# Impacts of intensive agriculture on soil fauna and ecosystem function

## Trading function for dependence?

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The candidate confirms that the work submitted is her own, except where work which has formed part of jointly-authored publications has been included. The contribution of the candidate and the other authors to this work has been explicitly indicated below. The candidate confirms that appropriate credit has been given within the thesis where reference has been made to the work of others.

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Scott Johnson (SNJ) designed the experiment based on knowledge of the existing experimental setup at the Hawkesbury Institute for the Environment (HIE), University of Western Sydney, with input from the candidate (Tiffany Aslam; TJA) and Uffe Nielsen. TJA collected the data with assistance from two research technicians at the HIE. TJA analysed the data, with input from Tim Benton (TGB). TJA wrote and revised the manuscript. SNJ produced Figure 3.1. All co-authors made suggestions to the manuscript and subsequent revisions.

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# Abstract

Soils form the basis of agroecosystems, generating the fuel, food and fodder needed to sustain human life. Soil biological communities contribute to almost all ecosystem processes, yet our understanding of how intensive agriculture impacts on these communities, and on fauna-function relationships, lags far behind that of above-ground systems. This thesis investigates the impacts of intensive agriculture, and in particular fertiliser use, on relationships between soil invertebrate abundance, community structure and ecosystem function both above-ground and below-ground.

The impacts of fertilisation, including organic and inorganic fertiliser regimes applied at different rates, and irrigation were quantified using realistic experimental field plots in temperate arable and plantation systems. Furthermore, the effects of a gradient of arable management intensity and the value of non-crop habitats in providing refugia for soil fauna were investigated using woodland-to-field transects. Impacts on soil invertebrates, including soil mites, springtails and nematodes, were quantified in terms of changes in abundance and shifts in community structure. Measures of ecosystem function included above-ground productivity, plant nutrient bioavailability and organic matter decomposition.

Impacts of fertilisers were complex and varied between systems and faunal groups. Notably, we observed that inorganic fertiliser application reduced soil mite and nematode abundance when applied with irrigation in water-limited, sandy soils. In general, astigmatid mites responded less negatively, or even positively, to intensive management. We observed strong evidence of non-crop habitats providing refugia for soil fauna, and in particular poor dispersers, in intensive arable landscapes.

This thesis advances our understanding of soil invertebrate ecology in intensively-managed agricultural systems. We discuss our findings in the context of the sustainable management of soils under a growing population, and suggest directions for future research.

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# Chapter 1

# General Introduction

## Abstract

Soils form the basis of agroecosystems, generating the feed, food and fuel needed to sustain human life. A healthy soil contributes to a vast number of ecosystem functions and services, including the cycling of water and nutrients, the storage of organic carbon and the provision of habitat for billions of organisms, many of which are yet to be identified. As such, human health is intrinsically linked to soil health. However, soils are under increasing pressure from a range of anthropogenic activities. The mismanagement of soils, sometimes associated with agricultural intensification, has accelerated rates of soil erosion globally, such that approximately one third of soils are now classified as being moderately to highly degraded. A lack of awareness, or regard, for soil health has meant that soil degradation has, until recently, been largely ignored. Subsequently, our understanding of the impacts of agricultural intensification on below-ground ecosystem functions and processes lags far behind that of above-ground systems. Here, we introduce the concepts of soil-derived ecosystem services and soil natural capital (Chapter 1.1), before briefly describing the diversity of the soil fauna and exploring their contribution to the provision of ecosystem functions and services (Chapter 1.2), in addition to ecosystem disservices (Chapter 1.3). Furthermore, we outline some of the major threats to soil fauna, focusing on the impacts of intensive agriculture, in addition to the role of invasive species and climate change (Chapter 1.4). Finally, we describe some of the major research gaps in soil research (Chapter 1.5) before defining the objectives of this thesis (Chapter 1.6).

## 1.1 Soil-derived ecosystem services and soil natural capital

Ecosystems provide a range of goods and services, both above-ground and below-ground, which help to sustain human life (Daily, 1997; Costanza *et al.*, 1998). Several frameworks attempt to quantify the value of these ecosystem goods and services to humans. Notably, the Millennium Ecosystem Assessment (2005) classifies ecosystem services into four key categories: provisioning, regulating, supporting and cultural services, and identifies the importance of soil functioning for almost all ecosystem services (Powlson *et al.*, 2011). For example, soil functioning plays a key role in the maintenance of the hydrological cycle, including flood mitigation, climate regulation and nutrient cycling. Together, these contribute to the production of food crops. In addition, soils form the basis of a stable physical environment for human settlements, including land used for infrastructure and farming.

Several soil-specific frameworks have been developed since the Millennium Ecosystem Assessment, offering quantitative assessments of ecosystem goods and services provided by the soil based on estimates of natural capital. Notably, Dominati *et al.* (2010) proposed a framework describing soil ecosystem services based on ‘inherent’ (e.g. depth, texture, slope, subsoil aggregate size) and ‘manageable’ (e.g. soil C and N, organic matter, temperature, pH, bulk density, topsoil aggregate size) properties of soil natural capital.

Natural capital stocks are defined in terms of mass (e.g. mineral and nutrient stocks, soil carbon, soil organisms and soil water), energy (e.g. thermal energy and soil biomass), and their organisation (e.g. physio-chemical structure, biological organisation, food web structure, spatio-temporal gradients) (Robinson and Lebron, 2010). Quantifying the value of natural products and services for human need in this way allows conservation bodies and policymakers to estimate the economic effects of change factors – for example, land use change – to humans, and to realise the actual costs of environmental degradation. If losses of natural capital can be compensated for by manufactured capital, or labour, no detrimental impacts will be observed (Millennium Ecosystem Assessment, 2005). However, the two cannot be infinitely substituted in either direction. For example, in the context of food production, a critical level of soil degradation will impair agricultural productivity regardless of manufactured capital inputs (Millennium Ecosystem Assessment, 2005).

Due to the array of natural capital stocks below-ground, soils can contribute substantially to a nation's wealth (Daily *et al.*, 1997). It is now recognised that environmental policies need to recognise the importance of preserving soil function and reducing soil erosion in order to preserve soil natural capital in the longer term (Dominati *et al.*, 2010). However, while many above-ground ecosystem services, such as pollination, can be relatively straightforward to value (i.e. the value of insect pollinated crops), the valuation of below-ground services is extremely complex. Firstly, there are logistical difficulties in measuring soil ecosystem processes due to the opacity of the soil and a lack of well-defined methodologies. Secondly, soil processes can be tightly interlinked, with some processes promoting others – for example, the decomposition of organic matter sustains soil nutrient cycling, and is regulated by soil biota and intrinsic properties of the soil – posing an additional challenge. Costanza *et al.* (1998) estimated the global value of ecosystem services derived from the soil to be worth tens of trillions of US dollars. In a more recent study, Brussaard *et al.* (2007) valued ecosystem services associated with soil biota alone to be worth $1.5 trillion.

## 1.2 Soil fauna and their contribution to ecosystem services

The soil food web, coined a "poor man's tropical rainforest" (Usher *et al.*, 1979), is characterised by high levels of species diversity, only a fraction of which is thought to have been identified (Wurst *et al.*, 2012). In addition, soil organisms exist in vast abundance, with the majority inhabiting the upper soil horizons, including the litter layer. One square metre of organic temperate agricultural soil can harbour 1,000 different species with population densities reaching $10^6$ nematodes and $10^5$ microarthropods (Altieri, 1999). In coniferous forest soils, enchytraeid worms can reach densities of 200,000 individuals $m^{-2}$ (Jeffery *et al.*, 2010). Soil microbial organisms are, however, the dominant organisms in soil communities both in terms of diversity and biomass (Jeffery *et al.*, 2010), with a single gram of soil supporting approximately $10^4$ microbial genotypes (Torsvik *et al.*, 2002) and over 45,000 genotypes occupying a hardwood forest soil (DeAngelis *et al*., 2015).

Soil fauna can be classified according to body size. At the smallest scale, soil microorganisms (< 0.2 mm diameter) include the microflora (bacteria and fungi) and microfauna (including nematodes, protozoans and rotifers), which require water-filled pores for mobility (Lavelle, 1997; Bonkowski *et al.*, 2011). Soil mesofauna range from 0.2-2 mm diameter, and include the microarthropods (soil mites and springtails), enchytraeid worms and tardigrades, which inhabit air-filled pores (Verhoef and Brussaard, 1990; Lavelle, 1997; Neher *et al.*, 1999). Soil mites include both predatory groups, including mesostigmatid (Acari: Mesostigmata) and prostigmatid (Acari: Prostigmata) mites, and detritivores, namely oribatid (Acari: Oribatida) mites. The astigmatid mites (Acari: Astigmata) were previously classed as a suborder of their own, but are now placed as a cohort within the Oribatida (Norton, 1998; O'Connor, 2009). Oribatid mites and springtails are the most well-studied soil microarthropods. At the largest scale, soil macrofauna measure > 2 mm diameter and can include earthworms and large arthropods associated with the litter layer, such as termites, centipedes, millipedes and woodlice (Lavelle, 1997; Jeffery *et al.*, 2010).

Biological communities are often self-organised (Lavelle *et al.*, 2006) and aggregated in distribution, with the greatest population densities occurring in resource-rich areas. However, aspects of below-ground community dynamics are fundamentally different to those above-ground. For example, above-ground biodiversity is influenced by a range of landscape-scale factors, including wider habitat heterogeneity and the availability of semi-natural habitat (Steffan-Dewenter *et al.*, 2002; Cunningham and Johnson, 2006; Gabriel *et al.*, 2006; Gabriel *et al.*, 2010). On the other hand, soil organisms are restricted in space due to their limited locomotory capacity. Therefore, below-ground patterns of biodiversity are thought to be influenced primarily by local-scale factors, such as microhabitat temperature, moisture and the local availability of organic matter (Bardgett *et al.*, 2005; Bardgett, 2005; Coleman *et al*., 2004).

Soil fauna contribute to the functioning of every terrestrial ecosystem through a combination of direct and indirect actions, including the cycling of nutrients, energy and materials (de Ruiter *et al*., 2002; Table 1.1). However, the relative contribution of different organisms to the provision of these services varies widely. It is thought that 80-90% soil processes are mediated by soil microbes (Nannipieri and Badalucco, 2003; Coleman *et al*., 2004). The relationship between soil microbial biodiversity and ecosystem functioning varies according to the activity rate, biomass and community structure (Joergensen and Emmerling, 2006 and references therein). Soil mesofauna and macrofauna primarily contribute to soil ecosystem functioning indirectly, for example by reducing particle size during the earlier stages of OM decomposition, and through the regulation of the soil microbial biomass by grazing (Lavelle and Spain, 2001).

**Table 1.1** Examples of ecosystem services provided by soil fauna, based on the classification of ecosystem services according to the Millennium Ecosystem Assessment (2005)

| Category | Ecosystem service | Soil-specific example | Reference |
|---|---|---|---|
| **Regulating** | Climate regulation | Soil microbial regulation of soil-land-atmosphere carbon exchange | (Conrad, 1996; Bardgett *et al.*, 2008) |
| **Regulating** | Flood mitigation | Infiltration and storage of water in soil through bioturbation and burrowing activity of earthworms | (Stockdill, 1982; Zachmann *et al.*, 1987) |
| **Regulating** | Disease regulation | Suppression of plant diseases by soil organisms, including springtails and nematodes | (Curl *et al.*, 1988; Lootsma and Scholte, 1997; Sabatini and Innocenti, 2001) |
| **Supporting** | Nutrient cycling | Decomposition of OM by multiple trophic groups | (González and Seastedt, 2001; Bradford *et al.*, 2002) |
| | | Rates of nutrient mineralisation and plant nutrient uptake affected by soil fauna, including springtails and nematodes | (Bardgett and Chan, 1999) |

| | | | |
|---|---|---|---|
| **Supporting** | Soil formation | Soil aggregate stabilisation by earthworm exudates | (Oades, 1993) |
| | | Contribution to OM layer formation by multiple trophic groups | (Lützow *et al.*, 2006) |
| **Supporting** | Primary production | Biocontrol of plant pests | (Akhtar and Malik, 2000) |
| | | Arbuscular mycorrhizal fungi symbioses promote plant nutrient uptake and above-ground productivity | (Jeffries *et al.*, 2003; Artursson *et al.*, 2006) |
| **Cultural** | Recreational | Use of earthworms as fishing bait | |
| **Cultural** | Educational | Use of earthworms as an educational tool for illustrating concepts such as soil porosity, bioturbation and OM recycling | |

An example of the complementarity of faunal roles is illustrated by the process of OM decomposition. Epigeic (litter-dwelling) earthworms and other decomposer macrofauna help to regulate the early stages of decomposition through the shredding, fragmentation and conditioning of plant material (Bardgett and Cook, 1998), increasing the surface area for smaller organisms. This earthworm activity quickly and directly alters detritivorous soil microarthropod (e.g. springtails) (Monroy *et al.*, 2011) and microbial (Aira *et al.*, 2008) communities, further promoting the decomposition of organic matter. Endogeic (soil-feeding) earthworms mediate later stages of decomposition through burrowing activity; modifying the soil structure for other soil organisms and transporting microbial populations. Furthermore anecic (deep-burrowing) earthworms physically redistribute organic matter by dragging it vertically through the soil profile. This process incorporates organic matter into the mineral soil, thus accelerating the rate of decomposition (Coleman *et al*., 2004). Microarthropods contribute to the decomposition processes by causing damage to plant material which may have been fragmented by earthworm activity, in turn further increasing the surface area available for microbial decomposition. Furthermore, microarthropods can shape microbial communities directly, through selective grazing, and indirectly, by supplying nutrients for microbial populations through the production and dispersal of faecal matter.

Within the soil invertebrates, much of the classical literature focuses on the contribution of earthworms to ecosystem function due to ease of sampling and their role as ecosystem engineers. Earthworms affect ecosystem services both directly and indirectly. For example, earthworms play a direct role in the formation of pores and channels within the soil profile to promote the cycling and mineralization of nutrients within the substrate and the creation of new habitat to promote the coexistence of multiple soil invertebrate groups (Maraun *et al.*, 1999), water infiltration, bioturbation and the stabilisation of soil aggregates (Eisenhauer, 2010). They also distribute P horizontally through the soil profile (Massey *et al.*, 2013). Soil microarthropods are one of the least well studied soil faunal groups. While their effects are likely to be smaller than those of the macrofauna or microfauna, mesofauna indirectly promote functions such as decomposition by increasing the surface area of organic material which the microbial biomass can act upon. This thesis will focus primarily on the impacts of intensive agriculture on soil mesofauna, and the relationships with ecosystem function. However, other faunal groups will be considered where appropriate.

Responses of soil faunal organisms to perturbation, and their recovery from disturbance, are likely to be dependent on both physiological traits, including those related to dispersal capacity, and life-history strategies. Firstly, the degree of exoskeleton sclerotisation affects the susceptibility of soil fauna to changes in the external environment, including soil moisture. Since soil moisture can vary with agricultural management directly, through the application of irrigation, and indirectly, for example through tillage (Frey *et al.*, 1999; De Vita *et al.*, 2007), exoskeleton sclerotisation is a key determinant of the ability to tolerate environmental perturbation. This will be explored throughout this thesis; particularly in Chapter 2. Generally, springtails and prostigmatid mites are more susceptible to changes in environmental conditions on account of their reduced cuticular sclerotisation (Convey *et al.*, 2003). On the other hand, oribatid and mesostigmatid mites have the greatest level of cuticular sclerotisation, and are therefore better able to withstand reductions in soil moisture levels (Convey *et al.*, 2003).

While soil moisture can affect fauna directly, as described above, their ecophysiology affects their ability to avoid – or escape from – adverse environmental conditions, including changes in soil moisture. For example, enchytraeid worms are unable to tolerate very low soil moisture levels, but, like earthworms, these organisms have the ability to respond to changes in the local environment by burrowing vertically through the soil profile to areas of more favourable (i.e. damper) environmental conditions (Springett, 1970; Nielsen, 1995a). Unlike enchytraeid worms, soil microarthropods lack the ability to burrow, instead relying on existing soil pores formed by burrowing organisms (earthworms and enchytraeid worms) for vertical movement, or by moving horizontally through the litter layer (Salmon, 2004; Cameron *et al.*, 2013).

While relatively little is known about how far and how fast soil mesofauna are able to disperse by active locomotion, the dispersal capacity of many microarthropod species is thought to be limited (Ojala and Huhta, 2001). In particular, detritivorous oribatid mites move slowly compared to predatory mesostigmatid mites and astigmatid mites. For these slow-moving mites, the additional cuticular thickness is of increased importance in order to tolerate existing environmental conditions and reduce the risk of desiccation. Dispersion of soil microarthropods can also occur passively, by wind and water or by phoresy; ‘hitch-hiking’ on another organism (Siepel, 1994). Astigmatid mites in particular rely on phoresy for movement across the landscape (Szymkowiak *et al*., 2007).

Unlike other soil organisms, springtails are unique in possessing a furcular; a tail-like appendage located on the ventral side of the fourth abdominal segment (Hopkin, 2007). The furcular acts as a ‘springing organ’, enabling the springtail to propel itself into the air. However, the direction of aerial movement is largely unpredictable and this rapid, erratic form of locomotion is mainly employed when individuals are under threat from predation or extreme adverse environmental conditions. Under typical conditions, springtails, like soil mites, are able to move across the landscape by walking. However, the extent to which the legs are developed varies between species (Ponge *et al*., 2006; Chapter 4).

In addition to the ecophysiological traits described above, soil mesofauna exhibit a diverse range of group- and species-specific life-history strategies, and this plays a significant role in their ability to recover from disturbance. For example, oribatid mites tend to undergo slow larval development, with life cycles lasting between 1-2 years (Behan-Pelletier, 1999). Under low temperatures, generation time can be extended to five years (Søvik *et al.,* 2003). In contrast, astigmatid mites are *r*-selected colonisers, with short generation times and high fecundity (Norton, 1999; Walter and Proctor, 1999; Chapter 2). Consequently, astigmatid mites thrive in disturbed sites, including agricultural soils under conventional tillage, where other groups struggle to survive (Wardle, 1995; Behan-Pelletier, 1999; Reeleder *et al.*, 2006).

While a wide range of species-specific differences exist; for example, in the ability to reproduce by parthenogenesis (Siepel, 1994; Lindberg and Bengtsson, 2005), crude differences in ecophysiology and life-history strategy can be observed between groups of soil mesofauna at the Suborder level. Therefore, it is possible to make predictions about the responses of different groups to perturbation. For example, it is likely that groups with good dispersal capacity, short generation times and high fecundity (e.g. astigmatid mites) would be less negatively affected by environmental perturbation (e.g. the application of a high dose of inorganic fertiliser) than poor dispersers with long generation times and low fecundity (e.g. oribatid mites).

## 1.3 Soil fauna and ecosystem disservices

In addition to playing a positive role in the functioning of the soil ecosystem through the provision of ecosystem services, soil fauna can also contribute to ecosystem disservices. Unlike ecosystem services, which describe ecosystem functions with positive impacts on human wellbeing, ecosystem disservices describe effects which are deemed undesirable, for example pollution, disease and biodiversity loss (Swinton *et al.*, 2007).

Whether soil biota promote ecosystem services or disservices can vary depending on resource availability. For example, nematodes transport soil microorganisms through ingestion and excretion or by adherence to the nematode surface coat (Bird, 2004). Thus, nematodes continually vary the structure of microbial communities and their activities. However, this service becomes a disservice if microbes are transported to resource-poor areas and are rapidly consumed by the nematodes (Fu *et al.*, 2005). In the absence of additional food, the nematode transporters then overgraze the limited prey available.

Furthermore, plant-associated nematodes at low densities cause minimal damage to plants through grazing, yet their presence provides resources for predatory fauna. However, overgrazing can lead to severe root damage, limiting the uptake of water and nutrients. These changes can restrict plant growth above-ground and, in turn, reduce food resources for the food web both above-ground and below-ground (Ferris, 2010). In order to successfully manage soil ecosystems and minimise the impacts of ecosystem disservices, we require a better understanding of the intricacies of the soil food web.

## 1.4 Threats to soil fauna

Relationships between soil organisms and intrinsic ecosystem functions can be disrupted through unsustainable land management (Wall and Six, 2015). Here, we briefly discuss some of the major threats to soil fauna and soil fauna-ecosystem function relationships appropriate to this thesis. Under the umbrella of agricultural intensification, the impacts of land use change, tillage and agrochemical use are explored. In addition, we also describe two additional threats to agricultural soil biodiversity: climate change and invasive species. While the soil food web comprises a number of different faunal groups, as discussed in Chapter 1.2, this thesis herein focuses on the effects on soil invertebrates and their contribution to ecosystem function. Impacts on soil microbes are briefly discussed in the context of soil invertebrates.

### 1.4.1 Agricultural intensification

Under a growing human population, increased crop yields are required, exerting increasing pressure on our food production systems. In addition, urban areas continue to expand into previously rural and semi-rural land (Goddard *et al.*, 2010), concreting over potentially fertile soils. If soil is used to support housing, rather than agriculture, its ability to deliver biological function is difficult to recover (Haygarth and Ritz, 2009). Furthermore, other land uses, such as biofuel production, also compete with productive farmland for space and resources (Fargione *et al.*, 2008). These pressures have resulted in the intensification of crop production on existing agricultural land. Agricultural intensification occurs through continuous cultivation, the loss of marginal habitats, increased agrochemical use and frequent disturbance (New, 2005; Smith *et al.*, 2008b). These factors promote productivity in the short-term, but exert increasing pressure on natural ecosystems.

Above-ground, agricultural intensification has been associated with declines in the abundance and diversity of a range of taxa, including farmland birds, mammals and arthropods (Fuller *et al.*, 1995; Chamberlain *et al.*, 2000; Donald *et al.*, 2001; Kremen *et al.*, 2002; Wickramasinghe *et al.*, 2003; Burel *et al.*, 2004; Wickramasinghe *et al.*, 2004). A causal factor in the decline in farmland biodiversity with increasing intensification is the change in landscape composition and, more specifically, the increased homogeneity of agricultural landscapes (Benton *et al.*, 2003; Bennett *et al.*, 2006). However, rather than the result of one factor, for example pesticide use or land use change, reductions in farmland biodiversity are likely to result from synergy between multiple changes in land management. This suggests that changes in the management of one factor will not act as a ‘cure all’ remedy in reducing biodiversity loss.

Despite hosting the majority of biodiversity in agronomic systems in terms of both abundance and diversity, relatively little is known about the effects of agricultural intensification on communities below-ground in comparison to our knowledge of above-ground systems. With increasing pressure exerted on global land, and particularly productive land, an improved understanding of the impacts of agricultural intensification on the complex relationships between soil biodiversity and ecosystem functioning is crucial if we are to manage soils in a sustainable way.

Soils are generally considered to be relatively stable habitats, buffered from diurnal and seasonal changes in abiotic conditions particularly in the presence of vegetative cover (Giller, 1996; Ettema, 1998). However, some soil properties are dynamic rather than static (e.g. soil moisture content), and are particularly susceptible to changes in land use (Robinson and Lebron, 2010). Below-ground, agricultural intensification accelerates rates of soil compaction, contamination and erosion and increases the vulnerability of the systems to perturbation. Since soil biota are tightly linked to soil properties, changes in land use may impair some soil processes and thereby contribute to a decline in ecosystem functioning in these systems. Here, we describe some of the major threats to soil biodiversity agronomic habitats and discuss consequences for ecosystem function.

#### 1.4.1.1 Tillage

Tillage can affect soil faunal communities both directly, through mechanical damage, and indirectly, via longer-term changes in soil moisture content, soil organic matter and the soil pore profile. Due to their larger body size, soil mesofauna and macrofauna are more susceptible to mechanical damage by tillage and changes in the habitable pore space (Kladivko, 2001). Within the soil macrofauna, epigeic earthworms are more sensitive to tillage than endogeic or anecic earthworms. Inhabiting the uppermost soil horizons makes epigeic species vulnerable to mortality caused by mechanical action and changes in resource availability (Kladivko, 2001). Movement of earthworm populations through tillage can also increase susceptibility to predation, for example by insectivorous birds (Giller *et al.*, 1997).

In general, microarthropods are also sensitive to tillage, with springtails, oribatid and mesostigmatid mites typically undergoing severe population declines in response to soil disturbance (Hendrix *et al.*, 1986; Wardle, 1995; Kladivko, 2001). However, astigmatid mites have been shown to recover rapidly from disturbance by tillage. Astigmatid mites are *r*-selected colonisers, characterised by short generation times and high fecundity (Norton, 1999; Walter and Proctor, 1999). This allows population densities to recover, or even increase, more quickly than groups with slow rates of development and low fecundity (e.g. oribatid mites) (Wardle, 1995; Behan-Pelletier, 1999; Reeleder *et al.*, 2006).

Tillage can also have indirect effects on soil invertebrates by modifying the soil structure and climate. Tillage physically disrupts the soil pore network through mechanical action, with complex effects on the soil microbial biomass (Young and Ritz, 2000). Changes in pore size and structure are only likely to have direct effects on larger soil invertebrates where body width exceeds pore size; however, these changes in the microbial biomass may have indirect bottom-up effects on microbial grazers. Furthermore, tillage disrupts the distribution of soil organic matter, with reduced soil organic matter observed in the upper horizons of tilled soils. Under reduced-till regimes (including no-till), where there is a greater amount of organic matter on the soil surface (Hendrix *et al.*, 1986), soils tend to be moister and cooler, providing favourable conditions for fungal growth and activity. Conversely, tillage disrupts the vertical stratification of the soil, incorporating crop resides through the soil profile. Consequently, tillage is associated with slow, fungal-dominated decomposition under reduced-till and no-till regimes, with a switch to bacterial-based pathways in conventionally tilled soils (Beare *et al.*, 1992; Frey *et al.*, 1999). These effects are fed up through the food chain, with rapid increases in the ratio of bacterial-feeding nematodes to fungal-feeding nematodes under disturbance regimes (Parmelee and Alston, 1986; McSorley, 2011). Furthermore, tillage can shift the composition of annelid assemblages, with a greater reduction in the abundance of metabolically slow earthworms compared to enchytraeids (Parmelee *et al.*, 1990).

#### 1.4.1.2 Agrochemical use

In conventionally managed agricultural systems, achieving maximum crop yields is largely dependent on agrochemical inputs (Matson *et al.*, 1997) and, in particular, inorganic fertilisers. However, soil fauna are sensitive to changes in soil chemistry, which influences their abundance and distribution through the soil profile (Edwards and Bohlen, 1996). Agrochemicals have been associated with reductions in soil fauna (Bünemann *et al.*, 2006; Tabaglio *et al.*, 2009; Thiele-Bruhn *et al.*, 2012). Furthermore, shifts in community composition have also been observed. For example, de Vries *et al.* (2006) observed the promotion of a bacterial-dominated nematode food web in response to increased N inputs. However, an absence of trends has been reported by others (Sarathchandra *et al.*, 2001). This lack of consensus may be due to a range of factors. Firstly, the effects of fertilisation are likely to be specific to particular soil faunal groups. As described in Chapter 1.2, differences in the ecophysiology and life-history strategies of different soil mesofaunal groups are likely to result in different responses to agricultural management. For example, it is hypothesised that groups with good dispersal capacity, short generation times and high fecundity (e.g. astigmatid mites) will recover more quickly following the application of fertiliser than those with poor dispersal capacity, long generation times and low fecundity (e.g. oribatid mites).

Furthermore, observed effects may be variable between systems, depending on the existing soil type and management history. Specifically, effects of fertiliser inputs are likely to depend on the N concentration and the duration of use. For example, Edwards and Lofty (1982) reported elevated earthworm population sizes under moderate nitrogen concentrations (up to 192 kg N $ha^{-1}$), while an excessive amount of liquid sludge applied in a single dose had a negative effect.

Few studies have attempted to investigate the effects of agrochemical use on the wider soil food web, including predator-prey interactions. Moreover, the effects of agrochemical application on soil biodiversity-ecosystem function relationships are relatively unknown. These gaps are addressed in greater detail in Chapters 2 and 5.

### 1.4.2 Invasive species

Invasive species pose a threat to the functioning of above-ground and below-ground ecosystems, within both terrestrial and aquatic environments. Since its introduction in the 1960s, the New Zealand flatworm (*Artioposthia triangulata* Dendy) has attained a widespread distribution across the United Kingdom, particularly across Ireland, Scotland and parts of NW England due to similarities to its native climate, and now poses a threat to native earthworms (Boag and Yeates, 2001, NBN Gateway, 2013). Murchie and Gordon (2003) predict that *A. triangulata* infestations could reduce total earthworm biomass by approximately 20% in agricultural lands, with particular effects on the common European earthworm (*Lumbricus terrestris* L.).

*A. triangulata* preys upon multiple native species, but is a particular threat to large, anecic earthworms including *L. terrestris*, the ‘night crawlers’, which feed on and migrate across the soil surface at night. Anecic earthworms form deep burrows through the soil profile, improving soil aeration and drainage. Therefore, a reduction in *L. terrestris* populations could affect the water holding capacity of soils, leading to localised flooding and crop failure. Additionally, these worms are a key component of the diet of multiple bird species, including blackbirds and song thrushes. Subsequently, reduced population densities of native earthworms may have bottom-up effects on higher trophic levels (Alford *et al.*, 1995).

### 1.4.3 Climate change

Climate change factors, including increased temperatures and drought, severely threaten food production systems worldwide. Their effects on above-ground faunal communities have been explicitly examined (Bezemer and Jones, 1998; Chen *et al.*, 2005; Dukes *et al.*, 2009; Visser *et al.*, 2009; Bentz *et al.*, 2010; Aslam *et al.*, 2013;

Romo and Tylianakis, 2013). However, below-ground effects are again under-represented within the literature.

It is likely that the direct effects of drought will be of particular concern to soil organisms. Soil ecosystems depend on the availability of water for optimal functioning and, while soils can buffer the effects of mild drought stress, extended periods of moderate to severe drought may not be tolerated so well. For example, nematodes rely on soil water-films for dispersal and feeding (Jones 1975); therefore, significant reductions in soil moisture content resulting from global climate change may have pronounced effects on their performance and survival, restricting feeding and ultimately leading to starvation or desiccation.

In the case of pest species, for example the root knot nematode (*Meloidogyne* spp. Goldi), these changes may impact positively on the provision of ecosystem services. Drought-induced reductions to pest populations would likely lead to improved crop yields and, in turn, economic benefits. However, reductions in other guilds are likely to have marked negative effects at the community and ecosystem scale. For example, shifts in the ratio of bacterial feeders to fungal feeders may alter rates of decomposition, with impacts on carbon sequestration. Since the importance of storing carbon below-ground is of increasing importance under proposed climate change scenarios (Lal, 2008), these changes could have consequences for the global carbon budget. On the other hand, reduced densities of predatory nematodes may lead to explosions of pest populations and subsequent damage to productivity.

Soil faunal recovery from climate change events is likely to depend not only on the severity of effect, but also on the life history strategies of organisms and their dispersal capacity. For example, Lindberg and Bengtsson (2005) found that abundances of collembolans, characterised by relatively short generation times lasting only a few months, recovered more quickly from the effects of experimental drought treatment than oribatid mites, which tend to have longer life cycles spanning multiple years (Chapter 1.2). Furthermore, a higher number of oribatid species able to reproduce parthenogenetically recovered within the four-year experimental period than those that relied on sexual reproduction. This work suggests that recolonisation of land following short-term climate change events is likely to take several years and, in the earlier stages of recovery at least, populations are likely to be dominated by species with fast generation times and good dispersal capacity such as astigmatid mites and some springtail species (Chapters 1.2 and 6).

As with above-ground systems, any impact on the provision of ecosystem services is likely to depend on the severity and variability of climate change factors, which are expected to vary on both spatial and temporal scales (IPCC, 2013). Since different climate change factors are expected to occur simultaneously, direct effects of drought on soil fauna are likely to be modified by increased temperature and subsequently the relative humidity of the soil. Therefore, future work should be set in a broader context to investigate how multiple climate change factors might interact with one another to influence the distribution of soil organisms and the provision of ecosystem services.

## 1.5 Research gaps

The importance of healthy agricultural soils in the drive for global food security under the pressure of a growing population cannot be underestimated. However, this challenge is made far more complex by our fragmented understanding of the relationships between below-ground biodiversity and ecosystem functioning. In particular, clear knowledge gaps exist in terms of the additive effects of multiple drivers of soil change. In order to satisfy the multifaceted challenge of sustainable food security, a broader, more comprehensive understanding of the drivers of below-ground agroecosystem dynamics is required. Here, we discuss some of the major knowledge gaps in soil diversity-function research.

### 1.5.1 Community and systems approaches

Numerous studies have explored the impacts of land-use change, including changes associated with agricultural intensification, on a single species or small group of soil-dwelling species. These studies offer valuable insights into specific relationships. In reality, however, soil organisms do not exist in the environment in isolation. Rather, the soil food web is a complex, inter-linking network of interacting organisms. Furthermore, soil organisms are characterised by a variety of physiological traits and life-history strategies that means they can exhibit a broad range of responses to the same environmental perturbation (Chapter 1.2). Consequently, studying the response of a single species or group of species to a stressors offers only a small insight into the effects on the soil community. Therefore, this thesis examines the impacts of intensive agricultural management on relationships between soil mesofauna and ecosystem function from a community perspective, including both detritivorous and predatory groups.

As discussed in Chapter 1.2, crude differences in the ecophysiology and life-history strategy of soil mesofauna at the suborder level enable us to make predictions about the responses of different groups to perturbation. For example, we can predict that groups with good dispersal capacity, short generation times and high fecundity (e.g. astigmatid mites) would be less negatively affected by environmental perturbation (e.g. the application of a high dose of inorganic fertiliser) than poor dispersers with long generation times and low fecundity (e.g. oribatid mites). Therefore, this thesis primarily assesses shifts in soil mesofaunal community structure at the suborder level, with some species-level work in Chapter 4.

### 1.5.2 Field observations

The soil poses a difficult medium to study due to its opacity and, therefore, sampling is typically, to a degree, destructive. In recent years, however, technological advancements have allowed researchers to view soil in its undisturbed state. For example, X-ray tomography has been used to revolutionise our understanding of rhizosphere interactions (Mooney *et al.*, 2012) and soil microhabitat structure (Nunan *et al.*, 2006). X-ray tomography has also been used to visualise the horizontal and vertical distribution of earthworm burrows in 3D space, which allows for predictions to be made as to how burrowing activity can affect the hydraulic properties of soil, e.g. water flow (Bastardie *et al.*, 2003). Additionally, this technique has been used to examine the trajectories of the root-feeding larvae of plant pests (Johnson *et al.*, 2004). A second advancement in the in-situ study of plant roots and root-associated soil microorganisms is the use of transparent substrate (Downie *et al.*, 2012; Downie *et al.*, 2014).

Methods such as these have the capacity to significantly advance research into soil processes. For studies of invertebrate populations, however, field studies using real soils in real environments, subjected to climatic effects and so on, are needed in order to make assessments of the effects of agricultural practices on diversity-function relationships. Therefore, this thesis examines the impacts of intensive agricultural management on relationships between soil mesofauna and ecosystem function in realistic field settings, including both plantation and arable systems.

Nevertheless, there are issues with field observations. Most importantly, soils are opaque and observations of soil dwelling-invertebrates necessitate careful extraction from the soil. A number of studies overcome this challenge by sampling the leaf litter only (e.g. Lensing *et al*., 2005), thus avoiding the need for the destructive sampling of the bulk soil. However, the spatial stratification of soil-dwelling invertebrates is transient, varying with soil properties such as moisture and pH. For example, the surface litter layer provides rich habitat for detritivores, including springtails (Irmler, 2006), and populations will aggregate in areas of high resource availability under favourable conditions. However, if soil moisture is reduced or temperature increased, springtails will migrate to the upper soil layers in search of damper, cooler conditions (Hassall *et al.*, 1986). Thus, sampling only the litter layer can give biased estimates of population densities and/or community composition under different environmental conditions. Furthermore, the effects of treatment variables may over-estimated, or indeed under-estimated, in the case of resource enrichment studies. Consequently, the studies described in this thesis explore changes in abundance and community structure within the upper 10 cm soil, where the majority of soil microarthropods are found (Al-Deeb *et al*. 2003).

### 1.5.3 Sustainable intensification for soil conservation

Agricultural intensification exerts increasing pressure on soils. Since soils are considered to be non-renewable on the scale of human generations, the fundamental challenge to food security within a soil framework is to manage soils in a sustainable way; maintaining productivity from existing farmland, or smaller amounts of land, while minimising negative environmental impacts and conserving ecosystem function. This concept is known as sustainable intensification. In the context of soils, maintaining soil health requires a reduction in the rate of soil erosion and acidification, and the conservation of soil biodiversity (Kibblewhite *et al.*, 2008). A key aspect of agricultural intensification is the use of high levels of synthetic inputs. Under the growing threat of diminishing resources, including the phosphorus crisis, and increasing costs, this is likely to be unsustainable and farmers may be forced to apply smaller amounts of fertiliser.

The role of soil mesofauna in ecosystem function is primarily manifested through their impacts on the microbial biomass, which affect rates of decomposition, nutrient bioavailability and seedling emergence (Coleman *et al*., 2004; Mitschunas *et al*., 2008). However, the extent to which soil mesofauna can contribute to ecosystem function, including productivity, remains unclear (Cole *et al*., 2004). It is likely that these effects will depend on the prior damage caused by agricultural management and the composition of the faunal community. The abundance of detritivorous fauna (e.g. oribatid mites and springtails) of particular importance here due to their role in decomposition and nutrient cycling.

Chapters 3 and 5 of this thesis will explore the relationships between soil mesofauna and ecosystem function, and how these relationships change under the application of different fertiliser types and N concentrations. This knowledge is particularly important under a sustainable intensification framework where, in addition to advances in crop breeding (e.g. low N-requiring varieties) and fertiliser use efficiency, consideration must be given to the application of varying types and quantities of fertilisers for maintaining, or increasing, crop yields while limiting adverse effects on the environment.

## 1.6 Objectives of the thesis

This thesis considers the issues raised in Chapter 1.5. Specifically, this thesis:

1. Investigates the effects of intensive agriculture on soil fauna-function relationships using realistic management practices in field systems.
2. Explores the effects of agricultural management practices on multiple soil invertebrate groups simultaneously.
3. Draws comparisons between the effects of intensive agricultural management in multiple systems, with varying soil types.
4. Makes recommendations for ways in which any negative observed effects of intensive agriculture on soil diversity-function relationships can be minimised.

## 1.7 Thesis outline

This thesis is presented in four main chapters, each addressing one or more of the objectives outlined in Chapter 1.6.

In Chapter 2, the contributions of biotic and abiotic factors in controlling temporal changes in populations of soil mesofauna are examined over the equivalent of a growing season. In particular, we consider the role of climatic variation, fertiliser application and predator-prey interactions. Interactions between fertiliser application, in varying forms and application rates, and soil parameters are also considered.

In Chapter 3, the impacts of intensive management on the abundance and community composition of different soil mesofaunal and microfaunal groups are considered in an Australian eucalypt plantation system. In particular, we evaluate the effects of fertilisation and irrigation regimes. Changes in abundance and community structure in response to management regimes are related to changes in soil nutrient bioavailability as a proxy for ecosystem functioning.

In Chapter 4, we explore changes in soil invertebrate abundance and community composition along a gradient of agricultural management intensity from woodland to field. The value of different non-crop habitats, including adjacent woodlands, hedgerows and grassy margins, as refugia for soil invertebrates are assessed and related to the conservation value for above-ground fauna.

In Chapter 5, we investigate the effects of fertiliser use, including different types and application rates, on relationships between soil invertebrates and ecosystem function above-ground and below-ground.

In Chapter 6, we review the key findings of the four studies described previously and discuss their relevance to agricultural soil management more generally. We also discuss priorities for future research.

# Chapter 2

# Complex drivers of soil mesofaunal population growth: density-dependence, environmental variation and fertiliser inputs

## Abstract

The population and community dynamics of organisms are a result of the complex interplay between stochastic, trophic, seasonal and competitive interactions. Soil organisms contribute to a broad range of ecosystem functions, yet our understanding of the impacts of intensive management on their population dynamics is far from comprehensive. Using a replicated, randomised field trial design, we explored the contribution of exogenous and endogenous factors in controlling the temporal dynamics of soil mesofaunal populations over the equivalent of a growing season. Furthermore, we investigated the impacts of a perturbation, in the form of fertiliser application, on these patterns. We observed strong evidence of seasonal patterns of abundance, which were modified by variation in the physical environment, and trophic and competitive interactions. This study is the first to show that soil mesofaunal community dynamics can be affected by perturbation in the form of fertiliser application.

## 2.1 Introduction

Intensive agricultural management has accelerated rates of soil erosion globally, such that approximately one third of soils are now classified as being moderately to highly degraded (FAO, 2015a). A recent FAO report states that, in some areas of the world, soils are degrading at such a rate that only 60 years of soil functionality remain. In the United Kingdom, it is predicted that only 100 harvests remain in agricultural soils (Edmondson *et al*., 2014). In Chapter 1, we discussed how soil biological communities contribute to a wide range of ecosystem functions and services. However, there are significant gaps in our understanding of how intensive management impacts on these communities. Understanding the impacts of intensive management is crucial if we are to manage soil biodiversity in a sustainable way.

Advances in the theory of the population and community dynamics of organisms mean that we have broad expectations about the interplay of stochastic, trophic, seasonal and competitive interactions. For example, we know that variation in the environment, e.g. the quantity or spatial arrangement of food, interacts with organisms' life histories to feed into population dynamics, ultimately influencing population size (Sæther, 1997; Beckerman *et al.*, 2003; Benton *et al.*, 2006). Different groups of organisms react to the same environmental stochasticity differently, with consequences for population size and structure (Coulson *et al.*, 2001). Consequently, organisms can be seen as biological filters, modifying environmental signals into changes in population dynamics (Benton and Beckerman, 2005).

Furthermore, delayed life history effects can be transmitted from parent to offspring (Rossiter, 1991; Mousseau and Fox, 1998; Beckerman *et al.*, 2002). Hence, an organism's performance is likely to depend on current conditions and those experienced by previous generations. The strength of parental effects, and particularly maternal effects, is again contingent upon the environment. For example, high food availability can erase the effects of the environment experienced by previous generations (Benton and Beckerman, 2005). In addition, we know that environmental effects depend on species assemblages and the age- or stage-structure of the population. For example, Cameron and Benton (2004) found that the stage-structure of mite populations before a perturbation, such as a harvesting event, can alter the structure of the population after the perturbation. Therefore, there is huge complexity in the interactions between the environment, the life histories of organisms and their biology, which ultimately affects their population dynamics.

Different species respond to variability in the physical environment, e.g. weather patterns and other abiotic stressors, and the biotic environment, e.g. food availability and predators, in complex ways. For example, soil moisture can be a strong driver of soil invertebrate abundance (Badejo and Van Straalen, 1993; Hopkin, 1997; Ferguson and Joly, 2002), with peak springtail population densities occurring after rainfall events (Badejo *et al.*, 1998). Furthermore, variation in the physical environment can affect life history by altering rates of fecundity; for example, springtail reproduction can be inhibited under low soil moisture (Van Gestel and Van Diepen, 1997; Choi *et al.*, 2002).

The temperature of the surrounding physical environment can also be a key driver of fecundity, as shown in fish (Kraus *et al.*, 2000; Pörtner *et al.*, 2001) and arthropods, both above-ground (Karlsson and Wiklund, 2005) and below-ground (Ydergaard *et al.*, 1997). In addition, temperature can affect juvenile development rate (Kasuga *et al.*, 2006). Again, interactions between organisms and their environment can involve trade-offs along the life history trajectory. For example, temperature may increase fecundity but this can result in a trade-off with size at maturity (Arendt, 2015).

The ecophysiology of different invertebrate groups shapes their responses to variation in the physical environment. For example, springtails have limited burrowing capacity and, while movement may occur between the litter and humus layers in response to changes in environmental conditions (Hassall *et al.*, 1986; Sgardelis *et al.*, 1993), under drought conditions individuals are forced to undergo horizontal migration, become immobilised until conditions improve (Bauer and Christian, 1993) or die. However, other groups, such as enchytraeids, have been shown to respond to changes in soil moisture through vertical migration to deeper, moister soil horizons (Nielsen, 1955b; Springett, 1970).

In addition to abiotic factors, biotic controls can also regulate biological communities in a complex way. A key question of population ecology is whether populations are controlled by resource availability and competition for resources (bottom-up control) or by effects of predation at higher trophic levels (top-down control). There is considerable evidence that detritus-based food webs are regulated by bottom-up forces, with densities of organisms at lower trophic levels controlling the abundance of detritivorous and predatory groups (Scheu and Schaefer, 1998; Chen and Wise, 1999; Laakso and Setälä, 1999). On the other hand, top-down forces can also play a role in the regulation of soil food webs (Bengtsson *et al.*, 1997; Hedlund and Öhrn, 2000; Lenoir *et al.*, 2007). While there is little evidence for top-down trophic cascades in soil systems, predator-prey interactions can affect herbivore and detritivore communities. For example, detritivorous mesofauna may become prey for mesostigmatid mites and some prostigmatid mites, in addition to larger arthropod predators, including carabids, centipedes and wolf spiders (Schaefer, 1995; Meek *et al.*, 2002; Lewis, 2007). Furthermore, predators above-ground can have trickle down effects on the below-ground food web (Wardle *et al.*, 2005).

In fact, soil community composition is likely to be determined by a combination of top-down and bottom-up regulatory factors, in addition to abiotic factors. For example, Ferguson and Joly (2002) reported that litter-dwelling soil springtail and mite communities were determined primarily by climate and density-dependent competition for food, assumed from a negative effect of lagged densities, and secondarily by predation by macroarthropods. The relative contribution of these factors in shaping soil community dynamics is likely to vary between systems and depend, for example, on the availability of resources. Indeed, Valiela *et al.* (2004) argue that top–down control becomes more important under low nutrient availability in aquatic environments, and there is also evidence for this in soil communities (Lenoir *et al.*, 2007).

Understanding changes in population abundance over time is a major challenge in population biology research (Cushing *et al.*, 1998). The majority of studies examining above-ground invertebrate population dynamics assess changes in abundance with yearly lags (Turchin, 1990; Perry *et al.*, 1993; Hunter and Price, 1998). There is strong evidence to suggest that soil communities are relatively stable in the longer-term, with little annual variation in abundance or community composition (Kampichler and Geissen, 2005; Irmler, 2006). However, due to the strong regulatory power of climatic factors in controlling soil faunal populations, most groups exhibit marked seasonal changes in abundance in response to seasonal changes in environmental conditions. Responses to climatic conditions are further determined by the strength and duration of climatic change; for example, Sulkava and Huhta (2003) reported greater reductions in microarthropod and enchytraeid worm abundances under severe frosts, compared to soils undergoing freeze-thaw cycles or constant benign temperatures.

While we have a broad understanding of the interplay of stochastic, trophic, seasonal and competitive interactions that affects population dynamics, there is a knowledge gap surrounding the temporal dynamics of soil communities and, in particular, the effects of perturbation on these dynamics. Therefore the aim of this study was to explore how a perturbation at the start of a season, through the application of fertiliser, impacted on the temporal dynamics of soil faunal populations. Using a field plot experiment, we investigated the effects of fertiliser inputs, in addition to climatic variation and biotic interactions, on changes in soil mesofaunal abundance over the equivalent of a growing season. We hypothesised that changes in soil mesofaunal abundance would be primarily driven by abiotic factors, mainly through resource enrichment, and secondarily by biotic factors, including competition and predator-prey interactions. In particular, we predicted that moisture content and soil temperature would promote the growth of springtail and soil mite populations respectively. It was further hypothesised that inorganic fertiliser inputs would slow the rate of population increase, while organic inputs would support the highest densities of detritivorous groups (e.g. springtails, oribatid mites and enchytraeid worms). Under inorganic fertiliser regimes, it was predicted that taxa with short generation times (e.g. springtails) would recover from any adverse effects more quickly than those with longer generation times (e.g. oribatid mites and enchytraeid worms).

## 2.2 Methods

### 2.2.1 Study site

The field site, comprising 16 4m$^2$ plots in a randomised block design, was situated on a grassy area at Spen Farm, West Yorkshire, UK (53°51'38.2"N, 1°19'46.7"W). The site had been out of cultivation for over 10 years prior to the study, with no agrochemicals applied during this period.

### 2.2.2 Experimental design

Each block of four plots comprised the following experimental treatments: standard dose ammonium nitrate fertiliser (175 kg N ha$^{-1}$; SD), double dose ammonium nitrate fertiliser (350 kg N ha$^{-1}$; DD), pig slurry and straw (175 kg N ha$^{-1}$; O), and an untreated control (C). Standard dose fertiliser application rates reflected those applied to the same area over the past 10 years (M. Langdale, pers. comm.). A free-draining, lime-rich clay loam soil type, characterised by a moderate water-holding capacity (Aberford type), dominated the field site (NSRI, 2013).

### 2.2.3 Soil sampling

Soil sampling took place during week 0 (9th May 2013), week 1 (immediately prior to the application of fertilisation regime; 16th May 2013), and weeks 2 (23rd May 2013), 3 (30th May 2013), 4 (6th June 2013), 6 (20th June 2013), 8 (4th July 2013), 10 (18th July 2013), 14 (15th August 2013) and 18 (12th September 2013). At each sampling event, six soil cores were collected from each experimental plot using a soil corer measuring 8 cm in diameter and 10 cm in depth, and combined to form a composite sample. A random number generator was used to select sampling locations over a grid of each experimental plot. This process was repeated at each sampling event to reduce the chance of sampling the same area on multiple occasions. Microarthropods were then extracted into 70% ethanol using a modified Tullgren funnel method with increasing light intensity over a six day period. During this time, the photoperiod was progressively extended to create a temperature gradient designed to drive soil fauna through the soil profile. Individuals were counted and identified to order level under a binocular microscope (Leica MZ75).

At each sampling event, two additional soil core samples measuring 8 cm in diameter and 10 cm in depth were taken from each sampling site, combined and homogenised. The locations of these cores were also selected using a random number generator, and this process was repeated at each sampling event. Soil moisture content was calculated by drying 25 g soil at 130 °C for 72 hours. A 10 ± 0.1 g subsample was then sieved, mixed with 50 ml distilled water and the pH of the resulting suspension measured.

### 2.2.4 Estimating soil temperature

Soil temperature data were obtained from an automated weather station (53°52'7.6''N, 1°19'7.9''W) at Headley Hall, University of Leeds Farms, West Yorkshire, UK. The weather station was situated approximately 1 km from the experimental plots. Soil temperature was measured 10 cm below the soil surface every minute by an automated temperature sensor. For all environmental variables, mean average values were calculated for the week preceding each soil sampling event.

### 2.2.5 Statistical analysis

Statistical analyses were conducted using R (R Core Development Team, 2014). Linear mixed effects models were used to analyse the effects of treatment on the abundance of soil fauna at different time points. Block was included as a random factor. Covariates included fertiliser treatment, soil moisture, soil pH and soil temperature. Where a non-linear relationship was observed between faunal abundance and soil temperature, a polynomial effect of temperature was modelled. A first-order autoregressive covariance structure (‘corAR1’) was used to account for temporal autocorrelation in the dependent variable using the R package *nlme* (Pinheiro *et al*., 2015). In each model, the log-transformed abundance of the faunal group of interest at t+2 or t+4 weeks was specified as the dependent variable. Using two- and four-week lags addressed the irregular sampling intervals (Chapter 2.2.3). Log-transformed abundances of relevant predator or prey groups at t were included as covariates, selected based on a priori knowledge of the system. The abundance of the group of interest at t was also included.

For each analysis, two maximal models were constructed in *nlme*, including all covariates with interactions and random terms, and abundance of the focal group at t+2 and t+4 weeks. The ‘dropterm’ function in the R package *MASS* (Venables and Ripley, 2002) was used to explore model structure by simplifying the over-parameterised full models to create a set of plausible candidate models. Models were then compared using second-order Akaike Information Criteria (Burnham and Anderson, 2002).

## 2.3 Results

The three best candidate models generated from the analysis of the abundance of oribatid mites (Table 2.1), mesostigmatid mites (Table 2.2), prostigmatid mites (Table 2.3), astigmatid mites (Table 2.4), springtails (Table 2.5) and enchytraeid worms (Table 2.6) are presented.

**Table 2.1** Model selection table for oribatid mite analysis. The best three candidate models are presented, with the best model indicated in bold. All models contained a random blocking term. Abundance at t+2 weeks was used as the dependent term

| **Model** | **Log *L*** | **AICc** | **K** | **wi** |
|---|---|---|---|---|
| time*treatment + abundance at t + predator abundance at t + treatment * moisture + temperature + treatment * pH | -93.02 | 220.50 | 14 | 0.02 |
| **time*treatment + abundance at t + predator abundance at t + temperature + treatment * pH** | **-87.67** | **212.84** | **15** | **0.84** |
| time*treatment + abundance at t + predator abundance at t | -84.77 | 216.74 | 18 | 0.12 |

**Table 2.2** Model selection table for mesostigmatid mite analysis. The best three candidate models are presented, with the best model indicated in bold. All models contained a random blocking term. Abundance at t+2 weeks was used as the dependent term

| **Model** | **Log *L*** | **AICc** | **K** | **wi** |
|---|---|---|---|---|
| time*treatment + abundance at t + prey abundance at t + treatment * moisture + temperature + treatment * pH | -124.05 | 312.99 | 24 | 0.05 |
| **time*treatment + abundance at t + prey abundance at t + temperature + treatment * moisture** | **-126.98** | **305.16** | **20** | **0.98** |
| time*treatment + abundance at t + prey abundance at t + temperature + treatment * pH | -135.07 | 321.35 | 20 | 0.00 |

**Table 2.3** Model selection table for prostigmatid mite analysis. The best three candidate models are presented, with the best model indicated in bold. All models contained a random blocking term. Abundance at t+2 weeks was used as the dependent term

| **Model** | **Log *L*** | **AICc** | **K** | **wi** |
|---|---|---|---|---|
| time*treatment + abundance at t + prey abundance at t + treatment*moisture + treatment*pH | -174.01 | 413.74 | 23 | 0.16 |
| time*treatment + abundance at t + prey abundance at t + treatment*moisture | -182.60 | 415.87 | 19 | 0.05 |
| **time*treatment + abundance at t + prey abundance at t** | **-186.48** | **410.45** | **15** | **0.79** |

**Table 2.4** Model selection table for astigmatid mite analysis. The best three candidate models are presented, with the best model indicated in bold. All models contained a random blocking term. Soil temperature was modelled as a quadratic effect. Abundance at t+4 weeks was used as the dependent term

| **Model** | **Log *L*** | **AICc** | **K** | **wi** |
|---|---|---|---|---|
| **time * treatment + abundance at t + enchytraeid abundance at t + temperature** | **-145.74** | **325.94** | **14** | **1** |
| time * treatment + abundance at t + predator abundance at t + treatment*moisture + enchytraeid abundance at t | -144.69 | 340.04 | 19 | 0 |
| time * treatment + abundance at t + enchytraeid abundance at t | -156.76 | 345.04 | 13 | 0 |

**Table 2.5** Model selection table for springtail analysis. The best three candidate models are presented, with the best model indicated in bold. All models contained a random blocking term. Abundance at t+4 weeks was used as the dependent term

| **Model** | **Log *L*** | **AICc** | **K** | **wi** |
|---|---|---|---|---|
| **time*treatment + abundance at t + predator abundance at t + temperature + moisture** | **-114.11** | **264.23** | **15** | **0.96** |
| time*treatment + moisture + predator abundance at t + temperature | -118.69 | 270.57 | 14 | 0.04 |
| time*treatment + abundance at t + predator abundance at t + temperature | -120.66 | 277.31 | 15 | 0.00 |

**Table 2.6** Model selection table for enchytraeid worm analysis. The best three candidate models are presented, with the best model indicated in bold. All models contained a random blocking term. Abundance at t+4 weeks was used as the dependent term

| **Model** | **Log *L*** | **AICc** | **K** | **wi** |
|---|---|---|---|---|
| **time * treatment + abundance at t + temperature + treatment*moisture** | **-190.28** | **422.41** | **17** | **0.96** |
| time * treatment + abundance at t + predator abundance at t + temperature + treatment*moisture | -190.35 | 428.69 | 19 | 0.04 |
| time * treatment + abundance at t + predator abundance at t + treatment*moisture | -198.71 | 442.31 | 18 | 0.00 |

The abundance of soil mesofaunal groups differed over the course of the study period under the unfertilised control treatment (Fig. 2.1). Declines in mite abundance after week 14 are likely to be a result of peak soil temperature and low soil moisture in the topsoil.

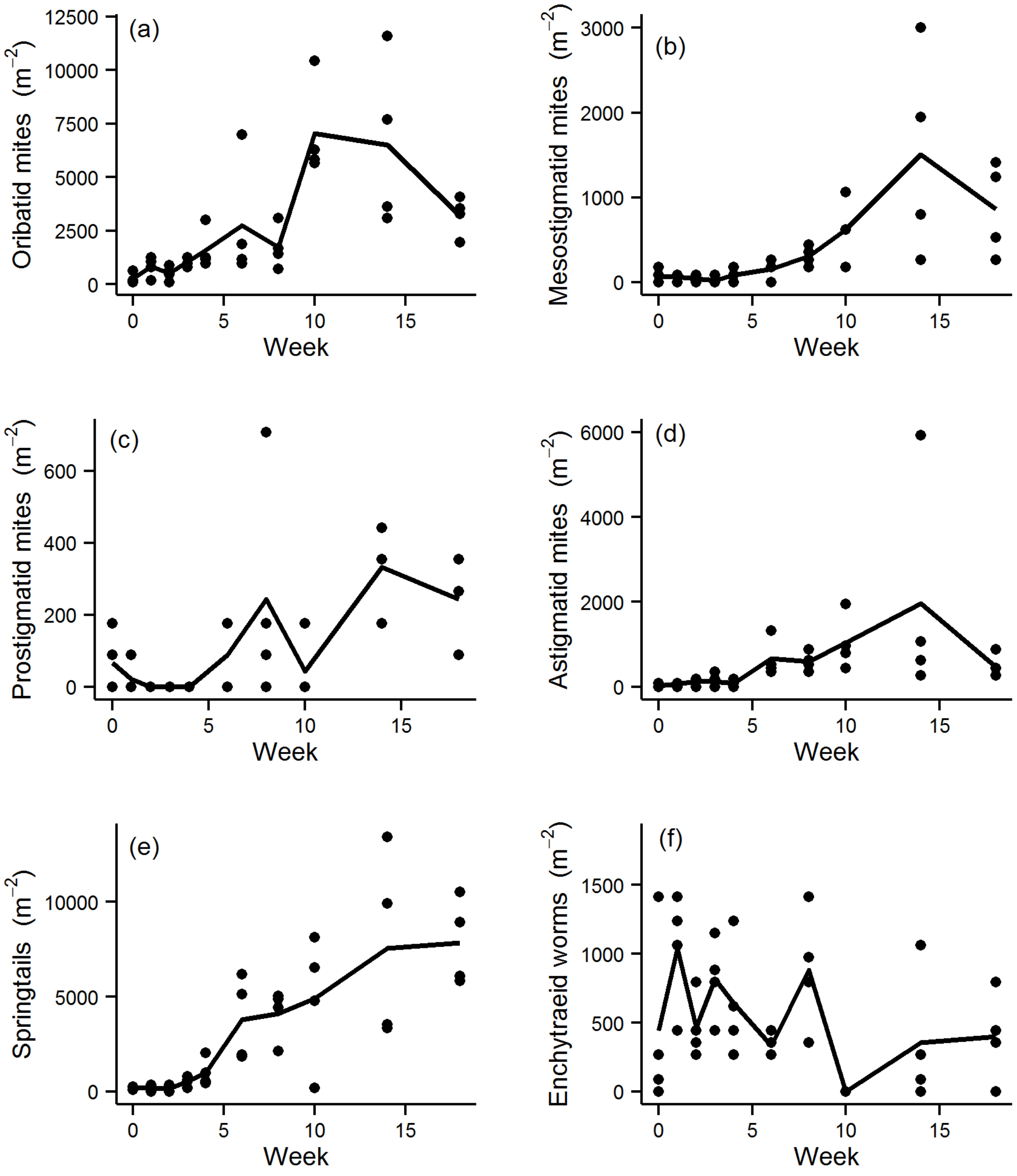


**Fig. 2.1** Changes in the abundance of (a) oribatid mites, (b) mesostigmatid mites, (c) prostigmatid mites, (d) astigmatid mites, (e) springtails and (f) enchytraeid worms over the equivalent of a growing season, from 9th May 2013 (Week 0) to 12th September 2013 (Week 18). Abundance data were estimated from unfertilised plots. The solid line represents the mean change in invertebrate abundance between time points, with dots representing individual data points

### 2.3.1 Impacts of soil environmental factors and fertiliser treatments

We observed a significant treatment × time interaction on the abundance of astigmatid mites ($F_{66} = 3.28$, $P = 0.03$). In particular, changes in population size under O differed to DD ($t_{66} = 4.29$) and SD ($t_{66} = 2.78$, both $P < 0.01$; Fig. 2.2a). Changes in springtail abundance over time varied between O and C ($t_{81} = 2.47$, $P = 0.02$; Fig. 2.2b). However, whilst treatment was retained in the best model using AICc, contrast tests performed on the best model indicated that the overall effect of fertiliser treatment was not statistically significant ($P > 0.05$).

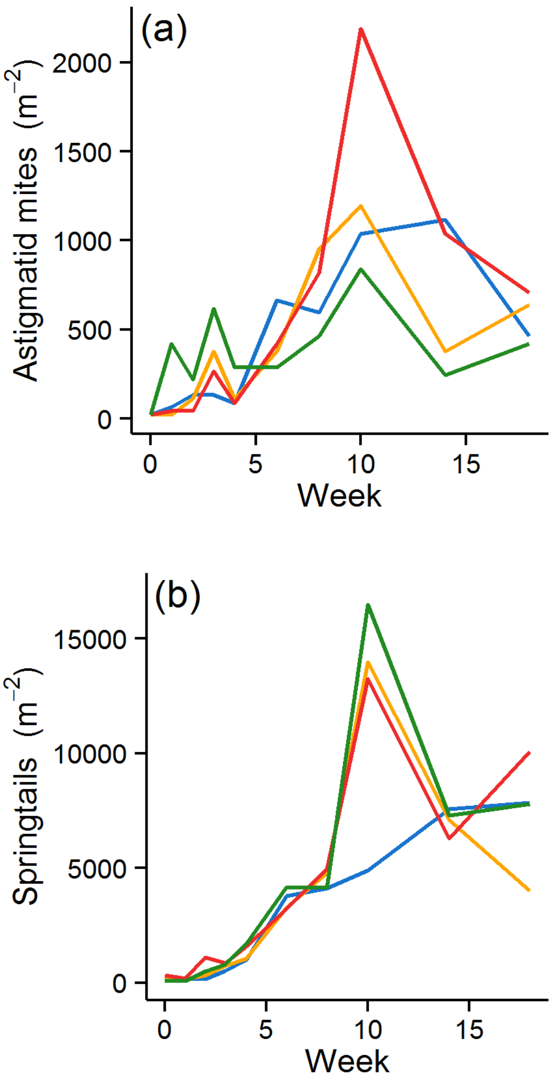


**Fig. 2.2** Changes in the abundance of (a) astigmatid mites and (b) springtails over the equivalent of a growing season under different fertilisation regimes. Abundance data were estimated under different fertilisation regimes: standard dose ammonium nitrate fertiliser (Nitram 34.5%N at 175 kg N ha$^{-1}$ (SD); orange), double dose ammonium nitrate fertiliser (Nitram 34.5%N at 350 kg N ha$^{-1}$ (DD); red), pig slurry and straw (175 kg N ha$^{-1}$ (O); green) and an unfertilised control (C; blue). Data are shown from 9th May 2013 (Week 0) to 12th September 2013 (Week 18)

We observed a significant treatment × moisture interaction on the abundance of enchytraeid worms ($F_{79}$ = 3.70, *P* = 0.02; Fig. 2.3), suggesting that the effect of fertiliser treatment was contingent upon soil moisture status. In particular, the effect of soil moisture under O differed to that of C ($t_{79} = 2.35$, $P = 0.02$), SD ($t_{79} = 3.15$, $P < 0.01$) and DD ($t_{79} = 3.72$, $P < 0.01$), with effects on abundance. Furthermore, we observed a negative effect of increasing soil temperature on the abundance of enchytraeid worms ($t_{79} = -4.31$, $P < 0.001$), with a four-week lag.

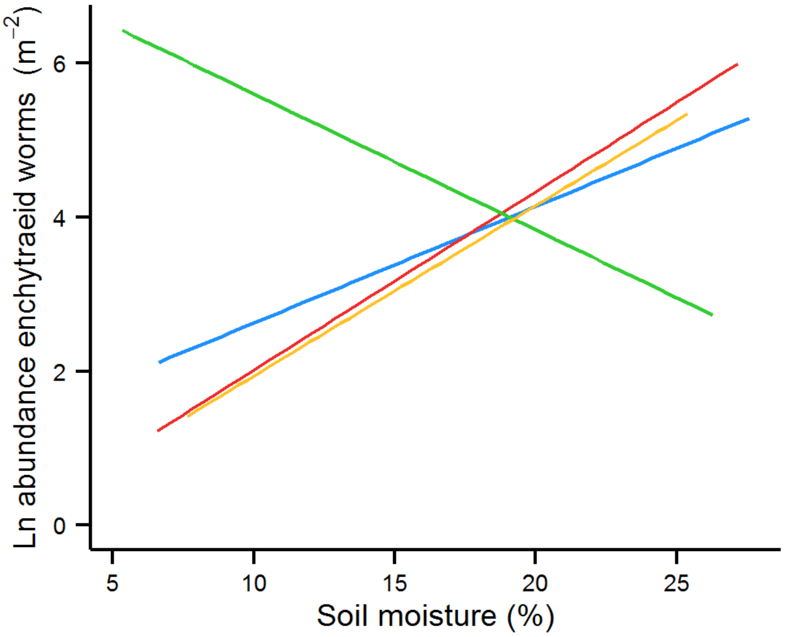


**Fig. 2.3** Model-predicted changes in enchytraeid worm abundance in response to fertiliser treatment under varying soil moisture levels. Abundance data were estimated under different fertilisation regimes: standard dose ammonium nitrate fertiliser (Nitram 34.5%N at 175 kg N ha$^{-1}$ (SD); orange), double dose ammonium nitrate fertiliser (Nitram 34.5%N at 350 kg N ha$^{-1}$ (DD); red), pig slurry and straw (175 kg N ha$^{-1}$ (O); green) and an unfertilised control (C; blue). Model-predicted data were generated from the best model presented in Table 2.6

An increase in the abundance of mesostigmatid mites ($t_{76} = 2.45$, $P = 0.02$) under O compared to C was associated with enhanced soil moisture with a four-week time lag.

Furthermore, overall soil moisture had a positive effect on springtail abundance ($t_{81}$ = 2.41, $P = 0.02$) with a four-week time lag, but this effect did not vary with treatment.

The effect of fertiliser treatment on the abundance of oribatid mites varied with soil pH (treatment × pH interaction: $F_{61} = 4.36$, $P < 0.01$; Fig. 2.4) with a two-week time lag. Specifically, differences were observed between C and SD ($t_{61} = -3.60$, $P < 0.001$), and C and DD ($t_{61} = -2.09$, $P = 0.04$).

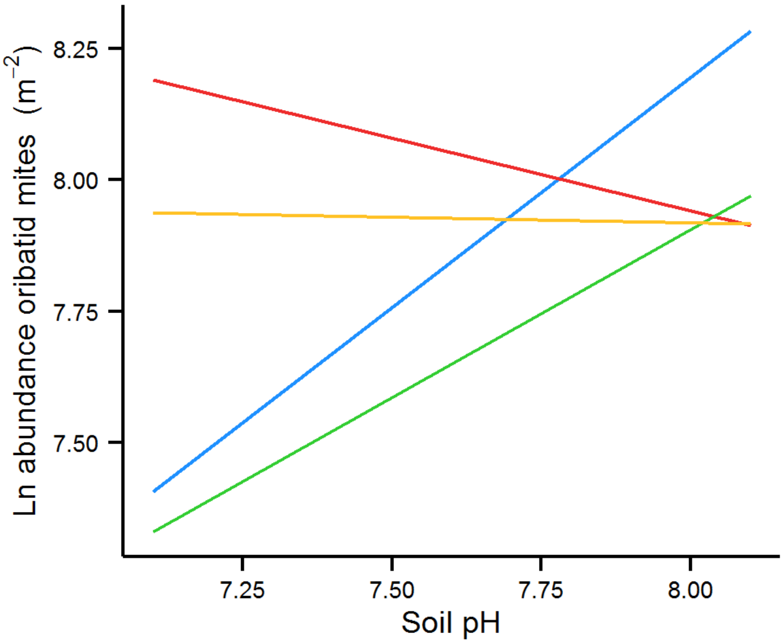


**Fig. 2.4** Model-predicted changes in oribatid mite abundance in response to fertiliser treatment under varying soil pH levels. Abundance data were estimated under different fertilisation regimes: standard dose ammonium nitrate fertiliser (Nitram 34.5%N at 175 kg N $ha^{-1}$ (SD); orange), double dose ammonium nitrate fertiliser (Nitram 34.5%N at 350 kg N $ha^{-1}$ (DD); red), pig slurry and straw (175 kg N $ha^{-1}$ (O); green) and an unfertilised control (C; blue). Model-predicted data were generated from the best model presented in Table 2.1

### 2.3.2 Predator-prey interactions

At a four-week lag, the abundance of predatory mesostigmatid mites was positively associated with the abundance of enchytraeid worms ($t_{76} = 2.17$, $P = 0.03$) and oribatid mites ($t_{76} = 2.25$, $P = 0.03$). We did not observe any effects of predator abundance on the abundance of prey groups.

### 2.3.3 Intraspecific patterns

We observed evidence of larger populations of mesostigmatid mites at t associated with smaller populations at t+4 ($t_{76} = -2.99$, $P < 0.01$). The same trend was also observed for enchytraeid worms ($t_{79} = -4.49$, $P < 0.001$). However, the abundance of astigmatid mites at t was associated with greater abundance at t+2 ($t_{75} = 2.38$, $P = 0.02$).

## 2.4 Discussion

The aim of this study was to investigate the seasonal community dynamics of soil invertebrates over the equivalent of a growing season. Additionally, we were interested in how these patterns were affected by the application of fertiliser as a form of perturbation. We observed seasonal patterns of abundance, which differed between taxa (Chapter 2.4.1). These patterns were modified by a range of seasonal variables (Chapter 2.4.2) and trophic and competitive interactions (Chapter 2.4.4). Furthermore, this is the first study to show that soil community dynamics are affected by perturbation in the form of fertiliser application (Chapter 2.4.3).

### 2.4.1 Temporal variation in soil mesofaunal abundance

In the absence of fertiliser amendments, the seasonal growth curves of oribatid, mesostigmatid and astigmatid mites showed a predictable pattern, similar to those observed by Chikoski *et al.* (2006) and Narula *et al.* (1996). The population increase of springtails followed a similar pattern. It is likely that favourable conditions between May and August increased rates of reproduction and juvenile development, resulting in a rapid increase in population densities during this period. This is followed by a decrease in habitat suitability later in the summer, including an increasingly dry topsoil, resulting in low rates of fecundity and increased mortality (Choi *et al.*, 2006). Evidence of this late season decline is shown in mite populations after week 14. We predict that population densities would have decreased to winter levels within a few weeks, with the decline in springtail abundance occurring slightly later. Abundances of prostigmatid mites followed a similar trend; however, a sharp decrease in abundance was observed in week 10. Unlike the microarthropod groups, the seasonal dynamics of enchytraeid worms were noisy, with several peaks in abundance observed throughout the sampling period. Since we observed a significant effect of soil temperature on enchytraeid abundance (Chapter 2.4.2), this may reflect changes in the vertical distribution of enchytraeids in response to changes in soil temperature.

While soil faunal abundances are affected by substantial within-year demographic change (Van Straalen *et al.*, 1997), populations are likely to remain relatively stable between years under comparable environmental conditions and management regimes. For example, using mean annual forest springtail abundance data or abundances from the same time point over successive years, Kampichler and Geissen (2005) found that forest springtail populations were fairly consistent over a five year period, with little directional change in community structure.

### 2.4.2 The role of abiotic factors in shaping soil mesofaunal populations

We observed a decrease in enchytraeid worm abundance in response to increased soil temperature. We observed a maximum soil temperature of 22 ºC, well below a critical temperature affecting mortality (Kools *et al.*, 2008; Johannesen *et al.*, 2013). Therefore, this reduction in enchytraeid abundance in the 0-10 cm soil layer is most likely to reflect changes in the vertical distribution of enchytraeid populations, with individuals undergoing vertical migration to deeper, cooler soil horizons (Briones *et al.*, 1998; Uhía and Briones, 2002; Briones *et al.*, 2009). Enchytraeids were extracted from the soil using a dry-funnel method, which is likely to have resulted in an underestimation of total community abundance with a bias towards hardier species able to withstand changes in soil moisture. Since soil temperature has complex, species-specific effects on enchytraeid worm abundance (Briones *et al.*, 1997), this pattern may not be representative of the whole enchytraeid community at the site.

Contrary to our predictions, we did not observe a significant effect of soil temperature on the population growth rates of all soil mite groups. However, it is possible that an increase in soil temperature, in excess of those observed in this study, would have resulted in a change in population growth. For example, Ydergaard *et al.* (1997) observed that the daily mean number of eggs laid by individual *Hypoaspis miles* (Berlese) females increased from 0.4 at 15 ºC to 2.3 at 25 ºC. Furthermore, the current study design only allowed two- and four-week time lags to be examined, but it is possible that temperature exerted more instantaneous effects on soil mites.

Soil temperature measurements were not treatment-specific due to the location of the weather station. However, some differences in temperature may have occurred between treatments. Specifically, the organic treatment is likely to have buffered changes in soil temperature due to the insulating effect of the straw-slurry mixture on the soil surface, reducing the transfer of heat generated by decomposition to the external environment. Phillips and Phillips (1984) showed that a mulched layer reduced evapotranspiration and was effective in moderating variation in soil temperature. Since temperature is a determinant of soil microbial and invertebrate development, fecundity and activity (Swift, 1979; Johnson and Wellington, 1980; Hopkin, 1997; Birkemoe and Leinaas, 2000; Choi *et al.*, 2002; Bardgett, 2005), an increase in soil temperature in the O plots would likely enhance habitat suitability for soil microarthropod populations. These conditions may have contributed to the accelerated rate of springtail population increase observed under the O treatment.

We observed an increase in springtail abundance with increasing soil moisture, as expected. The positive relationship between soil moisture and springtail abundance is well established (Badejo *et al.*, 1998; Convey *et al.*, 2002; Lindberg *et al.*, 2002; Chikoski *et al.*, 2006), while Jucevičа and Melecis (2002) observed that reduced soil moisture is also associated with reduced springtail species richness. Moreover, Choi *et al.* (2006) found that incorporating soil moisture data into stage-structured population models improved estimates of springtail abundance. In comparison to the heavily sclerotised Oribatida and Mesostigmata, soft-bodied collembolans have a more permeable cuticle and are therefore more sensitive to moisture stress (Convey *et al.*, 2003). Reduced soil moisture also has negative effects on the abundance and activity of soil microorganisms (Griffin, 1963; Wilson and Griffin, 1975; Orchard and Cook, 1983; Stark and Firestone, 1995; Milcu *et al.*, 2006). Since the availability of food resources (e.g. dead particulate organic matter) is a key driver of springtail density (Chen and Wise, 1997), increased soil moisture may have indirectly promoted springtail abundance through changes in food availability.

### 2.4.3 The role of fertilisers in shaping soil mesofaunal populations

The effects of fertiliser treatment differed between faunal groups. The rate of springtail population increase was enhanced under O compared to C and DD. This is likely to be due to resource enrichment in these plots, in addition to the temperature hypothesis suggested in Chapter 2.4.2. Furthermore, since the straw was not treated with insecticide prior to application, it is also possible that the O plots may have inoculated the soil with springtails directly, resulting in a faster rate of population increase.

Inorganic fertiliser inputs had diverse effects on soil mites. Astigmatid mites showed a greater increase in abundance under both high-dose and standard-dose ammonium nitrate treatments in comparison to the organic treatment, with a notable increase in these plots by week 8. The ecology of astigmatid mites is less well understood than other soil microarthropod groups. However, it is generally accepted that astigmatid mites are comparatively unaffected, or even positively affected, by the impacts of intensive agriculture. Subsequently, astigmatid mites can thrive where other microarthropod groups struggle to survive; for example, under conventional tillage (Reeleder *et al.*, 2006). Two potential explanations are offered for the enhanced population increase under the inorganic plots. Firstly, an increase in food availability via N enrichment under these plots may have promoted population growth. However, since population growth was dampened under the organic treatment, this hypothesis assumes species-specific responses of microorganisms to different fertiliser types. A more likely explanation is that astigmatid mites responded to a decrease in competition, for example by enchytraeids, in plots receiving ammonium nitrate fertiliser treatments, allowing populations to increase more rapidly over time. Astigmatid mites are *r*-selected colonisers, with short generation times and high fecundity (Walter and Proctor, 1999, Norton, 1999), enabling them to respond more rapidly to favourable conditions than K-selected species.

The effect of fertiliser treatment on the abundance of oribatid mites was contingent upon the pH of the soil. However, treatment-induced changes in soil pH were not as remarkable as predicted (mean pH under SD: 7.55 ± 0.04, DD: 7.50 ± 0.06, C: 7.79 ± 0.07, O: 7.76 ± 0.05). At these levels, oribatid mite abundance was higher under plots receiving inorganic fertiliser than under C, contrary to our expectations.

Enhanced soil moisture under the O treatment was associated with an increase in the abundance of mesostigmatid mites, compared to the untreated C treatment. This change in abundance is consistent with a similar study (Table 5.5). Chikoski *et al.* (2006) also observed an increase in the abundance of predatory mites under experimental water supplementation. While soil moisture can be a direct determinant of microarthropod abundance and distribution (Chapters 2.1 and 2.4.2), direct effects are unlikely to be a cause for elevated populations of mesostigmatid mites, which are heavily sclerotized with a thick waxy cuticle (Convey *et al.*, 2003). These physiological traits render these individuals less susceptible to changes in soil moisture.

We observed an increase in the abundance of enchytraeid worms – a key prey group of the Mesostigmata (Jeffery *et al.*, 2010; Whalen and Sampedro, 2010) – under the O treatment under typical soil moisture levels. Since a predator-prey interaction was identified between the predatory mites and enchytraeid worms (Chapter 2.3.2), whereby an increase in prey abundance enhanced predator abundances, this suggests a bottom-up control from the detritivore level. Alternatively, a bottom-up cascade could originate further down the soil food web, due to enhanced microbial biomass in response to resource enrichment in these plots. Indeed, changes in soil moisture content have been shown to affect interactions between microbes and soil fauna (Swift, 1979; Hopkin, 1997).

### 2.4.4 The role of biotic factors in shaping soil mesofaunal populations

Under our sampling regime, we did not detect strong evidence of interspecific interactions driving prey population dynamics, whereas we did observe strong responses to the abiotic environment. However, exposure to perturbation can have effects on the age- or stage-structure of the population (Cameron *et al.*, 2013). This may have led to directional shifts in the population structure of these communities, which were not captured by the study design.

The abundance of mesostigmatid mites was associated with an increase in the abundance of enchytraeid worms and oribatid mites with a four-week time lag. This suggests either a lagged predator-prey interaction or a delayed response of mesostigmatid mites to seasonal conditions. Indeed, mesostigmatid mite abundance peaked several weeks later than other microarthropod groups (Fig. 2.1). Since our sampling regime only allowed for the comparison of two- and four-week lags, it is not possible to conclude that this is the true time lag for biotic effects in this system. Consequently, trophic interactions may have been better estimated using a wider range of lagged densities.

In contrast to the findings of Schaefer (1995) and Hågvar (1995), we did not observe an effect of predation on springtail abundance. Soil mesofauna, including springtails, are preyed upon by a range of predators, including centipedes, spiders and beetles. Since only a subset of the soil predator community was sampled in this study, it is likely that predation effects were underestimated. Furthermore, the study was based on a productive grassland, where a vast availability of microbes and fungi would be expected. Therefore, prey abundances may have recovered too quickly from the effects of predation for a change in abundance to be detected, resulting in weak predation effects.

Soil mesofauna exhibit a diverse range of group- and species-specific life-history strategies. For example, some springtail species have several generations within a year (Schaefer, 1995), while the astigmatid mite species *Sancassania berlesei* (Michael) can have a generation time of 7-9 days in the laboratory (Beckerman *et al.*, 2003). However, oribatid mites exhibit slow larval development, with life cycles lasting between 1-2 years (Behan-Pelletier, 1999). In cool climates, the generation time can be extended to five years (Søvik *et al.*, 2003). The duration of the experiment may have only been long enough to capture fertiliser-induced mortality and predation, rather than population cycles. Therefore, it is more likely that evidence of density-dependence would be detected over a longer time series (Hassell *et al.*, 1989).

## 2.5 Conclusions

We observed evidence of the population dynamics of soil mesofauna being modified by complex interactions between variation in the physical environment, seasonal effects and biotic interactions. Furthermore, this study is the first to demonstrate that a perturbation, in the form of fertiliser application, can alter the temporal population dynamics of soil mesofauna over the course of a growing season. We observed some positive effects of fertiliser inputs, and particularly organic fertilisation, on soil mesofaunal abundance via changes in soil properties. Organic fertilisation provides a range of additional attributes, for example insulation and organic matter, which may become increasingly important for improving resilience in response to a range of environmental factors, e.g. drought and flooding. Subsequently, there is a need to evaluate how fertiliser-induced changes in soil faunal abundance and community structure affect ecosystem functioning (Chapter 5). Furthermore, future work should allow the comparison of additional time lags, rather than the two- and four-week time lags tested here, in order to gain a more detailed of soil mesofaunal population dynamics over the course of a growing season.

# Chapter 3

## Impacts of eucalypt plantation management on soil faunal communities and nutrient bioavailability: trading function for dependence?

## Abstract

Short-rotation forestry systems provide a range of ecosystem goods and services, yet the effects of intensive management on soil invertebrate community composition and ecosystem functioning are relatively unknown. Using an established eucalypt plantation study system, we investigated the effects of irrigation, inorganic fertilisation and a dual fertilisation and irrigation treatment on soil invertebrate abundance and community composition. Additionally, plant root simulator probes were used to estimate the effect of these interactions on nutrient bioavailability as a proxy for ecosystem functioning. Fertilisation reduced soil mite and nematode abundance when applied with irrigation, likely due to the increased solubilisation of inorganic fertilisers in water-limited soils. However, differences in soil invertebrate abundances were not associated with changes in plant nutrient bioavailability. Our findings suggest that high input systems can maintain productivity at the expense of shifts in the soil faunal community, which creates a “lock-in” whereby there is a continuous need for artificial inputs in order to maintain productivity. Reliance on artificial inputs may reduce the soil’s intrinsic capacity to maintain natural ecosystem function in the longer term and should therefore be considered in plantation planning and management.

## 3.1 Introduction

Terrestrial ecosystems provide a range of ecosystem goods and services, especially from agricultural and forestry systems (Swinton *et al.*, 2007; Jose, 2009; Power, 2010). Under proposed climate change scenarios (Collins *et al.*, 2013), the potential to rapidly accumulate biomass in crops is of increasing importance due to the value of sequestering atmospheric carbon and offsetting greenhouse gas emissions (Schroeder, 1992; Cannell, 2003). Therefore the value of intensive short-rotation forestry is growing in policy interest. Subsequently, there is a need to investigate the potential for the sustainable intensification of the short-rotation forestry sector globally (Almeida *et al.*, 2004; Weih, 2004; McNeely and Schroth, 2006; Smith *et al.*, 2010). In comparison with the agricultural sector, the relationship between intensive short-rotation forestry management practices and ecosystem composition and function is poorly understood, creating a knowledge gap around how best to manage for productive and sustainable systems.

Forestry systems can support diverse communities of organisms both above-ground and below-ground, if managed appropriately. In particular, nutrient-rich soils and enhanced soil organic matter content provide rich habitat for soil microbial communities (Chander *et al.*, 1998; Lee and Jose, 2003) and invertebrate communities, including earthworms, enchytraeid worms, springtails, soil mites and nematodes (Giller, 1996; Sileshi and Mafongoya, 2006; da Silva Moço *et al.*, 2009). Soil organisms contribute to a wealth of different ecosystem functions and processes, including decomposition, nutrient cycling and the biological control of invasive species (Brussaard *et al.*, 1997; Bardgett *et al.*, 2005; Bardgett, 2005). Moreover, soil fauna have been shown to directly increase the availability of soil nutrients (Bardgett and Chan, 1999; Wardle *et al.*, 2004).

Previous studies suggest that fertilisation and irrigation may affect soil faunal communities in contrasting ways. In a study of long-term management regimes on microarthropod communities in a Norway spruce stand, Lindberg and Persson (2004) observed a decline in soil microarthropod abundance in response to fertiliser application, while irrigation enhanced population sizes. Negative effects of inorganic fertilisers and other agrochemicals on soil biodiversity have been documented in other studies (Bünemann *et al.*, 2006; Tabaglio *et al.*, 2009; Thiele-Bruhn *et al.*, 2012). In addition, Birkhofer *et al.* (2008) found that the application of mineral fertilisers and synthetic herbicides can modify aboveground-belowground interactions, ultimately promoting negative environmental impacts of intensive agriculture. Since increased nutrient availability enhances biomass production, it would seem likely that soil faunal populations would respond positively to increased resource availability. However, observed decreases in abundance in response to the application of inorganic fertiliser may be caused by direct toxicity, desiccation from salinity effects or soil acidification. Conversely, irrigation regimes generally enhance soil arthropod abundance and diversity (Frampton *et al.*, 2000; Lindberg *et al.*, 2002; Tsiafouli *et al.*, 2005), primarily due to an increase in resource availability.

Using an established eucalyptus plantation system, we investigated the effects of irrigation and fertilisation on soil invertebrate abundance and community composition, and the effect of these interactions on the bioavailability of plant primary (N, P, $K^+$) and secondary ($Ca^{2+}$, $Mg^{2+}$, S) nutrients. We hypothesised that soil invertebrate communities would be largest and most diverse under irrigated treatments due to an increase in the quality and quantity of organic matter. Furthermore, it was predicted that these communities would be smallest and least diverse in plots receiving either fertiliser only or a dual fertilisation and irrigation treatment. It was further hypothesised that nutrient bioavailability would be highest where soil communities were dominated by groups likely to promote decomposition processes (e.g. oribatid mites and springtails).

## 3.2 Methods

### 3.2.1 Site description

The field site (5 ha), located at the Hawkesbury Forest Experiment, University of Western Sydney, Australia (33º36'39"S, 150º44’32”E), was converted from native pasture to a paddock in 1997. In March 2007, the site was prepared for planting by ripping shallow planting lines to 30 cm depth and treating a 1 m wide strip along each row with herbicide. In April 2007, Sydney Blue Gum (*Eucalyptus saligna* Sm.) were planted at a density of 1,000 trees $ha^{-1}$ (2.6 × 3.85 m tree spacing) in sixteen plots, each containing 160 trees in ten rows of 16 trees. From November 2008, no pesticides or herbicides were applied. A sandy-loam soil type characterised by poor water-holding capacity and moderate-low fertility with low organic matter content, as described in Barton *et al.* (2010), dominated the field site.

### 3.2.2 Experimental design

Fertilisation and irrigation treatments were applied across sixteen plots using a randomised block design replicated four times (Fig. 3.1). Each block comprised four plots receiving different treatments: irrigation only (I), solid fertiliser only (F), irrigation and liquid fertiliser (IL) and an untreated control plot (C). Irrigation treatments were applied every four days throughout the year using an *in situ* watering system to deliver the equivalent rainfall of 24,000 L $ha^{-1}$ $year^{-1}$ evenly across the designated plots using 65 spray heads. Liquid fertiliser (N:P:K 20:8:7) was applied every four days during the growing season (September - April), while solid fertiliser (N:P:K 21:6:8) was applied at quarterly intervals throughout the growing season. Different fertiliser types were used to reflect typical plantation management. Both fertilisation regimes were applied at a rate of 150 kg N $ha^{-1}$ $year^{-1}$.

**Fig 3.1** Layout of the experimental plots at the Hawkesbury Forest Experiment, University of Western Sydney, Australia. Letters indicate treatment codes (C: control; I: irrigation only; F: solid fertiliser only; IL: liquid fertiliser and irrigation)

### 3.2.3 Soil invertebrate abundance and community composition

In October 2012, three microarthropod samples were collected from five randomly selected subplots within each experimental plot using a soil corer measuring 8 cm in diameter and 10 cm depth. Microarthropods were extracted into 70% ethanol using a modified Tullgren funnel method over an eight day period. During this period, the light intensity was progressively increased to create a maximum soil surface temperature of 40 ºC. Individuals were enumerated and identified to order level under a binocular microscope (Olympus SZX10). Abundance data were cube root transformed prior to analysis.

To determine nematode community composition, a further three soil cores measuring 8 cm in diameter and 10 cm depth were collected from each subplot and combined to form a composite sample. This sample was gently homogenized and a subsample weighing 50 g ± 0.1 g was taken for extraction of nematodes using a Baermann funnel technique over 72 hours. Nematodes were enumerated, transferred to a graticulated counting dish and the first 100 individuals from each sample identified to trophic group level (bacterial feeders (BF), fungal feeders (FF), predators (Pr), omnivores (Om) and plant parasites (PP)) based on the morphology of mouthparts at 100-400 x magnification using an inverted microscope (Olympus CKX41). Proportions were arcsine square root transformed prior to analysis.

Soil macrofauna (e.g. earthworms and millipedes) and enchytraeid worms were found in very low abundance across the site, thus counts were excluded from the analysis.

### 3.2.4 Estimated plant nutrient bioavailability

Plant root simulator (PRS™) probes (Western AG Innovations Inc., Saskatchewan, Canada; Bengtson *et al.*, 2007) were used to estimate the bioavailability of multiple nutrients (including N, P, $K^+$, S, $Mg^{2+}$ and $Ca^{2+}$) *in situ.* At each sampling site, six probes (three anion and three cation) were inserted to a depth of 10 cm. After 40 days the probes were retrieved and returned to the manufacturer for processing. Data were square root (N, P, $K^+$ and $Ca^{2+}$) or cube root (S and $Mg^{2+}$) transformed prior to analysis. The appropriate transformation was selected by testing for goodness-of-fit; specifically, checking how well the model-predicted residuals fitted the observed data and testing for heteroscedasticity.

### 3.2.5 Soil chemical analysis

Soil chemical analyses were conducted on the remaining composite sample used for nematode extraction. Soil moisture content was estimated by drying a 25 ± 0.5 g sample at 130 °C for 72 hours. A 10 ± 0.1 g subsample was then ball-milled, mixed with 50 ml distilled water and the pH of the resulting suspension measured after one hour. A further subsample was used to estimate total soil C and N content using a LECO TruMac C/N determinator (LECO Corporation, USA) with thermal conductivity detection of $N_2$ and $CO_2$. C and N concentrations were determined by comparison with known standards.

### 3.2.6 Statistical analysis

All statistical analyses were conducted in R (R Core Development Team, 2014). Linear mixed effects models were used to analyse the effects of treatment on the community composition of soil fauna, using an offset function to account for soil core mass (faunal community analysis) or total nematode abundance (nematode community composition analysis). Block was included as a random factor. Covariates included soil C, soil N and soil pH. A spherical spatial correlation structure (‘corSpher’) was used to model the geographical coordinates of each subplot using the R package *nlme* (Pinheiro *et al.*, 2015), to control for the observed effect of spatial autocorrelation.

Abundances of soil invertebrates were also included in plant nutrient bioavailability models as covariates.

A maximal model, including all covariates and random terms with interactions, was constructed for each analysis in *nlme*. The 'dropterm' function in the R package *MASS* (Venables and Ripley, 2002) was used to explore model structure by simplifying the over-parameterised model to create a set of plausible candidate models. Models were then compared using second-order Akaike Information Criteria. Pairwise z-tests were performed, with *P*-values corrected using the Tukey method, in the R package *multcomp* (Hothorn *et al*., 2008).

## 3.3 Results

### 3.3.1 Soil faunal abundance

Total soil mite abundance varied between 199 and 19,893 individuals m$^{-2}$ across all treatments and springtail abundance ranged from 0 to 6,963 individuals m$^{-2}$. Total nematode abundance ranged from 2,076 to 12,650 individuals kg$^{-1}$ dry soil. Significant differences were observed between treatments and these varied across the different faunal groups (treatment × group interaction, $P < 0.001$; Fig. 3.2). Oribatid mites were less abundant under IL than under C ($z_{297} = 2.29$, $P = 0.02$) (Fig. 3.2a). Mesostigmatid mites were also observed in lower abundance under IL than under C ($z_{297} = 2.71$, $P < 0.01$) and I ($z_{297} = 2.30$, $P = 0.02$) (Fig. 3.2b). No significant treatment effects were observed for springtail abundance. Nematodes were observed in lower abundance under IL than under C ($z_{297} = 3.92$, $P < 0.001$), F ($z_{297} = 2.49$, $P = 0.01$) and I ($z_{297} = 3.37$, $P < 0.001$) (Fig. 3.2c). We observed a significant treatment-induced change in soil pH, with lower pH under F (mean pH 5.20, $t_{313}= -2.13$, $P = 0.03$) and higher pH under I (mean pH 6.57, $t_{313}= 21.75$) and IL (mean pH 6.49, $t_{313} = 20.34$; both $P <$

0.001) treatments compared with C (mean pH 5.33). However, this was not found to have a significant effect on soil faunal abundances.

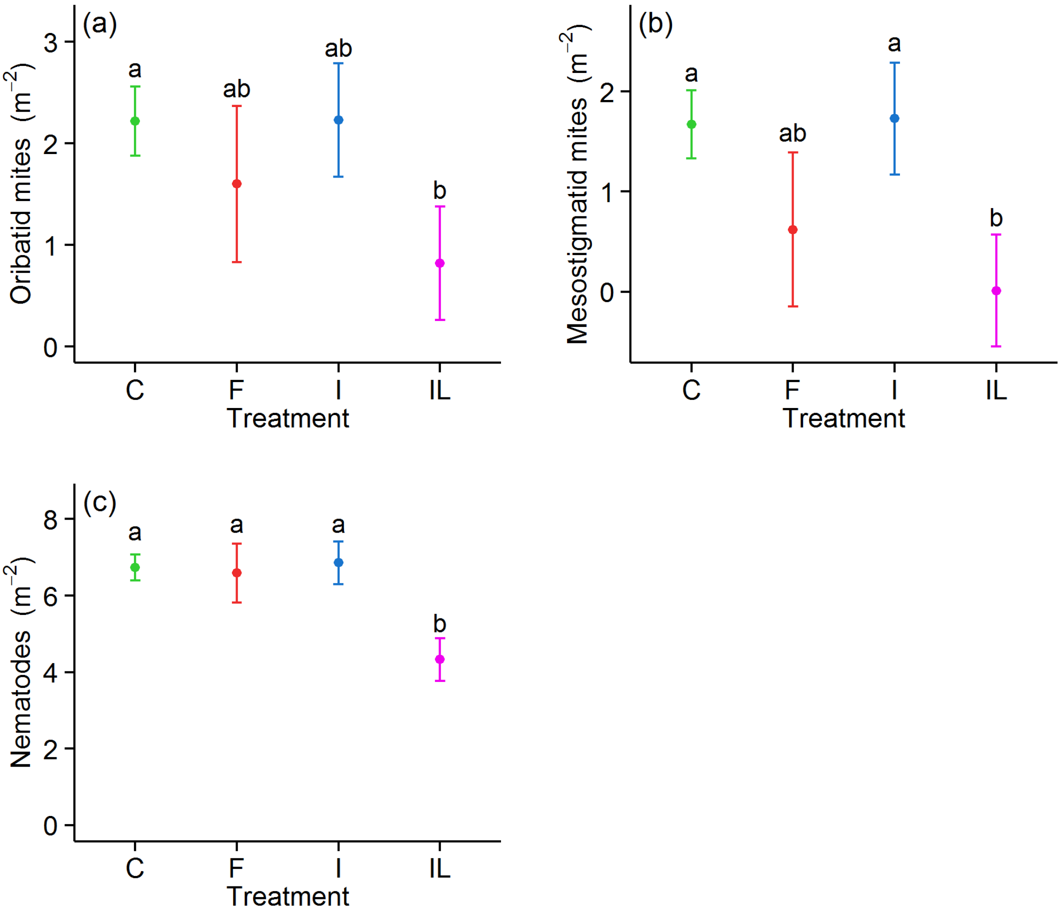


**Fig. 3.2** Model-predicted estimates (means ± SEs) of the cube root transformed abundance of oribatid mites, mesostigmatid mites and nematodes under experimental fertilisation and irrigation treatments (C: control (green); F:solid fertiliser only (red); I: irrigation only (blue); IL: liquid fertilisation and irrigation (purple)). Data are presented on the transformed scale. Annotations denote statistically significant differences

### 3.3.2 Nematode community composition

Significant differences in the proportion of nematode trophic groups were also observed between treatments and these varied across different trophic groups (treatment × trophic group interaction, $P < 0.001$; Fig. 3.3). The proportion of bacterial feeding nematodes observed under I was lower than under C ($z_{377} = -3.27$, $P = 0.001$) and IL ($z_{377} = -3.56$, $P < 0.001$) (Fig. 3.3a). Conversely, the proportion of fungal feeders was higher under I than under C ($z_{377} = 2.09$, $P = 0.04$; Fig. 3.3b). The proportion of plant parasites observed under IL was lower than under F ($z_{377} = -3.30$) and I ($z_{377} = -3.81$; both $P < 0.001$), and higher under I than C ($z_{377} = 2.10$, $P = 0.04$) (Fig. 3.3c). The proportion of omnivores decreased under F, compared to all other treatments ($z_{377} = -2.89$, $P < 0.01$; $z_{377} = -3.13$, $P < 0.01$; $z_{377} = -4.02$, $P < 0.001$, for C, I and IL respectively; Fig. 3.3d). No significant treatment effects were observed for the proportion of predatory nematodes (back-transformed model-predicted mean proportion under C: <0.01, F: 0.01, I: <0.01, IL: 0.01; $P > 0.05$).

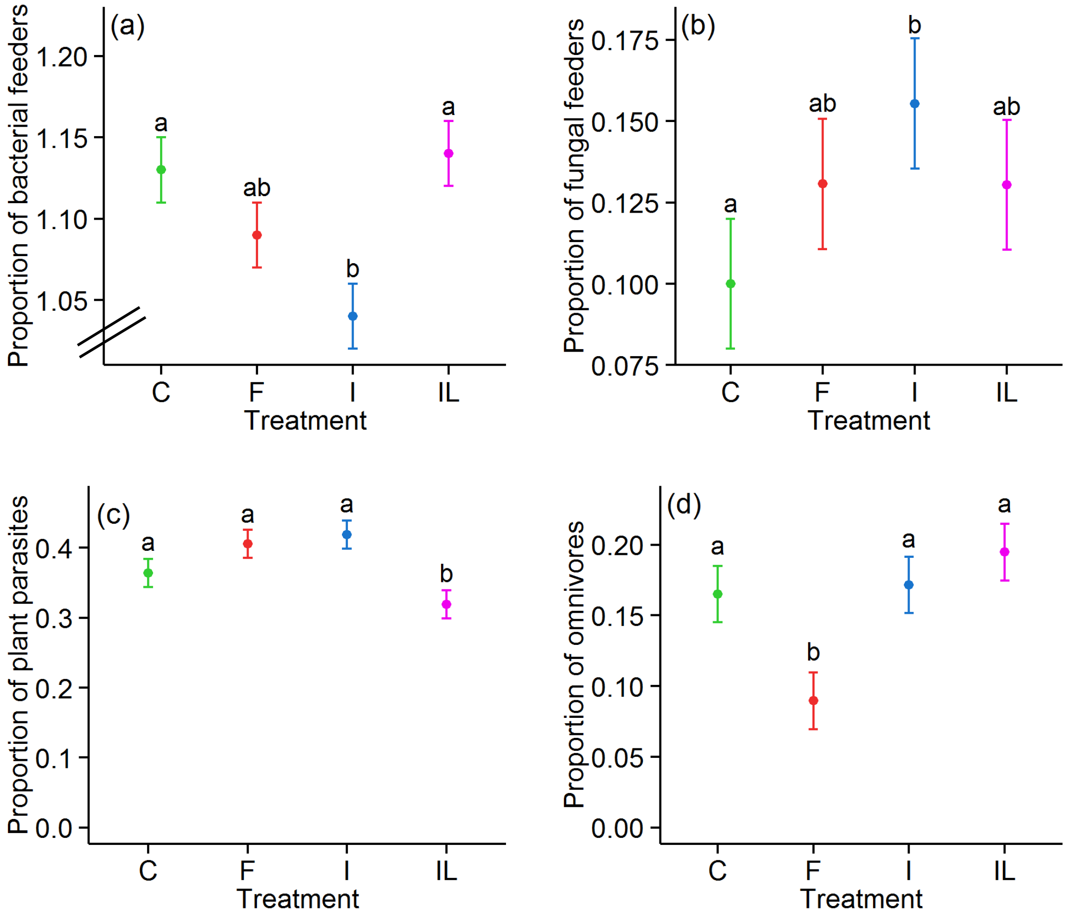


**Fig. 3.3** Model-predicted changes (means ± SEs) in nematode community composition under experimental fertilisation and irrigation regimes (C: control (green); F: solid fertiliser only (red); I: irrigation only (blue); IL: liquid fertiliser and irrigation (purple)). Proportional abundances of each trophic group relative to total nematode abundance were arcsine square root transformed prior to analysis and model predictions are presented on the transformed scale. The *y*-axis origin differs between plots. Annotations denote statistically significant differences

### 3.3.3 Estimated nutrient bioavailability

The estimated bioavailability of plant primary and secondary nutrients responded differently to treatment and soil chemistry (Fig. 3.4). Treatment-induced changes in soil microarthropod and nematode abundances were not useful predictors of nutrient bioavailability. Fertilisation increased availability of N ($t_{294}$ = 9.67, $P < 0.001$; Fig. 3.4a), P ($t_{302}$ = 8.39, $P < 0.001$; Fig. 3.4b), $K^+$ ($t_{294}$ = 7.64, $P < 0.001$; Fig. 3.4c), S ($t_{294}$ = 4.38, $P < 0.001$; Fig. 3.4d) and $Ca^{2+}$ ($t_{298}$ = 3.92, $P < 0.001$; Fig. 3.4e), but decreased availability of $Mg^{2+}$ ($t_{298}$ = 2.76, $P = 0.02$; Fig. 3.4f). Irrigation increased availability of $Ca^{2+}$ ($t_{298}$ = 4.53), S ($t_{294}$ = 5.07) and $Mg^{2+}$ ($t_{298}$ = 4.22; all $P < 0.001$), but decreased availability of N ($t_{294}$ = 4.47, $P < 0.001$) and $K^+$ ($t_{294}$ = 2.13, $P = 0.03$). Dual fertilisation and irrigation increased availability of N ($t_{294}$ = 2.03, $P = 0.04$), but decreased availability of $K^+$ ($t_{294}$ = 2.63, $P < 0.01$).

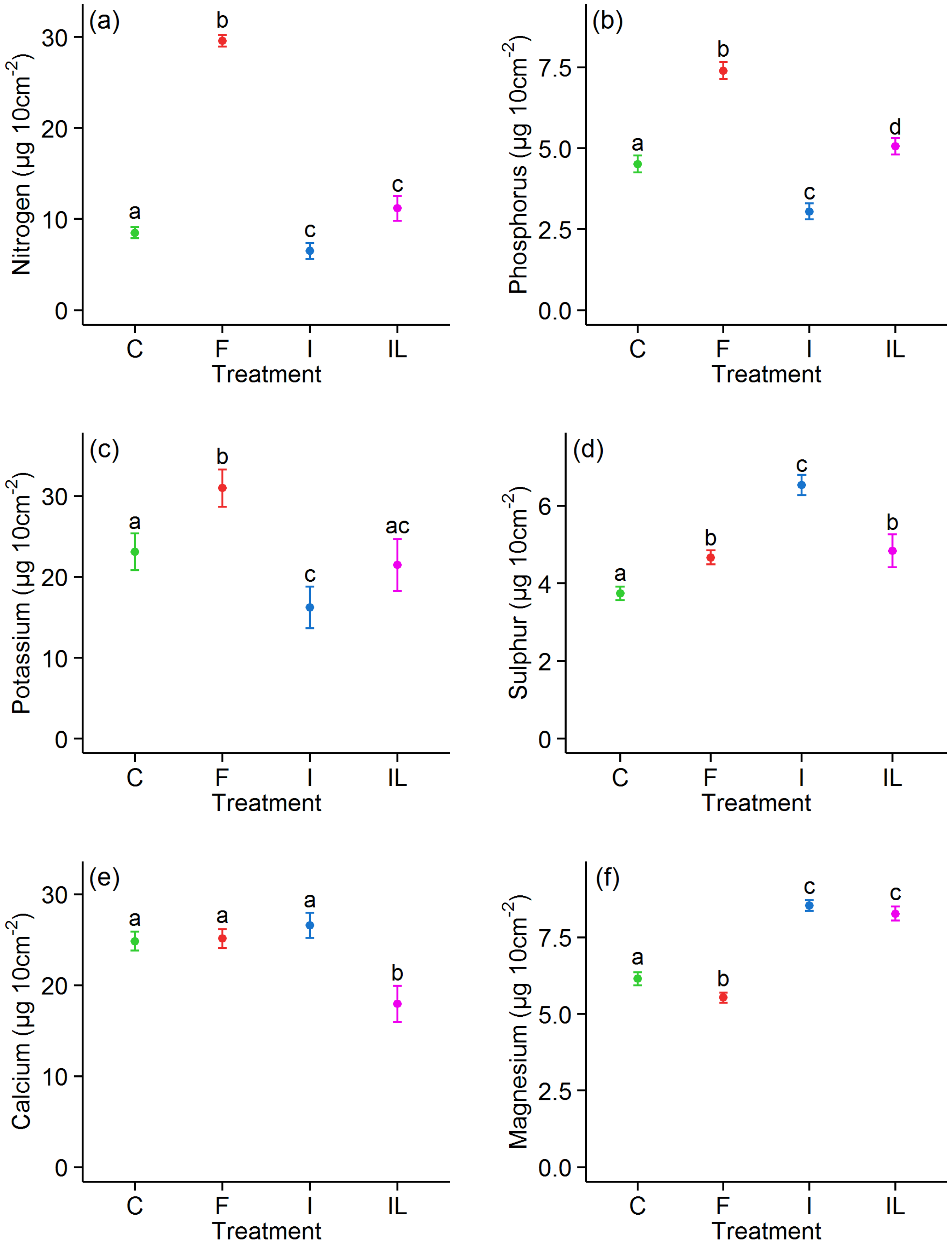


**Fig. 3.4** Model-predicted estimates (means ± SEs) of plant nutrient uptake under experimental fertilisation and irrigation treatments (C: control (green); F: fertiliser only (red); I: irrigation only (blue); IL: fertilisation and irrigation (purple)) over 40 days. *n* = 4 per treatment. Data were square root (N, P, K$^+$ and Ca$^{2+}$) or cube

root (S and $Mg^{2+}$) transformed prior to analysis and model predictions are presented on the transformed scale. Annotations denote statistically significant differences

## 3.4 Discussion

We observed a consistent pattern of decreased abundance under the dual fertilisation and irrigation treatment for both soil mites and nematodes, as predicted. However, contrary to our predictions, significant changes in abundance were not observed under the solid fertiliser treatment. It is likely that the application of irrigation with liquid fertiliser increased the solubilisation of fertiliser under the low soil moisture conditions observed in this study. Negative effects on soil organisms may have been direct, due to ammonium toxicity (Moursi, 1970; Wright, 1975; Wei *et al.*, 2012) or desiccation resulting from increased soil osmotic pressure (Jacobs and Timmer, 2005), or indirect, due to fertiliser-induced changes in the activity, biomass and composition of soil microbial communities. Indeed, reductions in soil microbial biomass (DeForest *et al.*, 2004; Wallenstein *et al.*, 2006; Demoling *et al.*, 2008) and activity (Bowden *et al.*, 2004; Demoling *et al.*, 2008), as well as altered community composition (Peacock *et al.*, 2001; Belay *et al.*, 2002; Marschner *et al.*, 2003; Ramirez *et al.*, 2010), have been associated with fertiliser use. This may have driven the observed changes in invertebrate abundance and nematode community composition through reduced grazing opportunities. It should be noted that using mite groups at order level may not have captured underlying shifts in soil mite food web composition due to species-specific life history strategies, particularly within the Oribatida.

Nematode community composition varied with treatment in a complex way. The nematode community was consistently dominated by bacterial feeders; however, the proportion of fungal feeders and plant parasites relative to bacterial feeders increased under irrigation, indicative of lower rates of decomposition and nutrient turnover (Twinn, 1974), greater root biomass or fungal hyphal length. The promotion of a bacterial-dominated food web under the dual fertilisation and irrigation treatment compared with irrigation alone is consistent with increased N inputs (de Vries *et al.*, 2006).

The estimated bioavailability of plant primary nutrients increased with the application of solid fertiliser, as expected. Conversely, irrigation alone decreased the availability of N and $K^+$; however, this trend was reversed for all secondary nutrients, suggesting the liberation of water-soluble $Mg^{2+}$, $Ca^{2+}$ and S. Irrigation enhances the transportation of dissolved nutrients locked in the soil via mass flow (Silber *et al.*, 2003; Hu and Schmidhalter, 2005), thus promoting nutrient uptake. Contrary to our predictions, changes in soil invertebrate abundance and community composition were not associated with differences in plant nutrient bioavailability. We therefore suggest that nutrient inputs compensate for changes in soil ecosystem composition, but that this creates a “lock in”. If fertilisation is reduced or stopped in the future, as is likely with limited resource availability and rising costs, we hypothesise that productivity will decrease rapidly.

We further suggest that soil communities will recover from the effects of mineral fertiliser use only in the longer term, since recovery from land use change tends to occur over relatively long timescales (Chapter 6.2.3). Rates of population recovery are likely to differ between faunal groups depending on dispersal ability and generation time, further altering food web composition. For example, the community recovery rate of detritivorous oribatid mites is slower than that of predatory mesostigmatid mites (Lindberg and Bengtsson, 2006). Coupled with a limited abundance of soil macrofauna, this is likely to lead to organic nutrient sources (e.g. leaf litter) taking longer to decompose and liberate nutrients than in previously unfertilised treatments, particularly if irrigation is also reduced or stopped.

## 3.5 Conclusions

Our findings suggest that the use of a dual fertilisation and irrigation regime reduces soil invertebrate abundance either directly, through toxic or osmotic effects, or indirectly, via changes in the activity, biomass and composition of microbial communities. Despite such changes, estimated plant nutrient bioavailability responded positively to the application of fertiliser, suggesting more broadly that artificial inputs can supersede the role of soil biota in intensively managed systems. We consider that there are several innovative aspects of this research. Firstly, the duration of the experimental setup and the use of realistic management practices is uncommon in the literature. Secondly, the use of PRS™ probes allowed us to investigate the effects of management on nutrient bioavailability in ‘real time’ rather than taking a snapshot of soil and plant nutrient pools at a single time point. Thirdly, we consider that this is the first study to have linked fertilisation to both soil biotic responses and changes in available plant primary and secondary macronutrients in a field study site.

Our findings can be regarded as a snapshot into the study system; while some variation would be expected over time, the duration of management suggests that our observations are likely to be well-established. In the long-term, continuous reliance on artificial inputs to maximise productivity may result in a reduction in the capacity of soils to maintain natural ecosystem function. The substitution of ecosystem function for inputs creates a risk to the system’s performance in the event that input availability becomes constrained. Considering more sustainable soil management options may reduce this risk and also increase the resilience of the system.

# Chapter 4

## The value of non-crop habitats for soil mesofauna in intensive arable landscapes

### Abstract

Grassy field margins are a key component of agroecosystem habitat heterogeneity, and have been associated with an increase in agricultural biodiversity above-ground. However, the effects of field margins and other non-crop habitats on soil invertebrates are relatively unknown. In 2013, seven transects representing a gradient of agricultural intensification were established in productive fields growing vining peas. Soil mesofaunal abundance and springtail community composition were estimated in a range of non-crop (adjacent woodlands, hedgerows and grassy margin) and cultivated (field edges and field centres) habitats. We observed strong evidence of intensive agriculture impacting on soil mesofaunal populations, with reduced abundances of all surveyed groups observed in cultivated areas compared to non-crop habitats. Furthermore, non-crop habitats, and in particular structurally complex habitats (woodlands and hedgerows), supported more diverse springtail communities. We discuss the value of non-crop habitat as refugia for soil mesofauna and the importance of agricultural habitat heterogeneity for the conservation of biodiversity-function relationships.

## 4.1 Introduction

Since the 1950s, the intensification of agricultural systems through continuous cultivation, the development of high-yielding varieties, advanced mechanisation and increased agrochemical use has dramatically increased crop yields globally. In addition, the enlargement and amalgamation of fields has increased the area of land available for seeding and allowed for more effective management. Global wheat production alone rose from 0.22 billion tonnes (Bt) in 1961 to 0.71 Bt in 2013, while the total land used for agriculture increased from 34.18% to 37.64% during the same period (FAO, 2014). However, these changes have resulted in a reduction in the abundance of natural and semi-natural habitat, particularly around field boundaries (Robinson and Sutherland, 2002; Cornulier *et al.*, 2011). Historically, boundary habitats (e.g. hedgerows) were used to define land ownership, act as a windbreak to protect crops, restrict the entry or exit of livestock and other animals, and provide a source of food and fuel (Marshall and Moonen, 2002). Reductions in these habitats have been associated with declines in farmland biodiversity, with complex natural communities becoming simplified (Robinson and Sutherland, 2002; Benton *et al.*, 2003; Jeanneret *et al.*, 2003; New, 2005; Goulson *et al.*, 2008).

In 1985, the European Union published a Green Paper addressing the environmental impacts of agriculture (CEC, 1985) and reformed Common Agricultural Policy (EEC Regulation 797/85). Since then, member states have been permitted to introduce agri-environment schemes; offering subsidies for environmentally-sensitive land management with the long-term aim of reversing the decline of farmland wildlife. In 1991, the Countryside Stewardship Scheme (CSS) was introduced in the United Kingdom, aiming to improve the environmental value of farmland by enhancing natural diversity. Under the scheme, existing wildlife habitat can be improved, or new areas of habitat created by taking a given amount of land out of cropping (Marshall *et al.*, 2006). From 1994 - 2003, 16,101 land management agreements covering 530,620 ha were enrolled under the CSS (DEFRA, 2005). Additionally, 3,048 km hedgerows were restored or maintained under the scheme between 1991 - 2013 within Yorkshire and Humberside alone (DEFRA, 2005). Furthermore, the Hedgerows Regulations 1997 prevent the uprooting or removal of hedgerows from agricultural, forested or common land providing they are at least 30 years old.

A key practice prescribed under the CSS, and subsequent schemes, is the promotion of field margins. Field margins are areas of linear, semi-natural habitat associated with the field boundary or between the field boundary and crop edge, including grass and wildflower strips, bird cover, sterile strips and beetle banks (Marshall and Moonen, 2002). Field margins are designed to buffer the detrimental effects of agricultural intensification by promoting landscape diversity, increasing resource availability for native flora and fauna, and acting as corridors for the movement of species from one habitat to another (Verboom and Huitema, 1997; Altieri, 1999). Grassy strips in particular can also act as an environmental buffer, by protecting watercourses from the potential effects of sediment movement (Abu-Zreig *et al.*, 2004; Le Bissonnais *et al.*, 2004) and agrochemical runoff (Blanco-Canqui *et al.*, 2004; Krutz *et al.*, 2005; Dorioz *et al.*, 2006) via increased infiltration at field edges. In the case of inorganic fertilisers, this allows for the immobilisation or transformation of nutrients within field boundaries and can reduce some of the negative environmental impacts associated with conventional agriculture, including the eutrophication of surrounding catchments.

The establishment or re-establishment of field margins have been associated with increases in above-ground biodiversity, with a number of studies recognising positive effects of field margins and other within-farm non-crop habitats on invertebrate (Lagerlöf *et al.*, 1992; Dover and Sparks, 2000; Woodcock *et al.*, 2005; Marshall *et al.*, 2006), farmland bird (Wilson *et al.*, 1999; Douglas *et al.*, 2009) and mammal populations (Fitzgibbon, 1997; Verboom and Huitema, 1997; Michel *et al.*, 2006). Furthermore, margins can act as overwintering habitat for beneficial arthropods, including carabids, which move into adjacent crops in the spring (Sotherton, 1984; Pfiffner and Luka, 2000) and act as biocontrol agents. Field margins and other areas of non-crop habitat have also been identified as important landscape structures for other predator and natural enemy populations (Thomas *et al.*, 1991; Dennis and Fry, 1992; Thomas *et al.*, 1992; Lys and Nentwig, 1994; Pfiffner and Luka, 2000; Sutherland *et* *al.*, 2001), most likely due to the increase in habitat complexity. The management of field margins further affects their value for farmland biodiversity. In general, minimal management, increased vegetative density and a combination of cover types (e.g. grass and wildflower strips) increases the value of field margins for a range of taxa (Feber *et al.*, 1996; Vickery *et al.*, 2002; Smith *et al.*, 2008b).

However, variation in the effectiveness of non-crop habitat in promoting agricultural biodiversity is apparent, both between taxa and studies. For example, Kleijn *et al.* (2001) reported neutral or negative impacts of agri-environment schemes on plants and birds in the Netherlands; though some of these effects may have been a result of the scale of the analysis. Moreover, field margins commonly harbour pest and pathogen species, which may therefore promote ecosystem disservices by hindering crop production.

While the value of farmland habitat complexity has been widely studied above-ground, effects on below-ground biodiversity are relatively unknown. Using paired transects in arable fields with and without a 6 m grassy strip between the hedgerow and crop, Smith *et al.* (2008a) investigated the effects of field margins on soil macrofaunal abundance and functional diversity. Abundances of soil feeders (including earthworms), litter consumers (including woodlice) and predators (including centipedes) all declined with increasing distance from the hedgerow. However, beneficial effects were confined to the grassy strip, with no increase in macrofaunal abundance in either the field or hedgerow. Positive effects of field margins on earthworm abundance are reported elsewhere (Hof and Bright, 2010), although Lagerlöf *et al.* (2002) observed fewer individuals in field boundaries under grass or forb cover in comparison to cropped areas, particularly in the field centre. Field margins have also been shown to enhance macrofaunal species richness (Smith *et al.*, 2008b). Despite this, the value of habitat heterogeneity within agricultural systems for soil mesofauna has not yet been considered.

This study aimed to evaluate the effectiveness of a variety of non-crop habitats as refugia for soil mesofauna in an intensive arable landscape. Firstly, we compared abundances of different functional groups, including decomposers and predators, between woodland, hedgerow, grassy margin and cropped habitats. Where woodland was present, it was hypothesised that the abundance of all soil mesofaunal groups would decrease with increasing distance from the woodland due to an increase in management intensity closer to the centre of the field. It was further hypothesised that grassy margin habitats would support greater densities of fauna than the field edge and field centre, but be of less value as refuge habitat than hedgerows and adjacent woodlands. Secondly, the value of hedgerows for soil mesofauna was compared with and without adjacent woodland. In the absence of adjacent woodland, it was hypothesised that hedgerows would support the highest numbers of soil mesofauna. Thirdly, we examined the effects of habitat complexity on springtail species assemblages, to assess whether communities in disturbed habitats (i.e. within-field) were separate to or subsets of those found in more complex habitats (i.e. non-cropped areas). It was hypothesised that springtail communities found in the most disturbed habitats (i.e. the field edge and field centre) would be more similar to those found in the grassy margins, and less similar to those found in the least disturbed habitats (i.e. hedgerows and adjacent woodlands). Since the range of taxa sampled exhibited a variety of habitat preferences and dispersal strategies, this study allowed us to quantify the value of different habitats for multiple groups simultaneously.

## 4.2 Methods

### 4.2.1 Study site

The field site was located at Spen Farm, West Yorkshire, UK (53° 51' 44" N, 1° 20' 38” W); a productive arable farm of approximately 263 ha. Multiple crops, including cereals and legumes, are grown in rotation. The majority of fields are bounded by hedgerows, some of which are likely to be pre-Enclosure. Some small wooded areas occur adjacent to hedgerows. Permanent grass margins of 1-2 m width are set out between the hedgerows and cropped areas. Across the site, the soil type is predominantly Aberford series; a free-draining, lime-rich, loamy soil with moderate water holding capacity (NSRI, 2013).

### 4.2.2 Experimental design

In July 2013, seven transects were laid out across seven fields perpendicular to the field boundary (Fig. 4.1). All fields were planted with vining peas. In four fields, transects were arranged from 2 m into the woodland adjacent to the hedgerow to 32 m into the cropped area (Fig. 4.2). In the remaining three fields, where adjacent woodland was not present, transects were arranged from the hedgerow to 32 m into the cropped area (Fig. 4.3). Transect markers were erected along each transect at 2 m into the adjacent woodland from the copse edge (if present; hereafter referred to as ‘adjacent woodland’), in the centre of both the hedgerow (‘hedgerow’) and grassy margin strip (‘grassy margin’), and at 2 m (‘field edge’) and 32 m (‘field centre’) into the cropped area. The field edge sites were chosen to represent the transition zone between cropped and non-cropped areas. The field centre sites were located approximately in the centre of the area designated for cropping, and were likely to be representative of the highest intensity of agricultural management within the field.

**Fig 4.1** Location of field transects at Spen Farm, West Yorkshire, UK. Four transects were arranged from 2 m into adjacent woodland to 32 m into the cropped area (green lines). Three transects were arranged from the hedgerow to 32 m into the cropped area (blue lines)

**Fig. 4.2** Sampling design showing approximate layout of transect markers along a woodland-to-field transect, occurring in four of the seven fields sampled

**Fig. 4.3** Sampling design showing approximate layout of transect markers along a hedgerow-to-field transect, occurring in three of the seven field sampled

### 4.2.3 Soil invertebrate sampling

Four soil cores were collected from each sampling site using a soil corer measuring 8 cm diameter and 10 cm depth, and combined to form a composite sample. Soil cores were collected from sampling points located at a 30 cm radius of each transect marker (Fig. 4.4). Soil mesofauna were extracted into 70% ethanol using a modified Tullgren funnel method over a six day period. During this time, the photoperiod was progressively extended to create a temperature gradient designed to drive fauna through the soil profile. Soil mites and enchytraeid worms were counted, and soil mites identified to order level under a binocular microscope (Leica MZ75).

Springtails were transferred to 7 ml plastic tubes and immersed in lactic acid for 48 hours to reduce pigmentation. Individuals were then transferred to distilled water, followed by a series of increasing ethanol concentrations ranging from 70% to 100%, in accordance with the protocol described in Hopkin (2007). Individuals were counted and identified to species level (Hopkin, 2007) under a binocular microscope (Leica MZ75). Where necessary, individuals were slide mounted with Canada balsam and identified under a compound microscope.

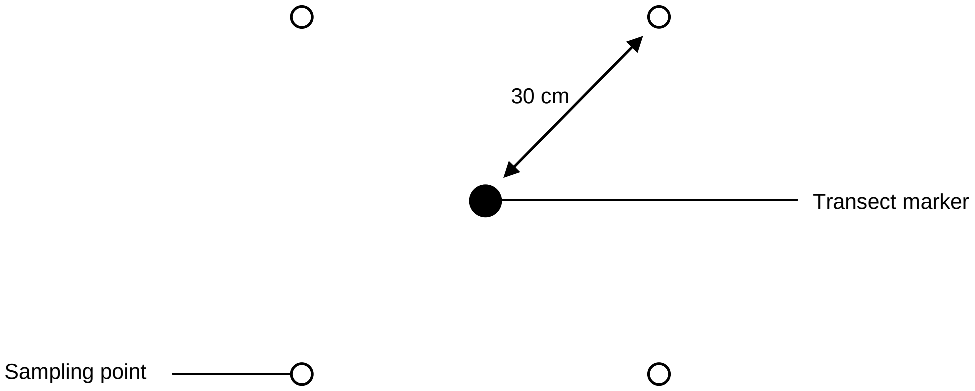


**Fig. 4.4** Location of soil core sampling sites at each transect marker

### 4.2.4 Statistical analysis

All statistical analyses were conducted in R (R Core Development Team, 2014). General linear mixed effects models were used to analyse the effects of habitat on log-transformed soil mesofaunal abundances and springtail species richness using the R package *nlme* (Pinheiro *et al*., 2015). In all analyses, field was included as a random factor. A group × habitat interaction term was included in the abundance analysis to investigate variation in response to habitat complexity between mesofaunal groups. Pairwise z-tests were performed, with *P*-values corrected using the Tukey method, in the R package *multcomp* (Hothorn *et al*., 2008).

A separate analysis was performed to analyse the effect of adjacent woodland presence or absence on abundances in the hedgerows. Again, abundances were log-transformed and a group × binary adjacent woodland interaction term was included.

Non-metric multidimensional scaling (NMDS) was performed using the ‘metaMDS’ function in the R package *vegan* (Oksanen *et al*., 2015) to analyse changes in springtail community composition over the woodland-to-field gradient. Bray-Curtis distances were used as a dissimilarity index to find the optimal ordination of species and habitats (Oksanen, 2011). A generalised analysis of variance (MANOVA) with 200 random permutations was performed using the ‘adonis’ function in the R package *vegan* (Oksanen *et al*., 2015) to analyse the effects of habitat and the presence of adjacent woodland on the ordination of springtail species assemblages. Singletons (species represented by a single individual) were removed from the dataset prior to analysis.

## 4.3 Results

### 4.3.1 Soil mesofaunal abundance from woodland-to-field

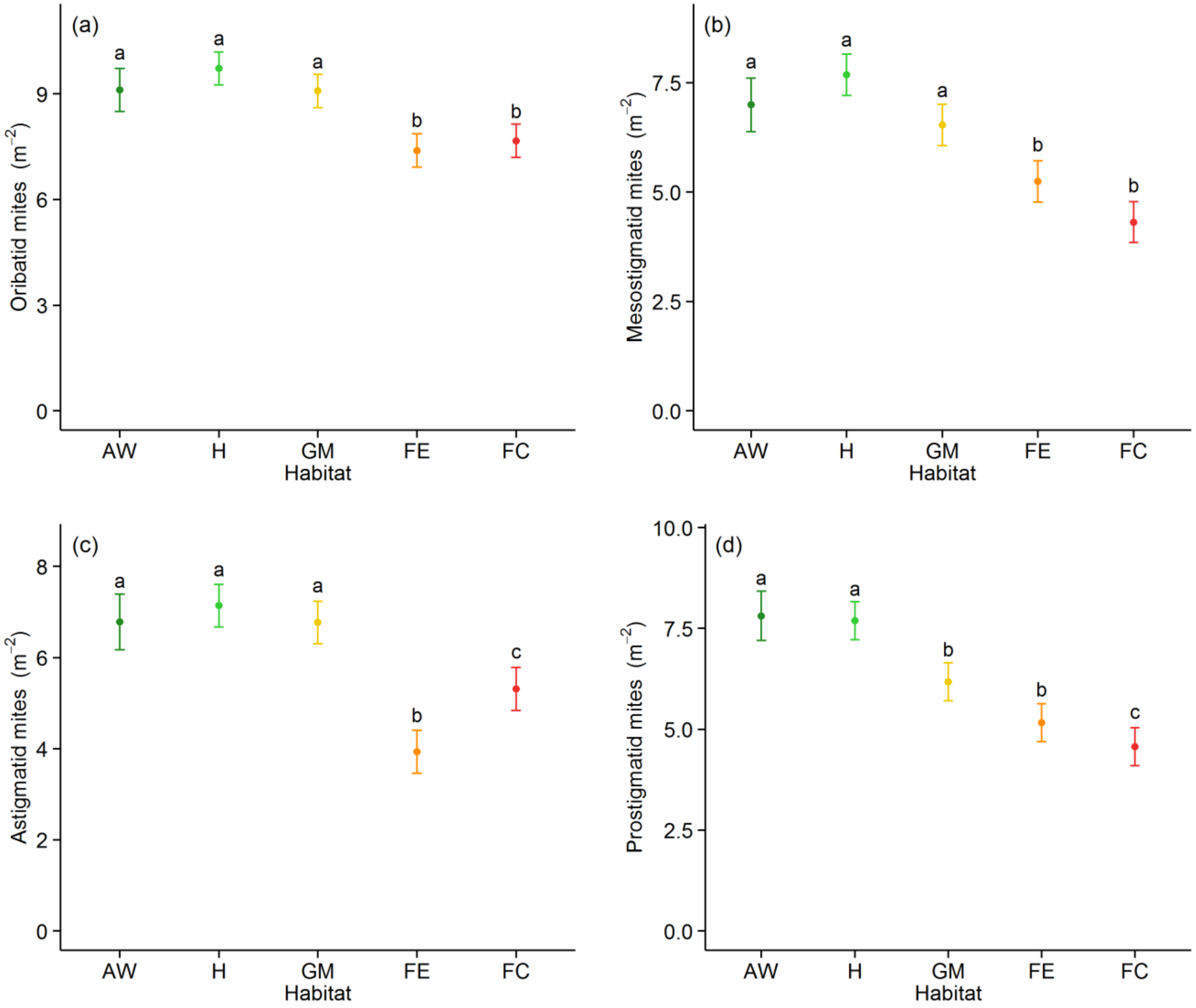
Total soil mite abundance varied between 531 and 48,012 individuals $m^{-2}$. Springtail abundance varied between 0 and 14,766 individuals $m^{-2}$, and species richness varied between 0 and 15 across all sites. We observed a significant effect of habitat on soil mesofaunal abundance ($F_{156} = 42.67$, $P < 0.001$), which varied between groups (group × site interaction $F_{156} = 2.02$, $P = 0.001$).

Contrast tests showed that oribatid mite abundance was higher in each of the non-crop habitats than at 2 m and 32 m into the cropped area (adjacent woodland - 2 m $z = 2.32$, $P = 0.02$; adjacent woodland - 32 m $z = 1.95$, $P = 0.05$; hedgerow - 2 m $z = 3.70$, $P < 0.001$; hedgerow - 32 m $z = 3.26$, $P = 0.001$; grassy margin - 2 m $z = 2.68$, $P < 0.01$; grassy margin - 32 m $z = 2.25$, $P = 0.02$; Fig. 4.5a). No significant differences in abundance were observed between the three non-crop habitats or between the two within-field sites.

The same pattern was observed for the abundance of mesostigmatid mites (adjacent woodland - 2 m $z = 2.36$, $P = 0.02$; adjacent woodland - 32 m $z = 3.61$, $P < 0.001$; hedgerow - 2 m $z = 3.87$, $P < 0.001$; hedgerow - 32 m $z = 5.35$, $P < 0.001$; grassy margin - 2 m $z = 2.04$, $P = 0.04$; grassy margin - 32 m $z = 3.52$, $P < 0.001$; Fig. 4.5b). Again, no significant differences in abundance were observed between the three non-crop habitats or between the two within-field sites.

Astigmatid mite abundance followed a similar pattern to the abundance of oribatid and mesostigmatid mites, with higher abundances observed in all non-crop habitats than at 2 m and 32 m into the cropped area (adjacent woodland - 2 m $z = 3.84$, $P < 0.001$; adjacent woodland - 32 m $z = 1.98$, $P = 0.05$; hedgerow - 2 m $z = 5.10$, $P < 0.001$; hedgerow - 32 m $z = 2.90$, $P < 0.01$; grassy margin - 2 m $z = 4.50$, $P < 0.001$; grassy margin - 32 m $z = 2.31$, $P = 0.02$; Fig. 4.5c). However, within-field abundances were significantly different, with a greater abundance of astigmatid mites observed at 32 m into the crop than at 2 m ($z = 2.19$, $P = 0.03$).

Prostigmatid mite abundance was higher in the adjacent woodland than the grassy margin ($z = 2.20$, $P = 0.03$), and at 2 m ($z = 3.56$, $P < 0.001$) and 32 m ($z = 4.37$, $P < 0.001$; Fig. 4.5d) into the cropped area. Moreover, greater abundances were observed in the hedgerow than in the grassy margin ($z = 2.40$, $P = 0.02$), and at 2 m ($z = 4.01$, $P < 0.001$) and 32 m ($z = 4.95$, $P < 0.001$) into the field. Abundance was greater in the grassy margin than at 32 m into the crop ($z = 2.55$, $P = 0.01$), but not at 2 m ($P > 0.05$). Again, abundance did not vary significantly between the hedgerow and adjacent woodland, or between the two within-field sites.


(a)
Oribatid mites (m$^{-2}$)
0
3
6
9
a
a
a
b
b
AW
H
GM
FE
FC
Habitat
(b)
Mesostigmatid mites (m$^{-2}$)
0.0
2.5
5.0
7.5
a
a
a
b
b
AW
H
GM
FE
FC
Habitat
(c)
Astigmatid mites (m$^{-2}$)
0
2
4
6
8
a
a
a
b
c
AW
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GM
FE
FC
Habitat
(d)
Prostigmatid mites (m$^{-2}$)
0.0
2.5
5.0
7.5
10.0
a
a
b
b
c
AW
H
GM
FE
FC
Habitat

**Fig 4.5** Model-predicted estimates (means ± SEs) of log-transformed (a) oribatid mite, (b) mesostigmatid mite, (c) astigmatid mite and (d) prostigmatid mite abundances in cropped and non-cropped habitats (AW: adjacent woodland (dark green), H: hedgerow (light green), GM: grassy margin (yellow), FE: field edge (orange) and FC: field centre (red)). Data are presented on the transformed scale. Annotations denote statistically significant differences

Enchytraeid worm abundance was significantly higher in adjacent woodland than all other surveyed habitats (adjacent woodland - hedgerow z = 4.40, *P* < 0.001; adjacent woodland - grassy margin z = 5.40, *P* < 0.001; adjacent woodland - 2 m z = 8.04, *P* < 0.001; adjacent woodland - 32 m z = 8.04, *P* < 0.001; Fig. 4.6). Furthermore, abundance was higher in the hedgerow and grassy margin when compared to both within-field sites (hedgerow - 2 m z = 4.28, *P* < 0.001; hedgerow - 32 m z = 4.28, *P* < 0.001; grassy margin - 2 m z = 3.11, *P* = 0.01; grassy margin - 32 m z = 3.11, *P* = 0.01). No significant differences in abundance were observed between the hedgerow and grassy margin or between the two within-field sites.

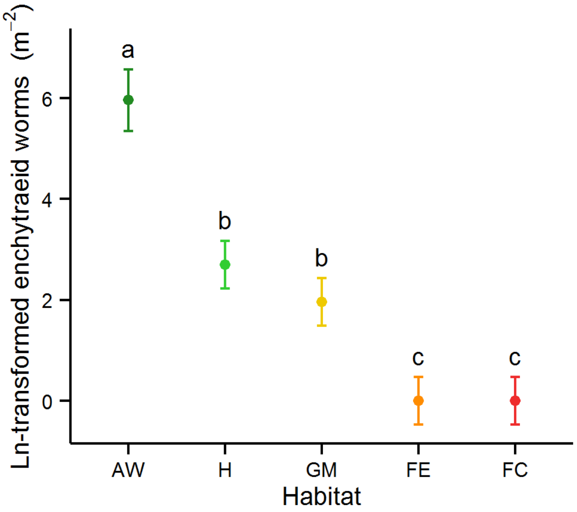

**Fig. 4.6** Model-predicted estimates (means ± SEs) of log-transformed enchytraeid worm abundance in cropped and non-cropped habitats (AW: adjacent

woodland (dark green), H: hedgerow (light green), GM: grassy margin (yellow), FE: field edge (orange) and FC: field centre (red)). Data are presented on the transformed scale. Annotations denote statistically significant differences

Springtail abundance was higher in the adjacent woodland and hedgerow than both within-field sites (adjacent woodland - 2 m, z = 2.07, $P = 0.04$; adjacent woodland - 32 m, z = 4.48, $P < 0.001$; hedgerow - 2 m, z = 2.88, $P < 0.01$; hedgerow - 32 m, z = 5.71, $P < 0.001$; Fig. 4.7a). Furthermore, abundance was higher in the hedgerow than the grassy margin (z = 2.07, $P = 0.04$). Abundance in the grassy margin was higher than at 32 m into the crop (z = 3.64, $P < 0.001$), but not at 2 m ($P > 0.05$). A significant difference was observed between the two within-field sites, with springtail abundance at 2 m greater than at 32 m (z = 2.83, $P < 0.01$).

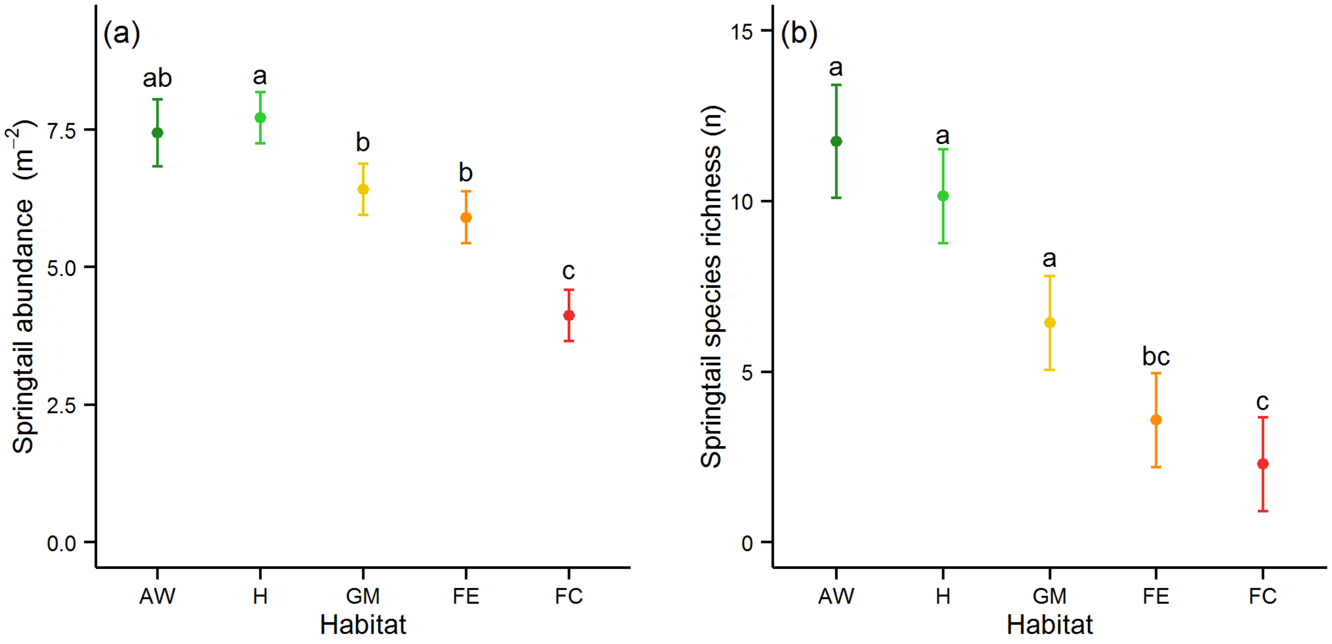

**Fig. 4.7** Model-predicted estimates (means ± SEs) of springtail (a) abundance and (b) species richness in cropped and non-cropped habitats (AW: adjacent woodland (dark green), H: hedgerow (light green), GM: grassy margin (yellow), FE: field edge (orange) and FC: field centre (red)). Abundance data are presented on a log-transformed scale. Annotations denote statistically significant differences

### 4.3.2 The value of hedgerows with and without adjacent woodland

We observed a significant interaction between soil mesofaunal group and the presence or absence of adjacent woodland on abundance within the hedgerows ($F_{20}$ = 3.30, $P$ = 0.03). Contrast tests showed that the abundance of mesostigmatid mites (z = 2.67, $P <$ 0.01; Fig. 4.8a), prostigmatid mites (z = 2.51, $P$ = 0.01; Fig. 4.8b) and springtails (z = 4.62, $P <$ 0.001; Fig. 4.8c) were all higher in hedgerows without adjacent woodland than hedgerows with adjacent woodland.

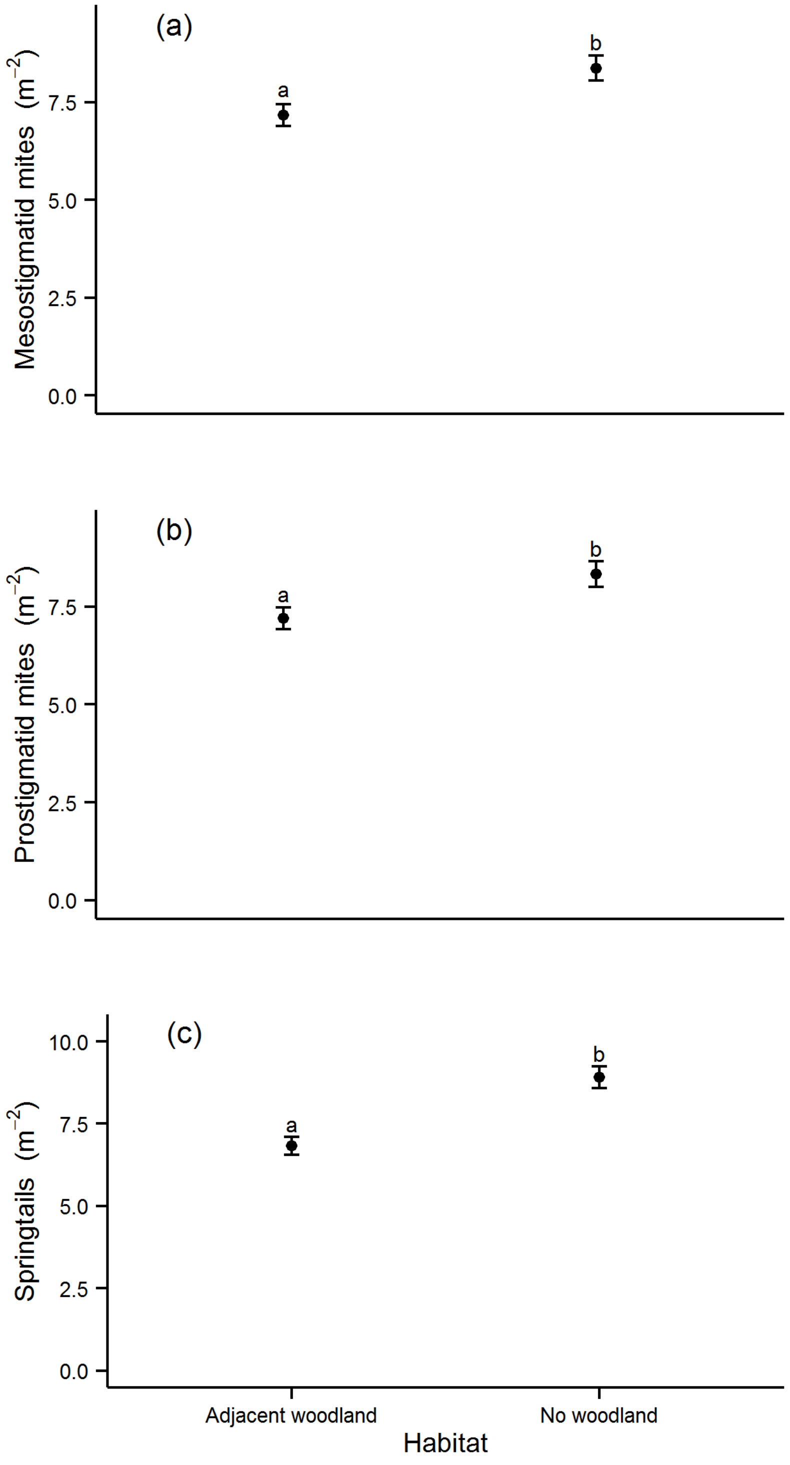

**Fig. 4.8** Model-predicted estimates (means ± SEs) of log-transformed (a) mesostigmatid mite, (b) prostigmatid mite and (c) springtail abundances in hedgerows with and without adjacent woodland. Data are presented on the transformed scale. Annotations denote statistically significant differences

### 4.3.3 Springtail species richness and diversity from woodland-to-field

Springtail species richness was higher in adjacent woodland (z = 2.90, $P < 0.01$) and hedgerow (z = 2.39, $P = 0.02$) sites than the grassy margin and both of the within-field sites (adjacent woodland - 2 m z = 4.46, adjacent woodland - 32 m z = 5.16, hedgerow - 2 m z = 4.23, hedgerow - 32 m z = 5.06, all $P < 0.01$; Fig. 4.7b). Furthermore, species richness was higher in the grassy margin than at 32 m into the crop (z = 2.67, $P = 0.01$), but not at 2 m ($P > 0.05$). No significant differences were observed between the two within-field sites.

A significant effect of habitat on springtail community composition was observed ($F_4 = 7.75$, $P < 0.01$). However, community assemblage did not significantly differ between sites with adjacent woodland and those without ($P > 0.05$). Furthermore, no interactive effect between the two variables was observed ($P > 0.05$). The optimal ordination of species and habitats using NMDS analysis is shown in Fig. 4.9. The ordination plot clearly separates within-field sites from hedgerow and adjacent woodland sites.

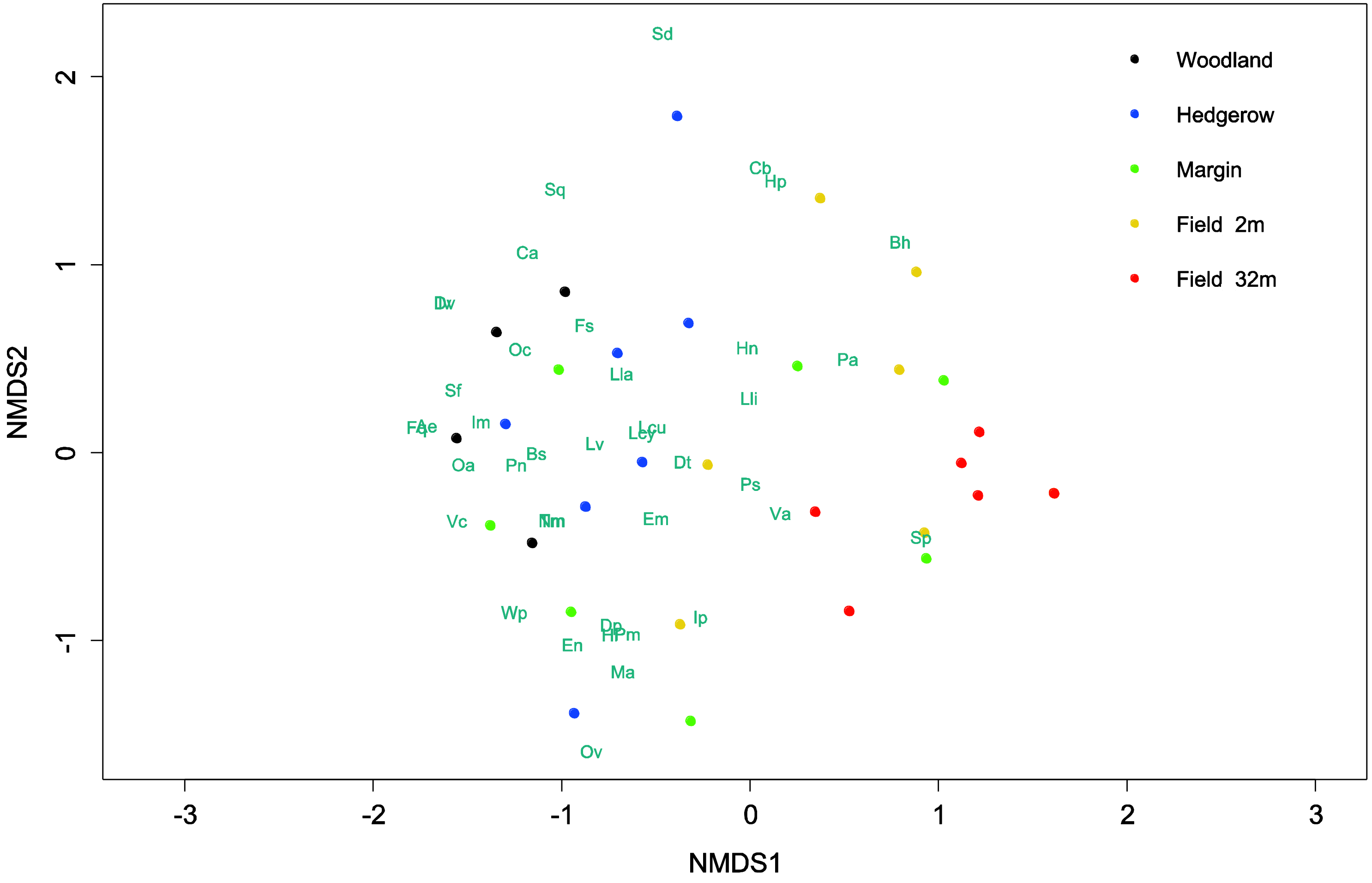
Sd
Woodland
Hedgerow
Margin
Field 2m
Field 32m
Cb
Hp
Sq
Bh
Ca
Dw
Fs
Oc
Hn
Pa
Lla
Sf
Lli
Fq
Ae
Im
Lcu
Ley
Lv
Bs
Oa
Pn
Dt
Ps
Va
Vc
Nm
Em
Sp
Wp
Ip
Dp
Pm
En
Ma
Ov
NMDS2
2
1
0
-1
-3
-2
-1
0
1
2
3
NMDS1

**Fig. 4.9** Ordination biplot based on NMDS analysis of springtail species data. Points indicate sampling sites. Text indicates species, labelled with first letters of the genus and species names. From L-R: Fq = *Folsomia quadrioculata*, Ae = *Allonychiurus edinensis*, Dv = *Desoria violacea*, Iv = *Isotoma viridis*, Sf = *Supraphorura furcifera*, Vc = *Vertagopus cinereus*, Oa = *Onychiurus ambulans*, Im = *Isotomiella minor*, Wp = *Willosia platani*, Pn = *Parisotoma notabilis*, Oc = *Oncopodura crassicornis*, Ca = *Cyphoderus albinus*, Bs = *Ballistura schoetti*, Nm = *Neanura muscorum*, Tm = *Tomocerus minor*, Sq = *Stenaphorura quadrispina*, En = *Entomobrya nivalis*, Fs = *Folsomia spinosa*, Ov = *Orchesella villosa*, Lv = *Lepidocyrtus violaceus*, Dp = *Deuterosminthurus pallipes*, Hi = *Heterosminthurus insignis*, Lla = *Lepidocyrtus lanuginosus*, Ma = *Metaphorura affinis*, Pm = *Proisotoma minima*, Lcy = *Lepidocyrtus cyaneus*, Lcu = *Lepidocyrtus curvicollis*, Em = *Entomobrya multifasciata*, Sd = *Stenaphorura denisi*, Dt = *Desoria tigrina*, Ip = *Isotomurus palustris*, Hn = *Heteromurus nitidus*, Lli = *Lepidocyrtus lignorum*, Ps = *Psuedoistoma sensibilis*, Cb = *Ceratophysella bengtssoni*, Hp = *Hypogastrura purpurascens*, Va = *Vertagopus arboreus*, Pa = *Pseudosinella alba*, Bh = *Bourletiella hortensis*, Sp = *Sminthurides parvulus*

## 4.4 Discussion

### 4.4.1 Soil mesofaunal abundance and community composition across a hedgerow-margin-field transition

All soil faunal groups surveyed were more abundant in hedgerows and adjacent woodland than within the cropped area, both at the field edge and field centre. For the majority of microarthropod groups, the cropped area proffered a hostile environment and abundances were low across within-field samples. Several factors are likely to have influenced this, including increased disturbance and agrochemical use (Chapter

1.4.1), and associated changes in the microbial biomass. Furthermore, reduced vegetative cover in crop fields during fallow months can leave the soil surface more susceptible to temperature fluctuations. For example, Pfiffner and Luka (2000) observed that the 0-5 cm soil surface layer became frozen during winter in cultivated areas, but not in semi-natural habitats. We would therefore expect increased mortality of non-burrowing groups (e.g. soil mites) in the cropped areas during the winter months, and also during the hottest summer months, due a reduced capacity to buffer extreme temperature changes. While we also observed an extremely low abundance of enchytraeid worms across the cropped area, it is possible that within-field abundances were underestimates of real population densities. Unlike soil microarthropods, enchytraeids are able to undergo vertical migration in response to changes in soil moisture and temperature (Nielsen, 1955a; Springett, 1970), so it is feasible that higher population densities were present in cultivated soils at deeper soil horizons.

Data collected using a similar protocol in 2012 showed that soil bulk density at 0-40 cm depth was lower in hedgerows than at the field edge (Lee *et al.*, 2013), indicating an increase in soil compaction and a reduction in the habitable soil pore space in cultivated soils. Since the majority of soil mesofaunal groups utilise existing soil pores and channels, including those created by earthworm activity, soil pore size is a key determinant of the distribution of fauna within the soil profile (Whitford, 1996; Larsen *et al.*, 2004). Increased soil bulk density would likely restrict the movement of many soil organisms, particularly larger-bodied individuals and poor above-ground dispersers, and also reduce soil water holding capacity (Gupta and Larson, 1979). Subsequently, mechanical disruption of the soil profile through tillage is likely to further reduce habitat suitability of within-field sites for soil mesofauna.

Our results show a decline in habitat suitability between the non-cropped and cropped areas, with reduced soil faunal population densities observed at the field edge and in the centre of the field. However, a notable exception to this pattern was observed; astigmatid mites were more abundant at 32 m than at 2 m. Unlike the other mite groups, the Astigmata can thrive in disturbed environments, including agroecosystems, and are not inhibited by tillage (Wardle, 1995; Behan-Pelletier, 1999; Kladivko, 2001;

Reeleder *et al.*, 2006). Indeed, populations appear to recover more quickly from disturbance, most likely due to their short generation times and high fecundity as *r*-selected colonisers (Norton, 1999; Walter and Proctor, 1999). Moreover, it is likely that reduced interspecific competition in the field centre would have further enhanced astigmatid abundance.

In addition to changes in abundance, cropped areas also hosted depauperate springtail communities, suggesting a decrease in habitat suitability with increasing distance from the field boundary. NMDS analysis clearly separated within-field springtail species assemblages from those found in the least disturbed habitats. Ponge *et al.* (2006) categorised common springtail species into slow-dispersers and fast-dispersers according to their ability to actively move across the landscape using locomotory appendages (i.e. legs and jumping apparatus (furcula)). For example, species with short legs, a poorly-developed furcula and incomplete visual apparatus are considered poor dispersers (Hopkin, 1997). These physiological traits have been associated with woodland-dwelling species, which are more susceptible to changes in land use due to limited locomotory capacity and poor protection from desiccation (Salmon and Ponge, 2012). In contrast, fast-dispersers – those species with longer legs, a well-developed furcula and complete visual apparatus – are likely to undergo longer, more frequent migrations across the landscape in response to changes in resource availability.

Several species clustered on the left-hand side of Fig. 4.9 are classified as slow-dispersers (e.g. *S. quadrispina, F. quadrioculata, C. albinus, O. crassicornis, P. notabilis, I. minor*), while those observed in field centres are classified as fast-dispersers (e.g. *P. sensibilis, S. parvulus, V. arboreus*) (Ponge *et al.*, 2006). Since no species were found exclusively in cropped areas, we suggest that springtails associated with these sites at the time of sampling were able to migrate across the habitat matrix through the growing season in response to changes in resource availability as the vining pea crop developed. Given the similarity in springtail and mite abundance patterns across the habitat gradient, we further suggest that soil mite communities may follow a similar trend to that observed for springtails. For example, we would expect the least motile oribatid mite species to be confined to the woodland and hedgerow habitats, with more motile, fast-moving mesostigmatid and astigmatid mite species (Chapter 1.2) able to move into the cropped area in response to changes in resource availability. However, relatively little is known about the locomotory capacity of soil mites and therefore a similar analysis to that described here for springtail species diversity is required to confirm this hypothesis. This area of future study is discussed in more detail in Chapter 6.2.3.

### 4.4.2 The value of non-crop habitats as refugia for soil mesofauna

The value of non-crop areas as refugia for soil mesofauna, and the grassy margin in particular, differed between taxa. Due to the increased structural diversity of plant species in hedgerows and adjacent woodlands versus grassy margins (pers. obs.), a denser, more complex litter layer is likely to form on the soil surface. Additionally, more complex root systems occur (Forman and Baudry, 1984). These vegetative conditions are likely to provide a favourable microclimate for soil fauna, with increased food resources for decomposers and grazers, and therefore enhanced prey populations for predatory groups. Furthermore, hedgerows modify micro-environmental conditions both above-ground and below-ground; for example, through a reduction in soil water evaporation, which helps to maintain higher levels of soil moisture in surrounding soils (Forman and Baudry, 1984).

In contrast, the grassy margins sampled in this study were botanically species-poor, dominated by perennial grasses and a small number of arable weeds. These habitats are likely to receive a moderate level of disturbance, although soil disturbance is likely to be significantly less than annually ploughed or harrowed within-field sites. Additionally, grassy margins may act as agrochemical sinks, accumulating fertilisers, pesticides and herbicides, which allows for nutrient transformation to occur before leaving the field (Marshall and Moonen, 2002). It is possible that these factors contributed to reduced abundances of prostigmatid mites and springtails in the grassy margins compared to the hedgerows studied; explored in greater detail in Chapter 6.2.2. Consequently, it is surprising that we did not observe a difference in the abundance of other mite groups, particularly detritivorous oribatid mites, between the more complex non-crop habitats sampled (hedgerows and adjacent woodland) and the grassy margins.

While grassy margins supported reduced abundances of springtail species, those present were a combination of slow-dispersing and fast-dispersing species. Studies have shown that hedgerows can be important habitats for the recolonization of arable fields by springtails (Alvarez *et al.*, 2000), and our findings suggest that grassy margins may also act as important refuge habitat for fast-dispersing springtails when within-field habitat suitability is low; for example during fallow periods. In addition, these areas are likely to support the abundance of some above-ground arthropod predators. For example, *Loricera pilicornis* (Fabricius) is a specialist springtail-feeding beetle (Meek *et al.*, 2002). In particular, it is an effective predator of *H. nitidus* (Hintzpeter and Bauer, 1986), which was associated with hedgerow and grassy margin habitats in this study. Thus, it is likely that enhanced populations of *H. nitidus* also promoted the abundance of *L. pilicornis*.

Within the microarthropod groups sampled, abundances of Oribatida, Mesostigmata and Astigmata were not significantly different between the adjacent woodland, hedgerow and grassy margin habitats. This suggests that less complex semi-natural habitats are comparable to more complex, well-established habitats as refugia for these groups. Enchytraeid worm abundance was higher in wooded areas than all other surveyed habitats, suggesting that adjacent woodland habitats were more valuable to enchytraeids than any other group. However, hedgerows and grassy margins offered a middle ground, with higher abundances observed in these habitats than in cropped areas. While the ecology of enchytraeids is poorly understood, enhanced population densities have been reported in woodland soils, compared with agricultural habitats (van Vliet *et al.*, 1995). The increased complexity of woodlands, including a well-established litter layer and diverse plant root system, is likely to have promoted habitat suitability for enchytraeids due to an increase in soil moisture content and enhanced food availability (e.g. microbes and decaying organic matter). Furthermore, the adjacent woodland habitats sampled in this study were likely to have been exposed to minimal levels of agrochemical runoff due to the buffering capacity of the grassy margin. Since enchytraeid worms are highly sensitive to anthropogenic disturbance (van Vliet *et al.*, 1997) and environmental toxicity (Römbke, 2003), physical and biochemical stability are likely to be important drivers of habitat suitability for this group.

The surrounding habitat affected the value of hedgerows as refugia for soil fauna. Hedgerows with adjacent woodland harboured reduced abundances of springtails, mesostigmatid mites and prostigmatid mites than those without, suggesting that the value of hedgerows increases as the complexity of the surrounding habitat declines. While some hedgerows were dominated by a single plant species, typically hawthorn, they were generally species-rich with multiple shrub species and a well-established ground layer. This suggests that the majority of hedgerows sampled were relatively old. Since the age of non-crop habitat affects its value for biodiversity (Denys and Tscharntke, 2002) and there may be a time lag for effect (Pfiffner and Luka, 2000; Smith *et al.*, 2008b), older hedgerows are likely to be more effective for maintaining biodiversity over time. Therefore, we would expect recently established hedgerows to have harboured reduced soil invertebrate populations.

Relative population densities of above-ground invertebrates are often lower in non-crop habitat during the summer than in the winter, with populations migrating out of the margins and into the crop in response to changes in within-field habitat suitability (Douglas *et al.*, 2009). Soil sampling occurred in July, when the vining pea crop was well-established but not yet harvested. If the dynamics of below-ground communities mirror above-ground communities, exhibiting a similar change in habitat preference and moving into the crop during the spring and summer, we would expect further reduced population densities during fallow months. Residual populations are likely to be extremely small and dominated by specialists (e.g. astigmatid mites). Thus, the role of non-crop habitat may become even more important for soil fauna during fallow months; the timing of which will vary depending on the when the crop is sown.

However, the extent to which soil organisms can move across the landscape, through both space and time, is relatively unknown and necessitates further research if the value of non-crop habitat for recolonisation is to be determined (Chapter 6.2.2). A comparative study examining the effects of different levels of intensive agricultural management on the seasonal migration preferences of both above-ground and below-ground fauna is needed to assess whether this is valid (Chapter 6.2.3).

Furthermore, the type of crop grown within the field may affect the value of non-crop habitat for soil mesofauna. In the study described here, vining peas were grown in all seven sampled fields. While legumes can provide additional plant N through symbiotic fixation, the presence of legumes has been shown to decrease springtail numbers in the surrounding soil (Milcu *et al*., 2006). Consequently, for springtails at least, it is suggested that non-crop habitat might harbour a higher proportion of existing soil mesofauna when a legume is grown instead of a cereal crop grown under similar management practices. Furthermore, cropping, and in particular crop rotation, can have significant effects on rhizosphere bacterial communities (Alvey *et al*. 2003), with potential bottom-up effects on mesofauna. As such, it is hypothesised that different mesofaunal species assemblages would be observed under continuous cereal cropping versus legume cropping or rotation management.

### 4.4.3 The importance on non-crop habitats in conserving ecosystem function and biodiversity

Since intensive farmland does not provide high-quality habitat for the majority of invertebrates (Morris and Webb, 1987), non-crop habitats act as important refuges for agricultural biodiversity and are therefore of considerable conservation value. Furthermore, this study shows that non-crop habitats, where present, support the majority of soil mesofaunal populations in intensively managed agricultural systems. Data collected in 2012 showed a similar decline in soil mesofaunal abundance between cropped and non-cropped areas. Despite this, crop yield remained high across the field. As in Chapters 3 and 5, we suggest that productivity is maintained by artificial inputs, and in particular nitrogen fertilisers. However, observed changes in within-field soil biodiversity and bulk density suggest that there is likely to be a decline in the buffering capacity of the soil in the longer term, for example in response to drought events. Furthermore, changes in the soil structure reduce the potential for reservoirs of soil fauna in adjacent non-crop habitats to re-colonise cropped areas if the intensity of farming is reduced or if fields are left to naturally regenerate.

## 4.5 Conclusions

We conclude that hedgerows and grassy strips are important components of within-farm habitat and should be promoted where possible. The addition of non-crop habitat is likely to be more important in the least diverse systems, i.e. fields with little or no adjacent non-crop habitat. However, further research is required to assess the effectiveness of promoting non-crop habitats adjacent to the field boundary versus within-field diversity, such as intercropping, in the maintenance of soil invertebrate communities in the longer term. Above-ground, semi-natural habitat is an important determinant of biodiversity at multiple spatial scales (Benton *et al.*, 2003). However, below-ground communities are governed predominantly by local abiotic conditions rather than landscape-scale factors (Bardgett *et al.*, 2005), so the function of neighbouring habitat is less likely to affect the value of within-farm habitat heterogeneity. Nevertheless, multiple landowners within a local area should be encouraged to adopt management schemes in concert in order to reap benefits to soil biodiversity on a landscape scale.

# Chapter 5

# Effects of organic and inorganic fertilisers on relationships between soil mesofauna and ecosystem function above-ground and below-ground

## Abstract

Soil fauna play a key role in ecosystem functioning above-ground and below-ground. However, relatively little is known about the effects of fertiliser use on relationships between soil fauna and ecosystem function. Understanding the impacts of artificial inputs on these relationships is crucial if soils are to be managed in a sustainable way. Using a classical litterbag technique, we investigated the interaction between fertilisers and soil faunal community complexity on the decomposition of organic matter. Additionally, we examined the effects of fertiliser inputs on relationships between soil mesofaunal abundance and above-ground productivity. We did not observe evidence of fertiliser-induced changes in litter decomposition. Above-ground, however, oribatid mite abundance was associated with enhanced crop yield in untreated plots and under moderate levels of fertilisation, but this relationship was disrupted in high input systems. Our findings suggest that the application of ammonium nitrate fertiliser in excess of crop requirements may compromise intrinsic relationships between soil fauna and above-ground ecosystem function.

## 5.1 Introduction

The diversity and composition of soil faunal communities contribute to the functioning of ecosystems both above-ground and below-ground. Decomposition – the fragmentation, redistribution and mineralisation of plant residues, fallen leaf litter and faecal material to bioavailable plant nutrients and soil organic matter – is one of the most widely studied ecosystem processes below-ground. The role of soil biota in litter fragmentation and decomposition has been studied in a range of systems, including forests (Heneghan *et al.*, 1998; Barajas-Guzmán and Alvarez-Sánchez, 2003; Powers *et al.*, 2009; Yang and Chen, 2009), grasslands (Hopkins *et al.*, 1990), deserts (Santos and Whitford, 1981; Belnap *et al.*, 2005) and microcosms (Cragg and Bardgett, 2001). Since decomposition regulates nutrient cycling and bioavailability, the rate of decomposition is a key determinant of soil fertility and, in turn, above-ground productivity. Over the past few decades, studies have identified a range of factors regulating the rate of decomposition, including local air temperature (Bothwell *et al.*, 2014), land management (Burgess *et al.*, 2002; Throop and Archer, 2007), resource quality (e.g. nitrogen, lignin and plant phenol content) (Conn and Dighton, 2000; Loranger *et al.*, 2002; Smith and Bradford, 2003) and a number of edaphic variables, including soil temperature (Xiao *et al.*, 2014), moisture (Jarvis *et al.*, 2007) and pH (Swift, 1979).

Additionally, decomposition rate is determined by the diversity and structure of the local decomposer community, including bacteria and fungi, oribatid mites, springtails and earthworms (Ayres *et al.*, 2009; Bardgett, 2005). At the largest scale, earthworms physically redistribute organic matter from the litter layer throughout the soil horizon (Nielsen and Hole, 1964; Scullion and Malik, 2000; Chapter 1.2). Furthermore, earthworms indirectly enhance decomposition rates by shredding plant material, thereby increasing the surface area upon which the soil microbial biomass can act, and by altering abiotic conditions; for example, increasing soil moisture through burrowing and the formation of nutrient-rich casts (Bardgett, 2005). Detritivorous mesofauna also stimulate microbial decomposition by further reducing litter particle size, in turn manipulating decomposition rate and nutrient availability (Heneghan *et al.*, 1999;

Bradford *et al.*, 2002). The extent to which soil mesofauna affect litter decomposition is climate-dependent, with fauna increasing the rate of decomposition unless temperature and moisture levels constrain their activity (Wall *et al.*, 2008).

The relative contribution of decomposer groups is commonly tested by replicating the classical litterbag technique using a range of pore sizes, designed to selectively exclude groups of soil organisms based on classification by body size. Such studies have typically shown that soil faunal community diversity is positively associated with the rate of litter loss due to the complementarity of functional roles (Wise and Schaefer, 1994; Setälä *et al.*, 1996; González and Seastedt, 2001; Wang *et al.*, 2010), but see Barajas-Guzmán and Alvarez-Sánchez (2003). However, these patterns can be affected by successional stage and litter type (Milcu and Manning, 2011), suggesting that litter quality can impact on fauna, and that these effects can in turn affect the rate at which the material is broken down.

In unmanaged terrestrial ecosystems, decomposition provides the primary source of bioavailable plant nutrients (Whittaker *et al.*, 1979). However, in conventionally-managed agricultural systems, achieving maximum crop yields is largely dependent on agrochemical inputs (Matson *et al.*, 1997). Synthetic inputs affect yields in interaction with a range of widely studied factors including climate (temperature, rainfall and solar radiation) (Monteith and Moss, 1977; Fischer, 1985; Lobell and Field, 2007; Asseng *et al.*, 2011; Aslam *et al.*, 2013), soil quality (e.g. pore size, organic matter content and chemical composition) (Letey, 1985; Kumar and Goh, 1999; Lal, 2004), soil fauna (Crossley Jr *et al.*, 1992; Pashanasi *et al.*, 1992; Li *et al.*, 2002), pests and diseases (Oerke, 2006).

Long-term studies suggest that up to half of major grain crop yields can be attributed to the use of artificial inputs, particularly nitrogen fertilisers. In the United States, a study of long-term nitrogen fertilisation at the Magruder Plots, Oklahoma State University, estimated that a relatively low application rate of 37-67 kg N $ha^{-1}$ $yr^{-1}$ accounted for approximately 40% wheat yield over a 71 year period (Stewart *et al.*, 2005). In the United Kingdom, the Broadbalk Experiment at Rothamsted, Hertfordshire, has shown that long term NPK fertilisation contributes to at least a doubling of winter wheat yield when compared to untreated plots (Rasmussen *et al.*, 1998). This gap is further increased through the use of improved crop varieties and additional agrochemicals such as fungicides and herbicides (Goulding *et al.*, 2008). While the effects of agrochemicals on soil biodiversity are thought to be generally negative (Bünemann *et al.*, 2006; Tabaglio *et al.*, 2009; Thiele-Bruhn *et al.*, 2012), little is known about how their application modifies relationships between soil fauna and simultaneous ecosystem functions, both above-ground and below-ground. A particular lacuna of knowledge is in the relationship between artificial inputs and the interactions between different faunal classes, and how this relates to ecosystem function in the field.

Using a factorial field plot experiment, we aimed to investigate the effects of organic and inorganic fertiliser application on relationships between soil fauna and ecosystem function, both above-ground and below-ground. Barley yield was used as a proxy for above-ground ecosystem function, while a classical litterbag study was used to assess the effects of treatment on decomposition below-ground. Alongside an increase in barley yield under both the inorganic and organic fertiliser treatments in comparison to the untreated plots, we predicted that increased soil faunal complexity would be associated with increased litter decomposition. Furthermore, it was hypothesised that litter loss would be negatively affected by the application of inorganic fertiliser, while the organic treatment would enhance decomposition due to localised changes in soil conditions.

## 5.2 Methods

### 5.2.1 Experimental design

The field site, comprising 16 4 m$^2$ plots in a randomised block design, was situated at the edge of a productive agricultural field at Stockbridge Technology Centre, North

Yorkshire, UK (53º49’30”N, 1º8’60”W). The area had been under arable rotation, comprising a combination of commercial cereal and vegetable crops, for over ten years prior to the study (Table 5.1). The land was always ploughed prior to seeding or planting, and left fallow during the winter months unless winter wheat was grown. All crops were grown according to the Code of Good Agricultural Practice. Fertilisation rate was commonly 180 kg N ha$^{-1}$ yr$^{-1}$.

Plots were physically separated from one another with polycarbonate sheeting (Liv Supplies, Hull, UK), to depth and height each 20 cm, to restrict movement of soil fauna between experimental plots. Each block of four plots comprised the following experimental treatments: standard dose ammonium nitrate fertiliser (Nitram 34.5%N at 175 kg N ha$^{-1}$; SD), double dose ammonium nitrate fertiliser (Nitram 34.5%N at 350 kg N ha$^{-1}$; DD), pig slurry and straw (175 kg N ha$^{-1}$; O), and an untreated control (C). A Qurondon soil series dominated the field site; a stoneless, rapidly permeable sandy loam soil, with poor water-holding capacity and low organic matter content (Bradley and Allison, 1979; Cranfield University, 2015).

**Table 5.1** Cultivation crops and practices at the field site, Stockbridge Technology Centre, North Yorkshire, for ten years preceding the study.
*Vegetable cultivation comprised mixed carrot, onion, cabbage and lettuce crops

| Year | Crop(s) grown |
|---|---|
| 2003 | Potatoes |
| 2004 | Winter wheat |
| 2005 | Vegetables* |
| 2006 | Vegetables* |
| 2007 | Vegetables* |
| 2008 | Vegetables* |
| 2009 | Spring barley |
| 2010 | Winter wheat |
| 2011 | Potatoes |
| 2012 | Spring barley |

### 5.2.2 Soil sampling

Soil sampling took place during week 0 (9th May 2013), week 1 (immediately prior to seed sowing and the application of the fertiliser treatments; 16th May 2013), week 2 (23rd May 2013), week 3 (30th May 2013), week 4 (6th June 2013), week 6 (20th June 2013), week 8 (4th July 2013), week 10 (18th July 2013), week 14 (15th August 2013) and week 18 (12th September 2013). At each sampling event, soil cores were collected from six sampling locations within each experimental plot using a soil corer measuring 8 cm diameter and 10 cm depth, and combined to form a composite sample. A random number generator was used to select sampling locations over a grid of each experimental plot. This process was repeated at each sampling event to avoid sampling the same area on multiple occasions.

Microarthropods were then extracted into 70% ethanol using a modified Tullgren funnel method over a six day period. During this time, the photoperiod was progressively extended to create a temperature gradient designed to drive soil fauna through the soil profile. All individuals were counted and soil mites identified to order level under a binocular microscope (Leica MZ75).

At each sampling event, additional soil core samples were taken at each sampling site and used to calculate soil moisture by drying 25 g soil at 130 °C for 72 hours. A 10 ± 0.1 g subsample was then sieved, mixed with 50 ml distilled water and the pH of the resulting suspension measured.

### 5.2.3 Estimation of decomposition

Litterbags measuring 8 $cm^2$ were constructed from nylon mesh (Northern Mesh, Oldham, UK) of different pore sizes to allow for the selective exclusion of different faunal groups based on body size; 5 mm mesh allowed entry of all faunal groups, 2 mm mesh excluded macrofauna (e.g. earthworms and myriapods) and 100 µm mesh excluded mesofauna (e.g. soil mites, springtails and enchytraeid worms) and macrofauna, while allowing entry of microfauna (e.g. nematodes) and microflora (bacteria and fungi). Bags were filled with 10 ± 1 g chopped (1 cm length) and homogenised dried barley litter, sealed and planted approximately 5 cm below the soil surface. Two bags of each size were buried in each plot. Litterbags were evenly spaced along the top grid row of each plot (Fig. 5.1) in a randomised order.

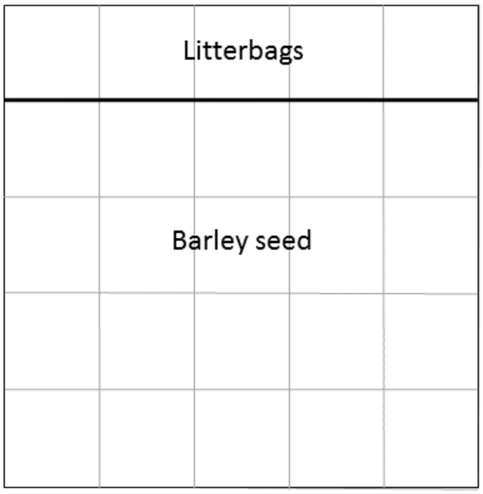

**Fig. 5.1** Location of litterbags and barley crop in each 2x2 m experimental plot. Soil cores were taken from the cropped area. Litterbags were buried in a randomised order along the top grid row

Litterbags were retrieved after 18 weeks (126 days) and dried at 40 °C until no change in mass was observed, which typically occurred between 2-4 days. Root material, soil aggregates and stones were carefully removed and litter was brushed with a small paintbrush to remove soil attached to the surface of the straw. Furthermore, care was taken to ensure that litter loss during burial, harvesting and analysis was minimal. For example, litterbags were placed into individual paper bags during transportation and drying, and contents were handled in a tray during processing in the laboratory. The remaining mass was calculated, and decomposition estimated using the original and remaining litter masses. While decomposition involves multiple processes of fragmentation and breakdown, we hereby refer to litter loss as decomposition.

### 5.2.4 Estimation of crop yield

Barley (*Hordeum vulgare* L. cv. Quench) seed was sown at a planting density of approximately 350 seeds m$^{-2}$, in line with commercial sowing rates, immediately after the baseline samples were taken at week 0. Seed was sown across the bottom four grid rows of each experimental plot (Fig. 5.1). Avoiding the top grid row, where the litterbags were buried, prevented barley roots penetrating the mesh and increasing resource availability within the litterbags. Throughout the study period, plots were weeded by hand and no pesticides or herbicides were applied. At week 18, after the final soil samples were taken, the crop was harvested and barley production estimated using three 20 cm$^2$ quadrats per plot in a random sampling design. Root and shoot material was harvested and dried at 40 °C, and yield estimated from weighed seed.

### 5.2.5 Statistical analysis

All statistical analyses were conducted in R (R Core Development Team, 2014). Linear mixed effects models were used to analyse the interactive effects of fertiliser treatment and soil fauna on litter decomposition and barley production. For the decomposition analysis, the arcsine square root transformed proportion of litter remaining at harvest was used as the dependent variable. Covariates included mesh size, soil moisture content and soil pH. For the yield analysis, covariates included soil mesofaunal abundance, soil moisture and soil pH, averaged across samples taken during the early barley tillering phase (Weeks 2-6); a key determinant of grain development and final crop yield (Engledow and Wadham, 1923; Hucl and Baker, 1989; Blake *et al.*, 2006).

A maximal model, including all covariates and random terms with interactions, was constructed for each analysis using the R package *nlme* (Pinheiro *et al.*, 2015). The ‘dropterm’ function in the R package *MASS* (Venables and Ripley, 2002) was used to inform sets of biologically plausible candidate models. Models were then compared using second-order Akaike Information Criteria (Burnham and Anderson, 2002). For each analysis, a best model was selected from the set of candidate models (Tables 5.1 and 5.2). Pairwise z-tests were performed, with *P*-values corrected using the Tukey method, in the R package *multcomp* (Hothorn *et al*., 2008).

Linear mixed effects models were also used to analyse the effect of fertiliser treatment on additional plant characteristics (plant height; fresh and dried root masses; fresh and dried shoot masses). In all analyses, block was included as a random factor.

**Table 5.2** Model selection table for decomposition analysis. The three best candidate models are presented, with the best model indicated in bold. Litter mass at harvest was used as the dependent term. All models contained a random blocking term

| Model | d.f. | Log *L* | AICc | K | wi |
|---|---|---|---|---|---|
| Treatment + size + treatment*pH | 81 | 68.22 | -110.57 | 12 | 0.01 |
| Treatment*size + pH | 84 | 65.35 | -108.59 | 9 | 0.03 |
| **Size + pH** | **87** | **65.22** | **-100.14** | **6** | **0.96** |

**Table 5.3** Model selection table for yield analysis. The three best candidate models are presented, with the best model indicated in bold. All models contained a random blocking term. Estimated barley yield ha$^{-1}$ was used as the dependent term

| Model | d.f. | Log *L* | AICc | K | wi |
|---|---|---|---|---|---|
| **Count*group*treatment + treatment*pH + treatment*moisture** | **37** | **25.59** | **249.79** | **58** | **0.99** |
| Count*group*treatment + treatment*moisture | 41 | -38.72 | 330.32 | 54 | <0.01 |
| Count*group*treatment | 45 | -80.36 | 374.05 | 50 | <0.01 |

## 5.3 Results

### 5.3.1 Decomposition

We did not observe a significant effect of increased faunal complexity or soil pH (both $P > 0.05$) on litter decomposition. Treatment was excluded during the model selection process (Table 5.2).

### 5.3.2 Yield

Estimated crop yield differed between experimental treatments ($F_{37} = 64.99$, $P < 0.001$; Fig. 5.2), with all fertiliser treatments producing a higher estimated yield than the unfertilised control (SD - C: $t_{37} = 5.15$, DD - C: $t_{37} = 7.51$, O - C: $t_{37} = 4.83$; all $P < 0.001$). Estimated yield was higher under O ($t_{37} = 6.06$) and SD ($t_{37} = 6.09$; both $P < 0.001$) than DD.

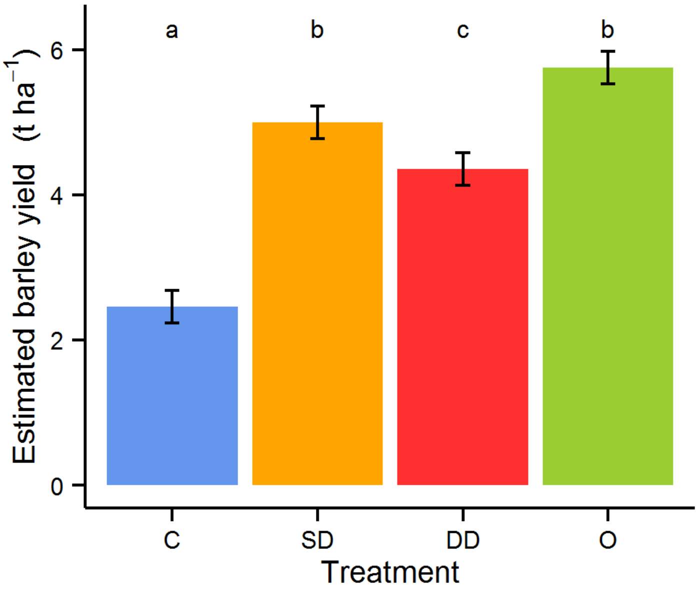

**Fig 5.2** Model-predicted estimates (means ± SEs) of spring barley yields under different experimental fertiliser treatments (C: unfertilised control (blue); SD: standard dose ammonium nitrate fertiliser (Nitram 34.5%N at 175 kg N $ha^{-1}$; orange), DD: double dose ammonium nitrate fertiliser (Nitram 34.5%N at 350 kg N $ha^{-1}$; red); O: pig slurry and straw (175 kg N $ha^{-1}$; green)). Estimated yields are extrapolated from yields per 2 $m^2$ plot (mean ± SE yield under C: 0.93 ± 0.01 kg; SD: 2.00 ± 0.03 kg; DD: 1.80 ± 0.17 kg; O: 2.30 ± 0.03 kg). Annotations denote statistically significant differences

## 5.3.3 Plant characteristics

Plant height was higher under all fertilised treatments than under the unfertilised control (SD - C: $t_{41} = 5.06$, DD - C: $t_{41} = 3.71$, O - C: $t_{41} = 6.51$; all $P < 0.001$, Fig. 5.3a). Furthermore, plant height was greater under O than DD ($t_{41} = 2.81$, $P < 0.01$).

Above-ground, fresh shoot mass was higher under all fertilised treatments than under the unfertilised control (SD - C: $t_{41} = 4.59$, DD - C: $t_{41} = 5.66$, O - C: $t_{41} = 4.73$; all $P < 0.001$, Fig. 5.3b); however, there were no significant differences between fertilised treatments. Dry shoot mass followed the same pattern (SD - C: $t_{41} = 4.90$, DD - C: $t_{41} = 4.70$, O - C: $t_{41} = 5.76$; all $P < 0.001$, Fig. 5.3c).

Below-ground, fresh root mass was higher under all fertilised treatments than under the unfertilised control (SD - C: $t_{41} = 2.26$, $P = 0.03$; DD - C: $t_{41} = 4.81$, $P < 0.001$; O - C: $t_{41} = 2.15$, $P = 0.04$, Fig. 5.3d). Furthermore, fresh root mass was also greater under DD than both SD ($t_{41} = 2.55$, $P = 0.01$) and O ($t_{41} = 2.66$, $P = 0.01$). Dry root mass followed the same pattern (SD - C: $t_{41} = 1.98$, $P < 0.05$; DD - C: $t_{41} = 4.71$, $P < 0.001$; O - C: $t_{41} = 2.17$, $P = 0.04$; DD - SD: 2.73, $P < 0.01$; DD - O: $t_{41} = 2.54$, $P = 0.02$, Fig. 5.3e).

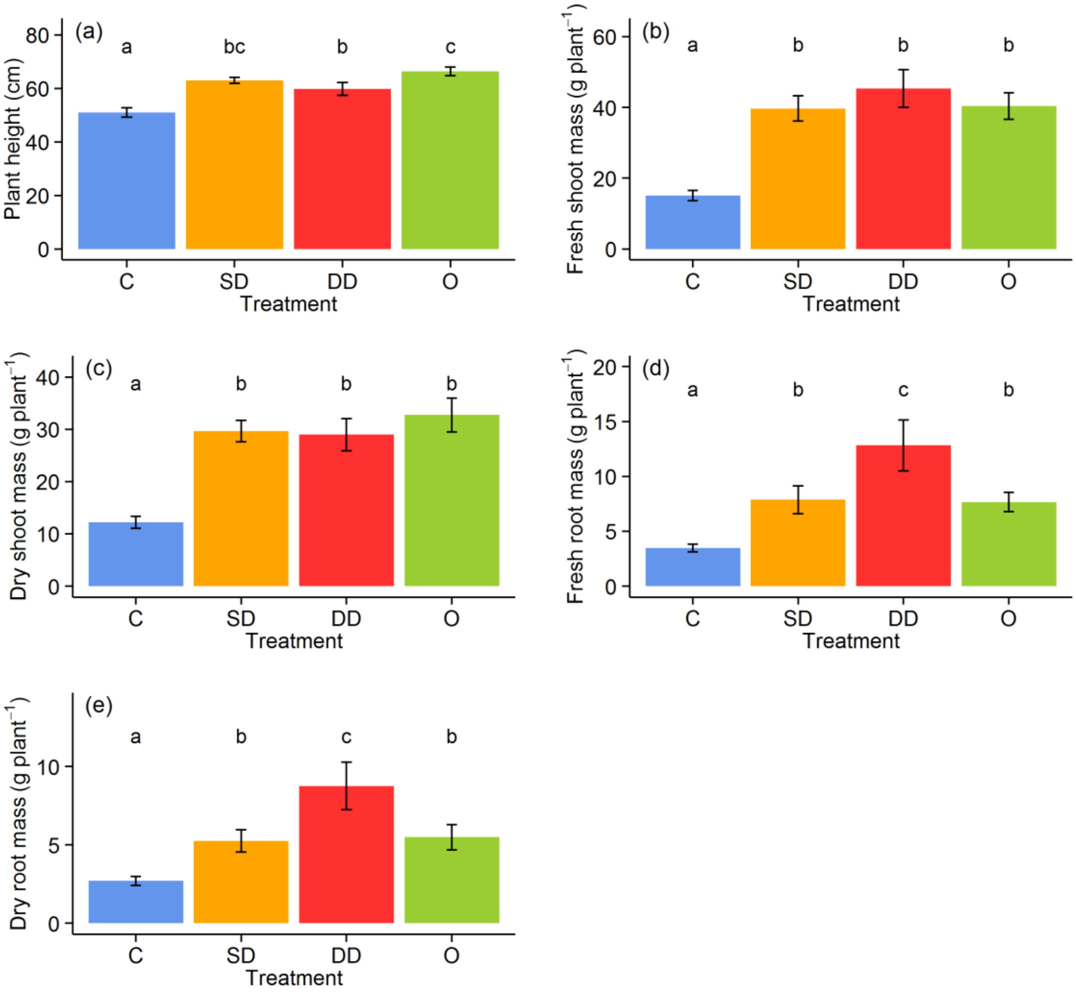

**Fig 5.3** Measurements (mean ± SE) of plant characteristics under experimental fertiliser treatments (C: unfertilised control (blue); SD: standard dose ammonium nitrate fertiliser (Nitram 34.5%N at 175 kg N ha$^{-1}$; orange), DD: double dose ammonium nitrate fertiliser (Nitram 34.5%N at 350 kg N ha$^{-1}$; red); O: pig slurry and straw (175 kg N ha$^{-1}$; green)). Annotations denote statistically significant differences

Estimated yield was influenced by mesofaunal abundance during the tillering period, which varied between treatments (count * group * treatment interaction: $F_{37} = 4.48$, $P < 0.001$; Table 5.4). In particular, contrast tests showed that a decreased abundance of oribatid mites under the DD treatment was associated with a decrease in estimated barley yield ($t_{37} = 2.16$, $P = 0.04$; Fig. 5.2). We also observed effects of soil moisture (soil moisture * treatment interaction: $F_{37} = 190.83$, $P < 0.001$) and soil pH (soil pH * treatment interaction: $F_{37} = 75.638$, $P < 0.001$) on estimated yield, which again varied between treatments.

**Table 5.4** Model-predicted abundances (mean ± SE) of soil mesofaunal groups during the barley tillering period under different fertiliser treatments (C: unfertilised control; SD: standard dose ammonium nitrate fertiliser (Nitram 34.5%N at 175 kg N $ha^{-1}$), DD: double dose ammonium nitrate fertiliser (Nitram 34.5%N at 350 kg N $ha^{-1}$); O: pig slurry and straw (175 kg N $ha^{-1}$))

| | **Treatment** | | | |
|---|---|---|---|---|
| | C | SD | DD | O |
| Oribatid mite abundance (individuals $m^{-2}$) | 1419.14 ± 220.33 | 1193.67 ± 378.63 | 1167.14 ± 192.91 | 1432.40 ± 202.92 |
| Mesostigmatid mite abundance (individuals $m^{-2}$) | 106.10 ± 21.66 | 194.52 ± 63.35 | 225.47 ± 26.40 | 380.21 ± 38.54 |
| Astigmatid mite abundance (individuals $m^{-2}$) | 172.42 ± 49.16 | 97.26 ± 21.05 | 137.05 ± 41.71 | 340.42 ± 167.51 |
| Prostigmatid mite abundance (individuals $m^{-2}$) | 97.26 ± 23.39 | 79.58 ± 21.05 | 66.32 ± 30.95 | 119.37 ± 44.14 |
| Springtail abundance (individuals $m^{-2}$) | 168.00 ± 35.73 | 243.16 ± 80.19 | 168.00 ± 30.20 | 605.68 ± 265.10 |

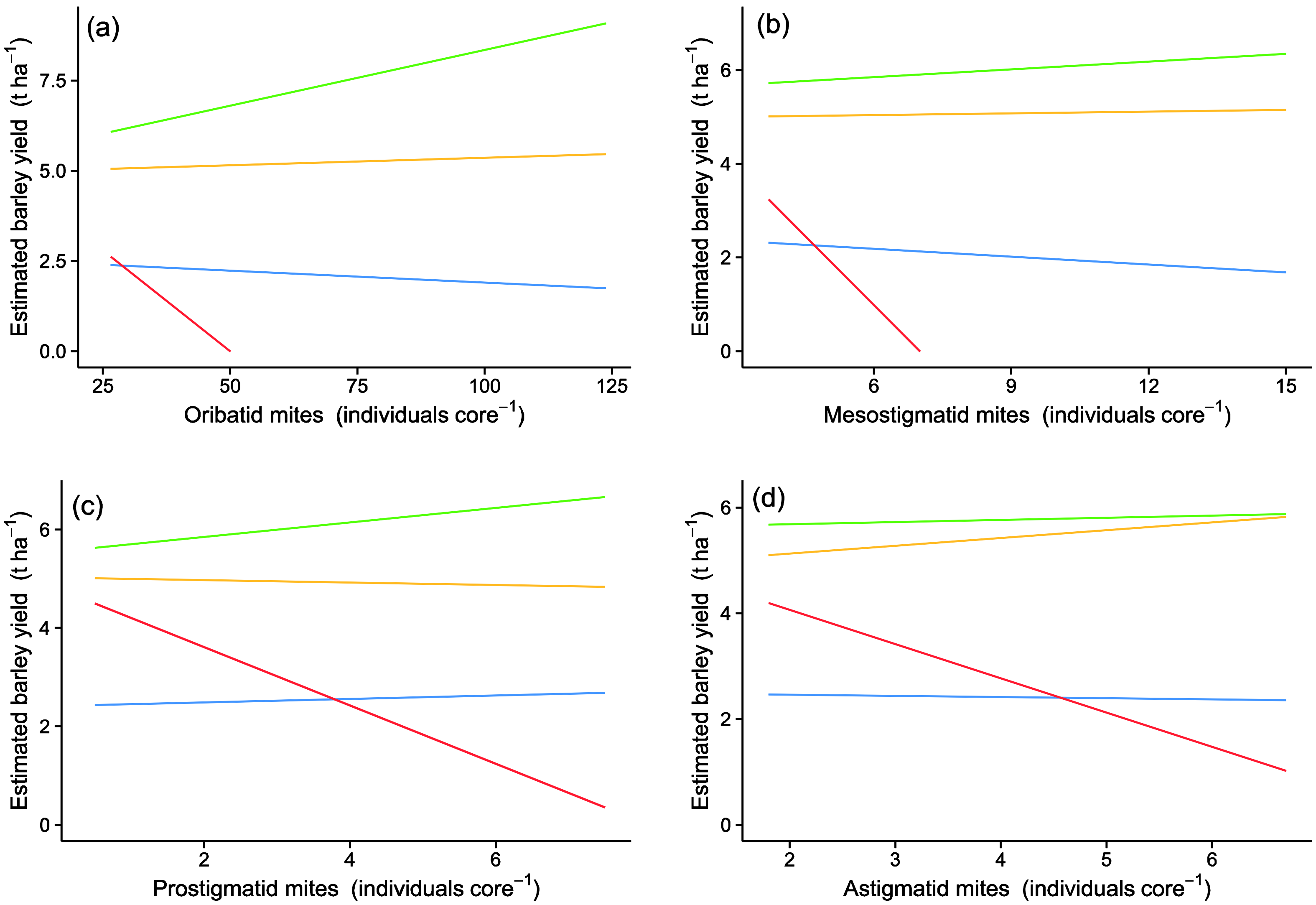
(a)
Estimated barley yield (t ha$^{-1}$)
0.0
2.5
5.0
7.5
25
50
75
100
125
Oribatid mites (individuals core$^{-1}$)
(b)
Estimated barley yield (t ha$^{-1}$)
0
2
4
6
6
9
12
15
Mesostigmatid mites (individuals core$^{-1}$)
(c)
Estimated barley yield (t ha$^{-1}$)
0
2
4
6
2
4
6
Prostigmatid mites (individuals core$^{-1}$)
(d)
Estimated barley yield (t ha$^{-1}$)
0
2
4
6
2
3
4
5
6
Astigmatid mites (individuals core$^{-1}$)

**Fig 5.4** Model-predicted spring barley yields under different experimental fertiliser treatments with varying soil mite abundances. Fertiliser treatments are colour-coded (C: unfertilised control (blue); SD: standard dose ammonium nitrate fertiliser (Nitram 34.5%N at 175 kg N ha$^{-1}$; orange), DD: double dose ammonium nitrate fertiliser (Nitram 34.5%N at 350 kg N ha$^{-1}$; red); O: pig slurry and straw (175 kg N ha$^{-1}$; green))

## 5.4 Discussion

### 5.4.1 Decomposition

Decomposition rate is determined by a range of climatic and edaphic factors, resulting in substantial variation in average litter losses between studies. The litter losses observed in this study fell within the range observed in other systems over a similar time period (Oladoye *et al.*, 2008; Peng *et al.*, 2014). However, we did not observe a significant increase in litter loss associated with increasing soil faunal community complexity, as observed in other studies (Vossbrinck *et al.*, 1979; Wise and Schaefer, 1994; Setälä *et al.*, 1996; González and Seastedt, 2001; Bradford *et al.*, 2002; Smith and Bradford, 2003). Since litter loss was approximately equal across all mesh sizes (macromesh: 71.15%, mesomesh: 73.68%, micromesh: 70.73%), we conclude that the decomposition process was dominated by the activities of the soil microbial community in this system, with little contribution of soil mesofauna or macrofauna. Indeed, mesofaunal abundances observed within the plots (Table 5.4) were lower than expected. Oribatid and mesostigmatid mite population densities were comparable to those observed under the IL treatment in Chapter 3 and at 32 m into cultivated field in Chapter 4. Under a simultaneous treatment regime at a different site (Chapter 2), abundances of springtails were approximately ten times greater than those observed here.

Additionally, we did not observe any evidence of earthworm activity in the 0-10 cm soil layer over the course of the study. The distribution of earthworm populations is governed by a range soil properties, including soil moisture content and the availability of organic matter (Lavelle, 1988; Edwards and Bohlen, 1996; Fonte *et al.*, 2009), in addition to anthropogenic factors, such as land-use type and management intensity (Curry, 2004; Smith *et al.*, 2008c). The sandy nature of the soil type at the site, with low organic matter content and poor water holding capacity, is likely to have decreased habitat suitability for earthworms. Since earthworms are typically the dominant soil macrofaunal decomposers, a lack of earthworm activity in the macromesh bags may have further reduced the strength of a mesh size effect. It is likely that continuous, high-intensity agricultural management, coupled with the soil characteristics listed above, depleted soil mesofauna and macrofauna, which resulted in a depauperate system dominated by microorganisms.

Estimating decomposition using the litterbag technique has been subject to criticism due to the potential for additional litter loss or leaching from larger mesh sizes through handling and rainfall (Bradford *et al*. 2002) and changes in microclimate within the litterbag (Vossbrinck *et al*. 1979) such as increased soil moisture, which could further vary with mesh size. Furthermore, this technique artificially alters resource availability, potentially promoting soil faunal population growth which could lead to elevated estimates of decomposition. However, we would expect no bias in these effects between fertiliser regimes, thus our results are likely to be consistent across treatments.

Litter decomposition was not significantly different between treatments, suggesting that the activity of soil microorganisms was equal between treatments. We propose two possible explanations for this. Firstly, fertiliser inputs may not have exerted adverse effects on the soil microbial biomass through the direct (e.g. ammonium toxicity) or indirect (e.g. soil acidification) effects suggested in Chapter 5.1. However, reductions in soil microbial biomass (DeForest *et al.*, 2004; Wallenstein *et al.*, 2006; Demoling *et al.*, 2008) and activity (Bowden *et al.*, 2004; Demoling *et al.*, 2008), as well as altered community composition (Peacock *et al.*, 2001; Belay *et al.*, 2002; Marschner *et al.*, 2003; Ramirez *et al.*, 2010), have been widely reported in response to fertiliser use. Alternatively, it is possible that any negative effects were offset by the increase in local resource availability, via enhanced root biomass, in the fertilised plots over time. The microbial biomass may have recovered rapidly following the fertiliser application in week 0, with compensatory microbial activity resulting in an increase in decomposition in these plots over time, versus the control plots which may have shown a steadier rate of decomposition. Since litterbags were retrieved at one time point only, we are unable to conclude whether these trends are reflective of long-term decomposition dynamics in this system. Future work should consider the effects of fertiliser and other agrochemical treatments on decomposition rates over time.

### 5.4.2 Barley yield

Above-ground, estimated barley yield was significantly enhanced under all three fertiliser treatments in comparison to the unfertilised control. Furthermore, plant height and root and shoot masses also followed this pattern, with the unfertilised control treatment producing the shortest and smallest plants, both above-ground and below-ground.

We observed that the relationship between detritivorous oribatid mites and estimated barley yield was either neutral or positive under the C, O and SD treatments. However, this positive impact of increasing soil nutrients on oribatid mite abundance was reversed under the high input regime. Here, we observed that a decreased abundance of oribatid mites was associated with a negative effect on barley yield. In contrast, both fresh and dry root masses were lower under DD than SD and O, suggesting that the negative impacts of this high ammonium nitrate dose on oribatid mites were not offset by enhanced root growth and a likely associated increase in the microbial biomass.

Detritivorous fauna can contribute to plant nutrient uptake and growth via changes in the biomass and structure of the soil microbial community (Laakso *et al.*, 2000). Since the abundance and distribution of oribatid mites are closely related to their food availability (Maraun and Scheu 2000), abundance tends to be higher in arable soils where crop residues or green manure are enhanced (Kautz *et al.* 2006, Ponce *et al.* 2011).

However, soil microarthropods are sensitive to ammonia (Moursi 1962, 1970). Furthermore, Bosch-Serra *et al.* (2014) observed that the abundance of oribatid mites decreases in response to fertilisation in excess of crop requirements. The standard dose fertiliser treatments used in this study contained 175 kg N ha$^{-1}$; within the optimum range of N concentrations for utilisation during the early stages of crop development. However, the high dose ammonium nitrate treatment was applied at double the standard rate of N fertilisation. Therefore, it is likely that fertiliser applied in excess of crop requirements may have resulted in an accumulation of ammonia in the soil and some localised leaching. Furthermore, a lack of soil organic matter in the study soil would likely reduce the denitrification capacity of the soil (Burford and Bremner, 1975), exacerbating these effects.

The Oribatida exhibit a wide range of life-history strategies (Maraun and Scheu, 2000), and egg development can range from <40 to >250 days between families (Luxton, 1981). Subsequently, populations may not have been able to recover from the effects of fertiliser toxicity over the course of the study period. Since the experimental plots were physically separated from one another using polycarbonate sheeting, we suggest that decreased oribatid mite abundance resulted from mortality rather than emigration. Consequently, we conclude that oribatid mites, as detritivores, contributed to productivity in untreated plots and plots under moderate levels of fertilisation, but that this relationship was disrupted in high input plots in this study. Some microarthropod detritivores, including springtails, stimulate N mineralisation (Bardgett and Chan, 1999; Partsch *et al.*, 2006) and can promote plant growth indirectly by grazing upon, and therefore upregulating the activity of, the microbial biomass (Kreuzer *et al.* 2004). However, the mechanisms behind this are not fully understood and it is unclear whether oribatid mites affect plant growth in this way. The role of oribatid mites in promoting plant growth should be explored; for example, in a microcosm experiment using soils inoculated with varying densities of oribatid mites and microbes in previously defaunated soils. This suggestion is further explored in Chapter 6.2.4.

## 5.5 Conclusions

We observed some evidence of high dose fertiliser treatments modifying the relationships between soil invertebrates and above-ground ecosystem functioning. Despite this, productivity remained high, although not as high as under moderate fertilisation. Under continuous supply, this substitution of function for inputs might be manageable, but it implies a substitution of natural function that may create a lock-in, whereby reliance on continuous artificial inputs is required for productivity to be maintained. If the cost of inorganic fertilisers increases, this is likely to force farmers to apply less N but raises questions over the potential for processes to recover. We did not observe evidence that fertilisation inputs affected relationships between soil fauna and ecosystem functioning below-ground. However, the depauperate nature of the study soil suggests that damage from intensive agriculture may have already taken effect, disrupting relationships between soil invertebrates and the decomposition of organic matter.

In Chapter 2, we observed some detrimental effects of inorganic fertilisers on soil mesofauna and positive effects of organic fertiliser. In addition, organic fertilisation provides a range of environmental attributes, for example organic matter and increased moisture, which may become increasingly importance for improving resilience in response to a range of environmental factors (e.g. drought and flooding). However, achieving high productivity using organic inputs relies on access to large amounts of organic material, which may not be feasible in many large-scale systems. Hence, we suggest that combinations of organic and inorganic fertilisers may offer a compromise that contributes to both high productivity and resilience to environmental change, and that these should be explored. Some trade-offs between biodiversity and productivity are discussed in Chapter 6.

# Chapter 6

# General Discussion

In Chapter 1, the key objectives of this thesis were established. Specifically, this thesis aimed to:

1. Investigate the effects of intensive agriculture on soil fauna-function relationships using realistic management practices in field systems.
2. Explore the effects of agricultural management practices on multiple soil invertebrate groups simultaneously.
3. Draw comparisons between the effects of intensive agricultural management in multiple systems, with varying soil types.
4. Make recommendations for ways in which any negative observed effects of intensive agriculture on soil diversity-function relationships can be minimised.

We first evaluate the extent to which this thesis achieved these aims and explore the implications for this research in a wider context. Subsequently, in Chapter 6.2, we suggest priorities for future research based on the findings of this thesis and gaps in the wider literature.

## 6.1 Review of main findings

### 6.1.1 Negative impacts of fertiliser use on soil biodiversity

Agricultural intensification has involved changes in management practices, including the continuous cultivation of arable land, the development of high-yielding crop varieties, advanced agricultural mechanisation and increased agrochemical use. These changes have contributed to a dramatic increase in crop yields globally (FAO, 2014). Agricultural intensification can exert negative effects on biological systems above-ground and below-ground, with consequences for agroecosystem function. In a soils context, the regulation of ecosystem function by soil fauna is progressively substituted for by regulation via artificial inputs (Giller *et al.*, 1997).

The use of agrochemicals in intensive agricultural management have been associated with adverse impacts on soil faunal abundance and community structure (Joy and Chakravorty, 1991; Bünemann *et al.*, 2006; Tabaglio *et al.*, 2009; Thiele-Bruhn *et al.*, 2012). In Chapter 1, a knowledge gap was identified around how fertilisation affects multiple soil faunal groups and, additionally, the consequences of these changes for agroecosystem function. Consequently, within this thesis, the effects of organic and inorganic fertiliser regimes on multiple soil faunal groups were tested in a number of agricultural systems, including both arable and plantation systems. We observed some negative effects and some neutral effects of inorganic fertilisers on soil fauna, with variation between taxa and sites.

We observed that, at least in water-limited sandy soils, the negative impacts of inorganic fertiliser on soil invertebrates were exacerbated by the addition of irrigation (Chapter 3). We suggest that this is due to the increased solubilisation of fertiliser. In areas of higher rainfall, or in moister soils, we would expect that the application of fertiliser without irrigation would have also exerted observable negative effects. The study soil was characterised by low organic matter content and low water-holding capacity (Barton *et al.*, 2010), similar to the study soil of Chapter 5. As these soils become saturated with water, excess ammonia is leached into the soil profile (Pathan *et al.*, 2002; Yao *et al.*, 2012), coming into contact with the soil fauna. Therefore, incorporating organic matter into these soils, for example through mulching, may have the potential to reduce these effects and increase the nitrification capacity of the soil (Burford and Bremner, 1975; Yao *et al.*, 2012), thereby reducing effects on soil fauna.

We have suggested that this thesis supports the argument that inorganic fertilisers exert negative effects on soil fauna through direct ammonia toxicity, as suggested by Moursi (1970), and Chapter 6.2 contains suggestions as to how this could be more explicitly tested. However, we have also observed evidence of fertiliser-induced soil acidification, which led to reductions in oribatid mite abundance (Chapter 2). While the mechanism by which fertiliser applications impact on soil fauna was not explicitly tested in this thesis, this finding lends some support to the hypothesis that fertiliser-induced soil acidification negatively impacts on soil organisms. In Chapter 3, however, models containing pH were excluded during the model selection process. This suggests that the mechanism, or dominance of mechanisms, by which fertiliser use affects soil fauna may differ between systems. The inclusion of data containing soil physical and chemical properties (e.g. soil composition, including OM content) in these analyses may help to suggest which mechanisms dominate in systems with different soil properties.

We observed evidence of populations of soil organisms recovering to baseline levels within the equivalent of a growing season following a single application of nitrogen fertiliser at the start of the season (Chapter 2). This is the first study to show that fertiliser applications can modify temporal changes in the abundance of soil fauna. However, this study took place in soil that had been out of cultivation for over a decade. In a more intensively managed system, with a history of frequent perturbations, recovery would be expected to take longer. Under long-term, continuous cultivation, we would also expect to see stronger, more immediate effects on soil fauna with greater differences in average abundance between treatments; similar to Chapter 3 where fertilisation regimes had been in place for over five years.

Soil food webs can be characterised by a high degree of species diversity (Usher *et al.*, 1979; Torsvik *et al.*, 2002; Bardgett *et al.*, 2005; Wurst *et al.*, 2012). In this thesis, we did not specifically investigate whether fertiliser inputs had species-specific effects on soil organisms. Thus, we are only able to draw broad comparisons between mite groups, springtails and enchytraeid worms. While we would expect inputs to have broadly similar effects across species within the same group, some taxa exhibit substantial variation in tolerance to environmental stressors, e.g. springtails (Irmler, 2006), and species-specific effects are therefore more likely to occur within these taxa. Furthermore, some groups, such as the Oribatida, have a wide range of life-history strategies (Behan-Pelletier, 1999; Søvik *et al.*, 2003). Therefore, studying effects on broad level taxonomic groups may not have captured underlying shifts in soil mite food web composition in response to treatment.

Soil invertebrate research can be broadly separated into two approaches. Firstly, detailed, species-level work may be carried out using a single study taxa, typically springtails or earthworms. Alternatively, abundances of a subset of fauna groups, e.g. soil microarthropods, can be estimated. While neither of these approaches allows for both a comprehensive and detailed analysis of the community to be performed,, difficulties in taxonomic identification and the labour-intensive nature of soil invertebrate community characterisation means that combining these approaches is uncommon. Throughout this thesis, attempts were made to gain a comprehensive overview of changes across the soil mesofaunal community (Chapters 2, 3, 4, and 5) and also nematodes (Chapter 3). Furthermore, we attempted to combine these approaches by a) estimating the abundance of all soil mesofaunal groups observed and b) undertaking species identification of a study taxa (springtails), with which we were able to make predictions of species-level trends (Chapter 4). In the future, advancements in DNA barcoding will allow rapid, reliable, financially-viable methods of characterising the entire soil biota, enabling a wider range of taxa to be characterised simultaneously. At present, however, this approach is prohibitively expensive and the database for soil mesofaunal species is incomplete (Orgiazza *et al.*, 2015.

### 6.1.2 Relating changes in soil biodiversity to ecosystem function

Throughout this thesis, a range of measures were used to estimate the effects of arable management on soil fauna-ecosystem function relationships. Changes in soil mite and nematode abundance and trophic structure were related to the estimated bioavailability of plant nutrients (Chapter 3). Furthermore, changes in soil fauna along a gradient of agricultural intensity were discussed in the context of yield in the previous year (Chapter 4). Finally, plant growth and organic matter decomposition were used as measures of above-ground and below-ground ecosystem respectively (Chapter 5). However, the relation of changes in soil faunal community abundance and structure in terms of ecosystem function are complex and still remain unclear.

We observed some evidence of high-dose fertiliser treatments disrupting relationships between soil fauna (oribatid mites) and ecosystem function (yield) (Chapter 5). Without a procedural control where mites were removed from the soil, it is not possible to estimate the extent to which oribatid mites, through their contribution to decomposition and nutrient cycling, affected yield under each fertiliser treatment. However, this result does suggest that there is a relationship between the abundance of detritivorous mites during the early tillering phase and subsequent yield, which is disrupted in high-input systems. It is more likely that this is the result of a shared driver – for example, high fertiliser doses impacting on soil mesofauna through lower trophic levels – than a direct causal relationship. Despite this, we observed limited evidence of treatment effects on soil fauna-ecosystem function relationships elsewhere in this thesis (Chapter 3). We have argued that these patterns suggest that, in intensive arable systems, artificial inputs substitute for the role of soil fauna in regulating agroecosystem function (Giller *et al.*, 1997). However, future work should compare these results to defaunated soils in order to evaluate the extent to which this is valid. Further discussion of this topic is contained in Chapter 6.2.4.

### 6.1.3 Evaluating the potential for mitigating negative effects of intensive arable management

Throughout this thesis, we have observed evidence of intensive agricultural management severely reducing population densities of soil invertebrates, particularly after several years of continuous management. This was most starkly illustrated in Chapter 4, where we observed clear decreases in abundance along a gradient of increasing management intensity. However, this work has also identified a number of different ways in which these effects can potentially be reduced.

The first option is a ‘land sparing’ approach; encouraging, or continuing to encourage, the setting aside of areas of existing farmland for conservation purposes at the farm or landscape scale. Areas of non-crop habitat have benefits for above-ground agricultural diversity (Lagerlöf *et al.*, 1992; Dover and Sparks, 2000; Woodcock *et al.*, 2005; Michel *et al.*, 2006) as well as below-ground (Hof and Bright, 2010, Smith *et al*. 2008b, see also Chapter 4), and so are likely to benefit both above-ground and below-ground communities. In Chapter 4, the value of non-crop habitats for soil mesofauna was shown to vary between taxonomic groups. However, one or more non-crop habitats adjacent to an arable field supported increased numbers of all groups sampled, in addition to springtail species diversity, when compared with cropped areas. Non-cropped areas, including grassy margins, act as refugia for soil mesofaunal communities and are likely to aid the re-establishment of populations if land is left fallow or the intensity of management decreases (Chapter 6.2.3).

The second option is a ‘land sharing’ approach, where impacts on soil fauna are considered when designing agricultural management regimes and steps are taken to reduce the risk of these inputs. We observed some positive effects of organic fertiliser inputs on soil invertebrate abundance (Chapter 2). Organic fertilisation was later shown to produce equivalent yields to ammonium nitrate fertiliser (Chapter 5). While this result is not consistent with findings on a larger scale – organic yields are typically 25-50% lower than conventional yields (Kirchmann and Bergström, 2013) – our findings do support the large body of work identifying benefits of organic agricultural management for soil conservation (Watson *et al.*, 2002; Peigné *et al.*, 2007; Verbruggen *et al.*, 2010).

Farming practices that result in low yields will not be able to support the needs of a growing population, thus organic fertilisation is not a viable option for sustainable intensification on a global scale. In particular, organic fertilisation requires large amounts of organic material, including animal manures and green matter, which individual farms do not typically produce in sufficient quantities to use as a sole method of fertilisation on a large scale. However, as suggested in Chapter 5, there may be scope for combining organic and inorganic fertiliser types to limit adverse effects on soil fauna while maintaining productivity. We suggest that the most ‘at risk’ soils, including those with low organic matter, would benefit most from such an approach. Since there is a lack of experimental evidence evaluating the potential for organic and non-organic fertiliser combinations for soil sustainability, this is an area that requires further research. Specifically, the benefits for soil mesofauna under different proportions of fertilisers and the subsequent effects for ecosystem function should be assessed alongside trade-offs in productivity under these fertiliser regimes. A larger-scale version of the sampling design used in Chapter 5, using multiple sites with different soil types, could be usefully applied here.

## 6.2 Future directions and wider perspectives

### 6.2.1 The importance of soil conservation

Soils are under increasing pressure from a range of anthropogenic activities. One third of soils are moderately to highly degraded due to unsustainable management (FAO, 2015a). Globally, soils are degrading at such a rate that, in many parts of the world, only decades of soil functionality remain. In Chapter 1, we discussed the breadth of functions that soil fauna contribute to, including the cycling of water and nutrients, productivity and the suppression of plant diseases. Therefore, it is clear that soil fauna-function relationships need to be conserved before populations are unable to recover. In an agricultural context, the capacity of a system to recover will depend on a combination of factors, including the resilience of the existing biotic community, the shape of the surrounding landscape, including the proportion of non-crop and corridor habitats, and the duration and intensity of management. As suggested by Godfray *et al.* (2010), there is a risk that measures of ecosystem health that are more difficult to quantify will be ignored in favour of more easily measureable characteristics that may not be appropriate. Due a lack of taxonomic knowledge of below-ground systems and the challenges of characterising change (Chapter 1), there is a danger that changes in soil biodiversity will be ignored until it is too late. This is particularly pertinent when it is thought that a huge number of soil-dwelling species, with potential benefits to human health in terms of pharmaceuticals and also indirectly through ecosystem services, are as of yet unidentified.

Some progress has been made recently to recognise the importance of soil for providing ecosystem services. For example, the UN Convention on Biological Diversity recognises the importance of soil biota for ecosystem health and has launched an initiative targeting the conservation and sustainable management of soil biodiversity, including agricultural systems. Furthermore, the FAO has declared 2015 the International Year of Soils, aiming to promote awareness of the importance of soil health in sustaining human life, while supporting a number of national and international policies supporting sustainable soil management. These changes in mind-set are vitally important if the preservation of soils and soil biodiversity is to be recognised as a fundamental component of sustainable intensification. However, it is imperative that the link between soil health and human health is communicated clearly, and that the preservation of intrinsic soil fauna-function relationships becomes a priority for sustainable intensification.

### 6.2.2 Evaluating the potential for non-crop habitat as refugia for soil mesofauna in intensive arable landscapes

In Chapter 4, the value of different non-crop habitats (adjacent woodland, hedgerows and grassy margins) for soil mesofauna was investigated. We observed that grassy margins were useful habitats for oribatid, mesostigmatid and astigmatid mites, and enchytraeid worms. The potential for grassy margins to act as refugia for farmland diversity has been well studied (Verboom and Huitema, 1997; Altieri, 1999; Smith *et al*., 2008a; Douglas *et al*., 2009; Hof and Bright, 2010). However, other options for the inclusion of non-crop habitat in intensive agricultural systems exist and a comparative study should be undertaken in order to evaluate their potential for conserving soil fauna-function relationships .

For example, an alternative to linear areas of non-crop habitat at the field edge, as is the case with field margins, may be the establishment of ‘islands’ of non-crop habitat within an arable field. Thomas *et al.* (1991) observed that island habitats provided useful overwintering ground for rove and ground beetles, with evidence of these natural enemies migrating up to 60 m into the field during the summer months. Furthermore, a follow-up study showed that these non-crop habitat islands harboured densities of these beneficial invertebrates similar to neighbouring field margins within three years of establishment. However, despite their potential for promoting abundances of above-ground invertebrates, the value of island habitats in arable fields has not yet been investigated for soil fauna.

In order to identify the optimal spatial distribution of non-crop habitat for the conservation of soil mesofauna, a replicated, comparative field study should be undertaken. Whether soil mesofauna mirror the temporal dynamics of above-ground invertebrates by migrating into the field through the spring and summer months in response to an increase in resource availability, and whether migration effects are more or less associated with different spatial arrangements of non-crop habitat, is also of interest (Chapter 4). Thus, the proposed study should monitor changes in abundance across the habitat matrix over time, with increased sampling effort during late spring, summer and early autumn.

A key factor determining the value of the spatial arrangement of non-crop habitats in an arable field is the extent to which they act as agrochemical sinks. In Chapter 4, we observed that, unlike the other mesofaunal groups studied, numbers of prostigmatid mites and springtails were not statistically different between grassy margins and the field edge. They were, however, observed in higher abundance in hedgerows and adjacent woodland, where lower levels of agrochemical runoff would be expected. Since one of the functions of field margins is to act as an agrochemical sink and protect neighbouring watercourses from the effects of agrochemical runoff (Blanco-Canqui *et al*., 2004; Krutz *et al*., 2005; Dorioz *et al*., 2006), it was suggested that these responses may be due to differences in the ammonia toxicity limits of different taxonomic groups. The extent to which the soil below the field margins studied in this study was contaminated is unknown. However, in order to determine whether grassy margins are accumulating agrochemicals and therefore impacting on some soil faunal groups, for example those with reduced sclerotisation (Chapter 1.2), toxicity analysis of the soil along the woodland-to-field transect should be carried out and related to the relative threshold limits of different mesofaunal groups. We suggest that the latter could be tested in the laboratory, by exposing laboratory-reared, clonal soil mesofaunal populations to environments containing different concentrations of ammonia and assessing mortality.

### 6.2.3 Recovery of soil mesofaunal populations in the field following perturbation

The value of non-crop habitat in promoting the abundance of soil mesofauna across the field, as opposed to localised increases in abundance in soils associated with non-crop habitats, also depends on the migration capacity of these organisms. Since the distribution of soil organisms across a landscape will affect the ecosystem functions and processes that they contribute to, this is of a wider concern. However, there is a significant gap in our understanding of how far and how fast soil fauna, and particularly soil mesofauna, move across the landscape, both horizontally and vertically.

The motility of soil mesofauna varies between groups. For example, *r*-selected astigmatid mites and predatory mesostigmatid mites are able to move faster than oribatid mites (Chapter 1.2). Furthermore, motility can vary between species of the same group. For example, springtail species can be classified as fast-dispersers and poor-dispersers depending on the development of the legs, furcular and visual apparatus (Ponge *et al*., 2006). However, how far and how fast organisms can move across the landscape, and whether species-specific differences in mobility among the soil mite groups exist, are important areas for future research. There may be potential for using transparent soil media here to track the movement of fauna in 3D space over time.

An improved understanding of the dispersal capacity of soil mesofauna would also help to make predictions about the recovery of populations following a perturbation; for example, tillage or a fertiliser event. In Chapter 2, the recovery of soil mesofauna to baseline levels (abundance prior to perturbation) following a fertiliser application occurred within the equivalent of a single season. However, this study took place in an uncultivated soil. How soil mesofaunal populations recover in the longer-term, for example following continuous cultivation, is relatively unknown.

Where long-term intensive cultivation has significantly impacted soil mesofaunal populations (as in Chapters 4 and 5), it is likely that the recovery of soil fauna in an affected system would take several years or decades and, at first, be dominated by specialists. For example, changes in nematode community composition in the decade following the cessation of fertilisation can be slow, with higher trophic levels taking the longest to recover (Verschoor *et al*., 2001).  Similarly, the community recovery of springtails following a forest fire has been shown to take over a decade, with only fast-dispersing species recovering to baseline abundance within this initial 10-year period (Malmström, 2012).

Such differences in recovery rates following perturbation are likely to be dependent upon both the life-history and dispersal capacity of organisms. Indeed, Lindberg and

Bengtsson (2005) observed that soil microarthropod species with larger habitat ranges recovered more quickly following experimental drought events than those restricted to smaller areas of habitat. Furthermore, oribatid mites recovered more slowly than springtails, likely due to differences in life-history and locomotion as discussed here and in Chapter 1.2. This finding lends some support to the idea that non-crop habitat dispersed throughout the wider habitat, for example through the establishment of several small ‘islands’ or an intercrop approach, may be useful for the recolonisation of species with slow rates of development, low fecundity and small habitat ranges. This would include the majority of oribatid mites (Chapter 1.2). While grassy margins such as those sampled in Chapter 4 may harbour high densities of mesofauna relative to the cultivated field, we therefore hypothesise that they are less likely to be valuable for the re-establishment of populations within the field.

Intercropping methods – growing two or more crops together, usually in alternating rows – may also aid re-establishment of soil faunal populations following years of intensive management by increasing habitat heterogeneity throughout the field rather than in one or two areas. Intercropping practices are widely used by African farmers, but less commonly nowadays in Western agriculture (Machado, 2009). Intercropping can reduce soil erosion while maintaining productivity if a high-yielding crop (e.g. a cereal) is grown alongside a soil-conserving crop (e.g. a legume), particularly if grown perpendicular to a topographical or weather gradient. The use of a leguminous crop acts as a living mulch, reducing soil evapotranspiration and, therefore, the need for irrigation. Intercropping has been shown to increase soil organic carbon content, likely due to an increase in plant root biomass (Manna and Singh, 2001; Cong *et al.*, 2015). Crucially, intercropping in this way has the potential to reduce the need for, or amount of, future fertiliser inputs due to the natural N-fixation (Danso *et al.*, 1987; Peoples *et al.*, 1995; Shah *et al.*, 2003). Therefore, this practice has potential for supplementing or replacing N fertiliser inputs in some systems, with predicted knock-on effects for soil fauna.

Increased microbial diversity (Chai *et al.*, 2005) and activity (Manna and Singh, 2001) have been observed in intercropped systems. Several reasons may exist for this, including increased habitat heterogeneity, variation in crop rooting depths, and changes in soil nutrient and moisture availability. While the literature on the impacts of intercropping practices on soil invertebrates is limited, intercropped systems have been shown to promote springtail population densities in comparison to wheat monocultures, reflecting increases in soil moisture and soil organic matter content under intercropped regimes (Gravesen *et al*., 2008).

While the methods suggested in Chapters 6.2.2 and 6.2.3 may benefit soil organisms, and ultimately soil health, it is essential that any trade-offs with yield are investigated. Existing research suggests that cereal yields are enhanced when intercropped with a leguminous plant (Jensen, 1996; Li *et al.*, 2001). Furthermore, yields have been shown to be more stable under intercropping systems (Sileshi *et al*., 2012). However, introducing areas of non-crop habitat to a conventionally managed field reduces the area available for production, while intercropping may reduce the total economic value of crop per hectare depending on the crops grown. A comprehensive analysis of trade-offs between ecosystem functions and services is essential to determine whether a reduction in overall farming intensity increases the overall benefits to the system through an increase in biodiversity and intrinsic biodiversity-ecosystem service relationships.

### 6.2.4 Trading function for dependence?

This thesis investigated whether the use of agrochemical inputs results in the trading of intrinsic relationships between soil mesofauna and ecosystem function (e.g. decomposition) for dependence. The term dependence has been used to describe a “lock-in” whereby the continual use of artificial inputs impacts negatively on soil fauna, resulting in mortality and a need for equal, or greater, amounts of fertilisers to be applied in order to maintain productivity. In the event that fertiliser resources become constrained, through reductions in availability and/or restrictive costs, this creates a risk to the resilience of the system.

This thesis has gone some way to address this question. In Chapter 3, the impacts of fertiliser-induced changes in soil mesofauna on the estimated bioavailability of plant primary and secondary nutrients were explored. Contrary to our expectations, we did not observe evidence of treatment-induced changes in faunal abundance impacting on plant nutrient bioavailability, and it was suggested that these soils were already in a state of ‘dependence’. In Chapter 5, changes in soil mesofaunal abundance in response to different fertiliser regimes were examined in relation to crop yields and decomposition. We observed evidence of high levels of inorganic fertiliser disrupting relationships between oribatid mites and productivity. However, this was only true for doses of ammonium nitrate fertiliser applied at double the typical dose for this crop-site combination (350 kg N $ha^{-1}$).

Consequently, there is insufficient evidence presented here to conclude that intrinsic relationships between soil mesofauna and ecosystem function are traded for dependence under intensive agricultural management. In order to test this hypothesis more rigorously, the studies described in Chapters 3 and 5 should be replicated to include a defaunated control treatment. Defaunation of a soil system in the field can be achieved using steam fumigation or chemical fumigation methods, although the latter may present risks to the wider ecosystem. Alternatively, defaunation could be more easily performed using a mesocosm experiment. For example, soil monoliths could be extracted, subjected to deep-freezing to defaunate the soil and sealed with 2 mm mesh (as used in the litterbag study in Chapter 5) to prevent immigration of soil mesofauna from the surrounding soil, and replanted. This approach would help to present a clearer idea of the contribution of soil mesofauna to the ecosystem functions assessed throughout this thesis, thus adding confidence to assertions of treatment-induced changes to intrinsic relationships.

## 6.3 Summary

Intensive, and unsustainable, agricultural management has accelerated rates of soil erosion globally, such that approximately one third of soils are now classified as being moderately to highly degraded (FAO, 2015a). In some areas of the world, the FAO predict that, under current rates of soil degradation, only 60 years of soil function remain. In the United Kingdom, it is expected that only 100 harvests remain in agricultural soils (Edmondson *et al.*, 2014). The work carried out in this thesis suggests that intensive agricultural management, including the use of inorganic fertilisers, has negative impacts on soil invertebrate communities and further suggests that these changes may have consequences for ecosystem function. If agricultural management continues to be unsustainable, and fertiliser use increases as expected (FAO, 2015b), this poses a threat to the resilience of the system as a whole. If it occurs, recovery is likely to be slow and favour species with short generation times and good dispersal capacity; further altering community structure.

However, there is room for optimism. There are a number of ways in which management can be made more sustainable, and awareness of the importance of this is increasing among academics, stakeholders, policy directors and the public. Nevertheless, research and policy need to progress rapidly in order to preserve arguably the most important natural resource on the planet for the health of future generations. In terms of research, it is vital that a collaborative, multidisciplinary approach is undertaken, integrating a range of soil expertise, including ecologists, hydrologists, microbiologists and soil physicists, in addition to terrestrial scientists. Each side of the soil surface is intrinsically linked; above-ground processes are sustained by the soil and below-ground processes are influenced by those above-ground. In order to expand our understanding of the impacts of agriculture on natural ecosystems, it is imperative that the two fields of research recognise one another more openly and work together towards a more sustainable future.

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