, and colonise new habitats was revealed; for example, at the margin:crop interface where there are compacted, traffic-related 'tramlines', abundances were particularly low while further into the field in less-disturbed areas, populations were more abundant.

The interaction effects between field margins, within-field crops and farm management highlighted the importance of well-designed and integrated agricultural strategies to maximise soil functions contributed-to by the soil fauna, such as litter decomposition and nutrient cycling, which in turn provide ecosystem services, such as maintenance of the soil fertility and structure, essential to sustainable food production.

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ACKNOWLEDGEMENTS

This study was funded by BASF as part of a doctoral training grant through Rothamsted Research, North Wyke and The University of Nottingham. I would like to thank these organisations for enabling me to conduct this work.

First of all, I would like to thank Prof. Phil Murray, my main supervisor at Rothamsted Research, for the amazing opportunity he gave me when I was offered this PhD. The last three years have been a life-changing experience and I could not have managed without his support – and his patience each time I was a bit over-enthusiastic. Thank you to Prof. Karl Ritz, my main supervisor at The University of Nottingham, for his invaluable writing and editing advice and the subtle humoristic note thorough all his comments on my manuscripts. At Rothamsted research, I would also like to thank Dr Lianhai Wu for taking over the supervision of my project and keeping it/me on good tack; and Dr Sam Cook for joining the team, always being cheerful and full of good advice. I would like to thank Graham Hartwell, Andy Beadle and Mike Green from BASF, for making this project a reality, for their expertise about farming systems; and, Graham for his incredible skill to tell stories and make them happen. And thanks to Andrew Mead and Jess Evans from the Computational and Analytical Sciences Department at Rothamsted Research. Their statistical expertise guided me all along the project.

I am also grateful for all the help and support I received from the North Wyke Staff. There are so many other people who have helped or supported me in one way or another, and made my PhD life at North Wyke a real pleasure: Megan who spent a year in the lab with me, volunteered to help in the field, shared much gossip and endured my changing moods; Rudi for being an excellent Dartmoor guide and a very good friend; Lizzy, always a friendly face at the reception; so much tea went down the wrong way as much as when you were telling stories at coffee time; all the PhD students, Andrew, Jamie, Stelian, Achilleas, with whom I have great memories and I hope to stay in touch. Finally, thank you to the two people I have shared a part of my life with, who were there whatever happened and became invaluable friends, Graham and Verena.

Je voudrais également remercier ma famille pour avoir été présents tout du long de cette thèse et ce malgré la distance. Mon père pour son soutien inébranlable et la garde de mon chien, ma mère pour les longues discussions au téléphone et pour beaucoup plus. Merci aussi à Joris, pour qui ces trois dernières années n'ont pas été faciles mais qui est resté et m'a fourni la stabilité nécessaire à l'accomplissement de cette thèse.

My work started in 'Paradise'*

** Paradise was the name of the first field I sampled*

AUTHOR'S DECLARATION

At no time during the registration for the degree of Doctor of Philosophy has the author been registered for any other University award without prior agreement of the Graduate Committee.

This study was financed by BASF.

A programme of advanced study was undertaken, including statistical packages and technical writing and a selection of supervised research skills training sessions organised by Rothamsted Research or external organisations.

Many conferences, with presentation (oral or poster) of the work, were attended, included: The soil Ecological Society meeting, the 2nd Global Soil Biodiversity Initiative Conference and the postgraduate conferences based at Rothamsted Research and The University of Nottingham.

Several publications, resulting from this PhD, are in preparation for publication.

Signed……………………

Date………………………

Word count of main body of thesis (references and captions included): 38,926

CHAPTER 1

INTRODUCTION

1.1. Soil ecosystems

1.1.1. General definition

Joffe (1936) was one of the first to characterise soils as a system. The definition he gave was: “*natural bodies, differentiated into horizons of mineral and organic constituents, usually unconsolidated, of variable depth, which differ from the parent material below in morphology, physical properties and constitution, chemical properties and composition, and biological characteristics*”. His view depicted a rather static system. Soon, the recognised importance of soil processes regulating fluxes between major earth compartments (lithosphere, hydrosphere, atmosphere and biosphere) forced researchers to reconsider soils as ‘dynamic components’ (Jenny, 1941), or as ‘fully-fledged ecosystems’ (Ponge, 2015). Nowadays, not only does the scientific community understand the great value of soils, but the topic is also well acknowledged by economists, governments (Costanza *et al.*, 1997; Millennium Ecosystem Assessment, 2005) and farmers. In the report “*The Status of the World’s Soil Resources”*, published for the 1st World Soil Day in 2015, the Food and Agriculture Organisation of the United Nations stressed the urgency to look after soils and preserve the essential functions they support (Montanarella *et al.*, 2015).

Soils provide a wide range of ecosystem services, such as food production, nutrient cycling, water storage and quality, support of biodiversity, regulation of climate, foundation material to build on, raw material supply, recreation and cultural value (Table 1.1; Bardgett and van der Putten, 2014; Bardgett and Wardle, 2010; Haygarth and Ritz, 2009; Wall *et al.*, 2015, 2013).

Table 1.1. Ecosystem services provided by soils.

Ecosystem service		**Soil Function**
Supporting	Primary production	Support for terrestrial vegetation
	Soil formation	Soil formation processes
	Nutrient cycling	Storage, transformation and cycling
Provisioning	Refugia	Habitat for soil dwellers
	Water storage	Retention of water in landscape
	Platform	Supporting structure
	Food supply	Provisioning plant growth
	Biomaterial	Provisioning plant growth
	Raw materials	Provisioning source materials
	Biodiversity and genetic resources	Unique biological materials
Regulating	Water quality	Filtration and buffering of water
	Water supply	Hydrological flows regulation
	Gas	Regulation of atmospheric flux
	Climate	Regulation of biologically mediated climatic processes
	Erosion control	Soil and colloid retention
Cultural	Recreation	Recreational activities
	Cognitive	Non-commercial activities
	Heritage	Holds archaeological records

Extracted and adapted from Haygarth and Ritz (2009).

Despite the important role of soils for human beings and their well-being, the last decades have witnessed a major loss of soil all around the globe and this is still an on-going trend (Montanarella *et al.*, 2016). Abrol *et al.* (2012) reported that five to seven million hectares of soils are degraded per year, meaning that they lose their ability to provide soil ecosystem services (Tóth *et al.*, 2008), and that rate could reach 10 million hectares before 2100. Considering the urgent situation, there is a real need to understand mechanisms occurring in soils and how they affect global ecosystem functioning in the hope that further degradation is prevented, and damage may be reversed.

Measuring the ability of soils to provide those ecosystem services, however, is no easy task; as defined by Joffe (1936), soil systems are a combination of physical, chemical and biological components, all playing important parts in the provision of ecosystem services. An integrated way to understand the mechanisms behind soil ecosystem services is to assess soil 'quality', which includes the capacity of soil to produce raw materials, such as food or fibre, and therefore covers the interaction between humans and soils. However, defining soil quality is not straightforward and the quality of soil cannot be determined simply by a degree of pollution which would affect animal health, in contrast with water or air quality (Bünemann *et al.*, 2018). Soil quality is, instead, determined by the abilities of a soil to respond to environmental changes, whether the causes are natural or artificial and its capacity to function in a given ecosystem (Karlen *et al.*, 2003). The heterogeneity of soils, the complexity of the physical, chemical and biological processes and the multitude of functions they provide, explain that the determination of soil quality indicators requires to be in line with the relevant context, threat, or function investigated (Bünemann *et al.*, 2018; Stone *et al.*, 2016). Stone *et al.* (2016) emphasised the ubiquity of biologically-based soil processes and therefore the relevance of using biological indicators, such as biodiversity, to assess soil quality; as instance one of their top-ten indicators is a soil mesofauna biodiversity index. Another concept assessing soil ecosystem services is soil ‘health’, which goes beyond the capacity of soils to produce and includes their ecological features (Bünemann *et al.*, 2018; Doran and Zeiss, 2000; Kibblewhite *et al.*, 2008). Health is defined by the World Health Organization as “the extent to which one is able to change or cope with the environment. Health is a resource for everyday life” (World Health Organization, 1984). Soil health refers to the living aspect of soils, a concept which focuses on dynamic systems, acting as ‘vital organs’ for the functioning of ecosystems (Doran and Zeiss, 2000). A healthy soil is the *sine qua non* condition of a fully-functioning and sustainable system, which can last and function throughout time (Bastida *et al.*, 2008; Doran and Zeiss, 2000). Although all soils do not have the same functions (e.g. food provisioning, biodiversity reservoirs, cultural purposes; Wall *et al.*, 2012), soil quality obviously need to be assessed by using the adequate soil quality indicators (Doran and Zeiss, 2000), which must be used in the appropriate context, to evaluate the relevant soil functions and meet environmental interests.

Assessing soil quality or soil health informs us about the ability of soil to provide ecosystem services, but it also reveals dysfunction inside the systems (Kibblewhite *et al.*, 2008), or provides additional information about impacts of anthropogenic practices on soils, which in turn would help to design appropriate environmental policies to preserve them (Doran and Zeiss, 2000). On a broader scale, soil quality is a promising tool to understand the impacts of global changes on soil ecosystems and the consequences for the ecosystem services they deliver (Bastida *et al.*, 2008).

1.1.2.Living soils

Soil invertebrates make a large contribution to many soil functions, such as carbon transformation and nutrient cycling; which, in turn, provide ecosystem services, such as maintenance of the soil fertility and structure or the production of food and raw materials (Bardgett and van der Putten, 2014; Brussaard, 2012; Wall *et al.*, 2015, 2013). The Food and Agriculture Organisation of the United Nations declared the study of soil organisms “a major tool to understand and alleviate impact of soil degradation” (Montanarella *et al.*, 2016). Soil biodiversity, measured in terms of community structure, functions carried, food-web interactions, is indeed a good indicator of soil quality, as it responds quickly to changes and disturbances and each component of the soil biodiversity has its specific response to various types of soil disturbance (Creamer *et al.*, 2016; Faber *et al.*, 2013; Stone *et al.*, 2016). For example, Creamer *et al.* (2016) applied a network analysis approach using multiple biodiversity and biological proxies (such as microbial and micro-fauna diversity, extracellular enzyme activity, respiration and other physiological processes) to discriminates soil ecosystem services between different climates and land uses across Europe; while Stone *et al.* (2016) adopted a 'logical sieve' method, consisting of a structured assessment and ranking of biological indicators based on their facility to be applied and their ability to be linked to more than one soil processes (Ritz *et al.* 2009), in order to determine soil biological proxies and monitor ecosystem services.

Soil biodiversity is extremely rich. In pioneering work, Torsvik *et al.* (1996) estimated the occurrence of ca. 10,000 genetically distinct bacterial types per square metre of forest soil, and the generality of enormous prokaryotic diversity in soils has consistently been supported by subsequent analyses (Curtis *et al.*, 2002; Gans *et al.*, 2005). Soil biodiversity can be classified in various ways (e.g. taxonomical, size-class or ecological classification) and the type of system used depend on the purpose and the scale of the study (Giller *et al.*, 1997). Taxonomical classification would preferably be used in species richness and biodiversity assessments, although the taxonomical identification of some taxa to species level can be a laborious and time-consuming task. This is one of the reasons why size-classes classification has been widely used to group soil organisms: the microscopic microbes (*Bacteria*, *Fungi*, and *Archaea*), the microfauna less than 0.2 mm (*Nematoda* and *Protozoa*), the mesofauna between 0.2 and 2 mm (*Acari* and *Collembola*), and the macrofauna larger than 2 mm (Bardgett, 2005; Coleman *et al.*, 2017; Orgiazzi *et al.*, 2016). None of the classifications above inform about the ecological functions of the soil biodiversity. Many of the functions carried by one taxonomical unit or size class are also carried by other groups and there is apparently much functional redundancy among soil organisms (Giller *et al.*, 1997). A functional classification assembles organisms of same reproductive strategy, distribution in their habitat and food resources (Table 1.2; Table 1.3; Brussaard, 1998; Crotty *et al.*, 2014; Kibblewhite *et al.*, 2008), making it easier to study soil ecological processes by disentangling the role of soil biodiversity in each process.

Table 1.2. Relationship between soil biodiversity, functional diversity and soil functions.

SOIL FUNCTIONS	**FUNCTIONAL ASSEMBLAGE**	**GUILDS**
Carbon transformation	Decomposers	Fungi
		Bacteria Microbivores Detritivores
Nutrient cycling	Nutrient transformers	Decomposers
		Element-transformers N-fixers Mycorrhizae
Soil structure maintenance	Ecosystem engineers	Megafauna
		Macrofauna Fungi Bacteria
Biological regulation	Bio-controllers	Predators
		Microbivores Hyper-parasites

Extracted and adapted from Kibblewhite et al. (2008).

Table 1.3. Classification of soil invertebrates. Taxa belonging to more than one trophic level (omnivorous phylum) were classified regarding their main food source.

	TROPHIC LEVELS				
INVERTEBRATE GROUPS	**Predators**	**Herbivores**	**Micro-predators**	**Microbivores**	**Decomposers**
Macrofauna	*Aranae* *Chilopoda* *Coleoptera* *Coleoptera* (larvae) *Hymenoptera*	*Coleoptera* *Homoptera (Aphidoidea)* *Thysanoptera (Frankliniella)*			*Diplopoda* *Diptera* *Diptera* (larvae) *Megadrilacea* *Isopoda* *Trichoptera* (larvae)
Collembola				*Entomobryomorpha* *Neelipleona* *Poduromorpha* *Symphypleona*	
Acari			*Mesostigmata* *Trombidiforme*	*Astigmata* *Endeostigmata* *Heterostigmatina* *Mesostigmata (Ameroseidae)* *Uropodina*	*Oribatida*
Others		*Tradigrada*	*Protura*		*Diplura* *Enchytraeidae*

Adapted from Crotty et al., (2011).

The mesofauna, typically composed of 95% mites (*Acari*) and springtails (*Collembola*) in most terrestrial systems (Harding and Stuttard, 1974), has a central role within the soil trophic network and members of this group are found at every trophic level (Figure 1.1; Brussaard *et al.*, 2007). The contrasting responses of the different groups to environmental changes reflect the life strategy of each of them and reveal the relationships and the dynamics within the soil community and their environment (Coudrain *et al.*, 2016), making the community structure of soil mesofauna an excellent indicator of changes and soil quality (Rieff *et al.*, 2016).

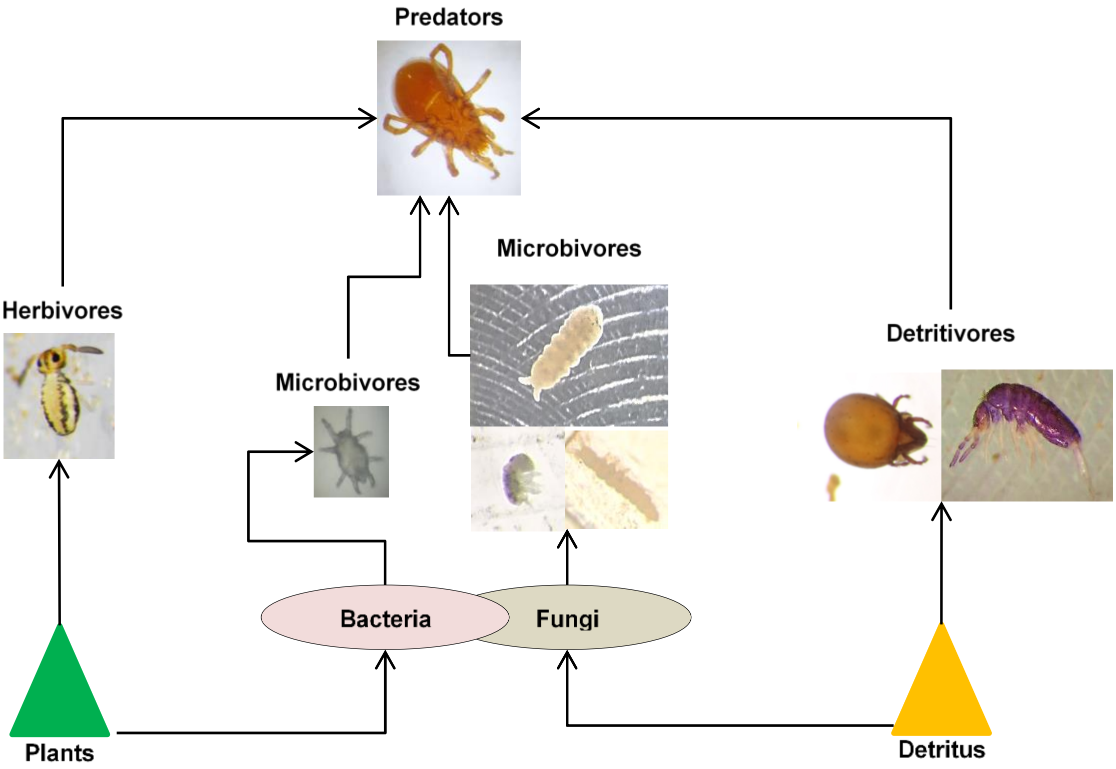

Figure 1.1. Simplified representation of the soil food-web, with all trophic levels only occupied by mites and springtails. Arrows show food resource / consumer relationship.

Collembola, also called springtails due to the presence on the abdomen of a jumping organ (the furca) are hexapods and known to be found in a wide range of environmental conditions, with abundance often reaching up to 100 000 indivuals.m^{-2}, and sometimes even more (Coleman *et al.*, 2017). Hopkin (2007) listed over 300 species in the United Kingdom, classified amongst four orders: *Poduromorpha*, *Entomobryomorpha*, *Symphypleona* and *Neelipleona* (Figure 1.2).

Collembola were often ranked as fungivores (Hunt *et al.*, 1987); however, they have shown abilities to switch their diet when required and could therefore be classified as an omnivorous taxon. They can feed on many fungal taxa, algae (Scheu and Folger, 2004), bacteria (Murray *et al.*, 2009) and detritus (Ponge, 2000), therefore having a strong impact on the regulation of microbial processes (Crotty *et al.*, 2012). They also make up an important food resource for predators in higher trophic levels (Bilde *et al.*, 2001; Oelbermann *et al.*, 2008; Wise *et al.*, 2006). Despite being opportunistic with fast reproduction rates (Coleman *et al.*, 2017); edaphic species of *Collembola*, such as *Poduromorpha* (Figure 1.2.a), which live below the soil surface, are particularly responsive to soil management and their populations can be greatly affected by soil disturbance, such as tillage (Coudrain *et al.*, 2016; Coulibaly *et al.*, 2017). As well as being important regulator of biofilm, fungi and plant detritus (Anslan *et al.*, 2018), *Collembola* are also the prey of many soil and surface predators (Bilde *et al.*, 2001) this central position within the soil food-web makes them valuable indicators of the trophic dynamics in the soil ecosystem. As show by Martins da Silva *et al.* (2016), the great diversity of life traits amongst *Collembola* species reflect their abilities to adapt to the diversity of soils and therefore their utility when assessing changes of environmental parameters or landscape uses.

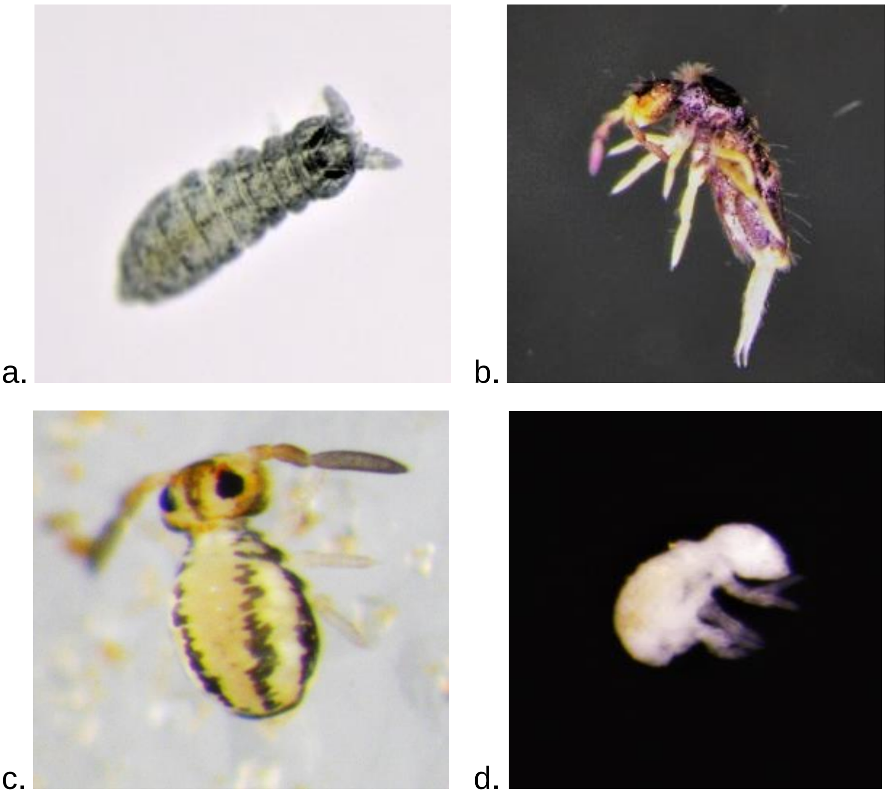

Figure 1.2. Main families of Collembola: Poduromorpha (a); Entomobryomorpha (b); Symphypleona (c); and Neelipleona (d). Image source: L. Carlesso, Rothamsted Research, Bioimaging unit, Microscope Leica M205; and, L. Carlesso, Rothamsted Research, Stereo Microscope Olympus SZX10.

Soil *Acari* (mites), are arachnids and the most abundant of the mesofaunal groups (Krantz and Walter, 2009). *Acari* are extremely diverse, Coleman *et al.* (2017) estimated that 100 genera of *Acari* could be found in forest floor, and can be related to many ecosystems. In soil four main suborders are found: the *Mesostigmata*, the *Oribatida*, the *Astigmata* and the *Prostigmata* (Figure 1.3). All can be associated to a specific trophic level; *Oribatida* (Figure 1.3.d) are generally detritivores, *Mesostigmata* (Figure 1.3.b) are largely predators, while *Astigmata*

(Figure 1.3.a) feed preferentially on fungi (Coleman *et al.*, 2017). Although, opportunistic and omnivorous species exist, the *Prostigmata* present a great variety in life strategies and feeding habits, and for the purpose of this thesis, we split them into two groups: the Trombidiformes (Figure 1.3.e), with the largest species feeding on small arthropods or nematodes (Coleman *et al.*, 2017), and the small opportunistic microbivore *Heterostigmatina* (Figure 1.3.c; Krantz and Walter, 2009; Ochoa *et al.*, 1991). Their relatively long-life span, and association with organic matter turn-over dynamics, makes the *Oribatida* one of the most studied group of soil mesofauna and an excellent indicator of the status of soils (Behan-Pelletier, 1999; Gergócs and Hufnagel, 2009). For instance, they are particularly affected by soil disturbance, such as tillage in an agricultural context (Hülsmann and Wolters, 1998). The range size distribution and the abundance of higher trophic level taxa, such as the predatory mite *Mesostigmata*, gives indications about the structure and organisation of the rest of the trophic network and can lead to inferences about the surrounding environment (Koehler, 1999, 1997; Ruf and Beck, 2005). *Astigmata* are found to a lesser extent in soils, although they can be abundant in agricultural soils rich in organic matter (Coleman *et al.*, 2017).

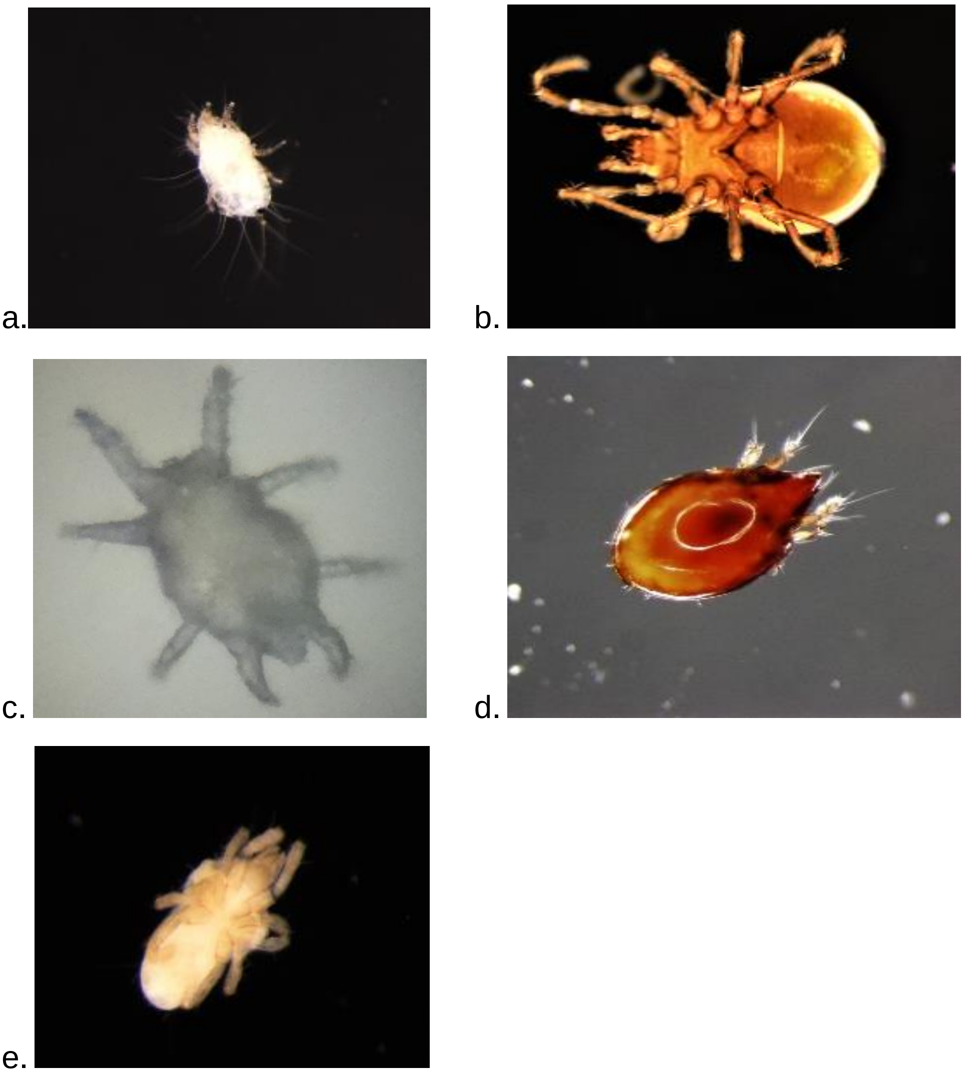

Figure 1.3. Main families of Acari: Astigmata (a), Mesostigmata (b) Heterostigmatina (c), Oribatida (d) and Prostigmata trombidiformes (e). Image source: L. Carlesso, Rothamsted Research, Bioimaging unit, Microscope Leica M205; and, L. Carlesso, Rothamsted Research, Stereo Microscope Olympus SZX10.

1.2. Interaction between soil biodiversity and its environment

1.2.1. Food resources shape the soil faunal community

In soils, above- and below-ground feedbacks are the origin of most ecosystem processes (Wardle *et al.*, 2004), and the interactions between plants, microbes and soil faunal communities are the mechanisms behind these processes. Plants are the primary producers of organic matter that fuel the soil food-web, either directly by the interaction between roots and herbivores or indirectly by the production of litter and exudates that will impact the community of decomposers (Glavatska *et al.*, 2017; Wardle *et al.*, 2004). Because the interactions are important to understand soil ecosystem processes, many studies have investigated the effects of plant-material quality, quantity and diversity entering the soil food-web on the composition and structure of the soil fauna community (García-Palacios *et al.*, 2013; Gergócs and Hufnagel, 2016; Ilieva-Makulec *et al.*, 2006; Milcu and Manning, 2011; Sauvadet *et al.*, 2016).

In agricultural soils, factors affecting litter decomposition are essentially determined by human activity. The amount and quality of organic matter returned to soils (Fierer *et al.*, 2005; Gergócs and Hufnagel, 2016; Milcu and Manning, 2011) together with the presence of the biotic communities (Murray *et al.*, 2009) are primary factors regulating decomposition rates. Thiele-Bruhn *et al.* (2012) noted the capability of agricultural practices to control the quality of primary organic matter entering soil systems and therefore its capability to modify the soil community and its activity, while Crotty *et al.* (2014; 2015) showed a contrasting effect of various types of crop residues on soil biodiversity. To understand the effects of litter quality, Johnson *et al.* (2007) tested the decomposition rates of three different organs of five crops that varied in relative proportions of their chemical composition and showed that crop types and plant parts affected decomposition rates at the soil surface, as most of the biological activity is in the topsoil (André *et al.*, 2002). This implies some potential for agricultural soil management via the manipulation of crop residues.

1.2.2. Impacts of agriculture on soil biodiversity

Very early, decreases in populations of *Acari* and *Collembola* were observed in cultivated habitats (Edwards and Lofty, 1975); and the recent decades unveiled the threats caused by dynamic land- use changes, such as urbanisation or agricultural intensification, to the detriment of soil quality (Montanarella *et al.*, 2016). The latter directly impacts soil biodiversity and leads to a decreasing complexity of belowground trophic networks, losses in specialist species (Tsiafouli *et al.*, 2015) and a reduction in abundance and diversity of the soil faunal communities (Postma-Blaauw *et al.*, 2010).

In the context of arable fields, many factors are applying pressures to populations of soil fauna. Field activities indirectly regulate the composition (abundance and structure) of the soil faunal community, by altering the quality and quantity of resource, such as food or oxygen, for the soil organisms (Thiele-Bruhn *et al.*, 2012). Agricultural activities are also a source of external inputs (fertilisers, pesticides, pollutions) which modify the dynamics and structure of soil fauna community (Bünemann *et al.*, 2006). In their review, Bünemann *et al.* (2006) identified agricultural parameters directly regulating soil organic matter, by addition of organic fertilisers, or indirectly regulating organic matter, by addition of mineral fertilisers, as the main force shaping soil fauna communities; although they found very heterogenous responses of the soil fauna to the type of organic amendment involved. On the other hand, pesticides have a general detrimental impact on community of soil invertebrates: neonicotinoid treatments showed reduced populations of non-targeted taxa, such as decomposers and predators (Atwood *et al.*, 2018), while fungicides impair litter decomposition mediated by soil fauna (van Wensem *et al.*, 1991).

Crop type as a direct effect on soil fauna community, Aleinikova and Utrobina (1975) demonstrated an increasing number of species and their density in maize, wheat and perennial grass crops in order; while, Crotty *et al.* (2015) showed the dominance of certain trophic groups was driven by the presence of the specific crop types. The response of each population of *Acari* also differs regarding the method of cultivation (crop rotation *vs.* monoculture; Aleinikova and Utrobina, 1975). However, Coudrain *et al.* (2016) did not observe such a clear effect of crop type on the abundance and structure of the soil fauna community, but showed that disturbing field activities, such as tillage, restricted the presence of certain groups of soil organisms. In the latter case, it could be hypothesised that field activities, such as tillage, offset the effect of crop on the composition of the soil faunal community. In this thesis project, attention was particularly directed to the effects of tillage practices and damage caused by soil compaction on community of soil mesofauna.

Many studies have investigated the effects of tillage on soil faunal community (Brennan *et al.*, 2006; Hülsmann and Wolters, 1998; Kladivko, 2001), most of them demonstrated that tillage directly affected the physical structure of soil and indirectly regulating food supply, by making it physically available or not, and therefore modified biologically-driven soil processes. For example, tillage regulates the amount of organic matter available to soil organisms (Balesdent *et al.*, 2000; Conant *et al.*, 2007), as well as changing the physical structure of their habitat (Kladivko, 2001; Loaiza Puerta *et al.*, 2018). In a review on the effects of no-till versus conventional tillage practices, Wardle (1995) calculated a magnitude index of response to tillage for different soil organisms and showed that most of the fauna (meso- and macro-fauna) is generally inhibited by tillage practices. The physical disruption of their habitat structure causes extreme inhibition of the macrofaunal community; while the response of the mesofauna depends on the taxonomical or functional group. *Collembola* are generally inhibited by tillage practices, however, the wide range of life-history strategies among the *Acari* community results in great variability in responses to tillage practices, such that some opportunistic taxa, for example

Heterostigmatina mites might benefit from the disturbance (Wardle, 1995).

In agricultural contexts, soil structure is also exposed to deterioration by heavy machinery traffic and many arable soils in the UK are sensitive to compaction, causing a decline in crop yield (Hamza and Anderson, 2005). Soil compaction results in a rearrangement and alteration of soil aggregates, which directly modify the soil pore network, and indirectly modulates the belowground oxygen supply, the physical habitat of the soil biodiversity and the functions it carries. The deterioration of the soil structure (principally reduction in porosity and connectivity of pores) via external factors has been shown to affect microbially-driven carbon and nutrient mineralisation processes (Beylich *et al.*, 2010; De Neve and Hofman, 2000), as well as the habitat and food resources that support the soil fauna (Althoff *et al.*, 2009; Beylich *et al.*, 2010; Larsen *et al.*, 2004). Although, other agricultural factors can impact soil mesofauna, it has been proven that soil disturbance is a strong factor regulating soil communities, Heisler and Kaiser (1995) proved that the reduction of pore space due to wheeling compaction, rather than crop species, had the more impact on density of populations.

1.3. The potential of field margins to support soil biodiversity in agricultural systems

In order to alleviate the impacts of agricultural intensification, the European Union, started to establish a series of agri-environmental policies in 1985 (European economic community, 1985; Agricultural and rural development, 2012). Most of them were designed to promote aboveground biodiversity in agricultural landscapes, and it was not until 2006 that ‘soil protection’ became a recurrent theme in these policies (Commission of the European communities, 2006). Since then, many studies have investigated the possible ways to reverse the degradation dynamics of agricultural soils and to promote the functional biodiversity and ecological functions in soils by managing the landscape heterogeneity (Bianchi *et al.*, 2013; Kovács-Hostyánszki *et al.*, 2017; Wezel *et al.*, 2014). Field hedgerows, such as field margins defined as a ‘non-cropped’ area at the edge of an arable field (Marshall and Moonen, 2002), had proven to sustain biodiversity in agricultural contexts providing shelters and habitat to pest controls (Mansion-Vaquié *et al.*, 2017) and pollinators (Kovács-Hostyánszki *et al.*, 2017; Wratten *et al.*, 2012) and to support a wide range of ecosystem services, such as quality regulation of water and soil resources (Marshall and Moonen, 2002; Wratten *et al.*, 2012). As part of the diversification of agricultural landscapes lounged by the European Union, the United Kingdom created a ‘Biodiversity Action Plan’ (BAP) and classified arable field margins as priority habitat (Department for Environment, Food & Rural Affairs, 2014; Maddock, 2008) to increase and support biodiversity in the agricultural landscape. This resulted in a stewardship for farmers, including a compensation for the establishment of field margins (Department for Environment, Food & Rural Affairs, 2014; Meek *et al.*, 2002). In 2012, the government released a ‘UK Post-2010 biodiversity Framework (JNCC and Defra, 2012), which aimed to redefine the direction of the BAP for the period 2011-2020, on the basis of the result obtained with the first action plan. It is stated that most of the stewardship plans were successful and must be pursued.

Despite the great potential of field margins to promote agricultural biodiversity, their impacts on belowground biodiversity had largely been overlooked. Studies on the effects of field margins on population of soil fauna had shown contrasted or limited responses of the various taxonomic groups to the presence of the margin and could not find a generalised effect on the soil community (Coudrain *et al.*, 2016; Frazão *et al.*, 2017; Meek *et al.*, 2002; Sechi *et al.*, 2017). There is a need to fill the knowledge gap in this matter and evaluate if field margins have any role in modulating the structure and function of the soil fauna community in arable contexts.

1.3.1. Thesis aim and hypotheses

This project principally aimed to investigate the effect of field margins and agricultural management on soil ecosystems in arable fields. We hypothesised that:

i) the soil mesofaunal community in crops will change in response to the presence, the time since establishment and the orientation of the field margin; the further in space and time the more different community between margins and crop will be (addressed in Chapters 3 and 4);

ii) agricultural practices (e.g. field traffic, crop residues) can partially mask or change the effects of the margin on the community of soil mesofauna; crop residues will facilitate the dispersal of margins communities into the field, while tramlines will prevent margin communities from dispersion into the crop (addressed in Chapters 4 and 5);

iii) the ecosystem services delivered by the soil biodiversity, such as litter decomposition, will be affected by soil and crop managements (addressed in Chapter 5); and

iv) historical landscape management is interacting with current field management to explain the distribution of soil mesofauna in the field (addressed in Chapter 6).

CHAPTER 2

MATERIALS AND METHODS

Those aspects of sampling design, materials and methods, and assays common throughout this PhD study are presented in this chapter. Details specific to each experiment are explained accordingly in each related chapter.

2.1. Experimental field sites

The experiments and soil sampling were carried out at two arable farms in the UK: The Grange farm, Northamptonshire, and the Rawcliffe Bridge farm, Yorkshire, with a distance of 153 km between them (Figure 2.1). The two farms are partners in the BASF Farm Network and were prescribed because of their contrasting soil types and their relatively similar cropping systems, despite existing differences in their field management.

Figure 2.1. BASF UK Network farm: The Grange farm, Northamptonshire, and the Rawcliffe Bridge farm, Yorkshire.

2.1.1.The Grange Farm

At the Grange Farm (52° 18' 2.73" N; 0° 45' 52.83" W), the field rotation was winter wheat (*Triticum aestivum* L.) in autumn 2015, oilseed rape (*Brassica napus* L.) in autumn 2016, and oilseed rape again in autumn 2017 to control a blackgrass outbreak. The fields were managed using minimum tillage techniques (i.e. no ploughing) for at least 15 years. Mineral fertilisation and chemical inputs were applied following the UK standard scheme management for farmers (Agriculture and Horticulture Development Board, 2017), all crop residues were left on the ground as soil organic amendment. Field margins (6 meters wide) had been set up around each field to promote biodiversity in the agricultural landscape (Department for Environment, Food & Rural Affairs, 2014; Maddock, 2008). Two fields were chosen for the studies; New Cover and Paradise (Figure 2.2). These fields were chosen as they had field margins that had been established 1 and 6 years (New Cover) and 10 years (Paradise) at the onset of this study. Margins of Paradise field were natural regeneration, red fescue (*Festuca rubra*), creeping bent (*Agrostis stolonifera*), couch grass (*Elymus repens*), Yorkshire fog (*Holcus lanatus*), docks (*Rumex sp.*) and dandelions (*Taraxacum*) were considered present. Margins of New Cover field were sown with a basic general purpose meadow mixture (EM1, Emorsgate Seeds, Norfolk, United Kingdom) comprising mainly crested dogstail (*Cynosurus cristatus*), red fescue (*Festuca rubra*), common bent (*Agrostis capillaris*), smaller cat’s tail (*Phleum bertolonii*), and in a smaller extent some wild flowers, such as common knapweed

(*Centaurea nigra*), lady's bedstraw (*Galium verum*), meadow buttercup (*Ranunculus acris*) The large size (312 m length) of New Cover field ensured that there was no interaction between the experimental areas at each end of the field. The two fields were approximately 700 m apart.

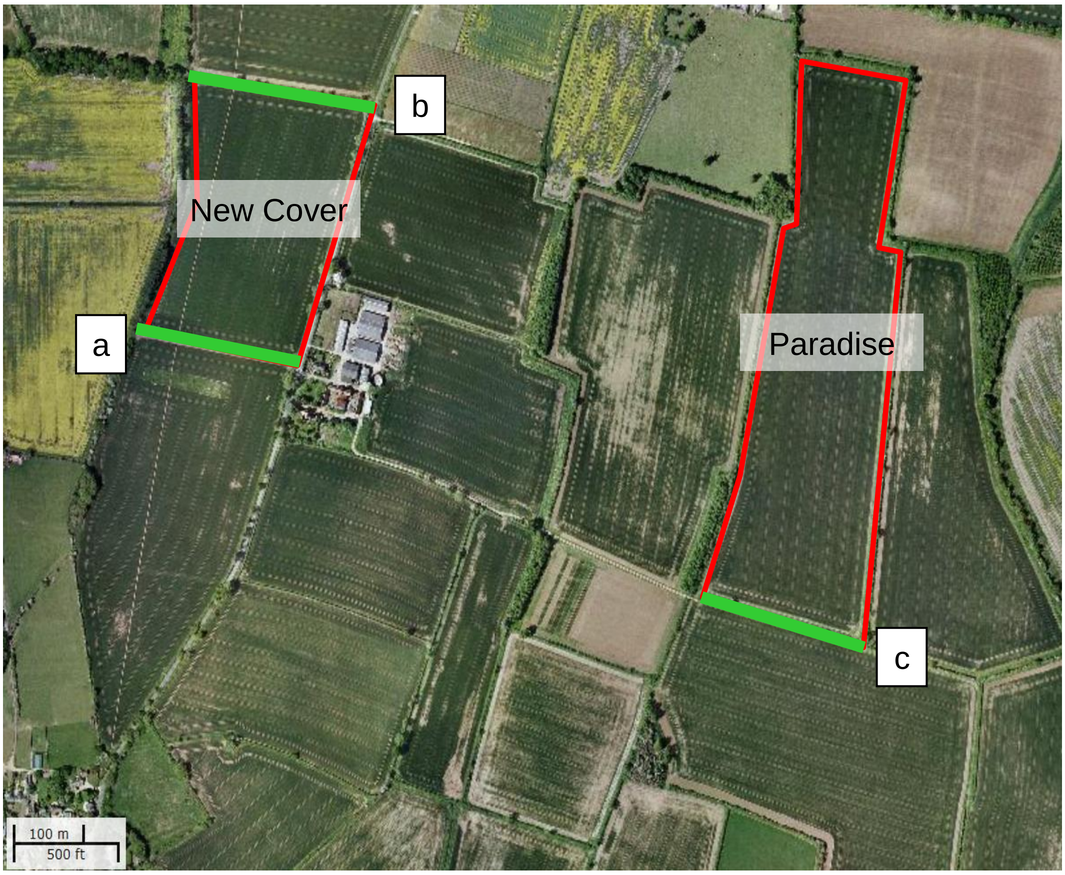

Figure 2.2. An aerial view of the Grange Farm. Red polygons delimit 'New Cover' and 'Paradise' fields; the green bands show the three field margins of different ages (a) 1-year-old (b) 6-years-old; (c) 10-years-old on which the study was based. Image source: RGB Aerial Photography - © Bluesky International Limited.

The soil of the fields was classified as Hanslope series, a typical calcareous pelosol from a clayey chalky drift series with poor drainage capacity and high sensitivity to compaction (Table 2.1; Cranfield University, 2017).

Table 2.1. Description and properties of the Hanslope soil series and Blacktoft soil series (Cranfield University, 2017).

	SOIL SERIES	
	Hanslope	**Blacktoft – "Warp soil"**
World Reference Base for Soil Resources *(Schad and Dondeyne, 2015)*	*Calcaric Stagnic Cambisols*	*Calcaric Fluvic Endogleyic Cambisols*
Description	Typical calcareous pelosols - Coarse blocky structure - Non-calcareous subsurface within 40cm - Calcareous subsoil	Gleyic brown calcareous alluvial soils - Deep stoneless permeable calcareous silty soils - Human-made topsoil (controlled flooding)
Geology	Clayey chalky drift	Marine alluvium
Drainage	Slowly permeable Risk of waterlogging	Permeable Low groundwater (controlled by ditches and pumps)
Chemical and nutrients properties	Potassium and Magnesium good Phosphorus related to management history Rare acidity	Naturally fertile Lime rich Manganese deficiency if high pH
Cropping land use	Winter crops - Winter cereals - Oilseed rape Restricted spring crops	Root vegetables - Sugar beet - Potatoes Cereals Field vegetables and Horticultural crops
Agricultural constraints	Shortage of soil moisture Timeliness with field work Sensitive to spring structural damage	Weak topsoil structure

2.1.2.The Rawcliffe Bridge Farm

Unlike the Grange Farm, the Rawcliffe Bridge Farm (53° 40’ 0.37” N; 0° 55’ 46.84” W) has been in no-tillage (no-till) practice over 10 years. The crop rotation was winter oilseed rape, winter wheat, winter oilseed rape, and spring beans (*Phaseolus vulgaris* L.). Mineral fertilisation and chemical inputs were applied following the UK standard scheme management for farmers (Agriculture and Horticulture Development Board, 2017) and like The Grange Farm, crop residues were also left after harvest. The field studied was bordered by 10-year-old (at onset of this study) grass-based field margin at least 6 m wide (Figure 2.3). The exact composition of the field margin was not know, records of botanical assessments suggested red fescue (*Festuca rubra*) and cockatoo grass (*Alloteropsis semialata*).

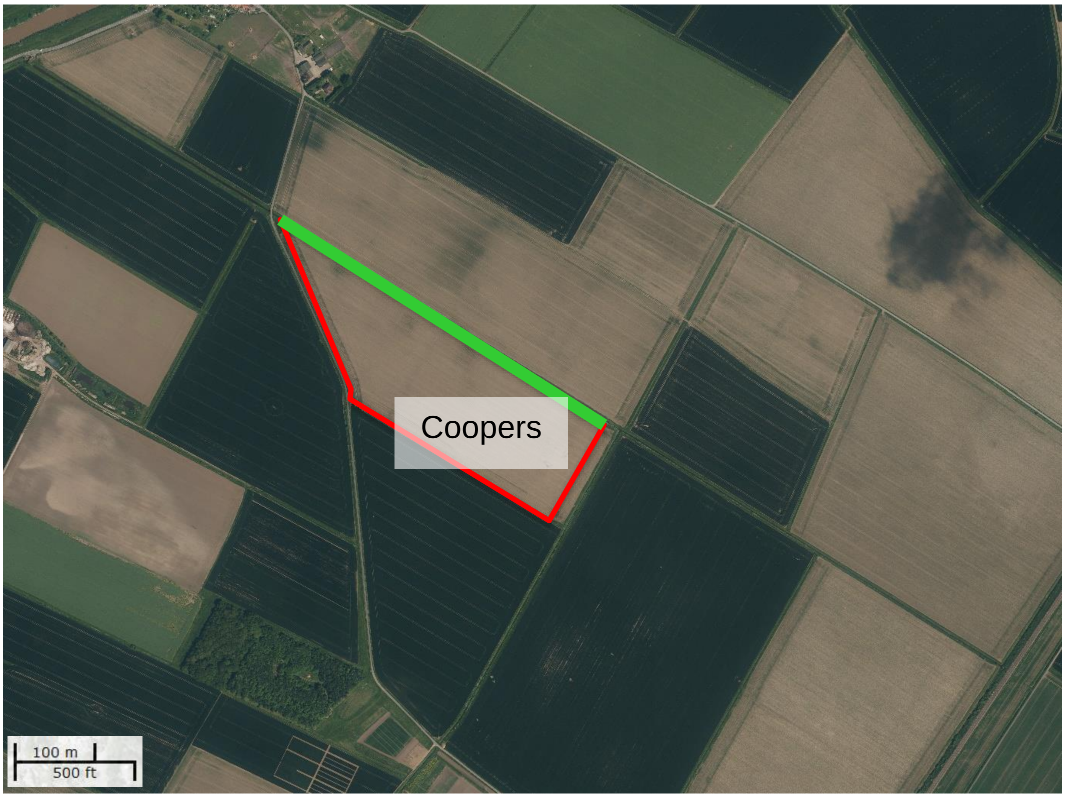

Figure 2.3. An aerial view of Rawcliffe Bridge farm. The red polygon delimits 'Coopers' field; the green band show the 10-year-old field margin on which the study was based. Image source: RGB Aerial Photography - © Bluesky International Limited.

Soils at Rawcliffe Bridge were classified as Blacktoft series (Cranfield University, 2017; Table 2.1). An artificial lime-rich top soil layer was created by historical flooding management (the warping method, Creyke, 1845; Creyke *et al.*, 1824).

2.2. Soil sampling

The sampling areas consisted of five adjacent transects in each field. Each transect was further divided into 6 subplots (6x6 m), the first being the field margin and five within the crop, at increasing distances from the margin (Figure 2.4). To offset the spatial correlation between the samples and to increase randomisation, one soil core was collected in each subplot following a "W" pattern along the transect.

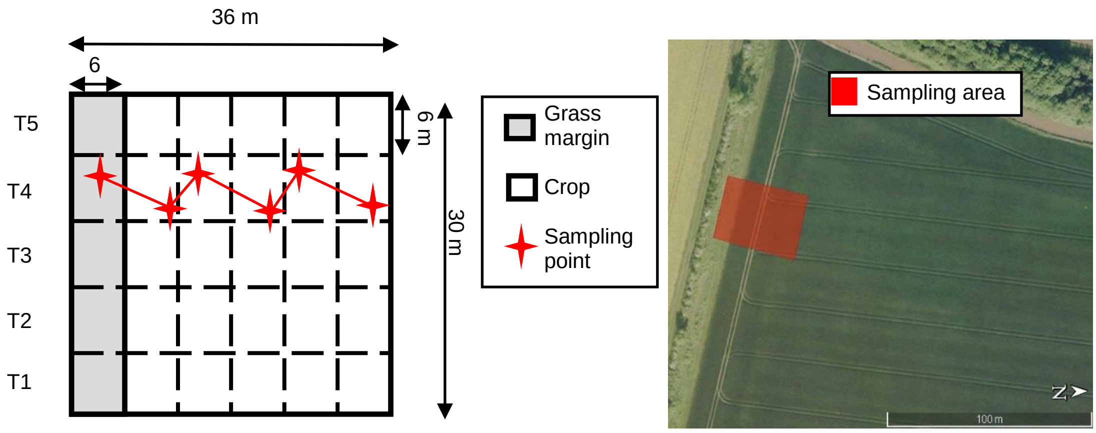

Figure 2.4. Experimental design of each study area (left) an aerial field-view (right) showing, as an example, the 10-year old margin at The Grange farm and adjacent crop in which the sampling area is marked in red. Soil cores were taken along five transects (T1 - T5) 6 m apart. Within each transect, soil samples were taken in a 'W' pattern along (just one depicted) from sample points, one in the margin and 5 from the crop at increasing distances from the margin (9, each 6m apart).

Soil samples were collected in autumn 2015 (October), spring 2016 (April), spring 2017 (April) and autumn 2017 (October), using a root corer (8 cm diameter x 10 cm depth, Eijelkamp, The Netherlands). Each intact soil core was placed in a labelled plastic bag and put in a cool box. All the cores were then transported to the laboratory where they were stored at 4°C until processing (approximately a couple of days to a week). Each core was vertically subdivided into two sub-samples. One half was used to measure soil characteristics (bulk density (BD), water filled pore space (WFPS), amount of plant residues, soil organic matter (SOM) content and pH), while the second half was kept intact for the invertebrate assessment by extraction.

2.3. Measurement of soil characteristics

Fresh soil samples (a volume of 251 cm^3 each) were weighed before being dried at 105°C to constant weight.

The sampling method used for the soil cores was considered appropriate to the requirements of this study as it has been shown not to affect BD measurement significantly (Özgöz *et al.*, 2006; Page-Dumroese *et al.*, 1999). BD was calculated as per Laryea *et al.* (1997):

$$\boldsymbol{SoilBD}(\boldsymbol{g.cm^{-3}}) = \frac{\boldsymbol{Drysoilmass}(\boldsymbol{g})}{\boldsymbol{Soilvolume}(\boldsymbol{cm^3})} \qquad \textbf{(1)}$$

Water filled pore space was determined as:

$$\boldsymbol{SoilWFPS}(\%) = \frac{\boldsymbol{\theta}}{\boldsymbol{P_s}}\boldsymbol{X100} \qquad \textbf{(2)}$$

where θ is volumetric water content:

$$\boldsymbol{\theta} = \frac{\boldsymbol{Soilwatermass}(\boldsymbol{g}) / \boldsymbol{Waterdensity}(\boldsymbol{g.cm^{-3}})}{\boldsymbol{Soilbulkdensity}(\boldsymbol{g.cm^{-3}})} \qquad \textbf{(3)}$$

and P_s is soil porosity defined as the inverse of the ratio BD to particle density (2.65 g cm^{-3}; Agriculture and Horticulture Development Board, 2015):

$$\boldsymbol{P_s} = \frac{\boldsymbol{Particledensity(g.cm^{-3})}}{\boldsymbol{BD(g.cm^{-3})}} \quad \textbf{(4)}$$

Visible plant residues in soil samples from the crop subplots and fine roots in those from the grass margins were handpicked or collected using a 2 mm sieve before the soil samples were dried and weighed for SOM. SOM was calculated with the loss on ignition method adapted from Davies (1974):

$$\boldsymbol{SOM}(\%) = \frac{\boldsymbol{M_B - M_C}}{\boldsymbol{M_B - M_A}} \times \mathbf{100} \quad \textbf{(5)}$$

where M_A is weight of an empty dish (g), M_B is total weight (g) after 20 g of dry and sieved soil were heated to 105°C for 24 h and M_C is total weight (g) after the sample was combusted at 400°C for 16 h.

Soil pH was measured at 1:2.5 soil:water ratio using a pH meter (Jenway Model 3320, Jenway, Staffordshire, United Kingdom).

2.4. Assessment of soil invertebrates

2.4.1. Extraction of soil invertebrates using the Tullgren Funnel Method

A soil sample was placed upside-down in a Tullgren Funnel unit with a 5 mm mesh (Figure 2.5; Burkard Manufacturing Co. Ltd, Rickmansworth, UK). Crotty (2011) established that 12 days was the optimal period to extract most of the active mesofauna organisms based on the soil types involved here. Invertebrates were collected in a tube placed below each funnel and preserved in 70% industrial methylated spirit (IMS) at 4°C before being hand sorted under a stereo-light binocular microscope (Olympus SZX10, Olympus, Essex, United Kingdom).

Figure 2.5. The Tullgren funnel units (Burkard Manufacturing Co. Ltd, Rickmansworh, UK) used for the extraction of soil invertebrates.

2.4.2. Identification of soil invertebrates

Soil invertebrates were classified to different taxonomic levels according to their type. The macrofauna (above 2 mm size range) were identified to the order level, while the mesofauna (size ranges between 2 mm and 2 µm) was divided into two subclasses: the *Collembola* (springtails) and the *Acari* (mites). *Collembola* were identified at the family level using the key by Hopkin (2007); and *Acari* at the sub-order or family level using the key by Krantz and Walter (2009). Such taxonomic resolution was chosen as the best compromise between considering sufficient differences amongst taxa in order to reveal environmental changes and time required to identify and classify each individual.

Soil *Acari* were identified into five sub-families: *Astigmata*; *Mesostigmata*; *Heterostigmatina*; *Oribatida*; and *Prostigmata* (Figure 1.3; Chapter 1). While soil *Collembola* were separated into the four main families: *Poduromorpha*; *Entomobryomorpha*; *Symphypleona*; and *Neelipleona* (Figure 1.2; Chapter 1).

2.5. Statistical analyses

All statistical models and analyses used for each experiment will be explained in full detail in the corresponding chapters. Analyses common to all work is explained below. Univariate ANOVA approaches were used to study single response variables and one or more explanatory variables; while multi-variate analyses (such as Canonical

Correspondence Analyses, Mantel test or Procrustes analyses) were used to test multiple response variables.

Effects of environmental treatment factors (margin age, habitat type, i.e. margin *vs.* crop, distance from the margin, sampling season (spring vs. autumn or year?)) and their interaction on the abundance of *Collembola* (*Poduromorpha*, *Entomobryomorpha*, *Symphypleona* and *Neelipleona*) and *Acari* (*Mesostigmata*, *Astigmata*, *Oribatida*, *Heterostigmatina*, and Trombidiformes) were estimated by multi-way analysis of variance (ANOVA). The difficulty in finding multiple fields with identical characteristics, to provide true replication of the effects of the application of these environmental treatment factors, and the decision, therefore, to focus on studying a few well-characterised fields in detail, rather than studying multiple fields in less depth, requires a number of assumptions to be made to allow the combined data to be analysed across different fields, seasons and years (and hence to assess the impact of the larger-scale environmental variables). The principal assumptions made are that variation in the response between the transects within each field is homogeneous across fields (after any required transformations have been applied) and that the pooled (across fields) between-transect variance provides an appropriate basis for the assessment of the effects of between-field environmental treatments, this between-transect variance mimicking the between-field variance that might be observed were true replicate fields available. Hence, multi-way ANOVAs for the assessment of large-scale environmental treatment factors include a blocking structure of samples nested within ‘replicate’ transects, but without any blocking component to allow for differences between fields (any differences therefore being assumed to be as a result of the different environmental characteristics, rather than the different locations of the fields). Smaller-scale environmental effects are then assessed relative to the between-sample (within-transect) variance. The same models were applied to determine the impact of the environmental factors on the soil characteristics, bulk density (BD), water filled pore space (WFPS), amount of plant residues, soil organic matter (SOM) and pH. The log transformation of the count data (invertebrate abundance), usually used to meet the assumption of normality of the residuals, was primarily applied to enable the assumption of homogeneity of variance (equal variance of the residuals with changing fitted value) to be met. This assumption was assessed by using the further model checking (residuals v. fitted values) plot, and was found to be improved by the log-transformation.

Canonical Correspondence analyses (CCA), Mantel test and Procrustes analyses were chosen for their rather similar approaches to describe relationships between response and explanatory variables. All three methods are based on ordination analyses, based on data matrix operations and which aimed to identify pattern into species community. The matrices are generally composed of species in row and environmental parameters in column, and the analysis rests on the calculation similarity (or its opposite the distance) between each community (the whole of the species) regarding the environmental parameters.

All univariate analyses were made using GenStat (GenStat 18th Edition, VSN International Ltd., Hemel Hempstead, UK), while R software 3.1.2 was used for multi-variate analyses.

This chapter is structured and formatted in accord with specification for the journal Agriculture, Ecosystems and Environment. Current status is: For submission.

CHAPTER 3

CONSEQUENCES OF TIME SINCE ESTABLISHMENT OF FIELD MARGINS ON THE STRUCTURE OF SOIL FAUNAL COMMUNITIES IN THE FIELD MARGIN AND ADJACENT CROP

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[Θ] Author contributions: L.C. led and conducted the experimental work, analysed the experimental results, drafted the manuscript and coordinated the revisions. A.M. contributed to development of statistical models. S.M.C., K.R., D.S., L.W. and P.J.M. contributed advice on the analyses. A.B., M.G. and G.H. contributed perspectives on the agricultural context. All authors contributed to the conceptual development and manuscript revision. P.J.M. and K.R. supervised the overall project. All authors give final approval for publication.

ABSTRACT

Understanding the abundance and composition of soil faunal populations is a required step to optimise ecosystem services delivered by agricultural soils. However, relatively little attention is given to ‘macrobiome’ compared to the plethora of studies on the effects of the microbiome on such phenomena. The aim of this study was to determine whether installed field margins changed the structure and population size of the associated soil invertebrate communities, and investigate if such effects extended into the field. We characterised soil mesofaunal communities in three field margins which had been established for different times, and their associated fields, over two seasons. Results showed that the responses to habitat (margin *vs.* crop), duration since establishment of the margin (i.e. margin age 1-year; 6-year; 10-year) and season (autumn *vs.* spring) differed with the taxa studied. Overall, populations were found in greater abundance in the margins than in the field, and populations increased margin age. The communities found in the margins, however, were dissimilar to the communities found in the adjacent cropped areas. In particular, the abundance in the area at the interface of the margin and crop, and in the tramlines were particularly low. Further into the field, population numbers increased but the community structure differed from that in the margins. While sustainable food production is critical to humans and environmental needs, tools to understand dynamics of agricultural ecosystems are lacking. This study shows the potential of field margin to help with establishment of complex soil mesofauna communities. It also highlights the possibility to use temporal dynamics and variation in life strategies of the different taxa as indicators of changes in the soil functions, required for sustainable uses of soil and food production systems.

Key-words: Mesofauna; Field management; Ecological succession

3.1. Introduction

Soil invertebrates make a large contribution to many soil functions, such as carbon transformation and nutrient cycling which in turn provide ecosystem services such as maintenance of the soil fertility and structure, and the production of food and raw materials (Bardgett and van der Putten, 2014; Brussaard, 2012; Wall *et al.*, 2015). Most of the biodiversity in agricultural ecosystems lies in the soil (Brussaard *et al.*, 2007a). However, in these systems, soil faunal communities are typically reduced both in size and diversity in comparison with those in semi-natural habitats. This can affect the overall functioning of the soil (Postma-Blaauw *et al.*, 2010). The mesofauna, mainly mites (*Acari*) and springtails (*Collembola*) (Harding and Stuttard, 1974) plays a central role within the soil trophic network, and members of this group are found at every trophic level (Brussaard *et al.*, 2007b). Each taxon tends to demonstrate a specific response to soil management and disturbance, such that the community structure of the soil mesofauna is an effective indicator of changes occurring in the soil system (Coudrain *et al.*, 2016).

Agricultural intensification has been, and prevails as, a major threat to European soils (Montanarella *et al.*, 2016) with land-use intensification leading to decreasing complexity of the soil web networks and losses of specialist species, which are very adapted to a type of food or/and environment (Tsiafouli *et al.*, 2015). Since 1985, agri-environmental policies have been established across Europe to reverse, or at least stabilise, the impacts of agricultural intensification on aboveground biodiversity (European Economic Community, 1985; European commission, 2012) but it was not until 2006 that the European Commission developed a “Thematic strategy for soil protection” (Commission of the European Communities, 2006). Several studies have shown that there is potential to mitigate the degradation of ecological functions in agricultural soils by managing the landscape and to improve the functional biodiversity within the soils (Bianchi *et al.*, 2013; Kovács-Hostyánszki *et al.*, 2017; Wezel *et al.*, 2014).

In the United Kingdom, the government has promoted the establishment of field margins as a priority habitat type, with the aim of encouraging above-ground biodiversity (Department for Environment, Food & Rural Affairs, 2014). Field margins are defined as non-cropped areas at the edge of arable fields (Marshall and Moonen, 2002). In addition to sustaining biodiversity in the agricultural landscape, they support a range of other ecosystem services such as pollination (Kovács-Hostyánszki *et al.*, 2017; Wratten *et al.*, 2012), and pest control (Mansion-Vaquié *et al.*, 2017), and also help to improve water and soil quality (Marshall and Moonen, 2002; Wratten *et al.*, 2012). Their effects on soil biodiversity and functioning have been less well studied. Coudrain (2016) showed that field margin management had various impacts on the different groups of soil invertebrates and could not generalize effects on the overall community structure. Other studies investigated the potential impacts of field margins on populations of soil fauna, although they found limited or contrasting effects of the margin on the soil biota. Frazão *et al.* (2017), as instance, found the same earthworm body mass and species richness between crop and margins, if they identified differences in community composition, the presence of the margin did not interfere with the community in the crops.

Bardgett *et al.* (2005) emphasises on changes in the soil communities occurring over timescales of tens of years and that the variation in the soil fauna community over decades is driven by the succession of vegetation which influences shifts in nutrient resources (Bardgett and van der Putten, 2014). Therefore, timescale is another fundamental factor likely governing soil faunal community development and the impacts of environmental changes on such changes (Bardgett *et al.*, 2005; Bardgett and van der Putten, 2014). Comparative studies on the effects of agricultural management on soil fauna are often focussed on vegetation cover or agronomic practices (e.g. tillage, fertilisation; Smith *et al.*, 2008). Neutel *et al.* (2002) found that over time the multiplicity of specific interactions within soil food webs strengthen the stability of the system. In agricultural ecosystems, Coudrain *et al.* (2016) demonstrated that the level of disturbance, embodied by tillage practices, was the main factor explaining shifts in soil fauna communities over time.

In the context of the UK agri-environmental schemes and the establishment of sown margins around arable fields, we investigated a field margin set up a year before the sampling started, to represent a recently disturbed system, and a 10-year margin as a model for a long-term undisturbed system, a 6-year margin was selected as an intermediate between the two extremes. We hypothesised that: i) the presence of grass strips margins supports the community of soil invertebrates and increases abundance and diversity of the community in the adjacent cropped area of the field; ii) the effects of the field margin on the structure of the soil fauna community are amplified with time since the establishment of the margin; iii) that the wide variation in life strategy of different taxa of springtails (*Collembola*) and mites (*Acari*) would result in different responses to disturbance and time succession.

3.2. Materials and methods

3.2.1. Site and soil characteristics

The experiment was carried at The Grange Farm, Northamptonshire, United Kingdom (52° 18' 2.73'' N; 0° 45' 52.83'' W) in arable fields where minimum tillage (i.e. no deep ploughing) has been applied for over 15 years with a conventional winter wheat (*Triticum aestivum* L.) - oilseed rape (*Brassica napus* L.) main rotation. Mineral fertilisation and chemical inputs were applied following the UK standard scheme management for farmers (Agriculture and Horticulture Development Board, 2017). The soil is classified as Hanslope series, a typical calcareous pelosol from a clayey chalky drift series with poor drainage capacity and high sensitivity to compaction (Cranfield University, 2017). Grassy strips of 6 m wide had been gradually set up around the different fields to promote biodiversity in the agricultural landscape. At the time of the study, the field was supporting winter wheat. The crop was sown two weeks before the first sampling in October 2015 and was at stem elongation stage at the time of the second sampling in April 2016.

3.2.2.Soil sampling

Three grass-based field margins of various ages since establishment (1, 6 and 10 years) and adjacent wheat crops were chosen for sampling. 1 and 6 years margins were located in the opposite side of the same field, while the 10 years margin was located in a neighbouring field 800 metres apart (Figure 2.2, Chapter 2). The sampling areas consisted of five adjacent transects 6 m wide x 36 m long in each field; each transect was divided into 6 subplots (6x6 m) the first of which was in the field margin and the other five in the crop (Figure 3.1). To offset the spatial correlation between samples and to increase randomisation, one soil core was collected in each subplot following a “W” pattern along the transect.

Soil samples were collected in autumn 2015 (October) and spring 2016 (April), using a root corer (8 cm diameter x 10 cm depth, Eijelkamp, The Netherlands). Each soil core was placed in a labelled plastic bag, in a cool box, and returned to the laboratory where they were stored at 4°C until processing. Each core was vertically subdivided into two sub-samples (i.e., each half covering the 0 – 10 cm depth of the core). One half was used to measure soil characteristics (bulk density (BD), water filled pore space (WFPS), amount of plant residues, soil organic matter (SOM) and pH), while the second half was kept intact for assessment of invertebrates.

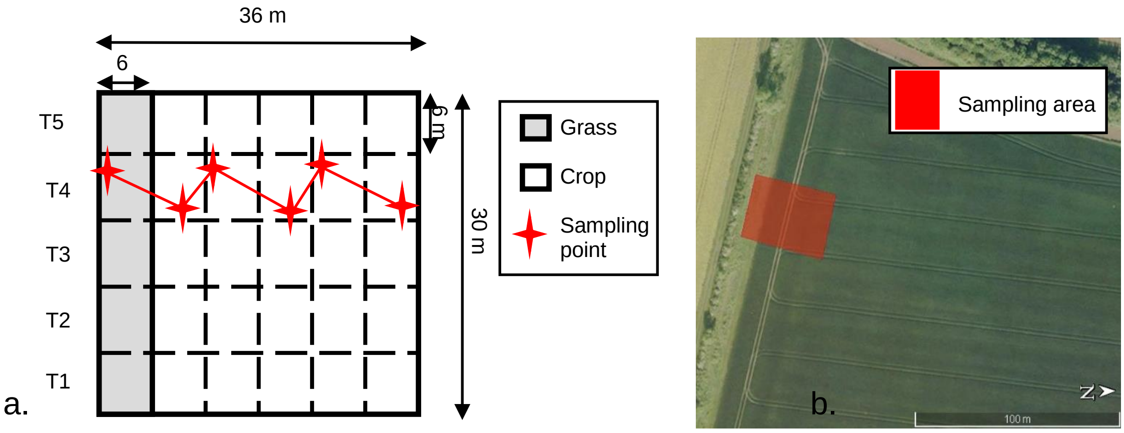


Figure 3.1. (a) Experimental design of each study field (left). Soil cores were taken along five transects (T1 - T5). Margin area is in grey and cropped area in white; red crosses show sampling points and the 'W' pattern along one of the transect. (b) Aerial view (right) of the 10-year margins and adjacent crop; the sampling area is marked in red.

3.2.3. Soil characteristics

For all measurements of soil characteristics, the fresh soil samples were weighed before being dried at 105°C until constant weight. The volume of a half-core was estimated as half the volume of an 8 cm diameter x 10 cm depth (i.e. 251 cm^3).

Bulk density (BD) was calculating following Laryea *et al.* (1997) Water filled pore space (WFPS) was determined from the ratio of volumetric soil water content to the total soil porosity. Soil porosity was the inverse of the ratio BD to particle density (2.65 g.cm^{-3}) (Agriculture and Horticulture Development Board, 2015).

Visible plant residues from the crop soil samples and fine roots from the grass margin soil samples were handpicked or collected using a 2 mm sieve, dried and weighed. Total soil organic matter content (SOM) was calculated from the loss on ignition method adapted from Davies (1974). Soil pH was measured at 1:2.5 soil:water ratio using a pH meter (Jenway Model 3320, Jenway, Staffordshire, United Kingdom).

3.2.4.Extraction and identification of the soil fauna

The other half of the soil sample was placed upside down in a Tullgren Funnel unit with a 5 mm mesh (Burkard Manufacturing Co. Ltd, Rickmansworh, UK) for 12 days. Invertebrates were collected in a tube placed below each funnel and preserved in 70% methylated spirit at 4°C before being hand sorted under a binocular microscope. The soil invertebrates were classified to different taxonomic levels. The macrofauna were identified to order level, while the mesofauna was divided in two subclasses: the *Collembola* and the *Acari*. *Collembola* were identified at family level using Hopkin’s key (2007); and *Acari* at sub-order or family level using Krantz and Walter’s key (2009).

3.2.5.Statistical analyses

Effects of the margin age, the habitat (field margin *vs.* crop), the distance to the boundary of the field (nested within habitat, with distance 0 corresponding to the margin), the sampling season (autumn *vs.* spring) and their interaction on the abundance of *Collembola* (*Poduromorpha*, *Entomobryomorpha*, *Symphypleona* and *Neelipleona*) and *Acari* (*Mesostigmata*, *Astigmata*, *Oribatida*, *Heterostigmatina*, and Trombidiformes) were estimated by a 3-way analysis of variance (ANOVA) with blocking structure. In order to compare the three margins and field areas, the blocking structure was taken such that each transect was sufficiently apart from one another, so they were considered independent and used as replication units. The same model was applied to determine the impact of the environmental factors on the soil characteristics (BD, WFPS, amount of plant residues, SOM and pH). Count data (invertebrate abundance) were log-transformed to meet the assumption of normality and the normal distribution of the residuals was assessed by using model checking plots (normal probability and quantile-quantile plots). This was done using GenStat (GenStat 18th Edition, VSN International Ltd., Hemel Hempstead, UK). We used a Canonical Correspondence Analysis (CCA) to identify and measure relationships between the different taxa of soil organisms and the soil characteristics. To verify that the CCA model is able to explain significantly more of the variance than expected by chance, we performed a permutation test (using 999 random permutations). Results of the CCA were displayed on a two-dimension biplot. The constrained model accounted for the variance explained by the soil characteristics and the unconstrained model accounted for the variance explained by the residuals. Eigenvalues represented the amount of variance explained by each axis of the CCA biplot. The magnitude of the CCA test scores informed us on the contribution of the individual variables to the corresponding canonical variable. The CCA analyses were done using R software 3.1.2 (http://www.r-project.org/).

3.3. Results

3.3.1. Soil sample characteristics

Soil bulk density significantly varied between sampling areas (margin and crop) ($F_{(2,179)}$=7.33, P=0.008) and between the margin/crop habitats ($F_{(1,179)}$=18.7, P=0.001). Bulk density was generally greater in the crop areas than in the margins; the highest value was recorded in the cropped area adjacent the 10-year margin sampled in autumn (Table 3.1). WFPS was significantly affected by the sampling season ($F_{(1,179)}$=509, P=0.001); values were twice as much in spring than in autumn. In spring, WFPS measured in the 6- and 10-year were greater in the margins than in their related field ($F_{(2,179)}$=7.31, P<0.001). The amount of plant residue found in the soil samples was not significantly different between the margin/crop habitats or within any distance to the field boundary. However, the interaction of the sampled area with the habitat significantly impacted the amount of SOM ($F_{(2,179)}$=157, P<0.001). The average SOM value was 8.9 % in the 10-year margin and 6.1 % in the related crop, while differences were less contrasted in the 1-year and 6-year margins and their related crop (Table 3.1). Soil pH differed between the sampling areas ($F_{(2,179)}$=791, P<0.001). The most acidic soil was recorded from the crop adjacent to the 10-year margin, and the margin itself (Table 3.1).

Table 3.1. Soil characteristics (average values) measured from grassy field margins of three different ages and adjacent cropped areas in two seasons.

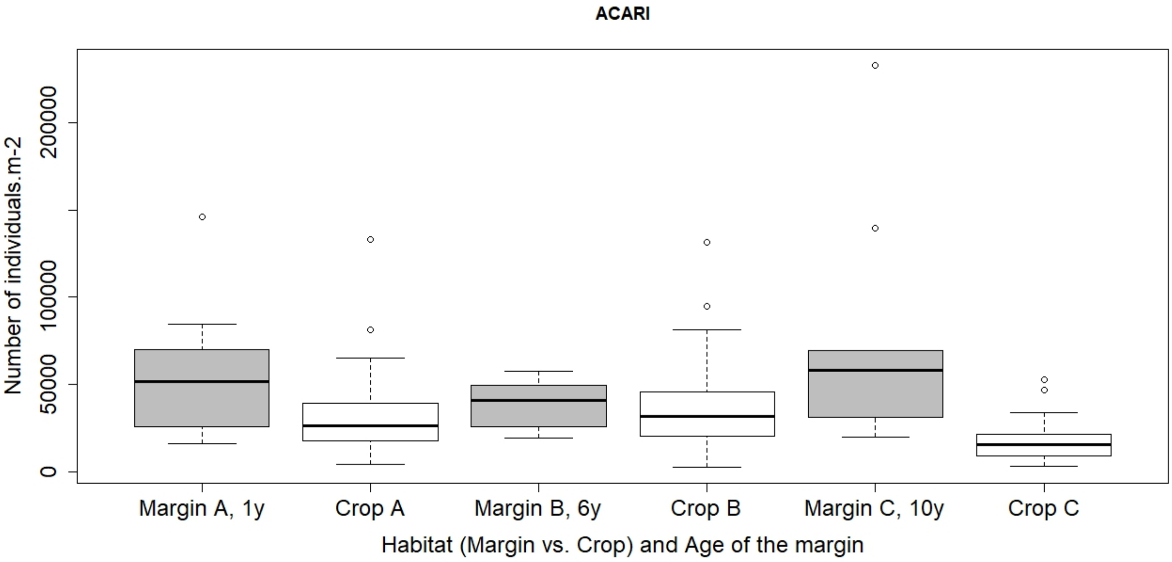
Season	**Autumn 2015**						**Spring 2016**					
Margin age	**1-year**		**6-year**		**10-year**		**1-year**		**6-year**		**10-year**	
Sample habitat	*Margin*	*Crop*	*Margin*	*Crop*	*Margin*	*Crop*	*Margin*	*Crop*	*Margin*	*Crop*	*Margin*	*Crop*
Bulk density (g.cm^{-3})												
Mean	1.03	1.13	1.05	1.10	1.02	1.28	1.01	1.01	0.94	1.04	0.90	1.12
±SE	0.04	0.04	0.03	0.03	0.10	0.03	0.06	0.03	0.05	0.02	0.08	0.03
WFPS												
Mean	7.45	9.10	7.60	8.65	8.32	9.09	15.94	17.02	18.64	16.44	21.85	14.97
±SE	0.16	0.20	0.25	0.31	0.55	0.25	0.36	0.30	0.62	0.57	4.53	0.46
Plant residues (mg.gSoil^{-1})												
Mean	3.94	9.53	4.44	15.10	13.26	7.45	13.59	10.48	18.30	12.46	19.00	9.29
±SE (x10^{-3})	0.51	1.43	1.09	1.74	4.51	1.40	3.97	2.31	3.93	2.40	4.49	3.50
SOM (%)												
Mean	7.09	7.57	7.22	7.03	9.16	6.12	6.54	7.21	8.11	6.61	8.67	6.02
±SE	0.09	0.07	0.08	0.17	0.72	0.05	0.17	0.09	0.24	0.06	0.44	0.08
pH												
Mean	7.26	7.31	7.39	7.47	6.37	6.25	7.48	7.44	7.51	7.56	6.52	6.33
±SE	0.03	0.02	0.04	0.01	0.17	0.06	0.04	0.02	0.03	0.02	0.11	0.08

3.3.2. Effect of margin age on abundance of *Acari* and *Collembola*

3.3.2.1. *Acari* populations

The population total of *Acari* varied with both sampling area and habitat ($F_{(2,179)}=6.89$, $P=0.002$); generally *Acari* were more abundant in the margins compared to the adjacent cropped area ($F_{(1,179)}=34.9$, $P<0.001$). In the crop habitat, the distance from the field boundary also affected the number collected ($F_{(4,179)}=9.93$, $P<0.001$) (Figure 3.2). Each taxonomic group of *Acari* (*Mesostigmata*, *Astigmata*, *Heterostigmatina*, Trombidiformes mites and *Oribatida*) showed variable responses to treatments (e.g. habitat, age of margin). The abundance of *Heterostigmatina* was not significantly different between the margins and the adjacent cropped area ($F_{(1,179)}=0.69$, $P=0.410$). However, all the other taxa were found in significantly greater abundance in the margins than the crop ($F_{(1,179)}=26.6$, $P<0.001$ for *Mesostigmata*; $F_{(1,179)}=10.9$, $P=0.002$ for *Astigmata*; $F_{(1,179)}=56.3$, $P<0.001$ for Trombidiformes; and $F_{(1,179)}=33.8$, $P<0.001$ for *Oribatida*). Furthermore, the numbers of *Mesostigmata* and *Oribatida* increased with increasing age of the margin (Figure 3.3). Unlike the overall population, distance from the margin had less impact on the abundance of the *Astigmata* ($F_{(4,179)}=2.34$, $P=0.065$) and *Heterostigmatina* ($F_{(4,179)}=2.49$, $P=0.052$) populations. The overall abundance of *Acari* did not vary with season ($F_{(1,179)}=0.83$, $P=0.367$) but the season in which the soil was sampled did affect each of the taxonomic groups ($F_{(1,179)}=21.7$, $P<0.001$ for *Mesostigmata*; $F_{(1,179)}=12.9$, $P=0.002$ for *Astigmata*; $F_{(1,179)}=24.0$, $P<0.001$ for *Heterostigmatina*; and $F_{(1,179)}=20.0$, $P<0.001$ for Trombidiformes) except *Oribatida* ($F_{(1,179)}=0.20$, $P=0.655$); *Mesostigmata* and Trombidiformes mites were found in greater numbers in spring, while *Astigmata* and *Heterostigmatina* were more abundant in samples taken in autumn (Figure 3.3).

a.



b.

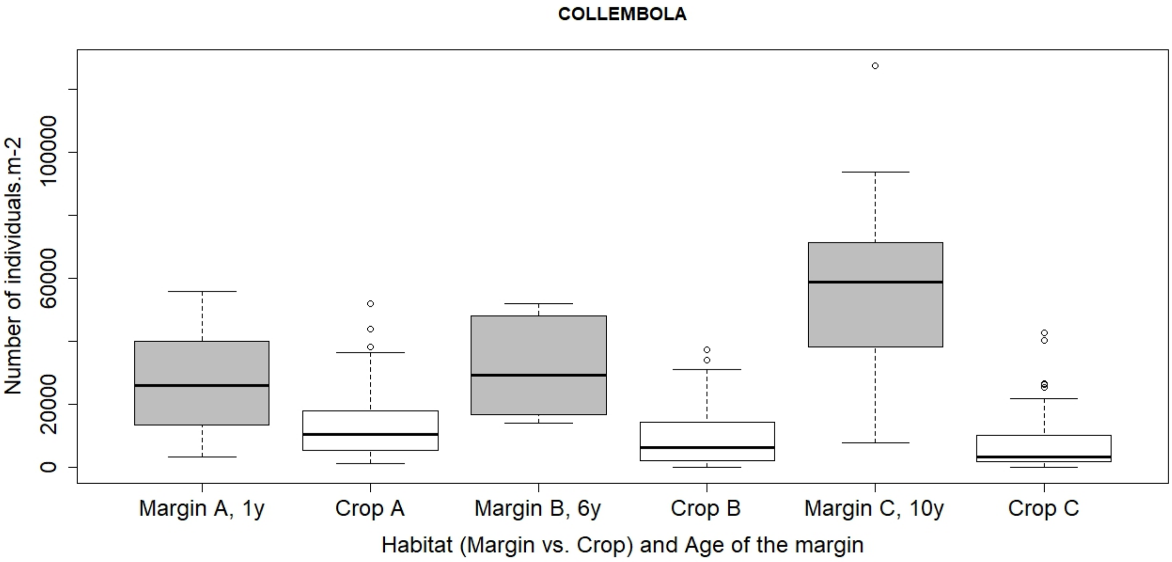
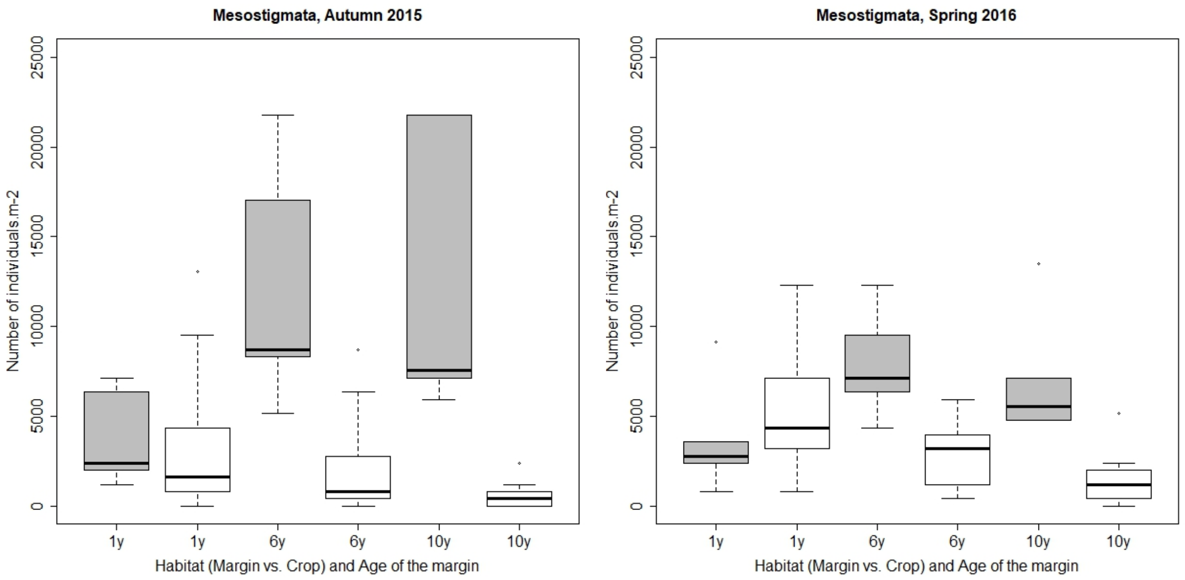
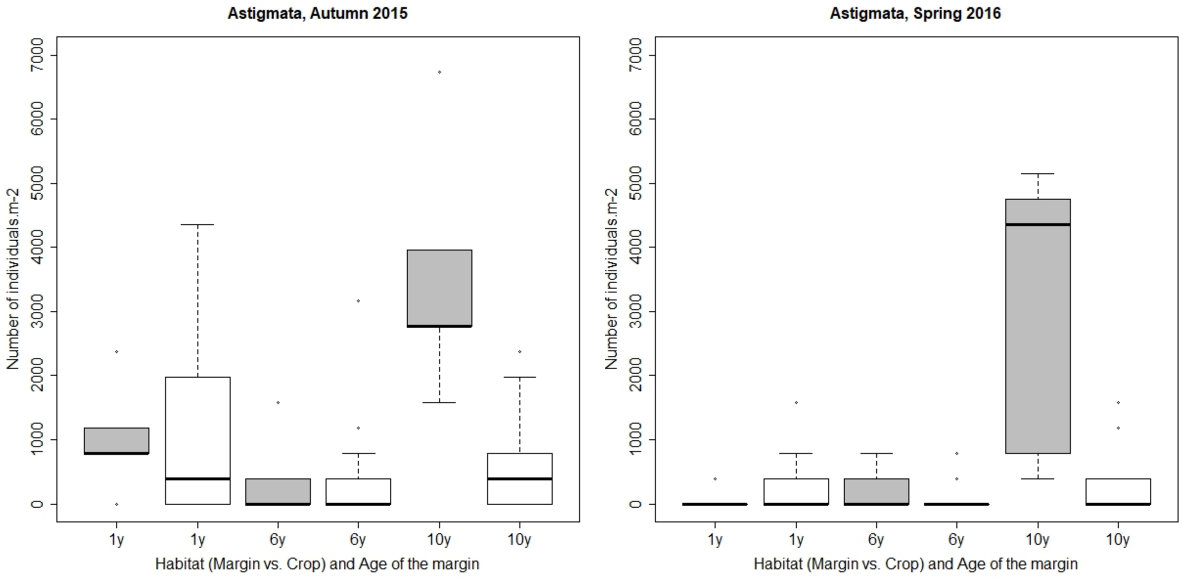


Figure 3.2. Abundance of (a) Acari and (b) Collembola sampled from grassy field margins of three different ages 1, 6 and 10-years (grey bars) and adjacent cropped areas (white bars). Upper and lower limit of boxes show the upper and lower quartile, respectively; the median is shown at the middle of the boxes and bars represent variability outside the upper and lower quartiles.

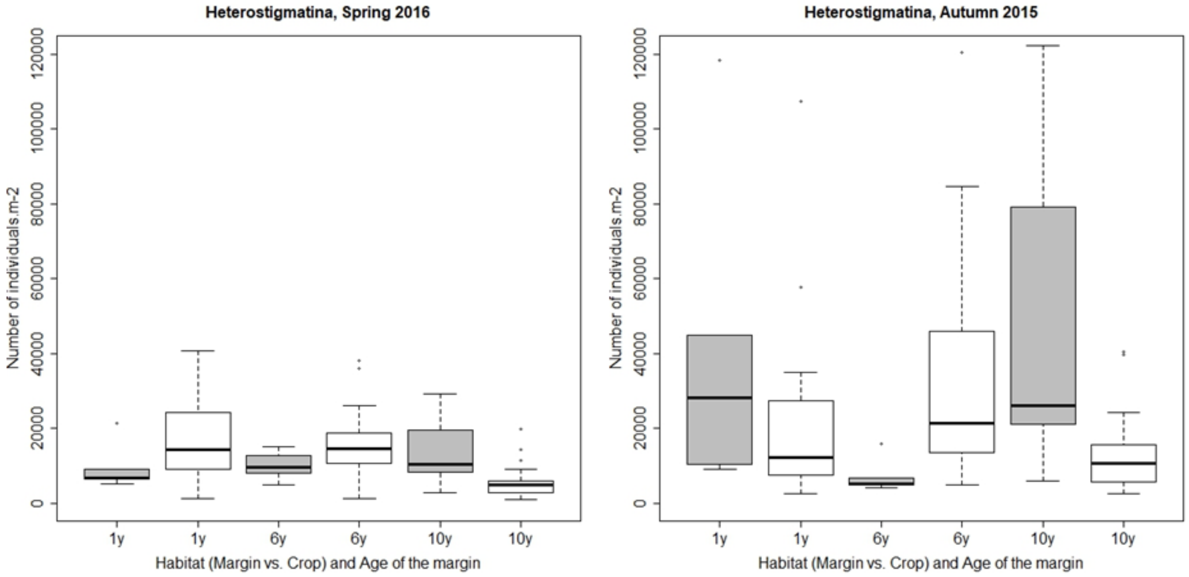
a.


Mesostigmata, Autumn 2015
Mesostigmata, Spring 2016
Number of individuals.m-2
0
5000
10000
15000
20000
25000
1y
1y
6y
6y
10y
10y
Habitat (Margin vs. Crop) and Age of the margin

b.


Astigmata, Autumn 2015
Astigmata, Spring 2016
Number of individuals.m-2
0
1000
2000
3000
4000
5000
6000
7000
1y
1y
6y
6y
10y
10y
Habitat (Margin vs. Crop) and Age of the margin

c.


Heterostigmatina, Spring 2016
Heterostigmatina, Autumn 2015
Number of individuals.m-2
0
20000
40000
60000
80000
100000
120000
1y
1y
6y
6y
10y
10y
Habitat (Margin vs. Crop) and Age of the margin

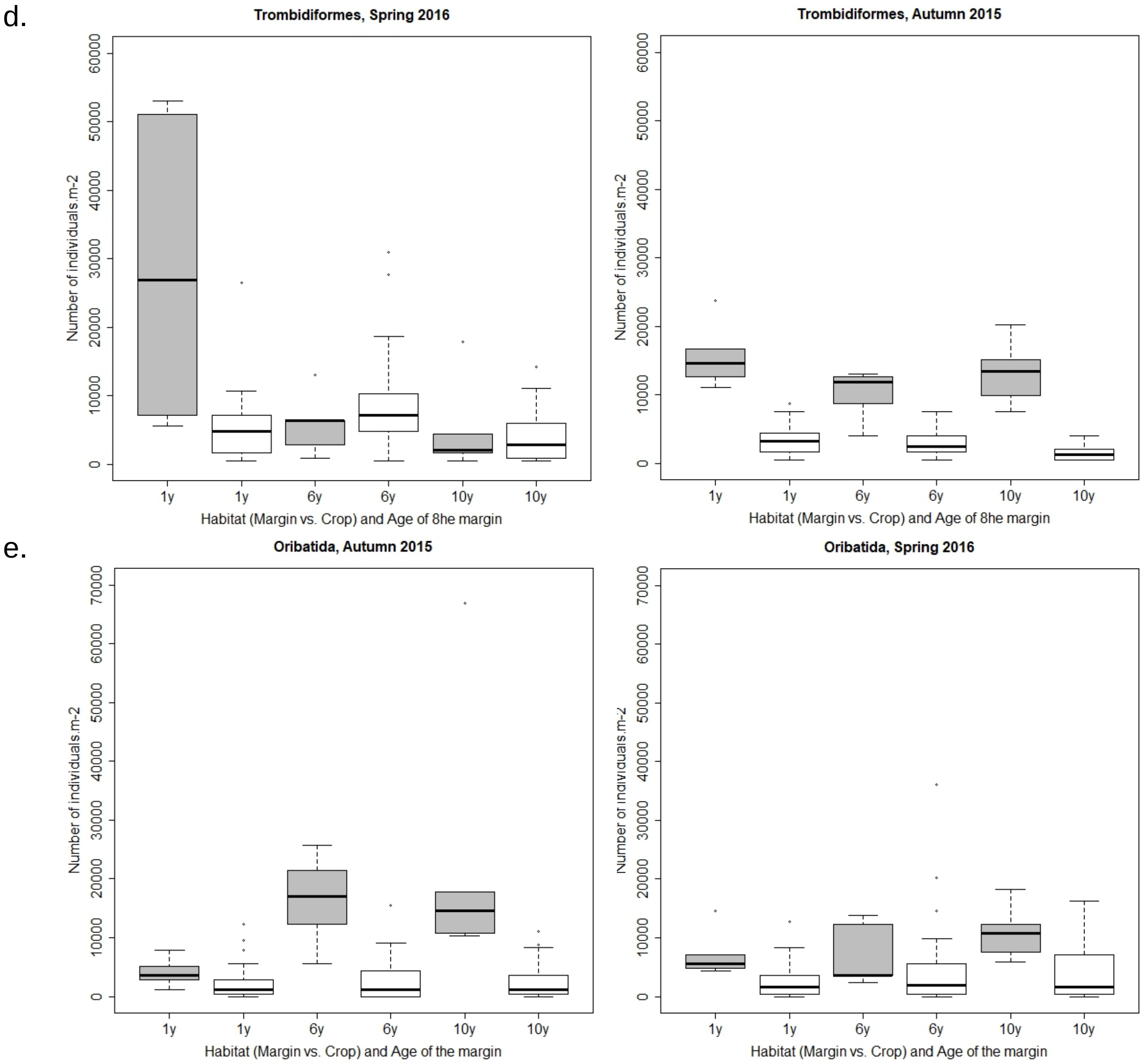


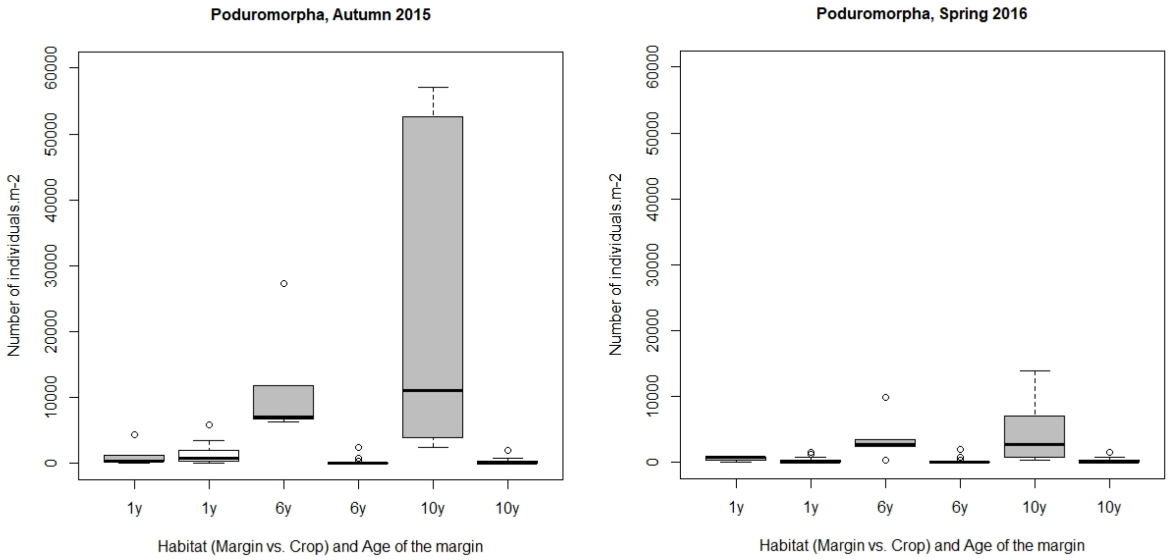
Figure 3.3. Abundance of (a) Mesostigmata, (b) Astigmata, (c) Heterostigmatina, (d) Trombidiformes and (e) Oribatida in the 1, 6 and 10-years old margins (shown in grey); their related cropped areas (shown in white) in autumn 2015 (left column) and in spring 2016 (right column). Upper and lower limits of boxes show the upper and lower quartile, respectively; the median is shown in the middle of the boxes and bars represent variability outside the upper and lower quartiles.

3.3.2.2.*Collembola* populations

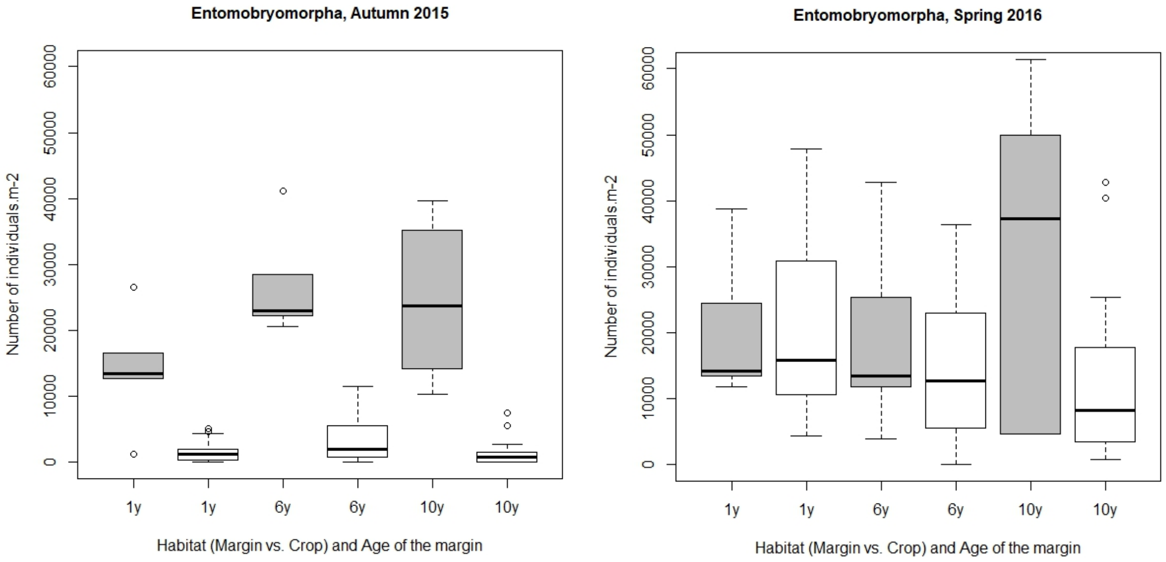
The plot location ($F_{(2,179)}$=5.77, P=0.018) as well as the habitat ($F_{(1,179)}$=28.2, P=0.001) affected the overall number of *Collembola*. The abundance in the field areas did not differ but the number increased with increasing age of the margin (Figure 3.2). Differences of relative abundance between the margins and their related crop were bigger for the population of *Collembola* than for the population of *Acari*; and low density of *Collembola* was found in the crop (Figure 3.2). Season had a strong impact on the overall population ($F_{(1,179)}$=60.0, P<0.001), yet this effect depended on the habitat ($F_{(1,179)}$=24.4, P<0.001); in autumn, lower densities were found in the crops than in the margins, while the differences between habitat were not evident in spring. In the crop, distance to the field boundary also affected the overall abundance ($F_{(4,179)}$=5.25, P<0.001).

Poduromorpha and *Entomobryomorpha* were two dominant groups in the sampled soils and the frequency of *Symphypleona* and *Neelipleona* was too low in some plots for differences between their populations to be analysed. *Poduromorpha* was significantly affected by all the factors (plot location, habitat, distance and season) and their interactions (need to give stats here) but abundance of *Entomobryomorpha* were affected by habitat ($F_{(1,179)}$=24.2, P<0.001) and distance only ($F_{(4,179)}$=4.71, P=0.002) (Figure 3.4). Both taxa were more abundant in the margins than the related crop areas, apart from in the 1-year margin, where the number of *Poduromorpha* was negligible.

a.


Poduromorpha, Autumn 2015
Poduromorpha, Spring 2016
Number of individuals.m-2
0
10000
20000
30000
40000
50000
60000
1y
1y
6y
6y
10y
10y
Habitat (Margin vs. Crop) and Age of the margin

b.


Entomobryomorpha, Autumn 2015
Entomobryomorpha, Spring 2016
Number of individuals.m-2
0
10000
20000
30000
40000
50000
60000
1y
1y
6y
6y
10y
10y
Habitat (Margin vs. Crop) and Age of the margin

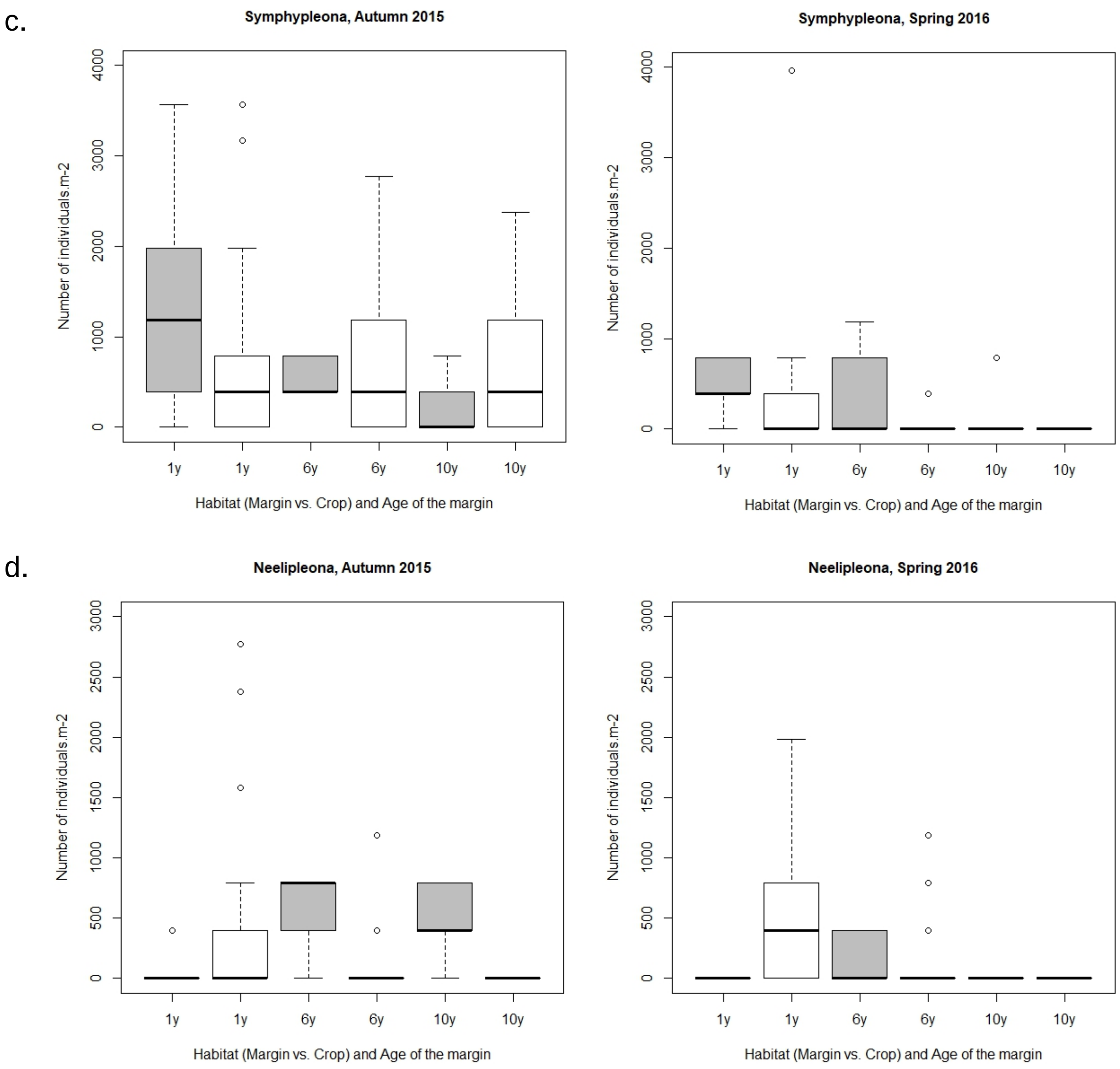


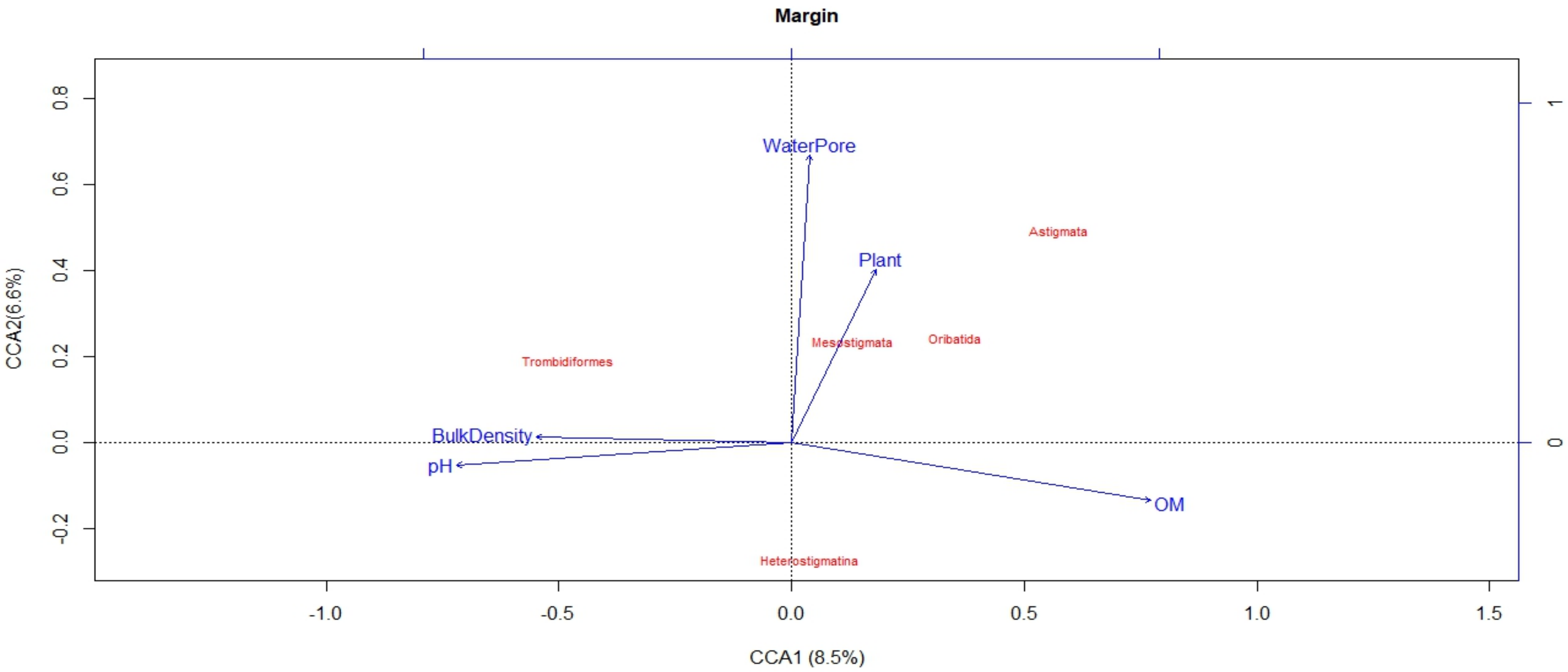
Figure 3.4. Distribution of (a) Poduromorpha, (b) Entomobryomorpha, (c) Symphypleona and (d) Neelipleona in the 1-year, 6-year and 10-year grass margins (shown in grey), and their related crop areas (shown in white) in autumn 2015 (left column) and in spring 2016 (right column). Upper and lower limit of boxes show the upper and lower quartile, respectively; the median is shown in the middle of the boxes and bars represent variability outside the upper and lower quartiles.

3.3.3.Relative distribution of the soil community *vs.* the soil characteristic variables

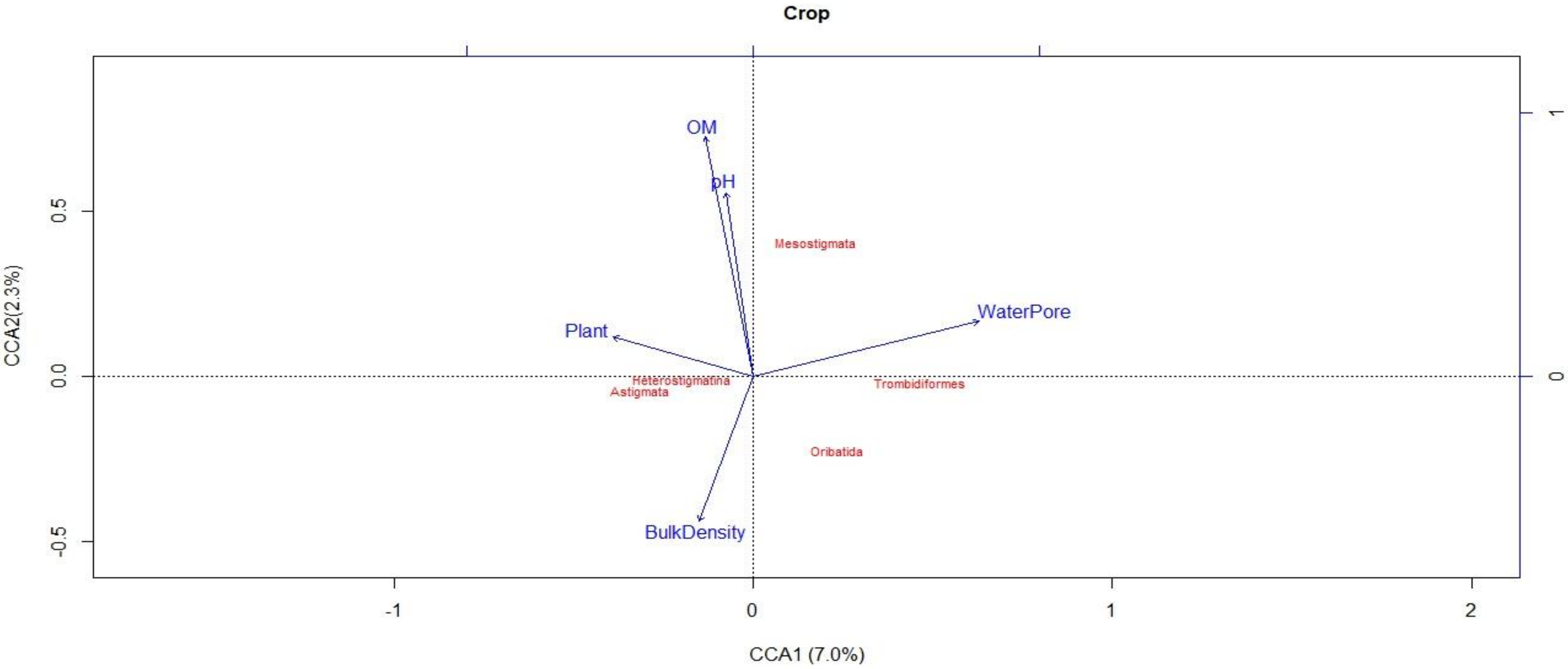
3.3.3.1.*Acari* populations

In the margins, only 37% of the variance was explained by the constrained model using the soil characteristics explanatory variables; while 63% was explained by the unconstrained analysis of the residues. The permutation test ($F_{(5,24)}$=2.82, P=0.052) was not significant, although the p-value was close to significance at the 5% level so the CCA analysis was relevant. When we tested the significance of each of the soil characteristics, we found that pH was significantly affected by the distribution of the different taxa of *Acari* ($F_{(1,24)}$=6.34, P=0.010). By interpreting the biplot, we found that the first axis was positively correlated with the soil organic matter (score=0.98) and negatively linked to bulk density (scores=-0.70) and pH (scores=-0.91); increasing organic matter content and low bulk density were associated with larger populations of *Astigmata* and *Oribatida*, while Trombidiformes were more related to high soil bulk density and low organic matter content. As the pH in the 10-year margin was lower than in the 1 and 6-year margins, it associated the population of *Oribatida* and *Astigmata* to the 10-year margin, while the Trombidiformes were linked to the 1 and 6-year old margins. The second axis associated to high water filled pore space (WFPS) values (score=0.85); was positively associated with populations of *Astigmata*, while *Heterostigmatina* were linked with low values of WFPS. (Figure 3.5.a)

Similarly, in the crop areas, the relative distribution of the different taxa was explained to a lesser extent by the soil characteristics; 19% of the variability was explained by the constrained model and 81% explained by the unconstrained model. Yet, the effect of soil characteristics on the observed frequencies of soil invertebrates was significant (permutation test, $F_{(5,144)}$=6.70, P<0.001). WFPS, plant residues, SOM and pH had significant effects ($F_{(1,144)}$=14.9, P<0.001; $F_{(1,144)}$=6.45, P=0.010; $F_{(1,144)}$=4.95, P=0.021; $F_{(1,144)}$=4.84, P=0.022, respectively) on the distribution of the different taxa. In the biplot, increasing values of WFPS (score=0.79), the low values of BD (score=-0.19) and low values of SOM (score=-17) were associated with the first axis and positively correlated to populations of Trombidiformes and negatively to populations of *Astigmata*. *Mesostigmata* were associated with increasing values of SOM (score=0.91) and pH (score=0.70) along the 2nd axis. The first axis discriminated for samples taken in Autumn (negative scores) and samples taken in Spring (positive scores). (Figure 3.5.b)


Margin
WaterPore
Plant
Astigmata
Mesostigmata
Oribatida
Trombidiformes
BulkDensity
pH
OM
Heterostigmatina
CCA2(6.6%)
CCA1 (8.5%)
0.8
0.6
0.4
0.2
0.0
-0.2
-1.0
-0.5
0.0
0.5
1.0
1.5
1
0

a.



b.

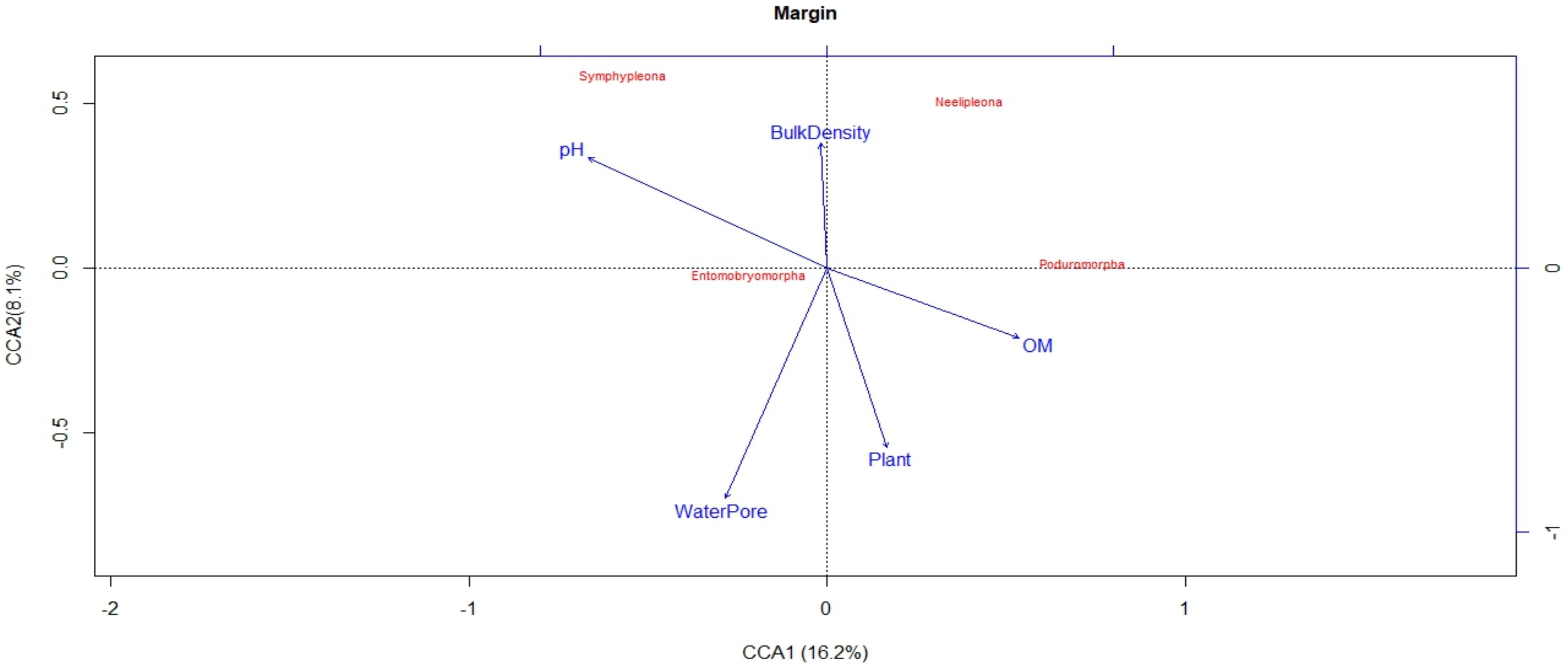
Figure 3.5. Ordination plot of the populations of Acari (Mesostigmata, Astigmata, Heterostigmatina, Trombidiformes, Oribatida) in relation to soil characteristics: (bulk density (BD), water filled pore space (WFPS), plant residues, soil organic matter (SOM), pH). (a) Relative distribution of each population in the margins; (b) Relative distribution of each population in the cropped areas.

3.3.3.2.*Collembola*

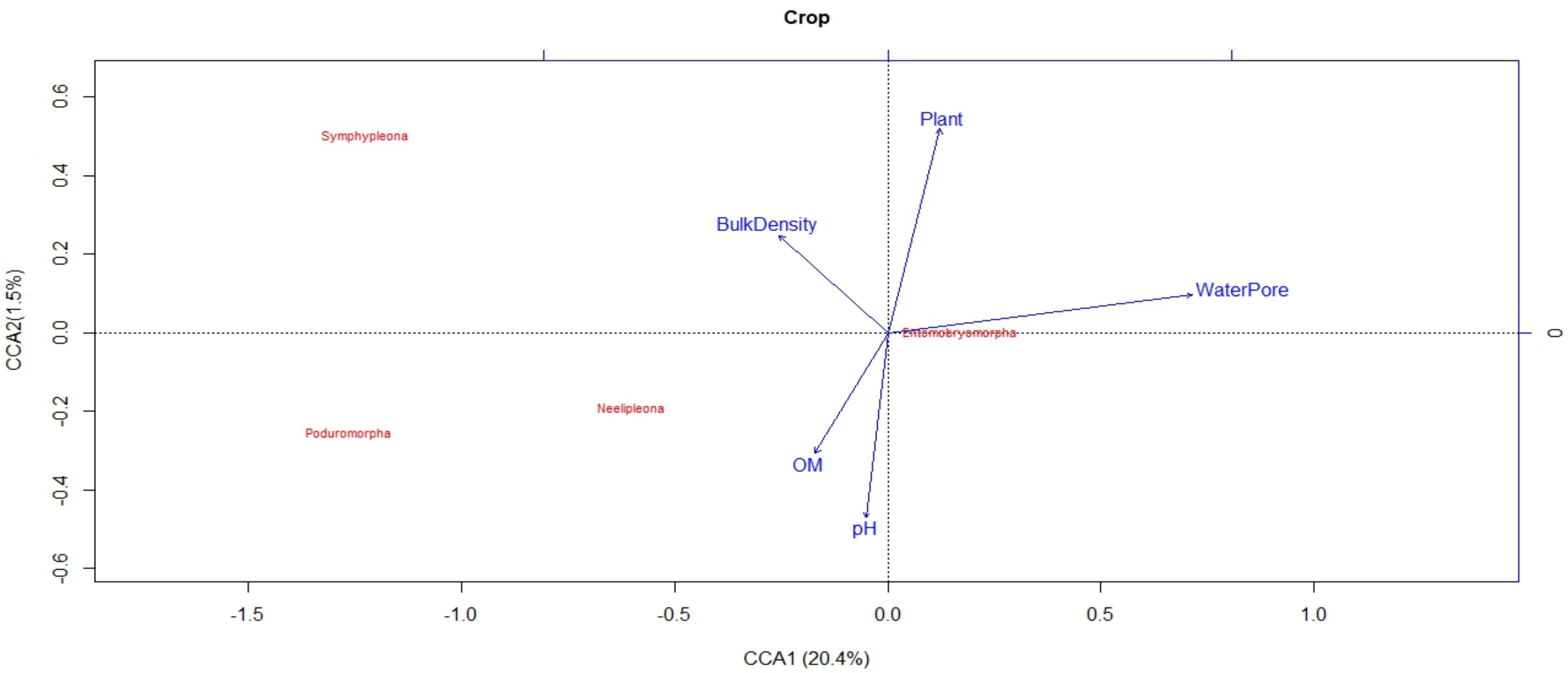
In the grass margin, 27% of the variance of the distribution of *Collembola* was explained by the soil characteristics and 73% by the unconstrained model. The combined effect of soil characteristics on the distribution of *Collembola* was not significant ($F_{(5,24)}$=1.81, P=0.455); the effect of pH alone however, tended to affect the distribution of *Collembola* ($F_{(1,24)}$=5.99, P=0.069). The analysis of the biplot confirmed this trend. The first axis only counted for 16% of the constrained model and represented mainly low pH (score=0.83) and increasing SOM values (score=0.67). It was positively correlated with population of *Poduromorpha* and negatively with *Symphypleona*. Samples taken in the 10-year margin were discriminates with more negative scores. The second axis weighted less but represented high BD values (score=0.47) and low plant residues quantities (score=-0.68) and WFPS values (score=-0.87), which was associated with populations of *Symphypleona* and *Neelipleona*. (Figure 3.6.a)

In the crop areas, slightly more of the variance (30%) was explained by the constrained model and the soil characteristics compared with the margin, while 70% was explained by the unconstrained model. Unlike the analysis for the margins, the overall effect of soil characteristics on the composition of the population of *Collembola* was significant ($F_{(5,144)}$=12.5, P<0.001). WFPS, SOM, and BD each had a significant effect on the distribution of *Collembola* ($F_{(1,144)}$=43.1, P<0.001; $F_{(1,144)}$=7.18, P=0.007; $F_{(1,144)}$=6.91, P=0.008, respectively); while plant residues could also have an influence

($F_{(1,144)}$=3.34, P=0.067). In the biplot, the first axis counted for 20% of the constrained model and was positively correlated to WFPS (score=0.89). Along this axis, all taxa, *Entomobryomorpha* apart, were strongly associated with low values of WFPS. The first axis also discriminated between samples taken in autumn (negative scores) and those taken in spring (positive score). The second axis was associated with an increasing amount of plant residues (score=0.64) and a low pH (score=-0.58). Populations of *Poduromorpha* and *Neelipleona* were related to low amount of plant residues and greater pH, while *Symphypleona* were associated with lower pH values and greater amount of plant residues (Figure 3.6.b).


Margin
Symphypleona
Neelipleona
BulkDensity
pH
Poduromorpha
Entomobryomorpha
OM
Plant
WaterPore
CCA2(8.1%)
0.5
0.0
-0.5
0
-1
-2
-1
0
1
CCA1 (16.2%)

a.



b.

Figure 3.6. Ordination plot of the populations of Collembola (Poduromorpha, Entomobryomorpha, Symphypleona, Neelipleona) in relation to soil characteristics (bulk density (BD), water filled pore space (WFPS), plant residues, soil organic matter (SOM), pH). (a) Relative distribution of each population in the margins; (b) Relative distribution of each population in the cropped area

3.4. Discussion

3.4.1. Comparison of soil characteristics along the age sequence of the field margins

Soil bulk density was greater in all the areas of the crop sampled than in the adjacent margins, suggesting that the fine roots of the grasses essentially ‘engineered’ the soil matrix, creating porosity and reorganising soil aggregates (Bronick and Lal, 2005; Feeney *et al.*, 2006). On average, the greatest bulk density was found in the 1-year old margin and decreased with the age of the margin (Table 3.1), indicating that successional vegetation cover and inherent soil processes drove changes in bulk density over the years of persistent grass cover. This is consistent with the results of Peukert *et al.* (2012) who showed that bulk density in a 25-year old established grass field was greater in the part of a field that was ploughed before establishment of the grass crop. They monitored a very wide range of soil properties and concluded that long-term grass systems without soil disturbance improve soil quality (Peukert *et al.*, 2012). WFPS values were mainly driven by the season, the presence of vegetation cover in the margin would explain lower values in the margin than in the crop in autumn, and similarly the presence of crop cover would reduce WFPS in comparison to grass in the margin in Spring (Nosetto *et al.*, 2012). SOM was greater in the margins than in the fields and increased with the age of the margins. The increased amount of SOM with the age of the margin reflected the start of the long-term dynamics between inputs of root material and carbon storage (Beniston *et al.*, 2014); while the depletion of SOM in the crop showed the impact of soil management, such as the distribution of crop residues or the soil disturbance, on carbon stocks and critical soil processes (Machmuller *et al.*, 2015).

3.4.2. Drivers of differences in the populations of *Acari* and *Collembola*

The community of *Acari* was subject to two different but interlinked temporal patterns: average abundance of the total population increased with the age of the field margin; however, the seasonality dynamics of soil invertebrates (Perdue and Crossley, 1989; Shakir and Ahmed, 2015) or the variation of vegetation cover between seasons (Rumble and Gange, 2013) would have interfered with the major patterns, explaining the increased population with age of the margin was observed in autumn only. The individual responses of each taxa to temporal patterns differed from one to another and did not reflect the global trend. The magnitude of abundance of each taxa that could be considered as establishment success, was possibly determined by position within the trophic network, life strategies of the taxa, or life stages at the time of sampling. Because the causes of this variability in responses to soil management and time succession are short-term dynamics, this would explain the seasonal difference observed in the overall community of *Acari*. Coundrain *et al.* (2016) found contrasting responses of different trophic groups of soil organisms to soil management and demonstrated that trophic identity of soil organisms was linked to the impact of agricultural practices over time. We can build an analogy with the time sequence of our three ageing field margins to indicate how the magnitude and the dynamics of the soil community changed in response to time. Opportunistic, fast-reproducing, omnivorous and small taxa appeared more adaptive to disturbance. For example, *Heterostigmatina* were found indiscriminately in the margins and the crop fields. In contrast, large and slow-reproducing taxa, such as the predatory *Mesostigmata* and the litter-decomposing *Oribatida*, increased in density with the age of the margin, while greatly reduced in the cropped areas.

In autumn, the density of *Collembola* was two to six times greater in the field margins than in the related crop areas, but no significant difference between the two habitats was observed in spring. *Collembola* are sensitive to soil disturbance (Coudrain *et al.*, 2016; Coulibaly *et al.*, 2017). Before the autumn sampling, crop management activities (e.g. ploughing) had just finished, which could explain why the density was so low. *Poduromorpha*, being mostly composed of true edaphic species, that live exclusively belowground, are particularly susceptible to soil disturbance, such as tillage practices (Coulibaly *et al.*, 2017); while *Entomobryomorpha*, composed of larger epigeic species, that evolve at the soil surface, could disperse and recolonise the crop areas more easily (Ponge *et al.*, 2013), especially in spring when the crop canopy would provide a shelter and food resource. The greater abundance of *Poduromorpha* found within the older margins could be linked to their dietary requirements. Sechi *et al.* (2014) reported the changing diet of *Poduromorpha* species in adaptation to their local environment. As field margins age, the plant communities within them change (De Cauwer *et al.*, 2005) which in turn drives changes in the soil microbial communities (Bardgett *et al.*, 2005; Bardgett and van der Putten, 2014) and this would have affected the communities of microbe feeders and consequently all trophic levels.

CCA revealed that soil characteristics, i.e. BD, WFPS, SOM and pH, had only small influence on the composition of the soil communities. However, the results suggested that abundance of *Oribatida* and *Poduromorpha* were correlated with BD and SOM, which resulted in greater abundance in the margins compared to the cropped areas, with 10-year-old margins having greater abundance then the younger margins. The association of *Poduromorpha* with WFPS has been previously reported (Bandyopadhyaya *et al.*, 2002; Davies, 1928). The correlation between acidic-pH and invertebrates should be carefully interpreted. Acidic pH values were associated with the 10-year old margin and its related crop area and the positive relationship between greater abundance of *Oribatida* and *Poduromorpha* at low pH could result from the stability and shelter offered by the 10-year margin, and not from the pH values directly. The CCA also discriminated species in the cropped areas which were affected by the seasons. *Entomobryomorpha* and *Mesostigmata*, for example, were correlated with samples taken in spring. Vegetation cover in the field would have favoured the presence of the epigeic *Entomobryomorpha*, which in turn would have provide a food resource for the *Mesostigmata* predators.

This study evidenced the impacts of field managements on abundance and composition of soil invertebrate communities and the importance of the time factor in ecological processes. Increasing age of the margins were associated with more abundant invertebrate communities, founded on larger and specialised organisms; while in the crop area, soil disturbances, such as harvest or tillage, prevent succession of vegetation and incorporation of a single type or low diversity of crop residues favoured opportunistic and fast-rate developing species. The presence of specialised detritivores in the older grass margin, together with the vegetation cover, could be correlated to organic matter turnover and storage (Bardgett and van der Putten, 2014; Brussaard, 2012; Brussaard *et al.*, 2007).

3.5. Conclusions

In this study, we investigated the effects of field margins of different ages on the structure of the soil biota communities. As hypothesised, the duration of time since establishment of the margin was critical in building-up suitable soil conditions that could sustain diverse soil communities. The sampling design presented confounding factors, as the 1-year and 6-year margins belong to the same field. Significant differences were observed between the 10-year margin and the two others; although effects of 1- and 6-year margins could be confounded, most of the interpretation is based on the difference occurring between the youngest (1-year) and oldest (10-year) margins, which do not belong to the same field. Results, despite being preliminary, were sufficient to be interpreted and justify future research. We demonstrated that duration since establishment of the margin affected not only the abundance of key taxa, but the structure of the community. The contrasted responses of the different taxa reflected the life strategy of each of them but also revealed the relationships and the dynamics within the soil communities of the field margins in regards with time successions. The presence of more specialised species and larger individuals in the older margin, suggests that long-term undisturbed field margins could favour the establishment of more complex communities. Dispersal mechanisms were not tested during this experiment and to understand the potential of field margins to act as reservoirs of soil biodiversity, which in turn could favour soil ecosystem function such as decomposition, or nutrient cycling in the adjacent arable crop, these colonisation processes should be further investigate. To meet the requirement of sustainable soil management, however, there is a real challenge for agri-environmental policy makers to consider the time factor in headland management and adapt policies to long-term dynamics in such systems.

This chapter is structured and formatted in accord with specification for the journal Soil Use and Management. Current status is: Manuscript for submission.

CHAPTER 4

IMPACTS OF FIELD MARGIN ORIENTATION ON POPULATIONS OF *ACARI* AND *COLLEMBOLA* IN RESPECT TO THE DIRECTION OF FIELD TRAFFIC

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ABSTRACT

Margin establishment around arable fields is a central part of many agri-environmental schemes which aim to improve biodiversity in agricultural landscapes. These margins may also serve to create a reservoir of functional biodiversity that could provide ecosystem services such as pollination and pest control for crops within the fields. However, the impacts of field margins on populations of soil invertebrates in the margins and the neighbouring cropped region remain unclear. In this study, we investigated the impact of margin orientation on populations of *Acari* (mites) and *Collembola* (springtails) in the field in respect to the direction of the tramlines. Two margins on adjacent sides of the same field and their neighbouring cropped areas were examined: a margin oriented perpendicular to the tramlines; and a margin oriented parallel to the tramlines. Soil cores were taken along transects from the margins and at increasing distances into the cropped area. The sampling was conducted at two farms with distinct soil management (no till vs. minimum tillage) and crop rotations (complex vs. conventional) in two seasons (autumn vs. spring) over two years. The distribution of invertebrates in the cropped areas depended on the orientation of the margin and the taxa studied at both farms. Lowest abundances of each taxonomic group were found in the tramlines. Effect of margin orientation was least in the farm under no-till with a complex crop rotation system. This study suggested the existence of an interacting impact of margin establishment with farm activities on population of soil mesofauna and highlighted the importance of well-designed and integrated management strategies in arable fields for maximizing ecosystem services in the system.

Key words: mesofauna; field margin; field management; tramlines

4.1. Introduction

Field margins are an important feature in sustaining ecosystem services in agricultural landscapes (Marshall & Moonen, 2002; Meek *et al.*, 2002; Falloon *et al.*, 2004). The British Government declared headland and field margins as priority habitats to sustain biodiversity (Department for Environment, Food & Rural Affairs, 2008), which was supported by new environmental stewardship schemes that remunerate farmers for setting up margins around their fields (Department for Environment, Food & Rural Affairs, 2014; Maddock, 2008). The primary aim of these policies was to improve above-ground biodiversity such as birds (Vickery *et al.*, 2009), butterflies and bees (Marshall & Moonen, 2002; Wratten *et al.*, 2012) and ecosystem services including pollination and pest management (Woodcock *et al.*, 2005; Wratten *et al.*, 2012; Kovács-Hostyánszki *et al.*, 2017; Mansion-Vaquié *et al.*, 2017). However, less is known about the impacts of field margins on the soil fauna and the ecosystem services provided from below-ground (Smith *et al.*, 2008). Limited studies about impacts of field margins on communities of soil invertebrates have shown an inconsistency of responses from the soil community to the presence of the margins although all of them highlighted the importance of time and space in regulating community dynamics (Roarty & Schmidt, 2013; Coudrain *et al.*, 2016; Sechi *et al.*, 2017).

Acari (mites) and *Collembola* (springtails) numerically comprise the majority of the soil mesofauna (Harding & Stuttard, 1974) and are key components of the soil trophic network as they are decomposers, microbivores and even predators (Brussaard *et al.*, 2007). The variability of life strategies amongst the communities of soil invertebrates makes a strong indicator of changes in resources, such as food supply or habitat structure (Coleman & Hendrix, 2000; Mulder, 2006; George *et al.*, 2017): one or more population dominating others depending on the resource availability. Studies have investigated aboveground – belowground relationships, such as the plant – soil feedbacks or the impact of herbivory on soil ecology, (Wardle *et al.*, 2004; Bardgett & Wardle, 2010; Bardgett & van der Putten, 2014), yet the nature of these interactions needs to be more precisely examined to entirely understand the nature of the major drivers of change in both above- and belowground ecosystems (Eisenhauer *et al.*, 2011). In arable fields, the quality and quantity of food substrates entering the system regulated by agronomic activities controls the composition and abundance of the soil fauna community (Thiele-Bruhn *et al.*, 2012). Soil management, such as tillage, impacts the community structure by modifying the habitat structure; as does crop management by altering the quality and quantity of food resource. Crotty *et al.* (2015) showed that different crops changed the composition of the soil food web; while Coudrain *et al.* (2016) did not find clear effects of crop residues on populations of soil invertebrates but demonstrated that tillage and other soil perturbations limited the establishment of certain populations of soil invertebrates.

Trafficking by heavy machinery has been shown to damage the soil structure (Hamza & Anderson, 2005), decrease crop yield (Arvidsson &

Håkansson, 2014), and generally reduce biologically-driven processes such as respiration or nitrogen mineralisation (Beylich *et al.*, 2010), and abundance of soil invertebrates including *Acari* and *Collembola* (Beylich *et al.*, 2010; Lees *et al.*, 2016). However, the effects on the community structure of these invertebrates have been rarely considered. These organisms are important for the concept of “soil self-organisation”, where small scale interactions of soil functions, driven by soil invertebrates, lead to larger scale processes such as soil ecosystem services (Lavelle *et al.*, 2006). Therefore, a greater understanding of how soil management affects community structure of invertebrates could help develop appropriate management practices to improve soil ecosystem services.

In this study, we investigated the effects of grass-based field margins, crop residues and tramlines on populations of *Acari* and *Collembola* in the field, and the effect of the orientation of the margin in relation to the location of the tramlines. We hypothesised that i) populations of *Acari* and *Collembola* would be more abundant and more diverse in the grass margin than in the crop area; ii) the impact of the grass margin on the community structure of the adjacent crop field would be strong (i.e. communities would be similar) and decrease its effect with the distance from the margin (i.e. communities would become less similar with distance from the margin) and iii) the turning area, where tramlines are perpendicular to the orientation of the field margin, would prevent dispersion of invertebrate from the margin into the field and this would result in strong differences of community structure.

4.2. Materials and methods

In this chapter, the data used for the perpendicular margin and its related field area at The Grange farm are the same than the data used for the 10-year margin and field area from Chapter 3.

4.2.1. Sites and soil characteristics

Soil sampling was carried out from The Grange Farm (Northamptonshire, UK; 52° 18’ 2.73” N; 0° 45’ 52.83” W) and Rawcliffe Bridge Farm (Yorkshire, UK; 53° 40’ 0.37” N; 0° 55’ 46.84” W) four times within two cropping years (autumn 2015, spring 2016, spring 2017, autumn 2017). The two farms practice different agronomic regimes, in relation to field practices (minimum tillage *vs.* no till), crop rotations (conventional *vs.* complex), and by the intrinsic properties of the local soil series (Table 4.1). All crop residues were left on the ground as organic soil amendment at both farms. In the two farms, grassy strip field margins of 6 m wide had been set up around the different fields to promote biodiversity in the agricultural landscape (Department for Environment, Food & Rural Affairs, 2014; Maddock, 2008). Each margin was between 10 and 12 year old at the time of the experiment. The Crops at The Grange Farm were winter wheat (*Triticum aestivum* L.) in autumn 2015 and spring 2016 followed by oilseed rape (*Brassica napus* L.) in autumn 2016 and spring 2017 and oilseed rape again in autumn 2017 to restrain a blackgrass outbreak. The field had been managed using minimum tillage techniques (i.e. no deep ploughing) for at least 15 years. The crops sampled at Rawcliffe Bridge farm were: oilseed rape in autumn 2015 and spring 2016 followed by winter wheat in spring 2017 and oilseed rape in autumn 2017. The farm has used zero tillage establishment methods for over 10 years. Both farms applied mineral fertilisers and chemical inputs following the UK standard scheme management for farmers (Agriculture and Horticulture Development Board, 2017) and crop residues were left in a systematic way on the ground as an organic soil amendment.

Table 4.1. Soil characteristics at the Grange and Rawcliffe Bridge farms.

Soil characteristic	**Rawcliffe Bridge farm** *Coopers field*	**The Grange farm** *Paradise field*
Soil series*	Blacktoft (wrap soil)	Hanslope
Soil type	Medium silty alluvium covered by loam from artificial flooding practices	Calcareous pelosol from clayey chalky drift series
Soil properties	Artificial drains and ditches High fertility Lime-rich	Poor drainage capacity High fertility High sensitivity to compaction
pH**	7.72	6.06
SOM** (%.gsoil^{-1})	5.35	6.13

** Soil series characteristics are typed according to 'The Soil Guide' (Cranfield University, 2017). ** pH and total soil organic matter content (SOM) are average values calculated over 2 years of sampling. *** Mineral fertilisation is applied followed by UK standard scheme management for farmers (Agriculture and Horticulture Development Board, 2017).*

4.2.2. Experimental design

At each farm, the area of study consisted of two grass margins of the same age and width in the same field, based on their orientation to the field traffic: a margin located perpendicular to the tramlines near to the tractor ‘turning area’ (marked as Area A in Figure 4.1a) and a margin oriented parallel to the tramlines within a ‘non-turning’ area (marked as Area B in Figure 4.1a). Each sampling area comprised a 6 m by 30 m margin area and a 30 m by 30 m adjacent cropped area. The total area was divided into 5 transects. Each transect was divided into 6 sections, one in the margin and 5 in the cropped area. A total of 30 soil samples were collected per sampling area (5 in the margin and 5 x 5 in the crop (Figure 4.1b).

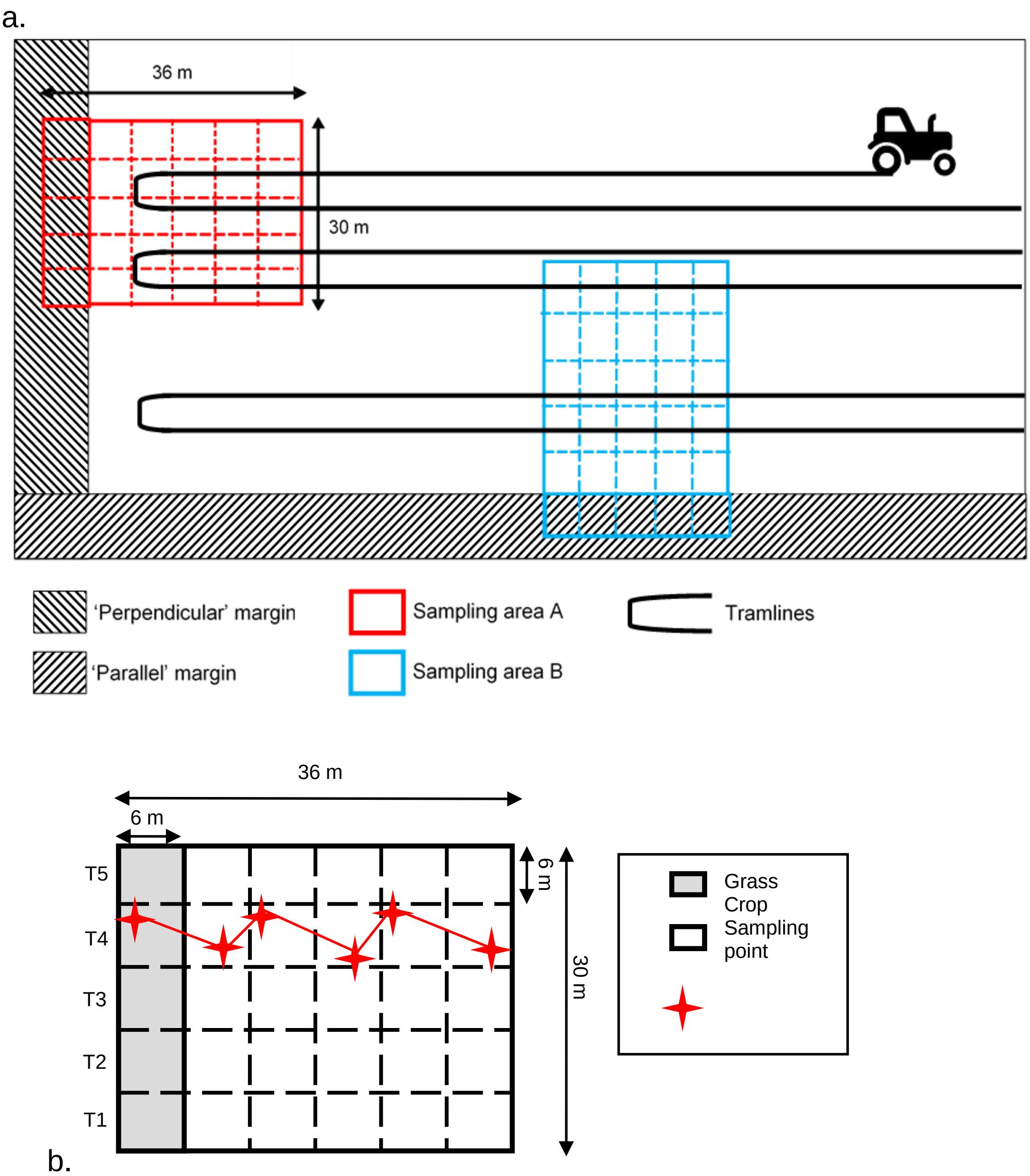


Figure 4.1. (a) Diagrammatic representation of the field margin and the sampling areas (Area A with margin perpendicular to tramlines in red; Area B with field margin parallel to tramlines in blue). Tramlines are shown by plain black lines and field margin areas indicated by diagonal strips. (b) Experimental design of each study field (left). Soil cores were taken along five transects (T1 - T5). Margin area is in grey and cropped area in white; red crosses show sampling points and the 'W' pattern along one of the transect. Aerial view (right) of the 10-year margins and adjacent crop; the sampling area is marked in red.

4.2.3. Soil sampling and measurements

Soil cores were collected along each transect following a ‘W’ pattern to offset spatial correlation and increase randomization using a root corer (8 cm diameter and 10 cm deep, Eijelkamp, The Netherlands). The perpendicular area was sampled in autumn 2015 and spring 2016 and the parallel area was sampled in spring and autumn 2017 at The Grange farm, while at Rawcliffe Bridge, the parallel area was sampled first in autumn 2015 and spring 2016 and the perpendicular area in spring and autumn 2017. The soil core samples were divided into two vertical halves, one used for soil property measurements and the other to extract soil invertebrates. The volume of each half soil core was 503 cm^3 (8 cm diameter x 10 cm depth cylinder). The fresh weight of the half intended for soil property measurement was first determined and was then dried at 105°C to constant weight. Visible plant residues from the soil samples taken from the cropped area and fine roots from the samples taken grass margin were removed by hand or by using a 2 mm sieve, then samples were dried and weighed. Soil bulk density (BD) was determined following Laryea *et al.* (1997). Water filled pore spaces (WFPS) was defined as the ratio of volumetric soil water content moisture to porosity (Laryea *et al.*, 1997). Soil organic matter (SOM) content was determined by loss on ignition, adapted from (Davies, 1974). Soil pH was measured at 1:2.5 soil:water ratio using a pH meter (Jenway Model 3320, Jenway, Staffordshire, United Kingdom).

4.2.4. Extraction and identification of *Acari* and *Collembola*

The second intact half of the soil core sample was placed upside down in a Tullgren Funnel unit with a 5 mm mesh (Burkard Manufacturing Co. Ltd, Rickmansworth, UK) for a 12-day period (Crotty, 2011). The heat gradient created by the light source forced all living and active soil invertebrates to move down the funnel. Invertebrates were collected in a tube placed below each funnel and collected in 70% industrial methylated spirit (IMS) and stored at 4°C before being hand sorted under a binocular microscope. All soil invertebrates were recorded and classified at the highest taxonomical level possible. However, only *Acari* and *Collembola* were considered in this study. *Collembola* were subdivided into families (*Poduromorpha*, *Entomobryomorpha*, *Symphypleona* and *Neelipleona*) and *Acari* into sub-order groups (*Mesostigmata*, *Astigmata*, *Oribatida*, *Heterostigmatina* and Trombidiformes). The taxonomical degree chosen reflected the different functions carried by each group.

4.2.5. Data analyses

The Mantel test method (Goslee & Urban, 2007) was used to assess the relationship between the structure of soil invertebrate communities structure and the spatial structure of the sampling. Simple Mantel tests investigated the correlation (or distance) between the two matrices; and whether the closer along the distance transects, the more similar the community structures. High Mantel coefficient (r-statistic value), characterised community structures more similar with reduced distance. Partial Mantel tests were done to correct for the influence of one or all of the soil predictor variables (BD, WFPS, plant residues, SOM and pH) on the relationship. To guarantee the validity of the tests, 9999 permutations were used to randomise rows and columns of one of the data matrix. All Mantel test analyses were done using the Ecodist package (Goslee & Urban, 2007) implemented in R software 3.1.2 (http://www.r-project.org/).

Effect of the margin orientation (‘perpendicular’ *vs.* ‘parallel’), the distance to the margin, the sampling season (autumn *vs.* spring), the cultivation strategy (No till + complex rotation *vs.* minimum tillage + conventional rotation) and their interactions on abundance of the different taxa of *Acari* and *Collembola* and soil properties (BD, WFPS, amount of plant residues, SOM and pH) were estimated by multiple-way analysis of variance (ANOVA). A blocking structure accounted for the differences between the two fields in each farm, the two margins and their related crop area within a field, the 5 transects within a sampling area, and the 6 distance points within each transect. The ten transects in each field (five per side) were considered sufficiently far-enough apart to be different and treated as independent and were used as replicates to assess differences between the two farms. We assessed normality of the data with model checking plots (normal probability and QQ plots), to meet the assumption of normality. Count data (abundances of invertebrates) were log-transformed. Multiple comparison method was used to correct for the significant critical values only due to chance, it adjusted for the false discovery rate using the Benjamini-Hochberg procedure. All ANOVA were done using GenStat (GenStat 18th Edition, VSN International Ltd., Hemel Hempstead, UK).

4.3. Results

4.3.1. Soil characteristics

Bulk density in the perpendicular area was lower compared to the parallel area at The Grange but the opposite was the case at Rawcliffe Bridge farm (Table 4.2).

Table 4.2. Average values of soil characteristics (bulk density; water filled pore space WFPS; plant residues; soil organic matter SOM and pH) within areas of 'perpendicular' and 'parallel' to the tramlines sampled from the field margins and at increasing distances into the crop area at The Grange farm and Rawcliffe Bridge farm over the four sampling seasons (October 2015, April 2016, April 2017 and October 2017; n=5).

THE GRANGE FARM	**Perpendicular area**						**Parallel area**					
	Margin	**6 m**	**12 m**	**18 m**	**24 m**	**30 m**	**Margin**	**6 m**	**12 m**	**18 m**	**24 m**	**30 m**
Bulk density (g cm^{-3})												
Mean	0.96	1.18	1.18	1.30	1.90	1.18	1.01	1.38	1.30	1.27	1.23	1.25
±SE	0.02	0.02	0.01	0.01	0.02	0.01	0.01	0.01	0.01	0.01	0.02	0.01
WFPS (%)												
Mean	15.1	12.6	11.5	11.2	12.2	12.3	13.8	13.3	13.0	11.2	13.2	12.1
±SE	0.90	0.35	0.27	0.35	0.33	0.31	0.28	0.23	0.11	0.23	0.18	0.20

THE GRANGE FARM	**Perpendicular area**						**Parallel area**					
	Margin	**6 m**	**12 m**	**18 m**	**24 m**	**30 m**	**Margin**	**6 m**	**12 m**	**18 m**	**24 m**	**30 m**
Plant residues (mg g^{-1}Soil)												
Mean	15.3	14.9	5.08	6.95	12.8	10.1	19.5	4.62	3.38	3.63	6.46	5.08
±SE (x10^{-3})	0.88	1.09	0.35	0.66	1.17	1.63	1.09	0.23	0.22	0.11	0.34	0.56
SOM (%)												
Mean	8.91	6.44	6.02	6.15	6.01	5.76	8.06	5.63	5.94	6.23	6.76	6.02
±SE	0.12	0.02	0.02	0.01	0.02	0.03	0.07	0.05	0.02	0.02	0.10	0.03
pH												
Mean	6.44	6.58	6.42	5.96	5.92	6.41	5.77	5.76	5.60	5.59	5.86	6.23
±SE	0.03	0.02	0.03	0.01	0.02	0.02	0.03	0.02	0.01	0.03	0.03	0.02

RAWCLIFFE BRIDGE FARM	**Perpendicular area**						**Parallel area**					
	Margin	**6 m**	**12 m**	**18 m**	**24 m**	**30 m**	**Margin**	**6 m**	**12 m**	**18 m**	**24 m**	**30 m**
Bulk density (g cm^{-3})												
Mean	0.97	1.38	1.38	1.33	1.27	1.11	1.07	1.21	1.15	1.21	1.21	1.25
±SE	0.03	0.01	0.02	0.02	0.01	0.06	0.02	0.02	0.01	0.01	0.01	0.01
WFPS (%)												
Mean	9.83	12.8	11.3	12.8	13.0	10.3	11.2	11.2	11.2	11.7	12.4	12.3
±SE	0.19	0.16	0.39	0.23	0.15	0.67	0.30	0.31	0.36	0.30	0.35	0.34
Plant residues (mg g^{-1}Soil)												
Mean	18.7	6.22	4.52	4.37	4.85	4.19	21.8	13.6	7.29	9.72	9.79	9.62
±SE (x10^{-3})	1.95	0.48	0.24	0.34	0.32	0.24	1.47	1.65	0.28	0.59	0.58	0.51
SOM (%)												
Mean	10.1	5.80	5.55	5.48	5.23	5.36	6.60	4.82	5.21	5.41	5.52	5.53
±SE	0.10	0.02	0.03	0.03	0.01	0.02	0.11	0.03	0.02	0.02	0.01	0.01
pH												
Mean	7.30	7.53	7.59	7.60	7.60	7.64	7.74	7.95	7.85	7.84	7.87	7.87
±SE	0.01	0.02	0.01	0.01	0.01	0.01	0.02	0.01	0.01	0.01	0.01	0.01

Neither cultivation strategy nor margin orientation alone significantly affected BD. However, there was significant interaction between the two factors (Table 4.3). Regardless of the farm or the margin orientation, BD was always lower in the field margin than in the crop (Table 4.2). Seasonal effects interacted with farm cultivation and orientation of the margin (Table 4.3).

Cultivation strategy significantly affected WFPS in the fields (Table 4.3) and greater average values were measured at The Grange farm than at Rawcliffe (Table 4.2). There was also a significant interaction between cultivation strategy and variation in WFPS with distance into the crop from the field margin (Table 4.3). On average, we measured greater WFPS values in the margin and decreasing WFPS in the crop with increasing distance at The Grange farm, while at Rawcliffe Bridge farm, WFPS was on average lower in the margin than in the adjacent crop.

The amount of plant residues depended on margin orientation in regard to the farm cultivation system (Table 4.3); the amount of plant residues left in the perpendicular area of Rawcliffe Bridge was significantly lower than in the parallel area, while it was the reverse at The Grange farm (Table 4.2). Plant residues also significantly varied with distance from the margin (Table 4.3).

SOM was significantly affected by the spatial factors (margin orientation and distance from the margin) of samples as well as by the cultivation system of each farm, and all interactions between them (Table 4.3). In the two farms, SOM content was significantly greater in the margin than any sample from the adjacent cropped. Average values of SOM in the field were lower at Rawcliffe Bridge farm (Table 4.2). Unlike the preceding soil variables, SOM did not vary with seasons.

Soil pH was significantly affected by the spatial and cultivation factors as well as their interaction. Soil pH of samples from The Grange farm were in general more acidic than at Rawcliffe Bridge farm. Spatial heterogeneity was observed at The Grange farm, were pH values in the crop and its related margin of the perpendicular area were greater than in the crop and margin of the parallel area; while Rawcliffe Bridge farm soil pH were more homogenous between all areas.

Table 4.3. Effects from analysis of variance of the margin orientation, either parallel or perpendicular to the tramlines (Orientation), the distance to the field margin (Distance), the sampling season (Season), the farm, either Rawcliffe Bridge or The Grange (Farm) and their interactions on soil characteristics. Significant values after False Rate Discovery adjustment (p < 0.05) are show in bold.

	Bulk density		Water filled pore space		Plant residues		Organic matter		pH		
	F	p	*F*	p	*F*	P	*F*	p	*F*	p	Df
TREATMENT											
Farm	0.11	0.825	7.21	0.054	0.19	0.789	75.6	**0.003**	3027	**0.002**	1, 239
Orientation	0.09	0.825	0.30	0.740	0.17	0.789	34.9	**0.003**	8.84	**0.017**	1, 239
Farm: Orientation	5.55	0.102	0.02	0.892	14.2	**0.015**	19.5	**0.003**	175	**0.002**	1, 239
Distance	8.76	**0.015**	0.84	0.731	10.4	**0.015**	159	**0.003**	9.20	**0.002**	5, 239
Farm: Distance	0.17	0.974	3.33	**0.034**	0.36	0.889	2.78	0.051	9.61	**0.002**	5, 239
Orientation: Distance	0.92	0.598	0.55	0.786	0.34	0.889	31.8	**0.003**	4.04	**0.006**	5, 239
Farm: Orientation: Distance	1.74	0.294	1.36	0.467	1.06	0.655	7.97	**0.003**	7.80	**0.002**	5, 239
Season	5.03	0.101	23.9	**0.008**	2.00	0.400	0.08	0.838	23.7	**0.002**	1, 239
Farm: Season	6.23	0.070	0.18	0.777	0.76	0.655	4.21	0.081	13.4	**0.002**	1, 239
Orientation: Season	2.37	0.294	0.75	0.645	6.25	0.053	0.17	0.838	3.25	0.082	1, 239
Season: Distance	1.22	0.459	0.88	0.713	2.37	0.132	2.09	0.122	2.10	0.082	5, 239
Farm: Orientation: Season	7.95	**0.045**	281	**0.008**	0.34	0.764	0.02	0.898	1.97	0.176	1, 239
Farm: Season: Distance	1.55	0.341	1.52	0.405	3.56	**0.025**	0.53	0.838	2.53	**0.050**	5, 239
Orientation: Season: Distance	1.23	0.459	3.30	**0.034**	1.14	0.655	1.18	0.445	1.53	0.185	5, 239
Farm: Orientation: Season: Distance	0.91	0.045	1.91	0.248	0.82	0.764	1.56	0.264	2.45	0.052	5, 239

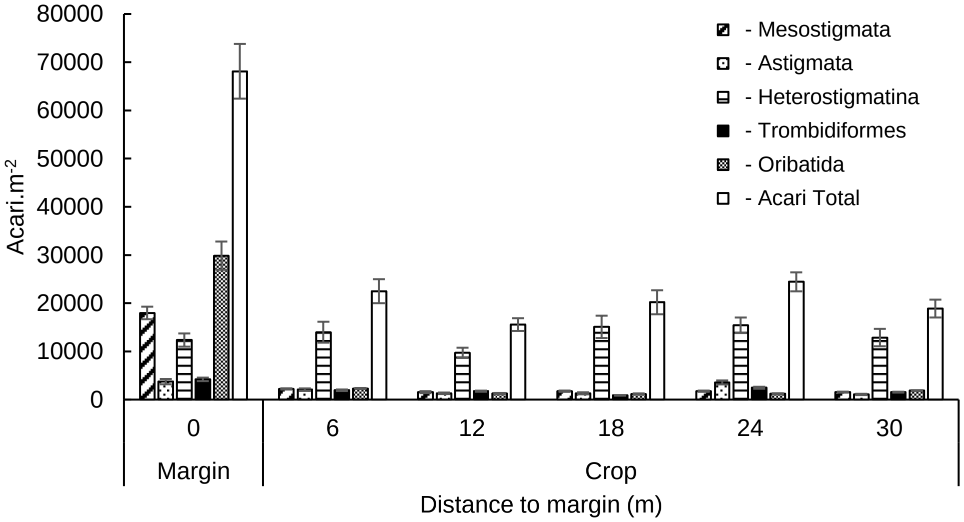
4.3.2. Abundance of soil invertebrates

4.3.2.1. *Acari*

The effect of the cultivation system on the whole population of *Acari* was not significant and average abundances between the cropped areas of both farms were similar (28,595 and 29,634 individuals m^{-2} at Rawcliffe Bridge farm and The Grange farm, respectively; Figure 4.2 and Figure 4.3). However, orientation of the field margin significantly affected the abundance of *Acari* in each field (Table 4.4). For both farms, average abundances in the perpendicular area were significantly lower in the crop than in the related margin (20,315 and 16,624 individuals m^{-2} in the crop and 68,112 and 72,508 individuals m^{-2} in the margin at Rawcliffe Bridge and The Grange, respectively). Abundances were less contrasted between the margin and crop in the parallel area (27,047 and 27,284 individuals m^{-2} in the crop and 38,214 and 63,558 individuals m^{-2} in the margin at Rawcliffe Bridge and The Grange, respectively). Distance from the margin was another significant factor explaining the variability of *Acari* abundances in the field. This factor interacted with the margin orientation to affect the abundances. (Table 4.4). Abundances across the perpendicular cropped area stayed low at every distance point (average values for the whole cropped area of 20315 individuals m^{-2} at Rawcliffe Bridge farm and 16624 individuals.m^{-2} at The Grange farm), while there was no certain spatial pattern in the crop of the parallel area. At both farms, the lowest abundances of *Acari* was found at 12 m from the margin (Figure 4.2 and Figure 4.3).

Each taxa of *Acari* did not respond in the same way to the different explanatory factors. Abundances of *Mesostigmata* and *Oribatida* were explained by spatial factors (margin orientation and distance from the margin), the cultivation system and their interactions (Table 4.4). Season also affected the abundances. *Mesostigmata* was always found in greater numbers in the margins than in the cropped areas (in average, 2,693 and 2,843 individuals m^{-2} in the crop and 9,742 and 9,504 individuals m^{-2} in the margin of the parallel area at Rawcliffe Bridge and The Grange respectively; and 1,758 and 863 individuals m^{-2} in the crop and 17,978 and 9979 individuals.m^{-2} in the margin of the perpendicular area at Rawcliffe Bridge and The Grange, respectively); This was also the case for *Oribatida* with less contrasted abundance between the average value across the cropped area and the margin (4,118 *vs.* 4,158 individuals.m^{-2} at Rawcliffe Bridge farm and 9,504 *vs.* 13,820 individuals m^{-2} at The Grange farm). The differences in abundances for taxa between the margin and crop were generally more significant in the perpendicular area than in the parallel area at both farms. Neither cultivation system, nor margin orientation significantly impacted the abundances of *Heterostigmatina* and Trombidiformes. But numbers in the crop area of the two sub-groups varied with distance from the margin. The spatial distribution patterns of them plus *Astigmata* followed that of the total abundance of *Acari*. Abundances of all the taxa but Trombidiformes varied with season.

a. ‘Perpendicular’



b. ‘Parallel’

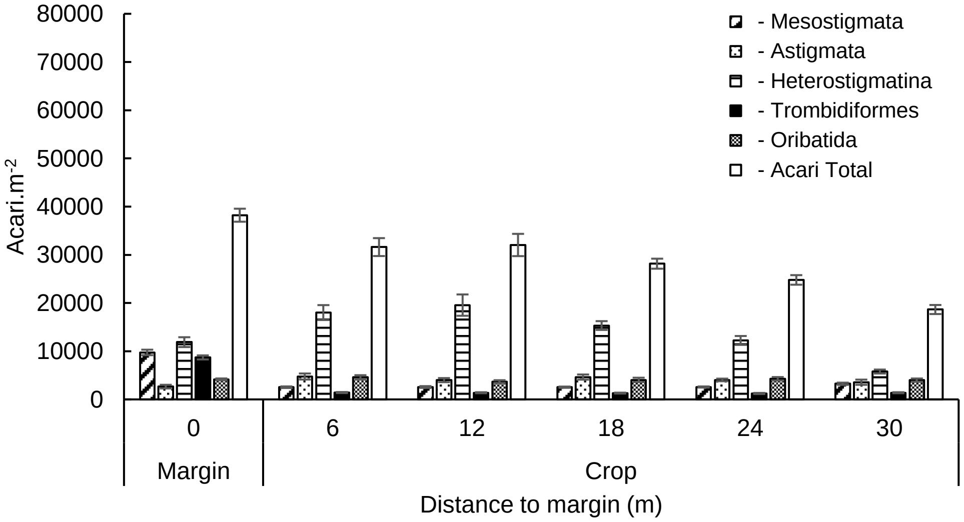
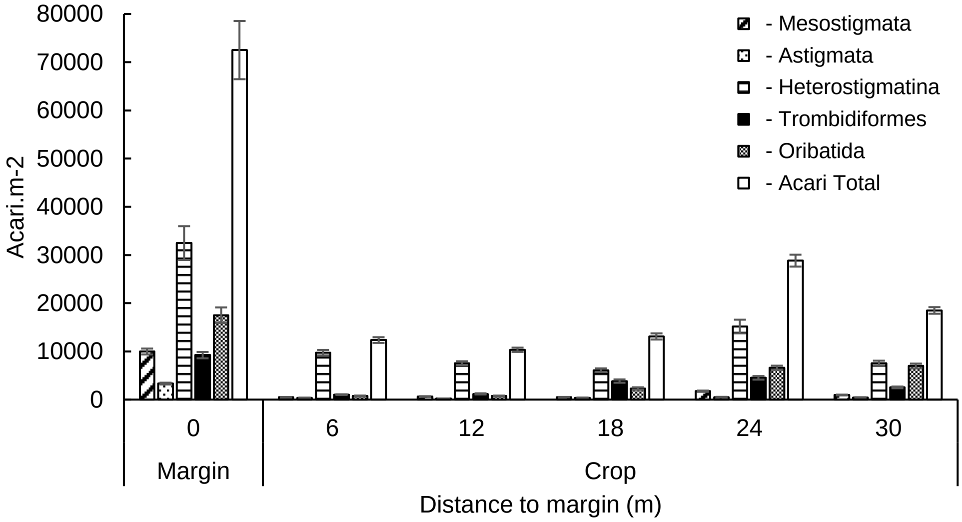


Figure 4.2. Average abundance of the different taxa of acari (individuals.m^{-2}) in the two sides field margins and at five distances from it into the crop at Rawcliffe Bridge farm (n=20). Figure 4.2.a represent the ‘perpendicular’ field margin and Figure 4.2.b the ‘parallel’ field margin. Bars denote standard error.

a. ‘Perpendicular’



b. ‘Parallel’

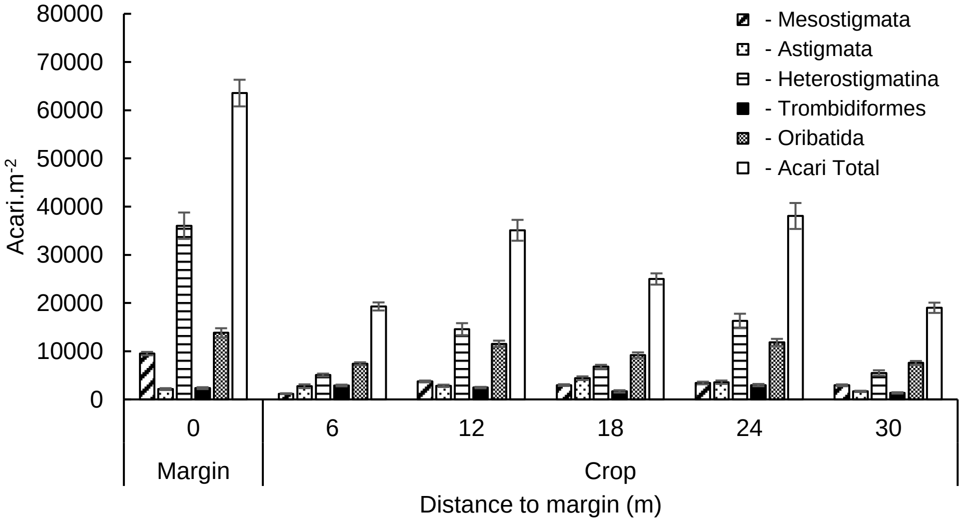


Figure 4.3. Average abundance of the different taxa of acari (individuals.m^{-2}) in the two sides field margins and at five distances from it into the crop at The Grange farm (n=20). Figure 4.3.a represent the ‘perpendicular’ field margin and Figure 4.3.b the ‘parallel’ field margin. Bars denote standard error.

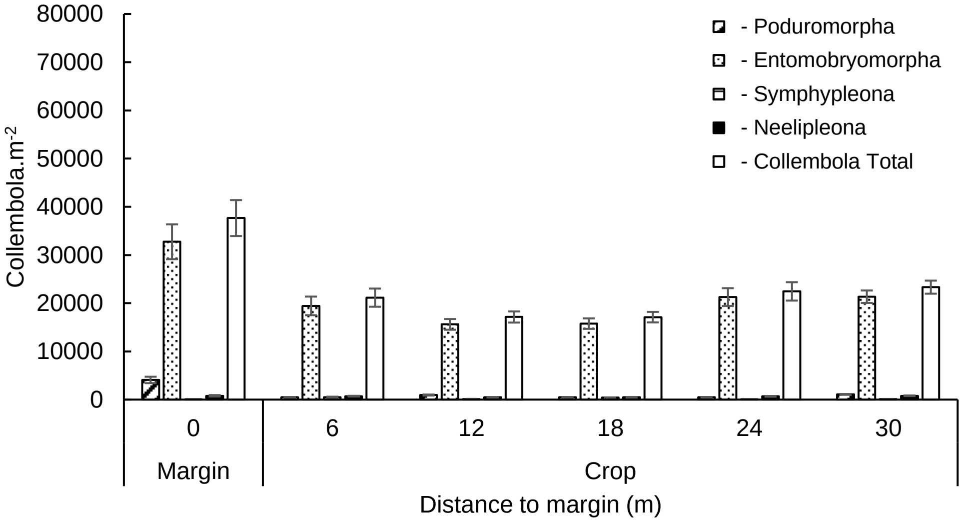
4.3.2.2. *Collembola*

Total abundance of *Collembola* varied significantly regarding to the orientation of the tramline to the field margin (Table 4.4). In the crop of the perpendicular area, abundance of *Collembola* reduced with the distance from the margin at first and then increased. However, the effect of the orientation of the margins on abundance in the crop area was different at two farms. No significant difference was observed between the cropped areas at Rawcliffe Bridge farm (Table 4.4) but the abundance in the cropped of the perpendicular area was less than half the number in the parallel area at The Grange farm (Figure 4.4 and Figure 4.5). There was a significant interaction between the cultivation system and the distance from the margin on the abundance (Table 4.4), which could explain the low abundance of *Collembola* between 6 and 18 m from the margin in the perpendicular area at The Grange farm (Figure 4.4 and Figure 4.5). Average abundance of *Collembola* in the field margins at The Grange farm was 8 times greater than the average abundance in the crop areas, while it was only 2 times greater at Rawcliffe Bridge farm.

The farming (cultivation system) and spatial (margin orientation and distance from the margin) factors affected the abundance of the four groups of *Collembola* in various ways (Table 4.4). Abundances of *Entomobryomorpha* and *Neelipleona* were significantly affected by the cultivation system, the margin orientation and their interaction. Abundance of *Entomobryomorpha* was always lower in the cropped areas than in the margins (in average, 14,113 and 15,246 individuals m^{-}

^{2} across the cropped area and 27,403 and 25,027 individuals m^{-2} in the margin of the parallel area at Rawcliffe Bridge and The Grange, respectively; 18,683 and 7,001 in individuals.m^{-2} across the crop and 32,749 and 28,116 individuals m^{-2} in the margin of the perpendicular area at Rawcliffe Bridge and The Grange, respectively). In general, greater abundance of *Entomobryomorpha* was found in every area (parallel vs. perpendicular; margin vs. crop) of Rawcliffe Bridge than at The Grange; only the abundance in the crop of the parallel area at Rawcliffe Bridge showed lower density than at The Grange (on average across the cropped area: 14,113 and 15,246 individuals m^{-2}, respectively; Table 4.4, Figure 4.4 and Figure 4.5). Abundances of *Neelipleona* at Rawcliffe Bridge farm were also greater than those at the Grange Farm (Figure 4.4 and Figure 4.5). Abundance of *Poduromorpha* was significantly affected by the orientation of the field margin (Table 4.4); in both farms the lowest abundance was observed in the crop of the perpendicular area (in average, across the cropped area: 689 and 237 individuals m^{-2} at Rawcliffe Bridge farm and The Grange farm, respectively), while the greatest abundance was in the margin of the parallel area (Figure 4.4 and Figure 4.5). Abundance of *Poduromorpha* in the margins was always greater than that at any points in the cropped areas but variation of abundance from one point to another differed from one farm to another (Table 4.4). Very low abundance of *Symphypleona* in the perpendicular area at Rawcliffe Bridge farm was observed (40 individuals m^{-2}; Figure 4.4 and Figure 4.5).

a. ‘Perpendicular’



b. ‘Parallel’

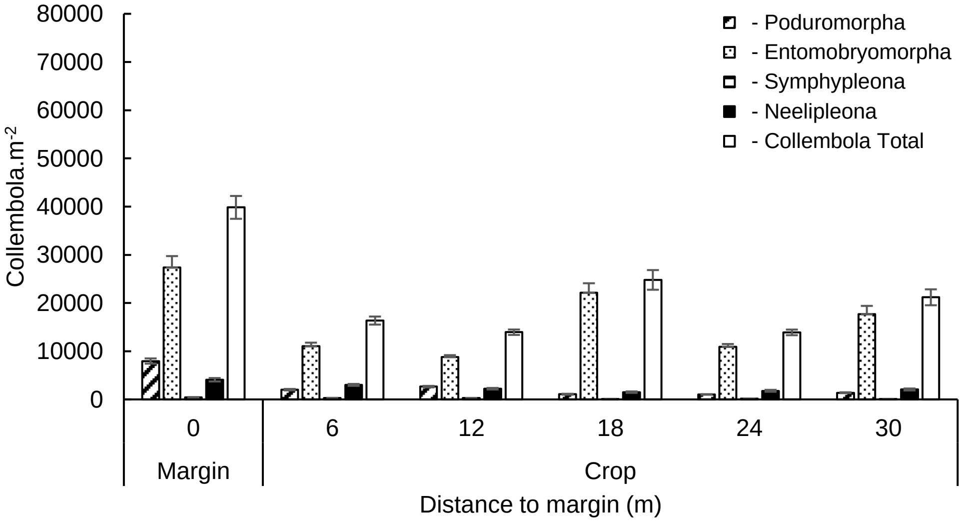
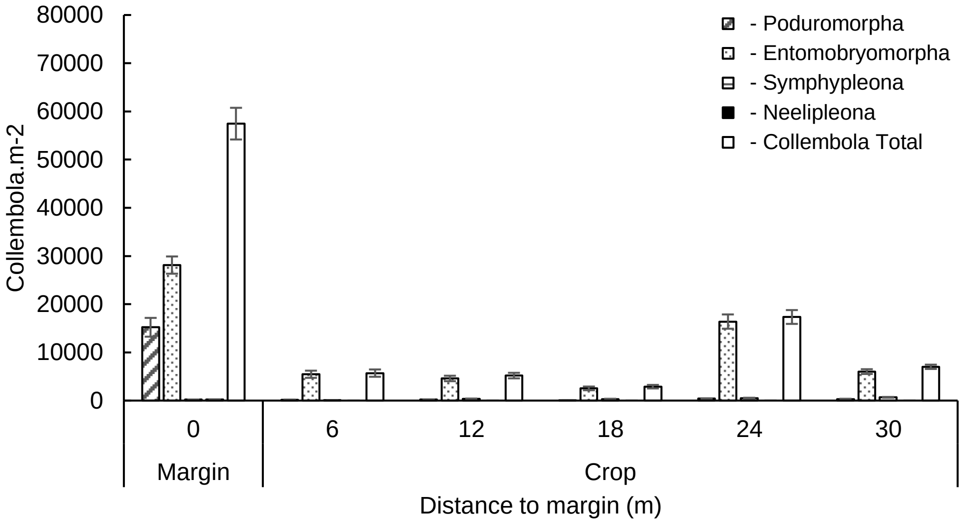


Figure 4.4. Average abundance of the different taxa of collembola (individuals.m^{-2}) in the two sides field margins and at five distances from it into the crop at Rawcliffe Bridge farm (n=20). Figure 4.4.a represent the ‘perpendicular’ field margin and Figure 4.4.b the ‘parallel’ field margin. Bars denote standard error.

a. ‘Perpendicular’



b. ‘Parallel’

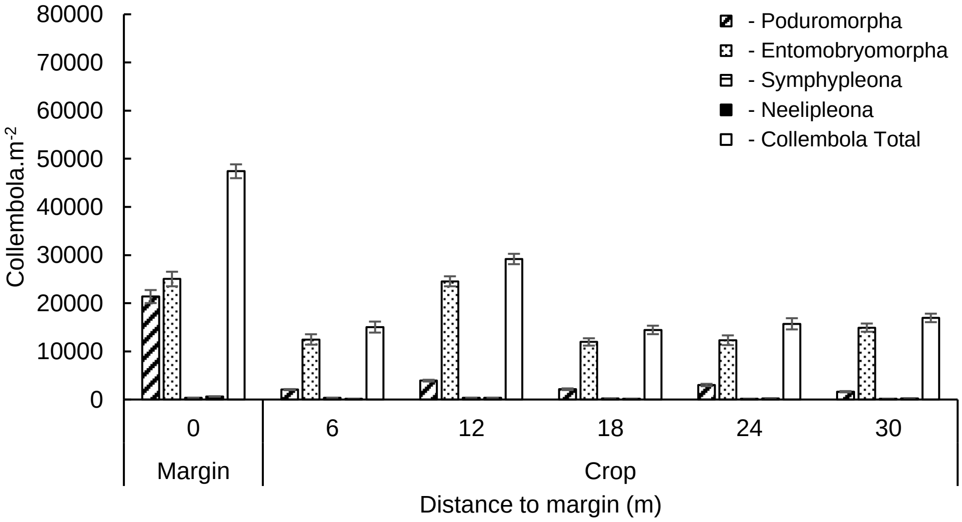


Figure 4.5. Average abundance of the different taxa of collembola (individuals.m^{-2}) in the two sides field margins and at five distances from it into the crop at The Grange farm (n=20). Figure 4.5.a represent the ‘perpendicular’ field margin and Figure 4.5.b the ‘parallel’ field margin. Bars denote standard error.

Table 4.4. Effects from analysis of variance of the margin orientation, either parallel or perpendicular to the tramlines (Orientation), the distance to the field margin (Distance), the sampling season (Season), the farm, either Rawcliffe Bridge or The Grange (Farm) and their interactions on log-transformed abundances of the different taxa of Acari and Collembola. Significant values after False Rate Discovery adjustment ($p < 0.05$) are show in bold.

	Mesostigmata		*Astigmata*		*Heterostigmatina*		Trombidiformes		*Oribatida*		*Acari* total		
	F	p	*F*	p	*F*	p	*F*	p	*F*	p	*F*	p	Df
Treatment													
Cultivation	8.41	**0.036**	5.61	0.099	0.91	0.412	3.20	0.160	114	**0.003**	0.19	0.835	1, 239
Orientation	36.6	**0.005**	39.5	**0.005**	1.56	0.316	0.84	0.433	177	**0.003**	10.4	**0.018**	1, 239
Cultivation: Orientation	5.53	0.085	2.30	0.199	3.35	0.191	1.92	0.256	38.9	**0.003**	0.48	0.682	1, 239
Distance	41.5	**0.005**	2.01	0.165	5.71	**0.003**	15.7	**0.008**	18.3	**0.003**	16.2	**0.004**	5, 239
Cultivation: Distance	2.41	0.096	1.65	0.199	6.22	**0.003**	2.87	0.055	3.37	**0.015**	2.51	0.081	5, 239
Orientation: Distance	3.78	**0.015**	4.03	**0.011**	1.68	0.253	2.84	0.055	11.5	**0.003**	3.12	**0.033**	5, 239
Cultivation: Orientation: Distance	0.79	0.598	0.39	0.855	0.94	0.466	10.6	**0.008**	3.81	**0.008**	0.39	0.915	5, 239
Season	25.5	**0.005**	39.1	**0.005**	71.3	**0.003**	0.58	0.479	30.2	**0.003**	14.8	**0.004**	1, 239
Cultivation: Season	0.00	0.999	39.4	**0.005**	43.9	**0.003**	9.13	**0.015**	2.26	0.169	23.3	**0.004**	1, 239
Orientation: Season	3.18	0144	2.03	0.199	17.6	**0.003**	0.05	0.819	8.64	**0.008**	12.3	**0.004**	1, 239
Season: Distance	1.29	0.340	0.90	0.516	0.41	0.841	1.80	0.179	2.77	**0.033**	0.54	0.861	5, 239
Cultivation: Orientation: Season	2.20	0.235	4.23	0.105	1.58	0.316	2.82	0.160	0.02	0.891	0.00	0.949	1, 239
Cultivation: Season: Distance	1.13	0.404	1.10	0.420	1.33	0.321	1.25	0.363	2.00	0.116	1.27	0.425	5, 239
Orientation: Season: Distance	1.31	0.340	2.06	0.163	2.21	0.145	2.08	0.159	1.58	0.197	2.05	0.146	5, 239
Cultivation: Orientation: Season: Distance	1.47	0.309	1.69	0.199	1.65	0.253	2.99	0.053	1.33	0.274	1.53	0.312	5, 239

	Poduromorpha		*Entomobryomorpha*		*Symphypleona*		*Neelipleona*		*Collembola* total		
	F	p	*F*	p	*F*	P	*F*	p	*F*	p	Df
Treatment											
Cultivation	1.73	0.350	23.0	**0.003**	8.54	0.055	118	**0.008**	13.9	**0.005**	1, 239
Orientation	92.8	**0.005**	16.7	**0.003**	0.02	0.915	53.8	**0.008**	21.5	**0.005**	1, 239
Cultivation: Orientation	6.86	**0.050**	27.8	**0.003**	0.18	0.850	9.11	**0.023**	15.0	**0.005**	1, 239
Distance	31.6	**0.005**	6.05	**0.003**	0.29	0.915	4.29	**0.007**	13.4	**0.005**	5, 239
Cultivation: Distance	5.03	**0.005**	3.65	**0.009**	0.87	0.691	1.44	0.299	7.06	**0.005**	5, 239
Orientation: Distance	1.23	0.429	2.14	0.101	1.43	0.415	1.98	0.155	3.90	**0.007**	5, 239
Cultivation: Orientation: Distance	0.83	0.615	3.16	**0.020**	1.63	0.351	1.13	0.377	3.90	**0.007**	5, 239
Season	2.83	0.204	25.2	**0.003**	28.0	**0.008**	10.6	**0.008**	9.46	**0.006**	1, 239
Cultivation: Season	2.06	0.291	8.22	**0.009**	24.4	**0.008**	2.19	0.213	4.05	0.064	1, 239
Orientation: Season	0.00	0.996	3.25	0.101	2.64	0.268	7.13	**0.023**	2.28	0.150	1, 239
Season: Distance	3.54	**0.015**	0.72	0.608	2.84	0.071	0.39	0.854	0.90	0.485	5, 239
Cultivation: Orientation: Season	0.03	0.931	19.2	**0.003**	1.07	0.455	5.78	**0.039**	10.5	**0.005**	1, 239
Cultivation: Season: Distance	1.14	0.429	1.24	0.318	1.35	0.415	1.34	0.307	1.70	0.150	5, 239
Orientation: Season: Distance	3.87	**0.011**	1.33	0.295	0.30	0.915	1.31	0.307	2.20	0.075	5, 239
Cultivation: Orientation: Season: Distance	1.19	0.429	1.83	0.140	2.16	0.192	1.95	0.155	2.35	0.064	5, 239

4.3.3. Spatial correlation of community structure with distance from the field margin

The Mantel tests revealed a weak but significant relationship between the structure of soil invertebrate communities of *Acari* and *Collembola* and distance from the field margin (Table 4.5). For both *Acari* and *Collembola*, the effect of distance on community similarity was observed to be the strongest at The Grange farm, and particularly in the perpendicular area (Table 4.5). The partial Mantel tests showed that relation between the community structure and the spatial distance varied while controlling for the effects of the different soil characteristics on this relation. The combination of all soil characteristics (SOM, BD, pH, plant residues and WFPS) significantly contributed to explain the spatial pattern of *Acari* community in the parallel area at Rawcliffe Bridge farm and *Collembola* community in the perpendicular area at The Grange farm; yet the Mantel coefficient (r-statistic values) resulting from these two tests (0.07 and 0.00 respectively; Table 4.5), showed that community structure was poorly correlated with increasing distance from the field margin. All soil characteristics (apart from SOM) in the perpendicular area at The Grange farm, contributed explaining the distribution of *Acari* and *Collembola* communities, while the correlation was not as strong between soil characteristics and invertebrates community in the parallel area or at Rawcliffe Bridge farm (Table 4.5).

Table 4.5. Results of simple and partial Mantel tests on dissimilarities between soil invertebrate communities (Acari and Collembola) and sampling distance from the field margin. The null hypothesis (H0) tested the absence of a relationship between dissimilarity values of the two dissimilarity matrices. H0 was rejected if the p-value < 0.05. Mantel test values and critical values are given for each farm (Rawcliffe Bridge farm, The Grange farm) and area of sampling (Perpendicular vs. Parallel). Significant values (p < 0.05) are show in bold and stars show significance levels >0.001 ***; >0.01 **; >0.5 *.

		RAWCLIFFE BRIDGE FARM				**THE GRANGE FARM**			
Orientation of margin side		***'Parallel'***		***'Perpendicular'***		***'Parallel'***		***'Perpendicular'***	
SIMPLE TEST Distance only		*Mantel r-value*	*p-value*	*Mantel r-value*	*p-value*	*Mantel r-value*	*p-value*	*Mantel r-value*	*p-value*
Acari		0.08	**0.019***	0.12	**0.003****	0.08	**0.042***	0.15	**>0.001*****
Collembola		0.09	**0.019***	0.07	**0.048***	0.12	**0.009****	0.21	**>0.001*****
PARTIAL TEST Distance + Soil properties									
Acari	***All***	0.07	**0.024***	-0.06	0.964	-0.02	0.645	0.01	0.329
	SOM	0.06	0.051	-0.06	**0.953**	0.03	0.220	0.01	0.414
	BD	0.07	**0.020***	0.11	0.004**	0.06	0.078	0.13	**0.002****
	pH	0.06	**0.047***	0.05	0.092	0.05	0.140	0.15	**>0.001*****
	Plant residues	0.06	**0.035***	0.10	**0.008****	0.06	0.084	0.15	**>0.001*****
	WFPS	0.09	**0.010***	0.12	**0.002****	0.07	0.052	0.15	**>0.001*****
Collembola	***All***	0.05	0.113	-0.09	0.994	0.04	0.166	0.00	**0.046***
	SOM	0.04	0.142	-0.12	1.000	0.06	0.095	-0.01	0.059
	BD	0.09	**0.020***	0.06	0.076	0.11	**0.011***	0.18	**>0.001*****
	pH	0.07	**0.041***	0.01	0.353	0.10	**0.015***	0.22	**>0.001*****
	Pant residues	0.08	**0.027***	0.03	0.262	0.11	**0.008****	0.21	**>0.001*****
	WFPS	0.09	**0.015***	0.07	0.046*	0.11	**0.008****	0.20	**>0.001*****

4.4. Discussion

4.4.1. Soil characteristics

Average soil bulk density from the field margins was similar between the two farms. However, differences existed in the crop areas. The difference in cultivation strategy between The Grange farm and Rawcliffe Bridge farm, together with the intrinsic soil properties (Table 4.1) could explain the response of BD to the field operations. The amount of plant residues varied independently regarding the orientation of the margin in each farm. This highlighted the difference of organic inputs distribution between the two agricultural systems; depending only on their former machinery traffic plans. It raised the importance that former field operations may have on the distribution of food resources for soil invertebrates in the crop, independently of all other environmental or agricultural factors. Surprisingly, the amount of soil organic matter was lower in the crop at Rawcliffe Bridge farm than at The Grange farm. We had hypothesised that the more complex crop rotation and the no-till system at Rawcliffe Bridge farm would enhance SOM in comparison to The Grange farm, but it is possible that the soil mineralogy, particularly the clay content of The Grange farm soils or the addition of organic matter, such as manure, might have facilitated SOM storage (Cranfield University, 2017). The greater spatial variation of soil pH at The Grange farm than Rawcliffe was likely due to the inherent heterogeneity of the soil texture or mineralogy (Cambardella *et al.*,

1994) rather than being a consequence of field operations or management.

The distinct site characteristics and management practices at each farm explained most of the differences between soil samples, although the difference of environmental background (soil type; climate; historical management) must be considered and a bold comparison between the two farms put in perspective. It has been shown that complex crop rotation and no tillage can improve soil quality (van Leeuwen *et al.*, 2015; Bünemann *et al.*, 2018). The perpendicular area in the field at Rawcliffe Bridge showed particularly high BD values (Table 4.2), while differences between the perpendicular and parallel areas at The Grange farm was not so evident (Table 4.2). The reduced tillage treatment on clay soils at The Grange farm could explain the reduced BD measured in the top 10 cm of soil (Morris *et al.*, 2010), while the no-till treatment at Rawcliffe Bridge farm would make the disruptive impact of field traffic more evident (Mäder & Berner, 2012). The minimum tillage management and the high clay content at The Grange farm (Table 1), may account for greater values of WFPS (Cranfield University, 2017). It is common practice in reduced or no-till practices to leave the crop residues on the field after harvest (Townsend *et al.*, 2015). The difference of spatial distribution and amount of residues found at the two farms could directly be linked to the type of soil work. The type of crop rotation of the two farms affected the amount of crop residues found in the samples too, while the crop type between the farms at one given season was unlikely to create a major difference as both farms included oilseed rape and winter wheat over the seasons. Unlike for crop residues, the impact of cultivation system on SOM at each farm could be confounded with the intrinsic soil characteristics at each site. Greater SOM content were found in the soils of The Grange farm, which can partially be explained by the amount of crop residues left after harvest, but could also result from stabilisation and strong bonds between SOM and clay particles (Six *et al.*, 2000).

4.4.2. Invertebrates

Studies have shown the detrimental impact of human activities on abundances of soil mesofauna (Tsiafouli *et al.*, 2015; George *et al.*, 2017). The result of this study also showed that variability in abundance of soil invertebrates across field areas and farms was heavily dependent on the taxonomical group studied: populations of *Acari* and *Collembola* did not responded in the same way to field management; and in a similar manner, families and sub-families. Populations of both *Acari* and *Collembola* reduced in their numbers in the cropped of the perpendicular area where machinery is turning, implying that at a broader scale the disturbance generated by the machinery prevented establishment of structured communities of soil invertebrates. These two invertebrate groups were, however, not affected by the cultivation systems in the same way. The average abundance of *Acari* did not vary between the sites while very low abundance of *Collembola* was observed in the field at The Grange farm. Edaphic *Collembola*n species that live their entire life cycle belowground, such as *Poduromorpha*, were particularly impacted by tillage (Coulibaly *et al.*, 2017). It is also possible that regular soil cultivation would have curtailed establishment of fungal mycelial systems that are a principal food resource for many *Collembola* species (Anslan *et al.*, 2018).

The trophic position and the life strategy of the different taxa observed was reflected in the variability of responses to the different treatments (cultivation system, orientation of the traffic, field margin). Larger specimens (large *Mesostigmata* predators), fungivores (*Poduromorpha*) or slow-reproducing taxa (*Oribatida*) were found in greater abundances at Rawcliffe Bridge farm, in the cropped of the parallel area or in the margins than at The Grange farm. Smaller and more opportunistic taxa, such as *Heterostigmatina Acari*, could be found in reasonable numbers in whatever the context. We saw here that R-strategist populations, including smaller, opportunistic and fast reproducing rates species (Pianka, 1970; Reznick *et al.*, 2002), dominated in the cropped of the perpendicular area while more complex communities, dominated by K-strategists, including by contrast bigger, stronger competitor and low reproducing rate species (Pianka, 1970; Reznick *et al.*, 2002), were found in the parallel areas. The result might imply that that recovery abilities of R-strategists favoured them in the more disturbed crop areas. Althoff *et al.* (2009) had similar results on communities of nematodes using military tanks to create disturbance and compaction under different soil conditions. They demonstrated that nematodes at different trophic levels were not affected to the same extent by the disturbance, with microbivores recovering better after disturbance than herbivores.

The community structure of *Acari* and *Collembola* in the crop areas was weakly correlated with spatial distance from the margin. Diversity and abundance of invertebrates varied differently along the distance transect, depending on the orientation of the tramlines. One explanation could be that traffic orientation impacted on intrinsic soil properties, such as BD or SOM, that affected changes among the soil fauna community. Modification in community structure therefore indirectly results from field operations.

4.5. Conclusions

In this experiment, the design had confounding factors (margin orientation was confounded with sampling year). However, we assumed that meteorological conditions between sampling years were sufffcently similar for study years to be comparable (appendix 6 and 7).

Setting up field margins may reduce (areas devoted to) crop production but have the potential to build up reservoirs of soil fauna biodiversity and be beneficial to adjacent crops. Field margins should be an integrated part of field management practices, which would involve considering in orientation regarding the direction field traffic in order to avoid reduction, or elimination, of potential ecosystem services provided by the margins. The results of this study suggests that soil disturbance generated by agricultural machinery might have shaped dispersion mechanisms of the soil fauna: a greater propensity for soil fauna to colonise the crop near the field margins parallel to the tramlines, rather than from the perpendicular margins at the ‘turning end’ of tramlines, where conditions would be disadvantageous to dispersion. Although factors facilitating dispersion are one thing, it could only happen within advantageous environmental condition that would allow in-field survival. It also emphasised that to set up proper field margins, the following environmental and agricultural factors should be considered: soil type, climate, cultivation type, disposition of the margin around the field, field activities. All these factors affect the soil fauna community and more replication on a greater number of farms would be needed to support the conclusion drawn from this study and fully understand the interaction between field management and more global environmental context. Dispersal mechanisms of the soil mesofauna populations should be tested to clearly elucidate the role of the margins and the traffic orientation on colonisation processes; while factors enabling the establishment, survival and perpetuation of populations (such as food resources or amplitude and frequency of disturbance) should be elucidated. In the context of this study and to fulfil the environmental purpose of field margin, we would advise to preferentially emphasise field margin management on the side parallel to the tramline rather than at the turning end of it. It should be noted that this recommendation is based on one in-depth study of field margins at one field site on two contrasting farms and further work is required to evaluate the generality of our results.

This chapter is structured and formatted in accord with specification for the journal Applied Soil Ecology. Current status is: Under second revision (accepted with minor revisions)

CHAPTER 5

SOIL COMPACTION EFFECTS UPON LITTER DECOMPOSITION IN AN ARABLE FIELD: IMPLICATIONS FOR MANAGEMENT OF CROP RESIDUES AND HEADLANDS

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ABSTRACT

Soil compaction is a major threat to agricultural soils. Heavy machinery is responsible for damaging soil chemical, physical and biological properties. Among these, organic matter decomposition, predominantly mediated by the soil biota, is a necessary process since it underpins nutrient cycling and provision of plant nutrients. Hence understanding factors which impact the functionality of the biota is necessary to improve agricultural practices. In the present study, to understand the effects of compaction on the soil system, we determined the effects of soil bulk density and soil penetration resistance on the decomposition rates of litter in three distinct field zones: margin, tramlines in the crop:margin interface, and crop. Three litters of different quality (ryegrass, straw residues and mixed litter) were buried for 1, 2, 4 and 6 months in litter bags comprising two different mesh sizes (<0.2 and >2 mm). Bulk density and soil resistance were greater in the compacted tramline than in the margin or the crop. The greatest loss of buried organic matter mass occurred in the grass margin and the lowest in the tramline. Differences between treatments increased with burial time. No significant difference in mass loss between the two mesh sizes was detected before the fourth month, implying that microbial activities were the main processes involved in the early stages of decomposition. Decomposition in the tramline was clearly affected by the degradation of soil structure and limitation of water and nutrient supplies due to heavy compaction. This study shows that prevailing soil conditions at the edges of arable fields affect major soil processes such as decomposition. It also reveals the potential to mitigate these effects by managing the headland, the crop residues and the machinery traffic in the field.

Key words: Decomposition; Compaction; Field margins; Environmental Stewardship Scheme; Soil quality

5.1. Introduction

Land-use is a primary determinant in driving soil processes (Holland *et al.*, 2014; Postma-Blaauw *et al.*, 2010; Sousa *et al.*, 2004). It was shown that vegetation cover modifies soil biodiversity (Crotty *et al.*, 2015) and that established grasslands have improved soil function compared to arable fields (Crotty *et al.*, 2014). In 1994, the United Kingdom government published a Biodiversity Action Plan, establishing arable field margins as priority habitat (Maddock, 2008) and supported by a new environmental stewardship scheme for farmers to increase and support biodiversity in the agricultural landscape in 2014 (Department for Environment, Food & Rural Affairs, 2014). This included compensation for the setting up of grass margins around arable fields with the primary aim of encouraging aboveground biodiversity (Department for Environment, Food & Rural Affairs, 2014; Meek *et al.*, 2002). Evidence suggests such margins can provide important ecosystem services including pollination and pest management (Lu *et al.*, 2014). However, the implications for the belowground biodiversity have been less considered even though it has been established that the soil biota can be adversely affected by field management (Sechi *et al.*, 2017). This may also have impacts on the functions supported by a diverse soil community which are less well understood. Field margins affect nutrient transformation and run-off (Marshall and Moonen, 2002), and the soil fauna plays a pivotal role in many of the soil processes that, in turn, deliver ecosystem services (Bardgett and van der Putten, 2014; Wall *et al.*, 2015). Among these services, decomposition, a biologically driven process, enables nutrient cycling and primary production (Coleman *et al.*, 2004; Hättenschwiler *et al.*, 2005). During the process, the interaction between the different classes of organisms (microbiome and macrobiome) is necessary to undertake the decomposition of primary organic matter (Bradford *et al.*, 2002). Although the role of the microbiome (bacteria and fungi) is reasonably well understood, Setälä *et al.* (1996) demonstrated the benefits of a more complex community for improved nutrient cycling. It has also been shown that macrofauna modify the processes of decomposition by its action on the microbiota (Hättenschwiler *et al.*, 2005; Joly *et al.*, 2015). In relation to the importance of the macrobiome to modify dynamics of organic matter degradation (Wolters, 2000), activity of this compartment (meso- and macrofauna) is required to achieve the decomposition of litter and should be regarded as a potential tool for crop management and nutrient cycling in agricultural contexts.

In agricultural soils, factors affecting litter decomposition are affected by human activity. The amount and quality of organic matter returned to the system (Fierer *et al.*, 2005; Gergócs and Hufnagel, 2016; Milcu and Manning, 2011) together with the presence of the biotic communities (Murray *et al.* 2009) are primary factors regulating decomposition rates. Thiele-Bruhn *et al.* (2012) noted the capability of agricultural practice to control the quality of primary organic matter entering soil systems and therefore its capability to modify the soil community and its activity. To understand the effects of litter quality, Johnson *et al.* (2007) tested the decomposition of five crops of varying chemical composition and three different organs of each plant, and showed that crop and plant parts affected decomposition rates and C-pools at the soil surface. This implies some potential for agricultural soil management via crop residues.

The architecture of the habitat and the associated propensity for belowground oxygen supply (modulated by the soil pore networks) are two more factors affecting decomposition rates. The deterioration of soil structure (principally reduction in porosity and connectivity of pores) via external factors has been shown to affect microbial mineralisation (Beylich *et al.*, 2010; De Neve and Hofman, 2000), as well as habitat and food resources that support the soil fauna (Beylich *et al.*, 2010; Althoff *et al.*, 2009; Larsen *et al.*, 2004). In agricultural contexts, soil structure is exposed to deterioration by heavy machinery traffic and many arable soils in the UK are sensitive to increased compaction, causing a decline in crop yield (Hamza and Anderson, 2005). Within the scope of environmental schemes and to prevent damage to improved biodiversity habitats, such as field margins, the policy requires that farmers do not manoeuvre on the field margins, obliging them to turn at the edges of the crop and thus creating a compacted area between the main crop and the margin. A better understanding of the effects of compaction on organic matter decomposition and biological activity in soils is a necessary step to improve soil management in agricultural systems and to mitigate the impacts of compaction.

In this study, we determined organic matter decomposition rates of plant material (wheat straw and ryegrass residues) in contrasting zones of an arable field that had been subjected to different pressures. We aimed to identify effects of machinery wheeling and agricultural management on decomposition and understand how the response changes with respect to litter type and soil faunal exclusion. We hypothesised: (i) decomposition rate would be lowest in more compacted soils; (ii) ryegrass litter, because of its lower C:N ratio, would decompose faster than straw residues; (iii) exclusion of the soil mesofauna would reduce the decomposition rate.

5.2. Materials and methods

5.2.1. Sites and soil characteristics

The experiment was carried out between October 2016 and April 2017 at The Grange Farm, Northamptonshire, United Kingdom (52° 18' 2.73" N; 0° 45' 52.83" W) in an arable field planted with oilseed rape (*Brassica napus* L.) which had previously been in winter wheat (*Triticum aestivum* L.). The field was managed using minimum tillage techniques (i.e. no deep ploughing) for c.15 years. Mineral fertilisation and chemical inputs were applied to the crop following the UK standard scheme management for farmers (Agriculture and Horticulture Development Board, 2017). The crop was planted in a field bordered by a 10-year-old grass margin that had been set up to promote biodiversity in the agricultural landscape (Department for Environment, Food & Rural Affairs, 2014; Maddock). The soil was classified as Hanslope series, a typical calcareous pelosol from a clayey chalky drift series (calcaric stagnic cambisol soil) with poor drainage capacity and high sensitivity to compaction (Cranfield University, 2017).

Climate conditions were characterised by two dry periods in October at the beginning of the experiment and in December. Temperatures were normal for the region for the time of the year and location.

The experimental area consisted of split plot design of 18 plots (6 x 6m) distributed within six blocks along the south side of the field. Each block comprised three plots; one in the grass margin, one in the tramlines between the margin and the crop, which were visibly compacted, and one in the actual crop. Total soil carbon (C) and total soil nitrogen (N) concentrations were measured using an elemental analyser (N1500, Carlo Erba, Milan, Italy). C:N ratio was determined as average values calculated from cores taken at each of the 18 plots.

5.2.2. Soil compaction assessment

Soil bulk density (Laryea *et al.* (1997) was determined from cores (8 cm diameter x 10 cm depth) taken at random from each of the 18 plots at the beginning of the experiment. This sampling method was considered appropriate to our requirements as it has been shown to not significantly affect bulk density measurement (Özgöz *et al.*, 2006; Page-Dumroese *et al.*, 1999). Samples were dried at 105°C for 24h, then plant residues and stones were removed by 2 mm sieving. Water content was calculated from the proportion of dry soil to wet soil (Table 1). Soil penetration resistance was recorded on April 1st 2017 with a penetrometer (Solution for Research Ltd, Silsoe, Bedfordshire, UK) fitted with a 9.45 mm diameter (base area 7 x 10-5 m2), 30-degree cone. At every sampling point, the soil resistance was measured at 14 depth points, each 3.7 cm apart. Penetrometer resistance was calculated by dividing force at each depth by the cone base area. Ten replicate measurements were randomly taken on each plot. Data were calibrated by Solution for Research Ltd, Silsoe, Bedfordshire, UK; and converted from mV to KPa as follows:

$$Force(KPa) = (Force(mV) - 57.48) \times 139.9 \times 0.0781 \qquad \textbf{(1)}$$

5.2.3. Organic matter decomposition experiment

Litter bags (6 cm length x 5 cm height) were made using two mesh sizes; one set with a mesh size of >2 mm allowed full access by the soil biota, and one set <0.2 mm which excluded most of the fauna and allowed microbial access only.

Three types of litter of different quality (C:N ratio) were prepared: a low C:N ratio perennial ryegrass (*Lolium perenne* L.), a high C:N ratio wheat straw (*T. aestivum*) and a 50:50 mixture of both types of litter. Ryegrass and wheat straw were oven dried to constant weight at 105°C. Then, 1.0 g of the litter was added to each of the litter bags (0.5 g of both litter types was added for the mixed litter treatment). Average values of total carbon and total nitrogen of wheat straw and ryegrass were measured from 5 subsamples of each of the initial materials (i.e. T0), and after 6 months (T6) for material remaining in both small and large mesh bags, for each of the three litter types (ryegrass, mixture 50:50, and straw) using an elemental analyser (N1500, Carlo Erba, Milan, Italy). The initial C:N ratio of the 50:50 mixture was taken as the arithmetic mean of the constituent ratios weighted by C and N concentration in the litters (equation 2).

$$C{:}Nmix = \left[\left(\left(\frac{\Sigma C_{straw}}{\Sigma m_{straw}}\Big/\frac{\Sigma N_{straw}}{\Sigma m_{straw}}\right)\right) + \left(\left(\frac{\Sigma C_{grass}}{\Sigma m_{grass}}\Big/\frac{\Sigma N_{grass}}{\Sigma m_{grass}}\right)\right)\right]/2 \qquad \textbf{(2)}$$

Where, C_{straw}; N_{straw}; C_{grass}; C_{grass} represent carbon and nitrogen content in straw and grass litter in mg.

And, m_{straw}; m_{grass} represent the mass of straw or grass in mg use for each measurement of C and N.

A total of 432 litter bags were distributed appropriately between the 18 plots and buried on 1 October 2016 and a sub-set of 108 bags were removed on 1 November 2016, 1 December 2016, 1 February 2017 and 1 April 2017, representing 1, 2, 4- and 6-months post-burial. The latter time is consistent with the cropping cycle, when the cultivated part of the field is then physically disrupted. The experiment was designed as a split-plot design, with 6 replicates (block) of 3 plots, each plot corresponding to the 3 zones in the same alignment (grass margin, compacted tramline and crop) treated at plot level, and all other treatment factors (2 mesh sizes x 3 litter types; exposed in the soil over 1, 2, 4 or 6 months) treated at bag level. The field zones (margin, margin-crop interface and crop) were spatially constrained and so randomisation of plots within blocks was not possible. Litter bags were buried in the top soil at 5 cm depth in each plot and the position of bags of each treatment combination was completely randomised within the plot. To minimise disturbance and to preserve the context of the inherent soil structure as far as possible, a vertical slit was made with a spade, just sufficient to locate the bag, and then closed up by firming the soil back into position. A string and a knot code system were used to identify each treatment. One bag was missing on the first and third collection dates, and 5 bags were missing on the last date.

After removing the litter bags from the ground, the litter was removed from the bags, soil particles were gently washed away from the litter using a 15 µm sieve to retain plant materials. The litter was then dried and weighed as described above. The proportion of litter remaining following each given time period spent in the ground was then calculated.

5.2.4. Statistical analyses

Impacts of field zone on bulk density was estimated by a 1-way analysis of variance (ANOVA). An analysis of covariance (ANCOVA) was used to test the effect of field zone (grass margin, tramline and crop) on the soil resistance, controlling for the effects of depth, which co-vary with the field zone effect. We tested the similarity of soil resistance in the “grass margin” and the “crop” zone by using a sub-model nested in the full model; the ANCOVA therefore tested for the differences between the effects of the field zone on soil resistance at the same time as the effect of the uncompacted zones (grass margin and crop) vs. the compacted tramline.

The five samples, taken from the initial litter material are pseudoreplicates in terms of testing for treatment effects and as such were excluded from the main statistical analysis model. However, means and standard errors were used as a basis for comparison between litter type. A two-way mixed-design analysis of variance (ANOVA) was used to test for the differences of C:N ratio between two treatment factors (mesh size and litter type) and their interaction. No transformation of the data was required when we assessed the normal distribution of the residuals by using model checking plots (normal probability and quantile-quantile plots). We used a post-hoc comparison Tukey test at 95% confidence level to see where differences between factors lied.

A four-way mixed-design ANOVA was used to determine effect of the treatment factors (mesh size, litter type, field zone and time period in the ground), and their interactions, on the quantity of litter remaining at the end of the experiment. No transformation of the data was required when we assessed the normal distribution of the residuals by using model checking plots (normal probability and quantile-quantile plots). Because of the destructive sampling of the litter bags, time did not need to be considered as a repeated measurement. We used Fisher's Least square difference method (LSD) to assess whether pairwise combinations were different from one another, with Bonferroni adjustment. Similarly, the effect of mesh size, litter type and field zone were analysed using a 3-way ANOVA for month 1, 2, 4 and 6 separately. All statistical analyses were done using R software 3.1.2 (http://www.r-project.org/).

5.3. Results

5.3.1. Soil Compaction

Bulk density was significantly greater in the compacted area of the tramline compared to the grass margin or the crop ($F_{(2,13)}$=18.59, P<0.001; Table 5.1).

Table 5.1. Average values (n=6) and standard error (±SE) of various soil properties measured in three zones of an oilseed rape field (October 2016). Superscript letters show significant difference of means between the field zones (Least square difference test, Bonferroni adjustment).

Field zones		**Water content (%. gSoil^{-1})**	**Bulk density (g.cm^{-3})**	**Total C (% .gSoil^{-1})**	**Total N (% g.Soil^{-1})**	**C:N ratio**
Grass margin						
	Mean	17.4 ^{a}	0.89^{a}	4.08 ^{a}	0.40 ^{a}	10.20 ^{a}
	± SE	*1.02*	*0.03*	*0.39*	*0.02*	*0.39*
Tramline						
	Mean	11.7 ^{b}	1.25^{b}	2.32 ^{b}	0.27 ^{b}	8.61 ^{b}
	± SE	*0.62*	*0.03*	*0.14*	*0.01*	*0.46*
Crop						
	Mean	14.6 ^{a}	1.02^{a}	2.36 ^{b}	0.25 ^{b}	9.58 ^{b}
	± SE	*0.25*	*0.06*	*0.19*	*0.02*	*0.42*

The soil resistance increased significantly with depth in all of the three field zones ($F_{(1,246)}$=1003,17, P<0.001). A peak was observed at 7.4 cm in the tramline, whereas the slope of the resistance in the crop increased below the ploughed layer at 23 cm depth (Figure 5.1). There was no difference in soil resistance between the crop and the field margin zones ($F_{(1,246)}$=0.23, P=0.63) and overall, the soil resistance was significantly greater in the compacted zone (tramline in the crop-margin interface) than in the uncompacted zones (crop and field margin zones combined) ($F_{(1,246)}$=128.83, P<0.001).

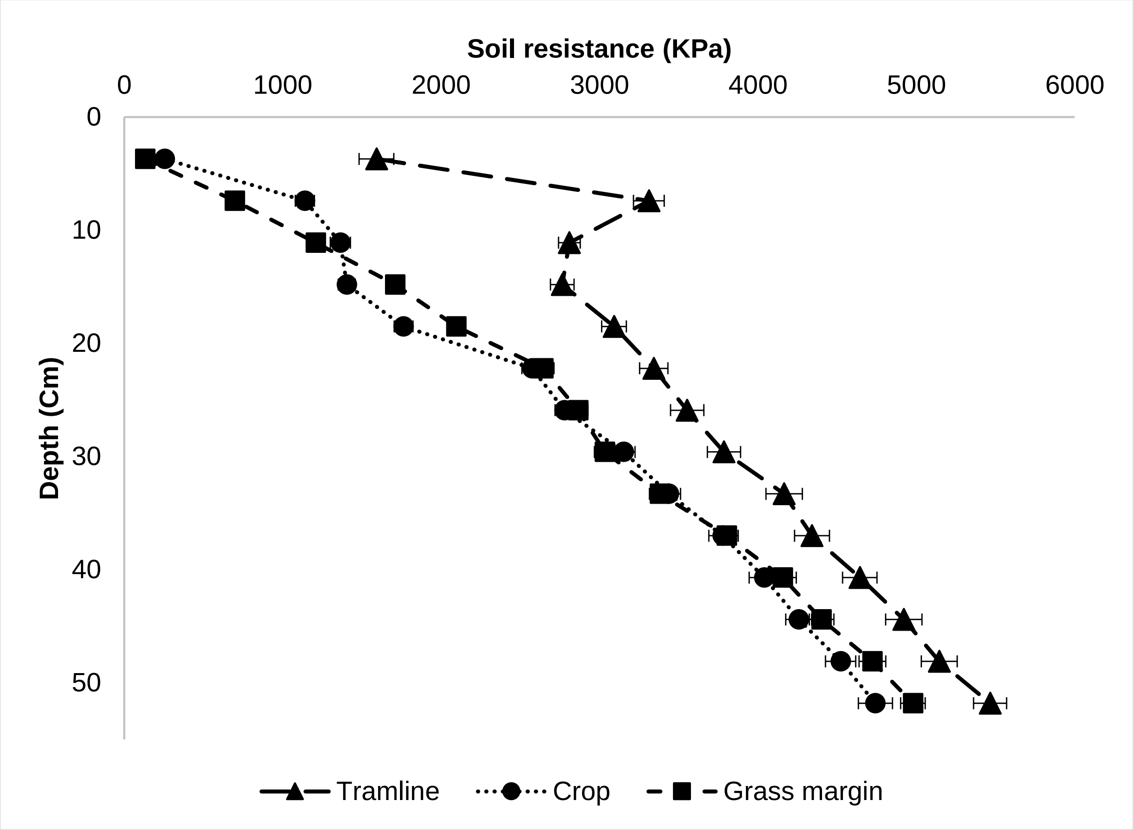


Figure 5.1. Profiles of soil resistance (KPa) within three field zones (grass margin ■, tramline wheeling in the crop-margin interface ● and, crop ▲) at 14 depth points (3.7 cm to 51.8 cm depth) within a field containing oilseed rape, 2017 cropping season. Points show means (n=60); bars denote standard error. In some instances, these fall within the confines of the symbols.

5.3.2. Litter decomposition

5.3.2.1. Comparison of the two mesh sizes

In the first two months of the experiment, regardless of the field zone or the litter type, there was no significant difference in decomposition between the large and small mesh size bags (for Month 1 and Month 2, $F_{(1,74)}$=0.63, P=0.431 and $F(_{1,75})$=0.67, P=0.415, respectively). However, from Month 4, there was more litter remaining undecomposed in the small mesh than in the large mesh size bags ($(F_{1,74}$=69.27, P<0.001; Figure 2). This effect was persistent from Month 6 ($F_{(1,70)}$=92.73, P<0.001). Overall the combined effect of mesh size on decomposition over time was significant ($F_{(3,350)}$=34.84, P<0.001). The effect of the field zone combined with the mesh size was also significant ($F_{(2,350)}$=3.65, P=0.027), with relatively less litter decomposed in the large compared to the small mesh bags when these were buried in the tramline or the crop rather than in the grass margin (Figure 5.2).

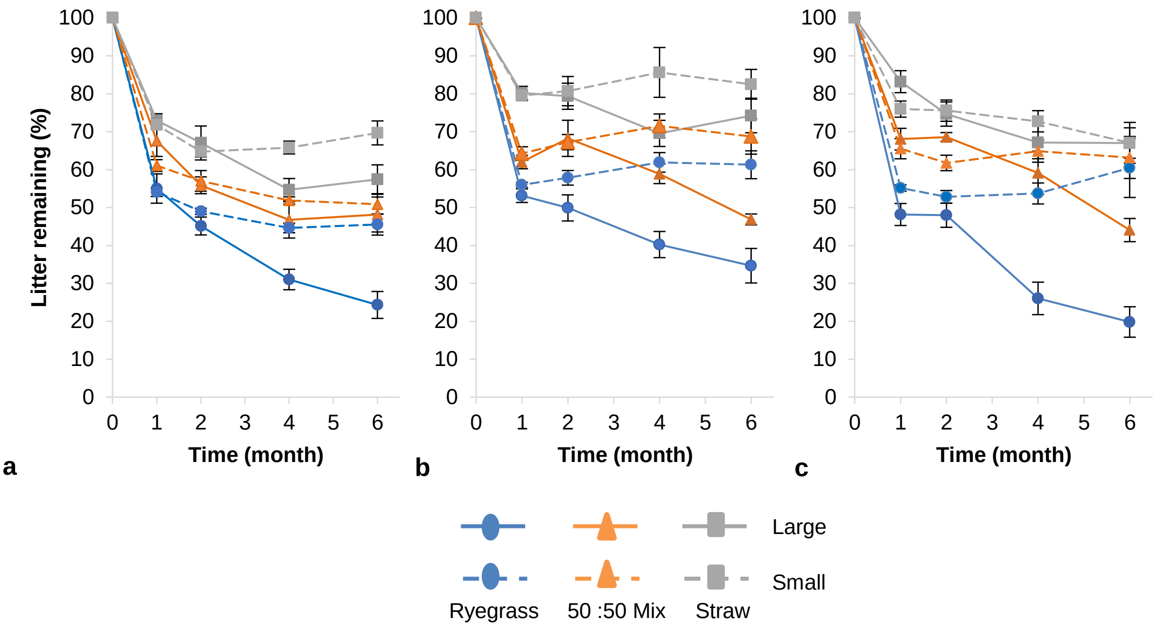


Figure 5.2. Percentage of different litter types (perennial ryegrass (Lolium perenne) blue ●, wheat straw (Triticum aestivum) grey ■, and a 50:50% mixture of both litters orange▲) remaining after 1, 2 ,4 and 6 months buried in three different zones of a field containing oilseed rape, in litter bags with small (<0.2 mm) and large (>2 mm) mesh sizes and in the three field zones (Figure 2.a. grass margin, Figure 2.b. compacted tramline and, Figure 2.c. crop). Month 0 corresponds to the start of the experiment (1st October 2016) and Month 6 to the end of the experiment (1st of April 2017). Points show means (n=18); bars denote standard error.

5.3.2.2. Effects of crop litter quality

Litter type significantly affected the proportion of plant material remaining in the bags at the end of the experiment ($F_{(2,350)}=385.94$, $P<0.001$); 72.6 ± 7.3 % of the straw remained after 6 months, while 47.1 ± 8.1 % of the ryegrass was left. Mixed litter had an intermediate decomposition rate, with 60.4 ± 8.0 % of material remaining. There was a significant interaction of the combined effects of litter type and mesh size ($F_{(2,350)}=22.43$, $P<0.001$), with more ryegrass decomposed in the large litter bags than straw residues or mixed litter in small and large mesh size bags (Figure 5.2). Even though the difference in litter remaining between the two mesh sizes at Months 1 and 2 was not significant, mass loss of ryegrass in the large mesh size litter bags was marginally greater than the loss in other treatments ($F_{(2,74)}$=3.08, P=0.052 and $F_{(1,75)}$=2.94, P=0.059 for Month 1 and Month 2, respectively; Figure 5.2).

The C:N ratio of the litter declined over time only in the case of straw and the mixture (Table 5.2). After 6 months decomposition, there was no significant interaction between litter type and mesh size, but a highly significant main effect due to litter type ($F_{(2,74)}$, P<0.001), where the ratio was circa three-fold greater in the case of straw compared to ryegrass (Table 5.2). In the case of the mixture, the C:N ratio was circa half that of the straw, but significantly greater than that for ryegrass alone (Table 5.2). There was also a significant effect of mesh size upon C:N ratio after 6 months where the ratio was 10% smaller in small compared to large mesh bags ($F_{(1,75)}$, P=0.02; Table 2).

Table 5.2. C:N ratios of the three plant residues used in the litter bags of two mesh sizes at the outset of the study (T0), and main effects of litter type and mesh size after 6 months burial (T6). Superscript letters show significant difference of means between the respective treatments for T6 (Least square difference test, Bonferroni adjustment).

	T0		**T6**		
	mean	s.e.	mean	pooled	P_F
Ryegrass	17.5	0.19	15.4^a	1.03	<0.001
Straw	84.2	0.45	40.3^b		
Mix	50.8*	n/a	22.1^c		
Large mesh			27.6^x	0.84	0.02
Small mesh			24.7^y		

** calculated as the arithmetic mean of the constituent ratios weighted by C and N concentration in the litters (equation 2).*

5.3.2.3. Effect of the field zone on decomposition

The location of the litter bags in the field (zone) significantly affected the decomposition rate of all litter types within bags of the two different mesh sizes ($F_{(2,10)}$=34.0,P<0.001). With a mean of 64.8 ± 7.8 % of litter remaining, mass loss was lowest in bags placed in the tramline and similar decomposition rates were observed in bags buried in the grass margin and in the crop (on average 55.0% and 60.2% of litter remaining, respectively).

5.4. Discussion

We hypothesised that in the field, litter decomposition at the interface between the crop and the margin would be reduced in comparison to the grass margin. This particular area was distinguished by degraded soil conditions: trafficking would deteriorate the soil structure and therefore impact soil processes such as litter decomposition (Hamza and Anderson, 2005).

5.4.1. Soil compaction

Soil bulk density acts as a simple surrogate to indicate the pore space and therefore soil compaction (Buckman and Brady, 1960). Bulk density was greater in the compacted area of the tramlines at the margin:crop interface than in the crop or the grass margin zones, and indicates inappropriate habitat and conditions for soil life (Beylich *et al.*, 2010; Horn *et al.*, 1995). We assessed compaction of the whole soil profile by taking soil resistance measurements. Penetrometer data is a measure of soil strength (Bengough *et al.*, 2000), here implying that the compacted soil was stronger than that associated with crop and grass, which were not different from each other on the day the measurements were made. All three treatments show an increase in strength with depth which is usual and probably due to the soil overburden (Horn *et al.* 2007). The increased strength may be due in part to differences in water content and or bulk density (Bengough *et al.*, 2000), but whatever the underlying causes of soil strength, the compacted soil was stronger than the grass or the crop (Figure 5.1). All the penetrometer curves were the same basic shape apart from bulge in the compaction curve at 7.4cm depth, which could be explained by wheeling pressures compacting the soil (Figure 5.1). This could be interpreted as an indicator of degraded soil condition (Duiker, 2002) and result in an impermeable layer of soil, preventing water drainage, increasing the likelihood that water capacity over the winter season would be exceed and consequently the absence of oxygen would limit decomposition processes (Beylich *et al.*, 2010; Horn *et al.*, 1995; Whalley *et al.*, 1995). Although only soil strength at the soil surface was used as a data to relate to effects of compaction on litter decomposition. The shallow angle of the slope observed in the cropped soil resistance measurements correspond to the plough layer at 23 cm. Above this layer, soil resistance in the grass margin and the crop zone behaved differently but reached similar intensities below this interface. Even though the field had been farmed using minimum tillage cultivation techniques for the past 15 years, this could reflect the long-term effect of previous ploughing practices on soil structure. The potential impact of this on soil processes (e.g. Peigné *et al.*, 2013) warrant further investigation. Our results showed that decomposition occurs more slowly in the compacted soil of the tramlines at the crop-margin interface regardless of the litter type or the mesh size of the bags used in the experiment.

5.4.2. Impact of mesh sizes

The two different mesh sizes of litter bags used in the decomposition experiment enabled conclusions to be drawn about the effects of microbial communities and larger soil fauna on decomposition since the large mesh size allowed access of all soil fauna and the small mesh size excluded this fraction and would therefore be predominantly microbial (Bokhorst and Wardle, 2013). Before Month 4, there was no difference in mass loss between litter bags of the two mesh sizes, implying that the initial decomposition (Month 1 and Month 2) was primarily carried out by microbes or that effect of the soil fauna was negligible. In this study, the addition of an exogenous source of organic matter might have stimulated primary microbial colonisation, resulting in mineralisation of the fresh organic matter, leaving humified organic matter (Wardle and Lavelle, 1997). Over time, the mass loss of litter in the large mesh size bags was more important than in the small mesh size bags implying that the activity of larger invertebrates become significant as they break down this recalcitrant pool of organic matter, making it available to mineralisation (Bradford *et al.*, 2002; Schädler and Brandl, 2005). Carrillo *et al.* (2011) observed that changes in litter decomposition process, induced by the presence of meso- and macro-invertebrates, was time dependent and highlighted the importance of temporal dynamics in effects on the soil fauna. The amplitude of the difference between decomposition rate in the large and small mesh sizes was the greatest in the compacted tramline. The inclusion of larger soil organisms may have supported litter decomposition despite restricted conditions. In the large mesh size bags buried in the grass margin, the decomposition of the mixed litter contrasted with the previous conclusion and no difference was observed compared to the small mesh size. This suggests that microbial decomposition in the grass margin could benefit from a ‘priming effect’ from the grass litter (Fontaine *et al.*, 2003), which would compensate for the effect of the soil fauna inclusion observed in the large mesh size bags. Unlike the mixed litter, straw residues alone decomposed faster in the large than small mesh size bags. This contrasting effect could result from the inabilities of the microbial populations in the grass margin to overtake decomposition of wheat straw without a ‘priming effect’.

5.4.3. Impact of litter quality

Litter quality (expressed here as C:N ratio) is well established as a driver of decomposition (Hamza and Anderson, 2005; Wardle and Lavelle, 1997) and accordingly in this study, the decomposition rate was influenced by litter type and its quality; the greater the C:N ratio of the litter (Table 5.2), the slower the decomposition (Figure 5.2). After 6 months in the soil, significantly more litter remained in the bags containing wheat straw than those containing ryegrass. Decomposition of mixed litter varied between the different treatments; showing that functions of decomposition (C and N mineralisation) were affected differently by synergistic, antagonistic or additive effects of the residues mixtures and thus depended on the mixture heterogeneity. It was shown by Redin *et al.* (2014), that the diversity of functional and chemical traits of crop residues mixture (regarding the plants alone) influences decomposition rates of residue mixtures. Because the effect of the mixed litter on decomposition rates was null only in the small mesh size treatment - where only microbial decomposition occurred - it might be evidence for the ‘resource concentration hypothesis’ presented by Pan *et al.* (2015). This posits that the diversity of plants in a litter mixture decelerates decomposition of litter because decomposers of each species suffer from a reduced availability of their preferred food resource. Because this was not observed in the large mesh size litter bags, it implies the role of larger soil invertebrates regulating and promoting the microbial decomposition (García-Palacios *et al.*, 2013; Schädler and Brandl, 2005). After 6 months decomposition, we observed that the C:N ratio of the straw and the mixture diminished while the C:N ratio of the ryegrass did not change (Table 5.2). We hypothesised that the chemical process of decomposition took part in the transformation of high C:N materials, such as straw, homogenising the composition of the soil organic matter until it tended towards an equilibrium, similar to the average C:N ratio 11.5 found in cambisol soils (Batjes, 1996), from which the C:N ratio of ryegrass would be closer explaining the small difference between the C:N ratio measured at T0 and at T6. Unlike for the decomposition rate, there was a greater C:N ratio in the large mesh size bags than in the small ones, evidence that most of the chemical decomposition was controlled by the microbial compartment, while the physical breaking down of the litter was as a result of the action of larger organisms (Bradford *et al.*, 2002).

5.4.4. General conclusions

We have shown that prevailing soil conditions at the edge of arable fields affect major soil processes such as decomposition. Soil porosity is particularly affected in this area due to heavy machinery traffic, and inputs (fertilizers, crops residues) are less homogenously distributed here than in the middle of the field. The uneven management and the increased disturbance at the edge of the field are probably causal factors of the observed lower crop yields in this area. For instance, Sparkes *et al.* (1998) recorded 3-19% less yield at the edge than in the middle of cereal fields and Wilcox *et al.* (2000) reported high variability in yield in the same zone of winter wheat fields. This results in a “sensitive zone” between the margin and the crop where soil biological and chemical dynamics are reduced if not appropriately managed. However, this study also revealed that there is potential to mitigate the effects of compaction in this sensitive zone. We have shown that the quality of organic amendments can partially mitigate the lower decomposition rates in the compacted zone, yet the inclusion of larger soil organisms helped to support litter decomposition in this specific zone. As stated by Baveye *et al.* (2016), both the characteristics of the habitat and the structure of the soil fauna community living there are of importance to sustain soil ecosystems. The presence of low C:N ratio crop residues, such as grass cover or cover crops, would sustain an adequate community of soil invertebrates that could carry decomposition of main crop residues and support soil structure in field area subjected to compaction.

We underline the important role of soil dwelling invertebrates in the decomposition process. In the current United Kingdom subsidy schemes, farmers are paid to manage crop margins to enhance botanical diversity, thereby supporting farmland birds and pollinators (Dept. for Environment, Food & Rural Affairs, 2014; Hatt *et al.*, 2017; Kovács-Hostyánszki *et al.*, 2017; Mansion-Vaquié *et al.*, 2017). These schemes also tend to benefit soil functions supported by the belowground diversity (Frazão *et al.*, 2017; Roarty and Schmidt, 2013; Smith *et al.*, 2009), but the resulting compacted zone, created by machine turning in the tramlines of the margin-crop interface (as operations are not allowed on the margins), impairs the ability of soil to function (Arvidsson and Håkansson, 2014; Beylich *et al.*, 2010; Hamza and Anderson, 2005). The ban on driving on the field margin exacerbates this. One option would be to increase the width of the margin to allow turning on this additional area. Grasslands are more resistant to compaction (Matthews *et al.*, 2010) and we believe that such a system would minimise the “sensitive zone” and maintain soil processes such as decomposition despite the high pressures and disturbances applied on soil in this specific zone.

This study highlights that the current regulations for the use of grass margins could be modified to optimise the ecosystem services they provide. We propose that adapting the rules regarding grass margins could result in a combined benefit for growers and ecosystem services. For instance, extending the field margin over the compacted tramline and allowing farmers to drive and turn in this extra-margin could result in improvement of soil structure, increase of above and belowground biodiversity, enhancement of ecosystem services, and reduction of the costs resulting from farming this non-profitable part of the field, thereby contributing to achieve more sustainable food production systems.

CHAPTER 6

DOES HISTORICAL LEGACY OF SOIL MANAGEMENT AFFECT SOIL FAUNAL COMMUNITIES IN ARABLE FIELDS? A CASE STUDY FROM AN ANCIENT WARPED FIELD IN YORKSHIRE (UNITED KINGDOM)

6.1. Introduction

Agriculture has clearly-demonstrated effects on ecosystem functions and dynamics (Stoate *et al.*, 2001; Tsiafouli *et al.*, 2015). Field management practices, such as fertilisation, tillage regimes or irrigation, are all contributing factors to changes in soil biodiversity (Tsiafouli *et al.*, 2015) and the functions they perform (Bardgett and van der Putten, 2014). Cuddington (2011) defined these effects, also called legacy effects, as ‘the long-lasting impacts of a species on the abiotic and biotic features of an ecosystem’. Perring *et al.* (2016) define legacies as not only influences of land-use history on a system at a given moment, but as a “trajectory of change” leading the system dynamics. In the case of agriculture, these definitions could be extended to the long-term consequences of field management on current abiotic and biotic soil features and dynamics. Many studies have reported the effects of previous land management on soil over a medium (seasons to decades) timescale (e.g. Crotty *et al.*, 2016; de Vries *et al.*, 2012; Liiri *et al.*, 2012), but very few have considered a longer timescale. As a necessity to interpret current ecosystem properties, Foster (2003) emphasised the importance of recognising impacts of historical land uses on those ecosystems. Soils, at the interface of terrestrial ecosystems, are consequently accumulating all ‘memories’ of ancient practices (Janzen, 2016), which can be reflected for centuries on the soil properties and dynamics, with implications for current land-use (Cuddington, 2011; Foster *et al.*, 2003). Examples of changes in soil physical and chemical properties arising from land-use that happened centuries ago, such as a settlement, pastoralism or irrigation practices, are often reflected at the vegetation level (Dambrine E. *et al.*, 2007; Dupouey J. L. *et al.*, 2002; Fisher *et al.*, 1996). Aboveground-belowground relationships (Bardgett and Wardle, 2010), as well as dynamics of soil communities over time and space, are well studied and understood (Bardgett and van der Putten, 2014). However, little attention has been given to long-term historical effects of soil use on belowground biodiversity. Capturing the heterogeneity of the soil fauna is challenging, as changes occur at multiple scales, from the soil pore, to the plant, to field or landscapes. Some of this spatial heterogeneity can be explained by alterations of soil organic matter, soil water or nutrient availability (Bardgett and van der Putten, 2014), but the implications of historical managements in driving changes of these physical and chemical features and its consequences for soil biodiversity are often overlooked.

Concurrently with a study on impacts of field margins on the community structure of soil invertebrates in arable fields (Chapter 4), we hypothesised that historical land management could interact with current farm activities to the extent where the distribution of soil invertebrates observed may be disconnected from the recent farm operations and result from a long-term legacy effect beyond the life time of the farm. The interference of pervious managements with current physical, chemical and biological soil process raises two fundamental challenges: understanding the interaction of all drivers of changes (present and past) to maximise the efficiency of current practices; and apprehending the impacts these current practices will have on future landscape uses.

6.2. Materials and Methods

6.2.1. Experimental Site

Rawcliffe Bridge Farm is located in the county of Yorkshire in the North of England (53° 40’ 0.37” N; 0° 55’ 46.84” W). The land at Rawcliffe Bridge is part of a distinctive “man-made” landscape. Before the 19th century, the area was mainly of peatland, still visible nowadays at the ‘Moorends’ area at the south boundary of Rawcliffe Bridge (Figure 6.1). The land was considered to be cost-effective to farm, but with a low yield potential, and in 1821 a so-called ‘warping’ method was used to improve the yielding capacities of the land (Creyke, 1845; Creyke *et al.*, 1824). This entailed the installation of drains and canals to manage natural tides of the river Ouse, and bringing a lime-rich deposit by intentional flooding with the aim to enrich the land. After the fields had been warped, trenches (‘grips’) were dug 5 to 10 m apart to assist drying out (Creyke, 1845; Creyke *et al.*, 1824). Before the warping of the land, it was mainly unfarmed peatland; but after gripping the ground, oats, rye-grass and clovers were sown and maintained for 2 years to build up organic matter and to enable use as pasture. The rotation then involved wheat and potato crops (Creyke, 1845).

The current crop rotation of the field sampled at the Rawcliffe Bridge farm included oilseed rape (*Brassica napus* L.) in autumn 2015 and spring 2016, winter wheat (*Triticum aestivum* L.) in autumn 2016 and spring 2017, oilseed rape was sown in autumn 2017 followed by spring beans (*Phaseolus vulgaris* L.) in 2018. The field was under a no-till strategy since at least 2008 (James Hinchliffe, personal communication). Mineral fertilisation and chemical inputs were applied following the UK standard management scheme for farmers (Agriculture and Horticulture Development Board, 2017) and crop residues were left in a systematic way on the ground as an organic soil amendment. Field margins of 6 m wide had been set up around the different fields to promote biodiversity in the agricultural landscape (Department for Environment, Food & Rural Affairs, 2014).

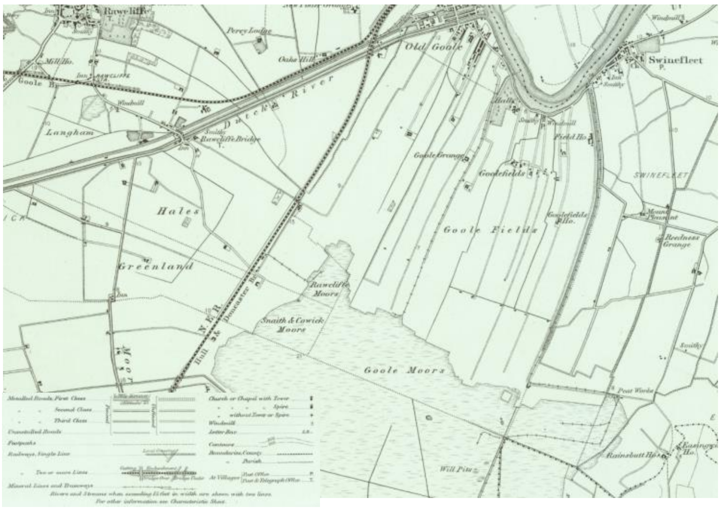


Figure 6.1. Ordnance survey One-Inch to the mile map of the Rawcliffe Bridge area, published in 1895. Drainage facilities from the river Ouse and the Dutch canal are shown, as well as Moorends (Smith and Corwick Moors, Rawcliffe moors and Goole Moors).

6.2.2. Measurement of soil characteristics and soil fauna survey

Soil samples were taken from two adjacent field margins and their related crop areas within the same field (Figure 6.2) in autumn 2015 and spring 2016 on the side of the field parallel to the tramline; and in spring 2017 and autumn 2017 on the other side, where tramlines formed an acute angle with the margin. In order to simplify the semantic, we called this margin ‘perpendicular’. Each field sampling area was 42 m long and 30 m wide; and included a 6 x 30 m grass margin strip. The field sampling area was divided into 5 transects, starting in the margin and extending 36 m into the crop. This was divided into 6 sections in the crop. A total of 40 soil samples (5 in the margin and 6 x 5 in the crop) were taken per sampling area (Figure 6.2b).

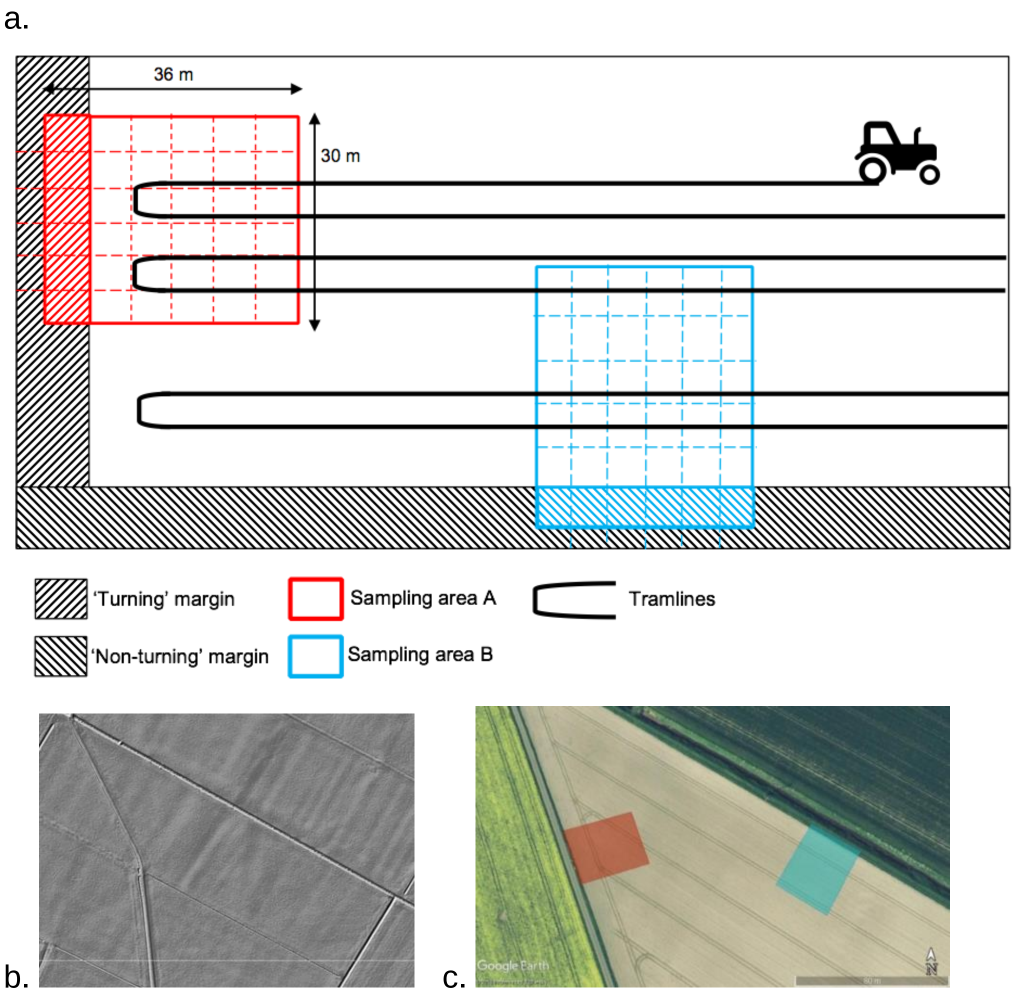


Figure 6.2. (a) Diagrammatic representation of the sampling areas at the Hinchliffe and Sons Rawcliffe Bridge Farm, Yorkshire UK; (margin perpendicular to the tramline in red =A A; margin parallel to the tramline in blue = Area B) with regard to orientation of field margins in relation to the of tramlines (field traffic). Tramlines are shown by plain bold lines and field margin areas by diagonal strips. (b) 'Google-Earth' Aerial and (c) high-resolution LIDAR (light detection and ranging) images of the sampled field. In the aerial picture (b), sampled areas are shown by squares coloured blue (field margin parallel to the tramlines) and red (field margin perpendicular to the tramlines). The LIDAR aerial view (c) shows soil topography.

Soil cores were collected using a root corer (8 cm diameter x 10 cm depth, Eijelkamp, The Netherlands) and stored in a plastic bag at 4°C until processed. One half of each core, covering the 0-10 cm depth of the core, was weighed before being dried at 105°C until constant weight and used to measured soil properties. Bulk density (BD) and gravimetric dry soil moisture content were determined following Laryea *et al.* (1997). pH was measured at 1:2.5 soil:water ratio using a pH meter (Jenway Model 3320, Jenway, Staffordshire, United Kingdom).

Soil-active/dwelling *Collembola* (springtails) and *Acari* (mites) were collected from the second half of the soil cores. Each half was kept intact and placed upside down in a 5 mm mesh Tullgren funnel unit (Burkard Manufacturing Co. Ltd, Rickmansworth, UK) for 12 days. The invertebrates extracted were preserved in 70% industrial methylated spirit (IMS) at 4°C before being counted and classified using a stereo-light binocular microscope (Olympus SZX10, Olympus, Essex, United Kingdom). *Collembola* were identified at family level and *Acari* at sub-order level using the key to the "*Collembola* (springtails) of Britain and Ireland" by Hopkin and the "manual of Acarology" by Krantz and Walter (2009).

6.2.3. Data analyses

A non-metric multidimensional scaling (NMDS) was first used to ordinate the spatial and biological data based on dissimilarity matrices (Paavola *et al.*, 2006). We used only two dimensions of the NMDS to correspond with the two dimensions of the spatial factor (distance to the margin and transect). For each sampling area (with field margins perpendicular or parallel to the tramlines) at each season (autumn and spring), we used Procrustes analyses to study the concordance between the spatial conformation and the biological data (*Acari*, *Collembola* and whole community). The method involves fitting one ordination to another by superimposition, minimising the residual sum of squares (m^2) between the two (Lisboa *et al.*, 2014; Peres-Neto and Jackson, 2001), the lower the m^2 value, the stronger the concordance between the two ordinations. To guarantee the validity of the test, 999 permutations were used for pairwise comparison between the spatial (i.e. location in the field) and biotic (i.e. community structure) ordination (PROTEST analyses). NDMS was conducted using the Ecodist package (Goslee and Urban, 2007), while Procrustes analyses were performed with the Vegan package (Oksanen *et al.*, 2013), both implemented in R software 3.1.2

As data used were the same as Rawcliffe Bridge data from Chapter 4, we used multiple-way analysis of variance (ANOVA) to test the effect of the margin orientation (‘perpendicular’ *vs.* ‘parallel’), the distance to the margin, the sampling season (autumn *vs.* spring) and their interactions on soil properties (BD, WFPS, and pH). The ten transects in each field (five per side) were considered sufficiently far-enough apart to be different and treated as independent and were used as replicates to assess differences between the two farms. We assessed normality of the data with model checking plots (normal probability and

QQ plots), to meet the assumption of normality. All ANOVA were done using R software 3.1.2.

6.3. Results

6.3.1. Soil characteristics

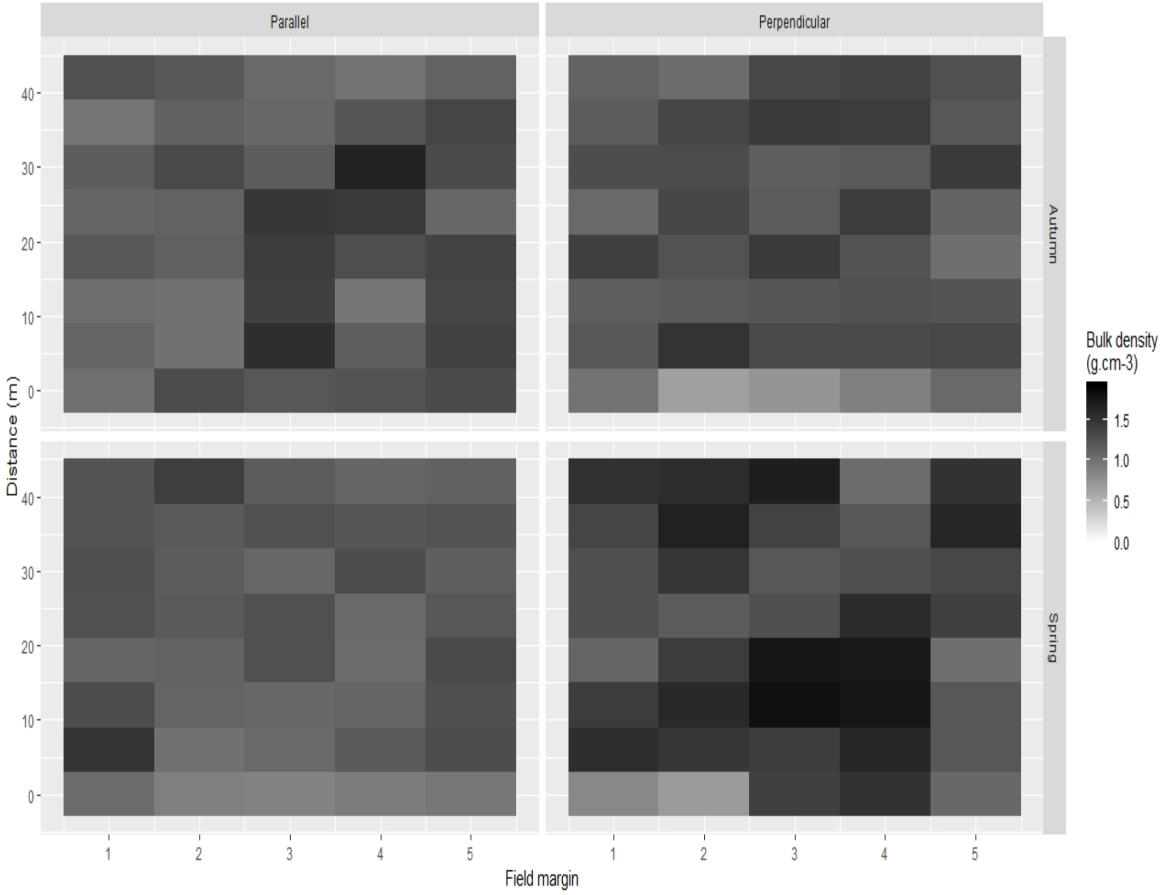
Bulk density in the perpendicular area was greater compared to the parallel (see Chapter 4, Table 4.2). None of the parameter studied had an effect on bulk density (Table 6.1).

Only pH was significantly affected by the three field parameters (margin orientation, distance to the margin and sampling season; Table 6.1). Soil pH were greater in the parallel sampling area and decrease at further distance from the margin in the perpendicular sampling area (Figure 6.3). Water filled porosity was on average lower in the margin than in the adjacent crop (see Chapter 4, Table 4.2), although distance was not significant. The sampling season and the interaction season / margin orientation significantly influenced water filled porosity (Table 6.1). None of the parameter studied had an effect on bulk density (Table 6.1).

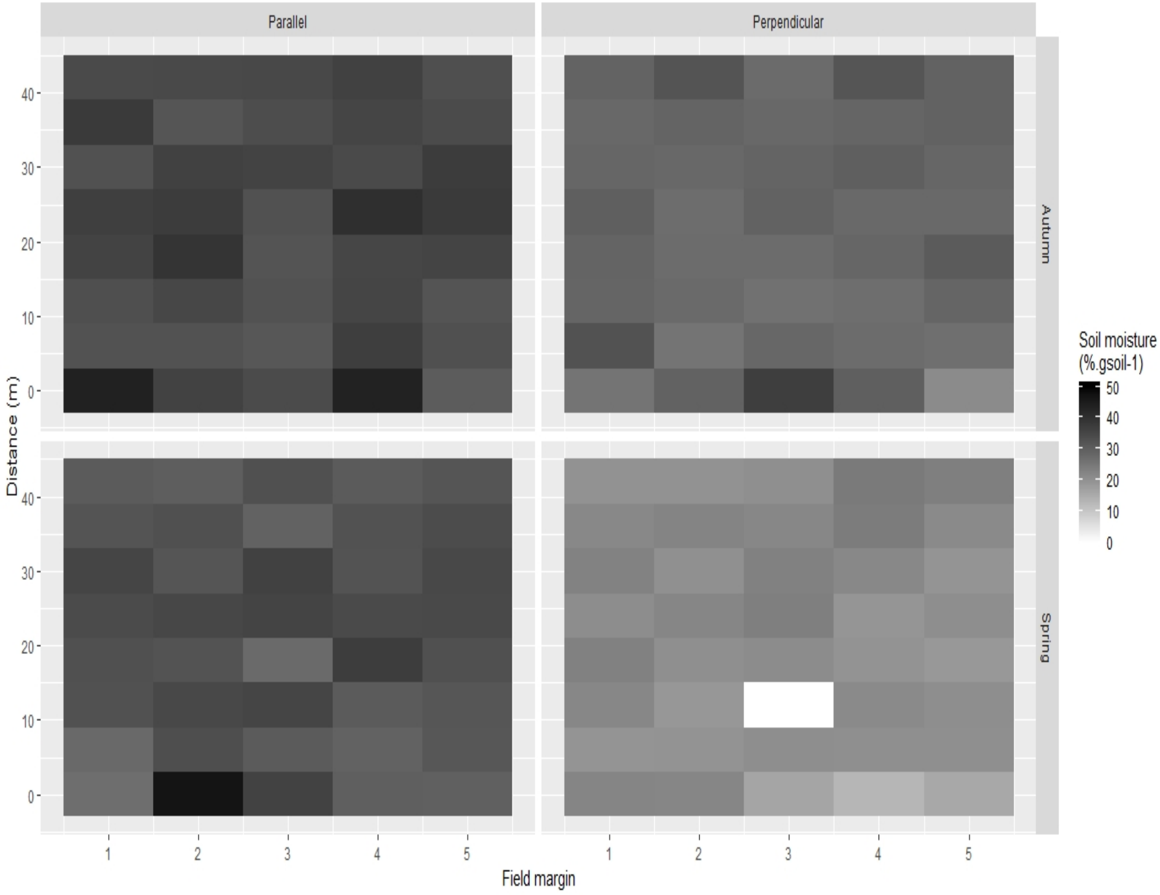
Table 6.1. Effects from analysis of variance of the margin orientation, either parallel or perpendicular to the tramlines (Orientation), the distance to the field margin (Distance) and the sampling season (Season) at Rawcliffe Bridge and their interactions on soil characteristics. Significant values (p < 0.05) are show in bold.

	Bulk density		Water filled pore space		pH		
	F	p	*F*	p	*F*	p	Df
TREATMENT							
Orientation	1.42	0.236	0.11	0.746	259	**<0.001**	1, 112
Distance	1.51	0.222	1.31	0.256	36.4	**<0.001**	1, 112
Orientation: Distance	0.49	0.505	0.78	0.378	15.1	**<0.001**	1, 112
Season	0.02	0.902	8.01	**0.006**	93.5	**<0.001**	1, 112
Orientation: Season	4.52	**0.036**	102	**<0.001**	0.24	0.627	1, 112
Season: Distance	1.50	0.223	0.16	0.694	0.10	0.753	1, 112
Orientation: Season: Distance	3.21	0.076	2.30	0.132	0.13	0.722	1, 112

a.


Parallel
Perpendicular
Autumn
Spring
Distance (m)
0
10
20
30
40
Field margin
1
2
3
4
5
Bulk density (g.cm-3)
0.0
0.5
1.0
1.5

b.


Parallel
Perpendicular
Autumn
Spring
Distance (m)
0
10
20
30
40
Field margin
1
2
3
4
5
Soil moisture
(%.gsoil-1)
50
40
30
20
10
0

c.

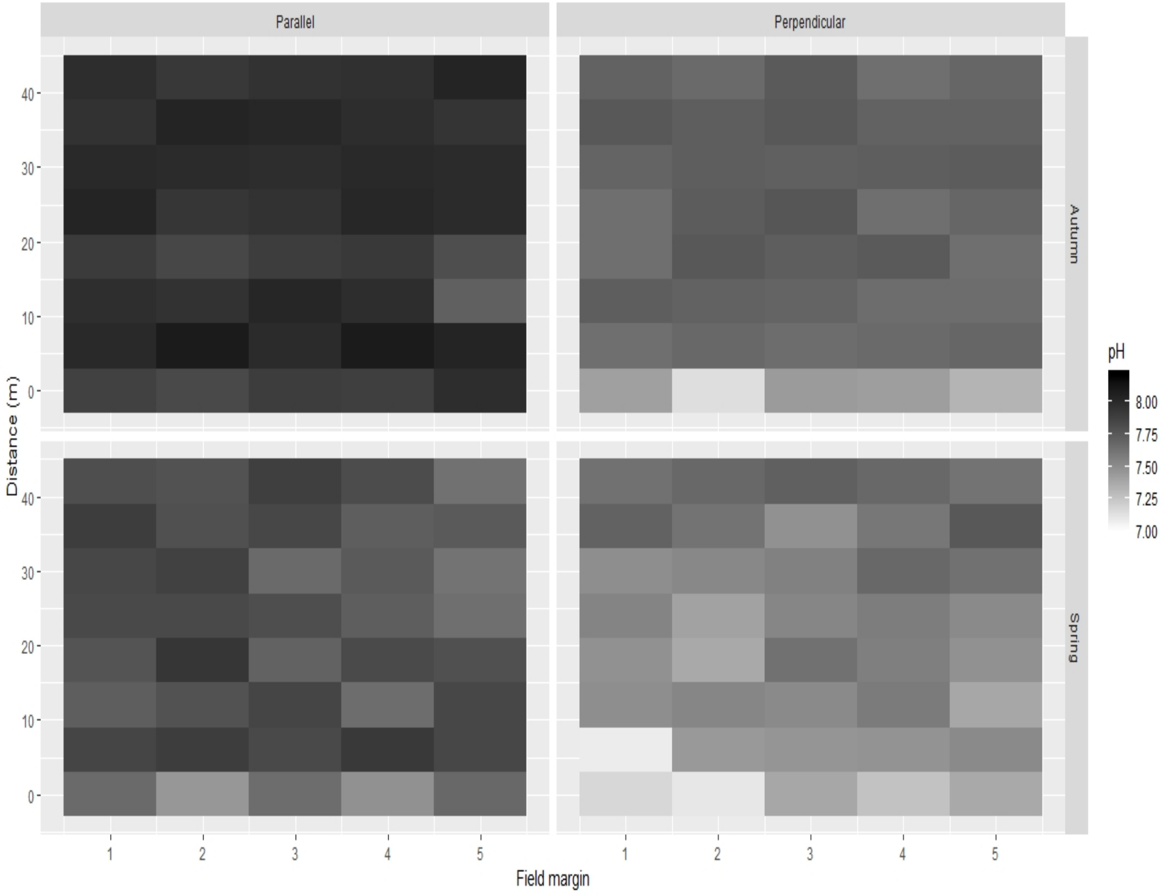


Figure 6.3. Spatial representation of the soil characteristics in Coopers field: (a) bulk density (BD), (b) soil moisture and (c) pH. Each square represents the average value per square metre in each 6 x 6 m sample point along each transect. Distance 0 represents the margin, and distances 6, 12, 18, 24, 30, 36, 42 the sample points in the crop. Values in the perpendicular area are shown in the left column and densities in the parallel area in the right column; while values in Autumn are shown in top row and densities in spring in bottom row. The darker the greyscale, the greater the value.

6.3.2. Biological data

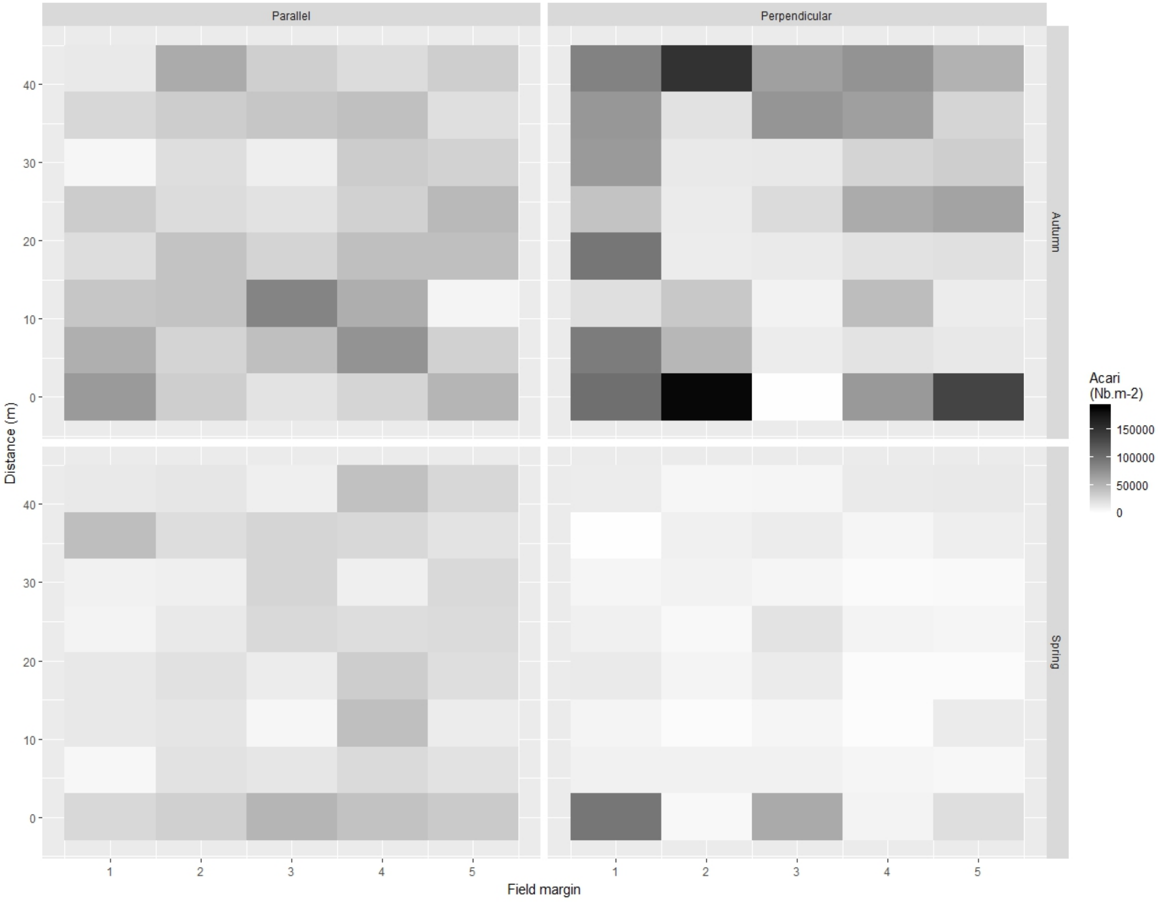
The permutation test (PROTEST analyses) indicated/identified significant concordances between the matrix of the *Acari* community and the spatial arrangement of the parallel area in autumn (P=0.016, 999 permutations), and between the whole community matrix fitting the spatial arrangement of the perpendicular area in autumn (P=0.006, 999 permutations).There was a weaker trend of concordance between the whole community matrix and the spatial arrangement of the parallel area in both seasons (Table 6.1). In addition, we observed a trend between the *Acari* community matrix and the perpendicular in autumn and the parallel area in spring (Table 6.1). In contrast, the *Collembola* community matrix did not fit the spatial organisation of either area (Table 6.1). From the Procrustes analyses, we could discern a differentiation between the concordance of *Acari* and *Collembola* communities to the spatial factor. While the variability of the community of *Acari* seemed to be explained by the spatial factor, particularly in the autumn season; the *Collembola* community did not show a similar pattern of spatial organisation (Figure 6.3). The spatial organisation of the community of *Acari* appeared especially stronger in the parallel area, where field margin was parallel to the tramline and field activities (tractors turning) were less likely to disturb the effects of natural explanatory factors.

Table 6.2. Results of the Procrustes analyses on the spatial (perpendicular and parallel area) and biological (Acari, Collembola communities and all mesofauna communities) non-metric multidimensional scaling (NMDS) ordinations; m² represents the Procrustes sum of squares and P the significance of the test calculated from 999 permutations (significant results are in bold). Number of samples per sampling area and season n=40, with 5 taxa of Acari, 4 taxa of Collembola and a total of 9 taxa for the whole community.

	Invertebrate community					
	Acari		*Collembola*		All mesofauna	
	m²	P	*m²*	P	*m²*	P
Perpendicular area						
Autumn	0.93	0.066	0.99	0.789	0.87	**0.006**
Spring	0.97	0.357	0.98	0.468	0.95	0.118
Parallel area						
Autumn	0.88	**0.016**	0.98	0.560	0.93	0.076
Spring	0.93	0.067	0.96	0.220	0.93	0.073

The initial purpose of the study was to assess the hypothesis that if populations of soil invertebrates would be more abundant in the field margins and numbers would be decreasing with distance to it, or that field activities will interfere with the margin and the distribution of invertebrates will be correlated to the orientation of the field traffic. After the sampling of the margin parallel to the tramline and its related field area, the data visualisation of soil *Acari* and *Collembola* populations showed a distribution pattern which could not be matched to any of the recent farm operations (Figure 6.3). Aerial images confirmed the current field management and field traffic (Figure 6.2.b) but did not reveal any aspect of the soil biological patterns observed.

a.



b.

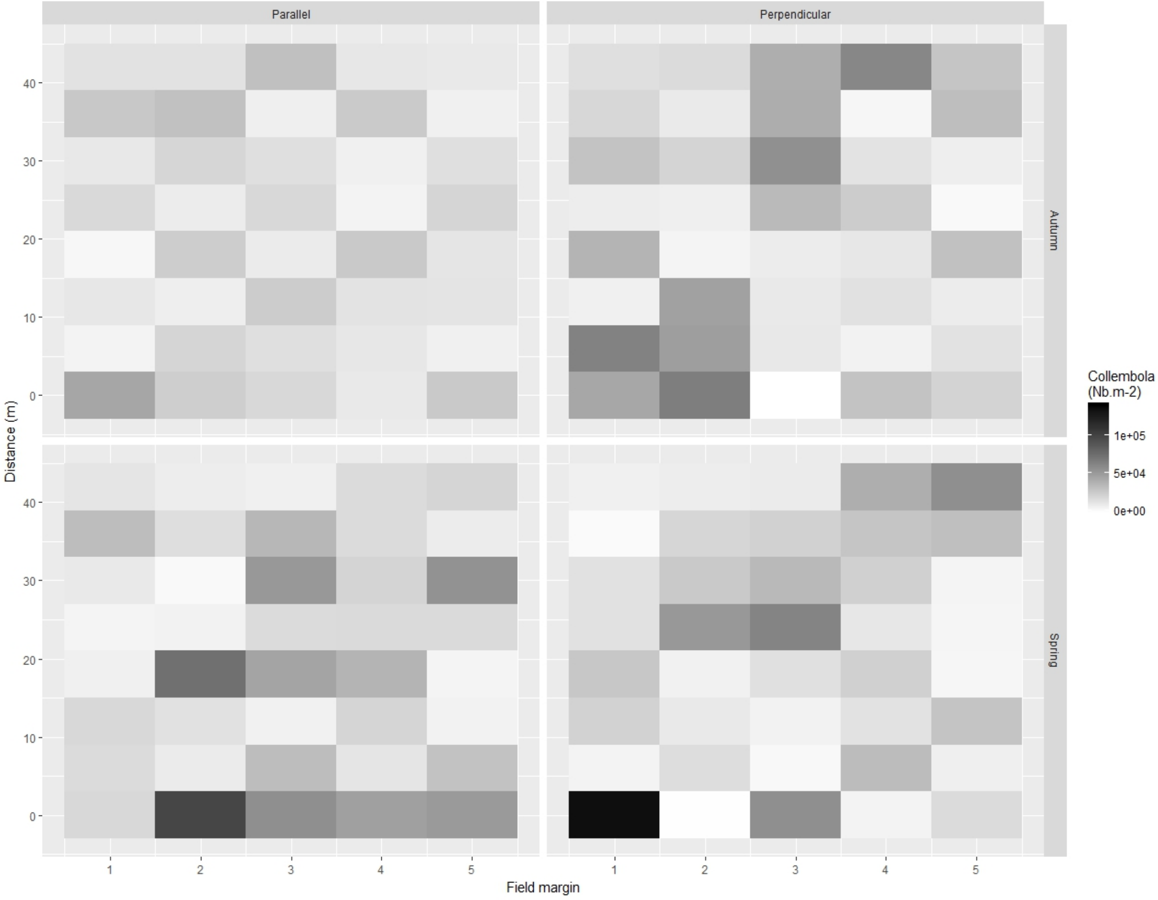


Figure 6.4. Graphical representation of the spatial distribution of populations of (a) Acari and (b) Collembola. Each square represents the average density of individuals per square metre in each 6 x 6 m sample point along each transect. Distance 0 represents the margin, and distances 6, 12, 18, 24, 30, 36, 42 the sample points in the crop. Densities in the perpendicular area are shown in the left column and densities in the parallel area in the right column; while densities in Autumn are shown in top row and densities in spring in bottom row. The darker the greyscale, the more abundant the population.

6.4. Discussion

In Chapter 4, the main hypothesis was that abundance of mesofauna would gradually decreased from the margin at increasing distance in the crop and that dissimilarities in community structure would get greater with distance; or if a difference of the soil mesofauna distribution was observed between the perpendicular area and the parallel area, any relationship to the spatial distribution of the invertebrate populations was unclear.

In chapter 4, Mantel tests failed to explain relationship between the combination of all soil characteristics and the spatial pattern of *Acari* and *Collembola* communities (Table 4.5). Although, in this chapter soil characteristics, pH apart, were not significantly explained by any of the field parameters (Orientation of the field margin, distance to the margin and sampling season). More data would be required to explain the spatial allocation of soil characteristics regarding the field parameters, and to link this to the distribution of soil fauna.

The diagonal distribution pattern of soil invertebrates could not be justified by either the field layout and management, or by the soil characteristics. Recognising the strong legacy of ancient landscape managements on soil ecology (Dupouey *et al.*, 2002; Fisher *et al.*, 1996), we hypothesised that the observed pattern could result from long-term legacy effects before the life time of the current farm, such as heritage of formal anthropogenic activities, historical floods or deeper soil features. High-resolution imagery of the area revealed hidden soil topographic features (Figure 6.2.c), which we assume to be related to the ancient flooding and drainage management of the land (Creyke, 1845; Creyke *et al.*, 1824). The grips used to drain the water out of the field would have potentially changed the soil characteristics at a small scale (Fisher *et al.*, 1996) and thus may have affected the current distribution of soil invertebrates. The resolution of the soil sampling in our study (a 6-m scale) enabled us to capture a potential legacy effect from the grips as they were dug 5 to 10 m apart.

Janzen (2016) wrote “*The soil remembers*”, elaborating on how changes and events affect soils on a long-term time scale and what lessons we could draw from it. He emphasised the importance of soil legacy in managed ecosystems, where present processes result from ancient anthropogenic activities; questioning us about the type of footprint we would like contemporary agriculture to leave for future generations. Here we captured a snapshot of effects of land fertilisation practices that happened 200 years ago on soil faunal distributions. Further investigations will be required to support our findings by showing a significant correlation between the distribution of current soil invertebrate populations to historical drains. An appropriate sampling design would be needed to address the spatial context of the study, and a map of the water levels at the field scale would be required to evaluate the impact of old drains on soil water properties (Fisher *et al.*, 1996).

CHAPTER 7

SYNTHESIS

7.1. Introductory restatement of PhD research project

Our understanding of soil functions, including organic matter decomposition and nutrient cycling is closely linked to our comprehension of soil community dynamics. The soil mesofauna (mainly mites [Acari] and springtails [Collembola]) underpin a wide range of the functional diversity found in the soil food web. Upholding these functions is essential to sustainable food production and the study of the soil food web provides insight to enable optimisation of ecosystem services delivered by agricultural soils.

This PhD project addressed this issue by looking at the abundance of populations and community structure of soil mesofauna in the context of arable fields. We aimed to understand whether installed field margins changed the structure and population size of the associated soil invertebrate communities; and we investigated if such effects extended into the field. To test our hypotheses, we used the facilities of the two BASF demonstration sites at Rawcliffe Bridge, Goole and The Grange, Northamptonshire, where field margins had been established at different times around arable fields. Over four seasons (autumn 2015, spring 2016, spring 2017, autumn 2017), we sampled, counted and identified soil mesofauna organisms in various field margins of different ages, with different orientations regarding the field traffic, and their associated main-crop areas.

7.2. General discussion

7.2.1. Impacts of field management practices on abundances of soil fauna and structure of communities

7.2.1.1. Effects of field margins and time since establishment of the margin

A study [Chapter 3] was conducted to test the impact of time since establishment of sown margins around arable fields upon mesofaunal communities. Dissimilarities in community structure and population abundances were found between the field margins and the crops. We hypothesised that the lower abundance of Acari and Collembola observed in the crops, in comparison to their related field margin, was due to the regular soil disturbance caused by field activities, such as tillage practice, harvest, machinery driveway: populations of these fauna in the crop would have to re-establish after every disturbance, while in the margins an essentially intact ecological succession could continue. The heterogenous distribution of abundances and the different community structures in the cropped areas reflected the degree of disturbance in the field and the abilities of certain type of soil invertebrates to adapt and recolonise: for example, at the margin:crop interface where there are tramlines, abundances were particularly low; while further into the field in less-disturbed areas, populations increased. Mechanistic factors, such as the degree of compaction or the quality and quantity of crop residues, regulating mesofaunal populations in the cropped areas should be further tested in more controlled environments, such as meso- or microcosms. Abundance and dynamics of the soil invertebrate community were also driven by the time since establishment of the margin, with numerous, larger organisms and specialist taxa found in the older margins. From an ecological perspective, the change in community structure over time was expected, as ecological succession of the grass margin aboveground happened, the community of soil invertebrates, much affected by the vegetation, followed a similar trend: specialist and competitor species (K strategists) overtaking on opportunistic species (R strategists) as the habitat changed toward a more stable state.

7.2.1.2. Impacts of field traffic regarding the margin orientation

The second experiment [Chapter 4] focused on impacts of field operations and farm practices on the soil mesofauna, in relation with the orientation of the margins. In both farms, the distribution of invertebrates in the field depended on the orientation of the margin and the taxa studied. Generally, in relation to abundances of invertebrates found in the perpendicular areas, the lowest abundances were found at a distance corresponding to the tramline location, before increasing at further distance into the crop (Section 7.2.1.1); while in the parallel areas, abundances decreased more gradually from the margin into the crop. Change in abundances driven by tramlines and margin orientation might be explained by an interference in dispersal mechanisms and abilities of the soil mesofauna and disturbance caused by field activities, such as wheeling. One can hypothesise that horizontal active migration of soil invertebrates would be affected by the topology of the soil surface for epigeic (or semi-epigeic) species, or the connectiveness of the pore network for endogeic species, while colonisation might result from the aptitude of populations to persist in a new environment. Indeed, regarding the morphology and size of the invertebrates, the topology of the soil surface architecture resulting from tillage or residues will affect migration paths and distances involved, contingent on the size of the organisms and their mode of motility. In the farm under a no-till strategy and a complex crop rotation, effects of margins and tramlines orientation was more similar. Dispersion might still be limited but the gathering of favourable environmental conditions (e.g. food resources, habitat structure) would support population establishment. The study pointed up the complexity of undertaking appropriate field managements to optimise soil ecosystem services. The heterogenous responses of the soil mesofauna demonstrated that mechanistic causes of changes in agricultural soils must be understood before being considered to support decisions regarding agri-environmental schemes. To elaborate environmental policies with the aim of managing the soil biological compartment, it would first need to design biodiversity indices; which must be easy to measure, reflect on changes caused by field management (such as tillage, fertilisation or crop residues) and ubiquitous to use in various agricultural contexts (Griffiths et al., 2016).

7.2.1.3. Implications of historical land management on current populations of soil fauna

In the context of the sampling carried out at Rawcliffe Bridge farm [Chapter 6], the visualisation of invertebrate data revealed an unexpected pattern that could not be explained by current field operations. However, we considered that historical irrigation and drainage practices could have potentially affected the community of soil mesofauna and interact with present environmental and agricultural factors. The data were indicative rather than conclusive, and only showed a trend that would need to be verified. Further investigations should aim to significantly correlate the distribution of soil invertebrates to historical drains, utilising an appropriate sampling design would to address the spatial context of the study and a map of the water levels at the field scale to evaluate the impact of old drains on soil water properties. In a pot experiment, Liiri et al. (2012) found that increasing land-use intensity (grass vs. wheat) impaired the functions of the soil fauna in the carbon cycling even after a short time of soil rehabilitation. Future study could usefully question the long-term consequences of current agricultural practices on soil fauna and associated ecosystem services. Would current intensive land management still be reflected in reduced population size and simplified community structure, even though environmental policies are moving towards more sustainable soil managements in agricultural contexts? This raises questions about the time of persistence soil management legacy effects.

7.2.2. Relationships between field management, soil fauna and soil functions

We observed that field traffic, because of soil compaction, and the distribution of crop residues, could be major factors driving the abundance and composition of population of soil mesofauna invertebrates. The third experiment aimed to understand the implications of field operation impacts on populations of soil invertebrates by looking at dynamics of litter decomposition in the field margin, the crop and the compacted tramline. Field traffic and limited input of organic materials at the interface margin / crop deteriorated soil structure, which in turn slowed down litter decomposition in all treatments. Despite poor soil conditions, a low C:N litter and the intervention of soil mesofauna promoted litter decomposition in the compacted tramline. The uneven management and the increased disturbance at the edge of the field were probably causal factors of the observed lower crop yields in what was called a “sensitive zone”. The interface margin/crop was qualified as such to demonstrate of the poor soil structure, the reduced populations of invertebrates and the lessened decomposition rates measured in this specific area. However, this study also revealed that there is potential to mitigate the impacts of compaction on litter decomposition in this sensitive zone. The quality of organic inputs can partially mitigate the lower decomposition rates, while the inclusion of larger soil organisms is a major factor to support litter decomposition in this specific zone. Limited soil ecosystem services in damaged or sensitive field areas could be optimised by integrating the living compartment of soil into field management plans: organic inputs that would enable the establishment, stabilisation and perpetuation of soil invertebrate communities, which in turn will favour soil processes, such as decomposition. Such practical implications are considered below.

7.3. Limitation of the study, practical implications and outcomes

7.3.1. Limited effects of the field margin on soil biodiversity in the crop, implications for soil mesofauna

We hypothesised that the soil mesofaunal community in crops would change in response to the presence, the time since establishment and the orientation of the field margin; the older the margin and the greater distance into the crop, the larger the difference in community size and structure; implicitly implying dispersal mechanisms between the field margin and the crops. In Chapter 3 and 4 we did not observe “a dilution” of community structure, nor of abundances, with respect to mesofaunal populations in the margin and into the field. Although, in Chapter 4 we disentangled the effect of the field margin on soil communities from the effect of other field activities, and we observed that there was a possibility that the disturbance caused by field activities, such as trafficking (tramlines), could interfere with the impact of the field margin and create a contrasting community in the crop area located nearby the margin or separated by the tramline. It is commonly accepted that active dispersion of soil micro-arthropods is slow and occurs mostly at small spatial scales, from cm-m per day depending on the taxa involved (Ettama and Wardle, 2002). Ojala and Huhta (2001) estimated that populations of micro-arthropods could move ca. 1 m y^{-1} (i.e. 30 m in 30 y), although they specified that edaphic collembolans were less capable of dispersion than acari. Lehmitz et al. (2012) found that active dispersion of Oribatid soil mites was an important factor of bare soil recolonization. However, in their study they revealed that aboveground dispersion was more important than belowground dispersion (Lehmitz et al., 2012). The physical constraint of the soil surface architecture in regard to the small size and the morphology of mesofaunal organisms, as well as the heterogenous supply of food resources (Ettema and Wardle, 2002), make active dispersion of soil mesofauna community limited at the field scale.

Ingimarsdóttir et al. (2012) studied the importance of environmental factors, mainly geospatial factors, constraining the dispersion of soil invertebrates from one isolated site to another, and showed that despite the importance of environmental barriers shaping community structure, dispersal mechanisms were still operating to homogenise the communities. At Rawcliffe Bridge farm, the field management strategy probably lessened the impact of the tramline in comparison to The Grange farm. The no till system and the complex crop rotation would create favourable conditions for dispersion and establishment, alleviating the consequences of disturbance caused by the tramline. It would be interesting to test the micro-topology of a no till vs. minimum tillage soil surface, see whether such practices make easier the active dispersion of soil invertebrate or not, or if it affects the dispersal capacities of soil organisms against different magnitudes of disturbance, like the presence of a tramline.

Many studies have emphasised the importance of environmental factors in survival of soil invertebrates populations (Coudrain *et al.*, 2016; Decaëns, 2010; Scharroba *et al.*, 2016). The combination of food resource (Crotty et al., 2014; Ferlian et al., 2015; Ponge, 2000) and disturbances (Coyle et al., 2017; Rousseau et al., 2018; Wardle, 1995) is directly driving the establishment or the collapse of important soil community. Therefore, effects of quantity, quality and type of organic amendments on establishment of populations of soil invertebrates, together with amplitude and frequencies of soil disturbances should also be evaluated to fully understand the mechanisms behind population establishment in specific field areas.

As developed, understanding factors of dispersion and colonisation from the margin into the crops, as instance by investigating the effects of agricultural practices on the active and passive dispersal abilities of soil invertebrates, would provide evidence for field margins to act as a biodiversity pool for soil invertebrates and provide a shelter from disturbance in the cropping areas.

7.3.2. Implication of body size and importance of functional redundancy for soil ecosystem processes

In Chapter 5, it was observed the important role of the soil fauna to maintain decomposition processes in comparison to microbial decomposition alone. It had been hypothesised that the change of habitat size caused by the soil compaction in the tramlines would negate the effect of the soil fauna; or in presence of a litter of low C:N ratio, such as ryegrass, the soil fauna maintained the decomposition functions. One explanation could be that the soil faunal community persisted despite strong habitat constraints in this particular area; which was corroborated by the observations made in Chapter 3 and 4. The populations of soil mesofauna found at the area of the margin:crop interface (where the tramlines are) were of smaller size-range than the populations in the margins. Besides the capacity of the smaller taxa of soil invertebrates to persist, compacted soils still have a lot of pores (Harris et al., 2003) that could provide an effective habitat to invertebrates; in addition, the mean bulk density of 1.25 mg m^{-3} measured in the tramline was probably not sufficiently high to provide significant physical constraints to mesofauna. In the latter case, the presence of a suitable food resources, such as ryegrass, would have been sufficient to allow the smaller invertebrates to maintain the decomposition process. Porre et al. (2016) explored the impacts of soil mesofauna on regulating nitrous oxide emissions by its action on soil structure; however, the role of the architecture of soil pore networks in regulating the size-range distribution of soil invertebrates is apparently unclear, and certainly warrants more study.

Furthermore, this questions the importance of functional redundancy occurring within the soil faunal community (Setälä et al., 2005). Functional redundancy implies that ecological functions can be delivered by more than one species, and that consequently the loss of one of the groups would not affect the function itself (Setälä et al., 2005). The soil food-web is characterised by a high degree of omnivory (Digel et al., 2014), in that soil organisms can switch their diet in response to the prevailing food supply (Murray et al., 2009) and one population can compensate for another in supporting soil functions. If this were true, then it could be argued that there is no need to manage the soil fauna communities in arable fields, as they could maintain a degree of functionality necessary to crop production. Many studies have addressed the question of the relationship between complex and connected soil food webs and the provision of ecosystem services (de Vries et al., 2013) and there would be a need to test if a more complex and less disturbed community at the interface margin:crop would ‘perform’ better than the reduced soil fauna community observed in Chapter 3 and 4.

7.3.3. Potential to overcome impact of field operation on soil biodiversity in the crop

In Chapter 3, we observed the importance of time in community dynamics of the soil mesofauna. Agricultural practices such as tillage or harvest ‘reset’ the system, after the disturbance only the presence of survivors and recolonisation from sheltered habitats around, such as the field margins, allow the successional process to restart.

Understanding mechanisms through which soil fauna disperse and recolonise the crop is therefore important to manage the field in the future and promote the establishment of soil faunal populations and favour the functions they deliver, such as litter decomposition or nutrient cycling (Brussaard, 2012). In Chapter 5, the type of crop residues, together with the presence of soil fauna, was shown to affect the decomposition rate in the compacted tramline to that almost similar than in the crop. Managing the quantity and quality of crop residues, or organic inputs in the field, could facilitate populations of soil fauna to recolonise disturbed areas, by recreating the minimal conditions required for those populations to carry out their functions. Nonetheless, there are very few studies looking at the direct impact of crop residues management on populations of soil fauna in arable fields (Sauvadet et al. 2017, 2016), and there is a need to fill this knowledge gap. Tillage practices and crop rotation may also be important factors to facilitate the dispersion of soil fauna communities from the margin into the field. As shown in Chapter 4, the community structure of soil invertebrates in the cropped area were more closely related to those in the field margin in the field under no-till practice and a complex crop rotation, than in the field with more conventional practices.

Despite different magnitudes of difference, all chapters have shown differences in abundance and community structure between the field margins and the cropped areas. There is potential to manage the biological component of soil by managing the field, but it could also be done by managing the field margin in order to more effectively connect the soil faunal community in the margin with that in the field. For example, one option would be to extend the margin from 6 m further inside the field and authorise farmers to drive in this enlarged area (Figure 1), thus managing the original margin for above-ground diversity. The presence of the grass, through the impact of roots and exudates, would reinforce the soil structure and minimise the impact of compaction (Matthews et al., 2010), and we can hypothesise that the lessened degree of disturbance would be sufficient to the soil fauna to disperse from the ‘real’ margin into crop and maintain their functions. The conversion of this cropped area would also limit the cost of farming as this area is exposed to an ‘edge effect’, resulting in poor crop yields (Sparkes et al., 1998a, 1998b) with higher per-hectare costs.

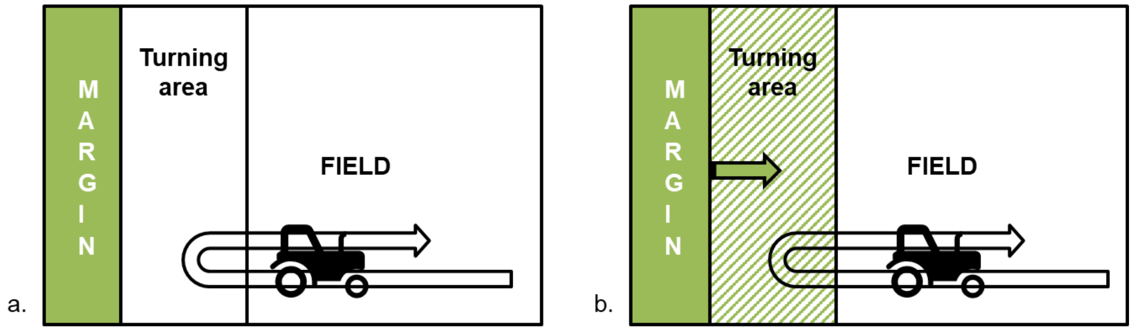


Figure 7.1. Schematic representation of changes in field margin management to facilitate dispersion of the soil fauna populations, cropped areas are in white and grassy field margins area in green, black arrows and tractor show field traffic. (a) represents current field management, where agricultural machinery is not allowed to enter the margin, which results in a 'sensitive zone' at the margin:crop interface; (b) concept for alternative margin management, where the green arrow represents an extension of the grass margin, on which agricultural machinery could drive.

7.3.3.1. Further prospects for agri-environmental schemes

Invertebrates provide soil ecosystem services that can be optimized by integrated field management. However, this research has indicated that there are apparently opportunities for improvement, via some potentially simple changes in agri-environmental policies. Future work should investigate in more detail the consequences of an extended margin on the soil community, major soil processes and the resulting ecosystem services, as well as on the economic viability for the farm enterprise. We showed that there is potential for soil biodiversity to spread out from the field margins, but the field operations, such as driving, that disturb the soil at the interface margin / crop makes it unlikely.

Many governmental schemes mainly recognise above ground biodiversity and aim to preserve it; yet they do not enhance soil fauna-based ecosystem services in the crop area. This PhD project highlighted that the current regulations for the use of grass margins could be modified to optimise the ecosystem services they provide as well as maintaining the financial sustainability of arable farming systems [Chapters 3 and 4]. It is proposed that adapting the rules regarding grass margins could result in a combined benefit for growers and ecosystem services. For instance, extending the field margin over the compacted tramline and allowing farmers to drive and turn in this extra-margin (Figure 7.1) could result in improvement of soil structure, increase of above and belowground biodiversity, enhancement of ecosystem services, and reduction of the costs resulting from farming this non-profitable part of the field, thereby contributing to achieve more sustainable food production systems. Other options could also be considered and the effects of different organic inputs to the crop (e.g. quality of the plant residues; manure; sewage) at the interface margin / crop should be tested. The “sensitive area” at the margin / crop interface could be improved by adding organic amendments that would facilitate the establishment of soil community and stimulate soil processes necessary to crop production, such as nutrient cycling or organic matter transformation. The Good Agricultural and Environmental Conditions (GAEC 4, 5 and 6), determined by the

European commission and applied at the national scale (Department for Environment, Food and Rural Affairs, 2014), set stewardship baselines requirements to preserve soils in agricultural contexts, among which keeping a minimum cover by returning crop residues to the ground. Physical and Chemical aspect of soil protection are well considered in these GAECs; whereas, the role of the biological compartment in soil preservation is not even mentioned; *de facto* reinforcing the need of more studies combining soil biodiversity and agricultural management to support agricultural policies.

Over the project we also emphasised the importance of time in regulating soil mesofauna communities [Chapter 4]. The presence of more specialised species, larger individuals, and more diverse functional and taxonomical community composition in the older margin, suggests that long-term undisturbed field margins help to build reservoirs of soil biodiversity and favour soil ecosystem function such as decomposition, or nutrient cycling in the adjacent arable crop (Bardgett and van der Putten, 2014; Brussaard, 2012; Brussaard et al., 2007a). The importance of time in management of soil is also discussed in Chapter 6. We noticed the potential impacts of historical soil managements on the present soil properties and community structure of soil mesofauna; implying consequences on the retribution of soil ecosystem services. This questioned the pertinence of short term agri-environmental plans, which do not enable to perceive soils at a long-time scale and prevent from managing soil properties and the functions they provide in the long term. Janzen (2016) said “The Soil

Remembers”, emphasising the importance of anticipating our impacts and preserving the soil resource for the future generations.

7.4. Conclusions

This project has ascertained that arable field margins are a consequential factor in regulating population of mesofaunal invertebrates in arable fields, and that their effects interact with field activities, such as tillage, driving pathways, crop rotation or crop residues management. The presence of field margins increases both the abundances of invertebrates populations and the complexity of community structure. Furthermore, it has been shown that the supporting effect of field margins on soil mesofauna communities has repercussions for soil processes, such as litter decomposition. Despite these findings, the impacts of field margins on soil mesofauna in the nearby crop areas depend strongly on other controlling factors in the fields.

The project has established facts about the composition of mesofaunal communities in field margins and their related crop areas; the precise mechanisms that could explain these observations remain unclear. Determining the mode of dispersion, the nature of the dynamics of soil mesofaunal populations and the causal factors behind these processes, is a necessary step to support the need for, and likely means of, implementation of successful agri-environmental schemes promoting soil biodiversity and sustainable food production. For example further experimental investigation could usefully target an evaluation of dispersal abilities of soil invertebrates under various field management, but, first, there will be need to test in-field survival abilities of different compartment of the soil food web under various environmental conditions.

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APPENCICES

Appendix 1. Examples of the different invertebrates extracted

1.a. *Acari*

Mesostigmata Ascidae

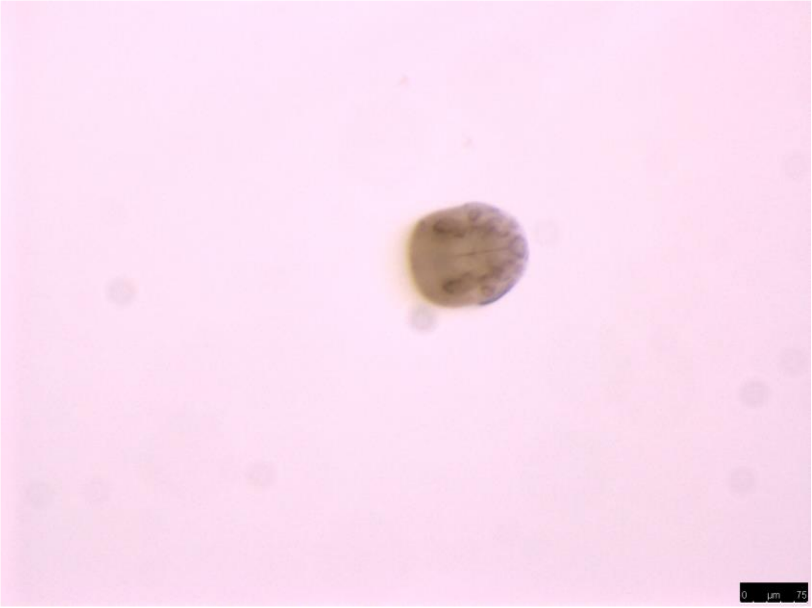
Mesostigmata Parasitidae

Mesostigmata Parasitidae

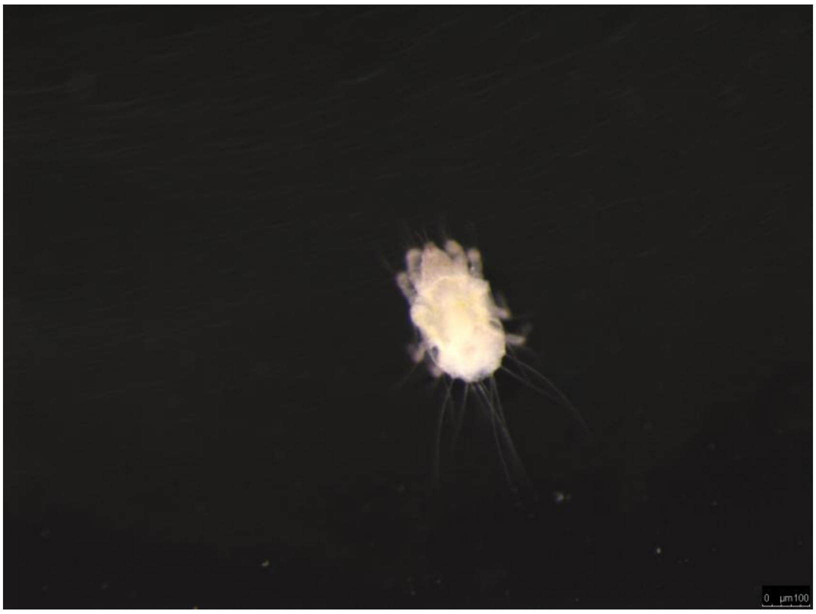
Mesostigmata

Mesostigmata Uropodina

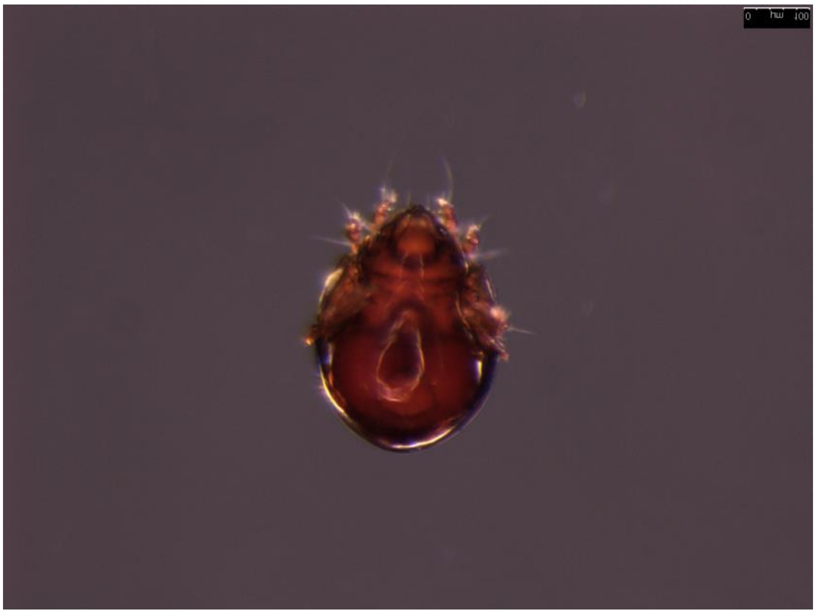
Heterostigmatina Scutacaridae (femelle)



Astigmata



Oribatida



Prostigmata

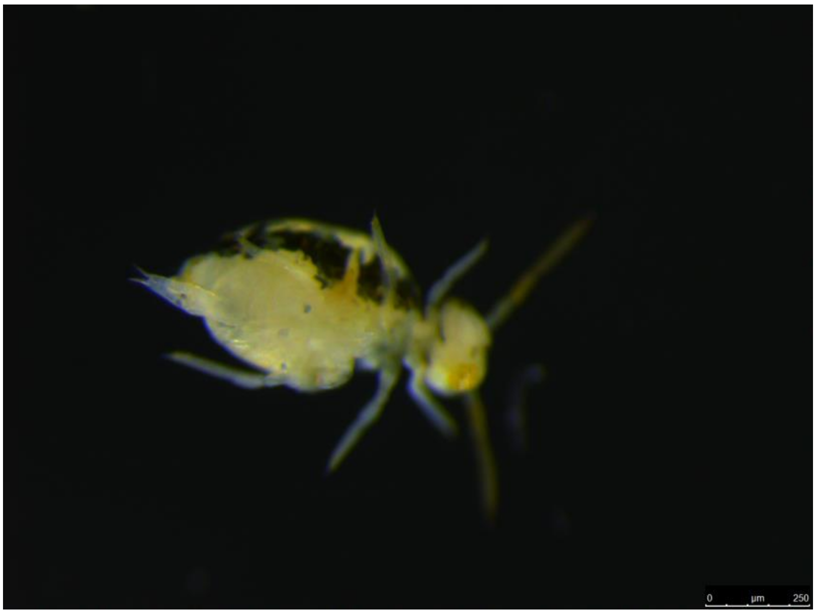
1.b. *Collembola*

Entomobryomorpha, Isotomidae

Entomobryomorpha Isotomidae

Entomobryomorpha Lepidocyrtus cyaneus

Symphypleona



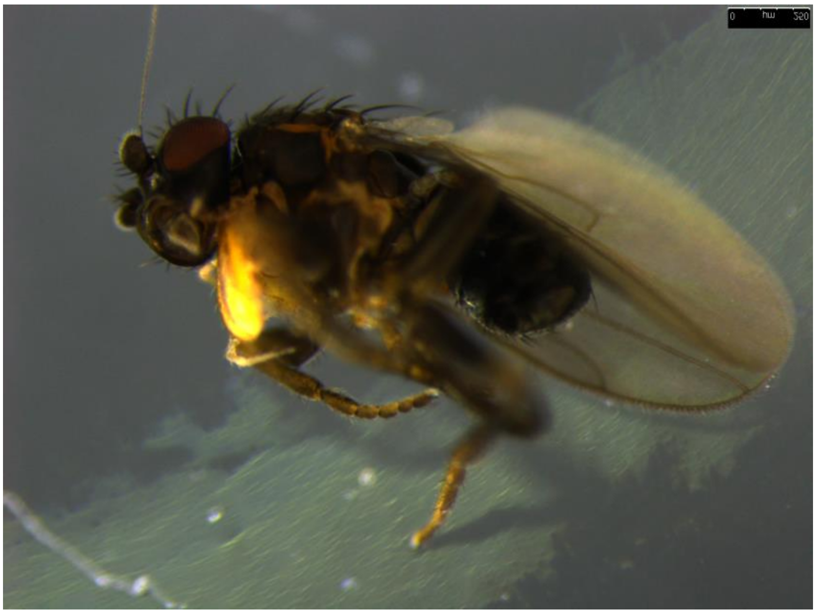
Poduromorpha Hypogastruridae

Poduromorpha Onychiuridae/Tullbergiidae

1.c. Macrofauna

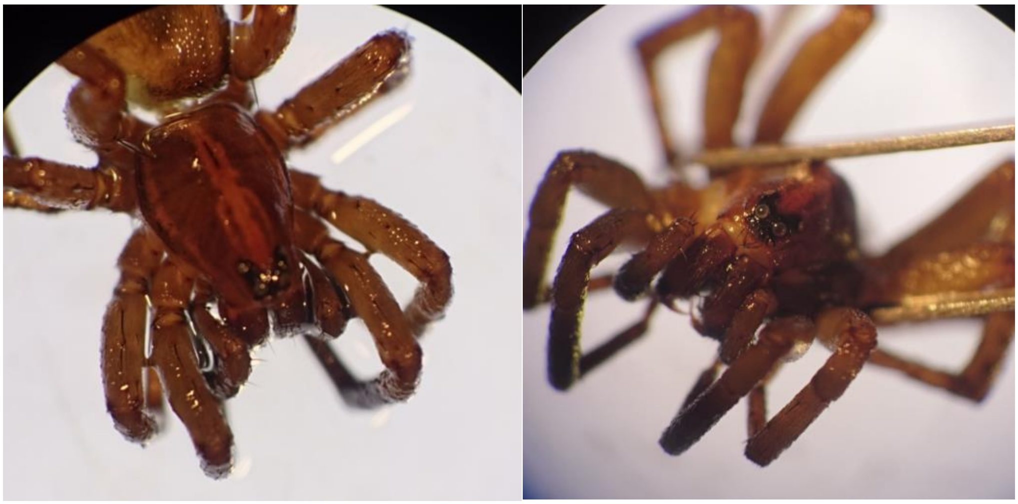
Diplopoda

Diptera Brachycera



Diptera Nematocera

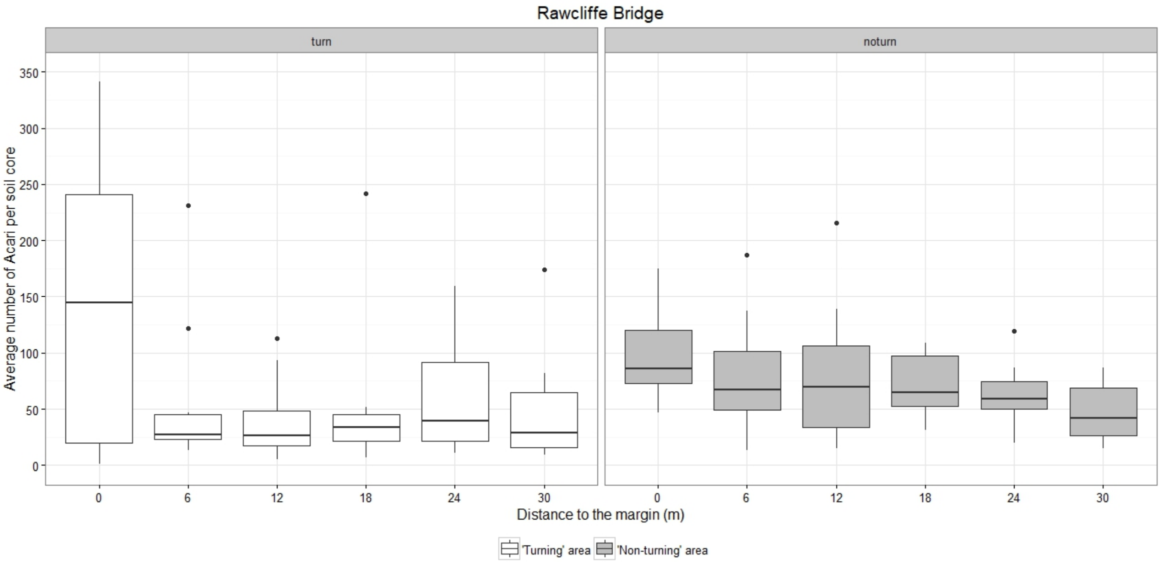
Arachnea



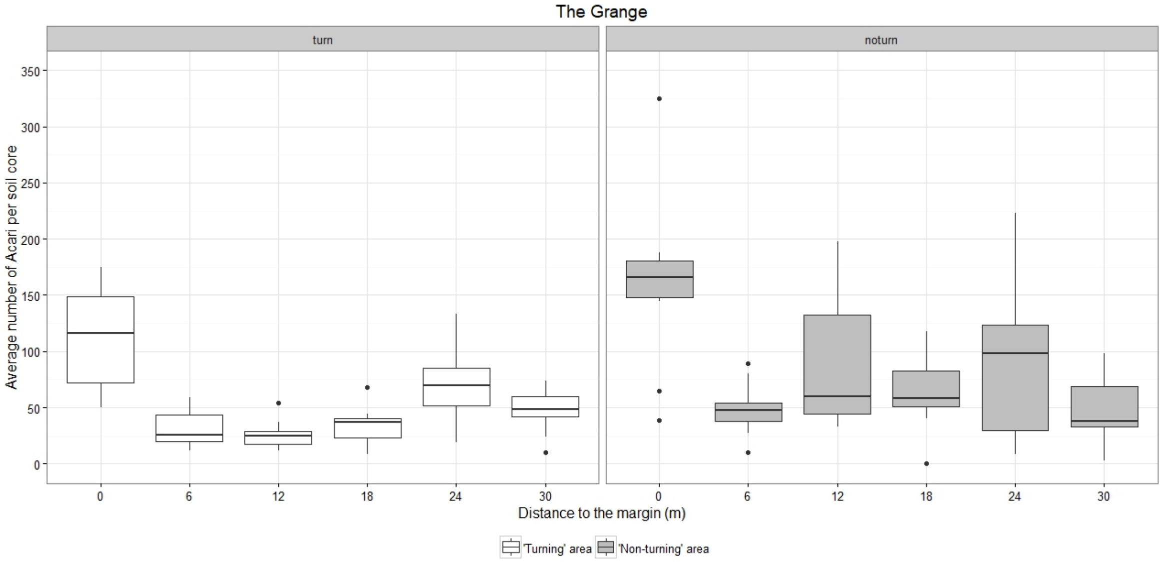
Larvae unidentified

Appendix 2. Distribution of Acari in the field margin (0 m) and cropped area at various distances from it at (a) Rawcliffe Bridge farm and (b) The Grange farm. Whites boxes show samples from the perpendicular area and grey boxes show samples from parallel area. Upper and lower quartiles are represented by upper and lower limit of the boxes; the middle of the boxes features the median and bars show variability outside the upper and lower quartiles. (Chapter 4)

a.

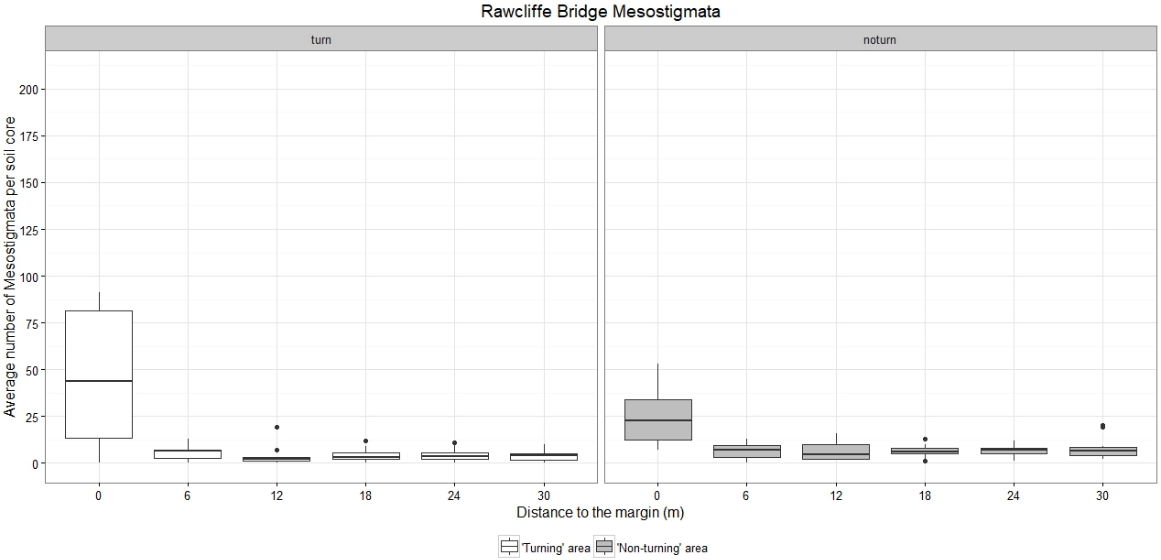


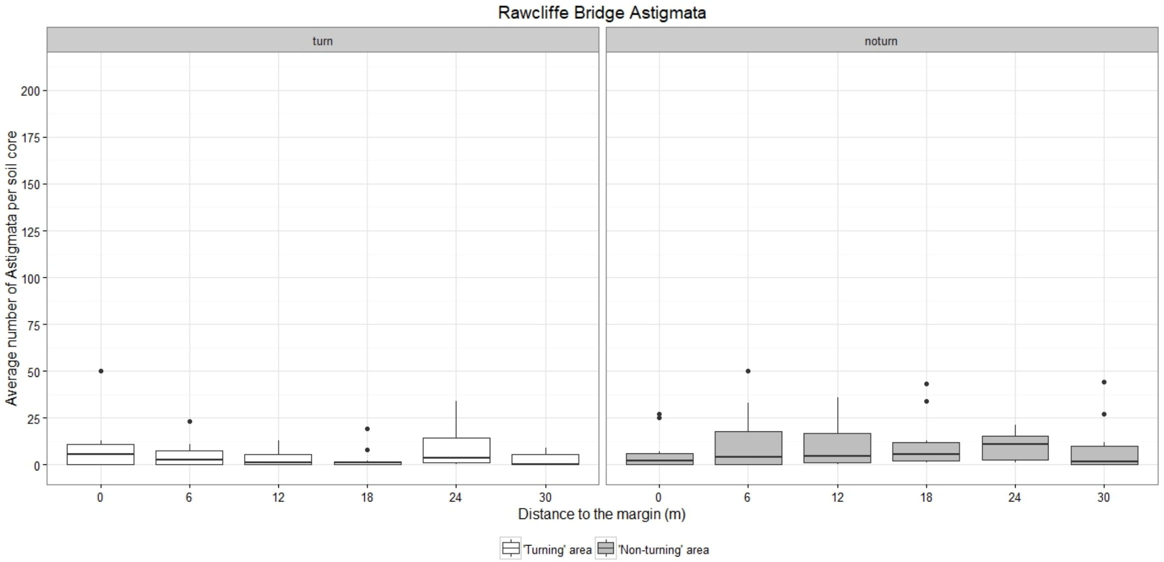
b.

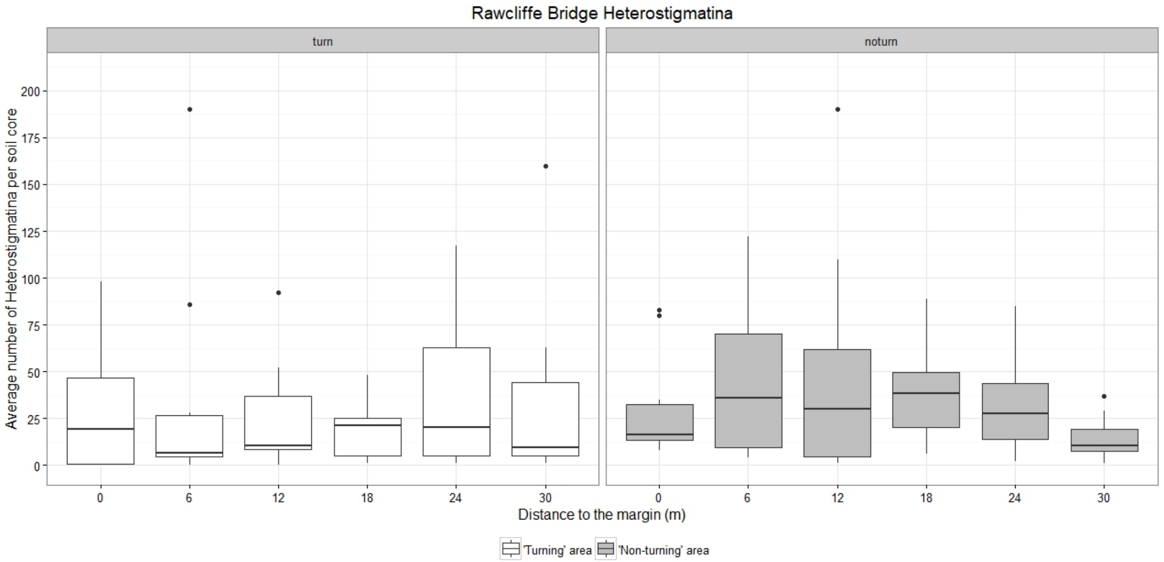

The Grange
turn
noturn
Average number of Acari per soil core
350
300
250
200
150
100
50
0
0
6
12
18
24
30
0
6
12
18
24
30
Distance to the margin (m)
'Turning' area
'Non-turning' area

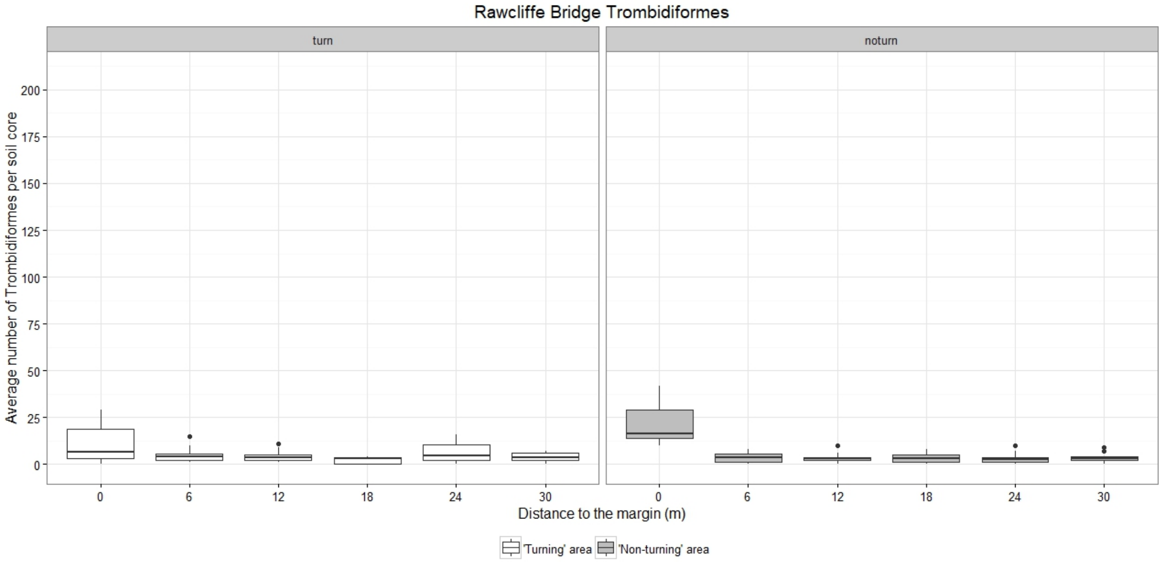
Appendix 3. Distribution of the different taxa of Acari (Mesostigmata, Astigmata, Heterostigmatina, Trombidiformes and Oribatida) in the field margin (0 m) and cropped area at various distances from it at (a) Rawcliffe Bridge farm and (b) The Grange farm. Whites boxes show samples from the perpendicular area and grey boxes show samples from parallel area. Upper and lower quartiles are represented by upper and lower limit of the boxes; the middle of the boxes features the median and bars show variability outside the upper and lower quartiles. (Chapter 4)

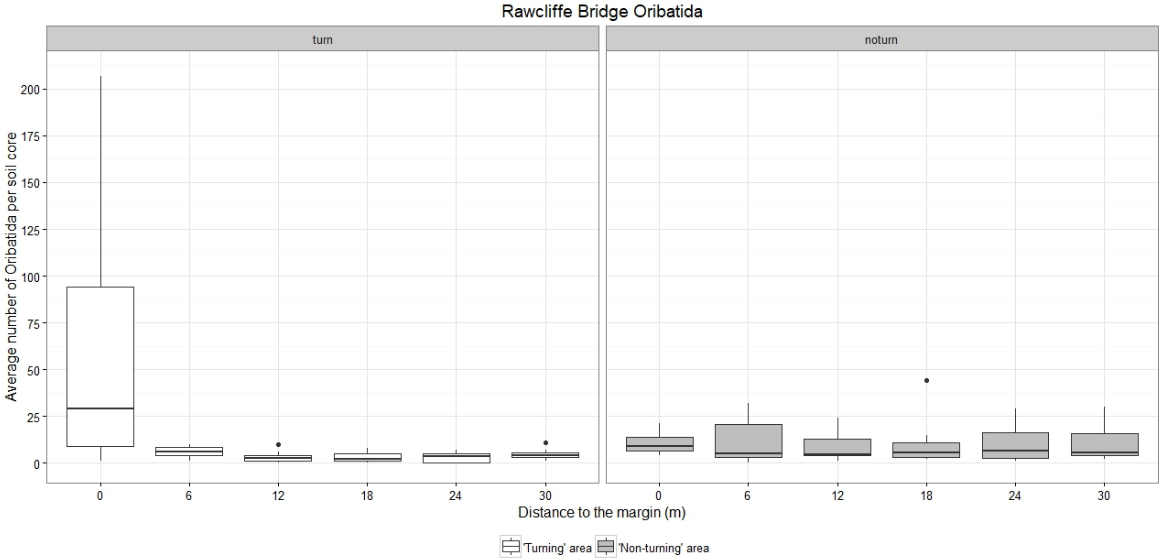
a.



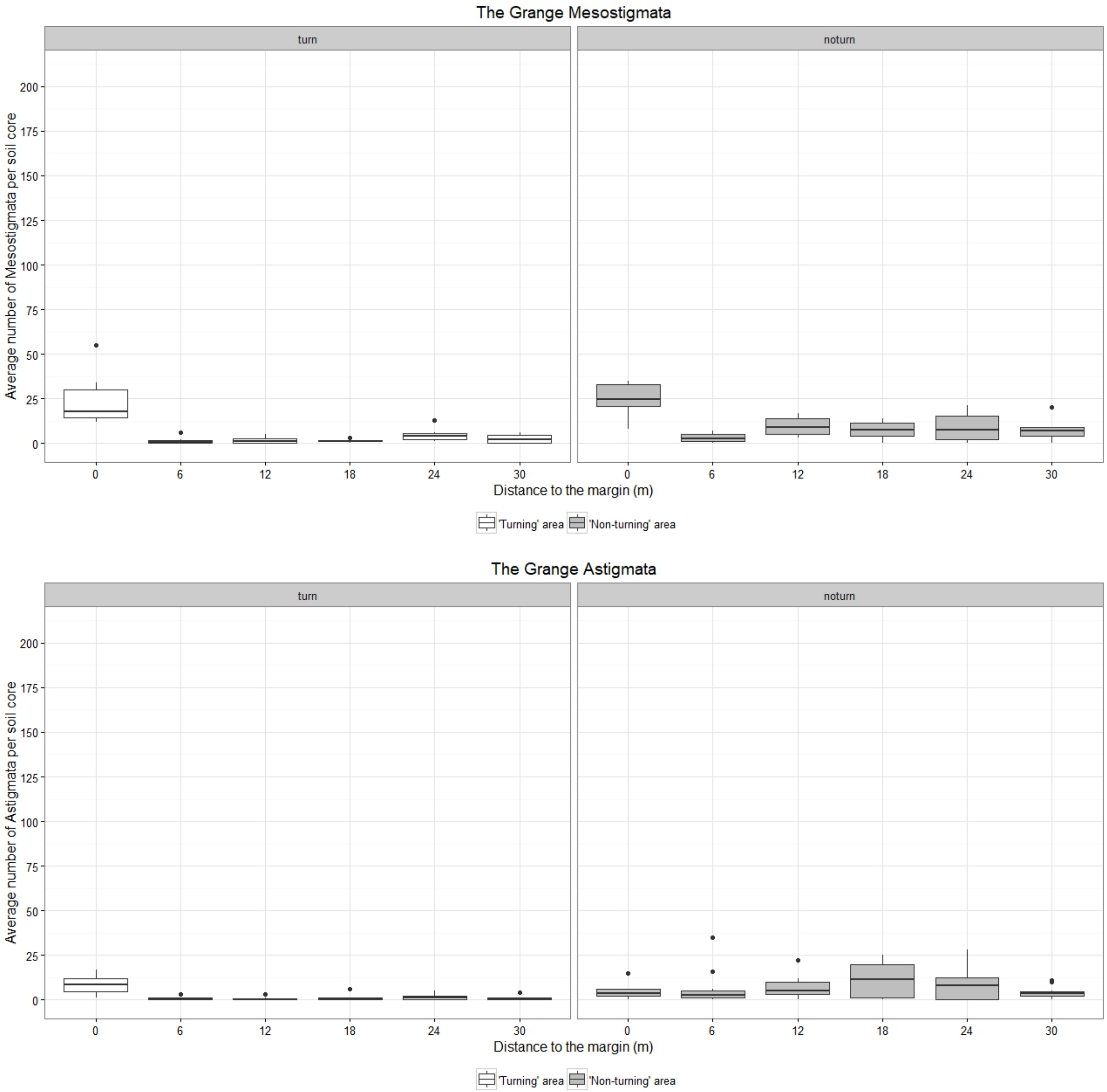

Rawcliffe Bridge Astigmata
turn
noturn
Average number of Astigmata per soil core
0
25
50
75
100
125
150
175
200
0
6
12
18
24
30
Distance to the margin (m)
'Turning' area
'Non-turning' area

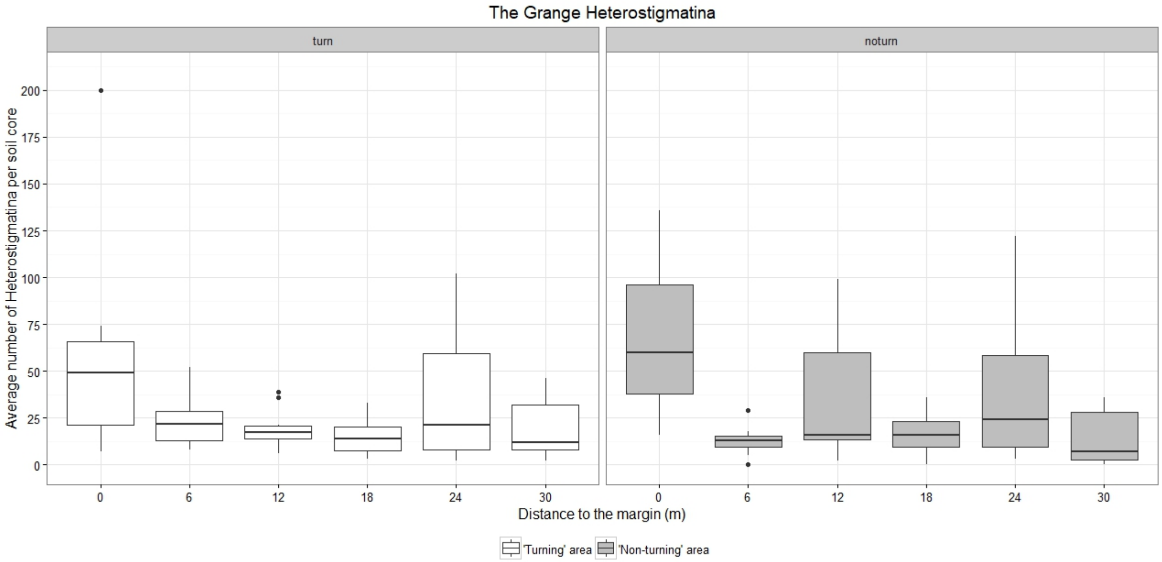

Rawcliffe Bridge Heterostigmatina
turn
noturn
Average number of Heterostigmatina per soil core
0
25
50
75
100
125
150
175
200
0
6
12
18
24
30
Distance to the margin (m)
'Turning' area
'Non-turning' area


Rawcliffe Bridge Trombidiformes
turn
noturn
Average number of Trombidiformes per soil core
0
25
50
75
100
125
150
175
200
0
6
12
18
24
30
Distance to the margin (m)
'Turning' area
'Non-turning' area


Rawcliffe Bridge Oribatida
turn
noturn
Average number of Oribatida per soil core
0
25
50
75
100
125
150
175
200
0
6
12
18
24
30
Distance to the margin (m)
'Turning' area
'Non-turning' area

b.


The Grange Mesostigmata
turn
noturn
Average number of Mesostigmata per soil core
0
25
50
75
100
125
150
175
200
0
6
12
18
24
30
Distance to the margin (m)
'Turning' area
'Non-turning' area
The Grange Astigmata
turn
noturn
Average number of Astigmata per soil core
Distance to the margin (m)
'Turning' area
'Non-turning' area


The Grange Heterostigmatina
turn
noturn
Average number of Heterostigmatina per soil core
0
25
50
75
100
125
150
175
200
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6
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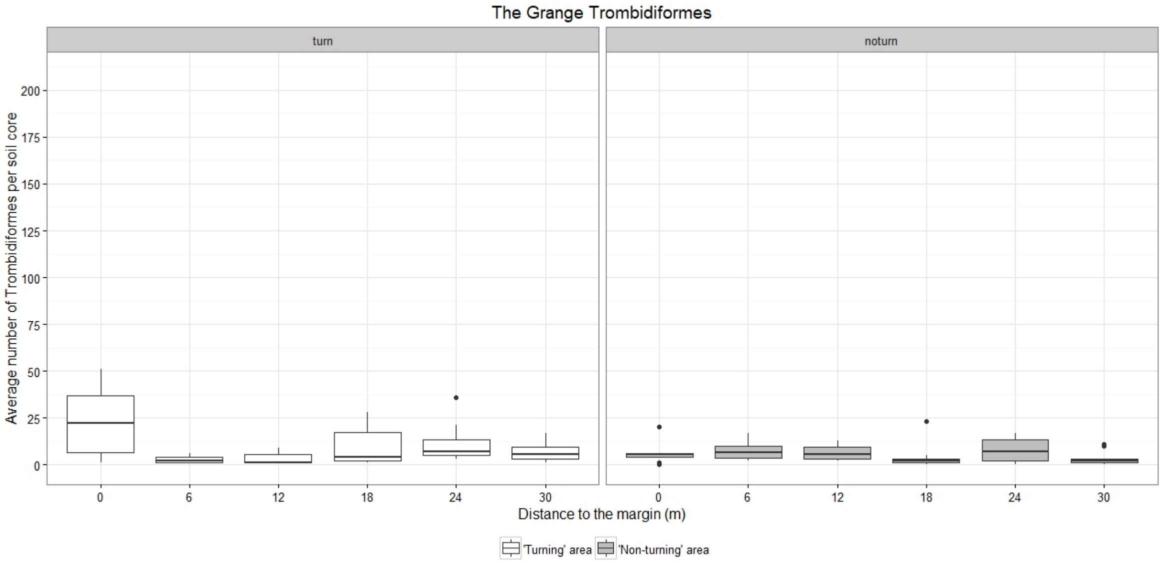
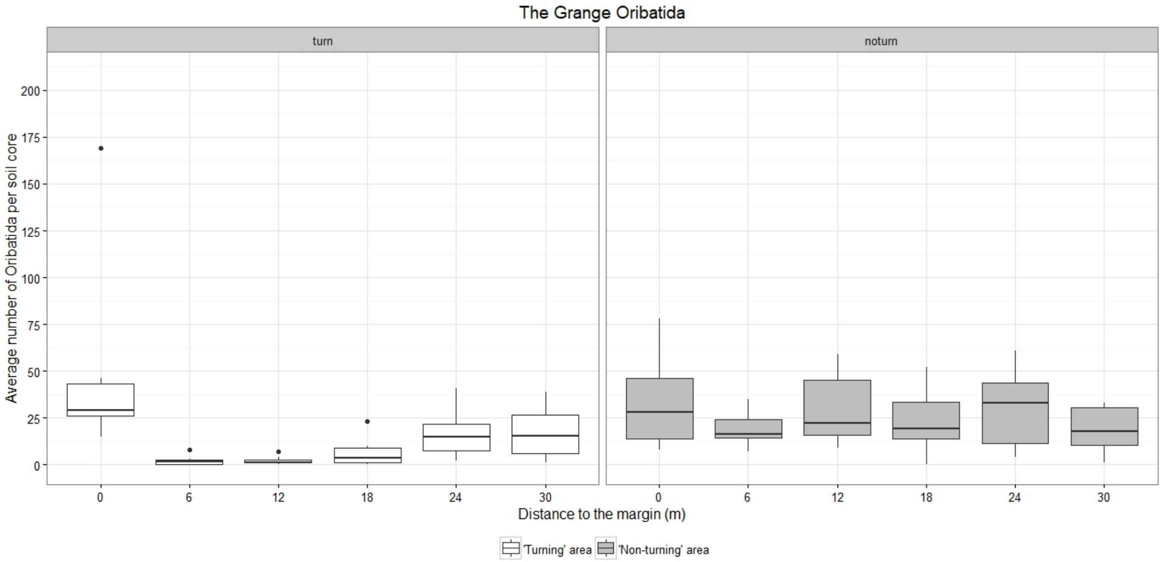
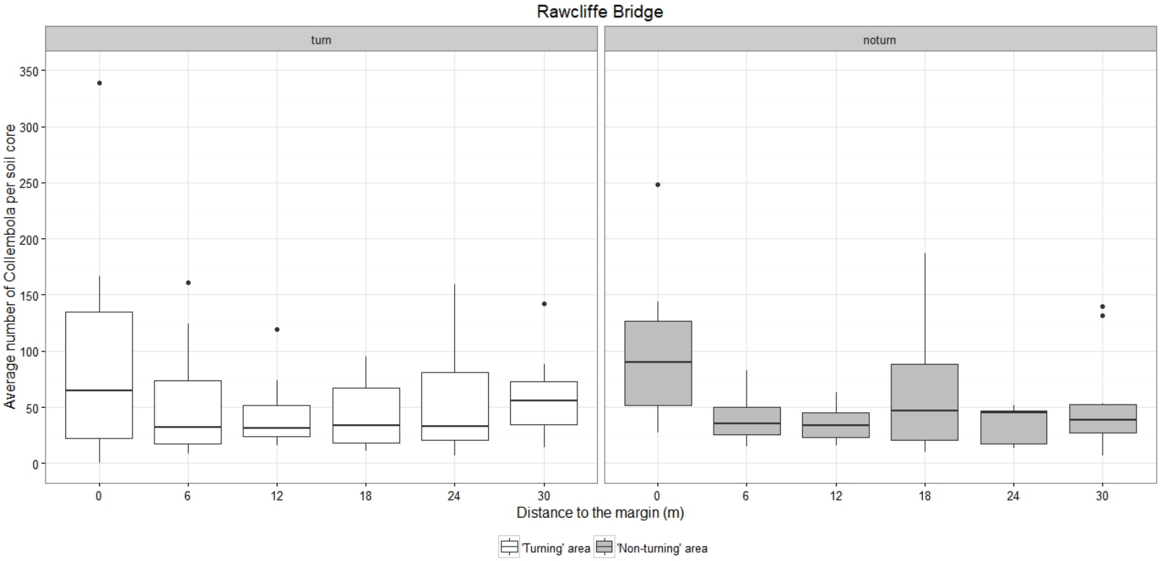
24
30
Distance to the margin (m)
'Turning' area
'Non-turning' area


The Grange Trombidiformes
turn
noturn
Average number of Trombidiformes per soil core
0
25
50
75
100
125
150
175
200
0
6
12
18
24
30
Distance to the margin (m)
'Turning' area
'Non-turning' area

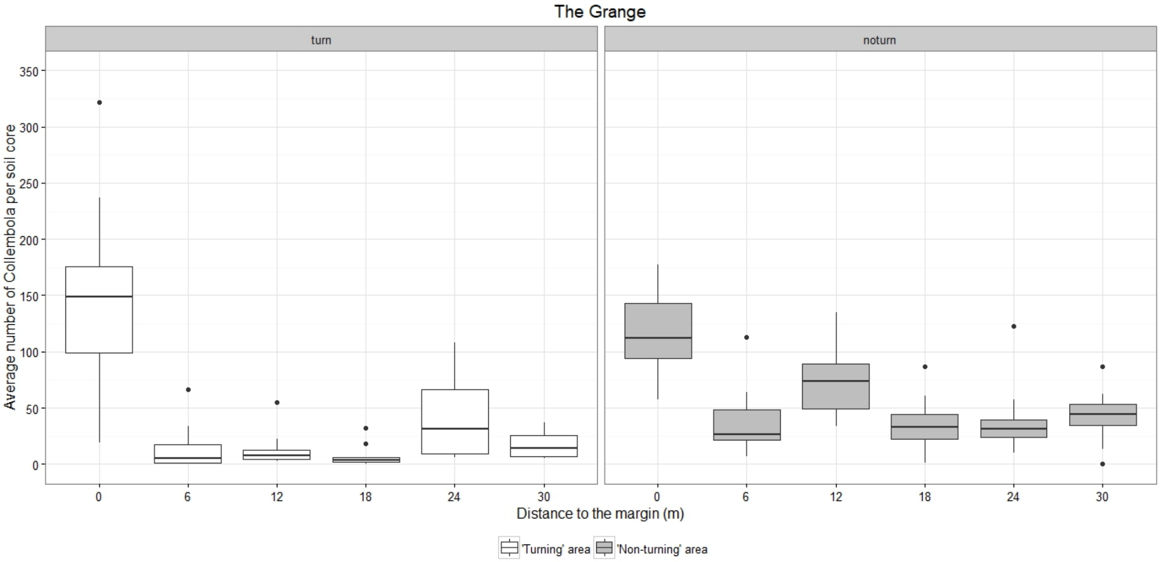

The Grange Oribatida
turn
noturn
Average number of Oribatida per soil core
0
25
50
75
100
125
150
175
200
0
6
12
18
24
30
Distance to the margin (m)
'Turning' area
'Non-turning' area

Appendix 4. Distribution of Collembola in the field margin (0 m) and cropped area at various distances from it at (a) Rawcliffe Bridge farm and (b) The Grange farm. Whites boxes show samples from the perpendicular area and grey boxes show samples from the parallel area Upper and lower quartiles are represented by upper and lower limit of the boxes; the middle of the boxes features the median and bars show variability outside the upper and lower quartiles. (Chapter 4)

a.

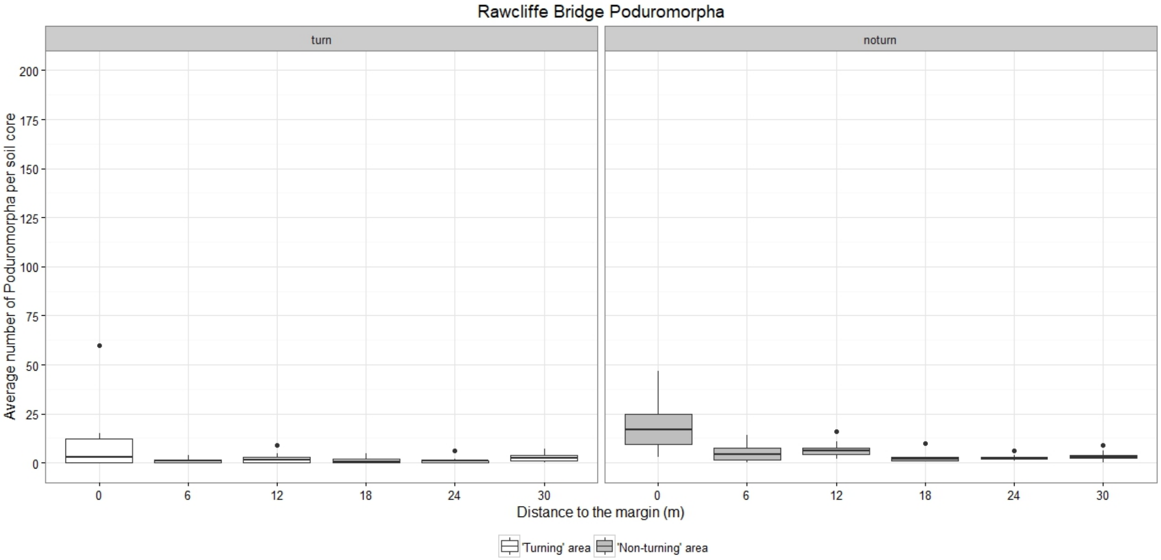


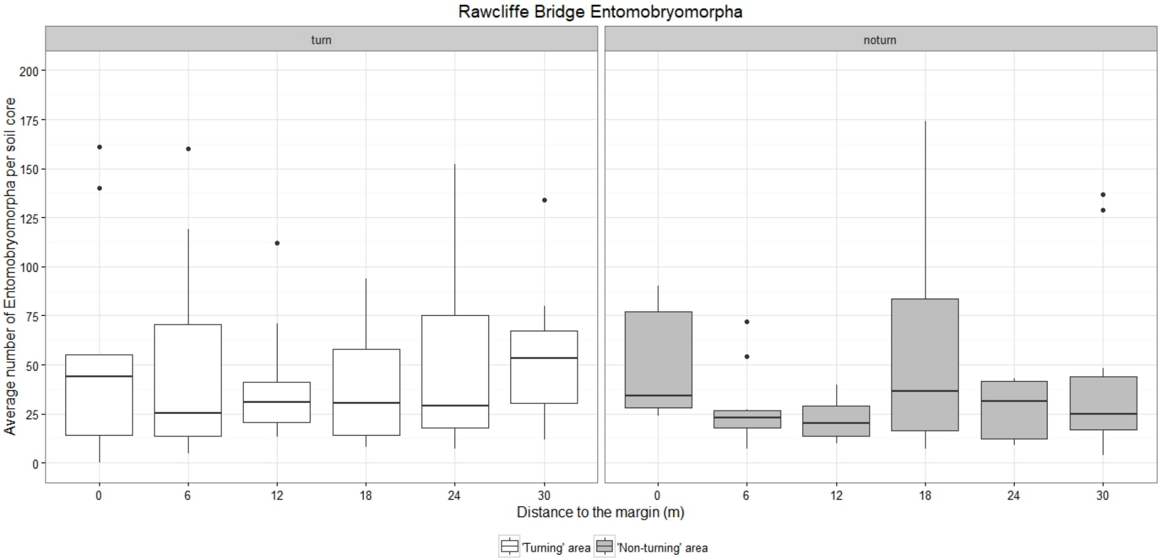
b.

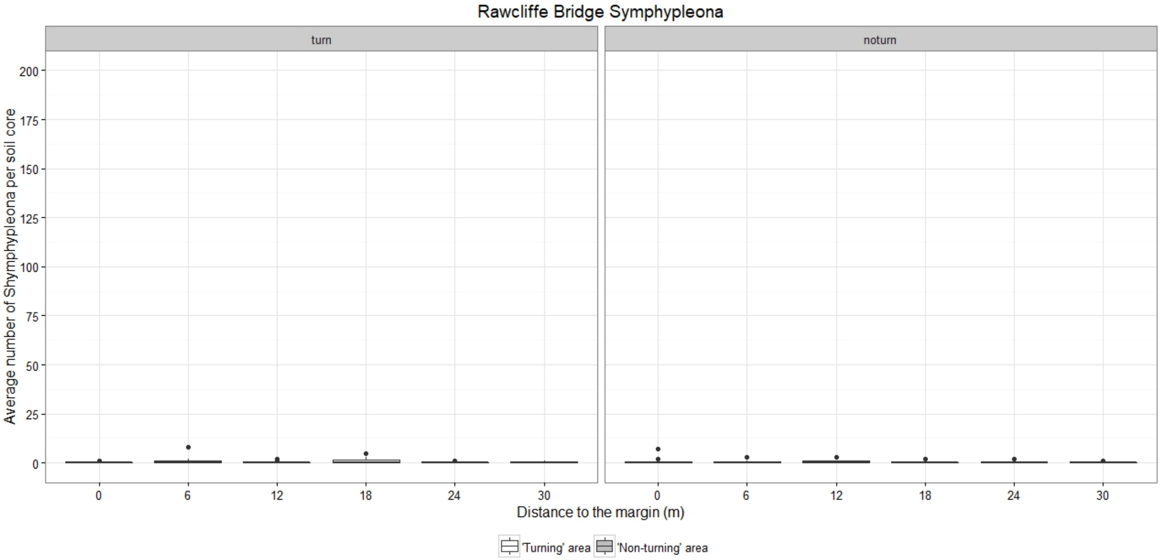


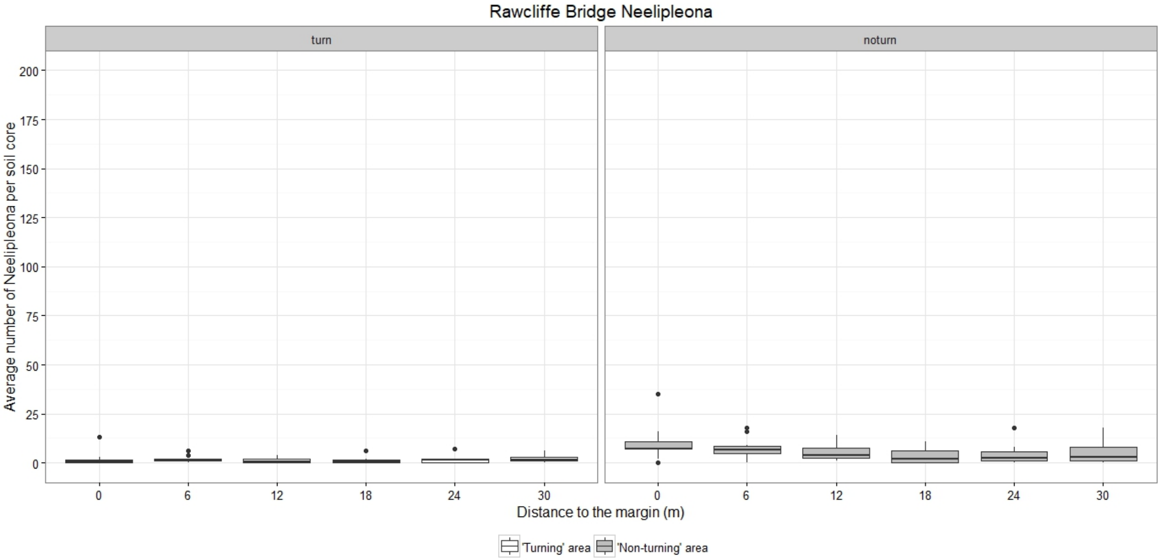
Appendix 5. Distribution of the different taxa of Collembola (Poduromorpha, Entomobryomorpha, Symphypleona and Neelipleona) in the field margin (0 m) and cropped area at various distances from it at (a) Rawcliffe Bridge farm and (b) The Grange farm. Whites boxes show samples from the perpendicular area and grey boxes show samples from the parallel area Upper and lower quartiles are represented by upper and lower limit of the boxes, the middle of the boxes features the median and bars show variability outside the upper and lower quartiles. (Chapter 4)

a.

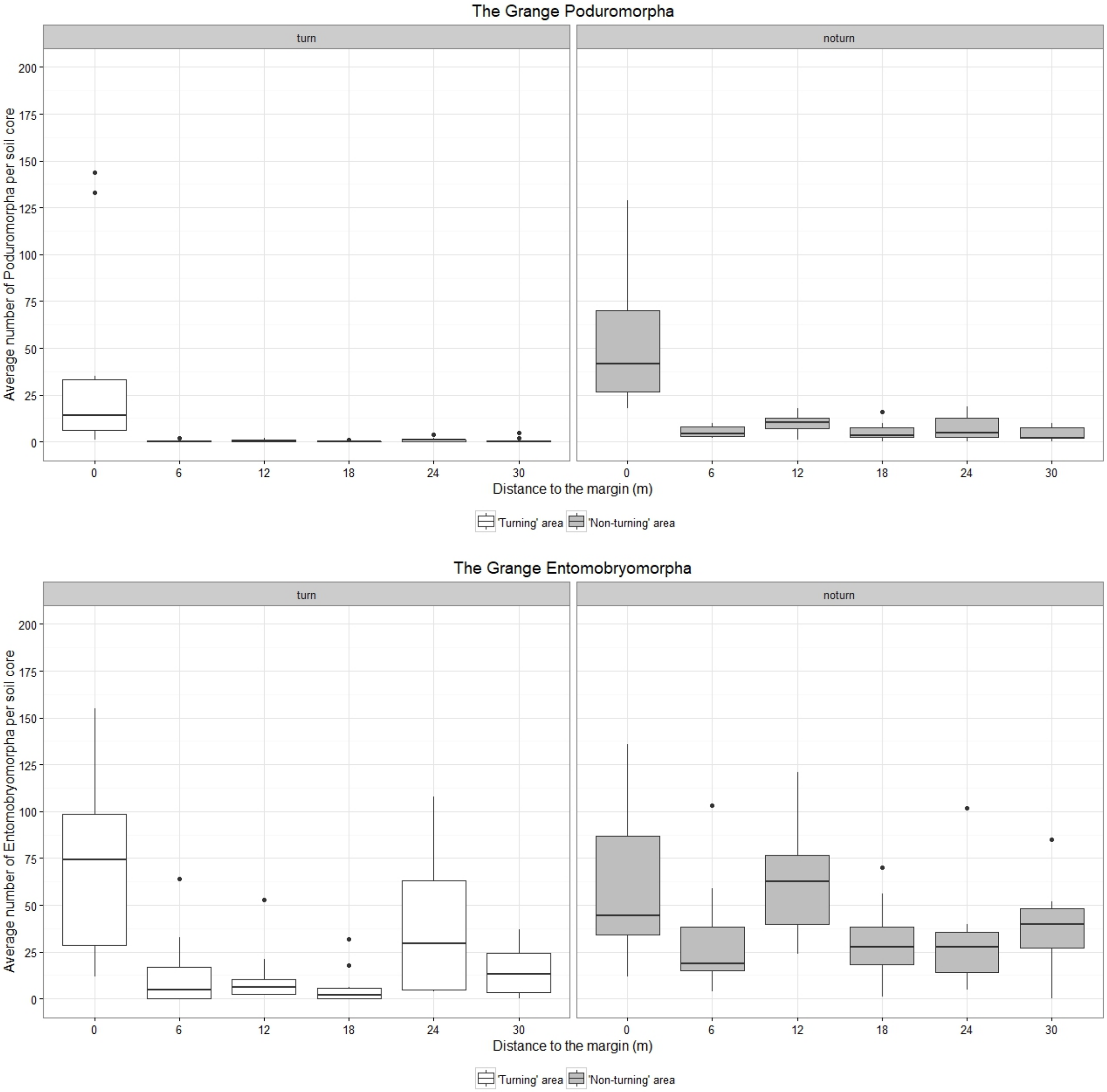


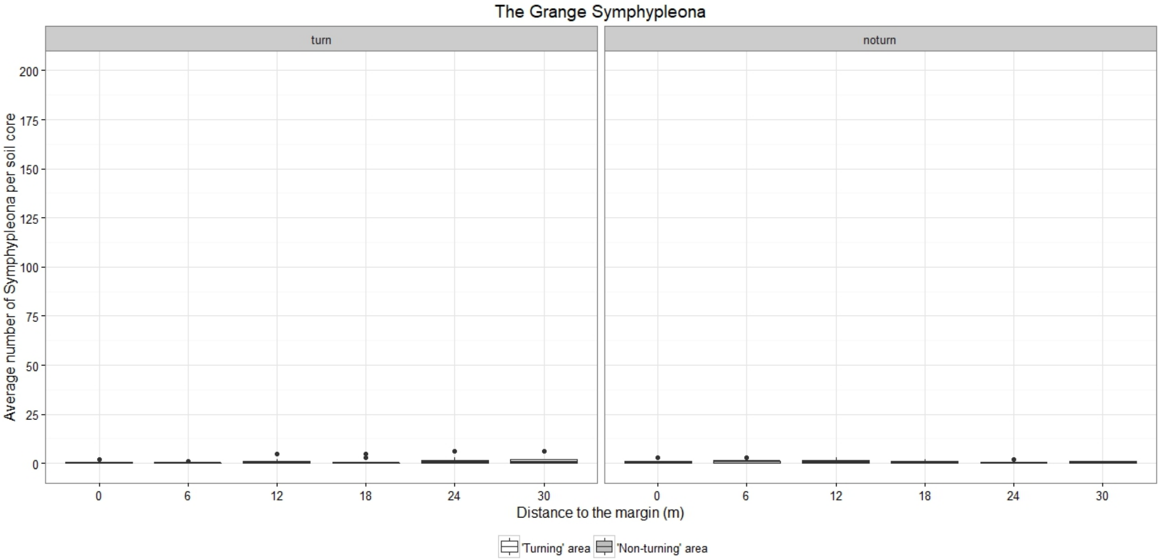

Rawcliffe Bridge Entomobryomorpha
turn
noturn
Average number of Entomobryomorpha per soil core
0
25
50
75
100
125
150
175
200
0
6
12
18
24
30
Distance to the margin (m)
'Turning' area
'Non-turning' area

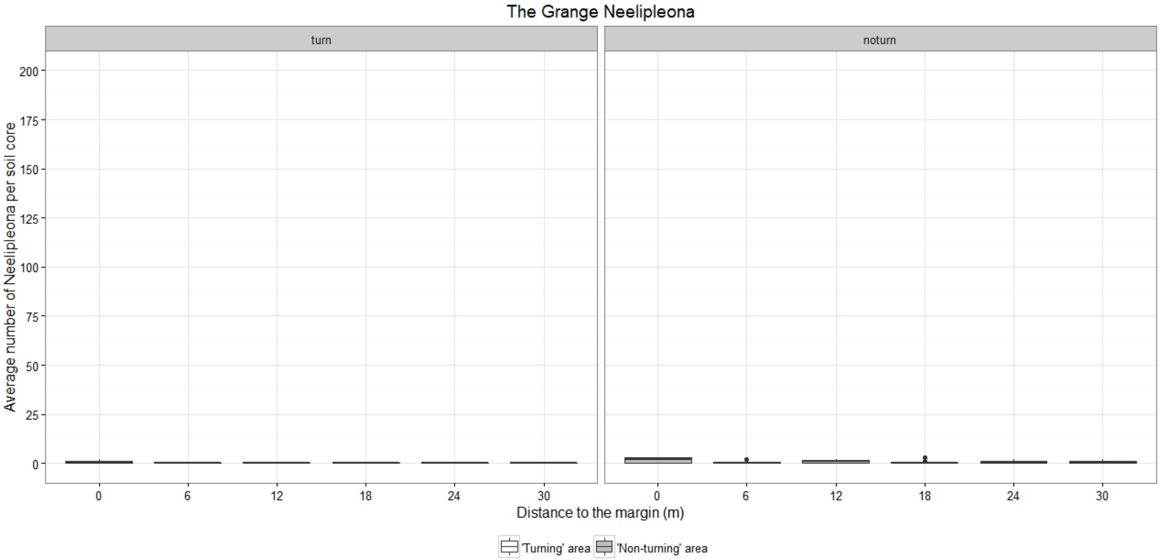

Rawcliffe Bridge Symphypleona
turn
noturn
Average number of Shymphypleona per soil core
0
25
50
75
100
125
150
175
200
0
6
12
18
24
30
Distance to the margin (m)
'Turning' area
'Non-turning' area


Rawcliffe Bridge Neelipleona
turn
noturn
Average number of Neelipleona per soil core
0
25
50
75
100
125
150
175
200
0
6
12
18
24
30
Distance to the margin (m)
'Turning' area
'Non-turning' area

b.

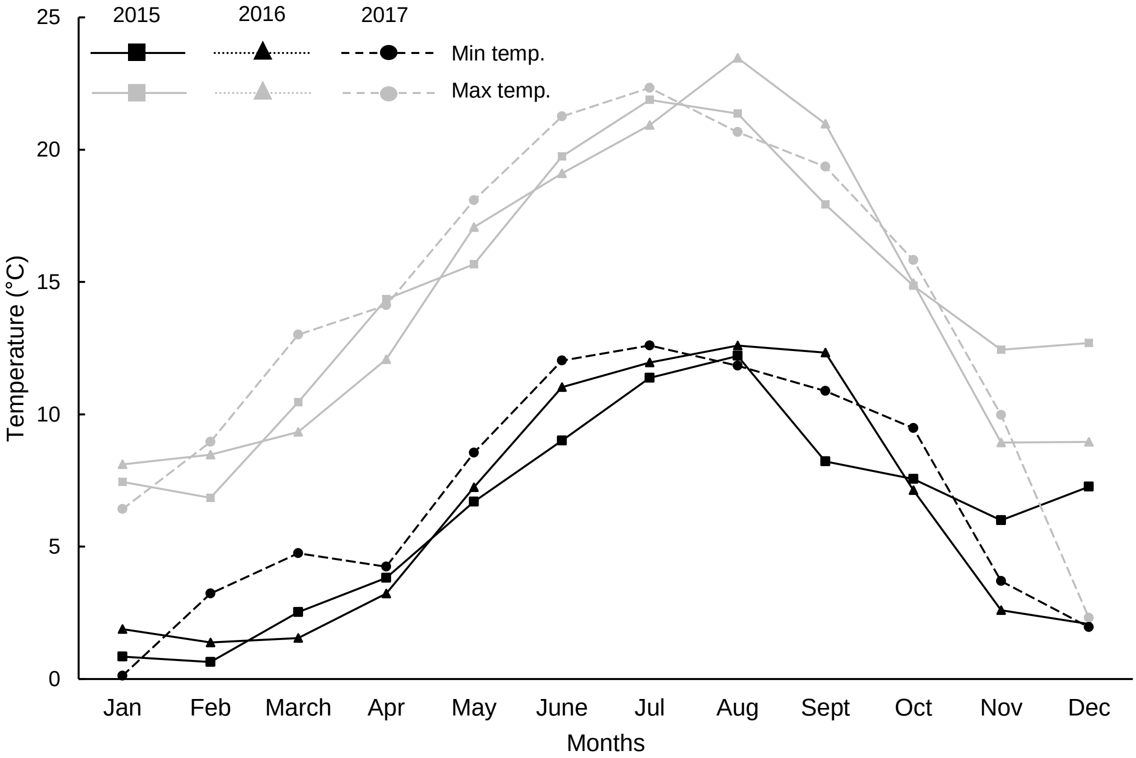

The Grange Poduromorpha
turn
noturn
Average number of Poduromorpha per soil core
200
175
150
125
100
75
50
25
0
0
6
12
18
24
30
Distance to the margin (m)
'Turning' area
'Non-turning' area
The Grange Entomobryomorpha
turn
noturn
Average number of Entomobryomorpha per soil core
Distance to the margin (m)
'Turning' area
'Non-turning' area


The Grange Symphypleona
turn
noturn
Average number of Symphypleona per soil core
200
175
150
125
100
75
50
25
0
0
6
12
18
24
30
Distance to the margin (m)
'Turning' area
'Non-turning' area

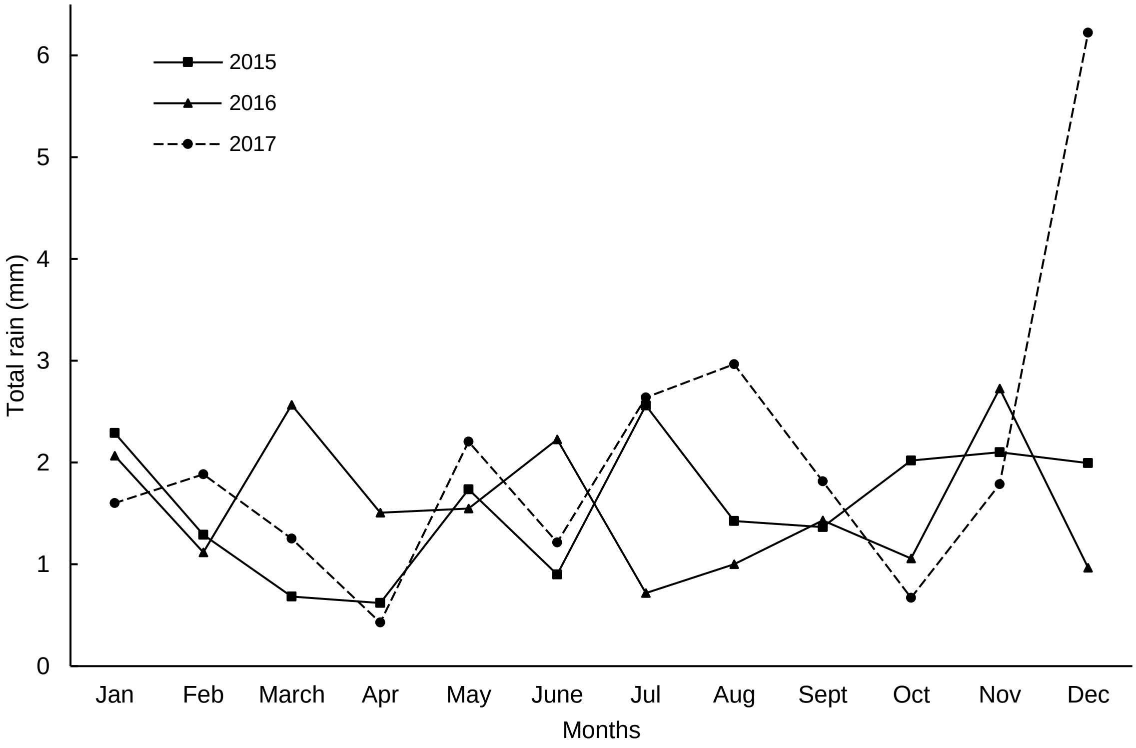

The Grange Neelipleona
turn
noturn
Average number of Neelipleona per soil core
200
175
150
125
100
75
50
25
0
0
6
12
18
24
30
Distance to the margin (m)
'Turning' area
'Non-turning' area

Appendix 6. Meteorological data for 2015, 2016 and 2017 at The Grange farm, Mears Ashby, Northamptonshire (52° 18' 2.73" N; 0° 45' 52.83" W).

6.a. Average minimum and maximum temperatures calculated each month form daily minimum and maximum temperature measured at Saws Bedford station in 2015, 2016 and 2017. Black lines show minimum temperatures and grey line maximum temperatures. Solid lines (■) stand for year 2015, doted lines stand for year 2016 (▲) and dash lines for year 2017 (●).

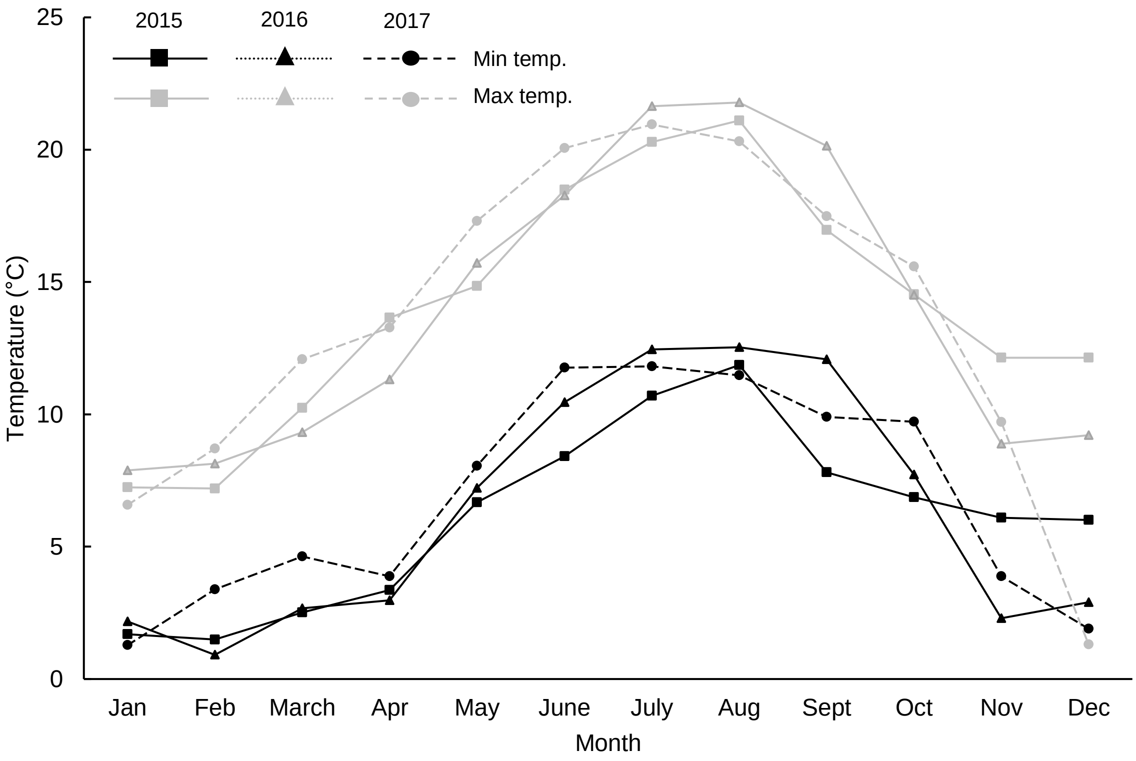


6.b. Average rainfall (mm) calculated each month form daily total rainfall measured at Saws Bedford station in 2015, 2016 and 2017. Solid lines (■) stand for year 2015, doted lines stand for year 2016 (▲) and dash lines for year 2017 (●).

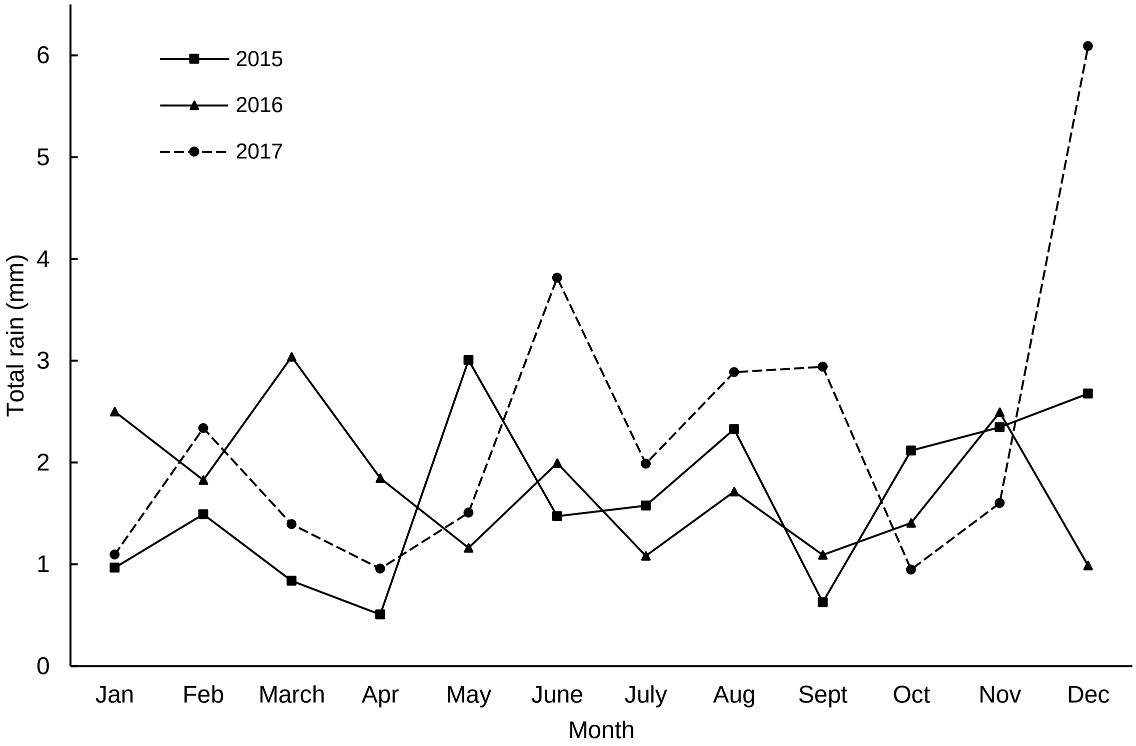


Appendix 7. Meteorological data for 2015, 2016 and 2017 at Rawcliffe Bridge farm, Rawcliffe Bridge, Yorkshire (53° 40’ 0.37” N; 0° 55’ 46.84” W).

7.a. Average minimum and maximum temperatures calculated each month form daily minimum and maximum temperature measured at Saws Leconfield station in 2015, 2016 and 2017. Black lines show minimum temperatures and grey line maximum temperatures. Solid lines (■) stand for year 2015, doted lines stand for year 2016 (▲) and dash lines for year 2017 (●).



7.b. Average rainfall (mm) calculated each month form daily total rainfall measured at Saws Leconfield station in 2015, 2016 and 2017. Solid lines (■) stand for year 2015, doted lines stand for year 2016 (▲) and dash lines for year 2017 (●).



Appendix 8. Abundance of Acari and Collembola in the perpendicular and parallel field margins of the two farms.

8.a. Mean abundance (individuals/m^{-2}) and standard error (±SE) of different taxa of Acari and Collembola in the ‘perpendicular’ and ‘parallel’ field margins and at five distances from each into the crop at Rawcliffe Bridge farm (n=20). Samples were repeatedly taken at over the four sampling (October 2015, April 2016, April 2017 and October 2017).

RAWCLIFFE BRIDGE FARM	**Perpendicular area**						**Parallel area**					
	Margin	**6 m**	**12 m**	**18 m**	**24 m**	**30 m**	**Margin**	**6 m**	**12 m**	**18 m**	**24 m**	**30 m**
***ACARI* TOTAL**												
Mean	34222	11301	7819	10147	12276	9491	19200	15877	16096	14146	12455	9371
±SE	5677	2489	1325	2488	1968	1850	1352	1858	2311	1041	994	941
Mesostigmata												
Mean	9033	1114	776	875	875	776	4895	1273	1293	1273	1293	1632
±SE	1301	132	204	134	131	106	569	160	179	127	113	228
Astigmata												
Mean	1870	1035	657	657	1791	537	1333	2386	2010	2328	2029	1791
±SE	548	266	159	217	413	131	376	627	427	534	268	541
Heterostigmatina												
Mean	6208	7023	4875	7581	7760	6466	5969	9053	9829	7700	6148	2905
±SE	1373	2171	1061	2319	1587	1802	1022	1546	2211	914	920	410
Trombidiformes												
Mean	2109	975	875	438	1234	776	4377	716	696	657	617	696
±SE	364	161	118	63	209	91	421	107	101	93	116	101
Oribatida												
Mean	15002	1154	637	597	617	935	2089	2308	1850	2029	2149	2010
±SE	2936	111	110	101	97	102	192	429	299	457	359	359
***COLLEMBOLA* TOTAL**												
Mean	18920	10624	8614	8594	11280	11718	18920	10624	8614	8594	11280	11718

RAWCLIFFE BRIDGE FARM	**Perpendicular area**						**Parallel area**					
	Margin	**6 m**	**12 m**	**18 m**	**24 m**	**30 m**	**Margin**	**6 m**	**12 m**	**18 m**	**24 m**	**30 m**
±SE	3734	1891	1159	1082	1910	1356	2368	836	559	2040	582	1651
Poduromorpha												
Mean	2049	239	477	239	239	537	3999	1015	1333	537	517	696
±SE	664	51	103	59	66	78	545	155	150	96	54	89
Entomobryomorpha												
Mean	16453	9768	7838	7918	10683	10723	13767	5551	4417	11121	5491	8873
±SE	3616	1929	1109	1090	1854	1300	2327	725	387	1965	559	1740
Symphypleona												
Mean	20	259	60	199	20	60	199	139	139	40	80	40
±SE	11	89	24	64	11	17	80	45	34	23	25	15
Neelipleona												
Mean	398	358	239	239	338	398	2049	1512	1114	756	895	1035
±SE	145	68	53	68	74	66	354	200	160	152	196	203

8.b. Mean abundance (individuals/m^{-2}) and standard error (±SE) of different taxa of Acari and Collembola in the ‘perpendicular’ and ‘parallel’ field margins and at five distances from each into the crop at The Grange Farm (n=20). Samples were repeatedly taken at over the four sampling (October 2015, April 2016, April 2017 and October 2017).

THE GRANGE FARM	**Perpendicular area**						**Parallel area**					
	Margin	**6 m**	**12 m**	**18 m**	**24 m**	**30 m**	**Margin**	**6 m**	**12 m**	**18 m**	**24 m**	**30 m**
***ACARI* TOTAL**												
Mean	36427	6207	5192	6585	14483	6261	31930	9689	17626	12553	19118	9549
±SE	6038	595	446	639	1234	690	2764	840	2165	1168	2692	1066
Mesostigmata												
Mean	5013	239	318	259	875	477	4775	597	1870	1492	1711	1472
±SE	611	68	69	38	130	82	351	87	188	178	274	191
Astigmata												
Mean	1671	179	99	179	259	219	1074	1373	1413	2208	1790	836

THE GRANGE FARM	**Perpendicular area**						**Parallel area**					
	Margin	**6 m**	**12 m**	**18 m**	**24 m**	**30 m**	**Margin**	**6 m**	**12 m**	**18 m**	**24 m**	**30 m**
±SE	185	43	35	67	57	58	197	394	239	384	357	132
Heterostigmatina												
Mean	16313	4894	3800	3064	7620	3780	18104	2546	7321	3402	8177	2765
±SE	3506	563	393	385	1411	547	2739	281	1244	405	1501	537
Trombidiformes												
Mean	4635	517	597	1930	2268	1273	1174	1452	1233	836	1492	676
±SE	654	71	118	350	370	177	195	175	142	244	230	141
Oribatida												
Mean	8793	378	378	1154	3322	3504	6943	3720	5789	4615	5948	3800
±SE	1626	89	79	257	426	499	946	295	666	567	718	410
COLLEMBOLA **TOTAL**												
Mean	28867	2865	2606	1452	8714	3521	23814	7560	14662	7261	7898	8515
±SE	3287	763	572	354	1432	446	1437	1142	1072	883	1162	882
Poduromorpha												
Mean	7639	7560	14662	7261	7898	8515	10743	1035	1970	1074	1512	816
±SE	1951	25	25	11	43	59	1351	110	177	173	244	128
Entomobryomorpha												
Mean	14125	2745	2307	1273	8236	3024	12573	6267	12335	6008	6187	7500
±SE	1792	25	25	11	43	59	1511	1081	1037	762	1008	857
Symphypleona												
Mean	99	40	179	159	259	338	179	179	179	99	80	80
±SE	31	15	58	63	70	97	43	36	40	26	25	19
Neelipleona												
Mean	199	0	0	0	0	0	318	80	179	80	119	119
±SE	30	0	0	0	0	0	46	25	32	35	25	30