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Mesofaunal Recolonisation of Degraded Soils

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By

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Copyright Statement

Mesofaunal Recolonisation of Degraded Soils

Abstract

JENNIFER KATE WILLIAMS

The degradation of soil quality due to anthropogenic causes is globally important, both in terms of ecosystem services and ecological biodiversity. Soil quality reduction is stated to be detrimental for population densities and species diversity of soil invertebrates, including the mesofauna (Acari and Collembola). Within the soil food web, mesofauna occupy several trophic levels and as such facilitate nutrient turnover, fulfilling vital ecosystem functions and services. Understanding soil invertebrate population dynamics not only during degradation, but equally upon ecosystem restoration, is vital to identify possible losses or benefits to healthy ecosystem functioning.

Prior to this investigation the Highfield site, Rothamsted Research, had been divided and maintained as grassland, arable cropping or bare fallow for 50 years. The latter resulted in a soil that had low soil organic matter levels, poor structure, low bacterial biomass and virtually no invertebrate population. Investigations into the invertebrate population changes, within both the experimental plots and surrounding land, upon alteration of the existing management strategies was completed over a two year period. Changes to mesofaunal populations were detected across all treatments following conversion. Generally, new fallow and arable management strategies produced low density fluctuating populations affected by the physical disturbance of ploughing and lack of soil organic matter as a basal food resource. Grassland management produced increased species diversity and abundance within a more stable soil food web. Each of the new management strategies developed towards its equivalent management strategy within the control treatments.

Although it was apparent that the mesofaunal populations were re-establishing under more favourable environmental conditions, there was no definitive conclusion as to the source of the population increases. An attempt to identify the physical mode of invertebrate movement was completed, utilising a prototype mesocosm to act as a physical barrier, this showed promise for future use in such studies.

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Abbreviations

ANOVA	Analysis of variance
DM	Dry Matter
ECN	Environmental Change Network
C	Carbon
LOG_{10}	Log scale
LOG_e	Natural log
N	Nitrogen
RMAVOVA	Repeated Measures analysis of variance
SE	Standard Error
SNK	Student Newman Kuels statistical test
SP-ANOVA	Split-Plot analysis of variance
∅	Diameter
√	Square root

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At North Wyke Research Station, I am indebted to Adrian Joynes, and a host of French placement students, who I worked in partnership with, for the completion of the Little Burrows experiment. Without their help this experiment would not have been able to continue past the data points discussed within this thesis. Additionally, constructive comments and advice from Felicity Crotty on experimental procedure and thesis chapters were also appreciated. Furthermore, I am grateful for all the help, support and friendship from all the North Wyke staff, I miss working with you, and the unique atmosphere that has been created there.

At Rothamsted Research I would like to thank the members of the Highfield Reversion project, particularly, Penny Hirsch and Ian Clark. Additionally, all the helpers and students that were 'volunteered' to assist with the experiments maintenance and sampling.

On a personal level, only the unwavering support of my whole family, but mostly, Rob, Owen and of course Noah (who arrived seven months into this work), has made the completion of this thesis possible. I will forever be proud of you all. I thank you all for your help and understanding. Whether it was proof reading, listening to problems, having a nap at the right time or endlessly taking the boys out all day so that I could work in peace and quiet, your support will never be forgotten. I love you all very much.

AUTHOR'S DECLARATION

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

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A programme of study was undertaken including statistical packages and technical writing. External institutions were visited for consultation purposes and several papers have been published, with several more in preparation for publication.

Presentation and Conferences Attended:

The Introductory Acarology course at Ohio State University was undertaken in June 2011 as part of the training programme for this thesis.

A presentation entitled 'Does changing agricultural management practice change soil invertebrate community structure' was completed at the joint meeting of the Royal Entomological Society of London and the Soil Ecology Society in September 2011 at the National Marine Aquarium, Plymouth.

The Post-Graduate conference based at Rothamsted Research, Harpenden was attended annually and poster presentations completed at each time.

Publications:

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Murray, P.J., Clegg, C.D., Crotty, F.V., de la Fuente Martinez, N., Williams, J.K., Blackshaw, R.P., (2009). Dissipation of bacterially derived C and N through the meso- and macrofauna of a grassland soil. *Soil Biology and Biochemistry* 41 (6), 1146-1150

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Experimental Overview

Due to the nature of the work conducted the following is a brief description of each experiment reported within this thesis, including; identifying those involved in the design, management and completion of each experiment, along with the time frame involved.

Chapter Two: Part B
The efficiency of the Tullgren Funnel experiment was designed by Jennie Williams and completed in summer 2011 at North Wyke.

Chapter Three
The Highfield Reversion Experiment was completed over two stages. Stage one, occurred in June 2006, and completed the collection of preliminary data. The original investigators involved were Penny Hirsch, Phil Murray, Ian Clark, Lucy Gilliam, Soran Sori and Jennie Williams. The preliminary mesofaunal data presented within this thesis was extracted, identified and analysed by Jennie Williams. Other aspects were completed by the other investigative team members, resulting in Hirsch *et al* (2009).

Stage Two was the completion of the Highfield Reversion project. As the investigation was multi-disciplinary, each of the researchers had a responsibility for a different aspect of data collection. The principal investigators were Penny Hirsch and Phil Murray, additional researchers involved were Ian Clark (PLFAs), Jennie Williams (mesofauna), Phil Brooks (microbial biomass), Rodger White (statistics) and Chris Watts (soil physics). The experimental design was developed by Penny Hirsch, Phil Murray and Rodger White. Due to the number and intensity of samples, a large team comprising of the researchers involved, students and volunteers completed each sampling. Between samplings the experimental area was maintained by the Rothamsted farm staff, as per the experimental instructions. However, once sampling had been completed, sample processing and analysis became the responsibility of the designated researcher. Within the context of this thesis the mesofaunal samples were extracted, identified and analysed by Jennie Williams, with statistical advice from Dan Dahona. Full data analysis will follow in a collaborative article.

Chapter Four
This chapter describes the Highfield Transect Project, an extension to the Highfield Reversion Project. This was designed, sampled and analysed between September 2008 and September 2010, by Jennie Williams, as an addition to the Highfield Reversion Project. Statistical advice for experimental design and data analysis were provided by Dan Dahona.

Chapter Five
Each of the experimental procedures were designed by Jennie Williams with statistical advice from Dan Dahona. The experiments described in Part A (invertebrate viability) and Part B (soil sterilisation techniques) were completed solely by Jennie Williams between April and June 2011. The Little Burrows Recolonisation project, described in Part C, was set up by Jennie Williams and

Adrian Joynes (North Wyke, Research Assistant) between June and September 2011. However, due to unforeseen circumstances the experimental maintenance and sample extraction was completed by Adrian Joynes (September 2011 to present). Mesofaunal extraction for the data presented within this thesis was completed by Mathieu Hirschy (French work experience student) between September 2011 and January 2012, following training by Jennie Williams. Data analysis was completed by Jennie Williams.

Chapter One

Introduction

1.1 Soil

Soil forms a thin layer uppermost in the earth's crust. It is an important natural resource often utilised by humans for their own gains; such as crop growth, raw material production or ground to build on (Haygarth and Ritz, 2009). Biologically, soil supports many ecosystems from the poles to equator and has been described as one of the most complex systems on Earth (Ritz, 2008). A significant proportion of worldwide biodiversity, at least 25% of described living species, live in soil (Bardgett and Wardle, 2010, Decaëns, 2010) often leading to claims that it is the poor man's tropical rainforest (Gilson, 1996). Soil provides many of life's requirements, including nutrients and structure to support plant, bacterial and fungal growth, pest suppression or facilitating chemical and physical processes (Doran and Zeiss, 2000). Soil is formed through interactions between inorganic minerals - with a range of particle sizes, derived from the weathering of the parental bedrock – and organic matter - water, air and organisms (Coleman and Crossley, 2003; Haygarth and Ritz, 2009). There are many definitions for soil quality or health, many of which are based on anthropogenic needs, either now or in the future (Haygarth and Ritz, 2009), but from an ecological perspective in order to be considered healthy a soil must be able to support life (Coleman, 2008). Factors that reduce soil quality include reduced nutrient availability, heavy metal deposition, structure loss or hydrological property changes. Soil degradation has a variety of sources; these can occur naturally, such as burning, desertification or volcanic activity. However, anthropogenic interference, for example agro-ecosystems landscape management, also results in poorer soil quality. Soil degradation is a concern due to the impacts on chemical, physical and biological processes, which may result in productivity reduction thus decreasing economic return. The

degradation of soil quality is problematic throughout the world, in the UK farming practice intensification since the second world war has resulted in carbon losses from soil of 0.6% yr^{-1} in England and Wales between 1978-2003 (Bellamy *et al*., 2005). In Córdoba Province, Argentina, the intensive management and agrochemical practices of corn and soya bean cropping have similarly led to degradation of the biological, chemical and physical soil condition (Cantú, 1998; Becker, 2006: Bedano, Cantu and Doucet, 2006). The quantification of soil quality through indicators is a key discussion point within the literature with suggestions for physical, chemical and biological parameters (Doran and Parkin, 1994; Karlen *et al*., 1997). However, to date there has been no consensus on the threshold values for the indicatory parameters including the soil biota (Arshad and Martin, 2002; Beylich *et al*., 2010).

1.2 Living Soil

As a habitat, soil provides a small space into which a large diversity and density of organisms are packed (Scheu and Falca, 2000). Within this space fauna are distributed both vertically and horizontally in soil pores (Ettema and Wardle, 2002), providing a challenging environment for researchers. The soil pores can be both air and water filled, the surface area, moisture content and pore size and connectivity affect an organism's ability to live within the environment provided (Adl, 2007). Small pore size can restrict the size of organisms able to live, feed and navigate through the tunnels (Kampichler, 1999). Whilst moisture and humidity levels affect the very survival and reproduction of organisms at risk from desiccation (Waagner, Bayley and Holmstrup, 2011) leading to the development of adaptations to overcome these environmental conditions (Greenslade and Greenslade, 1973; Greenslade, 1982; Holmstrup *et al*., 2001).

Within each square metre of soil it is thought that there could be more than 10 000 taxa (Bardgett, 2005). These organisms are commonly divided into groups by size; the

microflora (bacteria, Fungi, Green Algae) exist in large numbers, Tiedje (1995) believed there to be between 20 000 – 40 000 bacterial species / g of soil. The Microfauna are usually less than 0.2mm in size (Protozoa and Nematoda), the Mesofauna (Acari and Collembola) typically between 0.2 – 2mm in size and Macrofauna with individuals with a body size larger than 2mm (Coleman and Crossley, 2003). It is generally agreed that within soil there are two possible food webs to transfer energy and nutrients from one trophic level to another. Bacterial based food webs are usually found in ecosystems with high nitrogen inputs and high disturbance levels, whereas low nitrogen inputs and low disturbance levels lead to a fungal based food chain (Coleman, Reid and Cole, 1983; Wardle, 2002; van der Heijden, Bardgett and van Straalen, 2008; Kardol and Wardle, 2010). The presence of either a fungal or bacterial based food web has implications for the functional groups of species occupying higher trophic levels within the food web. An example of this is provided by Parfitt *et al*. (2010), where low fertiliser and livestock levels induced a fungal based food web with larger numbers of Acari (especially Oribatida) whereas the replica bacterial based food web with high fertiliser and livestock levels had more Collembolan species.

Anderson (1975) described soil animals as an "enigma", to date little further is known about the interactions, responses or behaviours that occur between different organisms inhabiting the soil (Hassell *et al*., 2006; Mills and Adl, 2006) or the services (benefits people obtain from ecosystems) and functions (natural processes completed within ecosystems) that these organisms provide (Foissner, 1997; Bengtsson, 1998). In comparison to above ground species and ecosystems, little information has been collected (Bardgett, 2002) and as a result most soil fauna are classified as generalist feeders, believed to be dependent on the available food sources within their immediate habitat (Scheu, 2002). Additionally due to the difficulties in reliably extracting and identifying these organisms (see André, Ducarme and Lebrun 2002 for a full review) they are often

over looked in large-scale investigations (Firbank *et al*., 2003, Kleijn *et al*., 2006), further limiting the knowledge that could be collected. Bengtsson (1998) argued that due to the soil environment's complexity and heterogeneity and the corresponding volume and specialist nature of the work involved, that it is unlikely any single system will ever be completely counted and identified.

This thesis will concentrate on the mesofauna, sometimes referred to as microarthropods, these are typically found at densities of 50 000 - 300 000 m^{-2} within temperate UK grassland soil (Bardgett and Cook, 1998). Soil mesofaunal movements and digestive processes facilitate the break down and turnover of organic matter within the soil from both living and dead sources (Hurej, Debek and Pomorski, 1992; Edwards, 2000; Endelweber, Ruess and Scheu, 2009), allowing the release of nutrients, most notably carbon (C) and nitrogen (N) but also phosphorus (Mckercher, Tollefson and Willard, 1979) for plant uptake (Wardle *et al*., 2004) and microbial utilisation (Petersen and Luxton, 1982; Heal, Anderson and Swift, 1997; Chamberlain *et al*., 2006). However, there is much debate as to the mesofaunal contribution to total nutrient turnover; Verhoef and Brussaard (1990) believed their role to be marginal, whereas, De Ruiter *et al*. (1993) and Griffiths (1994) suggested that as much as 30% of mineralised N was provided by the mesofauna. This is the dominant ecosystem function performed by mesofaunal communities. Other ecosystem functions and services have proven difficult to identify and study (Wolters, 2001) but include the movement of bacterial and fungal spores by passive transport (Kevan, 1965; Wallwork, 1976; Malloch and Blackwell, 1992; Shaw, 1992; Williams, Whipps and Cooke, 1998; Renker *et al*., 2005). It has been stated that due to large numbers of trophically equivalent organisms resulting from the high species richness, most species within the soil food web must be redundant (Bardgett, 2002) and therefore a plateau in ecosystem services and functions must be reached at moderate species diversity (Cardinale *et al*., 2006).

This diversity is demonstrated within the mesofauna. The Acari, often referred to as mites, are some of the most abundant soil arthropods (Koehler, 1999) with numerous species in the UK. Here, soil Acari are generally split into three superfamilies; Prostigmata, Oribatida and Mesostigmata, each group occupies a different functional role within the food web. The Mesostigmata are generalist predators (Karg, 1993), whilst the Oribatida are detritivores and have been described as unspecialized feeders (Maraun *et al*., 1998). Finally, the Prostigmata are omnivorous, detritivores or predators depending on the species. Many Acari species provide essential ecosystem services, for example the Oribatida facilitate soil structure maintenance and organic matter turnover (Crossley, 1977; Coleman and Crossley, 1996). Acari are also known to stimulate fungal and bacterial metabolism (Norton, 1986).

The Collembola are present in large numbers with over 300 UK species (Hopkin, 2007). Comprising some of the largest abundances of soil invertebrates (Bardgett and Wardle, 2003) with densities of up to 60000m^{-2} recorded by Gange and Bower (1997) in grassland soils. Collembola have been quoted to span all food web trophic levels, from predator level to, in some cases, acting as the first trophic level within the food web (König, Kaufmann and Scheu, 2011) depending on the available resources (Chahartaghi *et al*., 2005). Many Collembola are generalist, opportunist feeders, usually on a wide range of fungal taxa, algae and detritus (Anderson, 1975; Chen, Snider and Snider, 1996; Ponge, 2000), nematodes (Lee and Widden, 1996) and bacteria (Murray *et al.*, 2009). As a food source Collembola form an important part of the food web as prey for generalist predators including, carabid beetles and cursorial spiders in arable, grassland and forest ecosystems (Agustí *et al*., 2003; Wise, 2004; Birkhofer, Wise and Scheu, 2008; Oelbermann, Langel and Scheu, 2008).

However, due to the complex nature of studying invertebrate diets, true reflections of nature are difficult to reproduce in the laboratory. Many studies use gut or faecal content analysis (Ponge, 1999; Remén, Krüger and Cassel-Lundhagen, 2010), laboratory preference studies (Klironomos and Kendrick, 1995; Ponge, 2000; Addison, Trofymow and Marshall, 2003; Maraun *et al*., 2003; Chauvet, Ponge and Wolters, 2007) or morphological aspects of the mouthparts (Chen, Snider and Snider, 1997) to determine diet. These techniques have limitations including; only providing a snap shot of the immediate diet, which is possibly the least digestible food or when there was limited food availability. Additionally, consumption does not guarantee assimilation into the consumer's body. More recent techniques use stable isotopes to trace carbon and nitrogen movement through the soil food web (Scheu and Falca, 2000; Murray *et al*., 2009; Crotty, Blackshaw and Murray, 2011).

1.3 Soil Mesofaunal Population Dynamics and Dispersal

Within the literature there is much debate as to the natural control source over soil fauna populations, some argue top-down control, exerted by predators (Bardgett and Wardle, 2010), whilst others believe bottom up control, such as N availability (Cole, Buckland and Bardgett 2008) exist. Traditional views of species diversity controls are based on two factors; i) productivity/resource supply and ii) consumption/physical disturbance. In both instances species diversity is greatest at intermediate disturbance and resource availabilities. However, current literature does not support these theories within the soil ecosystem (Bardgett, 2002). Disturbance often results in huge population reductions (Bedano, Cantú and Doucet, 2006; Cole, Buckland and Bardgett, 2008; Hirsch *et al*., 2009) and there appears to be little regulation by competition for resources, as the heterogeneity of the environment (Nielson *et al*., 2010) leads to niche partitioning (Ladygina, Caruso and Hedlund, 2008) and microhabitats.

It is known that there is considerable interaction, both direct and indirect, between above and below ground organisms, with both positive and negative effects (Van der Putten, 2001; Bardgett and Wardle, 2003; Wardle *et al*. 2004). Above ground management induces the presence of either a fungal or bacterial based food web; which has implications for species composition and functional groups at higher trophic levels. Functional group change within the food web affects ecosystem functions and services, such as; plant production and plant community composition (Bradford *et al*., 2002) and nutrient cycling and decomposition (Wardle, 2002; Bardgett, 2005). A specific example is; Collembola grazing on fungal mycorrhizae caused damage, altering growth patterns, this disrupted the symbiotic fungi/higher plant relationship. This resulted in a reduction in carbon flow to the soil, thus affecting carbon cycling (Johnson *et al*., 2005). Partsch, Milcu and Scheu (2006) and Eisenhauer, Sabais and Scheu (2011) furthered the work to determine that non-leguminous forbs were particularly affected.

Population increase, however controlled, occurs either due to functional increases, such as reproduction, or numerical increases caused by population recruitment through dispersal (Krebs, 1978). Population growth, in response to an increase in available resources, occurs through reproduction or egg/larval reactivation from dormant developmental stages (Greenslade and Greenslade, 1973; Greenslade, 1982; Alvarez, Frampton and Goulson, 1999). Cole, Buckland and Bardgett (2005) determined that mesofaunal densities increased with enhanced soil fertility with a raised number of predators within the Collembola and Acari communities. However, there was no change to the mesofaunal diversity recovered. Joose and Testerink (1977), Walsh and Bolger (1990) and Chen, Snider and Snider (1996) believed that food source quality, in these studies fungi, was an important factor in driving population dynamics. Other studies on herbivores (Bernays and Bright, 1993) and predators (Toft and Wise, 1999; Oelbermann and Scheu, 2002) showed that a mixed diet was optimum for population growth and reproduction.

Moreover studies have shown that the quality of chemical inputs, whether by root exudates or incorporation of above ground material (Milcu *et al*., 2010), affects the mesofaunal community composition (Wardle, 2002) as well as population abundance. There is little direct evidence for the active dispersal capabilities of many mesofaunal species, Collembola have been shown to disperse at 10cm per day (Nielson *et al*., 2010), whilst radioactive isotope tracking experiments by Berthet (1964) recorded that Oribatida only travelled small distances (a few centimetres a day) and that they have no specialised dispersal stages. Acari are also thought to colonise soils through passive dispersal called phoresy, being carried by other larger animals such as other invertebrates, birds and rodents (Mašán and Halliday, 2009; Ulyshen, 2011). Other forms of dispersal include wind (Beckmann, 1988; Dunger, 1998; Skubala, 2004), Lehmitz *et al.* (2011) found some soil dwelling species amongst tree dwelling Oribatida 160m above ground level. Likewise, some species of Collembola produce eggs that are able to survive desiccation and freezing, which may allow dispersal by passive aerial movement (Alvarez, Frampton and Goulson, 1999).

A Mesofaunal movement stimulus is an over-looked subject within the literature, with very few direct studies due to the difficulties in studying their movement. However, it has been noted that soil organisms move between food resources at a slower rate than above ground organisms (Christensen *et al*., 2007). Furthermore, studies have shown that some species of Collembola direct their movements due to sensing fungi (Staaden *et al*., 2011). It is acknowledged that upon grazing by primary consumers some plants produce volatile compounds to act as a defence mechanism (Holopainen, 2004; Arimura *et al*., 2000). It has been postulated that secondary consumers, the primary consumers' predators, are able to detect these compounds and use them to find their prey species (Vet and Dicke, 1992). A recent laboratory study by Pfeffer and Filser (2010) looked at similar characteristics in fungi. The interactions between the soil fungus *Trichoderma viride*, fungivorous

Collembola *Folsomia candida* and predatory Acari *Hypoaspis aculeifer,* determined that the Acari were attracted to the ungrazed fungi, before grazed fungus or pure Collembola options.

1.4 Landscape Management, Soil Degradation and Effects on Biodiversity

The UK natural climax community is woodland, providing a diverse habitat for many different flora and faunal species, both above and below ground (Brown, 1997). However, anthropogenic management has changed the landscape resulting in managed grasslands, arable land and even bare fallow. Today, changes are still occurring so that between 1990 and 2003 there has been a 12.8% reduction in the area and quality of grasslands in European Union member states (FAO, 2006), with further changes expected due to the 2008 abolition of EU wide set-aside requirements (ENCA, 2008). Anthropogenic land use is considered a major factor in changes to biodiversity (Ribeiro *et al*., 2009) with cost effective management having detrimental impacts on wildlife (Benton *et al*., 2002), even small changes to the management techniques employed affect biological populations. Agricultural practices, such as; ploughing, pasture treatment, crop residues, crop rotation and pesticide and fertiliser application, are key variables in determining soil properties (Baker, 1998). These practices change the quality and quantity of plant inputs into the soil, altering the organic matter present, which in turn amends the physical and chemical soil properties, thereby influencing the soils microhabitats (Bardgett and Cook, 1998). The intensity of management determines the level of disturbance that is produced and its effects on soil communities. Bare fallow management - maintaining a vegetation free soil, through the removal of vegetation (by herbicides and cultivations) - results in low nutrient inputs and a combination of soil profile destruction and continuous lack of organic matter entering the soil reduces quality. Crop management results in a desired structured monoculture ecosystem, but inadvertently causes physical disturbance of the soil profile, by ploughing, seeding and compaction along with chemical changes through the addition of inorganic chemical inputs from fertiliser and pesticides (Kampichler, 1999). These crop

management systems alter soil properties, affecting moisture content, pore size and connectivity, pH, soil biota composition, temperature and nutrient availability and quality. Permanent grassland is either maintained through mowing or grazing to prevent succession to a climax community (Hoste-Danyłow, Ramanowski and Żmihorski, 2010). This management strategy provides a relatively stable and mature ecosystem, albeit with a highly heterogeneous nature (Roger-Estrade *et al*., 2010; Diekötter *et al*., 2010).

Intensive land management can lead to a reduction in invertebrate population sizes (Carvell *et al*., 2007). Pesticide applications have been shown to reduce Collembola populations (Vickerman, 1992; Filser, 1995; Frampton, 1997). Ploughing leads to the destruction of upper horizons, which has been demonstrated to expose soil inhabitants to desiccation, habitat modification and disrupted access to food sources, thus reducing Acari population sizes (Wardle *et al*., 1995; Coleman and Crossley, 1996; Hulsmann and Wolters, 1998; Neave and Fox, 1998; Fox *et al*., 1999). Work by Sánchez-Moreno *et al*. (2009) showed that predatory and omnivorous Acari were affected by the management strategies applied to agricultural land including ploughing. Further work by Cao *et al*. (2011) determined that unfertilised soils showed the highest Acari abundance, whilst organic farming and chemical fertiliser had no benefit or a negative population response respectively. When studying changes in populations, especially those due to habitat change, Wolters (2001) noted several factors to be taken into account; the scale of disturbance, habitat size, species physiological specialisation or stress tolerance and dispersal capabilities .

1.5 Restoration Ecology

Conservation efforts on degraded soils either aim to re-establish the natural ecosystem following anthropogenic interference, such as contaminated mine sites (Courtney *et al*., 2010, Andrés and Mateos, 2006) or land fill (Koehler, 1998) and natural damage to

ecosystems from fire (Malmström, 2010) or to increase crop yield or quality in arable systems (Smith, Potts and Eggleton, 2008a). This is achieved through ecological restoration, due to the beneficial relationship between biodiversity, ecosystem function and provision of ecosystem services (Balvanera *et al*., 2006; Rey Benayas *et al*., 2009). Most of the literature focuses on the management and reintroduction of larger above ground invertebrates and floral species (Pywell *et al*., 2011) to restore soil quality (Suding, Gross and Houseman, 2004; Eviner and Hawkes, 2008). Yet, the soil invertebrate communities within these ecosystems will also have been damaged by soil quality degradation. The reintroduction of mesofaunal populations boosts the soil food web, providing the linkages required to increase an ecosystems number of trophic levels. This promotes ecosystem maturity and stability (Neutel, Heesterbeek and de Ruiter, 2002), therefore naturally improving soil quality (Kardol and Wardle, 2010). Maraun, Visser and Scheu (1998) believed that the Oribatida facilitated the re-introduction of the microbial community by improving spore dispersal, hyphae decomposition and increased nutrient cycling. The resulting increase in microbial growth minimizes nutrient leaching. Studies investigating ecosystem disturbance determined that different groups of mesofauna recover at different rates (Lingberg and Bengtsson, 2005; Malmström, Persson and Ahlström, 2008). Whilst, Ayres, Dromph and Bardgett (2006) concluded that the floral species within the community encouraged the development of a soil community best suited to the rapid decomposition of the litter available. However, they only focused on the soil microbes as they believed that these are directly responsible for the majority of decomposition. Where the natural colonisation of an ecosystem has occurred, for example within glacial retreat (Kaufmann, 2001; König, Kaufamnn and Scheu, 2011), studies have shown the first colonisers of an area to be predators, followed by herbivores and decomposers (Hodkinson *et al*., 2001; Gobbi *et al*., 2006). Other investigations have shown that the evolution of terrestrial food webs begins with simple systems, comprising decomposing litter material and decomposer organisms with primary producers occurring

later (Labanderia 2005; Schaefer *et al*., 2010). A study by Dunger (1968) showed that Collembola are able to colonise a young soil within a few months of the start of primary succession. Oribatid mites were also shown to be able to colonise soils within the early stages of their development even though hostile conditions present (Beckmann, 1988; Skubala, 1995; Wanner and Dunger, 2002).

Predicting the consequences of ecosystem restoration is difficult due to the complexity of the processes involved. The models currently in existence reflect either end-point models (focus on desired restoration outcomes) or process based models (anthropogenic interference changes natural disturbance patterns that structure ecosystems). One example is the recovery cascade model (Robson, Mitchell and Chester, 2011) which outlines six stages to ecosystem recovery: i) physical ecosystem change, ii) creation of/improvement of habitat, iii) reconnection to adjacent ecosystems, iv) recolonization, v) resumption of ecological processes, vi) re-establishment of biotic interactions and reproduction. These models are difficult to test as many studies observe only one group of organisms, however, due to their widespread nature both Acari (Wang, Hooks and Marahatta, 2011) and Collembola (Courtney *et al*., 2010) have been suggested as bio-indicators for management induced changes to soil and habitat quality.

1.6 Aims and Objectives of the Thesis

This thesis aims to determine:

- Whether different mesofauna groups are able to recolonise heavily degraded soils.
- Whether changing the management regime of permanent grassland pasture leads to soil quality degradation and mesofaunal population change.

- The process of mesofaunal community dispersal, and whether populations are able to move across degraded soil to more favourable conditions, forming island habitats.
- New methodologies for determining the mode of mesofauna movement.

Chapter Two

Methods

2.1 Introduction

This chapter describes the methods used within this study to sample, collect, extract and identify soil mesofauna. The description has been divided into two sections. Part A describes the geographical locations and characteristics of each field site, followed by the standard protocols utilised to retrieve soil samples and process them within the laboratory. Any deviances from these standard protocols are described within the relevant experimental chapter. Part B describes an experiment designed to determine Tullgren Funnel extraction efficiency for the collection of soil invertebrates. A previous experiment by Crotty (2011), determined that invertebrates were still recovered, by Tullgren Funnel extraction, from soil samples 21 days after the samples were placed on the funnels. However, soil samples were removed from the Tullgren Funnels at this point and it remained unknown if any further invertebrates would be recovered. In this chapter, extraction samples were regularly collected until no further invertebrates were extracted from the soil samples.

All of the methods detailed within this chapter have been described within the literature for use in the extraction and identification of soil dwelling invertebrates. These have been utilised within this thesis to study the re-establishment of mesofaunal communities within degraded soils.

Chapter Two A

Field Sites and Standard Methodology

2A.1 Experimental Field Sites

2A.1.1 Introduction

Both of the experimental field sites are under the control of Rothamsted Research. The first site, Highfield, is based at the Rothamsted Estate in Harpenden, UK. The second, Little Burrows, is located at the North Wyke Research Station, Devon, UK. Each are located within a well-established research institute, however each site has a different agricultural use, soil type and climatic conditions. The geographical locations of both sites within the UK are shown in Figure 2A.1.

Both sites are part of the Environmental Change Network (ECN), therefore climatic, soil and environmental conditions are monitored on a regular basis and stored on the ECN database (http://www.ecn.ac.uk). Data from this source have been used to determine the climatic conditions of the experimental sites (Table 2A.1). The soil types of North Wyke Research station and the Rothamsted Estate have been extensively mapped (Figures 2A.8 and 2A.2 respectively), due to their locations and regular usage within agricultural research. Further details of the soil properties for the specific experimental sites can be found in Table 2A.1; these are based on soil within a grassland management regime.

Figure 2A.1 Map showing the geographical location of the Little Burrows and Highfield experimental field sites.

Table 2A.1 Soil properties and climatic conditions at the Little Burrows and Highfield experimental sites, ± standard error is shown in brackets where available.

	Highfield Site		Little Burrows Site	
Soil Properties				
Total C (%)	5.4	-	2.825	(±0.1)
Total N (%)	0.5	-	0.321	-
pH	5.5	-	5.3	-
Microbial Biomass Carbon (mgC/kg soil)	926.4	(±75.7)	890.52	(±87.1)
Climatic Conditions (01/01/2006 to 31/12/2010)				
Mean Annual Rainfall (mm)	718.9	(±40.7)	1040.3	(±100.5)
Mean Annual Temperature (^{o}C)	10.1	(±0.1)	9.8	(±0.1)
Maximum Air Temperature (^{o}C)	26.5	(±0.1)	22.6	(±0.1)
Minimum Air Temperature (^{o}C)	-2.5	(±0.1)	-3.3	(±0.1)
Average Soil Temperature at 10cm (^{o}C)	10.6	(±0.2)	10.8	(±0.2)
Average Annual Days of Rain (N^{o})	142.6	(±4.5)	173.2	(±7.6)
Average Hourly Solar Radiation (Wm^{-2})	125.9	(±16.3)	115.8	(±8.8)

2A.1.2 Highfield Site, Rothamsted Research, Harpenden, UK.

Rothamsted Research, Harpenden, UK (Highfield on Figure 2A.1) is a 330ha site, 25 miles north of London, with a minimum and maximum altitude of 94 - 134m respectively. Highfield is a well-established long term experiment to the south of the main buildings (global reference: 51:48:18N latitude, 0:21:48W longitude), whilst, the Geescroft Soil Mine site is within an immediately adjacent field. The Highfield and Geescroft experimental sites are on a Batcombe series soil, with a silty clay loam texture, Figure 2A.2. The original vegetation was maintained as permanent grassland for centuries, before conversion for experimental research purposes in 1949.

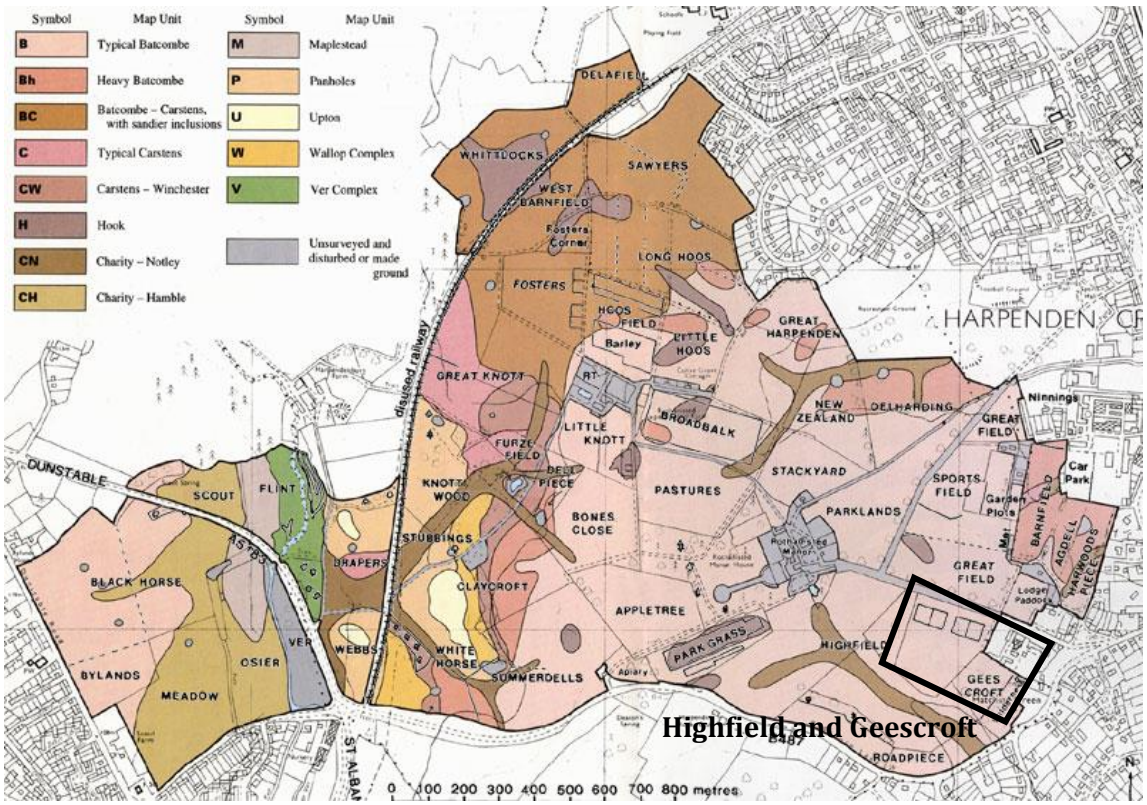


Figure 2A.2 Soil type map of Rothamsted Research (Avery and Catt, 1995). The Highfield and Geescroft experimental site is highlighted in black.

2A.1.3 Highfield Ley-Arable Experimental Design

The experiment was originally initiated to study the conversion of grassland pasture to arable farming practices. The Highfield experimental design consisted of 24 separate strips, each 7m x 50m. These strips were divided between two treatments (Figure 2A.3), maintained grassland pasture (reseeded, 1949 and 1991, as grass-clover) or conversion to ley-arable (3 years ley-3 years arable) management; see Johnson (1972) for a full description. Additional land was used in 1959 to create a bare fallow treatment, where vegetation was removed by tillage. This treatment was divided between two locations, shown in Figure 2A.4; the first location can be seen as a triangle of pale soil adjacent to the eastern edge of the Highfield plots. The second location was an area in the adjoining field, known as the Geescroft mine site. Full records of all treatments, applications and crops are available from the Rothamsted archives. The area surrounding the experimental plots is a maintained grassland border. The layout of the experimental site can clearly be seen in Figure 2A.4, with adjacent strips of differing agricultural practice.

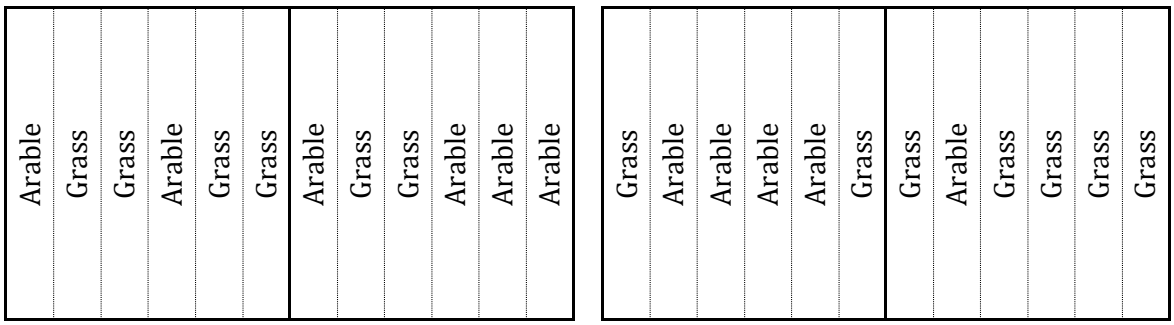


Figure 2A.3 Original Highfield Ley-Arable Experimental layout.

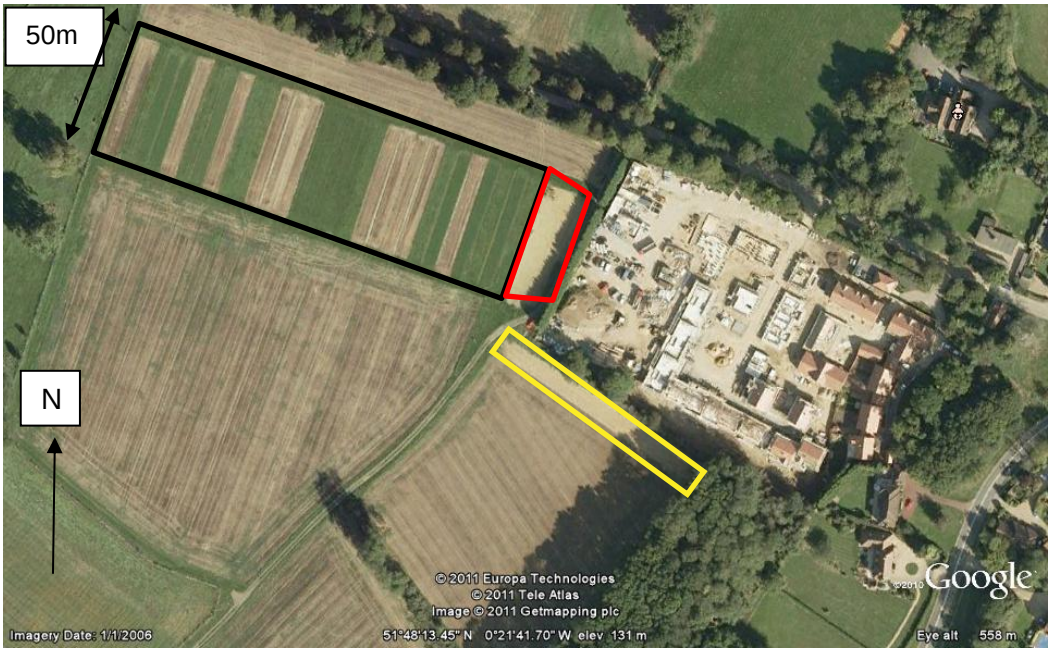


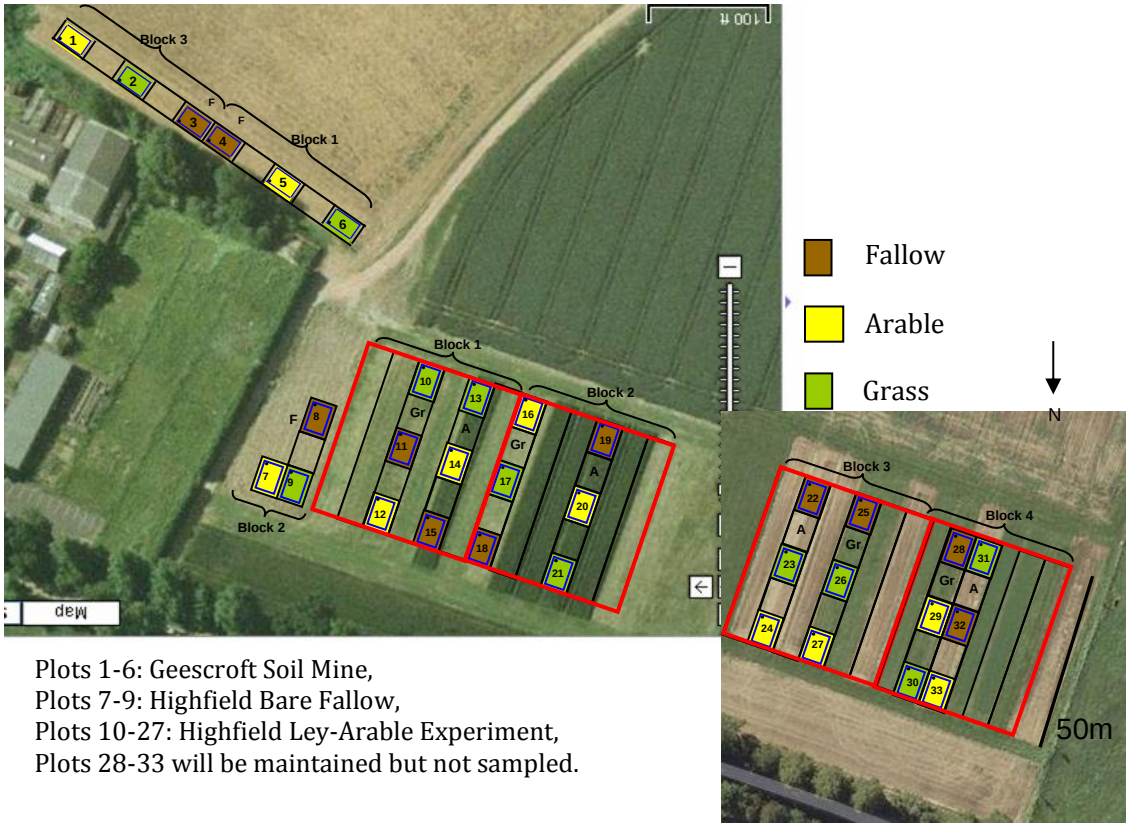
Figure 2A.4 Photo of the Highfield experimental site (black outline), the Highfield fallow (red outline) and the Geescroft Mine bare fallow (yellow outline).

2A.1.4 Highfield Reversion Project

Following a preliminary investigation in 2006 (Chapter Three), the Highfield reversion project was conducted. In total 11 of the Highfield strips; four arable, four grassland and three fallow treatments, were randomly selected and divided into smaller sub-plots (10m x 7m, with 10m separation for turning machinery between plots) (Figure 2A.5).

This provided 27 experimental plots on which nine treatments were replicated in triplicate from October 2008. The treatments are as follows:

- Maintained original treatment: Fallow (FF), Grassland (GG), Arable (AA)
- Fallow converted to: Grassland (FG), Arable (FA)
- Grassland converted to: Fallow (GF), Arable (GA)
- Arable converted to: Grassland (AG), Fallow (AF)



Plots 1-6: Geescroft Soil Mine,
Plots 7-9: Highfield Bare Fallow,
Plots 10-27: Highfield Ley-Arable Experiment,
Plots 28-33 will be maintained but not sampled.

Figure 2A.5 Aerial view of the Highfield experimental site with Highfield Reversion Project experimental treatment layout.

Following baseline sampling additional treatments were implemented to aid conversion, these included:

- *Grass-Arable conversion:* Glyphosate applied to eradicate grass during summer to facilitate subsequent cultivation.
- *Arable crops*: Herbicide and pest control as normal.
- *Grass*: No chemical treatments.
- *Bare Fallow*: Limed to equilibrate pH to the other plots, (pot trials conducted to assess the impacts of liming bare soil). Nitrogen (N), phosphate (P) and potassium (K), applied - amended at the minimum level required to support a crop and only during transition to arable and grass. Continuing bare soil was not fertilised.

2A.1.5 Highfield Reversion Project Plot Layout

Each sampling plot originally had the dimensions 10m x 7m. Each plot was sub-divided into a 0.5 x 0.5m grid, the central grid units (2 x 2m) were reserved 'pristine', plus a two-unit width perimeter designated buffer zone, Figure 2A.6.

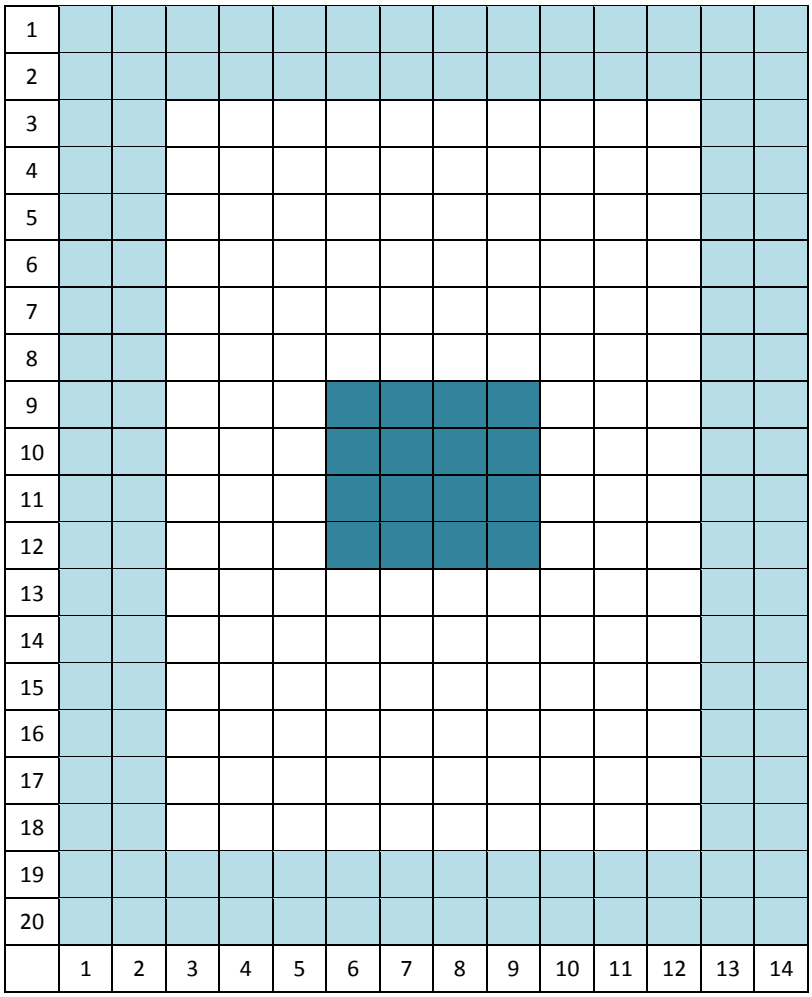


Figure 2A.6 Individual Highfield Reversion Experiment plot plan, showing the pristine , buffer zone nd sampling squares

2A.1.6 Little Burrows, North Wyke, Okehampton

The North Wyke Research Station, Devon, is a typical lowland grassland site, 250ha in size at a minimum altitude of 120m and maximum of 182m, with some of the wettest climatic conditions of western Britain. Little Burrows (global reference 3:54:14.0W longitude and 50:46:3.2N latitude) is a permanently maintained ungrazed grassland site with 25 years

recorded management history, Figure 2A.7. The soil is of the Hallstow series, a clayey typical non-calcareous pelosol in Head from clay shale (Harrod and Hogan, 2008) underlain by the Carboniferous Crackington, Figure 2A.8.

Figure 2A.7 An aerial photo of Little Burrows, with the experimental site marked with a red pointer.

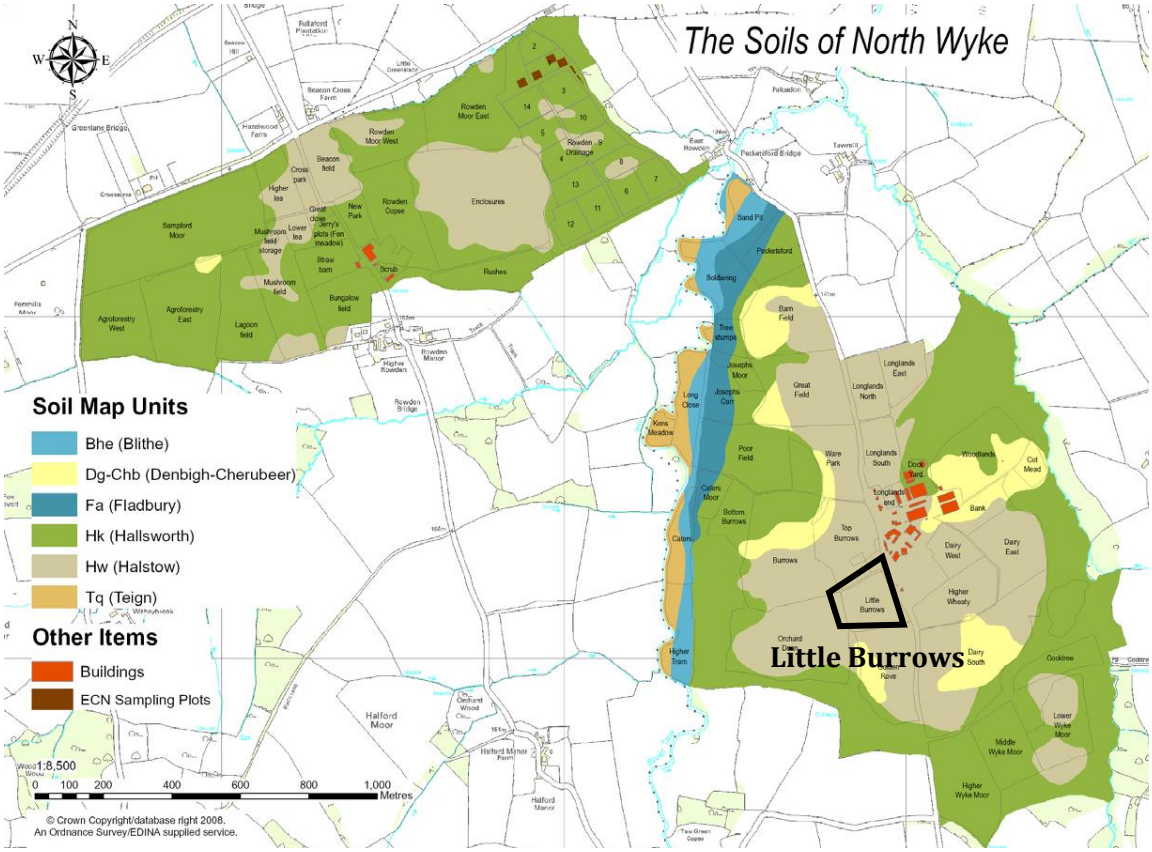


Figure 2A.8 Extract from the North Wyke Soils map, Little Burrows Experimental site highlighted with a black square (Harrod and Hogan, 2008).

2A.2 Soil Sampling

Soil samples were collected using the same methodology for all experiments. Soil cores 8cm Ø x 10 cm deep were removed intact from the ground (Figure 2A.9), using a Root Auger (Van Walt ltd, Surrey, UK) (Figure 2A.9). These were then stored individually in labelled sun bags (Sigma-Aldrich, UK). A 0.2µm filter within the sun bag allows gaseous exchange between the bags' interior and the environment. Additionally, this prevents moisture build-up, along with the associated risk of fungal growth. Immediately upon collection, the samples were placed in a chilled cool box for transportation.

Figure 2A.9 A fresh soil core (left) and soil core collection (right).

Invertebrates should ideally be extracted from soil samples as soon as possible after collection from the experimental site. The use of banked Tullgren Funnels, usually 12 funnels per unit, allows for multiple samples to be extracted simultaneously. However, where soil core numbers exceed Tullgren Funnel units, excess samples were stored at 8°C. The storage should be done on a random basis to prevent any bias in the results.

2A.3 Invertebrate Extraction Technique

Invertebrates were extracted by placing intact soil cores (Figure 2A.9), into Tullgren Funnels (Burkard Manufacturing Co. Ltd, Rickmansworth, UK) (Figure 2A.10). Tullgren Funnels are a dynamic method of soil invertebrate extraction. Disadvantageous environmental factors, in this case a temperature gradient and the resulting moisture loss, are exerted upon the soil sample. These conditions stimulate the organisms to move down the temperature gradient and eventually fall into the collection chamber. Organisms can be recovered alive or preserved in solution and are usually in good condition, making identification easier. However, biases can occur due to the reliance on the invertebrates' ability to move in conjunction with the temperature gradient, and therefore, egg and larval stages can be missed. This bias can, consequently, vary with seasonal and reproductive cycle stages of different organisms (Edwards, 1991).

Figure 2A.10 A Single Tullgren Funnel.

Multiple banks of 12 Tullgren Funnels (Figure 2A.11), are used within a controlled temperature chamber between 8-10^{o}C. A 25W light source within each funnel allows the production of a temperature and moisture gradient. The soil cores were left in the sample chamber, which had a mesh size of 2mm. Invertebrate samples were collected over a

period of seven days, as has been previously used (Bruckner, Barth and Scheibengraf, 2000; Querner and Bruckner, 2010; Parfitt *et al*., 2010; Beyer *et al*., 2011).

Figure 2A.11 12 Banked Tullgren Funnels.

Samples would traditionally be collected in a preserving fluid such as alcohol; Kautz, López-Fando and Ellmer (2006) used 70% isopropanol, whereas Sánchez-Moreno *et al*. (2009) preferred 70% ethanol. However, this method alters the invertebrate's chemical structure making them unsuitable for isotopic analysis. As the samples collected for this investigation were to be stored for possible use in isotopic analysis, they were collected in saturated salt solution, which has no effect on isotopic composition (Fábián, 1998; Ponsard and Amlou, 1999). Extracted liquid samples must be stored at -20^{o}C to prevent fungal growth and completely thawed before any further analysis.

2A.4 Invertebrate Identification

Invertebrate samples were separated and identified using a stereo-light microscope (Olympus SZX10, Olympus, Essex, UK), before being labelled and stored for future use. Within soil ecology, the separation and identification of invertebrates has been a time and resource consuming element of many investigations. There are numerous examples within the literature of attempts to use simpler, cheaper and less time consuming methods of assessing soil biodiversity than taxonomic identification. Examples include; abiotic

bioindicators of biodiversity (Ekschmitt *et al*., 2003) and DNA sequence-based methodology (Hamiliton *et al*., 2009; Wu *et al*., 2009; Seeber *et al*., 2010). However, it is still believed that taxonomic identification is required (André *et al*., 2001).

Due to the large number of samples collected and the time consuming nature of invertebrate identification to species, a compromise has to be made with regard to the identification of individual samples. Within these investigations individual invertebrates were at most identified to Superfamily. As the primary group of interest within the experiments were the mesofauna, the separation and identification of the macrofauna; for example the Coleoptera, Chilopoda and Diptera (Figure 2A.12), were only completed to the level of Order.

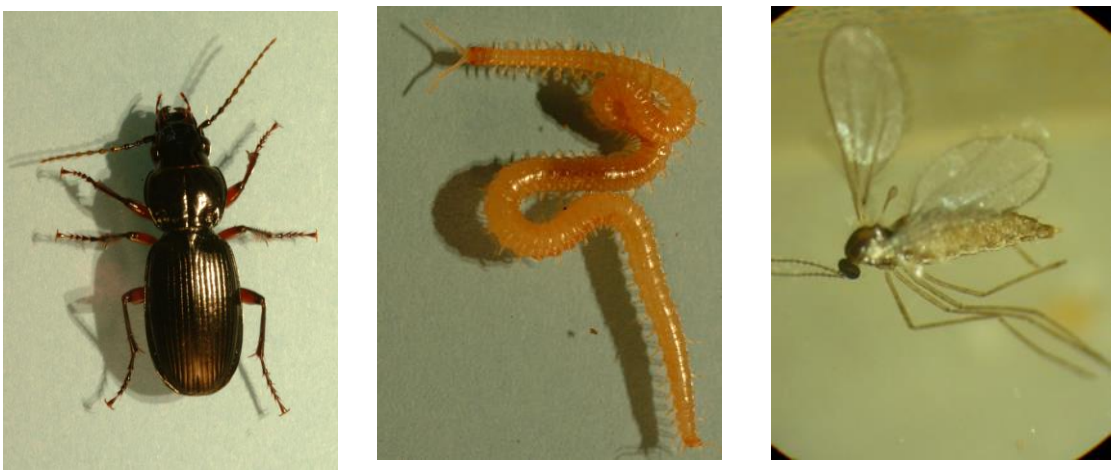


Figure 2A.12 Pictures of Coleoptera (live), Chilopoda (live) and Diptera (in saturated salt solution) through a stereo-light microscope as recovered from soil.

However, the mesofauna, consisting of the Acari and Collembola, were further separated into groups which approximately represent their function within the soil environment. The Acari were identified using the keys developed by Krantz and Walter (2009) (Figure 2A.13). Initial separation between the Superorders, Parasitiformes and Acariformes, allowed for the identification of the Order Mesostigmata. The Mesostigmata are the only soil inhabiting order of Parasitiform in the UK. All other parasitiform orders are parasitic,

whereas the Mesostigmata are usually predators (Karg, 1993). Further identification of the Acariformes provides two soil dwelling Suborders - the Prostigmata which has many different feeding types, and the Oribatida, which are usually detritivores.

Figure 2A.13 Typical Acari of the order Mesostigmata (left), and suborders Prostigmata (middle) and Oribatida (right).

Collembola were identified using the keys of Hopkin (2007). The initial separation was into the Orders Symphypleona and Neelipleona (grouped together due to very small abundance figures) or Arthropleona. This latter group was further subdivided into the Superfamilies' Poduromorpha or Entomobryomorpha (Figure 2A.14).

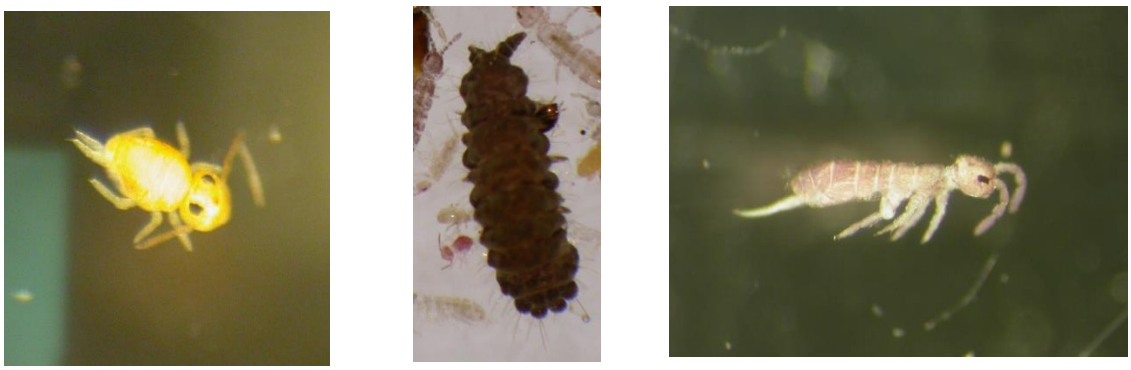


Figure 2A.14 Typical Collembola specimens: Symphypleona (left), Poduromorpha (middle) and Entomobryomorpha (right).

2A.5 Sample Storage

Following separation and identification into the different groups (Section 2A.4), all individuals from each group were placed together into an individually labelled container filled with saturated salt solution, and stored at -20^{o}C.

2A.6 Data Presentation

Invertebrate abundance is presented in a tabular, graphical and food web format (based on biomass). Where a mean has been calculated the standard error (±) will be displayed in brackets or as error bars as appropriate. Using the Network3D food web software package (version 1.0.0.0, Microsoft Corporation), to produce food webs based on the individuals recovered, is an alternative method for visualising the invertebrate populations, as it uses biomass rather than abundance. It utilises the linkages in the soil food web to determine predator-prey relationships between the different superfamilies present and the biomass of each.

Within each of the food web diagrams, the spheres represent population biomass. These were calculated using the recorded abundances (m^{-2}) x mean individual dry weights (µg) for each superfamily, as determined by Crotty (2011) (Table 2A.2). However, each food web is produced independently of one another within the software, and therefore are produced on different scales. The mesofaunal food web relationships have been based upon those described in Bezemer *et al*. (2010), and are denoted by the joining lines. Where invertebrate orders had not been broken down into superfamilies, by Bezemer, the same food web connections are shown for each individual superfamily biomass. As the basal food source biomass - Roots, Fungi and Soil Organic Matter - was not calculated, the representative figure used to create the food web is arbitrary. To maintain consistency an identical figure (1000µg) was utilised for each basal food source within every diagram.

Subsequently, the organism biomass, for each sphere, is shown in relation to each other and the basal food source, providing scale to each individual food web.

Table 2A.2 Mean individual organism biomass (µg) for the mesofaunal superfamilies for a grassland ecosystem, ± standard error shown in brackets where available (Crotty, 2011).

Mesofaunal Superfamily	Average Individual Organism Biomass (µg)
Acari: Oribatida	3 (±0.1)
Acari: Mesostigmata	13.5 (±1.8)
Acari: Prostigmata	0.8 (±0.2)
Collembola: Entomobryomorpha	3 (±0.6)
Collembola: Poduromorpha	2 (±0.2)
Collembola: Symphypleona	1

2A.7 Statistical Analysis

Statistical analysis was completed using GENSTAT (VSN Ltd, Hemel Hempstead, UK). Detailed descriptions of the statistical analysis applied are shown in the relevant chapters.

I would like to acknowledge Dan Dhanoa, our consultant statistician, for the statistical advice he provided.

Chapter Two B

Efficiency of Invertebrate Recovery Rates by Tullgren Funnel Extraction

2B.1 Introduction

There are many diverse methods for extracting invertebrates from soil; each has a different set of advantages and disadvantages (Macfadyen, 1955; Edwards, 1991). Physical methods fragment the soil and use methods, such as; hand sorting (Doblas-Miranda *et al*., 2008), centrifugation (Murphy, 1962) or flotation (Hale, 1964), to separate individuals from soil. These methods often recover all life cycle stages, but also collect dead organisms and can damage the specimens making identification difficult. Dynamic methods use external pressures to stimulate organisms to leave the soil of their own mobility; two examples of this are; wet funnel methods (Baermann, 1917) and Tullgren funnels (Nef, 1962). As a dynamic method of extraction Tullgren Funnels rely on the ability of invertebrates to be able to move within the soil core. Any sedentary stages of the life cycle, such as eggs and immobile larvae, are difficult to retrieve using this method (Edwards, 1991). In addition, samples can be difficult to retrieve from compacted soil where pore sizes are too small to allow movement. However, other methods, such as the flotation method described by Hale (1964), are often more time and resource consuming. Work by Smith, Potts and Eggleton (2008b) showed that for macro-invertebrates Tullgren Funnel extraction was more efficient at recovering species density and diversity than hand sorting. Edwards and Fletcher (1970, 1971) also believed that a Tullgren Funnel or Macfadyen type extractor with a steep temperature and moisture gradient offer the highest efficiencies.

Standard Tullgren Funnel methodology collects extracted invertebrates for seven days; recent examples include; Bruckner, Barth and Scheibengraf (2000), Querner and Bruckner (2010) and Parfitt *et al.* (2010). However, there are also many inconsistencies within the literature; Zhoa *et al*. (2011) and Monroy, Aira and Domínguez (2011) both used three days, whilst Cole, Buckland and Bardgett (2008) and Lindberg and Bengtsson (2005) extracted for four days and Crotty, Blackshaw and Murray (2011) recovered invertebrates for five days. Work by van Straalen and Rijninks (1982) found the optimum time for mobile invertebrate extraction to be 21 days, whilst Crotty (2011) was still recovering invertebrates after this time. This experiment aims to determine the optimum length of time for invertebrate extraction by Tullgren Funnel from intact soil cores.

2B. 2 Materials and Methods

Six intact soil cores (8cm Ø, 10cm deep) were collected by root auger as described in Section 2A.2, from Little Burrows, North Wyke (Section 2A.1.6), in June 2011. These were then placed on the Tullgren Funnels (Section 2A.3), within a controlled temperature room at 8^{o}C. Invertebrates were extracted into saturated salt solution; the collection tubes were individually labelled and changed on the following days; 1, 2, 3, 4, 5, 8, 9, 10, 11, 12, 15, 16, 17, 18, 19, 22, 23, 24, 25, 26, 29, 30. The number of invertebrates collected on each day were recorded, and individuals identified to the following levels: Acari – divided into two groups – the Parasitiformes: the Mesostigmata (predators) and then the Acariformes: Oribatida and Prostigmata (herbivores and decomposers); Collembola – divided into Symphypleona, Poduromorpha and Entomobryomorpha; all other invertebrates together in one group, as per the identification keys in Section 2A.4.

2B. 3 Results

Invertebrates were recovered daily from all soil cores from day one to day eight. After day eight some cores recorded a daily count of zero, however, a consistent zero count for all

cores was not recorded until day 18. After day 18 no further invertebrates were recovered from any of the soil cores, therefore all data displayed only show days 1-18. Table 2B.1 shows the average number of invertebrates recovered from the soil cores collected for each group.

Table 2B.1 Mean number (± Standard Error) of invertebrates recovered from the six replicate soil core for each sampling day, until day 18 after which no further invertebrates were recovered.

Sampling Day	Mean Number of Invertebrates Recovered			
	Collembola	Acari	Other Invertebrates	Total
1	7.5 (± 1.9)	5.6 (± 0.6)	3.2 (± 1.0)	16.3 (± 2.3)
2	7.8 (± 1.8)	4.3 (± 1.0)	3.8 (± 1.1)	16 (± 2.6)
3	14.7 (± 3.9)	7.3 (± 1.1)	0.8 (± 0.3)	22.8 (± 4.3)
4	3.8 (± 4.4)	18.3 (± 1.1)	0.8 (± 0.3)	23 (± 4.9)
7	4 (± 1.5)	5.8 (± 2.8)	0 (± 0.5)	9.8 (± 3.7)
8	0.7 (± 2.6)	5.8 (± 2.3)	0 (± 0.0)	6.5 (± 3.8)
9	0.7 (± 0.5)	5.8 (± 1.2)	0 (± 0.0)	6.5 (± 1.5)
10	0 (± 0.0)	7.2 (± 2.0)	0.3 (± 0.2)	7.5 (± 2.1)
11	0 (± 0.0)	2.2 (± 0.9)	0.3 (± 0.2)	2.5 (± 0.9)
14	0 (± 0.0)	4.5 (± 1.9)	1 (± 0.5)	5.5 (± 2.3)
15	0.5 (±0.2)	0.5 (± 0.3)	0.2 (± 0.2)	1.2 (± 0.6)
16	0 (± 0.0)	0.5 (± 0.8)	0.67 (± 0.2)	1.2 (± 0.8)
17	0 (± 0.0)	0.5 (± 0.2)	0.7 (± 0.3)	1.2 (± 0.5)
18	0 (± 0.0)	0 (± 0.0)	0 (± 0.0)	0 (± 0.0)

The cumulative curve (Figure 2B.1) shows the trend and numbers of each group extracted from the cores. The other invertebrates recovered were larger macrofauna and therefore would have had fewer individuals within the soil samples than the mesofaunal groups (Figure 2B.1). The Acari recorded the largest numbers of invertebrates, with lower Collembola numbers. In total, a mean of 120 individual invertebrates were recovered from the soil samples. Within a standard investigation, with this sample size, this would equate to 24000 individuals m^{-2}.

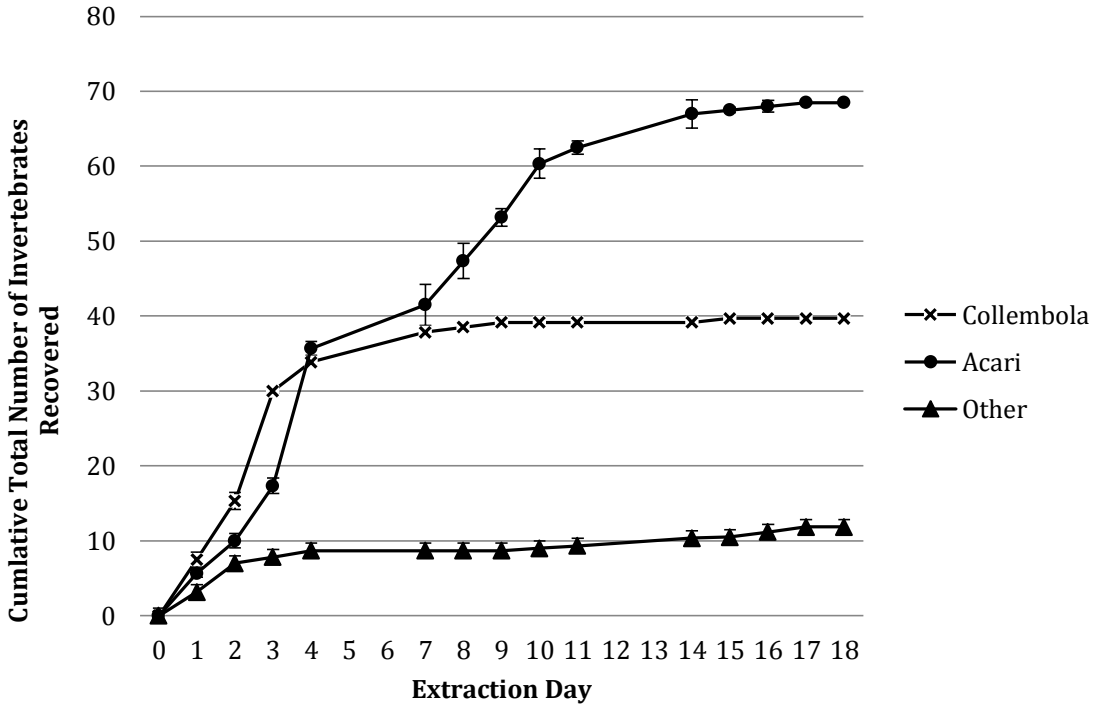


Figure 2B.1 The cumulative number of invertebrates recovered (Mean: 6 cores, plus standard error as error bars) from the three invertebrate groups.

The Collembola were extracted consistently from day one to day four, this is shown in Figure 2B.2, by day seven 95.4% of the total to be recovered were recorded. After seven days Collembola were only recovered in very small numbers, with 98.7% extracted by day 14, this group has the quickest extraction rate. The Acari were the slowest to be extracted with only 60% extracted after seven days; however, the rate becomes quicker than the other invertebrates after nine days and rising to 97.8% of the total after 14 days of extraction.

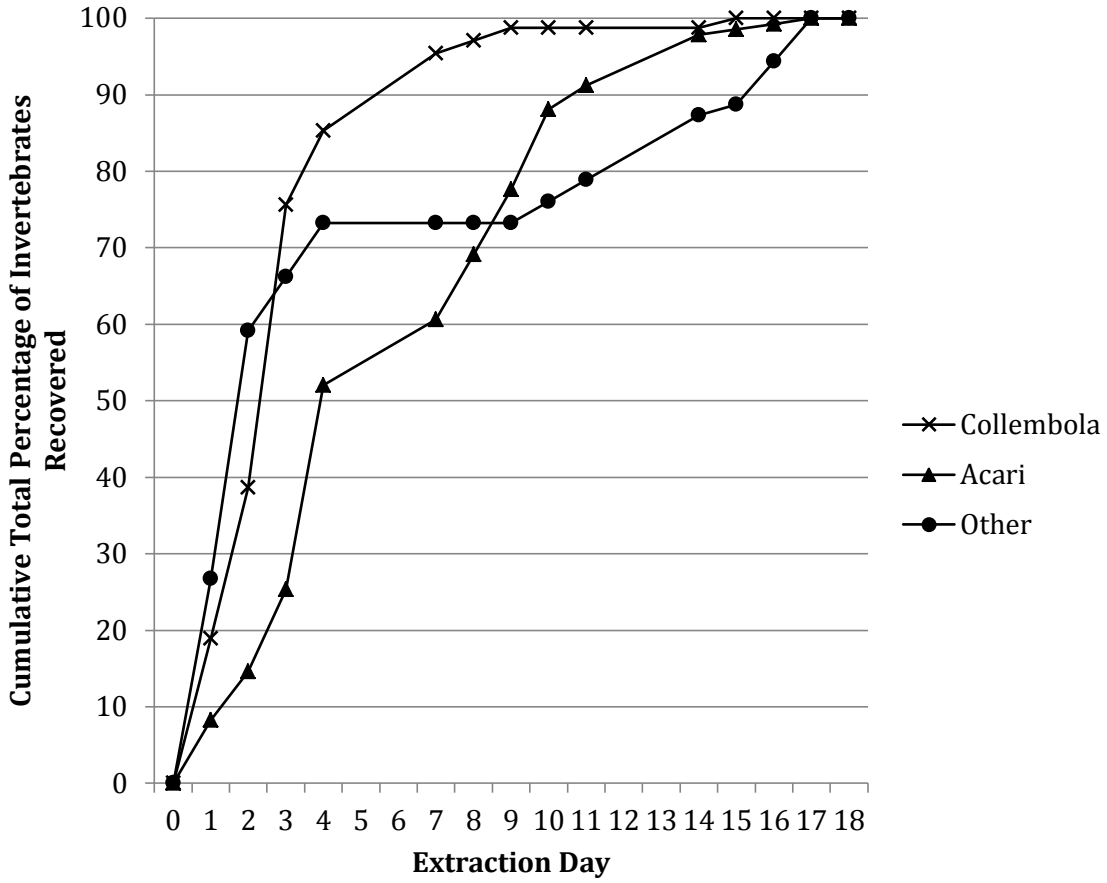


Figure 2B.2 The cumulative percentage recovered for each of the different invertebrate groups over the 18 days of successful extraction.

Of the other invertebrates, the majority were recovered at the start of the extraction process in days one and two, 73.2% of the total recovered was collected by seven days and 87% by day 14. The other invertebrates collected consisted of Arachnids, Annelid Worms, Coleoptera larvae, Diptera larvae and Diptera.

When the Acari and Collembola are further divided into the superfamilies, there are clear differences between the responses of the groups (Figure 2B.3). Within the Collembola, all groups were recovered by day nine; however, the Symphypleona and Entomobryomorpha were almost completely recovered by day five, with the Poduromorpha taking until day eight to reach the same point. Within the Acari, the Parasitiformes were almost completely

recovered by day eight, whereas the Acariformes group took much longer, with only half the population by day eight, taking a further eight days to be completely recovered.

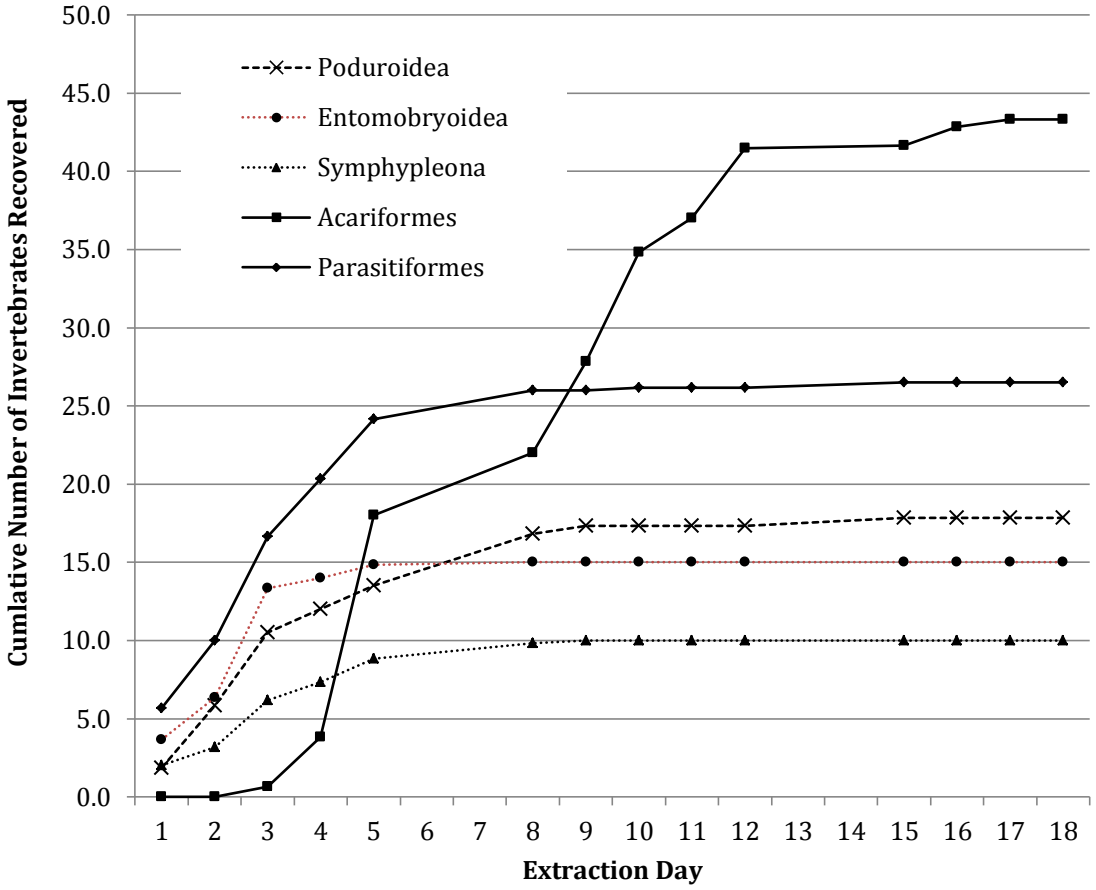


Figure 2B.3 The cumulative number of Acari and Collembola superfamilies recovered over the 18 day extraction period.

2B.4 Discussion

Within the literature various different methodologies for the extraction time required to recover invertebrates from soil have been described, ranging from three to 21 days, with the standard at seven days (Beyer *et al.*, 2011). As soil is a highly variable medium, even within the same geographical area, the soil's physical parameters, such as texture, moisture content, soil type, as well as season, may influence the extraction rate. Within the context of this investigation the extraction of invertebrates continued until day 18, therefore it could be suggested that in order to retrieve all soil invertebrates from a sample they must remain in the Tullgren Funnels for a full 18 days or slightly longer to allow for error. Previous investigations on the North Wyke site have suggested even longer, at a minimum of 21 days (Crotty, 2011). However, in that study, the soil was collected at a different time of year when the soil contained more moisture. This suggests that the results are only relevant for the specific site, soil sample size, soil type and possibly soil moisture content. Therefore, in order to standardise any results obtained it will be important to maintain methodological consistency for the entirety of any investigation. The determination of the extraction time length could be adapted to a specific investigation that would depend on the target species, soil characteristics and other investigation specific factors.

Further to this, when each of the mesofaunal groups are looked at individually they have different requirements for extraction time, this suggests that it could be possible to tailor extraction times or precise collection points to target specific organisms. The Acari were a good example of this, the Parasitiformes, as predators, are often large and highly mobile organisms, they are able to rapidly move away from the drying effects of the temperature-moisture gradient. Figure 2B.3 shows that this group were extracted quickly with the majority of individuals being recovered by day eight. However, the Acariformes (Oribatida and Prostigmata) took much longer, a total of 17 days. Therefore, if Acariformes are not

required the extraction period could be shortened to eight days to reduce the pressure on resources and remove these unnecessary individuals from the final samples.

Similarly, where Collembola are the only target organism the extraction time could be changed to reduce the number of other unrequired organisms within the sample. Collembola are quickly affected by the temperature and moisture changes and use behavioural means to move away from the external pressures (Hopkin, 1997). The results show that over 90% of the Collembola had been extracted by day seven, therefore, extending the extraction period would be of little benefit in relation to the time required to extract the final 10%. These results suggest that the standard time constraint of seven days used by most current experiments (Querner and Bruckner, 2010; Saitoh, Fujii and Takeda, 2011) are recovering a large proportion of the Collembola and other invertebrates from the soil cores. However, in experiments where the primary order required is the Acari, seven days may leave a significant number of individuals within the soil sample, especially within the Acariform group. Only 60% of the Acari were recovered by this point, which would be the standard point at which to stop collection. However, 97% were recovered by day fourteen. Further identification to genus or species could allow targeting to be more specific.

In most investigations there has to be trade-off between the recovery of all organisms within a sample and the resources available to do so. In an investigation, such as the Highfield Reversion project (Chapter Three), a total of 81 soil samples were to be collected from the experimental site on the same sampling day. These soil samples must then be extracted on the Tullgren Funnels. However, there is usually a restriction on the number that can be extracted at any one time, in the case of the Highfield Reversion project only 35 samples. Therefore, the remainder of the samples must be stored until the extraction funnels are available. The storage time length should be reduced as much as possible to

prevent changes from occurring within the soil samples during this time period. In order to complete the extraction of all 81 Highfield soil cores, two sets of 35 and one of 11 were extracted in immediate succession. If each soil core set were extracted for 18 days, the final set of soil cores would have been stored for 36 days before extraction. This is enough time for invertebrate life cycle progression or more sensitive organisms, such as Prostigmata, could have died, changing the population within the soil core. However, if a 70% count is acceptable as a trade-off, the third set would only be stored for 14 days, reducing the possibility of population changes.

2B.5 Conclusions

In conclusion the standard seven day extraction time applied to most invertebrate surveys by Tullgren Funnels appears to be too short, especially for Acari species (according to the data recovered here). This investigation and previous results suggest that the required extraction time will be specific for each individual investigation and will be determined by the variable factors. The soil type, soil moisture, soil sample size and target organism will all change the extraction rate. Whilst other factors such as number of soil samples to be extracted will alter the acceptable trade-off between available resources, facilities and extraction time. However, any methodology developed to meet the needs of a specific investigation must be consistent throughout the entire sampling period. Preliminary sampling before the main sampling regime will determine the requirements of the investigation. The compromise between resource usage and the requirement to recover all invertebrates within a sample must be carefully considered, before embarking on any new experiment.

In order, to further test this theory, additional sampling should take place. Firstly, the further identification of the organisms to species, would determine if particular species with distinct functions have different extraction rates. This would enable targeted extraction times to select these organisms, potentially reducing the number of other

invertebrates to be sorted within a sample, therefore saving time and resource use. Secondly, the weather prior to this sampling had been very dry and as a result the soil was also very dry. It would be useful to repeat this investigation under wetter conditions to determine if soil moisture content has an effect on invertebrate numbers and the rate at which they are extracted from intact soil cores.

Chapter Three

Highfield Reversion Experiment

3.1 Introduction

Within the current literature, recolonisation, recovery or re-establishment of mesofaunal communities has focused on land affected by; fire (Malmström, 2010; Beyer *et al.*, 2011), flooding (Russell, Hauth and Fox, 2004; Russell and Griegel, 2006), drought (Alvarez, Frampton and Goulson, 1999; Lindberg and Bengtsson, 2005; Waagner, Bayley and Holmstrup, 2011), soil pollution, such as copper (Böckl *et al*., 1998; Filser, Wittmann and Lang, 2000) and deglaciation (Doblas-Miranda *et al*., 2008; König, Kaufmann and Scheu, 2011). Few studies have focussed on soil degraded by agricultural management practices and its effect on mesofaunal populations. The unique nature of the Highfield ley-arable experiment (Section 2A.1.3), has provided a platform with which to study the effects of long term management practices on a wide range of multi-disciplinary observations. This includes the rate at which the mesofaunal populations are able to recover or decrease following management practice changes.

The Highfield ley-arable experiment was first implemented in 1949, on well-established permanent grassland pasture within the Rothamsted Estate (Section 2A.1). By dividing the field into strips, a long-term experiment to a compare continuous grassland pasture with a 3 year ley – 3 year arable rotation, was conducted. In 1959, an additional treatment of bare fallow, maintained by ploughing, was included using additional land from the Highfield and adjacent Geescroft mine site.

Previous studies on Highfield, such as Johnson, Poulton and Coleman (2009), showed that the organic carbon (C) levels between the arable and grass treatments had diverged in 1949, leading to a 30 tonnes per hectare difference by 2000. In 2006, a preliminary study determined that the fallow and arable strips of the Highfield experiment had a much reduced mesofaunal and microbial abundance; however, microbial biodiversity remained high. In addition, the soil of the fallow treatment plots was nutritionally and structurally degraded (Hirsch *et al*., 2009). This mirrors the finding of a crop cover experiment where the lack of vegetation decreases soil organic matter and increases soil erosion and compaction (Snapp *et al*., 2005). It also agrees with the statement by Wardle *et al.* (2004), that soil biota rely on the quality of plant derived resources to survive. The conclusions of the 2006 experiment led to the multi-departmental Highfield Reversion Experiment to change the long established management practices to test the hypothesis: Changes in the quantity and quality of carbon entering the soil are driven by plant species, soil communities and the functions that they perform.

This thesis primarily discusses changes to the mesofaunal community, in terms of individual density, community diversity and the presence/absence of functional groups. In particular the primary colonisers, rate of recolonisation and potential changes to the number of trophic levels, based on current understanding of food webs, will be analysed not only within previously degraded and restored soil but within previously well inhabited soil becoming degraded through management change.

3.2 Materials and Methods

3.2.1 Sample Collection

The experimental location, management and plot layout are described in Chapter Two (Sections 2A.1.4 and 2A.1.5). Experimental plots (10m x 7m, with 0.5m x 0.5m grid, Figure 2A.6), were sampled in three randomly designated grid points per sampling period; once sampled, that grid point became permanently unavailable for re-selection. This sample protocol is to be employed for the length of the Highfield Reversion experiment and was devised by Rodger White, statistician at Rothamsted Research, as part of the multi-disciplinary team.

3.2.2 Sampling Regime

In total four sampling times have occurred;

April 2006 – Preliminary investigation into mesofaunal communities of Grass, Arable and Fallow management; a different sampling protocol was employed, with five samples being collected from each treatment.

April 2008 – Pre-conversion baseline sampling; Grass, Arable and Fallow mesofaunal community estimates.

October 2008 – First post-conversion sampling, displays mesofaunal community change with ploughing. The nine treatments were described using the original followed by new management practice, i.e., the original Grass converted to Arable management treatment is displayed as Grass-Arable (GA). Producing the following treatments:

*Grass-Fallow (**GF**)*	*Grass-Arable (**GA**)*	*Grass-Grass (**GG**)*
*Arable-Grass (**AG**)*	*Arable-Fallow (**AF**)*	*Arable-Arable (**AA**)*
*Fallow-Grass (**FG**)*	*Fallow-Arable (**FA**)*	*Fallow-Fallow (**FF**)*

At the time of sampling the GF, AF and FF treatments had been recently ploughed and left fallow; the FA, FG, GA, AG and AA had been ploughed and seeded as

required and the GG remained undisturbed. The GG, FF and AA treatments were controls as management practices had not changed.

October 2009 – Second annual sampling of converted management regime continuation.

October 2010 – Final annual sampling with converted management regime continuation.

3.2.3 Sample Analysis

Analysis of mesofaunal populations were conducted on 8cm Ø x 10cm deep intact soil cores obtained as described in Section 2A.2. Mesofauna were extracted using a modified Burlese-Tullgren tunnel apparatus (Section 2A.3) and identified as described in Section 2A.4.

The invertebrate populations were determined as per Section 2A.6 and then reported in abundance (m^{-2}), percentage change from the control treatment and mesofaunal biomass ($\mu g\ m^{-2}$) food webs.

3.2.4 Statistical Analysis

In order to statistically analyse the data, the computer program GENSTAT was utilised (Chapter 2A.7). Due to the high proportion of zero results and variation in the data, transformation was required to normalise the distribution, for each sampling period and data type; the data was normalised using the most appropriate method as determined in GENSTAT.

Within the intra sampling period analysis, the preliminary data was analysed using a two-way analysis of variance (ANOVA) on actual values. Baseline data was transformed using $LOG_{10}(n+1)$, whilst October 2008, 2009 and 2010 were transformed using $LOG_e(n+1)$. Following transformation an ANOVA was performed between the different invertebrate groups to determine differences in populations between the nine treatments for each

sampling period. In order to locate any significant differences determined a Student-Newman-Kuels (SNK) (major orders) or Bonferroni (superfamilies only) test was applied, where the SNK test failed to produce distinct ranks the stricter Bonferroni test was utilised.

For the inter sampling period analysis a LOG_{10} transformation was completed on all data, before a repeated measures ANOVA (RMANOVA) was conducted. Where significant differences were determined a ranking system to show the differences was utilised. Where there were no significant differences for treatment x sampling time interactions, the data from all sampling periods was LOG_{10} averaged for each treatment and then an ANOVA was applied. Where significant differences existed between treatments the Bonferroni test was utilised to identify these treatments.

3.3 Results

3.3.1 Preliminary Results: June 2006

The 2006 preliminary investigation recorded significant differences (P=0.025) between the mean abundances of the three management regimes; Fallow, Arable and Grass (Figure 3.1) for both the Collembola and Acari invertebrate orders. The largest total mesofaunal abundance was within the Grass treatment, followed by the Arable and Fallow treatments (P=0.004). In all three treatments there were greater abundances of Acari species than the Collembola (P<0.001). The Acari showed the greatest variation in numbers between the three treatments. Whilst the Collembola numbers in the Arable and Grass were similar, but greater than the Fallow.

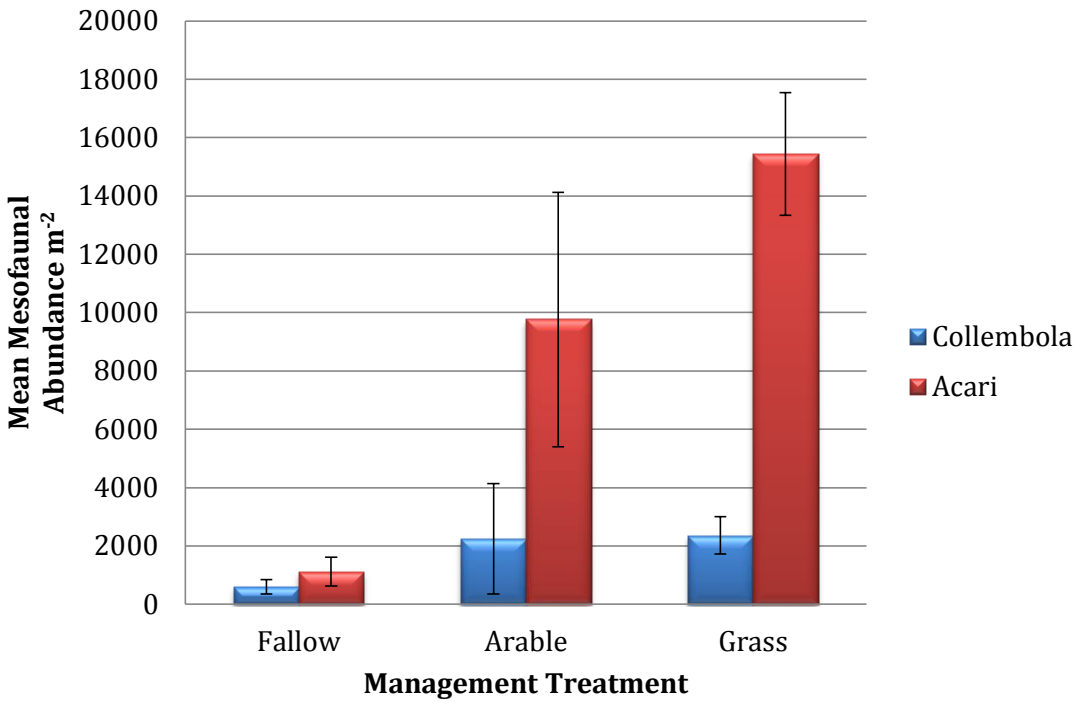


Figure 3.1 The mean abundance (m^{-2}) of the Collembola and Acari (±SE values as error bars) within the Highfield Reversion Project in June 2006.

3.3.2 Baseline Results: April 2008

Baseline results were obtained for the Fallow, Grass and Arable management treatments in April 2008. Sampling was completed before conversion to the new management treatments, the abundance results are shown in Table 3.1, $LOG_{10}(n+1)$ transformed data is shown in Figure 3.2.

Table 3.1 The mean invertebrate abundance (m^{-2}) baseline results for the original Fallow, Arable and Grass treatments, * indicates significant differences (P<0.001) to the other treatments for each group.

Treatment	Mean Invertebrate Abundance (m^{-2})		
	Collembola	Acari	Other Invertebrates
Fallow	630 (±192)	608 (±136)*	96 (±32)
Grass	6077 (±1093)*	24582 (±3456)*	1897 (±519)*
Arable	393 (±214)	1556 (±332)*	178 (±63)

As with the preliminary results, the Grass treatment had a significantly larger number of total invertebrates in comparison to the other treatments. The Acari were generally the most abundant order, with significantly larger abundances in the Grass than in the Fallow (P<0.001). The Collembola and other invertebrates had significantly (both P<0.001) larger abundances in the Grass treatment than the Arable or Fallow. Both the Arable and Grass treatments had similar patterns of community composition with the largest population proportion within the Acari, followed by the Collembola and other invertebrates. However, within the Fallow treatment the Collembola were the most numerous, followed by the Acari and other invertebrates.

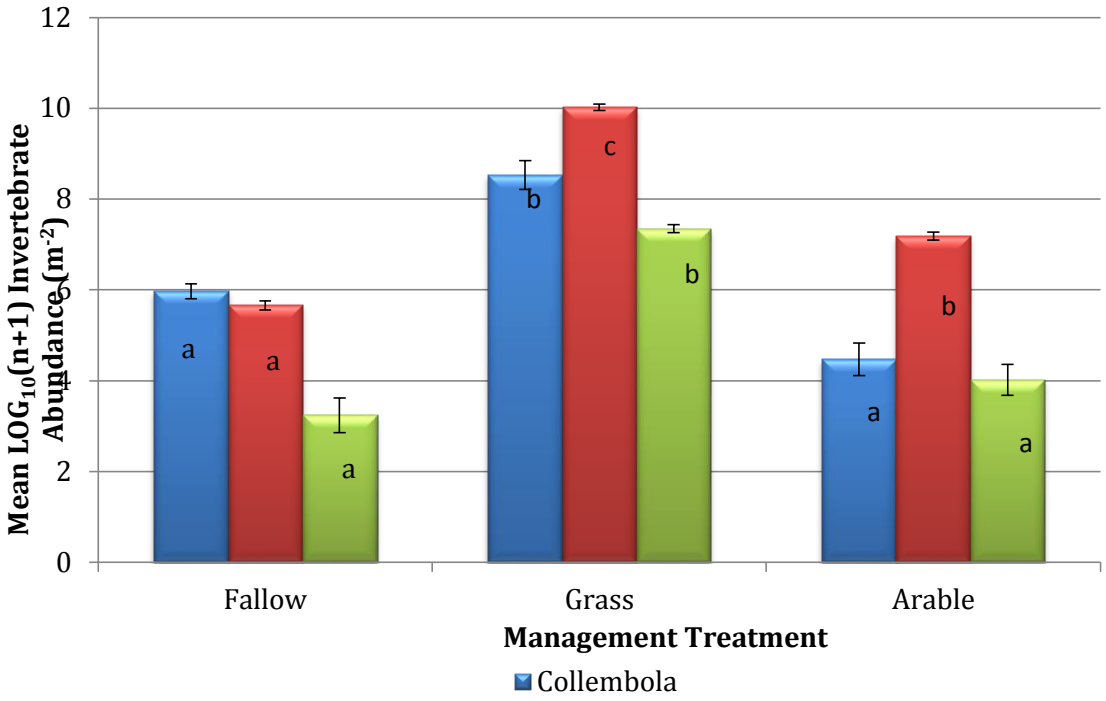


Figure 3.2 The April 2008 mean $LOG_{10}(n+1)$ invertebrate abundance (m^{-2}) (± standard error as error bars) of the Highfield Reversion Project, for the original treatments; Fallow, Arable and Grass. Alphabetical labels depict the statistical analysis results (ANOVA: $LOG_{10}(n+1)$ transformed data) between each invertebrate group for a treatment interaction, (e.g. - Fallow: Acari compared with Arable: Acari and Grass: Acari) differing letters determine significant differences.

Community composition is important for ecosystem function completion, such as the facilitation of organic matter decomposition. Proportional composition changes to the invertebrate community can potentially shift decomposition from the fungal to the bacterial channel (Bjorlund and Christensen, 2005). Therefore the comparison of community composition is important to understand how an ecosystem is functioning, the baseline sampling community composition is based on the invertebrate groups; Collembola, Acari and other invertebrates (Figure 3.3).

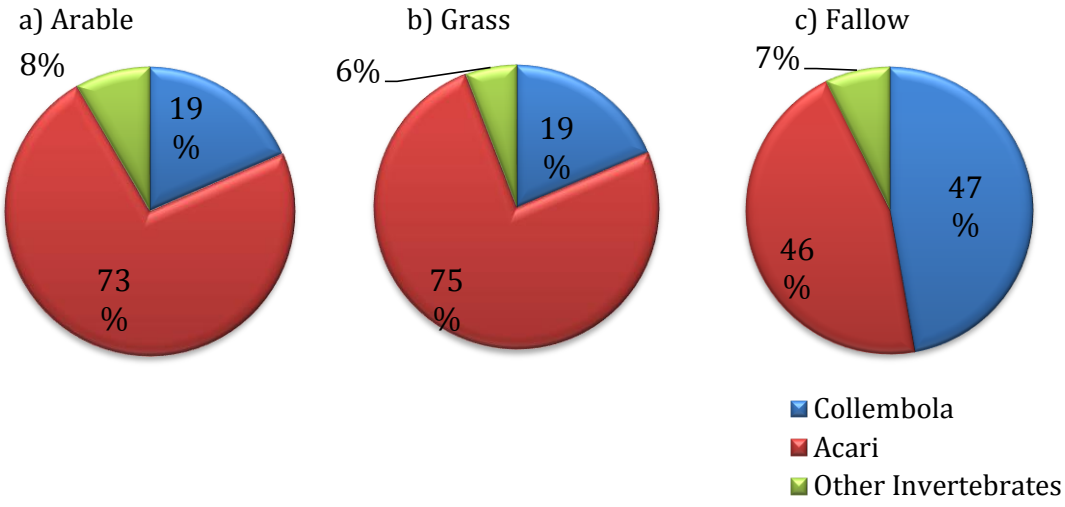


Figure 3.3 The invertebrate community composition recovered in April 2008 from the Highfield Reversion Project treatments.

The proportions of each invertebrate group within the Arable and Grass treatments were very similar even though the Arable abundance results were much lower than the Grass treatment. Both treatments had a community population based primarily on Acari species. The Collembola constitute a fifth of the community whilst the other invertebrates were the smallest group. However, the Fallow treatment had a larger Collembola proportion within the community, being approximately equal to the Acari.

The preliminary investigation and baseline sampling shared a number of similar results; firstly in every treatment the Acari were the most abundant mesofaunal group, secondly the Fallow plot Collembola abundances were very similar at both sampling times. However, there were also differences between the sampling times. Within the Grass treatments, the baseline sampling had a much higher Collembola and Acari abundance than preliminary sampling. However, within the Arable treatments this pattern was reversed with higher abundance levels in the preliminary results.

3.3.3 Post-conversion Invertebrate Population

3.3.3.1 Results Overview

Throughout the sampling period there were differences between the population densities and the community structure of the mesofauna. The baseline populations were recorded, with an average total of 12006 (±3305) invertebrates m^{-2}. This dropped in October 2008 to a mean of 3535 (±1342) invertebrates m^{-2}. Over the following two years the average number of total invertebrates increased, to 15052 (±4267) invertebrates m^{-2} in October 2009 and 30951 (±6804) invertebrates m^{-2} in October 2010 (Figure 3.4).

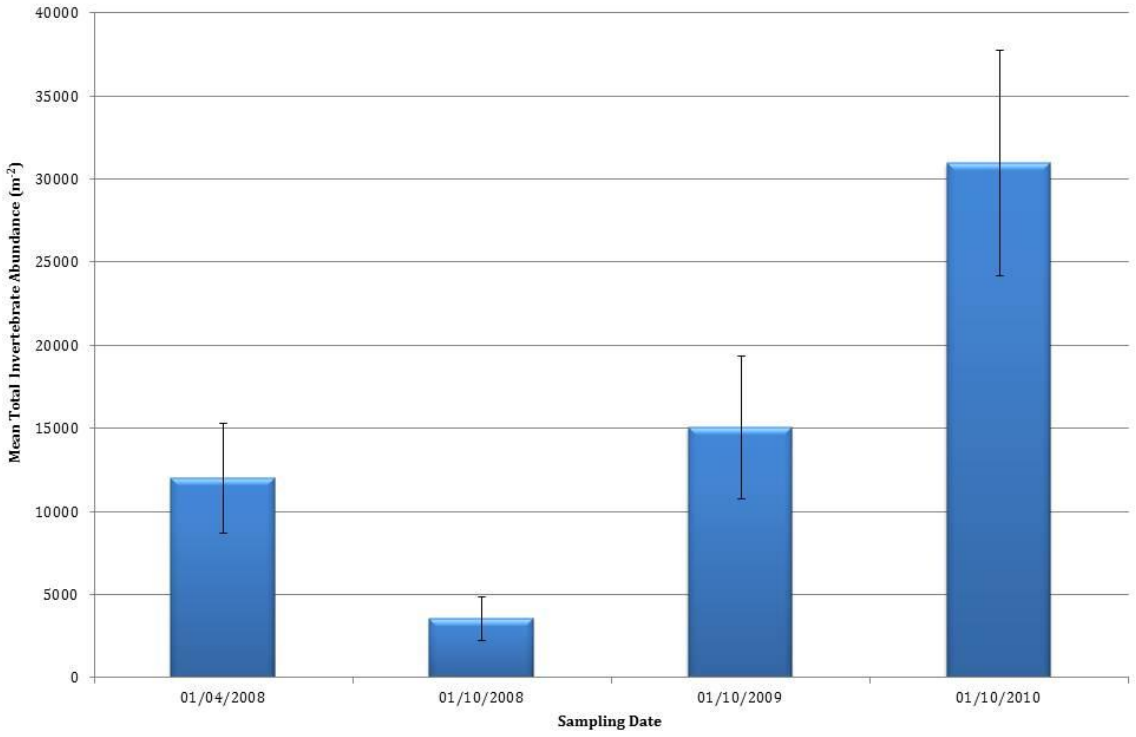


Figure 3.4 The mean total number of invertebrates (m^{-2}) (± standard error as error bars) recovered from the Highfield Reversion Project for the period April 2008 – October 2010.

The invertebrate and mesofaunal populations increased year on year, this difference was significant for all invertebrate groups and mesofaunal superfamilies. However, it can also be seen in the mesofaunal biomass food webs (Figures 3.5-3.13), where the relative size of

the basal resource spheres reduce over the experimental period. These did not decline quantitatively rather this was caused by an increase in the size of the other food web spheres. Full figures for the mesofaunal biomasses are displayed in Appendix I.

Overall the mesofaunal food webs show that the community composition of the AA and FF controls fluctuate throughout the experiment. The AA (Figure 3.5) begins with a Poduromorpha and Oribatida dominated food web, but by 2009 the Oribatida and Entomobryomorpha dominate with a smaller sub-group of Mesostigmata and Poduromorpha. However, this changes again in 2010 where the Oribatida and Mesostigmata dominate. The FF control (Figure 3.6) begins with very small biomass figures, mostly within the Poduromorpha and Entomobryomorpha. In 2009 larger biomass figures were recorded, these were within the Poduromorpha, Mesostigmata and Oribatida superfamilies. In 2010, although the Mesostigmata and Oribatida were still found as large biomasses, they were accompanied by the Entomobryomorpha.

The GG control (Figure 3.7) community composition was more stable; in 2008 the Oribatida and Mesostigmata dominate with a smaller sub-group of Entomobryomorpha and Poduromorpha. However, in 2009 and 2010 the dominant superfamily was the Mesostigmata, followed by the Oribatida and Entomobryomorpha.

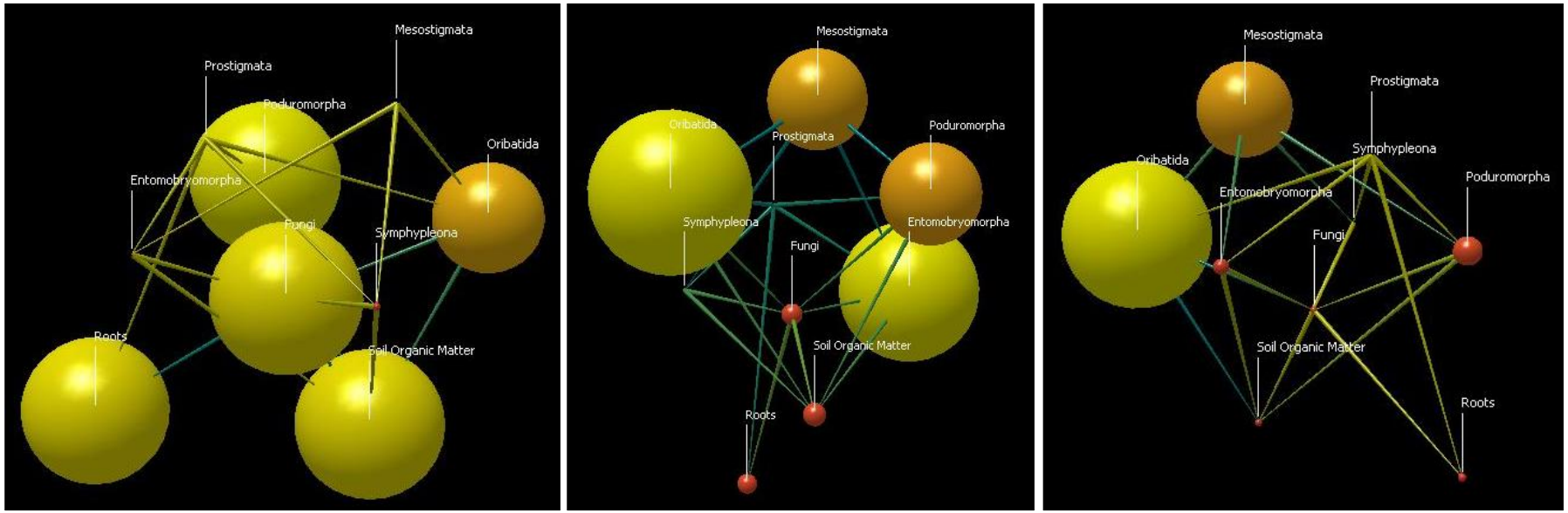


Figure 3.5 The mesofaunal biomass (µg m^{-2}) food web of the Arable-Arable control: 2008 (left), 2009 (middle) and 2010 (right)

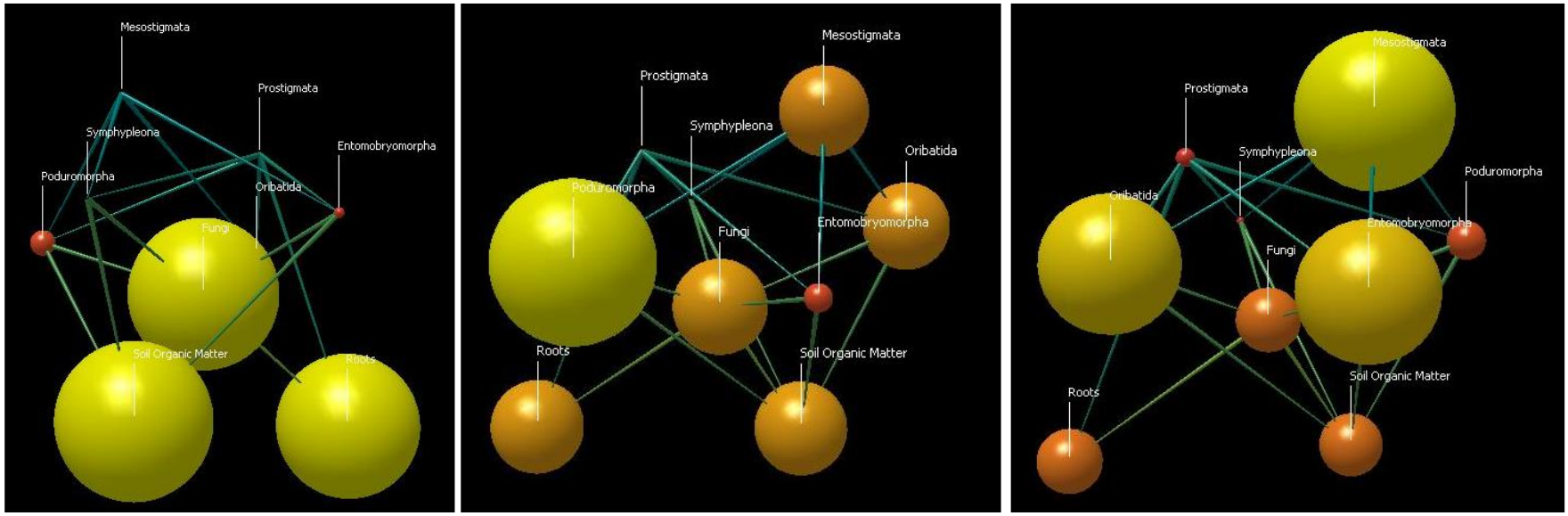


Figure 3.6 The mesofaunal biomass (µg m^{-2}) food web of the Fallow-Fallow control: 2008 (left), 2009 (middle) and 2010 (right)

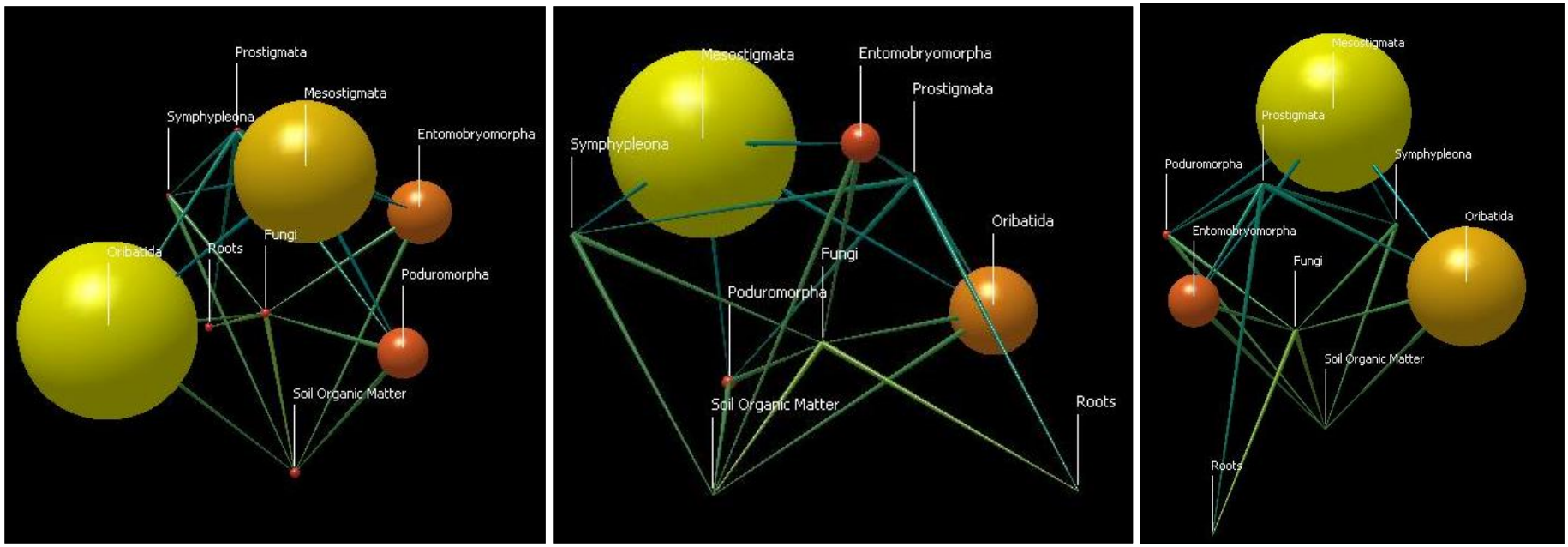


Figure 3.7 The mesofaunal biomass (µg m^{-2}) food web of the Grass-Grass control: 2008 (left), 2009 (middle) and 2010 (right)

The AF treatment (Figure 3.8) begins with a relatively equal split in the mesofaunal biomass between all six superfamilies. By 2009, the Oribatida became dominant with a smaller biomass of Poduromorpha, Mesostigmata and Entomobryomorpha, this pattern was then repeated in 2010. The AG treatment (Figure 3.9) community composition was more variable. In 2008, the Oribatida were dominant with a smaller Mesostigmata biomass. By 2009, there were three layers of biomass, again the Oribatida were most dominant, followed by the Mesostigmata and finally the Entomobryomorpha and Poduromorpha. Similar results were produced in 2010; however, the Mesostigmata had achieved higher biomass than the Oribatida.

The FA treatment (Figure 3.10) displays some variation between sampling years. In 2008, all superfamilies were present, with the Mesostigmata dominating followed by the Oribatida; these remain dominant throughout the sampling period. These were followed in 2008 by the Entomobryomorpha and Poduromorpha, in 2009 by the Poduromorpha, Entomobryomorpha and Prostigmata and in 2010 by the Entomobryomorpha, Poduromorpha and Prostigmata.

The FG treatment (Figure 3.11) begins with a dominant Poduromorpha biomass in 2008, changing to a food web with large Oribatida, Mesostigmata, Poduromorpha and Entomobryomorpha populations. In 2010, this had again changed, producing a Mesostigmata dominated community composition with smaller Entomobryomorpha, Poduromorpha and Oribatida populations.

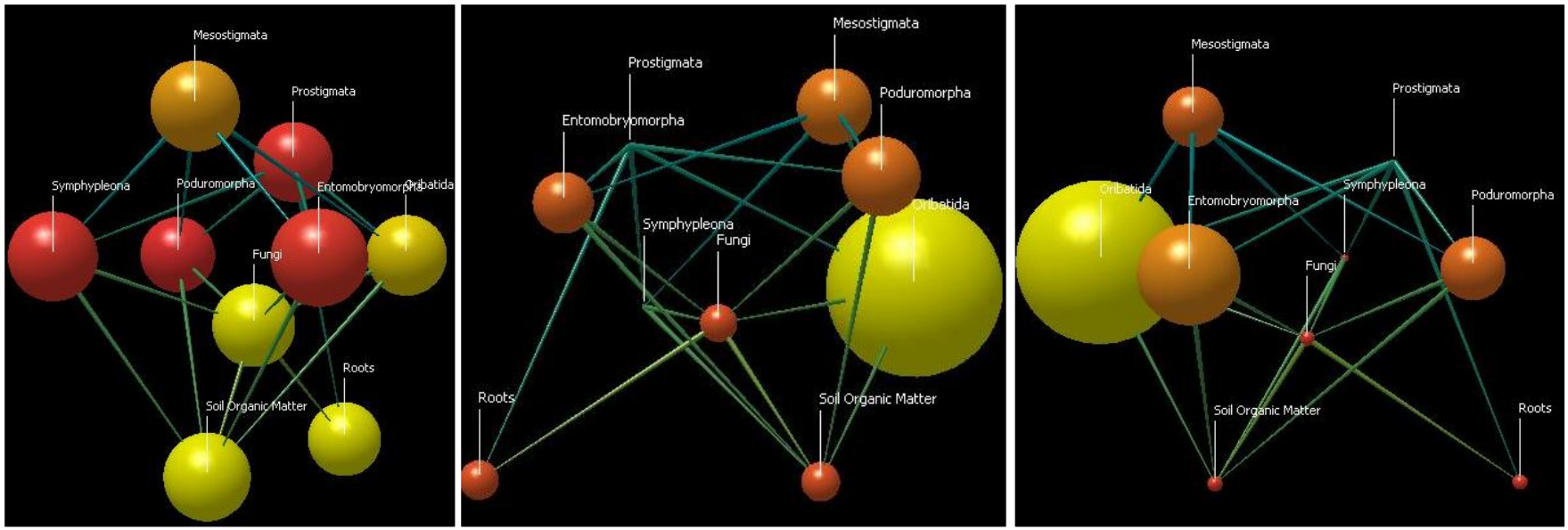


Figure 3.8 The mesofaunal biomass (µg m^{-2}) food web of the Arable-Fallow treatment; 2008 (left), 2009 (middle), 2010 (right)

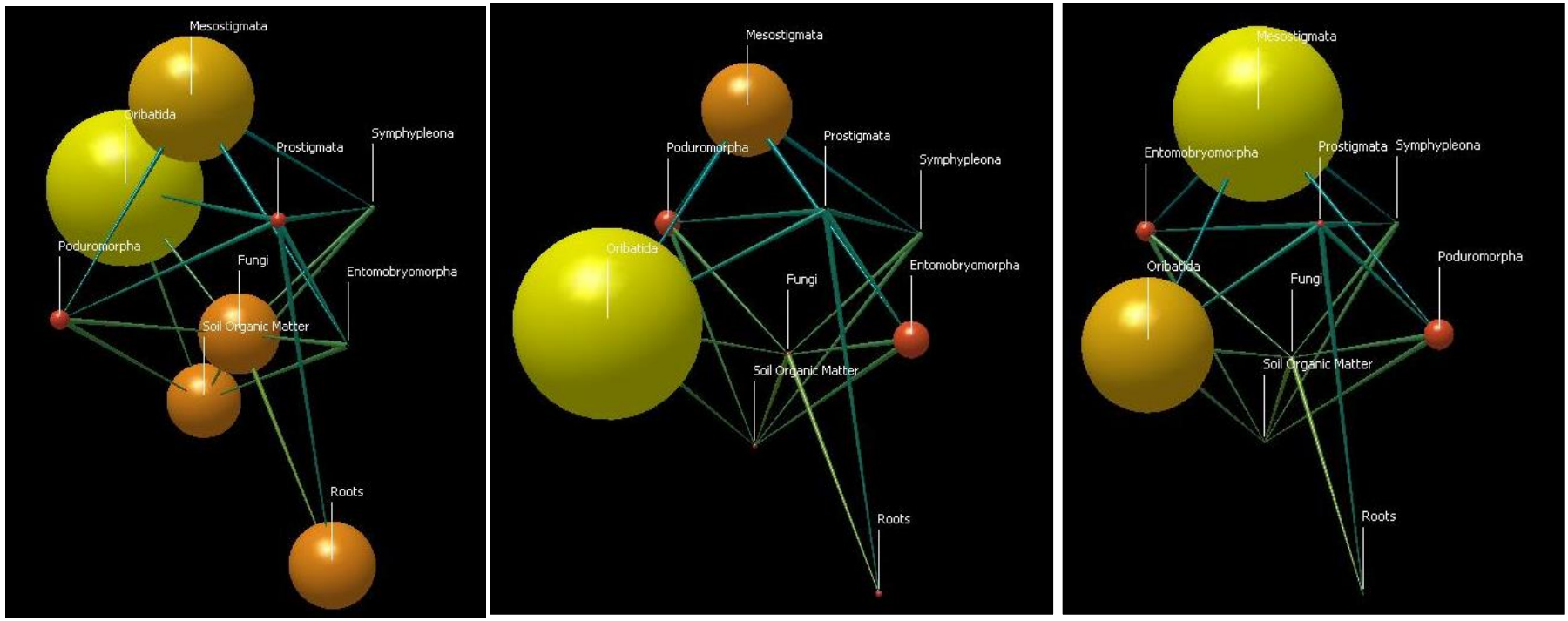


Figure 3.9 The mesofaunal biomass (µg m^{-2}) food web of the Arable-Grass treatment; 2008 (left), 2009 (middle), 2010 (right)

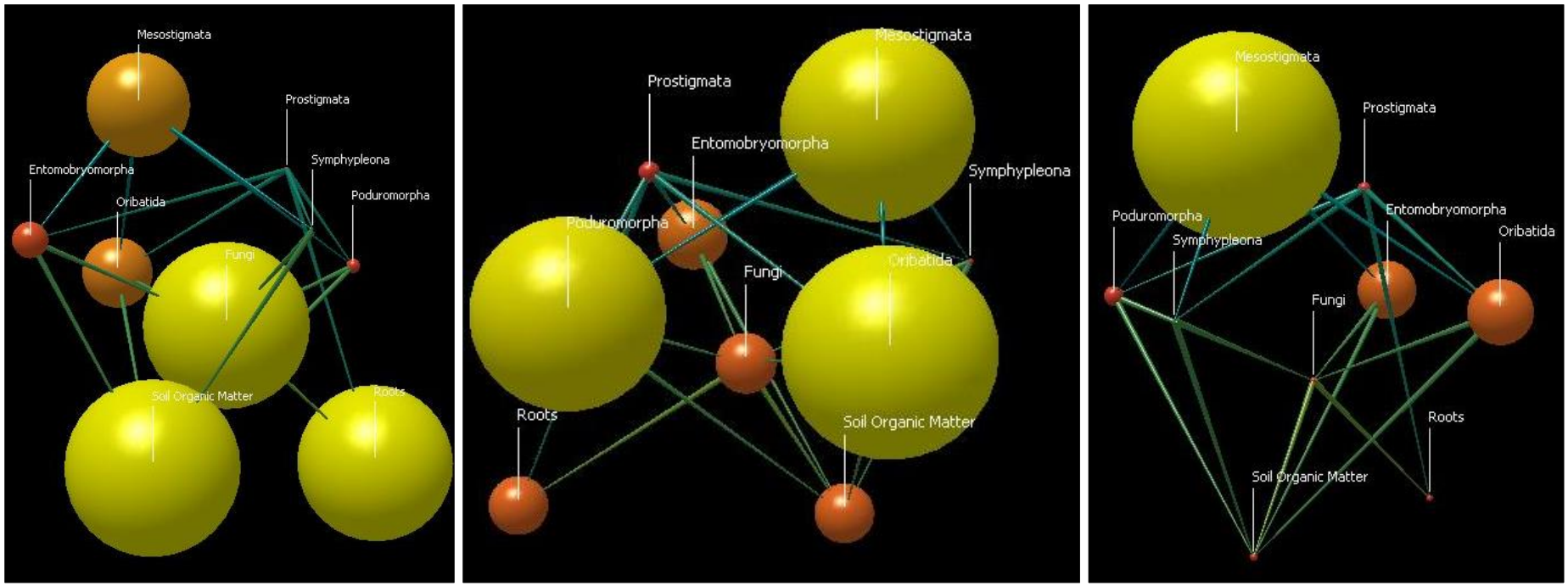


Figure 3.10 The mesofaunal biomass (µg m^{-2}) food web of the Fallow-Arable treatment; 2008 (left), 2009 (middle), 2010 (right)

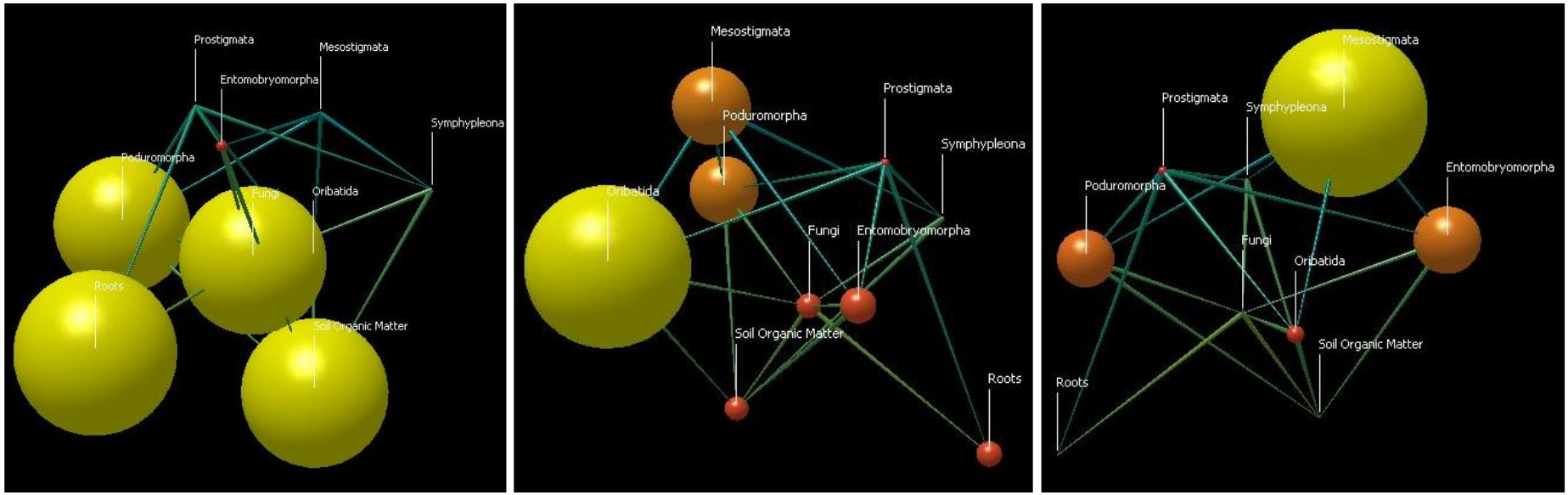


Figure 3.11 The mesofaunal biomass (µg m^{-2}) food web of the Fallow-Grass treatment: 2008 (left), 2009 (middle), 2010 (right)

The GA treatment community composition (Figure 3.12) displays changes between the 2008 and 2009 samplings and then a stabilisation in 2010. In 2008, the Entomobryomorpha and Mesostigmata were dominant with smaller populations of Oribatida and Symphypleona. In 2009 and 2010, the Entomobryomorpha population decreases, becoming equal to the Oribatida and the Mesostigmata became dominant, the Poduromorpha increase although do not match the Oribatida population size.

Within the GF treatment (Figure 3.13) the community composition also varies between years. In 2008, the most prevalent superfamily was the Oribatida, followed by the Mesostigmata and finally the Poduromorpha and Entomobryomorpha. By 2009, the Mesostigmata had the largest biomass; this was followed by the Poduromorpha and Oribatida and finally the Entomobryomorpha. In 2010 the community composition was more stable; however, the Entomobryomorpha and Poduromorpha had switched places.

It is noticeable, that throughout the experimental time the GG control was the most stable and had the largest organism diversity recovered from any treatment. Meanwhile, the treatments with regular ploughing (AA, FF, FA, GA, AF and GF) had the largest community composition variations. Those where ploughing had been removed, the AG and FG treatments, had community compositions closer to the GG controls community composition by the end of the investigation.

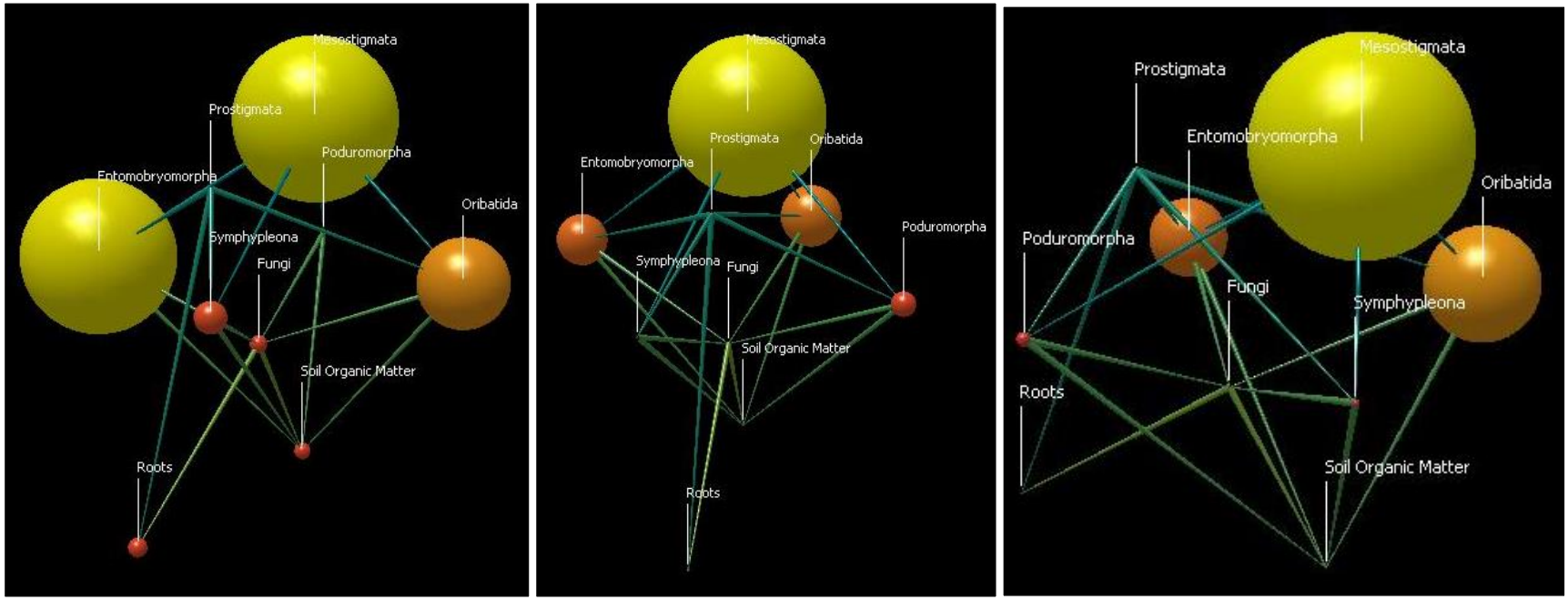


Figure 3.12 The mesofaunal biomass (µg m^{-2}) food web of the Grass-Arable treatment; 2008 (left), 2009 (middle), 2010 (right)

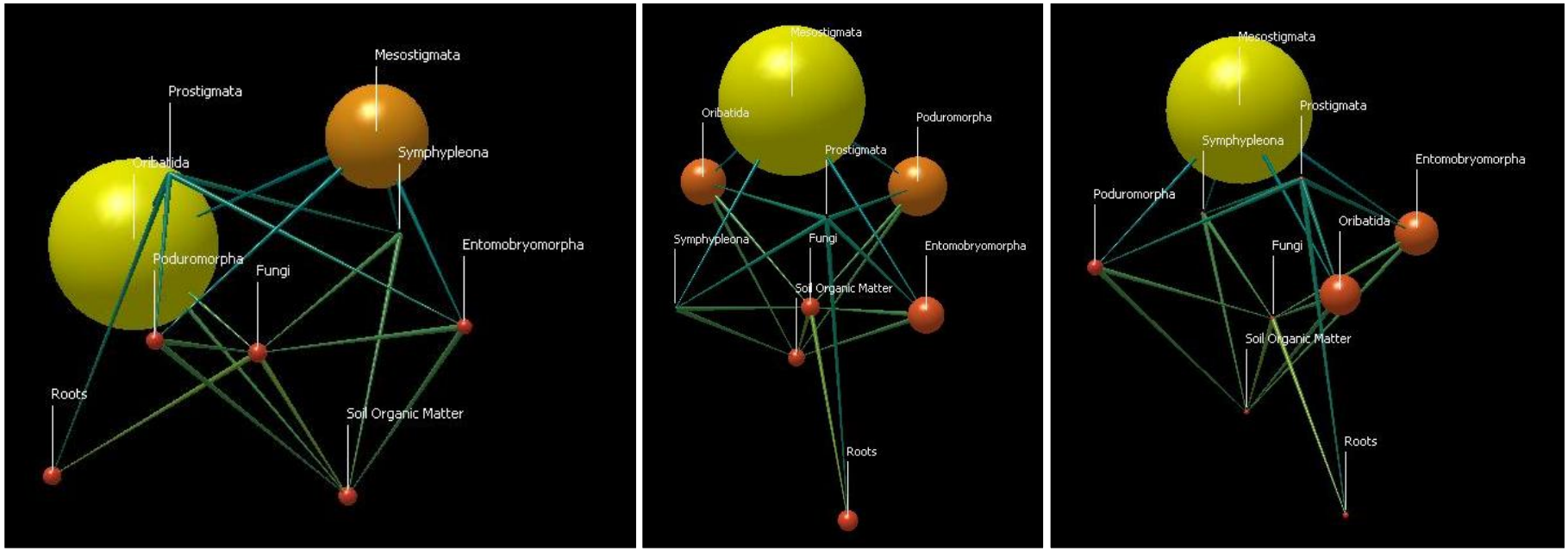


Figure 3.13 The mesofaunal biomass (µg m^{-2}) food web of the Grass-Fallow treatment: 2008 (left), 2009 (middle), 2010 (right)

3.3.3.2 Post-conversion Collembolan Population Differences between Treatments for Individual Years

The mean total Collembola abundance showed no significant differences by ANOVA analysis between the treatments in 2008 (Appendices II and V). However, the treatments were split into three groups; the GA and GG have the largest abundance, whilst the FA, FF, AF and AG have the lowest abundance, the remaining treatments (AA, GF and FG) produce a central group.

Within the 2009 results (Appendices III and V), there were four distinct SNK groupings; the GA and GG had the largest mean total Collembola abundance, a second group comprise FG, AG and AA, a third (FA, GF and AF) and finally the FF treatment with the smallest abundance. The GA and GG were significantly ($P<0.001$) larger than the FF, FA, GF and AF, whilst the FG, AG and AA were significantly larger than the FF only.

In 2010, the mean total Collembola abundance was significantly different ($P<0.001$) between the treatments, the mean abundance range was between 32772 m^{-2} (FG) and 1089 m^{-2} (FF) (Appendices IV and V). The FG treatment had the highest mean total Collembola abundance and was significantly different from the FF, AA, FA, GF and AF. The GG, GA and AG were significantly larger than the AA and FF treatments, whilst the FA, GF and AF treatments were also significantly larger than the FF treatment.

In 2008, the abundance and biomass of the Collembola superfamilies showed no significant differences between treatments for the Poduromorpha or Symphypleona (Appendix V). The Entomobryomorpha abundance was significantly different ($P=0.004$), as was the biomass ($P=0.005$) between the treatments, although there were differences in the statistical rankings (Table 3.2). In each case the AG and AA had the lowest biomass or abundance and the GG treatment had the highest.

Table 3.2 The statistical ranking for the Entomobryomorpha abundance and biomass results in 2008.

Abundance (P=0.004)		**Biomass** (P=0.005)	
Treatment	**Bonferroni Ranking**	**Treatment**	**SNK Ranking**
GG	B	GG	D
GA GF FA AF FF FG	AB	GA	BCD
		GF	ABCD
		FA	ABC
		FG FF AF	AB
AG AA	A	AA AG	A

The 2009 sampling displayed no significant differences in abundance or biomass between treatments for the Symphypleona (Appendix V). However, both the Entomobryomorpha and Poduromorpha have significant differences (abundance: $P<0.001$ and $P=0.008$, biomass: $P=0.002$ and $P=0.016$ respectively). The Bonferroni and SNK rankings are displayed in Table 3.3.

The Entomobryomorpha abundance had two distinctly different groups, firstly those with the highest mean abundance (GG, GA, AG, AA and FG) and secondly the lowest mean abundance (FF). The remaining treatments (AF, GF and FA), were within a group overlapping both the highest and lowest abundances. The Entomobryomorpha biomass was only divided into two groups, the FF treatment is significantly lower than the other treatments. Within the superfamily Poduromorpha, the abundance and biomass were divided into three groups, with the most abundant (GG and GA) being significantly larger than the FF treatment. The remaining treatments (AG, AA, FG, GF, FA and AF) were placed between the two extremes, without being significantly different.

Table 3.3 The statistical ranking for the Entomobryomorpha and Poduromorpha abundance and biomass results in 2009.

Superfamily	Abundance		Biomass	
	Treatment	Bonferroni Ranking	Treatment	SNK Ranking
Entomobryomorpha (P<0.001, abundance; P=0.008, biomass)	FG AA AG GA GG	B	GG GA AG AA FG AF GF FA	B
	FA GF AF	AB	FF	A
	FF	A		
Poduromorpha (P=0.002, abundance; P=0.016, biomass)	GA GG	B	GG GA	B
	AG AA FG GF FA AF	AB	AG AA FG GF FA AF	AB
	FF	A	FF	A

In 2010, there was no difference in mean abundance or biomass between the different treatments for the Symphypleona (Appendix V). However, the Entomobryomorpha had significant differences between the treatments, for both abundance (P<0.001) and biomass (P=0.002). The abundance of this superfamily was split into two extreme Bonferroni groupings (Table 3.4); the FF treatment has the lowest mean abundance, and was different from the GG, GA, FG and AG treatments which had the largest recorded abundances. The intermediate group contained the GF, AF, FA and AA treatments. The biomass SNK rankings were, however, more complex with the AG, GA and GG treatments all being significantly larger than the FF and AA, whilst the FG treatment is larger than the FF only.

Table 3.4 The statistical ranking for the Entomobryomorpha and Poduromorpha abundance and biomass results in 2010.

Superfamily	Abundance		Biomass	
	Treatment	Bonferroni Ranking	Treatment	SNK Ranking
Entomobryomorpha (P<0.001, both)	FG AG GA GG	B	GG GA AG	C
	AA FA GF AF	AB	FG	BC
	FF	A	GF AF FA	ABC
			AA	AB
			FF	A
Poduromorpha (P=0.005, abundance; P=0.011, biomass)	FG AG	B	AG FG	B
	AA GF FA GA GG AF	AB	GG AA GA GF FA AF	AB
	FF	A	FF	A

The Poduromorpha also revealed significant differences in abundance (P=0.005) and biomass (P=0.011), both had similar statistical test rankings with maximum (AG and FG) and minimum abundances (FF). This superfamily had a large intermediate group, consisting of the GG, GA, GF, AA, FA and AF; these treatments do not show significant differences between them or the maximum and minimum groupings.

3.3.3.3 Post-conversion Acari Population Differences between Treatments for Individual Years

In 2008, the GG, GF and GA treatments had a significantly (P=0.006) larger Acari abundance than the FF, whilst the five remaining treatments (AA, AG, AF, FA and FG) were in an intermediate group (Appendices II and V).

In 2009, the Acari were the most numerous invertebrate group, with a maximum abundance of 31727 m^{-2} within the GG treatment (Appendices III and V). The mean total Acari abundance displays significant differences ($P<0.001$) between treatments, divided into several SNK groupings. The largest abundance was recovered from the GG treatment; this was significantly larger than the FF, FA, AF, GF, FG and AA treatments; however it was similar to the GA and AG treatments. The GA and AG treatments were significantly larger than the FF, FA, AF and GF treatments, but were similar to the FG and AA treatments. The FG, AA and GF were significantly larger than the FF treatments. The FF treatments only had no differences from the AF and FA treatments.

During 2010, the Acari were the most numerous invertebrates recorded (Appendix V), with a maximum of 52871 m^{-2}. Within the mean total Acari abundance there were significant differences ($P<0.001$) between treatments (Appendix IV), different groups were identified by SNK, the maximum abundance (AG and GG) were significantly larger than the FF, AF, GF, FA and AA treatments, the GA and FG treatments were also significantly larger than the FF and AF treatments, whilst the GF, FA and AA were only significantly larger than the FF treatment.

Upon superfamily division statistical analysis of the 2008 data determined no significant differences between treatments for Prostigmata or Mesostigmata abundances (Appendix V). The Oribatida abundances, however, showed significant differences ($P=0.007$) between the abundances of the GG (highest) and FF (lowest) treatments, with the remaining treatments combining to form an intermediary group. The biomass of this superfamily was significantly different ($P=0.010$) between the treatments, with the largest biomass in the GF, GA and GG, whilst the lowest biomasses were found in the FF treatment (Table 3.5). The Mesostigmata biomass was also significantly different ($P=0.035$), although no SNK rankings were obtained.

Table 3.5 The statistical ranking for the Oribatida abundance and biomass results in 2008.

Superfamily	Abundance		Biomass	
	Treatment	Bonferroni Ranking	Treatment	SNK Ranking
Oribatida (Abundance, P=0.007; Biomass P=0.010)	GG	B	GG GA GF	B
	GA GF AF AG AA FG FA	AB	AG AF AA FA FG	AB
	FF	A	FF	A

Within the 2009 results, each of the Acari superfamilies; Prostigmata, Oribatida and Mesostigmata, had significant differences between the abundances (Appendix V) and biomasses recorded for the treatments. The significant differences (P=0.009) within the Prostigmata abundance were divided between three main groupings, those with the highest abundance (GG and GA), those with the lowest abundance (AF) and those in a group not significantly different from either extreme (AG, FG, AA, GF, FA and FF). The biomass also had significant differences (P=0.015) between treatments, the AF and FF treatments had the lowest biomass, whilst the GA and GG had the largest; the remaining group makes up a central non-significant group (Table 3.6).

The Oribatida had a similar pattern with significant differences (P=0.006) in the abundances of the highly populated GG and AG treatments and the FF treatment, with the GA, AA, AF, FG, FA and GF treatments forming a group not significantly different from the highest or lowest abundances. The Oribatida biomass measurements had very similar statistical rankings as the abundance, however, the GA was also significantly (P=0.008) larger than the FF treatment.

Table 3.6 The statistical ranking for the Oribatida, Mesostigmata and Prostigmata abundance and biomass results in 2009.

Superfamily	Abundance		Biomass	
	Treatment	Bonferroni Ranking	Treatment	SNK Ranking
Prostigmata (Abundance, P=0.009; Biomass, P=0.015)	AF	B	GG GA	B
	FF FA GF AA FG AG	AB	AG FG AA GF FA	AB
	AF	A	FF AF	A
Oribatida (Abundance, P=0.006; Biomass, P=0.008)	AG GG	B	GG AG GA	B
	AF AA FG FA GA GF	AB	AA AF FG FA GF	AB
	FF	A	FF	A
Mesostigmata (Abundance, P<0.001; Biomass, P=0.009)	AG	D	GG GA AG	B
	GA FG GG	CD	FG GF AA FA AF	AB
	FA GF	BCD		
	AA	ABC		
	AF	AB		
	FF	A	FF	A

The Mesostigmata abundances were more varied in their significant differences (P<0.001). The abundance of the AG treatment was significantly larger than the FF, AF and AA treatments, the GA, GG and FG treatments were also significantly larger than the FF and AA treatments. The biomass of the AG, GA and GG treatments were significantly (P=0.009) larger than the FF treatment, whilst the remaining treatments were not significantly different.

The 2010 sampling period results determined no differences in the abundance results between treatments for the Prostigmata (Appendix V). The Prostigmata biomass was significantly different (P=0.020) between treatments, although there was no SNK ranking differentiation between treatments, the AG and GG treatments had much larger biomasses than the FF and AF treatments. However, both the Oribatida and Mesostigmata had significant differences for the abundance and biomass (P<0.001) between treatments (Table 3.7). Within the Oribatida there were two isolated groups at the extremes of the mean abundance, the AG treatment was significantly larger than the FF treatment. Between these two treatments was a group that was not significantly different from either extreme, this contained the AA, FG and AF treatments. On either side of this central group two smaller groups were seen, the GA and GG treatments were significantly different from the FF treatment and the FA and GF treatments were significantly different from the AG treatment. The mean biomass of the AG is significantly larger than the FF, GF, FA, AF and FG, in addition the GG treatment is significantly larger than the FF, GF and FA treatments, the AA and GA treatments are also significantly larger than the FF treatment (Table 3.7).

The significant differences present in the Mesostigmata abundance were more complex than the Oribatida, with seven different Bonferroni groupings. The FF treatment was at the least populated end of the rankings and this treatment was different from the AG, GG, FG, GA and FA treatments; however it was not different from the GF, AA or AF treatments. At the top of the abundance rankings the AG treatment was significantly different from the AA, AF and FF treatments. The grouping closest to the AG treatment were the GG, FG and GA treatments, followed by the FA and GF treatments. The GF treatment was the only one that overlaps both the AG treatment at the maximum abundance and FF at the minimum abundance. The biomass rankings for these groups differ from the abundance, showing that the FF is also significantly different from the GF treatment in addition to the FA, FG, GA, GG and AG treatments.

Table 3.7 The statistical ranking for the Oribatida and Mesostigmata abundance and biomass results in 2010.

Superfamily	Abundance		Biomass	
	Treatment	Bonferroni Ranking	Treatment	SNK Ranking
Oribatida (Both, P<0.001)	AG	C	AG	D
	GA GG	BC	GG	CD
	AF FG AA	ABC	GA AA	BCD
	GF FA	AB	FG AF	ABC
			FA GF	AB
	FF	A	FF	A
Mesostigmata (Both, P<0.001)	AG	D	AG	D
	GA GG FG	CD	GG GA FG	CD
	FA	BCD	FA GF	BCD
	GF	ABCD	AA	ABC
	AA	ABC	AF	AB
	AF	AB		
	FF	A	FF	A

3.3.3.4 Post-conversion Total Other Invertebrates Population Differences between Treatments for Individual Years

In 2008, statistical analysis of the mean total other invertebrate abundance had significant differences (P=0.048) between the FA (lowest) and GG (highest) treatments, with the remaining making up the intermediate group (Appendices II and V). In the majority of treatments the mean total other invertebrates had the smallest abundances. However, within the FF treatment other invertebrates had the highest recorded abundance, with the AF and AA having a higher abundance than the mean total Collembola. During this sampling period the GG control records the most diverse range of other invertebrates, with a large number of Diptera larvae and Annelida. It was also evident that no herbivores were recovered during this period (determined using Wheater and Cook, 2003) (Appendix VI).

In 2009, a larger number of other invertebrate orders were identified, from more treatments, than 2008 (Appendix VI). Statistically, there was no difference between any treatments. However, there was a trend for the GG and AG treatments to have the highest numbers with greater diversity. Additionally, during this sampling period herbivores were recorded as part of the invertebrate community.

During 2010, there were a larger number of other invertebrates recorded than in any other year (Appendices IV and V). These were spread throughout all treatments and were from a diverse range of invertebrate orders (Appendix VI). Diptera larvae were recovered from all treatments; Coleoptera Larvae and Chilopoda were regularly recorded with abundances of over 100 individual's m^{-2}. Statistical analysis determined significant differences between the different treatments ($P<0.001$) (Appendix V), although the SNK ranking was more complex than the previous results. Here the AG treatment had a significantly larger abundance than the FF, GF, AF and FA treatments. The abundance of the GG and FG treatments were larger than the GF and FF treatments, whilst the FA, GA and AA treatments were significantly larger than the FF treatment.

3.3.4 All Years: Interactions between Time and Treatment - Invertebrate Population Changes

Statistical analysis to determine invertebrate population changes, caused by time, treatment or an interaction of the two, produced mixed results. Mean invertebrate populations significantly increased throughout the experimental period for all groups, over all sampling periods (Table 3.8). This increase was also seen in the mesofaunal biomass food webs (Figures 3.5 to 3.13), where the relative size of the basal resources got progressively smaller as the experiment progressed indicating that the mesofaunal biomass sizes were increasing.

Table 3.8 The mean abundance (m^{-2}) and biomass ($\mu g\ m^{-2}$) for all invertebrate groups throughout the investigation and the statistical significance of any differences.

Invertebrate Group	Mean Abundance (log)				Mean Biomass (log)			
	2008	2009	2010	P Value	2008	2009	2010	P Value
Other Invertebrates	4.61	6.18	6.52	<0.001	-	-	-	-
Acari	5.72	8.09	9.14	<0.001	-	-	-	-
Collembola	4.68	8.1	8.78	<0.001	-	-	-	-
Mesostigmata	2.56	6.19	7.44	<0.001	3.71	8.69	9.98	<0.001
Prostigmata	2.95	4.79	7.07	<0.001	2.82	4.61	6.82	<0.001
Oribatida	5.2	7.57	8.43	<0.001	6.13	8.67	9.55	<0.001
Entomobryomorpha	2.65	6.82	7.95	<0.001	3.18	7.87	9.01	<0.001
Symphypleona	2.03	2.32	5.55	<0.001	2.03	2.32	5.51	<0.001
Poduromorpha	3.8	7.53	7.58	<0.001	4.26	8.22	8.26	<0.001

Due to the general invertebrate population increase it is difficult to determine whether there is a time x treatment interaction. Where there were no significant time x treatment interactions, the results were reanalysed, using a mean log of all results (2008, 2009, and 2010) for each treatment, to determine if there were any treatment differences.

Statistical analysis determined that both the mean Acari and mean other invertebrate abundance data were significantly different (P=0.005 and P=0.018 respectively) for a time x treatment interaction (Table 3.9). It can be seen that treatments converted to Grass had moved up the abundance rankings, whilst those converted to Fallow had moved down. There was no difference in the mean Collembolan abundances, when analysed for the time x treatment interaction.

Table 3.9 The RMANOVA ranking of the mean Acari and mean other invertebrates abundance for each sampling period, for time x treatment interactions (significant differences are in brackets).

Invertebrate Group	The Bonferroni rankings for each sampling date (largest abundance uppermost)		
	October 2008	October 2009	October 2010
Acari (P=0.005)	GG	AG	AG
	GA	GG	GG
	GF	GA	GA
	AG	FG	FG
	AF	AA	AA
	AA	AF	FA
	FG	FA = GF	GF
	FA		AF
	FF	FF	FF
Other Invertebrates (P=0.018)	GG	FG	AG
	GA	GG	GG
	GF	AG	FG
	AA	GA	GA
	AG	GF	AA
	AF	AF	FA
	FF	AA	AF
	FG	FA	GF
	FA	FF	FF

Re-analysis (by ANOVA) of the mean abundance for each treatment for the Collembola revealed that there was a significant difference ($P<0.001$) between treatments for the full experimental time (Table 3.10). The GG treatment, at the top of the abundance scale, was significantly different from the AA, FA, AF and FF treatments, whilst the FF treatment was significantly different from the AG, FG, GA and GG treatments. There was an area of overlap in the centre of the abundance rankings.

Due to time constraints statistical analysis was not completed on the mean Collembola and Acari biomass data.

Table 3.10 The ANOVA and Bonferroni ranking for Collembola abundance using transformed results from April 2008, October 2008, 2009 and 2010.

Invertebrate Group	Treatment	Bonferroni Ranking
Collembola (P<0.001)	GG	e
	GA	de
	FG	cde
	AG	bcde
	GF	abcde
	AA	abcd
	FA	abc
	AF	ab
	FF	a

The RMANOVA was applied to the October 2008, 2009 and 2010 mesofauna superfamilies, for time x treatment interactions, for both abundance and biomass. The only superfamily with a significant time x treatment interaction was the Entomobryomorpha, for both abundance and biomass results (Table 3.11). Again experimental plots converted to Grass had moved up the statistical ranking table, whilst those converted to Fallow had moved down, with Arable in the middle.

In the superfamilies with no significant time x treatment interaction, the re-analysis by ANOVA was applied using the mean log data of all three sampling years. Following this only the Symphypleona continued to show no significant differences in the average results for either abundance or biomass.

The Poduromorpha had the simplest Bonferroni ranking outcome (Table 3.12). The AG, FG and GG treatments had the highest abundances and biomasses. These were significantly different (P=0.002 abundance and P=0.003 biomass) from the FF treatment, with the lowest abundance. The remaining treatments showed no significant differences between the top and bottom abundance rankings.

Table 3.11 The RMANOVA statistical ranking of the Entomobryomorpha for October 2008, 2009 and 2010.

	The RMANOVA rankings for each sampling date (largest abundance uppermost) Entomobryomorpha		
	October 2008	**October 2009**	**October 2010**
Abundance (P=0.009) Bonferroni Ranking	GG	GG	GG
	GA	GA	GA
	GF	AG	FG
	FA	AA	AG
		FG	GF
	FG = FF = AF	AF	AF
		GF	FA
		FA	AA
	AG = AA		
		FF	FF
Biomass (P=0.008) SNK ranking	GG	GG	GG
	GA	GA	GA
	GF	AG	AG
	FA	AA	FG
		FG	GF
	FF = FG = AF	AF	AF
		GF	FA
		FA	AA
	AA = AG		
		FF	FF

The three Acari superfamilies all showed significant differences between the treatments, thus statistical ranking was applied to determine the location of the differences. Within the Mesostigmata significant differences ($P<0.001$ both abundance and biomass) were recorded between the biomass and abundance (Table 3.12) of the GG and FF treatments. In addition, the FF, AA and AF treatments were significantly different from the abundance in the AG, GA and FG and biomass in the GA and AG treatments. Within the intermediate treatments there was a degree of overlap and they were not significantly different from each other.

Table 3.12 The ANOVA and statistical ranking analysis for treatment interactions, for the Mesostigmata, Poduromorpha, Prostigmata and Oribatida calculated from the average (October 2008, 2009 and 2010) transformed data.

	Abundance		Biomass	
Invertebrate Group	**Treatment**	**Bonferroni Ranking**	**Treatment**	**SNK Ranking**
Mesostigmata (P<0.001, both)	GG	D	GG	D
	AG	CD	GA	CD
	GA		AG	
	FG		GF	BCD
	GF	BCD	FG	
	FA	ABCD	FA	ABCD
	AA	ABC	AA	ABC
	AF	AB	AF	AB
	FF	A	FF	A
Poduromorpha (P=0.002 abundance; P=0.003 biomass)	AG	B	AG	B
	FG		FG	
	GG		GG	
	GA	AB	GA	AB
	AA		AA	
	GF		GF	
	FA		FA	
	AF		AF	
	FF	A	FF	A
Prostigmata (P=0.003 abundance; P=0.004 biomass)	FG	B	GG	A
	GG	AB	FG	
	AG		AG	
	GA		GA	
	FA		FA	
	GF		GF	
	AA		AA	
	FF		FF	
	AF	A	AF	
Oribatida (P<0.001 both)	AG	C	GG	C
	GG		AG	
	GA	BC	GA	BC
	AA	ABC	AA	
	GF		GF	ABC
	AF		AF	
	FG		FG	
	FA	AB	FA	AB
	FF	A	FF	A

Within the Prostigmata (Table 3.12) the only significantly different (P=0.003) abundances were found within treatments FG (highest) and AF (lowest). The biomass was also significantly different by ANOVA (P=0.004). The Bonferroni ranking was unable to differentiate between the treatments; however, the order was similar to the abundance, apart from the two largest populations (FG and GG) which were reversed. The Oribatida (Table 3.12) had a larger number of significantly different statistical rankings for both abundance and biomass. The abundances within the AG, GG and GA treatments were all significantly different from the FF treatment, the AG and GG treatment abundances were also different from the FA treatment. However, the AA, GF, AF and FG treatment were all consistent with treatments that had no significant differences from the high and low abundance treatments. Within the biomass measurements the GG, AG, GA and AA were all significantly larger than the FA and FF treatments Oribatida biomasses. With the GF, AF and FG producing a central overlapping group.

Due to the statistical difficulties caused by a generally increasing population, the control treatments were important to determine if population changes within treatments were caused by management change or were simply a reflection of the increasing population. Therefore, in addition to the statistical analysis of the abundance and biomass results, the use of percentage difference graphs (on the abundance results) compensated for the general population increase and highlighted any management induced population change within the results. The maintained treatment plots, FF, AA and GG, were the control plots, allowing any additional contributing factors, such as climate, temperature and soil moisture, which may have affected the mesofaunal populations, to be accounted for and the effect of management changes to be displayed.

The conversion of the Fallow to Arable management produced the FA treatment (Figure 3.14). The October 2008 sampling was immediately post-conversion, and the percentage

difference from the control treatment was almost 0% in every superfamily. Therefore, the control and experimental plots were equilibrated before the investigation commenced.

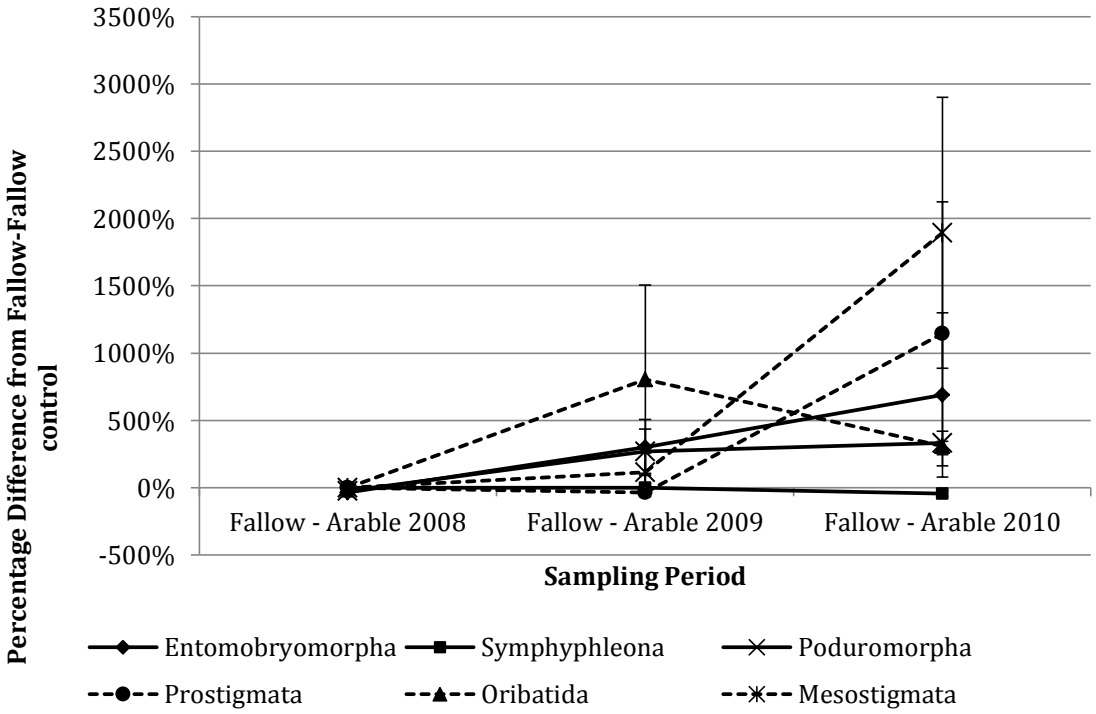


Figure 3.14 The percentage difference (± standard error as error bars) of the Fallow-Arable treatment from the Fallow-Fallow control (2008, 2009 and 2010).

Within the Collembola, the Entomobryomorpha and Poduromorpha had definite population increases in comparison to the FF control. The Entomobryomorpha increased from a negative difference, of -33% in 2008, to a positive difference in 2010 of 689%. The Poduromorpha showed a smaller increase, from -22% in 2008 to 333% in 2010. Both of these increases were sustained gradually over the two year period. However, the Symphypleona decrease in relation to the FF control, from 0% in 2008 to -42% in 2010.

Within the Acari superfamilies the differences between the FF control and the FA treatment were more varied. The Prostigmata showed a negative difference of -33%, between the FF control and the AF treatment in 2009, however, this was reversed in 2010

with a substantial increase to 1144%. The Oribatida showed a marked increase in 2009 with a population size 805% higher than the FF control. This, however, reduced to a 308% difference in 2010. The Mesostigmata increased the percentage difference slightly in 2009 to 117%; however, there was a huge increase the following year to 1894%.

The FG treatment also displays very little percentage difference in population abundances between the experimental treatment and the FF control in 2008 (Figure 3.15). The treatment areas were therefore starting from the same baseline populations. Both the Acari and Collembola mesofaunal orders show substantial changes to the population percentage difference over the two year treatment period.

When examined in more detail the Collembola superfamilies; Entomobryomorpha (4004%) and Poduromorpha (6497%) show huge differences from the control two years post-conversion. These were gradual increases, both having small increases in the first year, followed by a much larger increase in the final year. The Symphypleona showed no increase in the difference from the control in the first year, and a smaller one of 167% in the second year.

The largest difference from the FF control within the FG treatment was provided by the Mesostigmata, with an 8883% difference in the final year. The Prostigmata also had a substantial difference of 2263% in the final year, following a slight slump in the 2009 samples. The Oribatida population started at a lower level than the FF control, with the largest difference for this superfamily being the 2009 sampling, decreasing during the 2010 sampling period.

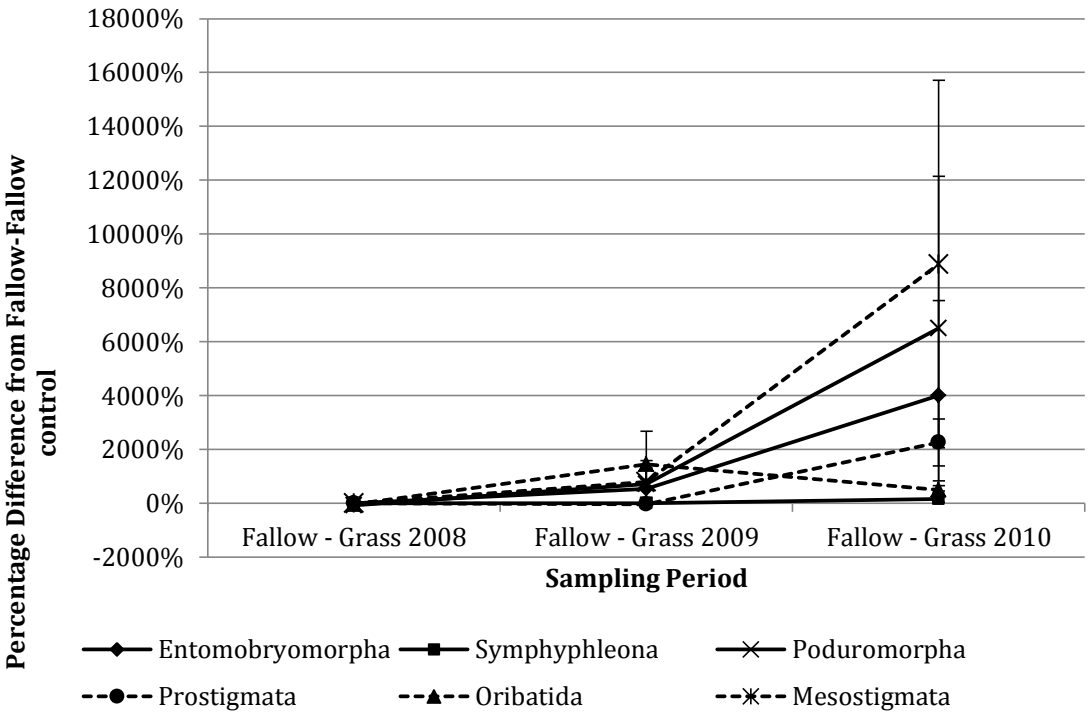


Figure 3.15 The percentage difference (± standard error as error bars) of the Fallow-Grass from the Fallow-Fallow control (2008, 2009 and 2010).

Within the Grass-Arable management treatment (Figure 3.16) it can be seen that the Entomobryomorpha (4435%), Prostigmata (757%) and Symphypleona (467%) had larger populations than the GG control. Immediately prior to sampling the plot had been ploughed and seeded for the new arable crop. The remaining three superfamilies only had a small difference whether positive or negative. In the years following conversion the difference between the control and the experimental treatment were positive, in favour of the experimental treatment. Following the conversion process, the largest difference between the GG control and GA treatment in 2009, was shown in the Symphypleona (1150%); this peaked during this sampling period and the difference was much reduced in 2010 (297%). This pattern, of the peak in the 2009 sampling results, was also repeated in the Entomobryomorpha, Prostigmata, Oribatida and Mesostigmata, although at a smaller percentage difference. Only the Poduromorpha showed a year on year increase in the

percentage difference from the control treatment, however, the differences here were small.

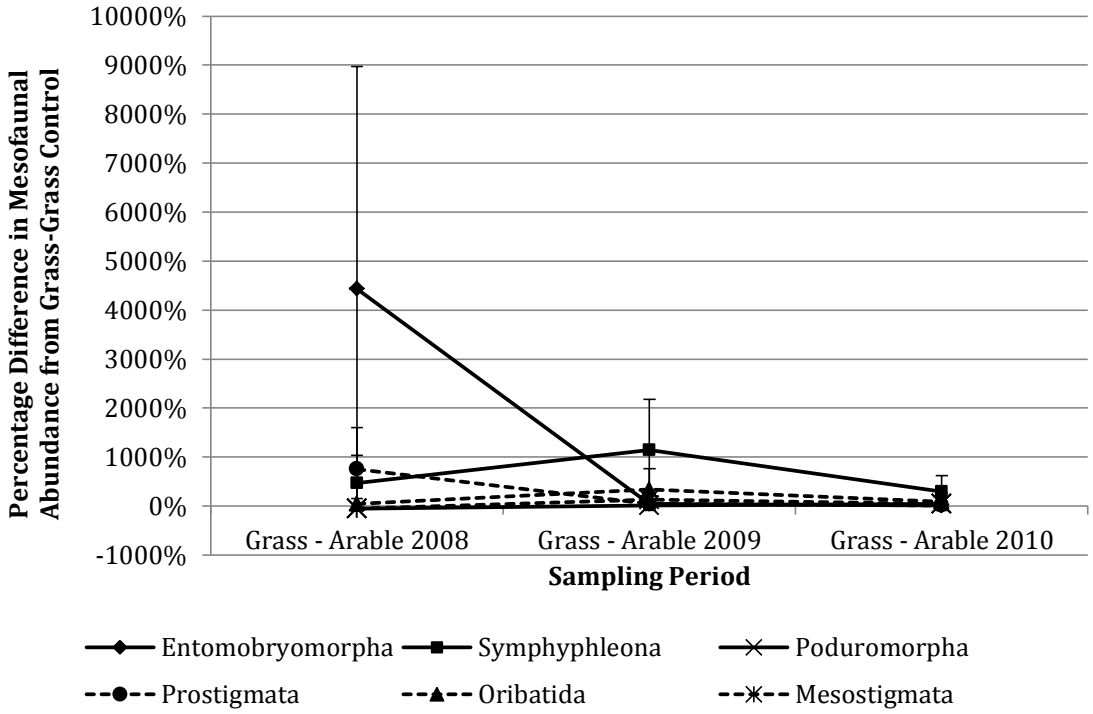


Figure 3.16 The percentage difference (± standard error as error bars) of the Grass-Arable from the Grass-Grass control (2008, 2009 and 2010).

Within the GF treatment the percentage differences in 2008 were relatively small and negative, the Symphypleona (-86%) has the largest difference and Prostigmata (-26%) the smallest (Figure 3.17). Over the two year experimental period the percentage difference of the GF treatment from the GG control did not vary greatly. In 2009, all of the superfamilies once again showed a negative percentage difference from the GG control, with a maximum difference of -99% (Symphypleona) and minimum difference of -66% (Poduromorpha). In 2010, however, the Symphypleona had a positive difference of 33%; all of the remaining superfamilies remained negatively different between -28% and -80%.

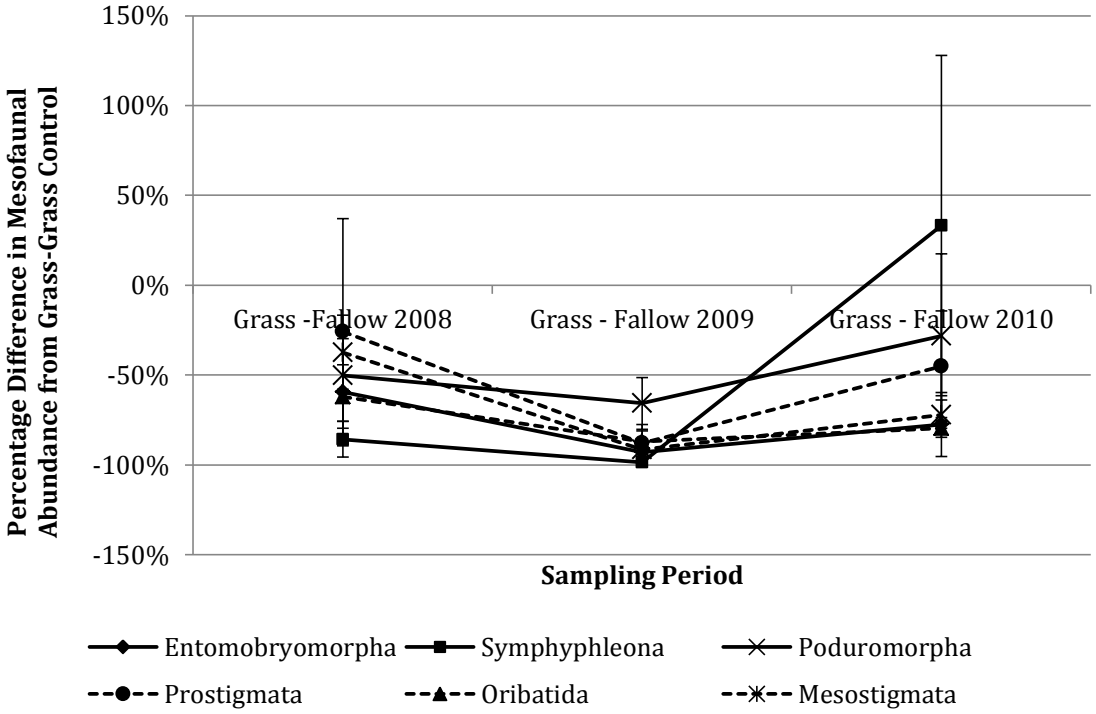


Figure 3.17 The percentage difference (± standard error as error bars) of the Grass-Fallow from the Grass-Grass control (2008, 2009 and 2010).

The Arable-Grass treatment plots showed little percentage difference in the mesofauna recovered immediately following the implementation of the conversion process in 2008 (Figure 3.18). The largest percentage difference was seen in the AG treatment for the Oribatida, with many of the superfamilies recording a 0% change from the control, the starting populations of the treatments were therefore similar. In the two years following conversion the AG treatment shows a great deal of change from the AA control. Following the first year, the 2009 results show that there had been a positive percentage increase for all of the superfamilies (apart from the Symphypleona which remained unchanged). The Prostigmata recorded a 32% difference in the population sizes and the maximum was recorded by the Oribatida at 353%, although all three Acari superfamilies were within the 0% to 300% range. The Collembola superfamilies showed the least amount of change with a range of 0% to 38%. The following year, 2010, the Symphypleona decreased in population size, indicated by a negative percentage difference of -58%. However, all of the

other superfamilies showed a positive percentage difference from the AA control and therefore an increase in the population size. The percentage changes here were large, with a minimum of 463% from the Oribatida and a maximum of 2027% for the Prostigmata.

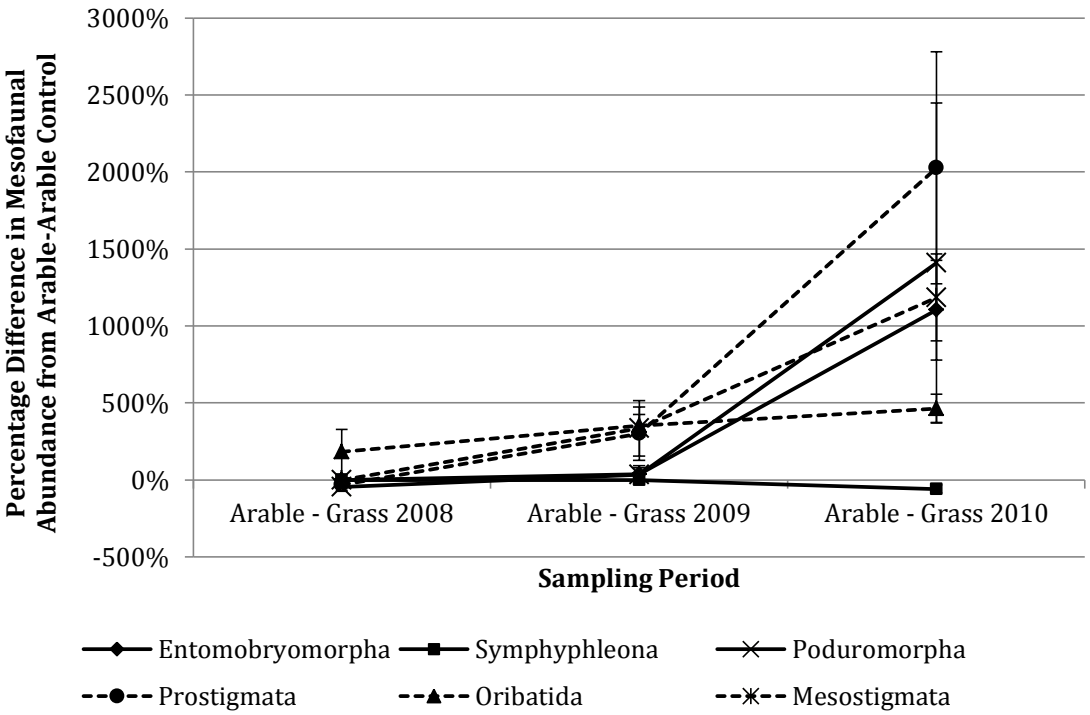


Figure 3.18 The percentage difference (± standard error as error bars) of the Arable-Grass from the Arable-Arable control (2008, 2009 and 2010).

The AF treatment shows very little difference from the AA control treatment immediately following conversion, however, the first year following conversion the treatment showed a negative percentage difference from the AA control (Figure 3.19). The minimum difference was 0% for the Symphypleona, and the maximum was -89% for the Prostigmata. Following a further years' management the only negative different percentages were for the Oribatida and Mesostigmata. The remaining superfamilies had all registered a positive percentage difference from the AA control, indicating a population increase. The Entomobryomorpha and Prostigmata had shown the largest percentage difference at 258% and 303%, respectively.

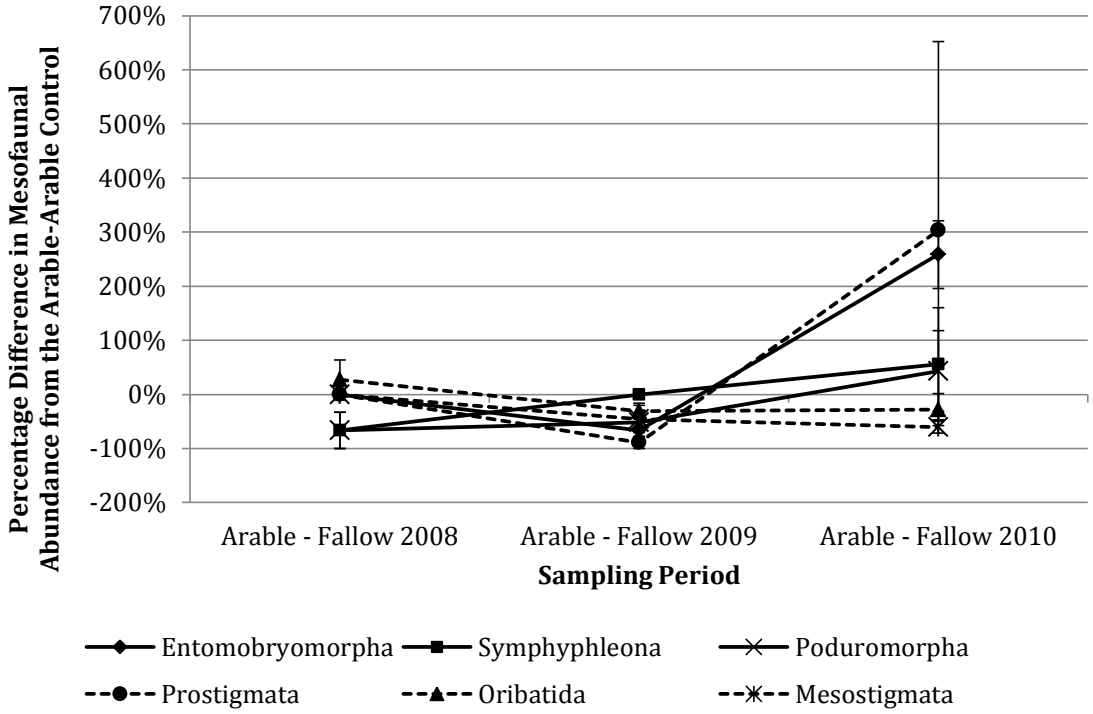


Figure 3.19 The percentage difference (± standard error as error bars) of the Arable-Fallow from the Arable-Arable control (2008, 2009 and 2010).

3.4 Discussion

3.4.1 General Discussion

The preliminary data determined differences in the Acari and Collembolan populations of the three management regimes; Grass management had the largest populations with the least in the Fallow. Hirsch *et al*. (2009) hypothesised that these differences were due to the level of carbon availability within the soil and its subsequent flow through microbial and invertebrate populations. Baseline sampling, on the pre-conversion experimental plots, revealed differences in the preliminary and baseline abundance results. For example, the Arable total invertebrate abundance was lower in 2008 than 2006. However, in addition to the two year interlude, seasonal variation between the sampling times existed, therefore natural temporal fluctuations may account for the differences. Temporal fluctuations have been observed within soil invertebrate populations (Koehler, 2000); Weigmann (2006) found the largest numbers of Oribatida in the early summer months. Whilst Alvarez, Frampton and Goulson (1997) concluded that Collembolan density was based on season and species life history strategy. Furthermore, the sampling regime utilised for preliminary sampling was altered before baseline data collection, making comparison difficult due to the lack of consistency. Poor methodology standardisation is a common problem with long-term data sets, which may impact on the results produced, distorting conclusions (Magurran *et al*., 2010).

Within the baseline data (Spring 2008), the Arable and Grass management have similar Acari dominated community compositions. However, the Grass recorded larger abundances. This community composition is consistent with other grassland management investigations (Curry, 1994; Koehler, 2000). Whereas, the Fallow management produced lower abundances, with Collembola dominated soil communities. Kampichler *et al*. (1999) found that Collembola migrated more easily than Acari possibly allowing them to disperse into the Fallow treatments more quickly following disturbance.

However, other studies reflect the reduced Acari abundance levels within the Arable and Fallow managements suggesting that disturbance had a more detrimental effect on this order than the Collembola resulting in a shift in community dominance. Bedano, Cantú and Doucet (2006) reported that increased levels of cultivation reduced Acari abundance. Likewise, Hulsmann and Wolters (1998), Neave and Fox (1998) and Fox *et al*. (1999) determined that Acari abundance reduced as a result of upper horizon destruction, which led to exposure to desiccation and disruption of access to food sources. Studies by Coleman and Crossley (1996) and Wardle *et al*. (1995) particularly singled out tillage as a cause of disruption and population reduction. Equally, Cao *et al*. (2011) determined a reduced Acari abundance and diversity where either organic or chemical fertiliser had been continuously applied.

It has been postulated that grass vegetation produces a microclimate within the soil that has a positive influence for mesofaunal communities (Koehler and Born, 1989). To complement this some species of Acari have been shown to have microhabitat preferences (Ruf and Beck, 2005), where these are present they cause an increase in both population size and diversity. Hirsch *et al*. (2009) suggested that the vegetation removal, such as crop harvest or bare fallow management, reduces soil carbon stores, decreasing the microbial population size and consequently resulting in a diminished invertebrate population. Wardle (2002) stated that the quality of resources found within soil affect the mesofaunal community composition, different vegetation inputs, such as grass or inorganic fertiliser will have different carbon and nitrogen input qualities. As separate plant species have different chemical compositions, there will be variations in the decomposition process. This in turn will have an indirect effect on the decomposer organisms present (Coleman, Reid and Cole, 1983; Bradford *et al*., 2002; Wardle, 2002; van der Heijden, Bardgett and van Straalen, 2008).

Alternatively it has been suggested that highly heterogeneous habitats, such as that provided by grassland, produce multiple niches, supporting increased species diversity (Diekötter *et al*., 2010; Roger-Estrade *et al*., 2010). Collembola have previously been shown to have larger species diversity in heterogeneous habitats (Nielson *et al*. 2010), with different species occupying distinct microhabitats (Klironomos and Kendrick, 1996).

Following conversion in 2008, the three control treatments (Grass, Fallow and Arable) provide the natural background variation of a typical mesofaunal population abundance and community composition for that management regime. During the experimental period the mesofaunal abundance significantly increased year-on-year within all control treatments. This increase was not a result of management change and was therefore due to favourable conditions within the control plots. Mesofauna are affected by environmental factors and have been shown to be strongly controlled by soil temperature and moisture (Laakso, Salminen and Setälä, 1995; Huhta and Hänninen, 2001). Both factors were beyond investigator control. However, knowledge of this natural population increase affected the experimental treatment analysis, as it needed to be ruled out as a cause of any recorded population change. The overall population increase was not observed in all superfamilies, in 2010 the Poduromorpha abundance decreased in both Grass and Arable controls. Poduromorpha are vulnerable to predators as many species have lost the ability to jump (Hopkin, 1997), abundance increases in predatory Acari and other Collembolan predators, such as Beetles (Hopkin, 1997) may have reduced the Poduromorpha population through predation. This would be confirmed by a reduction in predator abundance following a lag phase between excess prey and prey deficiency with the relationship conforming to a discrete generations predator-prey curve. However, unlike the purely mathematical predator-prey curve, real life systems have many different factors affecting population oscillations, for example the presence of other predators and

prey species (Krebs, 1978). Due to the investigation duration a possible predator-prey link had not been successfully determined.

Throughout the investigation the Grass control community composition is relatively stable; it has the largest invertebrate density and diversity of all controls and is mostly Acari dominated. The use of cover crops, such as grass swards, have been documented to build soil organic matter, increase aeration, nutrient supply and water holding capacity (Snapp *et al*., 2005), as such the abiotic conditions provided by Grassland provides a stable, undisturbed favourable ecosystem which facilitates the development of a diverse community (Cole, Buckland and Bardgett, 2008). Although, changes to the mesofaunal communities present should be expected, it is known that mature populations change even when they appear to be in a steady state, changes to general population turnover have been noted as an important factor often missed when abundance models are produced (Magurran *et al*., 2010).

Perturbation disturbance resulted in reduced population sizes and unstable community dynamics in several different investigations (Neave and Fox, 1998; Fox *et al*., 1999; Sánchez-Moreno *et al*., 2009). The process of ploughing turns the uppermost layers of the soil profile; this relocates invertebrates living in the uppermost layers to a deeper position. This process has previously been shown to negatively affect the invertebrate population within the soil (Kautz, López-Fando and Ellmer, 2006; Hussein *et al*., 2007; Cole, Buckland and Bardgett, 2008). Physically the process of ploughing can kill or injure organisms; additionally, relocation can lead to increased exposure to predators. Temporal changes to the ploughing regime can also affect species dominance, population sizes and biodiversity (Altieri, 1999). This is demonstrated within the Arable control where community composition and abundance differs between sampling periods, regularly switching in dominance from Acari to Collembola. These differences in the community

composition are large and indicated that the effect of ploughing is unpredictable. The Fallow control was also highly disturbed and displayed a variable community; however, unlike the Arable control residual organic matter and fertiliser are not ploughed back into the soil profile. This reduces nutrient availability within the soil. The low nutrient supply would suggest a fungal based food web; however repeated ploughing would damage mycorrhizae promoting a bacterial based food web (Kardol and Wardle, 2010). This is borne out by an earlier full PLFA analysis of the microbial population determined low densities of bacteria in these soils (Hirsch *et al*., 2009). Additionally, the mesofaunal population was primarily Collembola dominated for the whole investigation period. This group are known to feed on fungi (Scheu, 2002; Berg *et al.*, 2004), but are believed to be unspecific feeders, adapting to the food source available (Ruess *et al.*, 2007; Ladygina, Caruso and Hedlund, 2008; Murray *et al*., 2009; Crotty, 2011). Therefore, the high Collembola proportion suggests that they are possibly utilising coloniser mycorrhizae as a food source. Gange and Brown (1992) observed Collembola swarms in early succession and attributed the large abundances to grazing on mycorrhizae. Furthermore, Collembola are thought to be more mobile than Acari due to their body design (Coleman and Crossley, 2003) and have been demonstrated to disperse at scales greater than 10cm per day (Nielson *et al*., 2010), therefore providing them with opportunity to repopulate the experimental plots between sampling times. Dunger (1989) suggests that Collembola are involved in primary succession, and therefore, are more adaptable to continuous disruption and stressful environments. Whereas, the Acari have been determined to be the order most affected by disruptive management regimes (Ferraro and Ghersa, 2007).

Experimental plot conversion to the new management regime involved ploughing all but the grass control, including plots previously unploughed. As populations prior to ploughing reflected the ecological outcomes of the previous management regime, invertebrate populations recorded immediately following ploughing reflected its direct

impact. In all plots, the post-ploughing abundances were lower than the baseline populations. These differences where significant, for the Acari abundance, between the three original Grass treatments (Grass control, Grass-Arable and Grass-Fallow), and the Fallow control. The Collembola show no significant differences between treatments (including the Grass control). Furthermore, the population abundances within the Grass-Fallow and Grass-Arable treatments from the Grass control are not significantly different, suggesting that ploughing had no impact on the mesofaunal populations. However, both reversion treatments had large populations prior to the conversion process; therefore a proportion of these populations would have remained physically undamaged by ploughing and persisted within the soil. This finding suggests that single disturbances or reduced tillage regimes may have a reduced effect on population dynamics compared with repeated ploughing events. Within the microbial community, it has been shown that the sustained loss of soil organic matter through repeated ploughing is a greater disruption than the physical disturbance of ploughing itself (Simmons and Coleman, 2008). Moreover, ploughing relocated the plot's vegetation to a position lower in the soil profile. This makes the organic matter more available for decomposition; stimulating the microbial community. Increased microbial populations provide greater basal resources within the food web, instigating population increases at higher trophic levels (Roger-Estrade *et al*., 2010). At a higher taxonomic resolution the community composition of the ploughed treatments are very variable, even where the original management regime was identical and the starting populations were similar. This suggests that although general population density within ploughed treatments was not significantly affected, the community structure had been disturbed. This disturbance manifested differently for each experimental plot suggesting that predicting the effects of disturbances is difficult; Kladivko (2001) also found the responses of soil fauna to disturbance highly variable. This reflects trends reported in other long term data sets where temporal turnover was found to respond differently to the same disturbance (Svensson, Lindegarth and Pavia, 2009).

Carpenter and Brock (2006) argued that this variability indicates change from one state to the next.

Changes to the original fallow management regime included the introduction of seeds and fertiliser to produce Arable and Grass management strategies. Post-conversion, both treatments recorded invertebrate abundance increases over the investigation period, which was most pronounced in the Grass treatment. As with the Fallow control, both reversion management regimes remain Collembola dominated until the end of the reported investigatory period. As a typical Grass management regime usually produces an Acari dominated community (Koehler, 2000), the Fallow-Grass experimental plot has yet to reach its climax community. It can be argued that two years is not long enough to complete the soil ecosystem transformation, Woodcock *et al*. (2012) suggested that this could take up to seven years. Berch, Battigelli and Hope (2007) found that disturbances to the Acari and Collembola populations persisted for five years following site preparation. The conversion of Fallow to Arable management added plant and fertiliser inputs to the soil system. Unlike the Grass management the process of crop harvest and ploughing remove carbon from the soil and cause further soil profile disturbance, and these perturbations keep any invertebrate abundance increase at a reduced level. Over the investigation period the community composition moved towards that of the Arable control treatment.

The conversion of Grass to Fallow or Arable management involved vegetation removal and ploughing, post-conversion the invertebrate abundance immediately reduced within both treatments. However, within the experimental plots converted to Fallow invertebrate populations continued to reduce over the full experimental period. Additionally, the community composition altered to match the Fallow control. The ecosystem was regularly disturbed and lacked carbon inputs into the soil. This reduced carbon availability,

decreased its uptake into the soil food web, causing an invertebrate population crash (Wardle *et al.*, 1999). Conversely, the conversion of Grass to Arable management showed an initial population reduction followed by an abundance increase in comparison to the Grass control over the subsequent two years. This sustained increase was unexpected, although Koehler (2000) also showed that re-cultivation can lead to an increase in mesofaunal population. It has been hypothesised that ploughing incorporates residual organic matter from the vegetation into the soil, where it becomes available for assimilation into the food web, temporally increasing resource availability. This assimilation would have been completed within the detritivore population, including the Oribatida. Following the biological uptake of excess carbon into the food web, carbon stores would have depleted with the Arable crop removal each year, reducing inputs into the food web and therefore leading to a reduced populations. Although populations remained high in 2010, the food web had switched from an Acari dominated food web, typical of grassland to the more generalist Collembolan dominated food web. The reduction in the Acari population, particular the predatory Mesostigmata, is supported by work by Sánchez-Moreno *et al*. (2009). Within the study, Acari from the predator and omnivorous functional groups were affected by disruptive management strategies, including ploughing, applied to agricultural land.

The conversion of the Arable to Grass management left the plots undisturbed for two full years following seeding. This lack of disturbance and cessation in organic matter removal led to a more stable habitat, with increased nutrient availability for the invertebrate food web (Simmons and Coleman, 2008). This led to an increase in the mesofaunal abundance and alteration of the community composition from Collembolan to Acari dominance in line with the Grass control. Conversion of Arable to Fallow management reduced the population sizes and the diversity of the treatments; this is consistent with the removal of carbon inputs and the increase in ploughing disturbance.

3.4.2 Ecological Data Set Collection and Statistical Analysis

In addition to the ecological aspects of this study, the methodology used to collect, identify and analyse the data caused many points for discussion. Firstly, Tullgren Funnel extraction does not recover all invertebrates within the soil and misses full life stages of many of the invertebrates of interest (Edwards and Fletcher, 1971; Edwards, 1991). One method of reducing these biases is to combine extraction techniques, for example hand sorting and Tullgren Funnel extraction. However, due to the nature of the Highfield site, further destructive sampling, to allow the completion of additional methodologies was not permitted.

Secondly, the resolution of mesofaunal taxonomic identification proved to be a balancing act. Many studies identify the mesofauna solely to Collembola and Acari (André, Ducarme and Lebrun, 2002). However, within these orders there are many superfamilies and species, each with its own life history (Hopkin 1997; Krantz and Walter, 2009). Therefore, identification solely to order would have overlooked the 2010 Poduromorpha population decrease identified within the Collembola. However, identification to species level requires a highly specialised skill set that necessitates years to learn and apply reliably (André *et al*., 2001). Within this investigation, the number of soil samples and individual mesofaunal specimens to identify made this level of resolution prohibitive. A study by St John, Wall and Hunt (2006) in Kansas, USA produced 150 different species of Acari, with over 3000 specimens from a grassland ecosystem; Wu et al. (2009) estimated that this would have taken six person years to completely identify. However, without this information it is impossible to determine whether one species or several species of Poduromorpha were missing from the 2010 sampling. Identification to species may have provided a more definitive hypothesis for the superfamilies abundance reduction.

Thirdly, the statistical analysis applied provides limitations. Within each data set transformations have been applied to the raw data, this had the purpose of normalising it

before comparison. However, a different transformation was applied to different data sets. In each case, a set series of deductions were completed before deciding on the transformation applied, for example; the data was square-rooted (√) initially and then log scaled and then $LOG_{10}(n+1)$ until a transformation that allowed the data to normalise was determined. Following transformation the statistical analysis was completed. It has been argued that raw data should be used for ecological studies (O'Hara and Kotze, 2010), as the application of different transformation distorts the conclusions that are obtained from the results. However, many statisticians, including those connected with this experimental work, still believe that transformation is the best method to analyse the data effectively, whilst others argue that several different techniques need to be employed to analyse such data (Perry *et al*., 2002).

3.4.4 Future Work

Continuation of the Highfield Reversion Project would give a long-term picture of changes to population densities and diversity caused by altering management regime (Wardle *et al*., 1999). Previous studies have shown that the effects of management can persist for longer than two years; Bezemer *et al*. (2010) determined that sowing mix still impacted soil communities seven years after germination. To accompany the mesofaunal biomass data, the other invertebrates should be analysed for biomass differences. However, time was a limiting factor within this thesis. The addition of macrofauna biomass and any subsequent sampling data would give the opportunity to determine long-term changes to the whole soil food web and any alterations to the ecosystem functions and services that are completed by the soil biota. As this project is multi-disciplinary other forms of information have been collected simultaneously. The other measurements collected are:

- *PLFAs*: for determination of the bacterial community composition and abundance
- *Microbial respiration and microbial biomass carbon* - (discontinued 2009)
- *Soil properties*, including:

  - Moisture Content
  - Organic matter content
  - Water holding capacity
  - Bulk Density
- *Plant yield and seed bank studies* - (discontinued in 2009)

Currently, the collection of PLFA and soil properties data continues in line with the invertebrate data collection. All data must be looked at collectively to determine the whole system effects of management regime change. Therefore, changing the project's methodology including duration or sampling frequency could potentially cause flaws in the data and should be considered only if they improve the investigation. This is a common problem that affects many long-term datasets (Magurran *et al*., 2010). For example, increasing sampling frequency to an autumn and spring collection would allow identification of seasonal fluctuations in the data. This would also increase the biodiversity that is detected and therefore increase the possibility of diversity change identification (White, 2007).

In addition, further studies to determine the mode of invertebrate community movement should be undertaken. Whether invertebrates move over or through the soil or travel longer distances in an airborne manner are all important as these abilities may be affected by management practices or determine possible habitat restoration strategies.

3.5 Conclusions

The Grass, Arable and Fallow management regimes have revealed that differing mesofaunal community compositions and abundances are maintained with different management techniques. In addition, it was also determined that changing management techniques can rapidly affect both the mesofaunal community composition and

abundance. This, therefore, has important implications for land management practices, it suggests that under the correct management regime mesofaunal abundance and communities can be re-established to add the ecosystem functions that they perform.

Chapter Four

Highfield Transect Experiment

4.1 Introduction

In the UK, the Countryside Stewardship Scheme, and more recently the Environmental Stewardship Scheme, have promoted the retention or implementation of grass strips surrounding land used for arable production (Defra, 2005). The primary aim is to act as a pool for biodiversity, allowing organisms to move into the more intensively managed land. There are studies documenting the diversity and abundance of above ground fauna (Tscharntke, Batáry and Dormann, 2011) and the macrofauna (Smith, Potts and Eggleton, 2008a) within set aside or marginal strips. However, investigations into mesofaunal movement from these areas into other unpopulated habitats are rare.

An investigation into invertebrate populations, under different agricultural management practices, determined considerable differences in the mesofaunal communities (Chapter Three). The number of Collembola within the grassland management, were recorded as 10 times higher than the fallow and arable management populations. Similar figures were recorded for Acari and other invertebrates, recovered from the same locations. Therefore, grassland is a large potential source of mesofaunal populations. The Geescroft mine site has areas of fallow and newly converted fallow to grassland management, this is surrounded by a grassland perimeter. This unique experimental design enables investigation into the rate and method of invertebrate encroachment from the surrounding invertebrate populations into the newly converted grassland plots.

4.2 Materials and Method

4.2.1 Site Description

The Geescroft mine site (Figure 4.1) is part of the Highfield Reversion Project within Rothamsted Research, Harpenden (Section 2A.1.4). It is a strip of land, maintained as bare fallow, by tillage and vegetation removal for 30 years, a full history of management is available from Rothamsted Research.

Figure 4.1 The Geescroft site during initial experimental set-up showing the experimental plot and adjacent grassland border-hedgerow relationship.

4.2.2 Treatments and Plot layout

In April 2008, four plots (10m x 7m) were created (Section 2A.1.5), baseline invertebrate sampling was completed and results are available in Chapter Three. In October 2008, experimental management regimes were implemented. Two were converted to grassland

management, FG 2 and FG 6; two remained as bare fallow, FF 3 and FF 4 (Figure 4.2). During the conversion process some difficulties were encountered due to the harsh habitat within the bare fallow soil, details of applications to increase plant growth can be found in 2A.1.4.

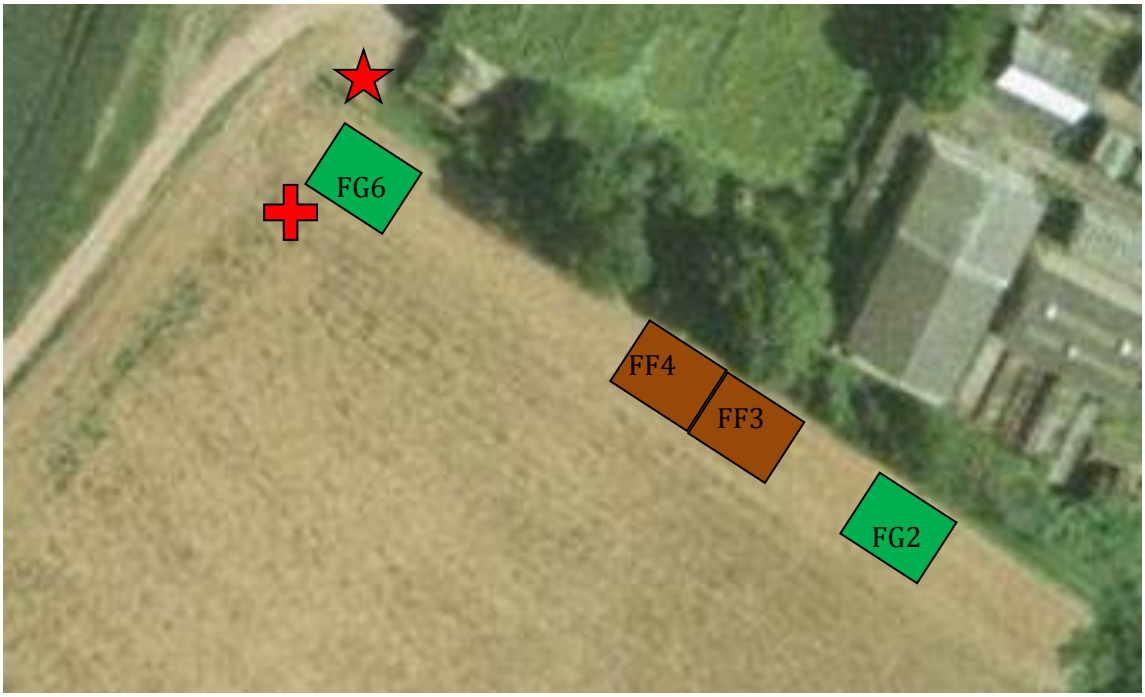


Figure 4.2 An aerial photograph of the Geescroft Mine Site showing the post-conversion treatment (grassland (FG2 and FG6), fallow FF3, FF4) - red star denotes transect start, red cross the end point.

Between plots FG2, FF3 and FF4, FG6, a minimum 10m buffer area (Figure 4.2) was ensured to allow machinery to turn without affecting adjoining treatments. Plots FF3 and FF4 were both retained as maintained fallow, and were immediately adjoining each other for ease of management. A 1m buffer area was maintained as bare fallow on the longitudinal sides of the plots. This created a barrier to the adjacent land uses.

4.2.3 Sampling Protocol

Sampling was completed on the Fallow-Fallow (FF3 and FF4) and experimental Fallow-Grass plots (FG2 and FG6). Samples were collected simultaneously with the Highfield Reversion Project in October 2008, May 2009 and October 2010. At each sampling event, 8cm ø x 10cm soil cores were collected, using the method in Section 2A.2.

For each reversion plot - FF3, FF4, FG2 and FG6 - a total of three sampling transects were devised. Each transect had five sampling points, at each a soil core was collected for analysis. Each transect started on the North-East of the experimental plots (Figure 4.2), within the permanently maintained grassland border. Transects travelled through the reversion plot, in a South-West direction, into the adjoining arable field (Figure 4.2). Transect point one (Grass Border), is 1m inside the permanent grassland border. This was an undisturbed grassland population. All 12 samples collected from this area, within each sampling period, were averaged to represent an undisturbed grassland population. The second transect point (Buffer Zone One), was approximately 1.5m along the transect from the Grass Border, was within the buffer area surrounding the reversion plot. This area was regularly ploughed and any vegetation removed. The sampling point was either adjacent to a maintained fallow or grass reversion plot, and referred to as; Buffer Zone One–Fallow (six samples/time period) or Buffer Zone One–Grass (six samples/time period) respectively. The third transect point; (Reversion Plot: either Grass or Fallow, each with six samples/time period) was within the reversion plot. The collection position was identical to the sample retrieved for the Highfield Reversion Project, and in effect the same sample was used (Section 3.2.2). By using the same soil sample the disturbance to the reversion plot was reduced. Additionally, this samples position determined the transect trajectory across the reversion plot, as the preceding and subsequent samples lined up with this central sampling point. The fourth transect sample (Buffer Zone Two), was collected from the second buffer strip, once again this was either adjacent to the grass or

fallow reversion plots. Where required these are referred to as Buffer Zone Two–Grass (six samples/time period) and Buffer Zone Two–Fallow (six samples/time period) respectively. The fifth transect sample (Arable Border) was 1m into the adjacent arable field from the buffer area edge (Figure 4.3).

4.2.4 Sample Handling Protocol

Once each of the samples had been collected, they were placed into a labelled sunbag (Section 2A.2) and then stored at 8°C until Tullgren Funnel extraction into saturated salt solution (Section 2A.3). Invertebrate identification was then completed as per Section 2A.4.

The number of invertebrates recovered were calculated as abundance (number m^{-2}), and biomass (µg m^{-2}). The Acari was subdivided into the; Mesostigmata, Prostigmata and Oribatida, the Collembola into the; Poduromorpha, Symphypleona and Entomobryomorpha, and the other invertebrates (no other sub division was completed). In order to determine invertebrate population changes within the reversion plots, mean abundances, percentage difference (from the Grass and Arable Border controls) and mesofaunal biomass food webs, for each sampling period was completed. Due to the continued buffer zone ploughing, and the resulting low abundance figures recorded, food webs were not produced for Buffer Zones One or Two.

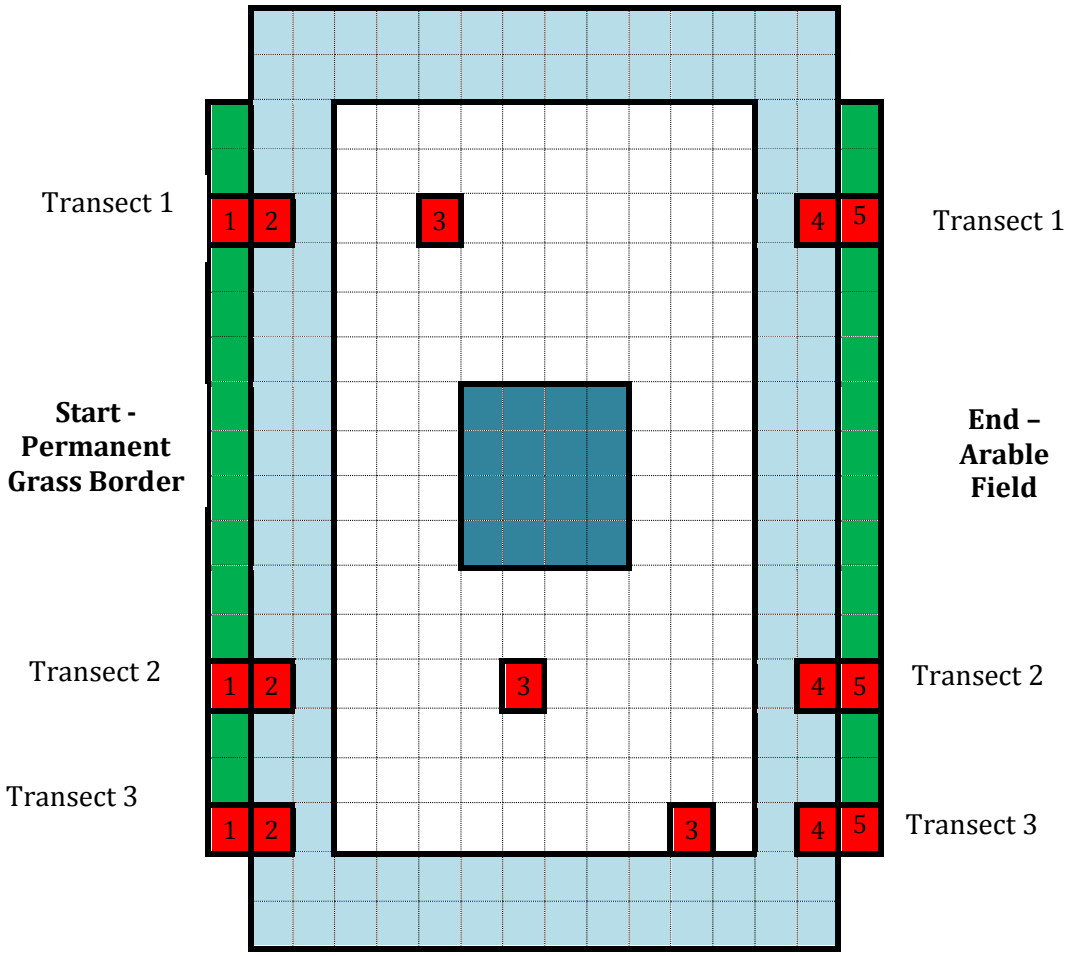


Figure 4.3 An individual reversion plot plan. Each sampling transect (red squares) line up with the predetermined location of the central transect sampling point (3). All transects start on the same side and traverse the treatment plot in the same direction.

4.2.5 Statistical Analysis

Statistical analysis was completed using several methodologies. Before analysis abundance data was square root (√) transformed and biomass data was LOG_{10} transformed to normalise it. Following transformation, repeated measures ANOVA (RMANOVA) was applied, to determine differences between the following variables, for each transect point; time, treatment, time x treatment interactions.

Differences between the invertebrate populations recovered from the transect points during one sampling period was determined using a split-plot ANOVA (SP-ANOVA), for the following variables; treatment, transect point, treatment-transect point

In order to compare all transect points, with the control invertebrate populations (the Grass and Arable Borders, used as separate reference points) two-sided Dunnett's tests, with 95% confidence, were used to determine significant differences between either of the controls in separate analyses.

4.3 Results

4.3.1 Invertebrate Abundance

4.3.1.1 Introduction

Prior to initial sampling (October 2008) the reversion plots and buffer zone areas were ploughed, culti-pressed and seeded, as required, in preparation for the commencement of the experimental treatments. The 2008 results provide a baseline for the initial invertebrate abundances and biomass food webs for each transect point. The second sampling (spring 2009) occurred 12 days following rotovation of the Fallow Reversion plot and buffer zones. Two further rotovations occurred prior to the October 2010 sampling, in August 2009 and June 2010.

4.3.1.2 Inter-Sampling Period Comparison

Differences between the abundance results, of each transect point, for all of the sampling periods, were determined by RMANOVA, with square root transformed data. The mean total abundance of the Acari, Collembola and other invertebrates are shown in Appendix VII. Significant population differences are apparent in all three invertebrate groups. RMANOVA determined that the mean Acari abundance had significantly increased throughout the investigation, for all experimental transect points (Buffer Zone One – $P=0.004$, Reversion plots - $P<0.001$, Buffer Zone Two – $P=0.003$) (Table 4.1; Appendix VII). The other invertebrates showed a similar trend, however, the increases between the initial 2008 sampling, and the larger abundances in 2009 and 2010, are only significant in the Reversion plot ($P=0.003$) and Buffer Zone Two ($P<0.001$). The mean Collembola abundance increased significantly, within the Reversion and Buffer Zone Two (both - $P<0.001$) transect points, during the experiment. Buffer Zone One, conversely, had a significantly higher Collembolan abundance in 2009 ($P<0.001$) than 2008 and 2010 (Appendix VII; Table 4.1).

Table 4.1 Probability values: RMANOVA for mean total invertebrate groups (√ transformed data) for the following variables: time, treatment and treatment x time (NS = no significant differences)

Variable	Invertebrate Group	Significant Difference probability (RMANOVA) for mean abundance (√ transformed) of Transect Points		
		Buffer Zone One	Reversion Plot	Buffer Zone Two
Time (2008, 2009, 2010)	Collembola	P<0.001	P<0.001	P<0.001
	Acari	P=0.004	P<0.001	P=0.003
	Other Invertebrates	NS	P=0.003	P<0.001
Treatment (Grass, Fallow)	Collembola	NS	P<0.001	NS
	Acari	NS	P=0.037	NS
	Other Invertebrates	NS	P=0.017	NS
Treatment x Time Interaction (2008xGrass, 2009xGrass, 2010xGrass, 2008xFallow, 2009xFallow, 2010xFallow)	Collembola	NS	P<0.001	NS
	Acari	NS	P=0.011	NS
	Other Invertebrates	NS	P<0.001	NS

The mean Acari, Collembola and other invertebrate abundances, of individual transect points, for the Grass or Fallow treatment, and any interactions between time x treatment, were only significantly different in the Reversion plots (Table 4.1). Significant differences, in treatment mean abundances, were apparent in the Grass Reversion plot, which had larger abundances than the equivalent Fallow plot (Acari (P=0.037), Collembola (P<0.001) and other invertebrates (P=0.017); Appendix VII). For all three invertebrate groups, the 2010 x Grass treatment interaction had significantly larger abundances than the other treatments (Table 4.1; Appendix VII; Figure 4.4). The other invertebrate percentage difference, from both the Grass and Arable Borders in 2010, display a larger population

size in the Grass Reversion plot than the Arable Border. Additionally, the differences between the Grass Border and the Grass Reversion plot were smaller than the Fallow reversion plot (Figure 4.4).

The line graphs presented in; Figure 4.4 and Appendices VIII and IX, show the percentage difference, of the invertebrate populations, from either the Grass (GB) or Arable Border (AB) separately, then for each different transect point; Buffer Zone One – subdivided into Grass (GBZ1) or Fallow transect (FBZ1), Grass (GRP) or Fallow Reversion plot (FRP), Buffer Zone Two – subdivided into Grass (GBZ2) or Fallow transect (FBZ2). This was then repeated for each sampling period, for each mesofaunal superfamily and other invertebrates.

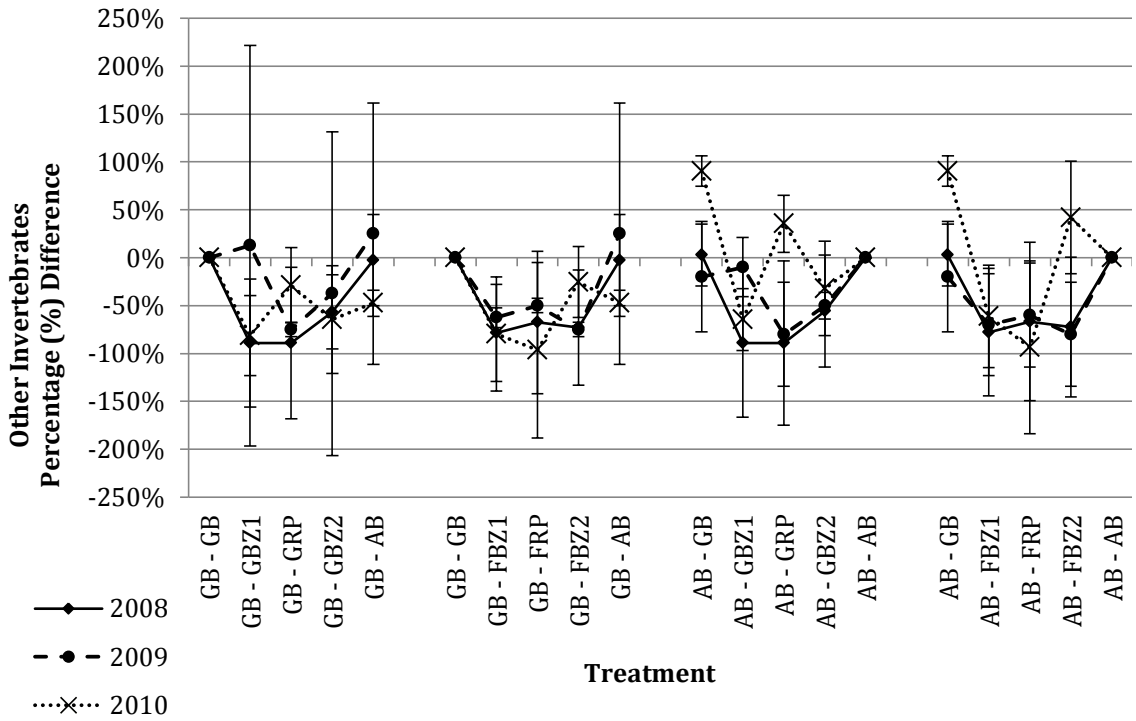


Figure 4.4 The percentage difference (± Standard Error as error bars) - from the Grass (GB) or Arable Border (AB) controls– for FG (G) and FF (F) treatments - for each transect point – Buffer Zones One (BZ1) and Two (BZ2) and Reversion plot (RP), for other invertebrate abundance throughout the experiment.

Upon division into the mesofaunal superfamilies, further differences in the populations were determined. Appendices X and XI show the mean abundances (m^{-2}), of the mesofaunal superfamilies, for each transect point (Grass Border, Buffer Zone One, Reversion plot, Buffer Zone Two, Arable Border), within each time period (2008, 2009, 2010), for the two reversion treatments (Fallow, Grass) (full figures; Appendix XII). As the graphs are on the same scale, it can be seen that, the populations generally increase in size over the investigative time period.

The Acari superfamilies; the Mesostigmata, Prostigmata and Oribatida, all display changes to the mean population abundances over time, (Table 4.2; Appendices X, XI and XII). The Mesostigmata show significant population increases in Buffer Zone One ($P=0.006$), Reversion plots ($P=0.002$) and Buffer Zone Two ($P=0.004$), throughout the experimental period. The Oribatida mean abundance significantly increases throughout the investigation, in both Reversion plots ($P<0.001$) and Buffer Zone Two ($P=0.029$). Prostigmata abundance also significantly increases, between the sampling periods, for Buffer Zone One ($P=0.014$), the Reversion plots ($P<0.001$) and Buffer Zone Two ($P=0.021$).

Comparisons between the Grass and Fallow treatments determined that the mean Mesostigmata ($P=0.005$) and Prostigmata ($P=0.001$) populations, of the Grass Reversion plot, was significantly larger than the Fallow Reversion plot (Table 4.2). Additionally, the population within Buffer Zone One-Grass, is significantly larger than Buffer Zone One-Fallow ($P=0.025$) (Table 4.2). Time x treatment interactions were only observed within the Reversion plots, where the largest Mesostigmata ($P=0.002$) and Prostigmata ($P=0.007$) abundances, were recorded in the 2010 x Grass treatment (Table 4.2; Appendix XII).

The percentage difference graphs, Appendix VIII, show that the 2010 Mesostigmata populations within the Grass Reversion plot are 530% larger than the Arable Border, but

are still -44% lower than the Grass Border. This trend is repeated, in the Oribatida (199%, AB and -48%, GB), however, the Prostigmata have a larger population size in the Grass Reversion plot than both the Arable and Grass Borders (247%, AB and 28%, GB). Additionally, the Grass Border has consistently larger abundances than the Arable Border for all three Acari superfamilies.

Table 4.2 Probability valves RMANOVA (√ transformed abundance) for each transect point, for changes to superfamilies for the following variables: time, treatment, treatment x time - NS = no significant differences.

Variable	Mesofaunal Superfamily	Significant Difference probability (RMANOVA) for abundance of Transect Points		
		Buffer Zone One	Reversion Plot	Buffer Zone Two
Time (2008, 2009, 2010)	Entomobryomorpha	NS	P=0.009	P=0.010
	Poduromorpha	P<0.001	P=0.005	P<0.001
	Symphypleona	NS	P=0.011	P=0.012
	Mesostigmata	P=0.006	P=0.002	P=0.004
	Prostigmata	P=0.014	P<0.001	P=0.021
	Oribatida	NS	P<0.001	P=0.029
Treatment (Grass, Fallow)	Entomobryomorpha	NS	P=0.019	NS
	Poduromorpha	NS	P=0.036	NS
	Symphypleona	NS	NS	NS
	Mesostigmata	P=0.025	P=0.005	NS
	Prostigmata	NS	P=0.001	NS
	Oribatida	NS	NS	NS
Treatment x Time (2008xGrass, 2009xGrass, 2010xGrass, 2008xFallow, 2009xFallow, 2010xFallow)	Entomobryomorpha	NS	P=0.015	NS
	Poduromorpha	NS	P=0.005	P=0.013
	Symphypleona	NS	NS	NS
	Mesostigmata	NS	P=0.002	NS
	Prostigmata	NS	P=0.007	NS
	Oribatida	NS	NS	NS

Similarly, the Collembolan superfamilies recorded abundance increases over the investigative period (Appendices; X, XI and XII). The Reversion plots had the most consistent differences (Table 4.2), with increases in the; Entomobryomorpha (P=0.009), Poduromorpha (P=0.005) and Symphypleona (P=0.011) mean abundances, over the experimental period (Appendices; X, XI and XII). Buffer Zone Two displays an abundance

peak in 2009, with the lowest abundance for that transect point in 2008, for all superfamilies (Entomobryomorpha, P=0.010; Poduromorpha, P<0.001; Symphypleona, P=0.012). Within Buffer Zone One, only the Poduromorpha abundance increase over the experimental period is significant (P<0.001).

All significant differences between the mean abundances, of the Grass and Fallow treatments, were within the Reversion plots (Table 4.2). Both the Entomobryomorpha (P=0.019) and Poduromorpha (P=0.036) had larger abundance results within the Grass Reversion plot than the Fallow.

Interactions between time x treatment, revealed further significant differences between the Collembolan superfamilies (Table 4.2). Within the Reversion plot, the Entomobryomorpha (P=0.015) and Poduromorpha (P=0.005) showed a significantly larger population in the 2010 x Grass treatment, although not significant the trend was repeated in the Symphypleona. Within Buffer Zone Two, the Poduromorpha had significantly (P=0.013) larger abundances in the 2010 x Fallow treatment, than the other treatment x time interactions.

The percentage difference, of the Entomobryomorpha and Poduromorpha, show similar trends throughout the investigation period (Appendix IX). Both have larger population sizes, in the Grass Reversion plot, than the Grass and Arable Borders by 2010 (Entomobryomorpha, 149% GB and 1010% AB; Poduromorpha, 190% GB and 1029% AB). The Symphypleona, however, displayed an alternative trend within the percentage difference results. The population within the Arable Border and Buffer Zone Two-Grass were larger (1000% and 500% respectively) than the Grass Border in 2008. However, by 2010, the Grass Border population was 372% larger than the Arable Border. Within the

experiment transect points; the only larger population size was within the Grass Reversion plot, in comparison to the Arable Border in 2010 (33%).

4.3.1.3 Intra-transect Abundance Analysis

Comparison of the mean invertebrate abundance of transect points, within the same sampling period, was completed using SP-ANOVA and Dunnett testing.

In 2008 ($P=0.030$) and 2009 ($P<0.001$), the mean Acari abundances of the Grass Border were significantly larger than all the other transect points. Conversely, in 2010, the Grass Reversion plot had the largest Acari abundance ($P<0.001$), though not significantly different from the Grass Border, whereas all remaining transect points had lower abundances (Appendix VII). Within the Acari superfamilies, there were significantly larger Mesostigmata abundances, in the Grass Border in 2008 (95%) and 2009 ($P<0.001$), than the other transect points. However, in 2010 ($P=0.047$), the Grass Reversion plot Mesostigmata abundance was also significantly larger than the other treatments, including the Arable Border (Appendices; X, XI and XIII).

In 2008, the Grass Border had a larger (Dunnett, 95%) Oribatida abundance than all other transect points for that sampling period (Appendices X, XI and XIII). Simultaneously, both Reversion plots had a significantly lower abundance than the Arable Border. In 2009, the Grass Border, Buffer Zone One–Grass, Buffer Zone Two–Grass and the Arable Border were not significantly different from each other, for Oribatida abundance; however, the remaining sampling points had a significantly lower abundance. In 2010, the Grass Border and Grass Reversion plot had Oribatida abundances significantly ($P=0.013$) higher than the Arable Border and the other transect points.

The 2008 Prostigmata abundance, was significantly larger in the Grass Border than all other transect points (P=0.042). In 2009, the Grass Border abundance was significantly larger than the other transect points. However, Buffer Zone One–Grass and Fallow, the Grass Reversion plot and Buffer Zone Two–Grass all have an intermediate abundance, with the lowest Prostigmata abundances in the remaining transect points (P=0.036) (Appendices; X, XI and XIII). In 2010, the Grass Border, Buffer Zone One–Grass and Fallow, Grass Reversion plot, Buffer Zone Two–Fallow and Arable border all have a statistically similar Prostigmata abundance size (Dunnett, 95%).

In 2008 and 2009, the Collembola had a significantly larger abundance (P<0.001) within the Grass Border than the other transect points. However, in 2010, there was no difference between the Grass Reversion and the Grass Border, although these were significantly larger than the remaining transect points (P<0.001) (Appendix VII).

Within the Collembolan superfamilies, the Entomobryomorpha showed larger (P<0.001) population sizes in the Grass Border in 2008 and 2009. However, in 2010, the Grass Reversion plot had the largest Entomobryomorpha abundance, in comparison with the other transect points (Appendices; X, XI and XIII). The Poduromorpha abundances, between transect points, were only significant different (P<0.001) in 2010, by SP-ANOVA. Here, the largest abundance was found in the Grass Reversion plot, however, intermediate abundances were recorded in the Grass Border and Buffer Zone Two–Fallow transect points. Conversely, Dunnett analysis determined that the Grass Border Poduromorpha abundance, was also significantly larger (95%) than all other transect points, in 2008 and 2009. In 2008, the Symphypleona showed a different pattern to the other Collembolan superfamilies, with significantly larger Arable Border abundances than the other transect points (P=0.035). In 2009, however, the Grass Border had the largest Symphypleona population size, followed by the Arable Border and then all other transect points

(P=0.036). Within the 2010 results, the Grass Border again has a significantly larger Symphypleona abundance than all other transect points (P=0.019). Additionally, the Grass Reversion plot, Buffer Zone Two–Fallow and the Arable Border all had similar abundances, these were larger than the remaining transect points (P=0.019) (Appendices X, XI and XIII).

The other invertebrates only had intra-transect significant differences in 2010, where similar populations were recorded in the Grass and Arable Borders, Grass Reversion plot, and both Buffer Zone Two treatments. These were significantly larger than the remaining treatments (P=0.003) (Figure 4.4; Appendix VII).

4.3.2 Mesofaunal Biomass

4.3.2.1 Mesofaunal Biomass Food Webs

Mesofaunal biomass food webs have been produced to diagrammatically display both the mesofaunal biomass and the food web linkages. These demonstrate, the currently known feeding interactions, between the different trophic levels, and mesofaunal superfamilies. Mesofaunal food web diagrams for the control plots: Grass and Arable Borders, along with the reversion plots - the Grass and Fallow, for each sampling period can be seen in Figures 4.5 (Grass border); 4.6 (Grass reversion); 4.7 (Fallow reversion) and 4.8 (Arable border) (mean biomass figures; Appendix XV).

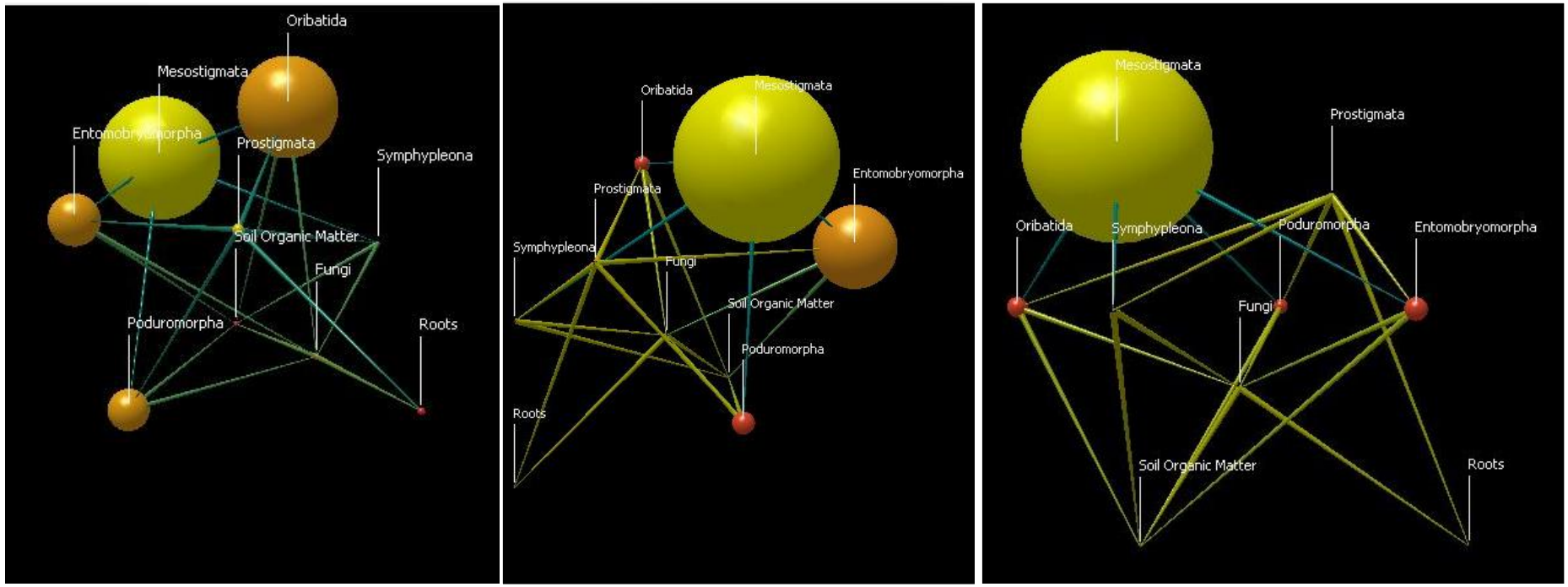


Figure 4.5 The mean mesofaunal biomass food webs (µg m^{-2}) for the Grass Border; 2008 (far left), 2009 (middle), 2010 (right).

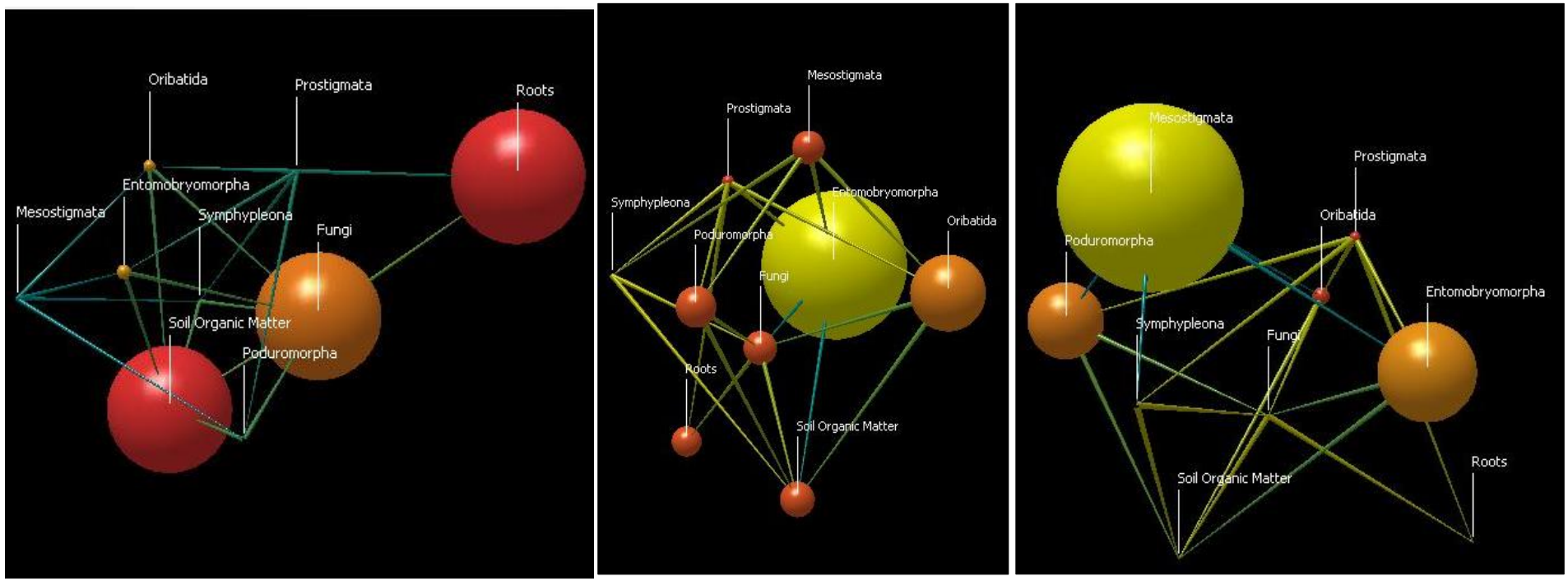


Figure 4.6 The mean mesofaunal biomass food webs (µg m^{-2}) for the Grass Reversion Plot; 2008 (left), 2009 (middle), 2010 (right).

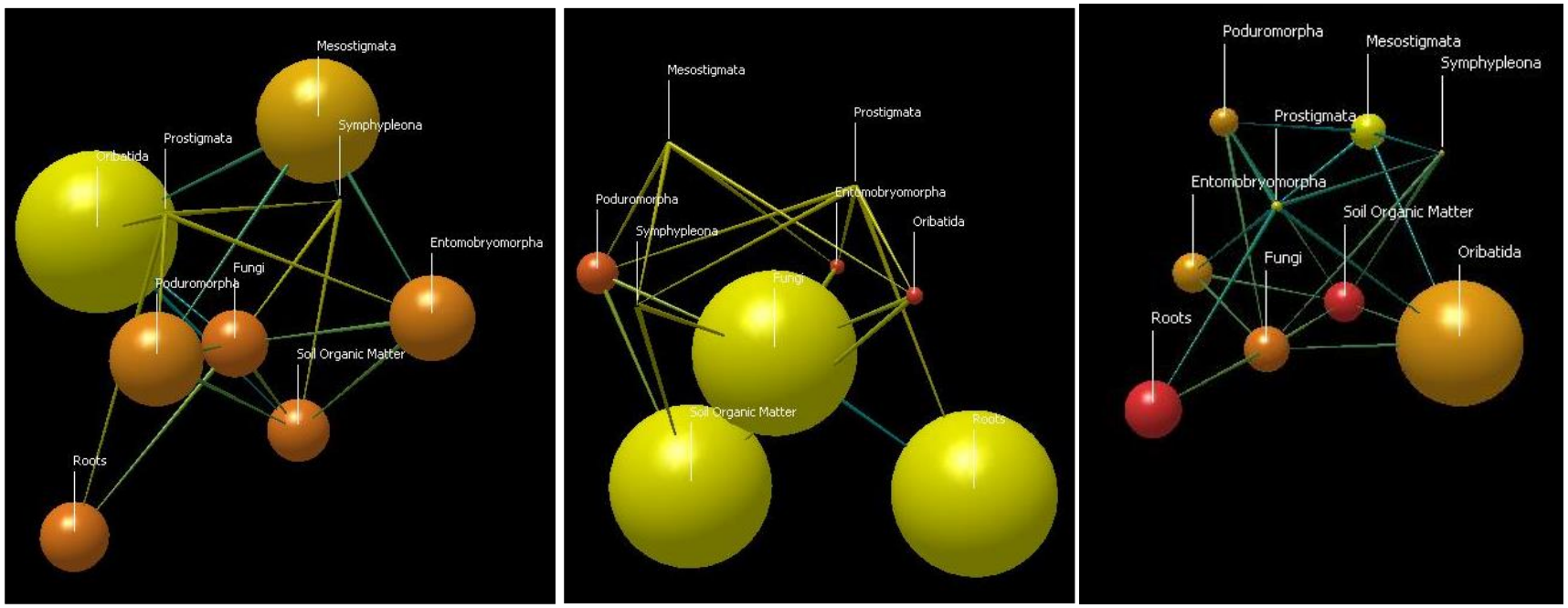


Figure 4.7 The mean mesofaunal biomass food webs (µg m^{-2}) for the Fallow Reversion Plot; 2008 (left), 2009 (middle), 2010 (right).

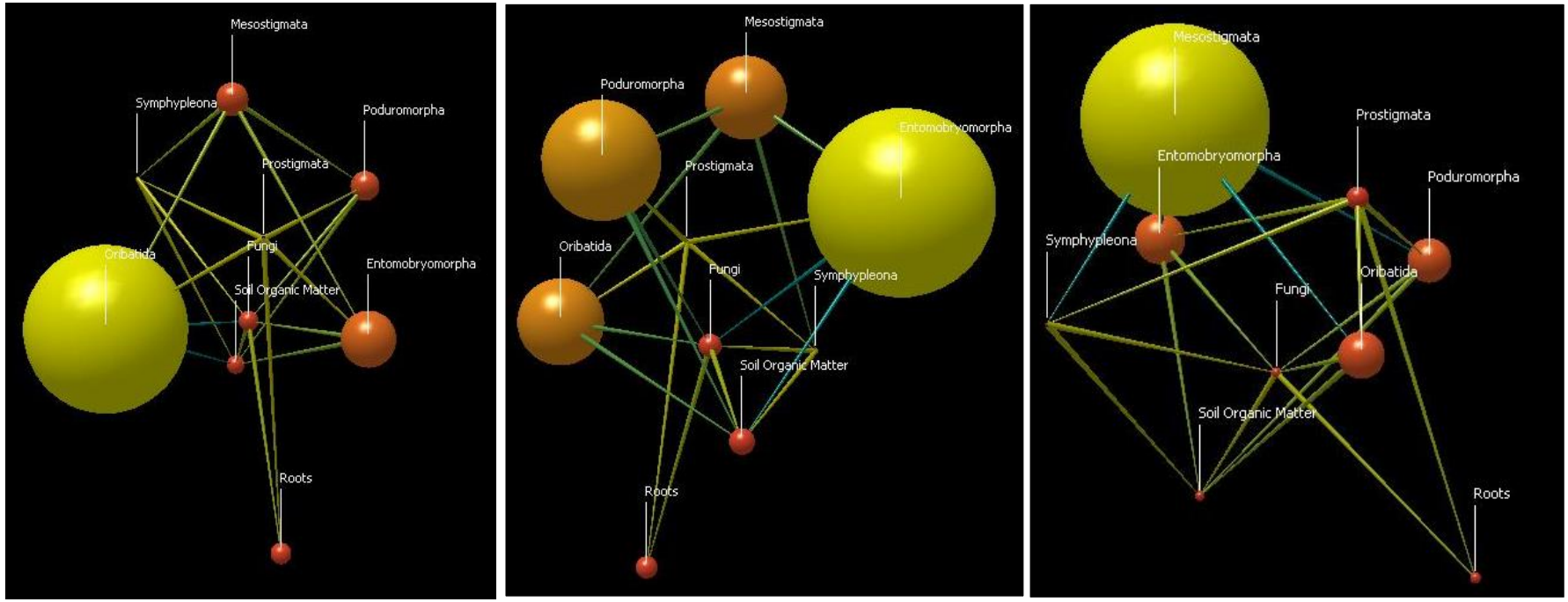


Figure 4.8 **The mean mesofaunal biomass food webs (µg m^{-2}) for the Arable Border; 2008 (left), 2009 (middle), 2010 (right).**

The food web diagrams show that the Grass Border generally has the largest biomass, and that this is dominated by Mesostigmata, in all sampling periods. The Grass Reversion plots began with small biomasses, which were Poduromorpha and Oribatida dominated in 2008. As the experimental time passes, the total mesofaunal biomass, of the Grass Reversion plot, increases and becomes Mesostigmata dominated by 2010. Within the Fallow Reversion plot, the mesofaunal biomass increases during the experimental time, by 2010, this food web was Oribatida dominated. Within the Arable Border the biomass food web was initially dominated by the Oribatida, however, by 2010, this becomes Mesostigmata dominated, although there is little change to the biomass size.

4.3.2.2 Inter-Sampling Period Comparison

The mesofaunal biomasses showed fewer significant differences, between sampling times, than the abundance data (inter-sampling period analysis is completed by RMANOVA). Within the mean Acari there was a general increase, year-on-year, in population biomass, this was significant in the Reversion plot ($P<0.001$) and Buffer Zone Two ($P=0.019$) (Appendix XIV). However, there were no significant differences in the mean Acari biomass, between the Grass and Fallow transect treatments, nor was there a time x treatment interaction within any of the possible variables.

The Collembola had significant biomass increases, year-on-year, in the experimental transect points (Buffer Zone One, Reversion plot - $P<0.001$, Buffer Zone Two – $P=0.032$), with the highest in 2010. There were time x treatment interactions in Buffer Zone One, where the biomasses recorded in 2008 x Grass and 2008 x Fallow were significantly lower than the remaining possible time x treatment interactions ($P=0.033$). The Reversion plot had a significantly larger Collembola biomass in 2010 x Grass ($P=0.003$) than the other time x treatment options for that transect point (Appendix XIV).

Within the superfamilies, the biomass increases with time are significant (RMANOVA) for the Symphypleona (P=0.007) within the Grass Border, and the Poduromorpha (P=0.009) and Prostigmata (P=0.005), within the Arable Border (Appendix XV). Comparison of the Grass and Fallow treatments determined significantly larger Entomobryomorpha (P=0.002) and Mesostigmata (P=0.018) within the Grass Reversion plot, than the Fallow. Within the reversion transect points there were time x treatment interactions, with significantly larger biomasses in the 2010 x Grass Reversion plot for the following superfamilies: Prostigmata (P=0.050), Entomobryomorpha (P=0.053), Poduromorpha (P=0.004) and Mesostigmata (P=0.005).

4.3.2.3 Intra-transect Biomass Analysis

SP-ANOVA analysis of the Acari biomass, determined that there were significant differences between the transect points in 2008 (P=0.006). The Grass and Arable Borders, Buffer Zone Two–Grass and Buffer Zones One and Two–Fallow, all have statistically similar Acari biomasses, these were larger than the Reversion plots. In 2009, all transect points had a significantly lower Acari biomass than the Grass Border. Moreover, Buffer Zone One–Fallow had the lowest biomass, which was statistically lower Acari biomass than the Arable Border (Dunnett 95%). In 2010, there were no significant differences revealed by SP-ANOVA. However, Dunnett analysis determined that the Grass Reversion plot had an Acari biomass higher than the Arable border, whilst Buffer Zone One–Fallow had a significantly lower biomass than the Grass Border; all other treatments had equivalent biomasses to the controls (Appendix XIV).

Upon sub-division into Acari superfamilies, SP-ANOVA analysis determined significantly larger Mesostigmata biomasses in the Grass Border than the Reversion plots in 2008 (P=0.009) and 2009 (P=0.002) (Appendix XVI). In 2010, Mesostigmata biomasses generally increased, on the 2009 figures, in many transect points, with only significantly

lower biomasses than the Grass Border recorded for Buffer Zone One–Fallow and the Fallow Reversion transect point (Dunnett, 95%).

The Oribatida, show no significant differences for any variable when analysed using SP-ANOVA. However, the Dunnett test revealed differences from the Grass and Arable Borders. Initially, significantly lower Oribatida biomasses were recorded within the Grass Reversion plot, Buffer Zone One–Grass and Fallow Reversion plot, than the Grass border (Dunnett 95%). By 2009, both Buffer Zone One-Fallow and Grass have a significantly (Dunnett 95%) lower Oribatida biomass than the Grass Border, although all other transect points were not significantly different. Following a further year of conversion, only Buffer Zone One-Fallow continues to have a significantly (Dunnett 95%) lower Oribatida biomass than the Grass Border (Appendix XVI).

The 2008 Prostigmata biomass, of all transect points, are significantly lower than the Grass Border (SP-ANOVA, P=0.004; Dunnett 95%) (Appendix XVI). During the 2009 sampling, there were no significant differences determined by SP-ANOVA. However, Dunnett comparison, between the transect points and the Grass Border determined that the Fallow Reversion plot and Buffer Zone Two-Fallow had significantly lower values (Dunnett 95%). The following year, 2010, there were no transect points with a significantly different Prostigmata biomass from either the Grass or Arable Border (Appendix XVI).

The 2008 Collembolan biomass, is significantly lower (SP-ANOVA, P=0.008) in Buffer Zone One–Fallow and the Grass Reversion plot than the other transect points (Appendix XIV). There were no other statistically different Collembolan biomasses, as determined by SP-ANOVA, within the intra-transect analysis. However, Dunnett testing determined that the Grass Reversion plot had a significantly lower Collembolan biomass than the Grass Border

in 2009. In 2010, the Grass Reversion plot had a biomass significantly larger than the Arable Border (Appendix XIV).

The most noticeable trend within the Collembolan superfamilies was that the Symphypleona had no significant biomass differences between any transect points, for any sampling times (Appendix XVI). In 2008, the Entomobryomorpha biomass within the Reversion plots and Buffer Zone One were significantly lower (P=0.010) than the Grass and Arable Borders. Whereas, all other transect points were equivalent to the Grass and Arable controls. In 2009, both Buffer Zone Two and the Grass Reversion plot had similar biomasses to the Grass and Arable Borders. Whilst the Fallow Reversion plot had a significantly lower Entomobryomorpha biomass than controls (P=0.033). By 2010, biomasses had increased and only the Fallow Reversion plot and Buffer Zone One-Fallow remained significantly lower than the Grass Border (Dunnett 95%).

The Poduromorpha biomasses increase over the investigation time period. In 2008, significantly higher biomasses were recovered in the Grass Border (P=0.042) than the other transect points (Appendix XVI). By 2009, the Poduromorpha biomass the Fallow and Grass Reversion plots, was significantly (P=0.023) lower than the biomass of the Grass Border. However, there was also a large Poduromorpha biomass in Buffer Zone One-Fallow. In 2010, the Grass Reversion plot Poduromorpha biomasses recorded in 2010, all had an equivalent biomass and were not significantly different from the Grass or Arable controls.

4.4 Discussion

4.4.1 Invertebrate Populations

The Grass and Arable Border transect points (one and five) were control plots, these reflected the natural invertebrate population changes within undisturbed grassland and disturbed arable habitat, respectively. The Grass Border maintains the largest total invertebrate abundance and biomass levels throughout the experiment; this population significantly increases over the experimental period. This suggests that the overall environmental conditions favourably change throughout the experiment, resulting in widespread increased invertebrate population sizes. Invertebrate populations are known to fluctuate both temporally and spatially, in response to changes in environmental conditions (Hopkin, 1997; Koehler, 2000; Bardgett and Wardle, 2010; Waagner, Bayley and Holmstrup, 2011). This general invertebrate increase within the Grass Border reached its maximum in 2010, although this pattern is reflected in the majority of superfamilies, the Entomobryomorpha were most prevalent in 2009. These differing superfamily responses may be attributed to seasonal differences in sampling times. Both spring (2009) and autumn (2008 and 2010) samplings were completed. Therefore, snap-shot sampling during different environmental conditions, may have recorded abundances during different life cycle stages, resulting in differences in the mesofaunal population abundance patterns. Sabais, Scheu and Eisenhauer (2011) recorded larger Collembola abundances in autumn than in spring, in a temperate grassland, demonstrating that such differences can occur as part of a temporal fluctuation. This highlights an issue with snap-shot sampling methodologies. Cyclic population changes can occur between sampling times or seasonal differences mask the change pattern, thus causing the true population dynamics to be overlooked (Beresford and Sutcliffe, 2009).

The Arable Border transect point, repeatedly has lower mesofaunal abundances than the Grass Border, additionally the population fluctuations throughout the investigation differ

between the two control management regimes. The arable land management required repeated ploughing during the experimental period. Repeated disturbances have been shown to affect the normal fluctuations of invertebrate life cycles and cause damage to the population sizes (Cole, Buckland and Bardgett, 2008). Soil invertebrate communities, in agricultural soils, have been described as being generally small species, with a high reproductive rate (Swift and Anderson, 1993). This is due to soil compaction causing a reduction in soil pore size, and therefore, species with larger body sizes are unable to move through the soil in search of food or to avoid stresses (Kampichler, 1999). Furthermore, the application of intensive management produces simple crop systems (Tscharntke *et al*., 2005) which induce a less diverse soil habitat, and therefore less opportunity for niche partitioning and high biodiversity (Birkhofer *et al*., 2011). These disturbances would also explain the low population sizes recovered from the Buffer Zone transect points, for all sampling times, for all superfamilies. Bare fallow has been used as a tool to reduce pests, including *Sminthurus viridis* an economically important pest in the southern hemisphere, as this removes the vegetation that the adults feed on (Walters, 1968; Greenslade and Ireson, 1986).

By 2010, the Grass Reversion plot contained larger populations than the Fallow Reversion plot. This suggests that the habitat, created by ploughing cessation and plant establishment promotion, was able to support larger mesofaunal population sizes than the plot which continued to be ploughed. Although this demonstrates an increase in the mesofaunal population, following the management change, the method of population increase is difficult to determine. One explanation is that organisms have travelled into the reversion plot from an external source; Berthet (1964) showed that Oribatida are able to move several cm every day. Whilst work by Nielson *et al*. (2010) determined that some Collembolan species are able to walk up to 10cm daily, and are known to be involved in primary succession (Dunger, 1989). Generally, Duelli and Obrist (2003) determined that

successful repopulation of an area, was higher in regions where a healthy source population existed in nearby habitats. But the importance of other traits within the species and the surrounding landscape was also found to be important (Tscharntke *et al*., 2005). However, many soil fauna groups have limited dispersal abilities, reducing the likelihood that the plot's increased biodiversity, was solely through translocation from surrounding areas (Wolters, 2001). A second explanation is that the population increases result from reproduction or eggs hatching within the soil (Hopkin, 1997; Krantz and Walter, 2009). However, as taxonomic identification was not completed past superfamily, it is impossible to determine the life history strategy of the organisms recovered, and therefore identify which of these mechanisms is most probable.

In 2010, larger Entomobryomorpha and Poduromorpha abundance and biomass were recovered in the Grass Reversion plot than the Grass Border. Whereas, when compared to the Arable Border all superfamily populations, were larger in the Grass Reversion plot. The Arable Border consistently had a lower invertebrate population than the Grass Border, suggesting that the developing Grass Reversion ecosystem was most similar to the Grass Border. This can be mostly clearly seen within the Dunnett analysis and percentage difference results. Although the biomass and abundance variations, for the total Acari and Collembola produce different statistical outcomes, by Dunnett analysis, both follow a similar pattern. With the general outcome that the Grass Reversion plots mesofaunal population was developing towards the Grass Border food web.

The shape of the other invertebrate percentage difference graphs, Figure 4.4, show that in 2008, all transects display a similar pattern, a "U" shape. Here, the smallest percentage difference is in the control borders - at the highest points of the "U" - and the buffer zones and reversion plots are within the dip, with negative percentage differences. In 2010, transects that pass over the Fallow Reversion plot, still display this pattern, however,

transects that pass over the Grass Reversion plot, now appear as a "W". Once again the Grass and Arable Borders make up the outside highest points, whilst the middle peak is the Grass Reversion plot; the buffer zones remain at the base of the troughs. This change shows that the other invertebrate populations, within the Grass Reversion plot have increased in the absence of ploughing, and are progressing to a population closer to the stable population within the Grass Border. Within this investigation, the other invertebrates were not identified to order; however, further analysis to determine the order or even species could clarify the process by which new habitats are invaded.

The level of taxonomic identification has been a source of contention within the literature for many years (André, Ducarme and Lebrun, 2002). There are pros and cons to the different resolution levels for identification, the higher the identification resolution, i.e. to species, is time consuming and requires a level of skill and training (André *et al*., 2001; Hamilton *et al*., 2009). However, the identification to a lower resolution level, such as order, can lead to the completion of a larger number of samples. The mesofaunal percentage difference graphs, Appendices VIII and IX, clearly show that determining organism identification, to superfamily, has revealed population differences that would otherwise not have been noted, if identification had only occurred to order. This is clearest in the superfamily Symphypleona, where the differences of this group, from the Arable and Grass Borders would have been masked, if the total Collembola figure had been used to calculate these results. Differences in the possible conclusions drawn, produced by a specific level of taxonomic resolution, have been noted elsewhere. Berg and Bengsston (2007) found that when whole functional groups are considered, there was little variation in the presence or abundance of these groups between treatments, however, at a species level there were large variations in the species present.

4.4.2 Methods of Data Analysis

Within this chapter, three different methods of manipulation were used to analyse the experimental data; the numerical abundances, biomass calculations and percentage difference from a control. Each of these different manipulations gave an alternative perspective on the populations present within the same samples. The numerical data, in the form of numbers m^{-2} (abundance m^{-2}), is used widely within the literature (Siira-Pietikäinen and Haimi, 2009; Sabais, Scheu and Eisenhauer, 2011). However, this does not take into account the size of the organisms relative to each other, and therefore, the volume of food consumption that is required by that organism or population. Biomass is often used to describe microbiological data, such as biomass carbon (Adl, Coleman and Read, 2006), where count data would be impossible. Within this work biomass provides an indication as to the movements of nutrients within the food web. The percentage difference indicates a direct change, from or towards the control population density. In this case, percentage change enables the determination as to whether the food web of the reverted management treatments, had begun to resemble the nearest population pools for each mesofaunal superfamily. At present there is no consensus within the literature of a reliable methodology to determine successful repopulation or restoration of an ecosystem (Bullock *et al*., 2011; Sodhi *et al*., 2011). Without such consensus, restoration efforts cannot be reliably assessed. Within this thesis, the different manipulation techniques have each provided an individual conclusion when used in isolation, however, the use of all three together, has allowed a more concise level of conclusion to be drawn.

4.4.3 Further Investigation

In order to further complement the data obtained, the continuation of data collection, for further sampling periods would be beneficial. This would include, at the minimum, another spring and autumn sampling point. This would allow identification of temporal population fluctuations. Furthermore, this would provide additional time, for differing

rates of population recovery, by different mesofaunal superfamilies, to occur (Lindberg and Bengtsson, 2005 and 2006; Malmström, Persson and Ahlström, 2008). To supplement this, investigation into the mode of transport; passive or active, above or below ground, would provide additional information, as to mesofaunal movement between populations or habitats. This would also confirm whether populations are numerically or functionally repopulating the regenerated soil. In order to complete this, additional sampling would be required along the transects, this would include: sticky traps (Lehmitz *et al*., 2011) placed at different heights, to collect airborne invertebrate movement, pitfall traps (Edwards, 1991) would determine soil surface movement, physical barriers to movement such as litter bags (Berg *et al*., 1998) may help to determine belowground movement.

4.5 Conclusions

The conversion of degraded bare fallow soil, back to a grassland pasture can be achieved, with the natural recolonisation of the habitat by invertebrates, including the mesofauna. In addition, this can be achieved, even where there is a break between the source population and the new habitat, in this case ploughed bare fallow. The food web that developed reflected the food web of the equivalent habitat, not the closest food web. The Grass Reversion plot came to resemble the Grass Border, not the Arable Border, whereas the Buffer Zones showed signs of organisms that could tolerate ploughing. Further work is required, to determine the mode of transport utilised by these organism, and the total time required to reach a stable community.

Chapter Five

Mesocosm Invertebrate Exclusion

5.1 Introduction

The Highfield Reversion and Transect experiments (Chapters Three and Four), determined that invertebrates move across areas of degraded or bare soil to occupy more suitable habitat. However, the mode of travel and the stimulus to move, have only been studied by a handful of investigations (Irmler, 2004; Pfeffer and Filser, 2010; Lehmitz *et al*., 2011; Stadden *et al*., 2011) and are often laboratory based (Bengtsson *et al*., 2004; Nilsson and Bengtsson, 2004; Pfeffer and Filser, 2010; Boiteau, Lynch and MacKinley 2011).

In situ investigations into the physical mode of movement are difficult, due to the nature of soil and difficultly in removing invertebrates (Murray *et al*., 2010). Sticky traps and pitfall traps are used above ground and indicate aerial or soil surface movement. However, techniques employed for use on below-ground populations such as hand sorting, litter bag analysis and soil core collection only determine the presence or absence of the fauna and not method of movement, especially over longer distances. The development of new methods using intact soil cores or physical barrier methods could help determine the mode of soil biota movement. This chapter describes a methodology trial to determine such movement at field scale, using transplanted invertebrate-free soil. To achieve this, it was necessary to determine effective methods of invertebrate removal from soil. Additionally, issues with long-term soil storage and the retention of dormant life cycle stages (e.g. eggs/ inactive larval stages) within Tullgren funnel extracted soil are addressed.

Chapter Five A

Viable Invertebrate Survival within Soil Cores Previously Processed by Tullgren Funnel Extraction

5A.1 Introduction

The standard Tullgren Funnel soil invertebrate extraction methodology applies a temperature gradient to the sample for seven days (Bruckner, Barth and Scheibengraf, 2000; Querner and Bruckner, 2010; Parfitt *et al.*, 2010; Beyer *et al.*, 2011). As seen in Chapter Two Part B, invertebrates were able to survive within the soil sample and be extracted for a considerable period following standard extraction time. This experiment aims to determine, whether invertebrates survive within soil cores previously treated with standard Tullgren Funnel methodology, then stored (8^{o}C), before rehydration, incubation and re-extraction. The aim is to determine whether this method could be used to remove invertebrates from soil for community re-establishment investigations.

5A.2 Materials and Method

5A.2.1 Soil Sample Collection Sites

A total of 24 intact soil cores were collected (Section 2A.2) from the Geescroft mine site, (Section 2A.1.4) in November 2008. The sample collection location can be seen in Figure 4.2, with a description in Section 4.2.1. The Grass Border (G) provided 12 samples; this had well-established grass vegetation and soil invertebrate abundance. The remaining 12 were collected from Buffer Zone One (BZ), maintained as bare fallow by ploughing.

5A.2.2 Fresh Soil Core Invertebrate Extraction and Incubation Preparation

Invertebrates were extracted from all soil cores, by Tullgren funnel, for seven days and collected in saturated salt solution (Section 2A.3). Following extraction, the dry cores were stored in Sunbags (Section 2A.2), at 8^{o}C, until April 2009. At this time, each dry soil core was weighed and placed into a 10cm diameter plastic drain pipe, this prevented sunlight exposure to the core side. This was placed into a new sunbag with the top rolled onto itself several times and closed with a bulldog clip (Figure 5A.1). Each enclosed soil core was then re-weighed, placed onto a labelled tray and 100ml de-ionised water added to the core's base. The soil core was re-wetted from the base as previous attempts had shown that top-down rehydration caused water pooling on the core's surface, whilst the middle remained dry. All soil cores were stored at 8^{o}C for five days; following this rehydration was repeated with 100ml deionised water, and the cores returned to storage (8 ^{o}C) for a further five days.

Figure 5A.1 An example of a soil core sealed inside a sunbag to prevent invertebrate contamination whilst maintaining gaseous exchange with the environment.

5A.2.3 Incubation and Second Invertebrate Extraction

Following rehydration for a total of 10 days, all soil cores were moved (sealed within the sunbag) to the glasshouse and incubated for either seven, 14 or 21 days. This provided the following treatment types based on vegetation cover and incubation period: G7 (grass, 7 days), G14 (grass, 14 days), G21 (grass, 21 days), BZ7 (buffer zone, 7 days), BZ14 (buffer zone, 14 days) and BZ21 (buffer zone, 21 days).

Following the required incubation period, all soil cores were removed from the sunbag and plastic pipe and extracted on the Tullgren Funnels for seven days. The extricated invertebrates were collected in saturated salt solution (Section 2A.5) and stored at -20^{o}c until separation and identification of invertebrates (Section 2A.4).

5A.2.4 Statistical Analysis

Following statistical advice, it was deemed unnecessary to complete statistical analysis. This was due the difficulties associated with completing analysis with such a small number of results that were not zero readings, in addition to the extreme differences displayed in the results.

5A.3 Results

5A.3.1 Initial Invertebrate Extraction

During the fresh core extraction invertebrates were recovered, separated and identified from all soil cores (Table 5A.1). The mean number of invertebrates recovered from the Grass Border was 63.7 (± 16.59). Within this sampling point, the Oribatida were the most numerous, followed by the Entomobryomorpha with the Symphypleona least abundant. Within the Buffer Zone, the mean number of individual invertebrates recovered per core, was lower than the Grass Border (Table 5A.1). The most abundant superfamily, within the Buffer Zone, were the Entomobryomorpha, followed by the Oribatida, and Poduromorpha, the least abundant were the Symphypleona.

Table 5A.1 Mean number of invertebrates (± SE) recovered during the fresh soil core Tullgren Funnel extraction from the Grass and Buffer Zone sampling areas.

	Mean (±SE) Number of Invertebrates						
	Acari			**Collembola**			**Other**
TREATMENT	Prostigmata	Oribatida	Mesostigmata	Entomobryomorpha	Symphyphleona	Poduromorpha	
Grass	6.9 (± 3.7)	22.9 (± 8.0)	4.7 (± 1.5)	13.9 (± 5.1)	0.7 (± 0.4)	9.4 (± 4.1)	5.2 (± 1.5)
Buffer Zone	0.7 (± 0.3)	1.9 (± 0.7)	0.75 (± 0.4)	3.9 (± 1.1)	0.3 (± 0.3)	1.8 (± 0.7)	1.2 (± 0.3)

5A.3.2 Dry Weight of Tullgren Funnel Extracted Soil Cores

Invertebrate extraction, by Tullgren Funnel, results in the soil becoming very dry due to the heating, and therefore, drying technique utilised. Following the first Tullgren Funnel extraction all soil cores were weighed to determine the soil dry weight (g), before rehydration with water. The average dry weight of the Grass Border soil cores was 605.0g

(±45.3); the Buffer Zone soil cores were heavier with an average dry weight of 742.7g (± 34.7).

5A.3.3 Post-Incubation Invertebrate Extraction Results

Following storage, incubation and second invertebrate extraction, the numbers of organisms recovered fell dramatically (Table 5A.2). Most noticeable is that no Collembola were recovered following incubation from any soil cores, although they had been present during the fresh soil core extraction procedure. The Oribatida, which had been most prevalent within the Grass Border cores during fresh soil extraction, were no longer recovered from these same soil cores. However, a limited number were recovered from the Buffer Zone samples. Prostigmata and Mesostigmata were recovered in small numbers from the Grass Border samples, but were absent from the Buffer Zone samples. The other invertebrates recovered from the Grass Border and Buffer Zone soil cores were all Diptera.

A comparison between the fresh soil core and post-incubation extraction results for each vegetation type can be seen in Figure 5A.3. As there were no differences between the different incubation times, an average of all soil cores has been used. It is clear that the fresh soil core extraction does not remove all invertebrates, and that a very small number are able to survive storage and be extracted at a later date.

Table 5A.2 Mean number of individual invertebrates per soil core (±SE) recovered by Tullgren Funnel extraction, for each treatment post- incubation.

Treatment	Mean (±SE) Number of Individuals/Treatment						
	Acari			Collembola			Other Invertebrates
	Prostigmata	Oribatida	Mesostigmata	Entomobryomorpha	Symphypleona	Poduromorpha	
Grass 7 days	1.0 (± 1.0)	0 (± 0.0)	0.25 (± 0.25)	0 (± 0.0)	0 (± 0.0)	0 (± 0.0)	0 (± 0.0)
Grass 14 days	0 (± 0.0)	0 (± 0.0)	0 (± 0.0)	0 (± 0.0)	0 (± 0.0)	0 (± 0.0)	0 (± 0.0)
Grass 21 days	0 (± 0.0)	0 (± 0.0)	0.25 (± 0.25)	0 (± 0.0)	0 (± 0.0)	0 (± 0.0)	0.25 (± 0.25)
Average	**0.33 (± 0.28)**	**0 (±0.10)**	**0.17 (± 0.10)**	**0 (± 0.0)**	**0 (± 0.0)**	**0 (± 0.0)**	**0.17 (± 0.10)**
Buffer Zone 7 days	0 (± 0.0)	0.25 (± 0.25)	0 (± 0.0)	0 (± 0.0)	0 (± 0.0)	0 (± 0.0)	0.25 (± 0.25)
Buffer Zone 14 days	0 (± 0.0)	0.25 (± 0.25)	0 (± 0.0)	0 (± 0.0)	0 (± 0.0)	0 (± 0.0)	0.25 (± 0.25)
Buffer Zone 21 days	0 (± 0.0)	0.25 (± 0.25)	0 (± 0.0)	0 (± 0.0)	0 (± 0.0)	0 (± 0.0)	0 (± 0.0)
Average	**0 (± 0.0)**	**0.16 (± 0.11)**	**0 (± 0.0)**	**0 (± 0.0)**	**0 (± 0.0)**	**0 (± 0.0)**	**0.08 (± 0.08)**

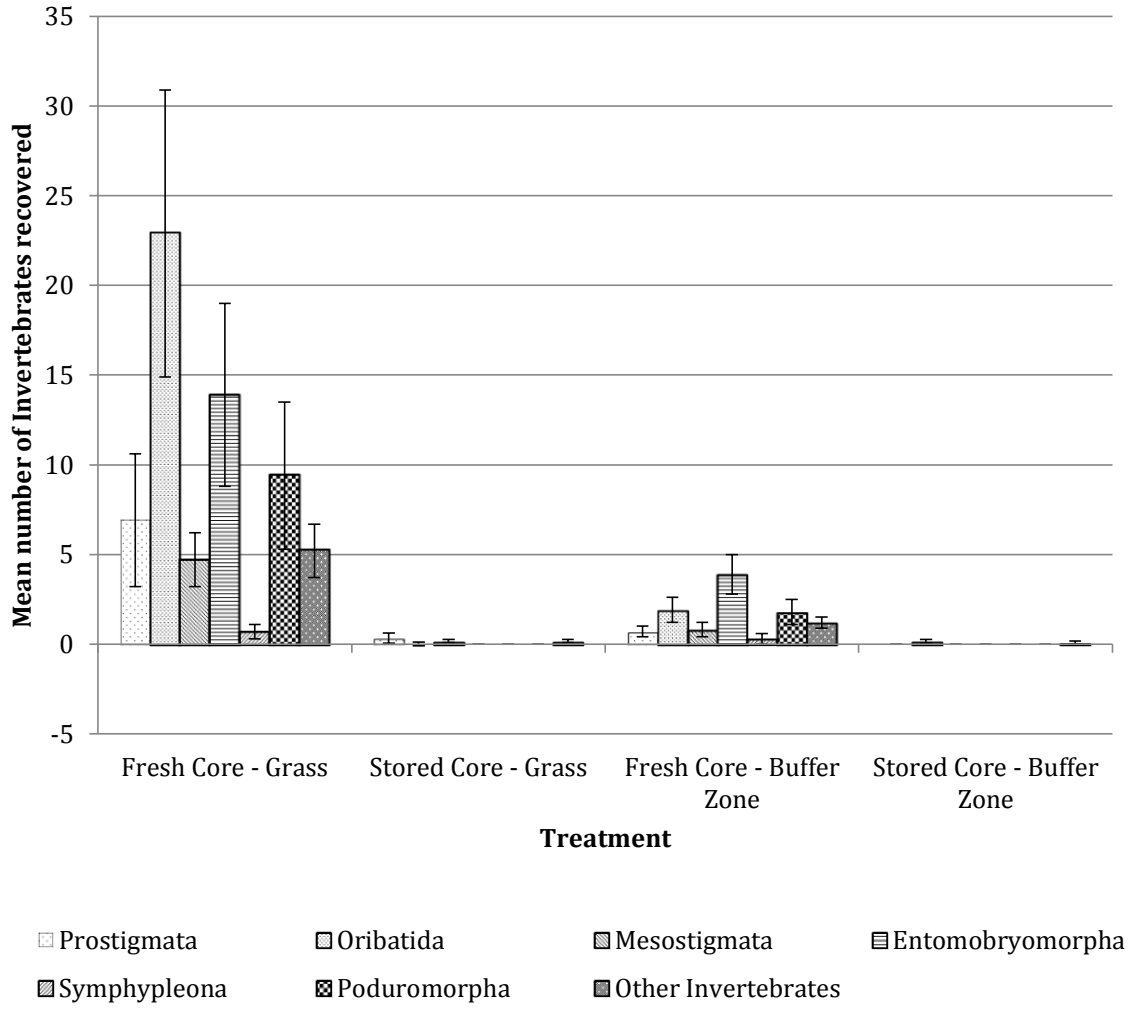


Figure 5A.2 Mean number (±Standard Error as error bars) of invertebrates recovered from fresh cores compared with post-incubation cores for each invertebrate group.

5A.4 Discussion

The differences between the invertebrate populations of the Grass Border and Buffer Zone, within the fresh core extraction time, are due to the variations in the ecosystems present. The Grass Border is a stable, plant driven, mature ecosystem with all major mesofaunal superfamilies present. The Buffer Zone is continually disrupted by ploughing; this leads to a lack of vegetation and poor soil structure, leading to a lower invertebrate abundance and diversity level (Chapters Three and Four). Vegetation removal by ploughing, leads to a reduction in carbon inputs into the soil, this was noted by Watts *et al*. (1996) and Watts, Dexter and Longstaff (1996) and Johnson, Poulton and Coleman (2009). This therefore, reduces available food sources for detritivores, with subsequent impacts on the remainder of the food web, leading to reduced total invertebrate population abundance. The lack of plants and associated root structure are reflected by the larger dry weights of the Buffer Zone soil, with a denser, more compacted and crumbly soil structure (Hirsch *et al.*, 2009) that lack the soil pores required for invertebrate survival (Kampichler and Hauser, 1993; Waagner, Bayley and Holmstrup, 2011).

The invertebrate population difference between the fresh and post-incubation soil cores was large. The difference is vast, with a large number of zero results in the incubated soil cores, that it was unnecessary and impractical to complete any statistical analysis. As no Collembolan species were recovered following storage, either all Collembolan were recovered during the first extraction or these species did not survive storage in dry, cool conditions. The results of the Tullgren Funnel extraction efficiency experiment (Chapter Two Part B) recorded that after seven days extraction 95.4% of the total Collembola had been recovered. Therefore, this suggests that only a small number remained following the fresh extraction and that these were unable to survive the storage process. Collembolan species usually inhabit moist environments, however, some species such as *Sminthurinus elegans*, *Sminthurus viridis* and *Bourletiella hortensis,* have been demonstrated to survive

drought as eggs. These are species found predominately, although not exclusively, within arable ecosystems (Alvarez, Frampton and Goulson, 1999).

The recovery of adult Diptera and Acari from the incubated soil cores, suggests that the eggs or larvae were present in the fresh soil cores before being sealed into plastic bags. These had later developed into adults during incubation, and had then been collected during the post-incubation Tullgren Funnel extraction. Chapter Two Part B determined that over 60% of Acari remain in the soil core following seven days of Tullgren funnel extraction. Therefore, it was expected that based on this figure and the numbers recorded during fresh core extraction, 13.8 and 0.58 individuals would have been recovered post-incubation from the Grass Border and Buffer Zone respectively. These figures were not recorded, although some Acari were recovered (0.58, Grass Border and 0.17, Buffer Zone). Therefore, the few individuals recovered in the post-incubation extraction had survived the storage conditions. However, the majority were not extracted and presumed to have died. This has important implications for the soil sample storage prior to analysis, as although the Acari were able to survive for short periods in fresh soil cores, they were not able to survive long-term within dried soil core, during the storage period.

Edwards and Fletcher (1971) and Leinaas (1978) both suggested that under cooled conditions cores could be stored for several weeks. However, it is evident that pre-analysis long-term soil sample storage can be detrimental to any results obtained. As this type of storage can cause biases in the results. Where invertebrate's life cycles continue within the stored soil, there are changes to the relative population abundances. For example, some Prostigmata species can complete a life cycle in one week (Behan-Pelletier, 2003). However, if the storage conditions are unfavourable, i.e. very dry, the invertebrates can die, reducing the population levels within the sample.

Additionally, as individuals were not identified to species, it is not recorded whether the Prostigmata and Mesostigmata extracted were small adults or juveniles. Juveniles would potentially have developed from eggs or from an inactive larval stage, induced by the unfavourable conditions, which then developed once the soil had been rehydrated. This has been observed in Collembola (Hopkin, 1997) and Acari (Walter and Proctor, 1999) species. Further identification of the specimens to species level would have given a better insight into the life history of that individual and therefore would allow the categorisation of the life cycle stage before rehydration of the soil core. Oribatida were recovered from the Buffer Zone incubated soil cores. Oribatida, especially the sub-group Astigmata, are known to be better at surviving soil disturbance due to their life history strategies than other Acari (Adl, Coleman and Read, 2006). Generally the Oribatida have evolved to survive desiccation and environmental stress. For example, they have highly sclerotised bodies and an ability to produce offspring, which can return to dormant stages of the life cycle, which promotes their ability to survive within the soil (Paoletti *et al*., 2007).

5A.5 Conclusions

This investigation shows that soil core environmental conditions caused by the process of Tullgren Funnel extraction and storage were not favourable for survival. Any invertebrates remaining either enter into an inactive larval state or hatch from eggs when more favourable conditions return or die. This process could be used as an invertebrate removal method prior to soil uses within invertebrate reintroduction investigations. However, this method is time consuming and requires a long storage time, plus storage space at the appropriate temperature and therefore may not be of benefit to many studies.

Chapter Five B

Core Sterilisation Techniques

5B.1 Introduction

In order to study the re-establishment of mesofaunal communities within soil, it is often necessary to remove any organisms already present. Once all mesofauna have been removed, a zero abundance start point is achieved. There are many methods described within the literature to achieve this, such as freezing to -22^{o}c for two weeks (Huhta, Wright and Coleman, 1989; Eisenhauer, Sabais and Scheu, 2011) and at -80^{o}C for 3 days followed by heating to 50^{o}C for 3 days (Maraun, Visser and Scheu, 1998). However, these methods are problematic, they are either time consuming, such as Tullgren Funnels, or destroy the soil structure, such as sieve-freeze-thaw method used by Bradford, Gancos and Frost (2008), or destroy the fungal community (Maraun, Visser and Scheu, 1998). Techniques into the investigation of mesofaunal movements and population re-establishment often use mesocosms of soil, reinserted into the natural environment. At present, these experiments use soil where the invertebrates have been removed by structure destroying techniques. A technique where soil can be removed from the natural environment intact, sterilised and replaced intact could reduce errors and more accurately stimulate natural processes. This investigation compared Bradford's well-established method with similar methods that have a reduced effect on the soil structure.

5B.2 Materials and Method

5B.2.1 Soil Sample Collection and Sterilisation Treatment

In total 25 intact soil cores (8cm ∅ x 10 cm) were collected (Section 2A.2), from the Little Burrows site, North Wyke, (Section 2A.1.6) and stored at 8^{o}C. To determine fresh soil core invertebrate abundance, five control cores were immediately Tullgren Funnel extracted (Section 2A.3), saturated salt solution collection pots were removed at seven days and replaced with fresh collection pots (Section 2A.5), these were removed at 14 days. The remaining 20 cores were split between four treatments:

B_o - Established Bradford technique: sieve 2mm, freeze (-20^{o}C) 76 hours, thawing (room temperature) 24 hours, re-freezing (-20^{o}C) 24 hours

B_i – Intact Bradford technique: keep soil cores intact, freeze (-20^{o}C) 76 hours, thawing (room temperature) 24 hours, re-freezing (-20^{o}C) 24 hours

B_{-80} – Intact deep freeze technique: keep soil cores intact, freeze (-80^{o}C) 76 hours, thawing (room temperature) 24 hours, re-freezing (-80^{o}C) 24 hours

B_h – Intact heating technique: keep soil cores intact, heat (80^{o}C) 76 hours, cool (room temperature) 24 hours, re-heat (80^{o}C) 24 hours

5B.2.2 Invertebrate Extraction

Following treatment, all cores were returned to room temperature. The B_h heated treatment had dried the soil which was rehydrated using 100ml de-ionised water per core. Soil cores were then placed onto Tullgren Funnels for invertebrate extraction; as treatment B_o is sieved soil, this was placed into a mesh bag prior to extraction to prevent soil from falling into the sample collection container. Collection pots were removed at seven days and renewed for a further seven days and invertebrates identified (Section 2A.4).

5B.2.3 Statistical Analysis

Following consultation with a statistician, due to the small number of results that were not zero readings, no statistical analysis was carried out.

5B.3 Results

The control samples were extracted immediately, and invertebrates collected for one-seven days and eight-14 days. All samples provided invertebrates at both sampling periods (Table 5B.1). During the first seven days, similar Acari and Collembola numbers were collected, with a small number of other invertebrates. During the second time period, the numbers reduce for all taxa collected; however, the Acari were more numerous.

Table 5B.1 Mean number (±SE) of invertebrates recovered by Tullgren Funnel extraction for all invertebrate removal techniques

Treatment	Mean Number (±SE) of Individual Invertebrates								
	Time Period 1-7 Days				Time Period 8-14 Days				Total Whole Time Period
	Acari	Collembola	Other Invertebrates	Total	Acari	Collembola	Other Invertebrates	Total	
B_o	0.4 (±0.4)	0 (±0)	0 (±0)	0.4 (±0.4)	0 (±0)	0.2 (±0.2)	0.2 (±0.2)	0.4 (±0.2)	0.8 (±0.4)
B_i	0.8 (±0.2)	0 (±0)	0.2 (±0.2)	1 (±0.3)	1.4 (±0.7)	0 (±0)	0.2 (±0.2)	1.6 (±0.7)	2.6 (±0.5)
B_{-80}	0.4 (±0.2)	0.2 (±0.2)	0 (±0)	0.6 (±0.4)	0 (±0)	0 (±0)	0.2 (±0.2)	0 (±0)	0.6 (±0.4)
B_h	0.8 (±0.4)	0.2 (±0.2)	0 (±0)	1 (±0.3)	0 (±0)	0.2 (±0.2)	0.4 (±0.2)	0.6 (±0.2)	1.6 (±0.2)
Control	40.2 (±3.2)	40.6 (±4.5)	8.8 (±1.7)	89.6 (±7.9)	23.8 (±6.7)	5.6 (±3.2)	1.2 (±0.6)	30.6 (±7.2)	120.2 (±14.4)

All of the trialled techniques recorded much lower invertebrate numbers than the fresh core controls (Table 5B.1). No specific method produced a zero count for all soil cores. The most successful was the freezing intact soil cores to -80^{o}C; however, there was no real difference between this technique and the remaining three techniques.

5B.4 Discussion

The invertebrates extracted from the fresh soil cores were recorded in large numbers for both one-seven and eight-14 days, with a reduction in the number recovered during the second period. This is to be expected and has been seen in Chapter Two Part B. These soil cores were collected at the same time and place as the soil cores used for the invertebrate removal technique comparison.

All of the techniques trialled were based on a similar process of freezing or heating in cycles over a four day period. However, it was also used to trial the possibility of removing the required soil sieving. The numbers recovered from all techniques were very small in comparison to the control results; therefore all techniques considerably reduced the invertebrate population. The established Bradford method produced the lowest results; this method included sieving, which destroyed the soil structure. However, the other techniques also produced very similar results. The choice of technique used would, therefore, be dependent on experimental requirements, and other side-effects of the techniques.

In general, soil freezing affects the microbial population and causes nutrient leaching due to demineralisation during the freeze-thaw process (Kampichler *et al*., 1999; Bradford *et al*., 2002). Additionally, freezing to -80^{o}C can be difficult due to the space required within what might be a limited resource depending on the capabilities of the establishment. Furthermore, Kampichler *et al.* (1999) determined that deep freezing sieved soils caused an increase in the ammonium (NH_4^+) levels. Moreover, soil heating has fewer complications for nutrient leaching. However, the soil cores are completely dry following the procedure and this may affect the microbial population within the soil.

Further investigation would be required to determine any detrimental effects of each technique on the soil properties, and the other soil organisms. Moreover, further work to reduce the amount of time required and possibly removing whole stages could be completed.

It must be noted that these techniques are suitable for the soils on which the trial was completed. For use on other soils the natural environmental conditions must be taken into account, for example in regions where the soil is regularly frozen to -20^{o}c the soil fauna would be acclimated to the process and therefore be unaffected.

5B.5 Conclusions

There are no differences in the invertebrate numbers recovered for the different removal techniques, and therefore, it can be concluded that any of the above techniques will have a similar outcome. Consequently, technique choice will depend on investigative requirements and resource availability. Further investigation of the different techniques could determine unwelcome effects on the soil, such as nutrient leaching, and on the other biota contained within it, including nematodes or microbial populations.

Chapter Five C

Mesocosm Invertebrate Exclusion

5C.1 Introduction

Following the completion of the Highfield Reversion (Chapter Three) and Highfield Transect (Chapter Four) experiments, the results indicated that mesofauna are able to repopulate an area of low abundance upon the return of favourable conditions. This also includes the repopulation of soil where the population has crashed to almost non-existent levels. In order to understand the physical movements of these populations, the mode by which they travel is important. One question that at present is unanswered is whether these organisms travel through the air, over the soil surface or if they travel within the soil they inhabit. A second question is the rate at which this occurs. The work previously described in this chapter (Sections 5A and 5B) has determined methods by which soils can be made devoid of invertebrates in order to answer the two questions above. The following section describes an experiment linking the previously tested soil sterilisation procedures, performed on soil extracted directly from the experimental area, and the identification of the mode of mesofaunal movement. Additionally, this experiment uses isotopic tracking techniques to determine any influence that the presence or absence of mesofauna might have on detritus turnover. However, due to time constraints only a limited proportion of this investigation's results will be presented within this thesis.

Within this experiment, soil obtained from the experimental field site was treated to remove mesofauna and returned to the field within a pot designed to produce a physical barrier; referred to as a mesocosm. Mesocosms are enclosed outdoor systems that are partially permeable to their surroundings (Odum, 1984). Kampichler *et al*. (1999) believed that mesocosms combined a high degree of realism with the repeatability of experimental

units and Coleman, Crossley and Hendrix (2004) stated that they are a well-established method for studying the short term population dynamics of soil fauna. In this study the mesocosms were manipulated to allow three different pathways for the recolonisation of soil by mesofauna; surface and airborne, airborne only and free movement. Shredded dry root material labelled with ^{15}N was added to the mesocosm soil to determine the mesofaunal effect on the turnover of the total N. In addition, each mesocosm was planted with either Ryegrass (*Lolium perenne*) or White Clover (*Trifolium repens*) to determine if the mesofauna have any influence on the uptake of ^{15}N or other nutrients within the soil.

5C.2 Materials and Methods

5C.2.1 Experimental Site, Mesocosm Soil Collection and Preparation

The experimental site was Little Burrows, North Wyke Research Station (Section 2A.1.6). The general field site conditions can be seen in Figure 5C.1. Soil for the mesocosms was collected by root augur (Section 2A.2), close to where the experiment was implemented. Completing soil collection adjacent to the experimental area ensured that the soil was biologically, chemically and physically similar to the experimental site and had previously received the same management regime. In addition this prevented any unnecessary damage and disturbance to the experimental site prior to mesocosm implantation.

The soil cores were placed onto Tullgren Funnels (Chapter 2A.3) and invertebrate extraction was undertaken for two weeks to remove the majority of invertebrates. As the soil was very dry following Tullgren Funnel extraction it was re-hydrated using 100ml deionised water per core. The surface vegetation was removed and the remaining soil core sieved to 3mm to remove the majority of plant material and stones. The soil was then stored (4^{o}C) in sealed plastic bags until required for the experiment. This was repeated until the required volume of soil had been processed.

Figure 5C.1 The Little Burrows field site during the plot marking out process.

5C.2.2 Plant Preparation

Ryegrass (*Lolium perenne*) and White Clover (*Trifolium repens*) seeds were germinated in trays containing sterile sand within a fully controlled growth cabinet (Sanyo 350FIT, Sanyo, Japan) (Figure 5C.2). The growth cabinet allowed total control of temperature, light intensity and daylight time, as well as providing a sealed environment to prevent the invertebrate contamination of the growth medium. The growth cabinet cycle was; 16 hours daylight (full light intensity available from the cabinet) at 21°C followed by eight hours dark at 15°C. Two weeks after germination the seedlings were separated into individual pots filled with invertebrate free soil obtained using the procedure in Section 5C.2.1, and placed back into the controlled growth chambers to establish. During this period the plants were fed using 20% modified (N-free) Arnon's nutrient solution (Hewitt, 1966) and shoot growth was trimmed approximately every three weeks to six-seven cm in

height to ensure good root development. All plant trimmings were retained, labelled and stored frozen for possible future analysis.

Figure 5C.2 The germination seed trays of White Clover (top left) and Ryegrass (top middle) seedlings, the separated White Clover seedlings (bottom left) and a growth cabinet containing both the source tray for Ryegrass and trays containing separated seedlings (right).

5C.2.3 Stable Isotope Preparation

The stable isotope used within this investigation was ^{15}N. Ryegrass was grown in a hydroponic system (Figure 5C.3) using an aerated modified Arnon's nutrient solution containing only ^{15}N labelled nitrogen sources (Hewitt, 1966). This ensures that the plants only incorporate ^{15}N labelled nitrogen into their tissues which is traceable with a mass spectrometer. Plastic trays filled with the ^{15}N nutrient solution were used as a reservoir. Within each tray an aeration pump added oxygen to the water. On top of the nutrient solution a layer of bubble wrap coated in silver foil prevented light from being transmitted

through to the nutrient solution and affecting root growth. In addition this layer prevents excessive evaporation. The Ryegrass seedlings germinated in sand, were gently washed with water to remove excess material, 4-5 seedlings were then wrapped in glass wool and fed through 1cm holes in the bubble wrap, with the shoots on top and roots underneath. The bubble wrap then floated on top of the nutrient solution.

Figure 5C.3 The hydroponic system within a growth cabinet, filled with freshly trimmed Ryegrass.

The hydroponic system was located within a controlled growth cabinet (Figure 5C.4) set with the same light/dark and temperature phases as the Ryegrass and White Clover seedlings. It was important that the ^{15}N plants were kept in isolation from the other experimental plants to prevent cross-contamination with the ^{15}N isotope as this would affect the final isotopic results. Once the seedlings were established the plant material was harvested on a regular basis, with roots and shoots kept separate. The material was dried

(85°C, 18 hours) and then roughly chopped to 2.5cm lengths before use. A total of 40g dried root material was required to add 0.3g to the isolation pots.

Figure 5C.4 The ^{15}N labelled Ryegrass, before harvesting within the bubble wrap (top left), after harvesting - only short roots and shoots remain (top right) and the harvested product divided into roots and shoots before drying (bottom).

5C.2.4 Mesocosm Preparation

In order to determine the mesofaunal movement path, mesocosms with specific routes of access, encasing both soil and plant, were produced for transplantation into the experimental field. The mesocosm is made of Shelterguard™, (Acorn Planting Products, Maldon, UK) a plastic mesh with 1cm squares. Each square was filled with plastic film, creating an impermeable boundary. This provided an isolating barrier to mesofaunal movement, but was also easily removed to allow invertebrate movement through selected points. The mesh was cut into 13cm x 20cm rectangles and then rolled to form a tube with a 7.5cm ø x 13cm length, the mesh was held in place using cable ties with the smallest possible heads (Figure 5C.5). A disc of mesh was added to the pot base and held in place with cable ties. This ensures that there was no deep mesofaunal movement into the mesocosm and that the experimental soil, which was very crumbly due to the absence of root material, placed in the pot did not fall out before transplantation.

Invertebrate free soil (Section 5C.2.1) was added to the mesocosm to a height of 10 cm, (not filled to the top). By leaving an overlap between the soil surface and the mesocosm top movement across the soil surface and the air immediately surrounding this can be controlled and isolated. The 0.3g of roughly chopped ^{15}N labelled plant root material (Section 5C.2.3) was mixed into the soil and the weight of the intact mesocosm was recorded before and after soil addition.

Figure 5C.5 A single mesocosm containing invertebrate free soil and ^{15}N labelled root material

Into each of these isolation pots either White Clover or Ryegrass was transplanted as required. The fully intact mesocosms were watered and left to establish for three days within the controlled environment growth cabinets. This was to prevent invertebrate contamination from the outside environment before transplantation into the experimental site.

Figure 5C.6 The planted mesocosms ready for transplantation into the experimental site.

5C.2.5 Mesocosm Transplantation

In total there were six treatments. Each treatment was produced by punching out the interlinking film between the Shelterguard™ mesh of the mesocosm as follows (Figure 5C.7):

Full Access Grass – Invertebrates enter mesocosm from all locations, all interlinking spaces are removed, topped with Ryegrass

Top Access Grass – Invertebrates enter mesocosm from the soil surface to the mesocosm top, top three rows of interlinking mesh removed. Will determine soil surface and airborne movement, topped with Ryegrass

No Access Grass – Invertebrates unable to access mesocosm through the walls, only airborne access, no interlinking areas removed, topped with Ryegrass

Full Access Clover – Invertebrates enter mesocosm from all locations, all interlinking spaces removed, topped with White Clover

Top Access Clover – Invertebrates enter mesocosm from the soil surface to the mesocosm top, top three rows of interlinking mesh removed. Will determine soil surface and airborne movement, topped with White Clover

No Access Clover – Invertebrates unable to access mesocosm through the walls, only airborne access, no interlinking areas removed, topped with White Clover

Figure 5C.7 Mesocosm examples before transplantation: from left to right the treatments are: Full Access Grass, No Access Grass, Top Access Grass, Full Access Clover, No Access Clover and Top Access Clover.

A total of 126 mesocosms were transplanted in September 2011. This provided three replicates at each time point, for a total of seven time points. Here data collections after one, two and four months are reported. Further samplings at six, eight, 10 and 12 months will be made and data reported elsewhere.

The mesocosm transplantation locations were determined using randomised treatment blocks. Three blocks, 12m x 4m, were marked out, these formed three replicate blocks. Each block was divided into $1m^2$ quadrats, and the treatment that was applied to each block was determined using a random number table, (Figure 5C.8). Each quadrat was then divided diagonally using a devised device (Figure 5C.9) to find the centre.

1	10	2	8
4	2	10	1
8	12	4	6
sp	6	sp	12
8	1	sp	10
4	6	2	8
sp	12	6	4
10	2	1	12
4	2	6	10
1	6	12	2
sp	10	8	sp
12	8	4	6

6	10	12	2
8	12	1	10
4	1	sp	4
2	sp	8	6
2	12	10	4
4	sp	6	1
8	1	2	8
10	6	12	sp
6	1	4	1
10	8	sp	2
sp	4	8	12
2	12	6	10

sp	6	1	sp
4	2	10	8
12	10	12	4
1	8	2	6
4	6	10	2
12	2	1	12
sp	8	4	8
1	10	6	sp
4	1	8	10
2	6	1	2
12	10	4	sp
8	sp	6	12

Figure 5C.8 Mesocosm experimental layout, the numbers represent the collection time of the transplanted mesocosm (plus one spare - sp) within each treatment as follows - Full Access Grass, o Access Grass, p Access Grass, Full Access Clover, No Access Clover, Top Access Clover, the three replicate blocks are shown.

Figure 5C.9 Left: The apparatus used to locate the quadrats centre; the point at which the mesocosm (right) will be placed into the soil.

The mesocosm was transplanted into the quadrat's centre point. An 8cm Ø x 10cm deep soil core is removed using the root auger (Section 2A.2). The sides of the remaining hole

were checked for clay smearing as the auger was removed, as this could act as a barrier for invertebrate movement. Where present, the smearing was removed by tapping the area with the bristles of a wire brush. Once the hole was empty the required mesocosm was fitted into place and secured using a little invertebrate free soil. The mesocosm was fitted intact with the wire mesh in place, as this acts as the barrier to movement. The removed soil core was retained, stored in a sun bag, labelled and placed in 4^{o}C storage. Of these soil cores, 18 were immediately transferred to the Tullgren Funnels and the invertebrates extracted and identified (Sections 2A.3 and 2A.4). This result determined the baseline invertebrate population of the experimental site and provided time zero results.

5C.2.6 Sample Collection

During each sampling time, three randomly selected mesocosms were collected from each treatment. The samples were collected intact, with the surrounding mesh, placed into labelled sunbags and transported back to the controlled environment room. The base disc was removed before Tullgren Funnel extraction (Section 2A.3). However, the remaining mesh had a protective effect, preventing evaporation from the soil core and decreasing the rate at which invertebrates left the sample. The soil samples remained on the Tullgren Funnels for a minimum of two weeks to ensure all invertebrates had been extracted. After two weeks the soil cores and invertebrate collection pots were inspected daily and were only removed from the Tullgren Funnels when there were no further invertebrates extracted.

5C.2.7 Sample Analysis

All invertebrates were identified and separated into groups (Section 2A.4). The results were analysed for abundance (m^{-2}) and biomass food webs (µg m^{-2}), using the methods described in Section 2A.6. In addition, vegetation samples were taken, dried (85^{o}C, 18 hours), finely ground using a ball mill (Glen Creston) and elemental analysis completed

using a 20-20 mass spectrometer (PDZ-Europa, Crew, UK) linked to a Carlo Erba NA 1500 elemental analyser (Carlo Erba, Milan, Italy). The following elements were analysed: Total N (% total Nitrogen), Total C (% total Carbon), ^{15}N (^{15}Nitrogen), ^{13}C (^{13}Carbon), Dry Matter (DM), N_mg (Nitrogen per mg), C_mg (Carbon per mg) and ^{15}N_mg (^{15}Nitrogen per mg). In addition soil moisture content was also recorded.

5C.2.8 Statistical Analysis

Statistical analysis has been completed on the abundance ($\sqrt{}$ transformation) and biomass (LOG_{10} transformation) data using ANOVA. In all ANOVA analyses, comparisons between the following variables were made:

Species: Grass, Clover

Treatment: Full Access, Top Access, No Access

Time Series: 1, 2, 3

Species x Treatment: Grass, Clover x Full Access, Top Access, No Access

Species x Time Series: Grass, Clover x 1, 2, 3

Treatment x Time Series: Full Access, Top Access, No Access x 1, 2, 3

Species x Treatment x Time Series: Grass, Clover x Full Access, Top Access, No Access x 1, 2, 3

ANOVA analysis was also completed on the soil moisture content and vegetation results.

5C.3 Results

5C.3.1 Invertebrate Populations

The invertebrate population results presented here are the time zero sampling and time series; one - one month, two - two months and three - four months following mesocosm transplantation. For nutrient and isotopic analysis only time series one and two are presented, soil moisture content is presented for all three post-transplantation time series.

Time Zero results were obtained from 18 soil cores collected from Little Burrows during the transplantation process (September 2011). The mean invertebrate abundance (m^{-2}) and biomass and associated mesofaunal food web were calculated (Section 2A.6). These results demonstrate the invertebrate population present within the Little Burrows site and therefore providing the reservoir population for mesocosm recolonisation.

The mean invertebrate abundance (m^{-2}) recovered during time zero sampling (Table 5C.1; Appendix XVII) had a large Acari population, consisting predominantly of Prostigmata, followed by Collembola and finally other invertebrates. When body mass ($\mu g\ m^{-2}$) was considered (Figure 5C.10) the food web is Acari dominated. Within this order the Mesostigmata were the most dominant superfamily, followed by the Oribatida and finally Prostigmata. The Collembola occupied a relatively small proportion of the food web, this was Entomobryomorpha dominated with smaller Poduromorpha and Symphypleona biomasses. Full data with standard error (±SE) are displayed in Appendix XVII.

Table 5C.1 Mean invertebrate abundance (m^{-2}), (±SE) recovered from Little Burrows during transplantation, representative of the starting population.

Mean (±SE) Invertebrate Abundance (m^{-2})								
Acari				Collembola				
Prostigmata	Oribatida	Mesostigmata	Total	Entomobryomorpha	Symphypleona	Poduromorpha	Total	Other Invertebrates
16822 (±2239)	7522 (±848)	8211 (±2380)	32555 (±3261)	3222 (±459)	1656 (±395)	3100 (±566)	7978 (±1199)	3644 (±241)

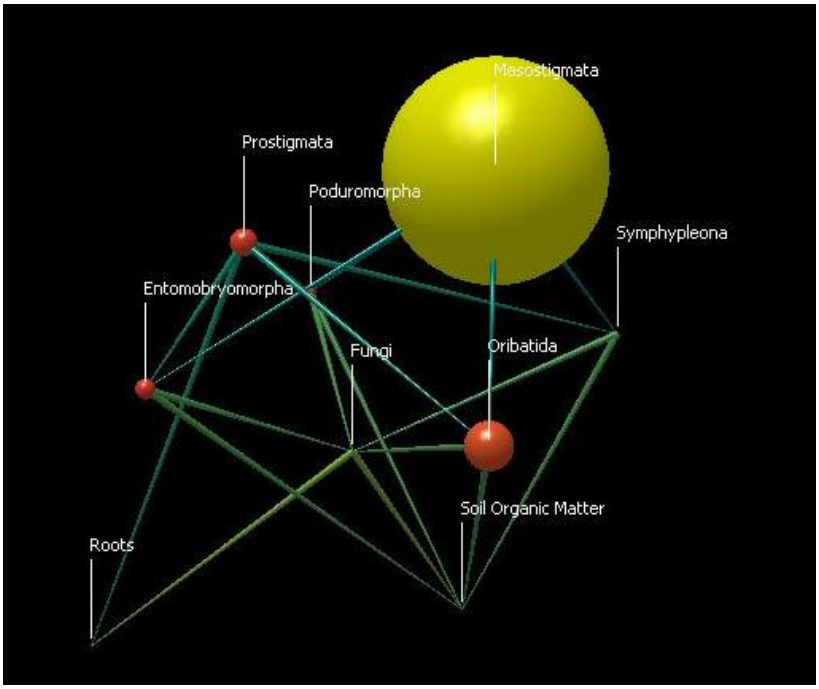


Figure 5C.10 Little Burrows mesofaunal biomass food web (µg m^{-2}), time zero.

Following the transplantation, collection and extraction of the mesocosms, invertebrates were recorded from all treatments, within all time series, the mean abundances (m^{-2}) are shown in Appendix XVII. Mean biomass data is displayed in Appendix XVIII.

Generally, the mean abundance and biomass was highest in time series one (October), decreasing to time series two (November) and then increasing slightly into time series three (January). The mean biomass food web diagrams (Figures 5C.11, 5C.12 and 5C.13) demonstrate that there was no overall pattern in the results obtained from the treatments throughout the time series. Commonly, within the Acari, the superfamily Prostigmata was consistently more abundant than the Mesostigmata and Oribatida; however, the mean biomasses determined that for some treatments the Mesostigmata were more dominant. The Collembolan superfamily Symphypleona were often the least numerous within each treatment throughout the experimental time. The mean biomass food web diagrams depict the Entomobryomorpha were the largest collembolan superfamily within most treatments.

When considering population changes over the experimental time period, the total mean Acari abundance had significant differences ($P<0.001$), with the largest abundances in time zero and time series one, with the smallest in time series two. Within the superfamilies, the Mesostigmata were notably absent from time series two (Appendix XIX; Figures 5C.11, 5C.12, 5C.13). The mean total Mesostigmata abundance ($P<0.001$) and biomass ($P<0.001$) was significantly larger in the time zero data. With intermediate amounts in time series one and three, with time series two population significantly lower (Appendix XIX). Both remaining Acari superfamilies had significant differences between sampling times. The mean total Oribatida had a significantly higher abundance ($P<0.001$) and biomass ($P<0.001$) in time zero data than the subsequent time series samplings, with time series one having a significantly different ($P=0.014$) abundance than the other time series (Appendix XIX). The mean total Prostigmata abundance is significantly ($P<0.001$) higher in the time zero data than the remaining time series. This is also reflected in the biomass data ($P<0.001$); within all time series. However time series one had a significantly ($P=0.005$) larger abundance than time series two and three.

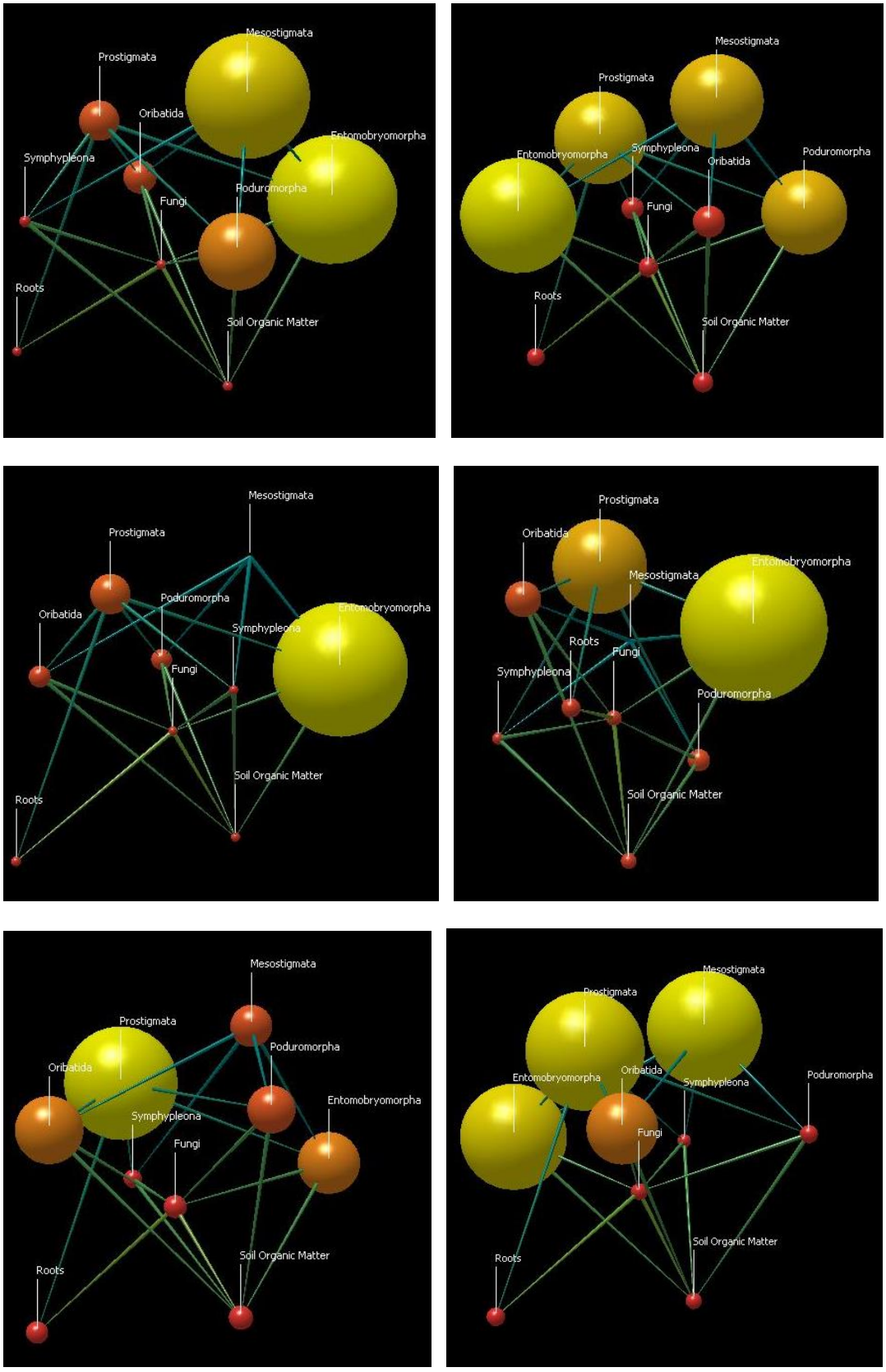


Figure 5C.11 The mesofaunal biomass food webs (µg m^{-2}) - Full Access treatments, left - White Clover, right - Ryegrass, top - time series one, middle – time series two, bottom - time series three

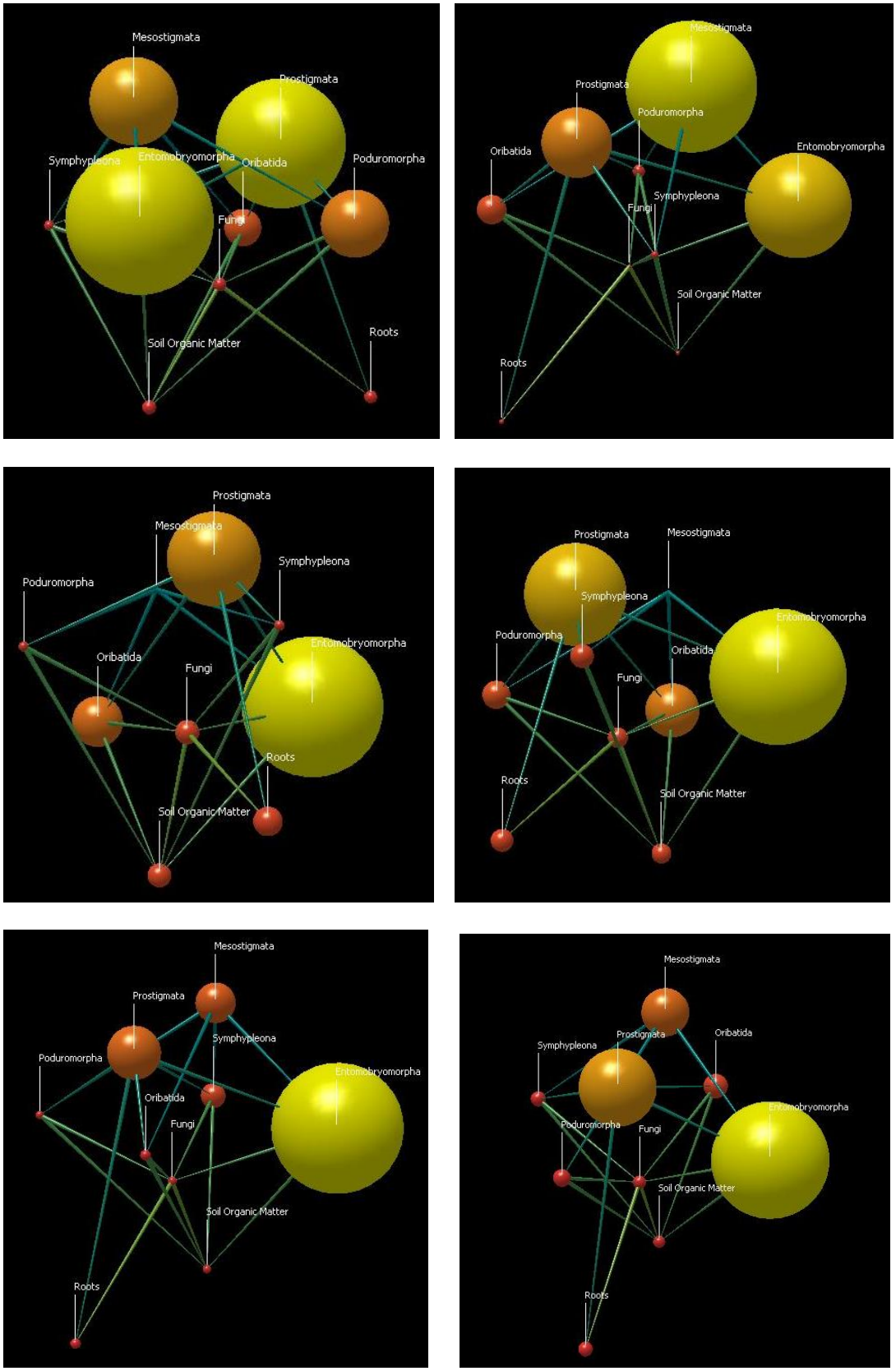


Figure 5C.12 The mesofaunal biomass food webs (µg m^{-2}) - Top Access treatments, left - White Clover, right - Ryegrass, top - time series one, middle – time series two, bottom - time series three

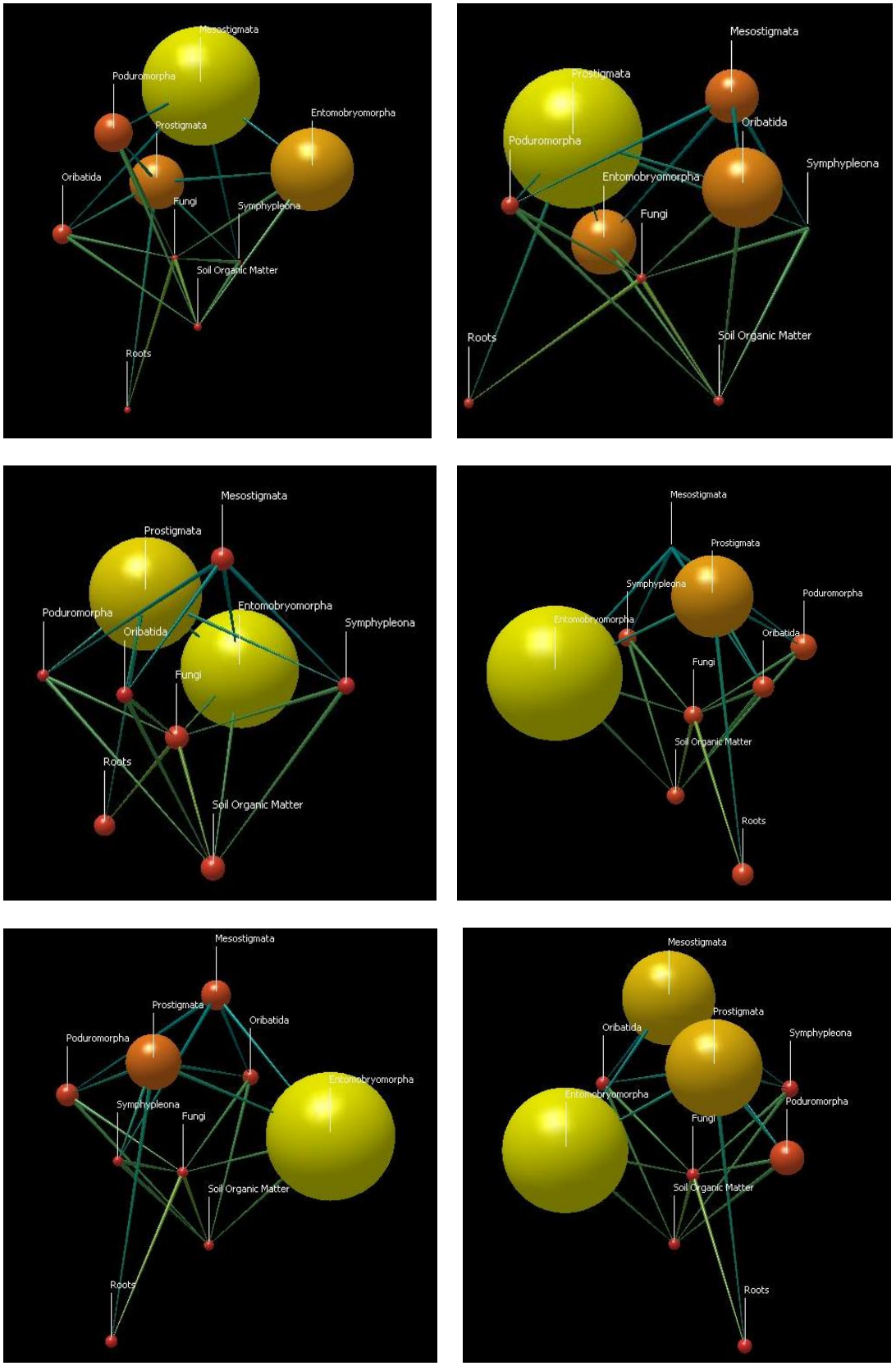


Figure 5C.13 The mesofaunal biomass food webs (µg m^{-2}) - No Access treatments, left - White Clover, right - Ryegrass, top - time series one, middle – time series two, bottom - time series three

The total mean Collembola abundance, for each sampling time, determined that the time zero and time series one data were significantly (P=0.016) higher than time series two and three. Upon subdivision into the superfamilies, the Poduromorpha abundance and biomass have significantly (P=0.004 – Abundance; P=0.023 - Biomass) higher figures in the time zero, time series one and three than time series two populations (Appendix XIX).

When the abundances and biomasses of each post-transplantation invertebrate group were averaged for vegetation type, there were no significant differences (Appendix XIX). However, upon comparison with the time zero data, the mean total Acari and other invertebrates were most abundant at time zero (P<0.001). Within the Acari superfamilies, all had significantly higher abundance (P<0.001) and biomass (P<0.001) in the time zero data, than within the Ryegrass and White Clover. The Poduromorpha also had a significantly larger mean abundance (P=0.025) and mean biomass (P<0.001) in the time zero data than within the mesocosms.

The mean total invertebrate abundance and biomass within the post-transplantation time series were not significantly affected by mode of access (Appendix XIX). However, time zero results were significantly higher than the mesocosm results for mean total abundance and biomass for the Mesostigmata (P<0.001), Oribatida (P<0.001), Prostigmata (P<0.001), Poduromorpha (P=0.047 – abundance, P=0.002 - biomass), other invertebrates (P<0.001 - abundance) and mean total Acari (P<0.001 - abundance).

When interactions between the different experimental variables were considered in the post-transplantation time series, there were no significant differences between; the mean abundance or biomass of time series or vegetation type or the vegetation type x mode of access or time x vegetation type x mode of access. However, when contrasted with the time zero data, there were differences between the vegetation type x time series

abundances (Appendices; XX and XXI). Overall, the mean total Acari had a significantly ($P<0.001$) higher abundance in the time zero and time series one/Ryegrass than the remaining treatments, this pattern was also followed by the Prostigmata mean total abundance ($P<0.001$). The Mesostigmata abundance is significantly ($P=0.021$) lower in both the Ryegrass/time series two and White Clover/time series two than the remaining treatments.

Within the time series and mode of access results, the mean total Acari abundance of time series one was significantly higher for top access and no access treatments ($P=0.007$) than the remaining treatments post-transplantation (Appendix XXI). The Poduromorpha abundance is significantly ($P=0.024$) lower in the top access/time series two treatment than any of the other treatments. The Prostigmata had significantly ($P<0.001$) larger abundances in the baseline sampling, top access/time series one and top access/time series three than the top access/time series two, with the remaining treatments between these two extremes. When considering the biomass data the Prostigmata had significantly ($P=0.006$) larger values in the baseline, top access/time series one and top access/time series three than the remaining treatments (Appendix XX).

5C.3.2 Soil Properties

The soil moisture content was determined simultaneously with sample collection for all sampling times. There were significantly ($P<0.001$) higher moisture contents as the experimental time increased (Figure 5C.14; Appendix XXII). Mesocosms that had a White Clover herbage coverage have a lower moisture content ($P<0.001$) than the Ryegrass (Appendix XXII). In addition, the treatments that had full mesocosm access had a significantly ($P=0.010$) higher soil moisture content than the remaining treatments (Appendix XXII).

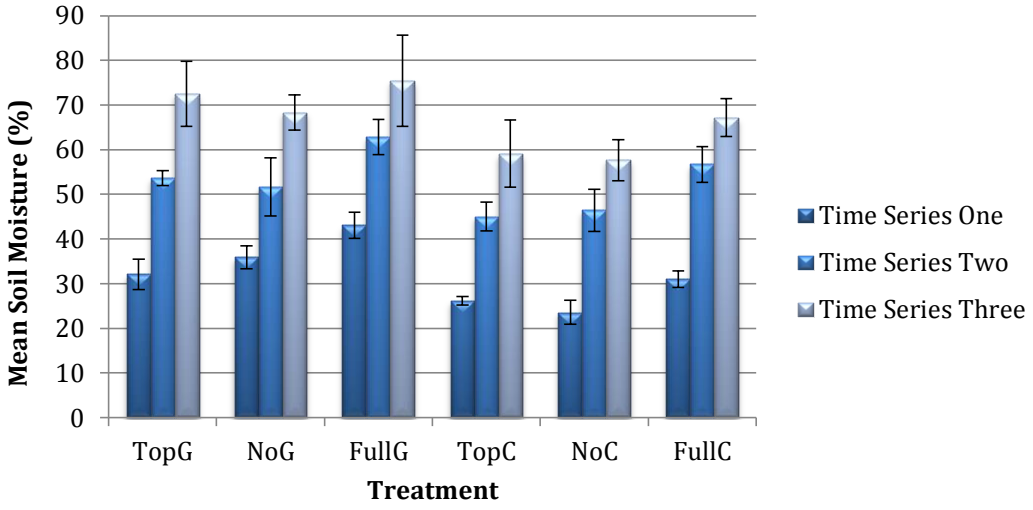


Figure 5C.14 Mean (± SE) mesocosm soil moisture (%) at each sampling point for all treatments.

The meteorological data (Section 2A.1.1) shows that the mean daily rainfall preceding the first extraction time was lower than the remaining two sampling times (Figure 5C.15).

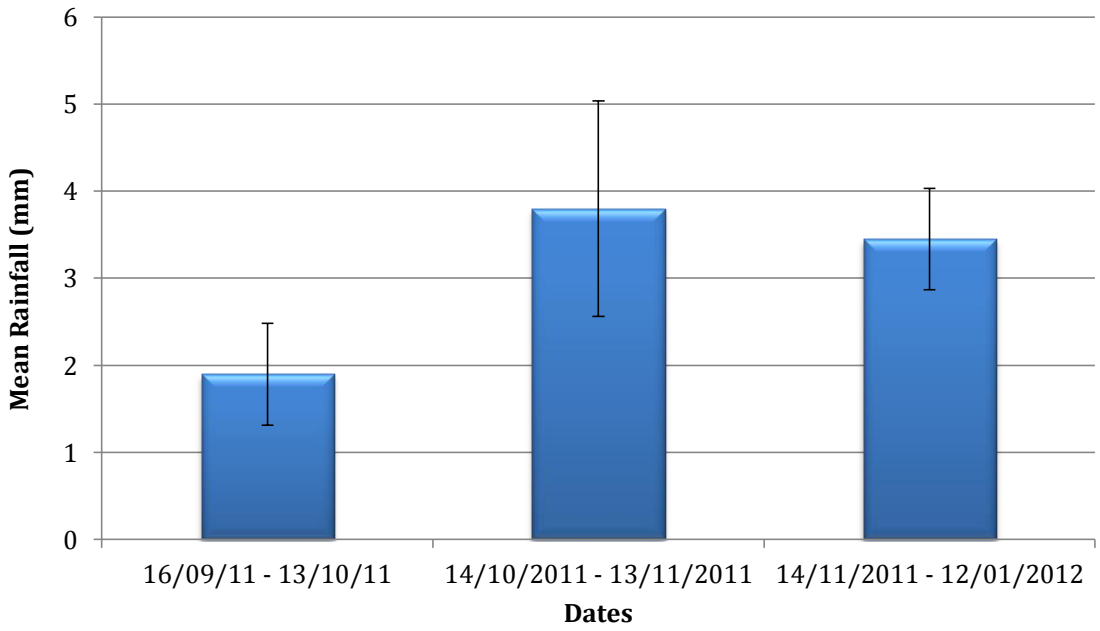


Figure 5C.15 Mean (± SE) daily rainfall (mm) at North Wyke during the experimental period.

The mesocosm plant growth was assessed using dry matter (DM) analysis, there were significant differences (P<0.001) between the mean Ryegrass (1.052g) and White Clover (0.454g) over the experimental period. There was also significantly (P<0.001) more dry matter in time period two (0.978g) than time period one (0.528g) (Appendix XXIII).

5C.3.3 Isotopic Analysis

Due to time limitations, the results for the ^{15}N isotopic analysis were limited to time series one and two only. Figure 5C.16 clearly shows that ^{15}N isotopes were detected in all of the herbage that had been analysed, for both time series one and two. In both time series, it is also apparent that the Ryegrass contains a significantly (P<0.001) larger amount of ^{15}N mg^{-2} than the White Clover. Time series two contains a significantly (P<0.001) larger ^{15}N mg^{-2} isotopic content than time series one. The ANOVA analysis also revealed that the interaction with the vegetation type and the time series was also significantly different (P<0.001) (Appendix XXIII).

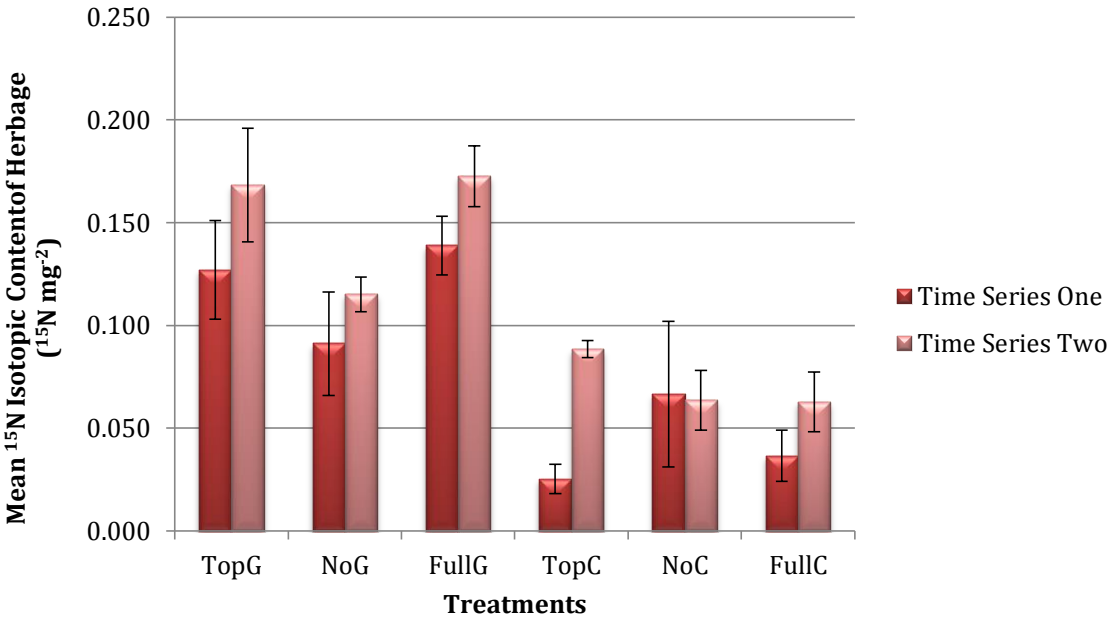


Figure 5C.16 Mean (± SE) weight (mg) of ^{15}N isotopic material detected per mg of mesocosm herbage for time series one and two, for all treatments.

5C.4 Discussion

5C.4.1 Invertebrate Populations

The time zero results indicate that the initial biomass food web and abundance was typical of managed grassland (Hopkin, 1997; Bardgett and Cook, 1998; Cole *et al*., 2006) and similar to that seen in Chapters Three and Four. The Acari were the most abundant, mostly dominated by the Prostigmata in numbers and Mesostigmata in biomass. The Collembola are dominated by the Entomobryomorpha by weight, but are also joined by the Poduromorpha in numbers, and these are finally followed by the other invertebrates. It demonstrates that a healthy population was present from which mesocosm recolonisation could be sourced.

Within the time zero mesofaunal food web diagram, there was a much larger Mesostigmata population than the other mesofauna. As predators the Mesostigmata would be expected to survive on lower trophic level populations, which in this instance appear to be smaller. However, this can be explained by the presence of other groups of prey organisms, such as microbial biomass and nematodes, that would have been present in the soil but were not included within the mesofaunal food web diagrams depicted within this chapter (Koehler, 1999; Bardgett and Wardle, 2010).

As invertebrate populations were extracted from all recovered mesocosms, it suggests that mesofauna quickly recolonized the transplanted soil. However, the abundances and biomasses recovered from the mesocosms were lower than the baseline population. This suggests that population sizes did not reach the same level as those in the surrounding environment. However, due to a lack of simultaneously collected control samples there was an inability to compare natural populations with experimental populations, highlighting a possible error in experimental design. Although there appears to have been significant changes to the mesocosm invertebrate populations throughout the

experimental time, temporal factors, such as changing seasons, are more likely to have caused these differences (Bardgett *et al*., 2005; Högberg *et al*., 2010; Schon *et al*., 2010). As the control samples were not collected, there is no record of any natural temporal fluctuation in the experimental sites invertebrate populations. These changes, such as the collapse of the Mesostigmata population in November, may therefore be temporal in nature and be unrelated to the application of the mesocosms. The collection of the remaining mesocosms may highlight whether or not the population then recovers as time progresses into the spring. The other invertebrates also show lower abundances in the mesocosms than the time zero data; although they were present in all treatments the numbers increase as the experimental time increases. These figures may demonstrate that the mesocosm design was effective for larger organisms. Many of the other invertebrates are much larger in body size (Swift, Heal and Anderson, 1979) than mesofauna and therefore their movements would have been more restricted by the mesocosm surrounds and access points. In addition, the other invertebrates are usually found in much lower densities than mesofauna (Peters, 1983) and therefore the incidence of interacting with the mesocosms within the field site may have been lower. In many cases however, larger invertebrates would have had the advantage of being able to move further distances at a much faster rate than mesofaunal groups.

The mesocosm mode of access had no effect on the size of the mesofaunal populations present in the soil throughout the investigation. This indicates that invertebrates were; a) already present in the soil due to ineffective experimental preparation, b) able to move into the mesocosms through the different access points provided or c) a mesocosm design fault provided unexpected access points.

Assuming that the experimental design had been successful, the similarities in abundance and biomass for all time periods and treatments, including the no access mesocosms,

suggest that all groups of invertebrates were able to move into the mesocosm soil to repopulate the soil within one month of transplantation. This indicates that the mesofauna were able to move through aerial dispersal or climb the mesocosm walls to enter through the top. This was completed at such a rate that after one month it equalled the rate achieved in the free access and soil surface access routes of movement. Aerial dispersal had been noted in some mesofaunal species, either as adults or as eggs (Alvarez, Frampton and Goulson, 1999; Lehmitz *et al*., 2011). However, Kampichler *et al*. (1999) determined that even after a six month time period Oribatida populations had not migrated into adjacent mesocosms. Mesocosm studies by Rygiewicz *et al*. (2010) using sieved soils determined that it took 3 years for the bacterial, fungal, nematode and amoebae populations to return to normal following construction. Lindberg and Bengtsson (2005, 2006) and Malmström, Persson and Ahlström (2008) all determined that different mesofaunal group populations recovered at different rates following a disturbance. Therefore assuming that the mesocosm isolation has been successful, a repetition of the experiment within a shorter time frame (one month), with a quicker succession of sample collection may indicate the rate at which the mesofauna are able to colonise the mesocosms. However, this assumes that the experimental design had been successful. The possibility that there had been an error in the preparation procedure or a flaw within the design is likely to have allowed mesofaunal to have entered the soil; these possibilities are discussed below.

The soil used to create the mesocosms was invertebrate free and both the soil and mesocosms had been carefully managed once assembled to ensure that they remained invertebrate free. Therefore the mesocosms should have been invertebrate free when they were transferred into the field site. However, although invertebrates had been removed through Tullgren funnel processing, sieving and 4^{o}c storage, the soil was not treated in any other way, for example freezing and thawing (Section 5B). Eggs and larvae may have

remained in the soil and then become reactivated and hatched once the soil had been added to the mesocosm pot, providing a basis for the mesofaunal population within the mesocosms. Collembolan eggs have been shown to survive desiccation and freezing (Hopkin, 1997; Alvarez, Frampton and Goulson, 1999) with similar survival adaptations within Acari species (Walter and Proctor, 1999). Additionally, some Prostigmata species have been shown to be able to complete a full life cycle in one week (Behan-Pelletier, 2003), therefore, the one month experimental time would have provided time for four generations to have developed. Although the results obtained in Section 5A suggest that Tullgren funnel extraction and storage would kill mesofaunal populations, the soil was not stored for the same time period, in addition it had be re-wetted to be sieved and then stored moist. The production and immediate extraction of control mesocosms before transplantation would have determined possible invertebrate contents before insertion and would have identified the existence of these problems.

A further error source in mesocosm design, may have allowed invertebrates to enter through alternative routes. Although the plastic walls provided a physical barrier the 4cm overlap in the Shelterguard™ sheet to produce a tube was not sealed completely. The small gap that remained may have allowed invertebrates to move into the mesocosms. Oribatida have been noted to travel at up to a few centimetres per day (Berthet, 1964) and Nielson *et al*. (2010) determined that Collembola were able to disperse at distances greater than 10cm per day, therefore one month would have been more than sufficient to complete the movement into the mesocosm. Any repetition of the experiment must seal the side of the mesocosm with silicone sealant to prevent this movement. This error is also repeated with the base disc; however, had this been completely sealed, water would not have passed through the mesocosm and caused mesocosm flooding.

The lack of significant differences in the mean invertebrate abundance and biomass between the two vegetation types, Ryegrass and White Clover, of the mesocosms suggests

that there was no link between the two at this stage in the investigation. This is in contrast to previous investigations into the benefits of leguminous plants on the soil biota (Habekost *et al*., 2008; Eisenhauer *et al*., 2009). Moreover, there was a general trend for the Ryegrass abundance to be larger than the White Clover, with further experimental time the development of ecosystem establishment may have produced a larger difference between the two vegetation types. Bezemer *et al*. (2010) determined that community composition of many soil fauna differed between plant species, although Collembola species were not affected. The causes of the differences between the time zero and the mesocosm populations are difficult to determine. As the samples were taken at different times, seasonal factors may have caused the population differences rather than vegetation factors. It was shown that the White Clover produced less dry matter than the Ryegrass and was less well-established within the mesocosms. However, investigations have determined that plant biomass does not affect community composition (Bezemer *et al*., 2010). However, a study by Eisenhauer *et al*. (2010) into the effects of legumes on invertebrate populations, displayed a four year lag phase between the introduction of the legumes and changes to the invertebrate populations. To ensure that this was not a future issue the mesocosms with the associated plants should be given longer to establish, within sunbags, before transplantation into the field. The structure of the mesocosms could have produced a microclimate, reducing the air flow around the soil surface and therefore increasing the temperature artificially (Krab *et al*., 2010).

5C.4.2 Soil Properties

The mesocosm soil moisture content increase, over the experimental time period, was consistent with the rainfall during the experiment. In addition, the presence of White Clover vegetation was associated with lower soil moisture content than Ryegrass vegetation, though this does not affect the mesofauna populations (Murray *et al*., 2006). White Clover may absorb water from the soil at a faster rate than Ryegrass, with a higher

evapotranspiration rate, causing the soil to remain drier. However, it is also noticeable that the dry matter of the two different vegetation types was also significantly different, with a larger weight in the Ryegrass treatments. The White Clover had not established as well as the Ryegrass within the mesocosms, previous studies have shown poor establishment in autumn (Herriott, 1958) and therefore the root system was not as well developed. A plants root system affects soil structure and a well-established root system will produce a soil profile where soil is well bound and held together by the roots (Jones, Lawton and Shackak., 1994; Jones *et al*., 2010). The lack of an effective root system may have caused water to move through the soil profile at a faster rate due to a poor soil structure. Both of the Full Access treatments had significantly higher soil water content than the other treatments. It would have been expected that the Full Access treatments would have better drainage than the mesocosms with restricted access and therefore the reverse would have been expected.

5C.4.3 Isotopic Analysis

The ^{15}N isotopic analysis of the herbage showed that the plants within all of the treatments for both time series had incorporated isotopes within their tissues. As the ^{15}N isotope was introduced into the system in the form of plant material, this indicates that the ^{15}N isotope was available for the plants to absorb into their root systems. In order, for this to have been achieved, the plant material will have been broken down by detritivores, such as the mesofauna and released into the soil (Pollierer *et al*., 2009).

As ^{15}N labelled isotope is not naturally present in the soil, any recorded from within plant or invertebrate tissues would have been sourced from the implanted ^{15}N material implanted into the original mesocosm soil. As the plant tissue analysed contained ^{15}N the organisms that facilitate the breakdown of plant material and nutrient release must have been present within the mesocosms. Collembola are known to graze plant and fungal

material, facilitating the release of nitrogen into the soil (Anderson, Ineson and Huish, 1983; Faber and Verhoff, 1991; Staadden *et al*., 2011). Oribatida feed directly on decaying plant material (Scheu and Setälä, 2002; Schneider *et al*., 2004) as one of their preferred food sources.

Within both time series the Ryegrass isolation pots had incorporated more of the ^{15}N isotopes than the White Clover. White Clover is a legume with the ability to fix nitrogen from the atmosphere and therefore has two possible sources of nitrogen (Elgersman and Hassink, 1997), whereas the Ryegrass only has the nitrogen available within the soil. The lower ^{15}N content within the White Clover could therefore be a result of the plants using atmospheric nitrogen as well as the nitrogen present within the soil. Time series two has a higher content than time series one. This shows that the incorporation of the ^{15}N isotope into the living plants was accumulating over time and therefore the isotopic material was still being absorbed into the plants.

5C.4.4 Further Work

In addition, to determining the ^{15}N isotopic ratios of the plant root and shoot material, it would be possible to determine the ^{15}N isotopic ratio of the invertebrates that had been collected from the mesocosms. This would be possible by cleaning all of the samples with ultra-pure water, to remove any salt solution as this would affect the results from the mass spectrometer. The samples are then weighed into a tin capsule within their individual superfamilies and placed in an oven (65^{o}C for 48h) to dry. Once dried, the samples are then analysed by mass spectrometry. Any ^{15}N present in invertebrate tissues must have been ingested either directly through consumption of the living or dead plant material or indirectly by the consumption of organisms that have utilised this material previously. Therefore analysing this material would enable further understanding of the soil food web in grassland soils under different botanical compositions.

5C.5 Conclusions

The mesocosm design and the preparation technique utilised within this investigation possibility had flaws that caused problems with the outcome of the results. Through this study, we now know how to avoid these flaws in future studies, having proven the effectiveness of the mesocosm design. Once these problems have been solved, the technique will prove to be useful in determining invertebrate mode of movement.

Although not successful in determining mesofaunal movement, the continuation of this investigation may provide further results as to the uptake of nitrogen into soil food webs and plants.

Chapter Six

General Conclusions

6.1 Introduction

The maintenance of global biodiversity at the 2010 level is a political objective (UNEP, 2002), this results from the acknowledgement that human actions are directly or indirectly responsible for biodiversity endangerment (Dirzo and Raven, 2003; Bradshaw, Sodhi and Brook, 2009). The importance of conservation and restoration of the insect community was noted by Arenz and Joern in 1996, but they also recognised that this was a difficult task due to the opaque nature of the soil environment. In recent years, most work in relation to soil mesofaunal populations has focussed on soil food web interactions (Murray *et al*., 2009), the movement of nutrients through the food web (Crotty, Blackshaw and Murray, 2011) and ecosystem services and functions (Diekötter *et al*., 2010; Pywell *et al*., 2011). The re-establishment of mesofaunal populations in degraded soil has been overlooked even given their importance as a cog within the 'biological engine of the earth' (Ritz, McHugh and Harris, 2004). This could be due to the noted difficulties in determining whether density and diversity changes are from natural or anthropogenic sources (Magurran *et al*., 2010). The complicated nature of the soil ecosystem and the resulting difficulties in attribution of the causes of population change, are highlighted repeatedly throughout this thesis.

6.2 Thesis Overview

6.2.1 Methodology: Tullgren Funnels

The use of Tullgren funnels for the invertebrate extraction from soil has been criticised for the inefficiencies, and bias towards mobile species or active stages of the life cycle (Edwards, 1991; André, Ducarme, and Lebrun, 2002). In addition, inconsistencies exist in

the literature for the time required for effective invertebrate extraction (documented in Chapters Two and Five). Investigations within this thesis have shown that extraction times for different invertebrate orders and superfamilies differ, with the "standard" five-seven days of extraction time potentially producing results biased towards Collembola recovery, at the expense of Acari individuals which take longer to exit the soil. This indicates that the methodology can be manipulated to tailor the extraction to target particular organisms or minimise the size of an unwanted sample.

In order to combat the issues of inefficiency the application of a combination of invertebrate extraction techniques could be employed. The completion of Tullgren funnel extraction with other techniques, such as hand sorting (Doblas-Miranda *et al*., 2008), centrifugation (Murphy, 1962) or flotation (Hale, 1964), would increase the recovery rates of invertebrates and reduce criticisms of this technique. This would increase the resources that are required to complete a single sampling event. However, due to the difficult nature of the substrate and other criticisms such as soil sampling depth inconsistencies, there may never be one extraction methodology that is 100% effective. However, where data are to be compared within a single investigation or even between investigations, consistency with the methodology is required, therefore the inefficiencies within the methodology will be comparable.

6.2.2 Methodology: Identification Issues

The importance of identification to the lowest taxonomic level possible is clearly demonstrated within the Highfield Reversion and Highfield Transect projects. When the data is looked at to the Order level, it appears that there are a particular number of either Acari or Collembola. However, both the Acari and Collembola have a wide range of superfamilies and species within the orders. These superfamilies and species have different life cycles, nutritional needs and abilities to obtain these needs. By differentiating

between the superfamilies further, patterns in the lifestyles and repopulation capabilities have been identified. For example, within the Highfield reversion experiment (Chapter Three) the total Collembola abundance rises year-on-year throughout the investigation, however, the abundance of the superfamily Poduromorpha is lower in 2010 than 2009. This difference would not have been noted if identification had only occurred to order. Identification to an even higher resolution (species level), could possibly have further determined differences within the superfamilies. However, within this investigation the volume of samples and invertebrates extracted would have required a huge amount of time and expertise of identify each specimen to species level. Therefore some degree of compromise must be made to best fit the required investigation outcomes. This is a problem not just within this investigation but across soil biodiversity as a whole. High resolution studies, where diversity and density have been studied to species level, have only covered a small number of ecosystems and taxonomic groups (Bardgett, 2005). In addition to the skill level required to identify soil organisms to species level, taxonomic identification keys are often incomplete with many undescribed species (Behan-Pelletier and Newton, 1999). Some estimates state that only 10% of species have been described (André, Ducarme and Lebrun, 2002), whilst others proclaim that for Acari, this figure could be as low as 4% (De Deyn and Van de Putten, 2005). Molecular techniques of identification have been described within the literature for many groups of soil invertebrates. However, as highlighted by André *et al*. (2001) without comprehensive taxonomic identification of the specimens to species linked to the development of a genomic library, molecular analysis can only indicate the number of genetically different species present. This was evident in a recent study by Wu *et al*. (2009), as specific species were not identified, conclusions related to life history strategy were lacking.

6.2.3 Temporal Fluctuations

Data from the Highfield Reversion project concluded that mesofaunal populations naturally fluctuated from year to year (Chapter Three); this corresponds with other investigations (Bardgett *et al*., 2005; Högberg *et al*., 2010; Schon *et al*., 2010). Favourable conditions for reproduction and nutritional support for the growth of the population have enabled significant increases in population to be demonstrated in control plots with no changes to management strategies (Chapter Three). It was important to ensure that conclusions relating to mesofaunal population changes, within the treatment plots, did not result from similar temporal fluctuations, but as a consequence of the implemented management changes. Shorter term temporal fluctuations were also seen within the results of Chapter Five C, where time sequence sampling from autumn (a traditional sampling time) through to winter, determined a reduction in population size. However, on this occasion control samples were not collected throughout the experimental time, consequently it is unclear as to whether the population reduction was in response to the treatments applied or a temporal fluctuation. This subsequently reduces the validity of the conclusions derived from the investigation. Both of these experiments highlighted the importance of understanding the natural temporal fluctuations in mesofaunal populations under investigation.

6.2.4 Differences in Mesofaunal Populations between Land Management Types

Chapters Three and Four reported studies of the mesofaunal populations that were naturally present in bare fallow, managed arable and managed grasslands within the same field. Each held a different mesofaunal density and diversity. The greatest densities and diversities were obtained from the managed grassland. This was Acari dominated and the communities were also relatively stable and mature, and this reflects previous investigations (Curry, 1994; Koehler, 2000). The bare fallow control plot community was

sparse and Collembola dominated but relatively stable in its composition. There are numerous explanations for the changes to community structure; Schon, Mackay and Minor (2011) determined that the Oribatida were sensitive to soil structure changes which would explain the reduction in Acari abundance. Whereas Sabais, Scheu and Eisenhauer (2011) determined that Collembola are able to survive relocation in the soil profile and then re-migrate back to their original position. The arable control plots were the most unstable with switching between Collembola and Acari dominated food webs occurring at different sampling times. The diversity and density was also lower than that of the grassland ecosystem. The interchanging between Acari and Collembola suggest a fluctuating community, this instability has been stated to reflect short term environmental changes (Chernova and Kuznetsova, 2000).

6.2.5 Effects of Ploughing

The disruptive effect of ploughing to the soil profile has been documented to disrupt mesofaunal populations (Cole, Buckland and Bardgett, 2008). Within these investigations, continuous ploughing clearly caused considerable disturbance to the mesofaunal populations. However, although population numbers dropped after the initial ploughing of the grass plots during conversion, the differences from the retained grass plots were not significant (Chapter Three). Within the grass to arable conversion, the populations increased following conversion. This may have resulted from the incorporation of the grass to the soil, making it available to the microfloral population for decomposition. This increases the populations at the food web base, and therefore the subsequent populations that feed upon them (Roger-Estrade *et al*., 2010). Therefore it could be hypothesised that occasional disturbance to the soil increases nutrient turnover and soil biota population sizes without damaging the overall population community structures. However, this increase in population may have been followed by a decline once the excessive nutrient availability had reduced. In order to test this hypothesis, time series sampling would be

required for both carbon availability and invertebrate populations within the soil. This would determine the presence of any pattern and time lag between the reduction in resources and reduction in population sizes. This hypothesis has similarities to the intermediate disturbance hypothesis, where species diversity within the Budonga Forest was highest where disturbances were intermediate in both intensity and frequency (Connell, 1978).

6.2.6 Effects of Management Change

Both the Highfield Reversion (Chapter Three) and Highfield Transect (Chapter Four) experiments demonstrated that, following management change, mesofaunal communities were able to repopulate soil that previously had reduced population sizes. The restoration of the grassland plant community was beneficial not only for above ground communities but also below ground, as determined in previous investigations (Bezemer *et al*., 2010). However, it must be noted that there is some evidence that species rich grasslands used for forage can be less productive than the fertilised equivalent (Bullock, Pywell and Walker, 2007) and therefore may not be commercially viable. Management change can produce soil conditions that are favourable to support mesofaunal life and allow reproduction, although Chazdon (2008) believed that once a soil has been degraded, a return to the original soil quality is difficult to achieve. The arable conversion also recorded changes to the supported populations, demonstrating that the management regime and plant species affect the development of the soil food web. Viketoft *et al*. (2009) recorded differences in nematode communities with different plant species; as nematodes are prey for many mesofaunal consumers this would affect mesofaunal community structure. It was unclear as to the origin of the population increase; whether this was caused by individual organism dispersal into the experimental plots or the result of a re-activation of larvae or eggs, or rapid reproduction of the organisms already present. Furthermore, Sabais, Scheu and Eisenhauer (2011) determined that some species of

Collembola were able to migrate vertically in order to return to their original position within the soil profile following a distributional disturbance, such as ploughing. Microbial populations have been shown to maintain the diversity of the population in the presence of low carbon inputs, even when the density has significantly dropped (Hirsch *et al*., 2009). Sala *et al.* (2000) stated that species composition change in the face of land use change will have a predictable pattern. However, results from the arable plots provided variable and unpredictable outcomes from ploughing even within the same sampling period. Further investigation into the predictability of community composition change, in the event of non-destructive or destructive management techniques, could determine predictability.

6.2.7 Mode of Re-Establishment

The mode of re-establishment was not determined within the Highfield project, as there was no conclusive data to suggest that populations were travelling across the buffer zone into the experimental plots. However, work completed for Chapter Five provided a basis on which to continue the investigation of mesofaunal movement in the field. Preliminary results suggest that the described methods could effectively determine the substrate through which the mesofauna were moving.

6.2.8 Ecosystem Restoration

There are various suggestions for the mode of ecosystem restoration; some have proven to be more successful than others. Kardol *et al*., 2009 determined that although whole turf transplantation was relatively successful for the floral species the soil fauna were more sensitive to their relocation. Smith, Potts and Eggleton (2008a) provided evidence that the close proximity of hedgerows to field boundary grass strips enhanced macrofaunal repopulation. Natural repopulation of the experimental plots in both the Highfield Reversion experiment (Chapters Three and Four) and the mesocosm repopulation

experiment (Chapter Five C) occurred when favourable environmental conditions were provided by the altered management regimes. The communities developing within the new management regimes of the Highfield Reversion experiment appeared to be similar to the populations within the control plots, at least to superfamily level. Similar experiments have proposed that, following restoration, the rate of recovery for different organisms will differ, even when they are inter-dependent (Wassenaar *et al*., 2005). This will have an impact on the ecosystem services and functions that are completed by the soil biota. As the food web develops and changes, alterations will occur to carbon and nutrient cycling rates, this will in turn affect plant growth and carbon sequestration rates (Van Dijk *et al*., 2009).

6.3 Further Work

6.3.1 Laboratory Scale Movement Experiments

The small scale, highly controlled environment of the laboratory would serve to investigate the stimulus for mesofaunal movement. The application of tracking software, could record and analyse mesofaunal movement within a controlled space to different stimuli, could ascertain whether movement was random or directional. This can be further developed with the addition of other objects within the controlled chamber to determine if the mesofauna are able to negotiate these obstacles.

6.3.2 Mesocosm Scale Movement Experiments

As a continuation of the laboratory video-tracking experiment, it may be possible to track organisms through mesocosm scale experiments with the use of florescent labelling. Florescent labelling has been utilised within the aquatic environment (Lard *et al*., 2010) to track zooplankton in both light and dark environments. This same technology could be applied to mesofauna in mesocosms. A simulated mesocosm environment can be structured with transparent sides and monitored by video tracking to determine movement within the soil profile and across the soil surface.

It has been hypothesised that mesofauna use pores within the soil profile as tracks to move around. In order to determine the effect of pore size and connectivity on mesofaunal movement and survival, the use of CT scanning techniques could be employed. Unpublished preliminary data (Williams, Otten and Murray, unpublished) has shown that CT scanning has the ability to map the size, shape, location and connectivity of soil pores within a soil core, however, analysis proved to be time consuming. By combining this technique with the extraction and reintroduction of mesofauna to a soil core, there is a possibility for the volume of habitable space to be calculated.

6.3.3 Field Scale Movements

At the field scale, continuation of the Highfield Reversion experiment would enhance the data already collected. Data of this type needs to be collected over a sustained time period, as it is unclear from the results whether a stable and mature population had been reached following management change. At present, the target for successful restoration of the ecosystem under the new management system has not been determined; a suitable reference point to allow evaluation should be selected (Aronson, Dhillion and Le Floc'h, 1995). Alternatively, the experiment would continue until a plateau had been recorded indicating that a climax community has been reached. Grassland restoration studies on aboveground food webs, based on plant species and beetle assemblages, took over six years to reach the comparable target grassland (Woodcock *et al*., 2012). Moreover, the information recorded must be considered alongside the other experimental results collected from the experiment, such as the microbial population data and soil physics data. Soil is a complex environment and is rarely studied from a holistic view point, however, this approach, termed the "Ecosystem Approach" is now being promoted by Defra (2007).

To complement this holistic approach, and to continue the investigation into the modes of mesofaunal movement, other invertebrate collection techniques should be employed on

the Highfield Reversion experiment. These techniques such as sticky traps (Lehmitz *et al*., 2011) and pitfall traps (Edwards, 1991) would allow the mode of transport or movement of the mesofauna to be determined. Sticky traps placed at differing heights would provide information on aerial movement of mesofauna, whilst pitfall traps will collect those animals that have travelled across the soils surface and fallen into the trap.

6.4 Conclusions

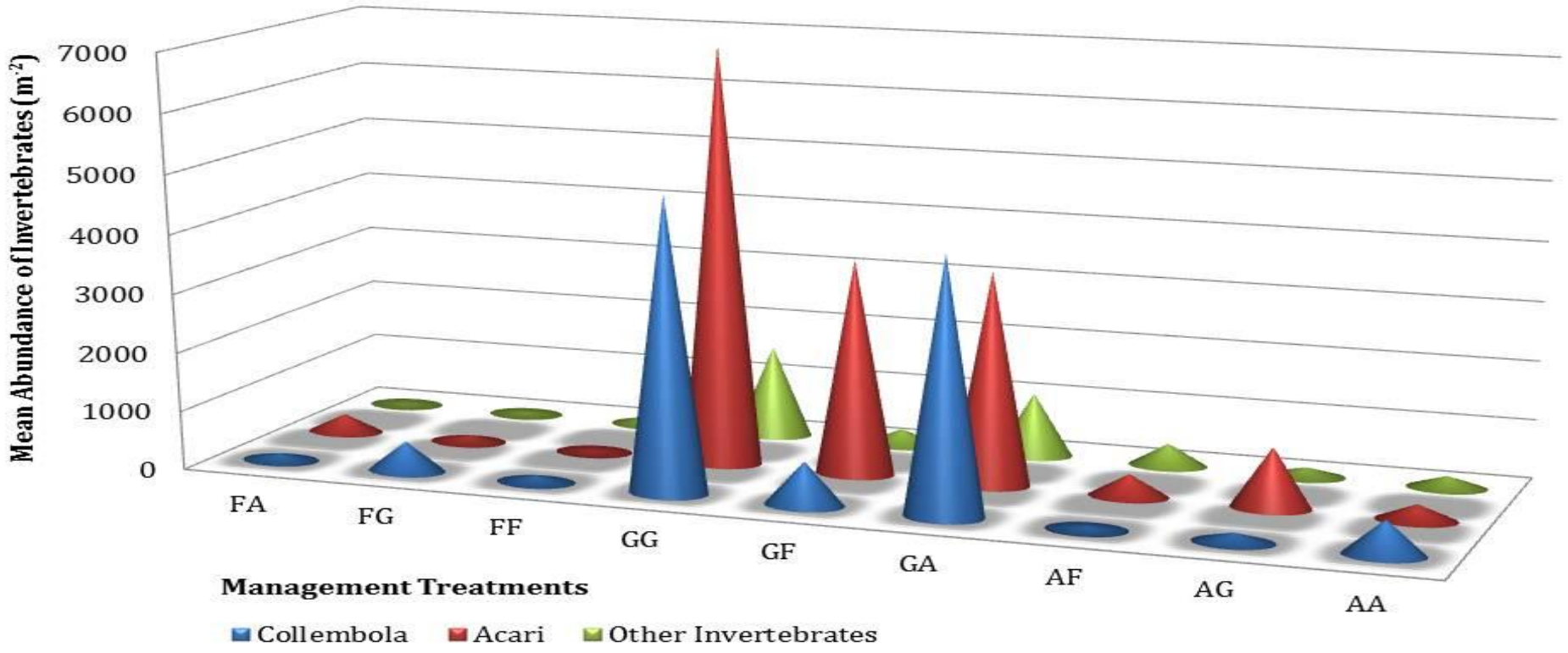
This thesis has determined that mesofaunal populations are able to repopulate heavily degraded soils, where the conditions have been changed by alterations to management practices. Conversion of arable or fallow land to grassland increases both the density and diversity of the organisms inhabiting the ecosystem. Additionally, it has been shown that conversion of grassland, with a healthy mesofaunal population, to either arable or fallow, leads to a dramatic decrease in the populations that were present. These changes to population occurred quickly and were maintained for the two years of the investigation.

However, although there were changes to the populations with changing management techniques, there is no evidence as to the mode of repopulation within these soils. Determining the mode of repopulation is important for the implementation and success of ecosystem restoration. This knowledge will enable ecologists to plan the management techniques employed to promote repopulation of an ecosystem. For example, either nearby populations in similar habitats provide source populations or physical reintroduction maybe required. The populations within this investigation were either able to repopulate the soil through reproduction (from within the experimental plots) or through dispersal into the plots, further experimental work would be required to determine this.

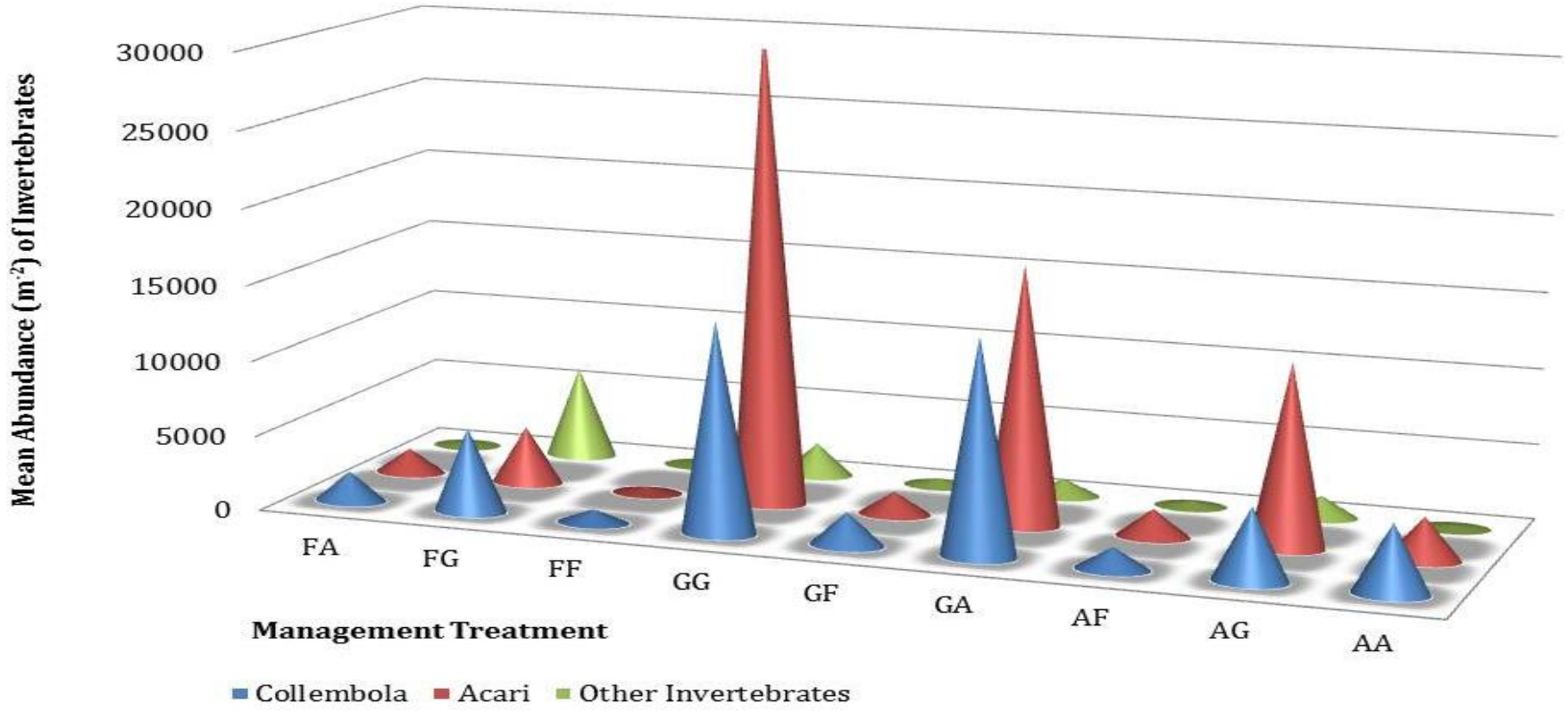
Appendix I The mean biomass (µg m^{-2}) (±SE) for each mesofaunal superfamily, for each treatment, within the Highfield Reversion Project.

Year	Treatment	Mean biomass (µg m^{-2}) (±SE) for the mesofaunal superfamilies for each treatment					
		Acari			Collembola		
		Prostigmata	Oribatida	Mesostigmata	Entomobryomorpha	Symphyphleona	Poduromorpha
October 2008	FA	36 (±18)	467 (±371)	600 (±600)	200 (±200)	0 (±0)	88 (±44)
	FF	0 (±0)	67 (±67)	0 (±0)	67 (±67)	0 (±0)	178 (±118)
	FG	18 (±18)	133 (±67)	0 (±0)	67 (±67)	0 (±0)	978 (±978)
	AA	18 (±18)	734 (±133)	0 (±0)	0 (±0)	44 (±22)	1067 (±937)
	AF	36 (±18)	867 (±176)	600 (±300)	67 (±67)	44 (±44)	0 (±0)
	AG	178 (±178)	2068 (±941)	1501 (±1082)	0 (±0)	44 (±22)	222 (±44)
	GA	961 (±882)	5069 (±2055)	9605 (±5103)	9205 (±9005)	378 (±378)	1690 (±1166)
	GF	142 (±36)	9271 (±7164)	5103 (±2668)	734 (±291)	67 (±39)	845 (±424)
	GG	712 (±339)	15875 (±9216)	12306 (±6416)	6537 (±3256)	556 (±424)	4447 (±3377)
October 2009	FA	338 (±312)	3068 (±996)	3002 (±1082)	1267 (±437)	111 (±111)	2979 (±618)
	FF	53 (±53)	934 (±406)	900 (±520)	267 (±176)	0 (±0)	1645 (±978)
	FG	409 (±280)	6136 (±2816)	17409 (±7958)	7337 (±3482)	178 (±178)	6047 (±3650)
	AA	125 (±36)	7104 (±1366)	4652 (±1051)	7037 (±3573)	0 (±0)	4424 (±790)
	AF	18 (±18)	5069 (±1813)	2101 (±794)	1534 (±437)	0 (±0)	1912 (±618)
	AG	391 (±139)	31149 (±6486)	16508 (±5703)	5870 (±706)	311 (±212)	5114 (±963)
	GA	1494 (±740)	30015 (±15662)	71436 (±37741)	23812 (±8304)	934 (±657)	10672 (±4138)
	GF	125 (±47)	2535 (±636)	7504 (±3902)	1734 (±811)	22 (±22)	3246 (±1051)
	GG	1352 (±329)	60897 (±29563)	131466 (±59600)	24212 (±8728)	623 (±523)	10539 (±2068)
October 2010	FA	1761 (±844)	8004 (±2665)	25213 (±5995)	8538 (±5737)	133 (±67)	2712 (±641)
	FF	285 (±94)	2068 (±734)	2401 (±1501)	1934 (±934)	133 (±77)	623 (±89)
	FG	5158 (±2998)	11272 (±983)	81341 (±61174)	41354 (±35199)	356 (±89)	35084 (±30224)
	AA	285 (±158)	20410 (±8089)	12906 (±5726)	1868 (±769)	400 (±176)	3735 (±1811)
	AF	285 (±158)	11206 (±58)	3902 (±600)	5736 (±1140)	600 (±534)	3958 (±2957)
	AG	6723 (±5310)	101651 (±32318)	142871 (±41461)	17809 (±1744)	222 (±118)	23434 (±1328)
	GA	2472 (±1224)	44222 (±25612)	77739 (±46039)	31816 (±10085)	2668 (±1816)	5203 (±2042)
	GF	996 (±125)	6870 (±1948)	28214 (±16639)	8671 (±2131)	978 (±488)	2846 (±664)
	GG	3593 (±1992)	90245 (±37466)	130565 (±48424)	38219 (±8340)	1045 (±235)	8004 (±3535)

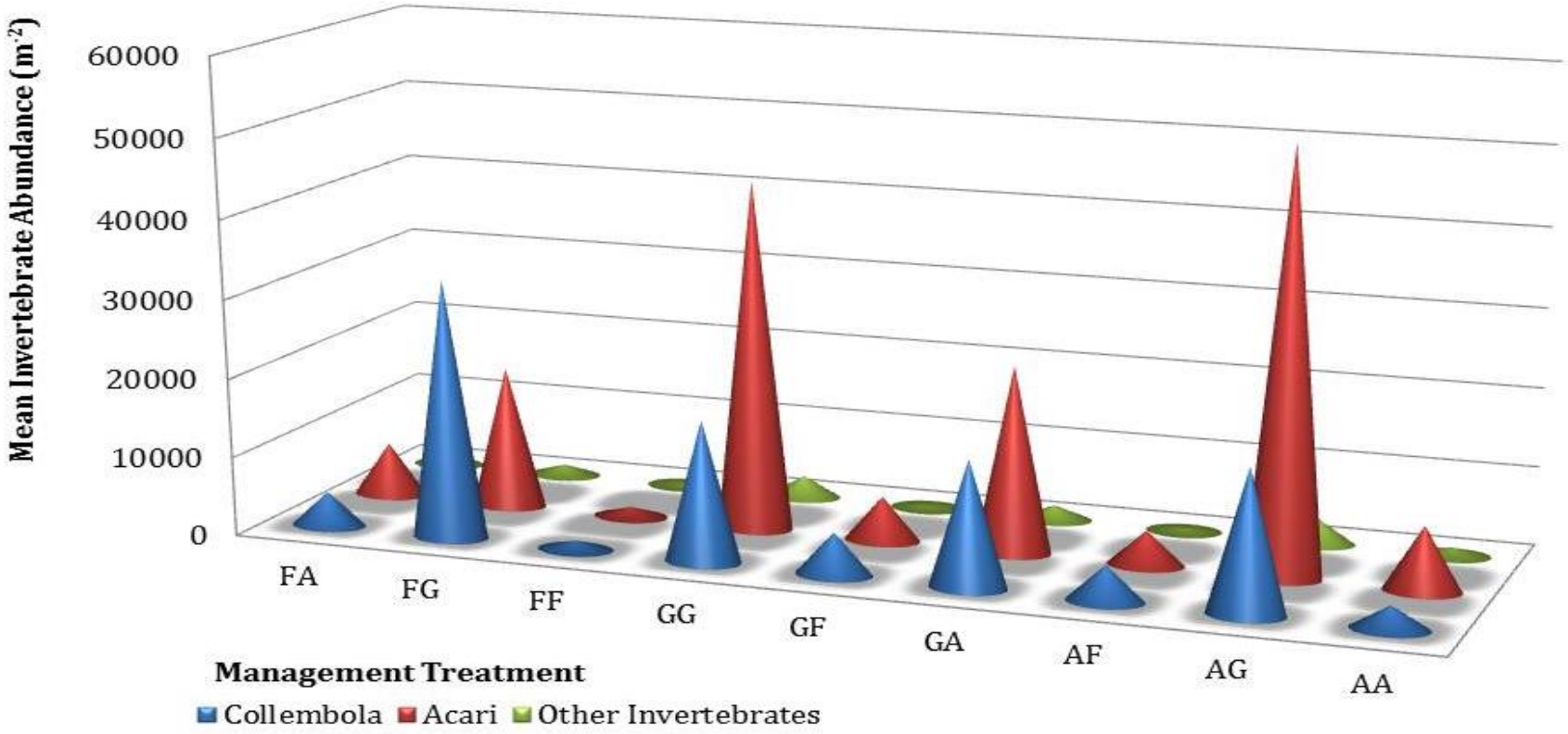
Appendix II The mean abundance of invertebrates (m^{-2}), divided into the Collembola, Acari and other invertebrates, collected from nine treatments (displayed as original treatment – reversion treatment) on the Highfield Reversion experiment in October 2008 during the conversion process.



Appendix III The mean abundance of invertebrates (m^{-2}), divided into the Collembola, Acari and other invertebrates, collected from nine treatments (displayed as original treatment – reversion treatment) on the Highfield Reversion experiment in October 2009 during the conversion process.



Appendix IV The mean abundance of invertebrates (m^{-2}), divided into the Collembola, Acari and other invertebrates, collected from nine treatments (displayed as original treatment – reversion treatment) on the Highfield Reversion experiment in October 2010 during the conversion process.



Appendix V The mean (±SE) mesofaunal superfamily abundance (m^{-2}), recovered throughout the post-conversion sampling of the Highfield Reversion Project, divided into three tables: 2008, 2009, 2010. Significant differences between treatments, obtained by ANOVA (on $LOG_e(n+1)$ transformed data) for each invertebrate group are indicted with *, probability values are shown at the base of the column (for each sampling period). Where significant differences exist, and statistical ranking has been applied, the reference below the probability value denotes the location within the text where a full description of the statistical ranking can be obtained.

2008

Sampling Period	Treatment	Mean Abundance of Mesofaunal Superfamilies (m^{-2}) (±SE)								Other Invertebrates
		Collembola				Acari				
		Entomobryomorpha	Poduromorpha	Symphyphleona	Total Collembola	Prostigmata	Oribatida	Mesostigmata	Total Acari	
2008	Fallow-Arable	67 (±67)*	44 (±22)	0 (±0)	111 (±80)	44 (±22)	156 (±124)*	44 (±44)	311 (±248)*	22 (±22)*
	Fallow-Grass	22 (±22)*	489 (±489)	0 (±0)	511 (±478)	22 (±22)	44 (±22)*	0 (±0)	111 (±44)*	44 (±22)*
	Fallow-Fallow	22 (±22)*	89 (±59)	0 (±0)	111 (±80)	0 (±0)	22 (±22)*	0 (±0)	44 (±44)*	133 (±77)*
	Grass-Grass	2179 (±1085)*	2223 (±1688)	556 (±424)	4958 (±3051)	889 (±424)	5292 (±3072)*	912 (±475)	7092 (±3563)*	1556 (±485)*
	Grass-Fallow	245 (±97)*	422 (±212)	67 (±39)	734 (±315)	178 (±44)	3090 (±2388)*	378 (±198)	3646 (±2525)*	267 (±102)*
	Grass-Arable	3068 (±3002)*	845 (±583)	378 (±378)	4291 (±3958)	1201 (±1102)	1690 (±685)*	711 (±378)	3602 (±2038)*	1067 (±462)*
	Arable -Fallow	22 (±22)*	0 (±0)	44 (±44)	67 (±67)	44 (±22)	289 (±59)*	44 (±22)	378 (±80)*	378 (±232)*
	Arable-Grass	0 (±0)*	111 (±22)	44 (±22)	156 (±22)	222 (±222)	689 (±314)*	111 (±80)	1023 (±508)*	156 (±44)*
	Arable-Arable	0 (±0)*	534 (±468)	44 (±22)	578 (±481)	22 (±22)	245 (±44)*	0 (±0)	267 (±39)*	200 (±0)*
		* P=0.004 pp.62					* P=0.007 pp.66		* P=0.006 pp.64	* P=0.048 pp.69

2009

		Mean Abundance of Mesofaunal Superfamilies (m^{-2}) (±SE)								
Sampling Period	Treatment	Entomobryomorpha	Poduromorpha	Symphyphleona	Total Collembola	Prostigmata	Oribatida	Mesostigmata	Total Acari	Other Invertebrates
2009	Fallow-Arable	422 (±146)*	1490 (±309)*	111 (±111)	2023 (±289)*	422 (±390)*	1023 (±332)*	222 (±80)*	1668 (±578)*	222 (±97)
	Fallow-Grass	2446 (±1161)*	3024 (±1825)*	178 (±178)	5647 (±3006)*	511 (±349)*	2045 (±939)*	1290 (±589)*	3846 (±778)*	6136 (±5444)
	Fallow-Fallow	89 (±59)*	823 (±489)*	0 (±0)	912 (±545)*	67 (±67)*	311 (±135)*	67 (±39)*	445 (±156)*	133 (±39)
	Grass-Grass	8071 (±2909)*	5269 (±1034)*	623 (±523)	13963 (±4463)*	1690 (±412)*	20299 (±9854)*	9738 (±4415)*	31727 (±13832)*	2223 (±988)
	Grass-Fallow	578 (±270)*	1623 (±526)*	22 (±22)	2223 (±370)*	156 (±59)*	845 (±212)*	556 (±289)*	1556 (±459)*	467 (±240)
	Grass-Arable	7937 (±2768)*	5336 (±2069)*	934 (±657)	14207 (±4795)*	1868 (±925)*	10005 (±5221)*	5292 (±2796)*	17164 (±8711)*	1156 (±540)
	Arable -Fallow	511 (±146)*	956 (±309)*	0 (±0)	1467 (±429)*	22 (±22)*	1690 (±604)*	156 (±59)*	1868 (±648)*	378 (±118)
	Arable-Grass	1957 (±235)*	2557 (±481)*	311 (±212)	4825 (±761)*	489 (±174)*	10383 (±2162)*	1223 (±422)*	12095 (±2758)*	1445 (±388)
	Arable-Arable	2346 (±1191)*	2212 (±395)*	0 (±0)	4558 (±1566)*	156 (±44)*	2368 (±455)*	345 (±78)*	2868 (±534)*	245 (±118)
		* P<0.001 pp.63	* P=0.008 pp.63		*P<0.001 pp.61	* P=0.009 pp.67	* P=0.006 pp.67	*P<0.001 pp.67	*P<0.001 pp.65	

2010

		Mean Abundance of Mesofaunal Superfamilies (m^{-2}) (±SE)								
Sampling Period	Treatment	Entomobryomorpha	Poduromorpha	Symphyphleona	Total Collembola	Prostigmata	Oribatida	Mesostigmata	Total Acari	Other Invertebrates
2010	Fallow-Arable	2846 (±1912)*	1356 (±321)*	133 (±67)	4336 (±1577)*	2201 (±1055)	2668 (±888)*	1868 (±444)*	6737 (±2094)*	600 (±139)*
	Fallow-Grass	14341 (±11440)*	17942 (±14907)*	489 (±118)	32772 (±13585)*	7070 (±3373)	3313 (±743)*	7604 (±3899)*	17987 (±7626)*	1334 (±77)*
	Fallow-Fallow	645 (±311)*	311 (±44)*	133 (±77)	1089 (±292)*	356 (±118)	689 (±245)*	178 (±111)*	1223 (±89)*	89 (±22)*
	Grass-Grass	12740 (±2780)*	4002 (±1768)*	1045 (±235)	17787 (±4662)*	4491 (±2490)	30082 (±12489)*	9672 (±3587)*	44244 (±17213)*	2735 (±1755)*
	Grass-Fallow	2890 (±710)*	1423 (±332)*	978 (±488)	5292 (±332)*	1245 (±156)	2290 (±649)*	2090 (±1232)*	5625 (±676)*	245 (±44)*
	Grass-Arable	10605 (±3362)*	2601 (±1021)*	2668 (±1816)	15875 (±6125)*	3090 (±1529)	14741 (±8537)*	5758 (±3410)*	23590 (±12462)*	1823 (±1085)*
	Arable -Fallow	1912 (±380)*	1979 (±1479)*	600 (±534)	4491 (±1060)*	356 (±198)	3735 (±1936)*	289 (±44)*	4380 (±2146)*	334 (±67)*
	Arable-Grass	5936 (±581)*	11717 (±664)*	222 (±118)	17876 (±1316)*	8404 (±6637)	33884 (±10773)*	10583 (±3071)*	52871 (±7000)*	3202 (±240)*
	Arable-Arable	623 (±256)*	1868 (±906)*	400 (±176)	2890 (±1234)*	356 (±198)	6803 (±2686)*	956 (±424)*	8115 (±2210)*	1023 (±212)*
		* P<0.001 pp.64	* P=0.005 pp.64		*P<0.001 pp.61		*P<0.001 pp.69	*P<0.001 pp.67	*P<0.001 pp.65	*P<0.001 pp.70

Appendix VI The mean other invertebrates abundance (m^{-2}) (±SE) results for all three post-conversion sampling years (2008, 2009 and 2010), Highfield Reversion project.

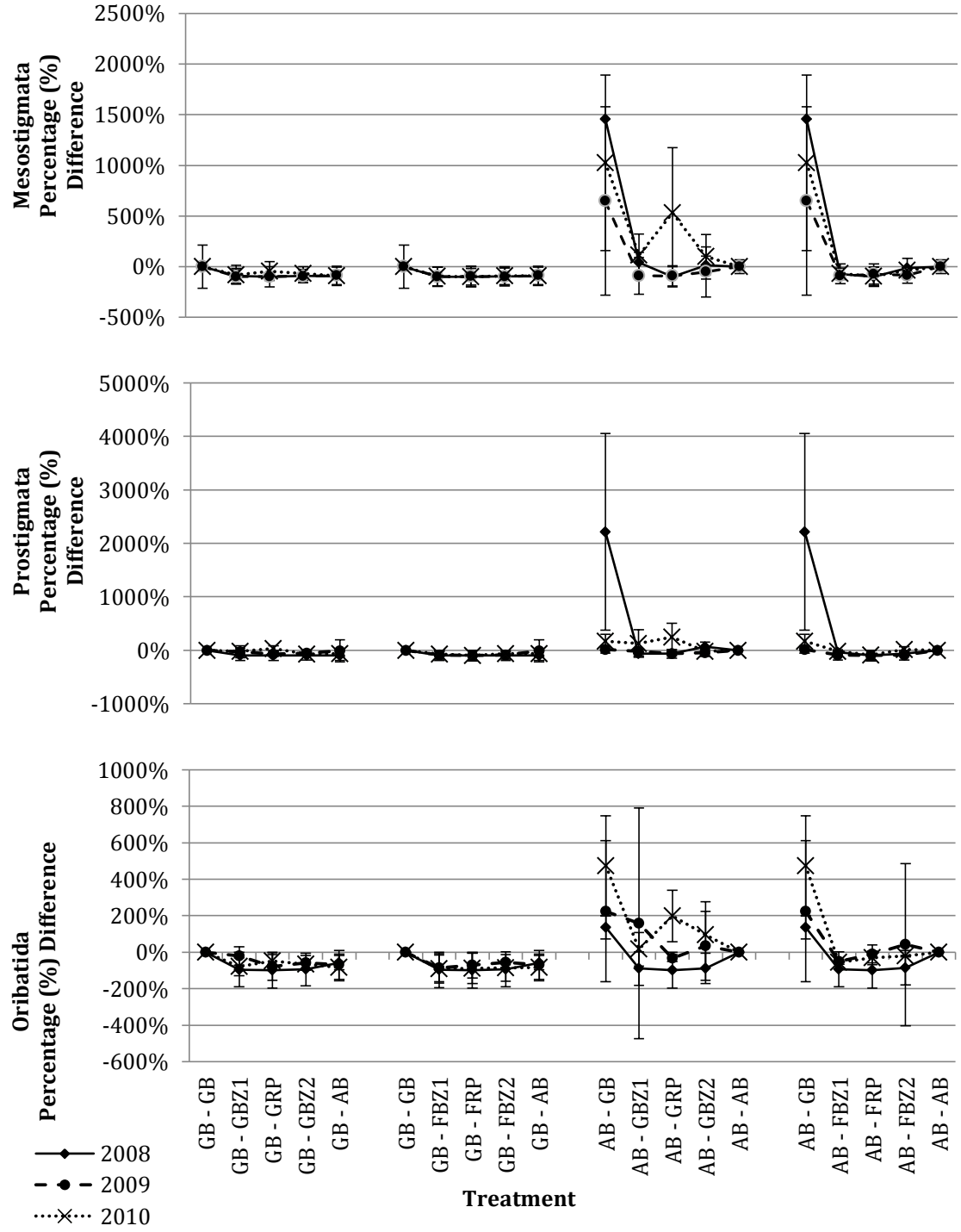
Sampling Year	Management Treatment	Mean (±SE) Abundance of Invertebrates (m^{-2})														
		Predators					Detrivores			Herbivores			Undetermined			
		Coleoptera larvae	Diptera larvae	Chilopoda	Coleoptera	Araneida	Isopoda	Annelida	Diplopoda	Gastropoda	Caterpillar	Hemiptera	Hymenoptera	Diptera	Diplura	Unidentified
2008	FA	0 (±0)	267 (±77)	0 (±0)	0 (±0)	44 (±22)	0 (±0)	0 (±0)	0 (±0)	0 (±0)	0 (±0)	0 (±0)	0 (±0)	267 (±267)	0 (±0)	22 (±22)
	FG	44 (±44)	311 (±311)	200 (±168)	111 (±111)	0 (±0)	0 (±0)	22 (±22)	22 (±22)	0 (±0)	0 (±0)	0 (±0)	0 (±0)	89 (±59)	22 (±22)	0 (±0)
	FF	0 (±0)	0 (±0)	0 (±0)	0 (±0)	0 (±0)	0 (±0)	44 (±22)	0 (±0)	0 (±0)	0 (±0)	0 (±0)	0 (±0)	400 (±168)	0 (±0)	0 (±0)
	GG	44 (±44)	1378 (1378)	311 (±311)	267 (±267)	44 (±22)	0 (±0)	267 (±204)	22 (±22)	0 (±0)	0 (±0)	0 (±0)	0 (±0)	1112 (±1078)	44 (±44)	156 (±156)
	GF	0 (±0)	0 (±0)	0 (±0)	0 (±0)	0 (±0)	0 (±0)	0 (±0)	0 (±0)	0 (±0)	0 (±0)	0 (±0)	0 (±0)	0 (±0)	0 (±0)	0 (±0)
	GA	0 (±0)	44 (±44)	0 (±0)	0 (±0)	0 (±0)	0 (±0)	0 (±0)	0 (±0)	0 (±0)	0 (±0)	0 (±0)	0 (±0)	200 (±168)	0 (±0)	0 (±0)
	AF	0 (±0)	267 (±267)	89 (±89)	67 (±67)	0 (±0)	0 (±0)	44 (±44)	0 (±0)	0 (±0)	0 (±0)	0 (±0)	0 (±0)	44 (±44)	22 (±22)	89 (±89)
	AG	0 (±0)	22 (±22)	0 (±0)	0 (±0)	0 (±0)	0 (±0)	22 (±22)	0 (±0)	0 (±0)	0 (±0)	0 (±0)	0 (±0)	0 (±0)	0 (±0)	0 (±0)
	AA	0 (±0)	44 (±44)	0 (±0)	0 (±0)	0 (±0)	0 (±0)	0 (±0)	0 (±0)	0 (±0)	0 (±0)	0 (±0)	0 (±0)	0 (±0)	0 (±0)	0 (±0)
2009	FA	0 (±0)	44 (±44)	0 (±0)	0 (±0)	22 (±22)	0 (±0)	0 (±0)	0 (±0)	22 (±22)	0 (±0)	22 (±22)	0 (±0)	67 (±0)	0 (±0)	22 (±22)
	FG	111 (±22)	89 (±89)	0 (±0)	200 (±102)	0 (±0)	0 (±0)	44 (±44)	0 (±0)	0 (±0)	0 (±0)	5558 (±5558)	44 (±22)	89 (±59)	0 (±0)	0 (±0)
	FF	22 (±22)	22 (±22)	0 (±0)	0 (±0)	0 (±0)	0 (±0)	0 (±0)	0 (±0)	0 (±0)	0 (±0)	67 (±39)	0 (±0)	22 (±22)	0 (±0)	0 (±0)

	GG	467 (±342)	200 (±101)	356 (±146)	422 (±219)	111 (±59)	0 (±0)	44 (±44)	22 (±22)	0 (±0)	0 (±0)	200 (±168)	44 (±44)	156 (±59)	200 (±139)	0 (±0)
	GF	178 (±146)	178 (±80)	22 (±22)	44 (±22)	0 (±0)	0 (±0)	0 (±0)	0 (±0)	0 (±0)	0 (±0)	0 (±0)	0 (±0)	44 (±22)	0 (±0)	0 (±0)
	GA	534 (±193)	67 (±67)	222 (±222)	67 (±39)	0 (±0)	0 (±0)	67 (±39)	44 (±22)	0 (±0)	22 (±22)	44 (±44)	0 (±0)	22 (±22)	0 (±0)	0 (±0)
	AF	44 (±22)	111 (±80)	0 (±0)	44 (±22)	0 (±0)	0 (±0)	0 (±0)	22 (±22)	0 (±0)	0 (±0)	67 (±0)	0 (±0)	67 (±67)	0 (±0)	0 (±0)
	AG	245 (±22)	334 (±168)	22 (±22)	133 (±39)	0 (±0)	0 (±0)	22 (±22)	178 (±44)	0 (±0)	22 (±22)	311 (±194)	0 (±0)	67 (±39)	111 (±59)	0 (±0)
	AA	0 (±0)	0 (±0)	0 (±0)	0 (±0)	0 (±0)	0 (±0)	0 (±0)	44 (±44)	0 (±0)	0 (±0)	44 (±22)	44 (±22)	67 (±39)	0 (±0)	0 (±0)
	FA	378 (±80)	245 (±80)	0 (±0)	44 (±22)	89 (±22)	0 (±0)	67 (±0)	0 (±0)	0 (±0)	0 (±0)	44 (±22)	0 (±0)	0 (±0)	44 (±22)	0 (±0)
	FG	334 (±102)	534 (±134)	22 (±22)	67 (±39)	44 (±44)	0 (±0)	44 (±44)	0 (±0)	0 (±0)	0 (±0)	245 (±146)	0 (±0)	22 (±22)	0 (±0)	0 (±0)
	FF	0 (±0)	44 (±22)	0 (±0)	0 (±0)	0 (±0)	0 (±0)	0 (±0)	0 (±0)	0 (±0)	0 (±0)	0 (±0)	0 (±0)	0 (±0)	0 (±0)	0 (±0)
	GG	356 (±44)	89 (±59)	578 (±358)	89 (±59)	0 (±0)	89 (±89)	67 (±39)	89 (±59)	0 (±0)	0 (±0)	245 (±212)	400 (±400)	0 (±0)	600 (±473)	22 (±22)
2010	GF	0 (±0)	44 (±22)	44 (±22)	0 (±0)	0 (±0)	0 (±0)	0 (±0)	44 (±22)	0 (±0)	0 (±0)	44 (±22)	0 (±0)	22 (±22)	22 (±22)	0 (±0)
	GA	222 (±124)	467 (±176)	400 (±336)	111 (±80)	67 (±67)	22 (±22)	44 (±44)	67 (±39)	0 (±0)	67 (±39)	22 (±22)	22 (±22)	22 (±22)	289 (±256)	0 (±0)
	AF	89 (±22)	22 (±22)	67 (±0)	22 (±22)	0 (±0)	0 (±0)	44 (±44)	44 (±44)	0 (±0)	0 (±0)	22 (±22)	0 (±0)	22 (±22)	0 (±0)	0 (±0)
	AG	578 (±198)	867 (±501)	711 (±232)	422 (±59)	67 (±39)	0 (±0)	156 (±22)	44 (±22)	0 (±0)	22 (±22)	0 (±0)	67 (±67)	0 (±0)	222 (±118)	44 (±44)
	AA	156 (±80)	400 (±139)	133 (±77)	22 (±22)	0 (±0)	0 (±0)	89 (±22)	133 (±102)	0 (±0)	0 (±0)	44 (±44)	0 (±0)	0 (±0)	22 (±22)	0 (±0)

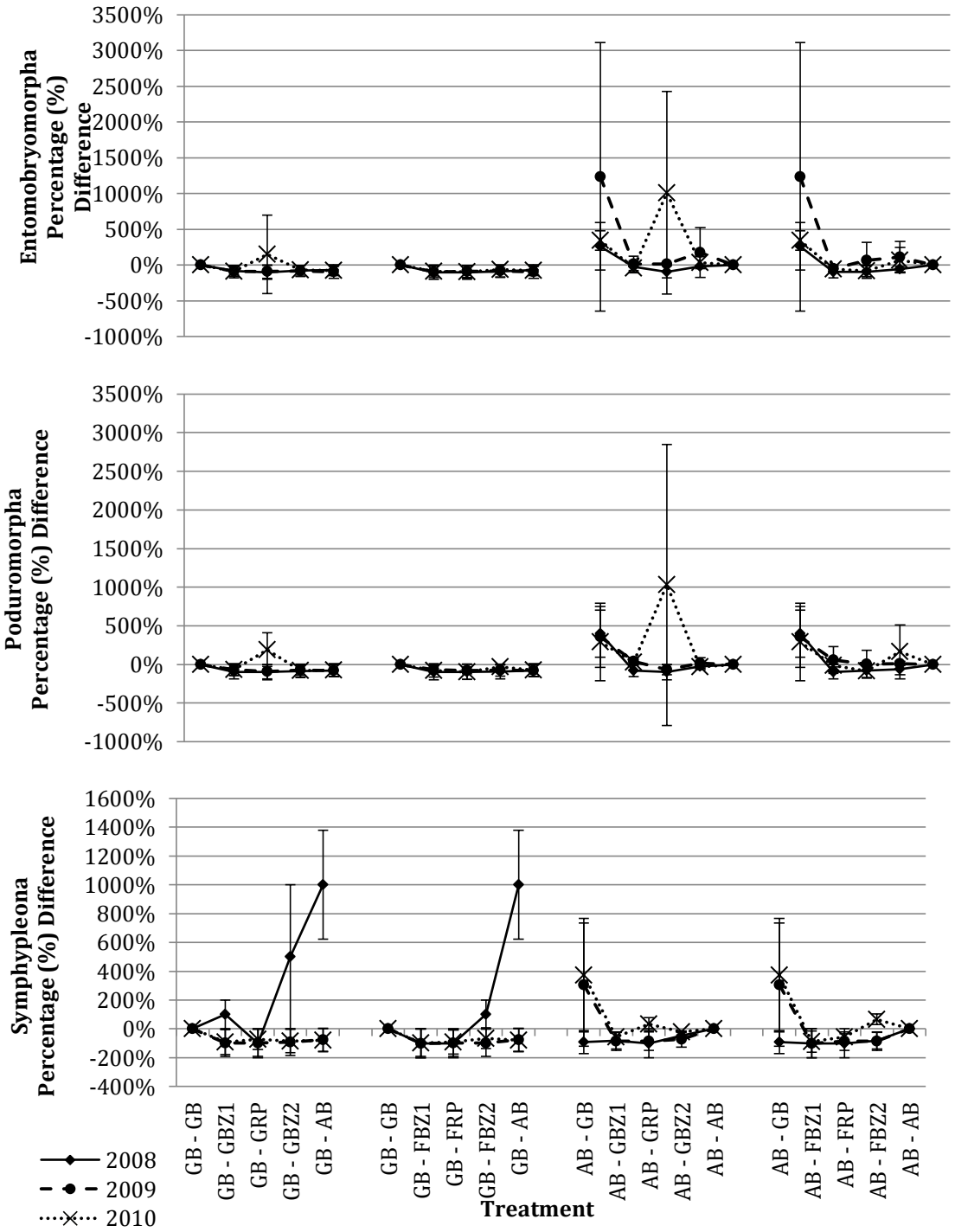
Appendix VII The mean invertebrate abundance (m^{-2}) (±SE) for each transect point, during each sampling time. The results of statistical analysis (by Dunnett test with 95% confidence limits) are denoted, with individual significant differences of each transect point from the (*) Grass Border and/or the (•) Arable Border for that sampling period (Section 4.3.1.3).

Sampling Time	Treatment	Transect Position	Number of samples	Mean Invertebrate Abundance (m^{-2})					
				Acari		Collembola		Others	
2008	Grass border		12	10083•	(±3801)	6900•	(±2441)	617	(±201)
	Grass	Buffer Zone One	6	467*	(±211)	833*	(±411)	67*•	(±67)
		Reversion	6	67*•	(±67)	33*•	(±33)	67*•	(±42)
		Buffer Zone Two	6	600*	(±339)	1367*	(±530)	267	(±123)
	Fallow	Buffer Zone One	6	267*	(±84)	67*•	(±67)	133*•	(±99)
		Reversion	6	33*•	(±33)	167*•	(±61)	200	(±52)
		Buffer Zone Two	6	500*	(±144)	700*	(±169)	167	(±80)
	Arable border		12	2750*	(±1610)	1800*	(±550)	600	(±296)
2009	Grass border		12	11550•	(±2537)	27683•	(±7275)	267	(±62)
	Grass	Buffer Zone One	6	3833*	(±1926)	4100*	(±1116)	300	(±191)
		Reversion	6	1233*	(±436)	2133*	(±513)	67	(±67)
		Buffer Zone Two	6	2500*	(±1059)	5967*	(±2293)	167	(±167)
	Fallow	Buffer Zone One	6	733*	(±256)	3500*	(±1424)	100	(±68)
		Reversion	6	1167*	(±307)	4200*•	(±2521)	133	(±67)
		Buffer Zone Two	6	1733*	(±1216)	5000*	(±1706)	67	(±67)
	Arable border		12	3233*	(±1799)	3400*	(±786)	333	(±146)
2010	Grass border		12	29867•	(±6326)	18283•	(±4382)	1967	(±497)
	Grass	Buffer Zone One	6	10300*	(±5560)	4000*	(±1261)	367*	(±289)
		Reversion	6	21433•	(±6596)	45967*•	(±8067)	1400	(±301)
		Buffer Zone Two	6	7400*	(±3887)	4267*	(±1477)	700	(±218)
	Fallow	Buffer Zone One	6	3067*	(±1728)	2833*	(±474)	400*	(±200)
		Reversion	6	1267*	(±267)	800*	(±263)	67*•	(±42)
		Buffer Zone Two	6	4800*	(±1937)	9467	(±3661)	1467	(±681)
	Arable border		12	5267*	(±1299)	4367*	(±953)	1033	(±428)

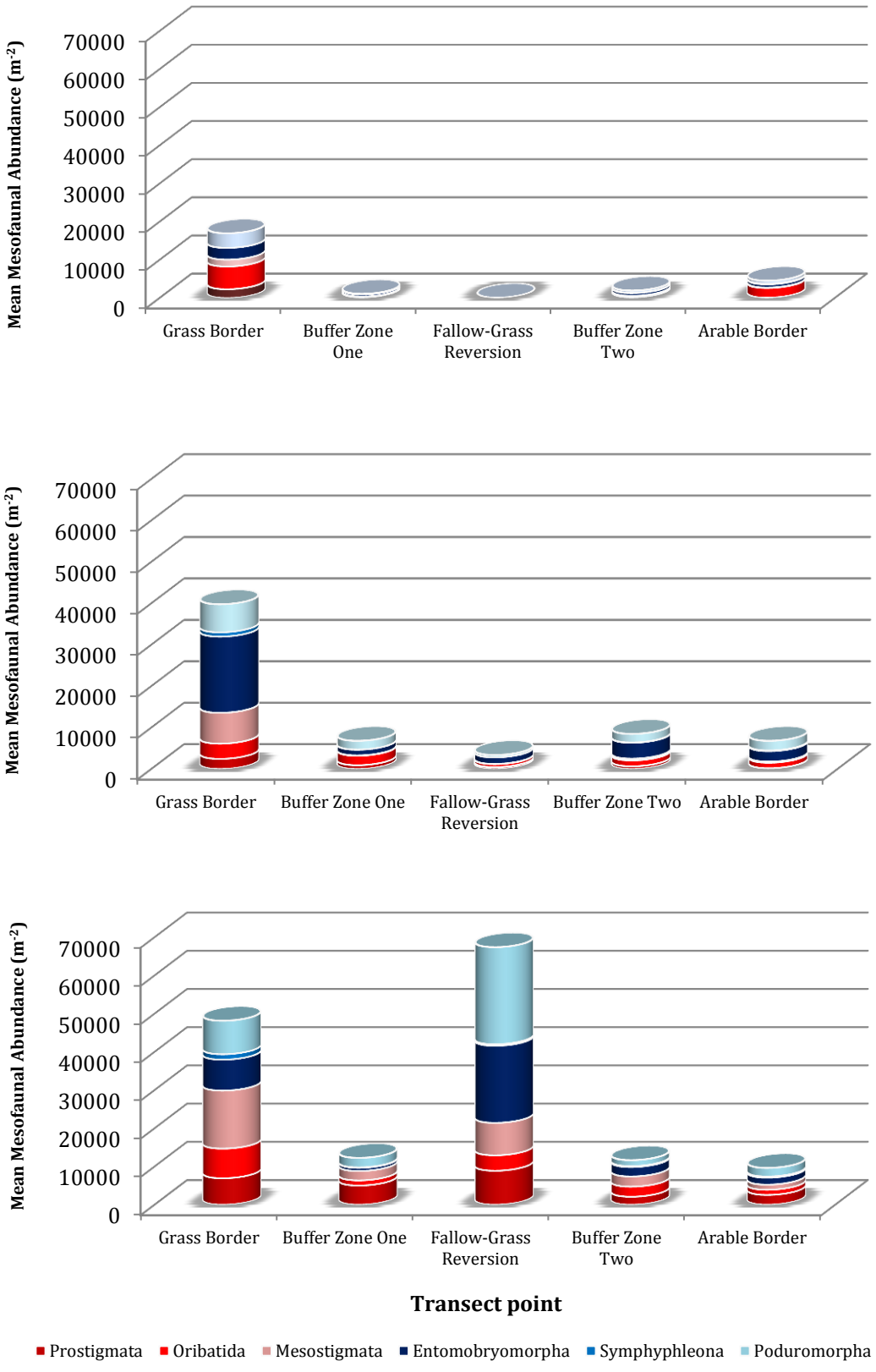
Appendix VIII The percentage difference (±SE as standard error bars)- from the Grass Border (GB) or Arable Border (AB) control populations – for Fallow-Grass (G) and Fallow-Fallow (F) treatments - for each of the transect points – buffer zones one (BZ1) and two (BZ2) and reversion plot (RP), for the Mesostigmata (top), Prostigmata (middle) and Oribatida (bottom) abundance throughout the experimental period.



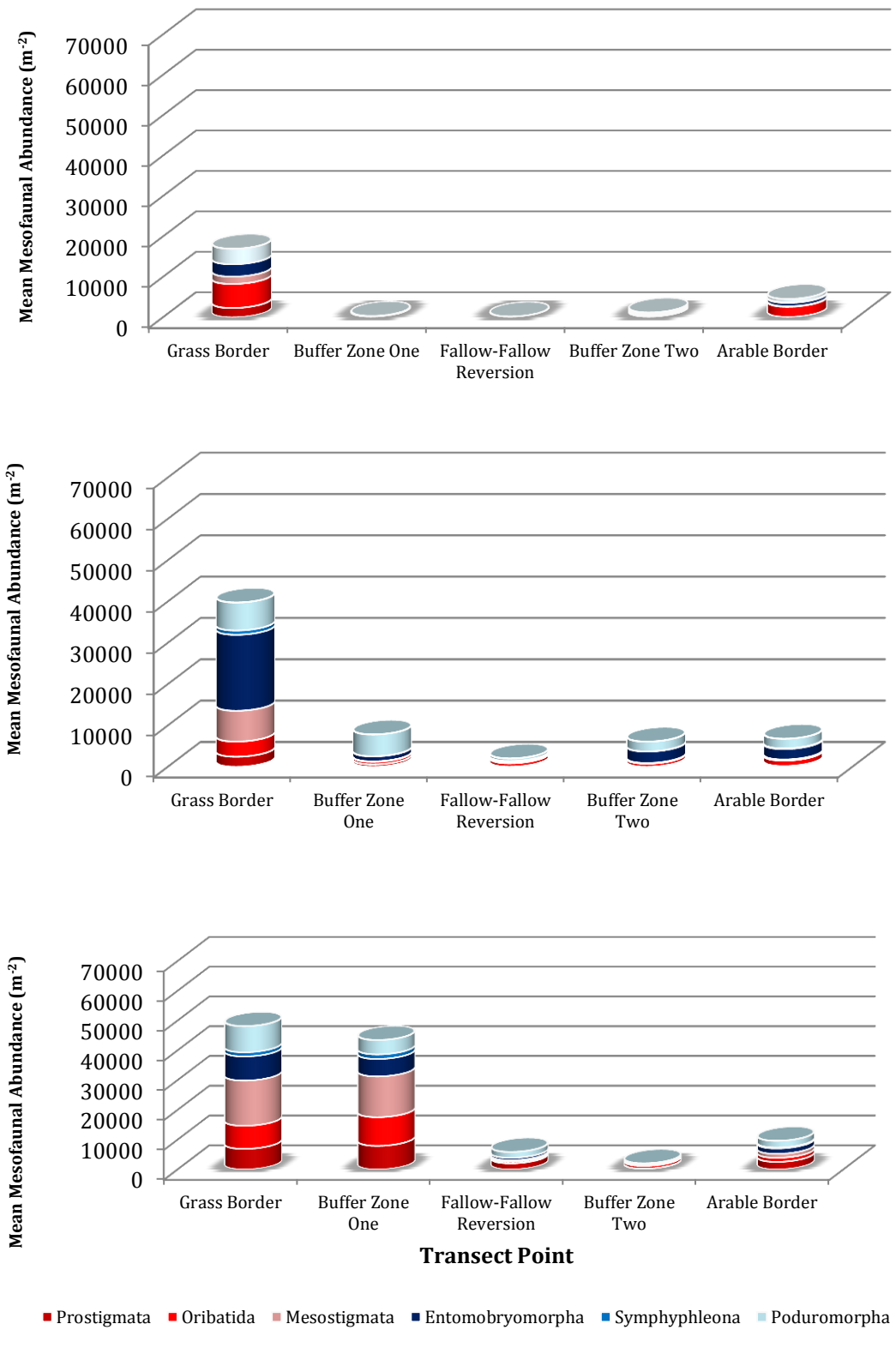
Appendix IX The percentage difference (±SE as error bars)- from the Grass Border (GB) or Arable Border (AB) control populations – for Grass (G) and Fallow (F) treatments - for each of the transect points – buffer zones one (BZ1) and two (BZ2) and reversion plot (RP), for the Entomobryomorpha (top), Poduromorpha (middle) and Symphypleona (bottom) abundance throughout the experimental period.



Appendix X The mean superfamily abundances (m^{-2}) recovered from the Grass Reversion Transects in 2008 (top), 2009 (middle) and 2010 (bottom) (Grass and Arable Borders are averaged from 12 soil cores).



Appendix XI The mean superfamily abundance (m^{-2}) recovered from the Fallow Reversion transects in 2008 (top), 2009 (middle) and 2010 (bottom) (Grass and Arable Borders are averaged from 12 soil cores).



Appendix XII The mean invertebrate abundance (m^{-2}) (±SE) recovered from transects crossing the Grass and Fallow Reversion treatments, from the Highfield Transect project, throughout the experimental period (Section 4.3.1.3).

Sampling Time	Treatment	Number of Samples	Transect Position	Mean Abundance (m^{-2}) (±SE) of Invertebrates											
				Acari						Collembola					
				Prostigmata		Oribatida		Mesostigmata		Entomobryomorpha		Symphypleona		Poduromorpha	
2008	Grass Border	12	1	2317	(±1013)	5950	(±2543)	1817	(±397)	3067	(±1037)	17	(±17)	3817	(±1885)
	Grass Reversion	6	2	33	(±33)	267	(±123)	167	(±109)	633	(±439)	33	(±33)	167	(±95)
		6	3	33	(±33)	33	(±33)	0	(±0)	33	(±33)	0	(±0)	0	(±0)
		6	4	167	(±95)	300	(±262)	133	(±133)	700	(±262)	100	(±100)	567	(±280)
	Fallow Reversion	6	2	67	(±67)	167	(±61)	33	(±33)	33	(±33)	0	(±0)	33	(±33)
		6	3	0	(±0)	33	(±33)	0	(±0)	33	(±33)	0	(±0)	133	(±42)
		6	4	33	(±33)	367	(±95)	100	(±68)	367	(±141)	33	(±33)	300	(±113)
	Arable Border	12	5	100	(±52)	2533	(±1558)	117	(±39)	850	(±240)	183	(±80)	767	(±468)
2009	Grass Border	12	1	2450	(±1087)	3667	(±886)	7450	(±1733)	18400	(±7369)	1033	(±490)	6767	(±2381)
	Grass Reversion	6	2	1067	(±796)	2667	(±1442)	100	(±45)	1600	(±771)	33	(±33)	2467	(±661)
		6	3	467	(±204)	700	(±235)	67	(±42)	1567	(±391)	33	(±33)	533	(±152)
		6	4	667	(±378)	1400	(±568)	433	(±196)	3833	(±1661)	67	(±42)	2067	(±757)
	Fallow Reversion	6	2	600	(±407)	633	(±442)	100	(±68)	1200	(±575)	33	(±33)	5267	(±1299)
		6	3	33	(±33)	833	(±260)	133	(±99)	400	(±171)	0	(±0)	633	(±275)
		6	4	0	(±0)	767	(±244)	167	(±80)	2767	(±1197)	33	(±33)	2367	(±1176)
	Arable Border	12	5	183	(±58)	1333	(±530)	267	(±99)	2533	(±635)	150	(±78)	2333	(±408)
2010	Grass Border	12	1	6933	(±2244)	7750	(±1501)	15183	(±4155)	8100	(±1535)	1417	(±615)	8767	(±3327)
	Grass Reversion	6	2	5867	(±3489)	1567	(±772)	2867	(±1333)	967	(±469)	133	(±84)	2900	(±772)
		6	3	8900	(±3525)	4033	(±974)	8500	(±3189)	20167	(±9924)	400	(±179)	25400	(±10592)
		6	4	2100	(±1435)	2633	(±1133)	2667	(±1371)	2467	(±1201)	233	(±120)	1567	(±543)
	Fallow Reversion	6	2	2067	(±1207)	600	(±358)	400	(±186)	833	(±356)	33	(±33)	1967	(±442)
		6	3	267	(±84)	933	(±251)	67	(±42)	333	(±123)	133	(±99)	333	(±99)
		6	4	2900	(±1493)	1067	(±389)	833	(±370)	3067	(±1808)	500	(±169)	5900	(±2486)
	Arable Border	12	5	2567	(±980)	1350	(±403)	1350	(±429)	1817	(±654)	300	(±124)	2250	(±552)

Appendix XIII The SP-ANOVA analysis results for invertebrate abundance (m^{-2}) ($\sqrt{}$ transformed) obtained from the Highfield Transect Project in 2008, 2009 and 2010. For each individual year the variables (transect point, treatment and transect x treatment), were analysed for each invertebrate group. Significant differences are denoted by italics, with the probability value (key shown at the table base) indicated by the adjoining letter (Section 4.3.1.3).

Invertebrate Group		Sampling year	SP-ANOVA analysis for transect abundance results within each sampling period															
			Transect					Treatment		Transect x Treatment								
			1	2	3	4	5	FG	FF	Grass Border	FG -2	FF -2	FG -3	FF -3	FG -4	FF -4	Arable Border
Acari	Mesostigmata	2008	*38.8a*	*4.9a*	*0a*	*5.2a*	*7.6a*	14.1	8.5	38.8	7.4	2.4	0	0	4.7	5.7	7.6
		2009	*68.3a*	*5.9a*	*7.7a*	*12.1a*	*19.2a*	*30e*	*15e*	*68.3a*	*7.1a*	*4.7a*	*4.7a*	*10.7a*	*16.2a*	*8a*	*19.2a*
		2010	*110.9a*	*30a*	*43.3a*	*31.2a*	*29.9a*	60.9	37.2	*111q*	*45.9q*	*14.1q*	*81.9q*	*4.7q*	*37.7q*	*24.7q*	*29.9q*
	Oribatida	2008	*64.1a*	*11a*	*2.4a*	*13.7a*	*33.9a*	24.9	25.2	64.1	11.5	10.4	2.4	2.4	9	18.5	33.9
		2009	*50.2j*	*27.3j*	*24.9j*	*30.4j*	*28.7j*	35.6	29	50.2	37.3	17.4	23.1	26.6	32.4	28.3	28.7
		2010	*81.5a*	*24.2a*	*43.4a*	*37.7a*	*31.9a*	45.6	41.9	*81.5f*	*32f*	*16.4f*	*59.5f*	*27.3f*	*45.3f*	*30.1f*	*31.9f*
	Prostigmata	2008	*34.6a*	*2.8a*	*1.2a*	*5.6a*	*5.6a*	13.9	6	*34.6m*	*2.4m*	*3.3m*	*2.4m*	*0m*	*8.8m*	*2.4m*	*5.6m*
		2009	*33.3i*	*15.6i*	*9.2i*	*11.9i*	*18.3i*	21.2	14.1	*33.3k*	*22.2k*	*9k*	*18.4k*	*0k*	*17.4k*	*6.4k*	*18.3k*
		2010	71.1	44.6	49.7	35.4	39.4	55.2	41	71.1	55.9	33.3	85	14.5	29.7	41.1	39.4
Collembola	Entomobryomorpha	2008	*43.8a*	*8.3a*	*2.4a*	*19a*	*25.8a*	24.9	14.9	43.8	14.3	2.4	2.4	2.4	22.9	15.2	25.8
		2009	*105.4a*	*26.1a*	*37.5a*	*50.48a*	*33.1a*	66.7	34.3	*105.4a*	*32a*	*20.2a*	*37.8a*	*37.2a*	*54a*	*46.8a*	*33.1a*
		2010	*82.8a*	*23.8a*	*67.5a*	*43.3a*	*34.5a*	61.3	39.5	*82.8b*	*25.3b*	*22.3b*	*199b*	*15.9b*	*42.9b*	*43.8b*	*34.5b*
	Poduromorpha	2008	*46.8a*	*5.6a*	*4.7a*	*16.7a*	*18.6a*	18.6	18.3	46.8	8.8	2.4	0	9.4	18.2	15.1	18.6
		2009	*81.3a*	*45.3a*	*27.3a*	*40.2a*	*36.8a*	48.2	44.2	81.3	46.4	44.1	20.5	34.2	41	39.4	36.8
		2010	79.8	47.2	76.6	53.3	42.1	68.8	50.9	*79.8a*	*51.6a*	*42.8a*	*135.8a*	*17.5a*	*36.7a*	*70a*	*42.1a*
	Symphypleona	2008	*1.18j*	*1.18j*	*0j*	*3.22j*	*8.42j*	3.37	2.23	1.18	2.36	0	0	0	4.08	2.36	8.42
		2009	*19.4d*	*1.2d*	*2.4d*	*3.5d*	*9.6d*	8.2	6.3	*19.4k*	*2.4k*	*0k*	*2.4k*	*2.4k*	*4.7k*	*2.4k*	*9.6k*
		2010	*27.1h*	*4.5h*	*11.1h*	*15.1h*	*11.7h*	12.5	15.2	27.1	6.7	2.4	15.8	6.4	10.5	19.6	11.7
Other Invertebrates		2008	*20.7g*	*4.9g*	*8.7g*	*10.9g*	*17.3g*	12.6	12.4	20.7	3.3	6.4	4.7	12.8	12.8	9	17.3
		2009	13.8	8.6	5.7	4.3	11.3	7.6	9.9	13.8	11.5	5.7	3.3	8	5.3	3.3	11.3
		2010	*40.3a*	*13.5a*	*20.3a*	*29.7a*	*27.3a*	25.3	27.2	*40.3c*	*11.8c*	*15.2c*	*35.8c*	*4.7c*	*24.8c*	*34.6c*	*27.3c*

a P<0.001, b P=0.001, c P=0.003, d P=0.004, e P=0.011, f P=0.013, g P=0.016, h P=0.019, i P=0.030, j P=0.035, k P=0.036, m P=0.041, q P=0.047

Appendix XIV The mean biomasses (µg m^{-2}) (±SE) of the total Acari and Collembola for transect points throughout the experimental time period. The results of intra-sampling period statistical analysis (by Dunnett test with 95% confidence limits) are denoted, with individual significant differences of each transect point from the (*) Grass Border and/or the (•) Arable Border for that sampling period (Section 4.3.2.3).

Sample Time	Treatment	Transect Position	Number of samples	Mean Biomass (µg m^{-2}) (±SE)			
				Acari		Collembola	
2008	Grass Border		12	44228	(±13417)	16850	(±5649)
	Grass	Buffer Zone One	6	3077*	(±1687)	2267	(±1262)
		Reversion	6	127*•	(±127)	100*•	(±100)
		Buffer Zone Two	6	2833	(±1796)	3333	(±1307)
	Fallow	Buffer Zone One	6	1003	(±377)	167*•	(±167)
		Reversion	6	100*•	(±100)	367	(±150)
		Buffer Zone Two	6	2477	(±1136)	1733	(±431)
	Arable Border		12	9255	(±4815)	4267	(±1279)
2009	Grass Border		12	113535•	(±24007)	69767	(±22419)
	Grass	Buffer Zone One	6	10203*	(±4313)	9767	(±2904)
		Reversion	6	3373*	(±1126)	5800	(±1391)
		Buffer Zone Two	6	10583*	(±4263)	15700	(±6199)
	Fallow	Buffer Zone One	6	3730*•	(±2131)	14167	(±4055)
		Reversion	6	4327*	(±1285)	2467*•	(±922)
		Buffer Zone Two	6	4550*	(±1729)	13067	(±5798)
	Arable Border		12	7747*	(±2247)	12417	(±2509)
2010	Grass Border		12	233772	(±59546)	43250	(±10067)
	Grass	Buffer Zone One	6	48093	(±23040)	8833	(±2875)
		Reversion	6	133970	(±46109)	111700•	(±21309)
		Buffer Zone Two	6	45580	(±22978)	10767	(±4151)
	Fallow	Buffer Zone One	6	8853*	(±4416)	6467	(±1119)
		Reversion	6	3913*	(±1119)	1800	(±582)
		Buffer Zone Two	6	16770	(±6646)	21500	(±8611)
	Arable Border		12	24328	(±6647)	10250	(±2444)

Appendix XV The mean invertebrate biomass (µg m^{-2}) (±SE) recovered from each transect point, from the Highfield Transect project, throughout the experimental period (Section 4.3.2.3).

Sampling Time	Treatment	Number of Samples	Transect Position	Mean Biomass (µg m^{-2}) (±SE) of Invertebrates											
				Acari						Collembola					
				Prostigmata		Oribatida		Mesostigmata		Entomobryomorpha		Symphypleona		Poduromorpha	
2008	Grass Border	12	1	1853	(±810)	17850	(±7629)	24525	(±5364)	9200	(±3112)	17	(±17)	7633	(±3770)
	Grass Reversion	6	2	27	(±27)	800	(±369)	2250	(±1465)	1900	(±1318)	33	(±33)	333	(±191)
		6	3	27	(±27)	100	(±100)	0	(±0)	100	(±100)	0	(±0)	0	(±0)
		6	4	133	(±76)	900	(±786)	1800	(±1800)	2100	(±786)	100	(±100)	1133	(±560)
	Fallow Reversion	6	2	53	(±53)	500	(±184)	450	(±450)	100	(±100)	0	(±0)	67	(±67)
		6	3	0	(±0)	100	(±100)	0	(±0)	100	(±100)	0	(±0)	267	(±84)
		6	4	27	(±27)	1100	(±286)	1350	(±922)	1100	(±422)	33	(±33)	600	(±225)
	Arable Border	12	5	80	(±42)	7600	(±4674)	1575	(±521)	2550	(±720)	183	(±80)	1533	(±935)
2009	Grass Border	12	1	1960	(±870)	11000	(±2658)	100575	(±23395)	55200	(±22106)	1033	(±490)	13533	(±4762)
	Grass Reversion	6	2	853	(±637)	8000	(±4326)	1350	(±604)	4800	(±2313)	33	(±33)	4933	(±1321)
		6	3	373	(±164)	2100	(±706)	900	(±569)	4700	(±1174)	33	(±33)	1067	(±304)
		6	4	533	(±303)	4200	(±1704)	5850	(±2647)	11500	(±4983)	67	(±42)	4133	(±1513)
	Fallow Reversion	6	2	480	(±325)	1900	(±1327)	1350	(±922)	3600	(±1725)	33	(±33)	10533	(±2598)
		6	3	27	(±27)	2500	(±781)	1800	(±1335)	1200	(±514)	0	(±0)	1267	(±551)
		6	4	0	(±0)	2300	(±733)	2250	(±1084)	8300	(±3591)	33	(±33)	4733	(±2352)
	Arable Border	12	5	147	(±46)	4000	(±1590)	12150	(±1343)	7600	(±1906)	150	(±78)	4667	(±816)
2010	Grass Border	12	1	5547	(±1795)	23250	(±4503)	204975	(±56094)	24300	(±4605)	1417	(±615)	17533	(±6654)
	Grass Reversion	6	2	4693	(±2791)	4700	(±2316)	38700	(±18000)	2900	(±1406)	133	(±85)	5800	(±1545)
		6	3	7120	(±2820)	12100	(±2921)	114750	(±43052)	60500	(±29771)	400	(±179)	50800	(±21184)
		6	4	1680	(±1148)	7900	(±3399)	36000	(±18506)	7400	(±3602)	233	(±120)	3133	(±1085)
	Fallow Reversion	6	2	1653	(±966)	1800	(±1073)	5400	(±2514)	2500	(±1067)	33	(±33)	3933	(±885)
		6	3	213	(±67)	2800	(±754)	900	(±569)	1000	(±369)	133	(±99)	667	(±198)
		6	4	2320	(±1194)	3200	(±1166)	11250	(±4999)	9200	(±5424)	500	(±169)	11800	(±4971)
	Arable Border	12	5	2053	(±784)	4050	(±1209)	18225	(±5796)	5450	(±1962)	300	(±124)	4500	(±1103)

Appendix XVI The SP-ANOVA analysis results for mesofaunal biomass abundance (µg m^{-2}) (LOG_{10} transformed) obtained from the Highfield Transect Project in 2008, 2009 and 2010. For each individual year the variables (transect point, treatment and transect x treatment), were analysed for each invertebrate group. Significant differences are denoted by italics, with the probability value (key shown at the table base) indicated by the adjoining letter (Section 4.3.2.3).

Invertebrate Group		Sampling year	SP-ANOVA analysis for Mesofaunal Superfamilies Biomass (Log transformation)															
			Transect					Treatment		Transect x Treatment								
			1	2	3	4	5	FG	FF	Grass Border	FG -2	FF -2	FG -3	FF -3	FG -4	FF –4	Arable Border
Acari	Mesostigmata	2008	*9.14b*	*2.12b*	*0b*	*2.15b*	*4.01b*	4.03	2.94	9.14	2.93	1.32	0	0	1.55	2.75	4.01
		2009	*11.07j*	*3.35j*	*2.73j*	*5.05j*	*5.57j*	6.04	5.07	11.07	3.95	2.75	2.63	2.86	5.91	4.18	5.57
		2010	11.08	7.24	6.86	7.29	7.89	8.92	7.22	11.08	9.86	4.63	11.1	2.63	6.85	7.72	7.89
		Average	*11.44i*	*7.80i*	*7.36i*	*7.22i*	*7.99i*	9.13	7.59	11.44	9.08	6.51	10	4.72	7.34	7.10	7.99
	Oribatida	2008	8.99	4.03	1.07	4.67	6.16	4.56	5.4	8.99	3.68	4.38	1.07	1.07	2.48	6.86	6.16
		2009	9.01	5.35	6.43	7.09	6.71	7.13	6.71	9.01	5.82	4.89	6.36	6.50	7.67	6.51	6.77
		2010	9.17	5.36	7.85	8.09	7.3	7.73	7.37	9.17	6.73	3.98	9.01	6.68	8.44	7.73	7.3
		Average	*9.57k*	*6.72k*	*7.77k*	*7.78k*	*8.02k*	7.98	7.96	9.57	6.66	6.77	8.16	7.39	7.98	7.58	8.02
	Prostigmata	2008	*5.25a*	*0.9a*	*0.42a*	*1.79a*	*1.79a*	2.48	1.58	5.25	0.85	0.96	0.85	0	2.72	0.85	1.79
		2009	6.14	3.52	2.43	2.63	3.49	4.27	3.01	6.14	4.27	2.77	4.86	0	3.38	1.88	3.49
		2010	7.45	5.87	6.99	4.73	5.94	6.11	6.28	7.45	6.26	5.47	8.43	5.55	3.89	5.57	5.94
		Average	7.58	5.58	6.03	4.91	5.12	6.31	5.38	7.58	6.23	4.93	7.43	4.64	5.11	4.71	5.12
Collembola	Entomobryomorpha	2008	*6.78c*	*1.96c*	*1.07c*	*5.6c*	*6.97c*	5.16	3.8	6.78	2.86	1.07	1.07	1.07	6.33	4.86	6.97
		2009	*9.44f*	*6.65f*	*6.57f*	*8.08f*	*8.56f*	8.59	7.12	9.44	6.71	6.58	8.25	4.88	8.75	7.42	8.56
		2010	9.18	5.84	8	7.78	6.9	7.83	7.25	9.18	6.39	5.30	10.3	5.75	7.25	5.48	6.9
		Average	*9.78g*	*7.48g*	*7.47g*	*8.28g*	*8.33g*	8.81	7.73	*9.78h*	*7.62h*	*7.35h*	*9.39h*	*5.54h*	*8.34h*	*8.23h*	*8.33h*
	Poduromorpha	2008	*7.36d*	*2.09d*	*2d*	*5.06d*	*4.67d*	3.89	4.58	7.36	3.18	1	0	4	4.78	5.34	4.67
		2009	*8.73e*	*8.57e*	*5.84e*	*7.38e*	*8.16e*	7.89	7.58	8.73	8.15	9.0	5.86	5.82	7.85	6.92	8.16
		2010	8.62	8.31	8.2	8.37	7.48	8.16	8.23	8.62	8.50	8.13	10.1	6.34	7.73	9.01	7.48
		Average	9.15	8.23	7.72	7.94	7.99	8.38	8.03	9.15	8.11	8.35	9.03	6.42	7.56	8.33	7.99
	Symphypleona	2008	0.44	0.44	0	0.98	2.47	1.12	0.61	0.44	0.88	0	0	0	1.07	0.88	2.47
		2009	4.14	0.88	0.44	1.33	1.97	1.87	1.64	4.14	0.88	0.88	0	0.88	1.77	0.88	1.97
		2010	4.75	1.44	3.06	4.11	3.1	2.98	3.61	4.75	2	0.88	4.18	1.95	3.02	5.2	3.1
		Average	5.55	1.58	2.53	4.27	4.03	3.7	3.53	5.55	1.75	1.40	3.47	1.59	4.17	4.36	4.03

a P=0.004, b P=0.009, c P=0.010, d P=0.042, e P=0.023, f P=0.033, g P<0.001, i P=0.020, j P=0.002, k P=0.023

h P=0.002

Appendix XVII Little Burrows Experiment: The mean invertebrate abundance (m^{-2}) (±SE) of retrieved mesocosms, for time series (0, 1, 2, and 3), Grass/White Clover foliage, Mode of Access (Top, Full and No).

Time Series	Treatment		Mean Invertebrate Abundance (m^{-2}) (±SE in brackets)						
	Foliage	Mode of Access	Prostigmata	Oribatida	Mesostigmata	Entomobryomorpha	Symphypleona	Poduromorpha	Other Invertebrates
0	Grass	Free	16822 (±2239)	7522 (±848)	8211 (±2380)	3222 (±459)	1656 (±395)	3100 (±566)	3644 (±)241
1	Grass	Top	17800 (±3904)	2133 (±67)	2133 (±786)	7733 (±1485)	1400 (±577)	1533 (±291)	1200 (±200)
		Full	6067 (±4689)	467 (±291)	333 (±240)	1867 (±267)	1267 (±786)	2200 (±2101)	1800 (±416)
		No	17800 (±2498)	2400 (±400)	400 (±115)	2400 (±757)	333 (±67)	867 (±133)	867 (±67)
	Clover	Top	12133 (±2440)	1000 (±306)	467 (±67)	3200 (±1249)	800 (±306)	2400 (±693)	1000 (±0)
		Full	5000 (±1102)	1200 (±400)	867 (±467)	4333 (±1162)	1067 (±636)	3400 (±1270)	1200 (±306)
		No	10667 (±240)	1000 (±416)	1267 (±371)	3800 (±306)	800 (±503)	2533 (±1298)	1067 (±371)
2	Grass	Top	6200 (±643)	1000 (±529)	0 (±0)	4400 (±643)	533 (±240)	1267 (±819)	1667 (±570)
		Full	7733 (±1729)	733 (±267)	0 (±0)	3067 (±1618)	867 (±133)	800 (±346)	2000 (±643)
		No	4867 (±521)	333 (±67)	0 (±0)	2200 (±503)	1067 (±570)	733 (±333)	1200 (±306)
	Clover	Top	4733 (±769)	800 (±346)	0 (±0)	2133 (±1157)	400 (±115)	200 (±200)	1267 (±133)
		Full	5000 (±872)	733 (±133)	0 (±0)	4733 (±2345)	867 (±371)	1200 (±416)	1733 (±521)
		No	6133 (±1947)	200 (±0)	67 (±67)	1800 (±917)	667 (±291)	267 (±176)	1467 (±291)
3	Grass	Top	6600 (±833)	667 (±371)	267 (±67)	2733 (±696)	1200 (±643)	600 (±200)	933 (±291)
		Full	8600 (±1510)	1267 (±467)	533 (±291)	2200 (±872)	933 (±133)	533 (±240)	1467 (±176)
		No	8400 (±2914)	400 (±306)	533 (±67)	2933 (±1048)	1400 (±721)	1200 (±611)	2000 (±529)
	Clover	Top	6733 (±1749)	333 (±176)	333 (±176)	4600 (±1747)	933 (±353)	1533 (±291)	1867 (±240)
		Full	6400 (±833)	933 (±467)	133 (±133)	933 (±406)	867 (±176)	933 (±133)	1533 (±353)
		No	5667 (±1378)	533 (±291)	200 (±200)	3600 (±2553)	800 (±611)	1067 (±353)	1200 (±200)

Appendix XVIII Little Burrows Experiment: The mean biomass (µg m^{-2}) (±SE) results of the mesofaunal superfamilies for all sampling time periods and treatments within mesocosms.

Time Series	Treatment		Average Biomass (µg m^{-2}) of invertebrate groups (±SE in brackets)					
	Foliage type	Mode of Access	Mesostigmata	Prostigmata	Oribatida	Entomobryomorpha	Poduromorpha	Symphypleona
0	Grass	Free	110850 (±32123)	13458 (±1791)	22567 (±2543)	9667 (±1376)	6200 (±1131)	1656 (±395)
1	Grass	Top Access	28800 (±10611)	14240 (±3123)	6400 (±200)	23200 (±4454)	3067 (±581)	1400 (±577)
		Full Access	4500 (±3245)	4853 (±3752)	1400 (±872)	5600 (±800)	4400 (±4202)	1267 (±786)
		No Access	5400 (±1559)	14240 (±1998)	7200 (±1200)	7200 (±2272)	1733 (±267)	333 (±67)
	Clover	Top Access	6300 (± 900)	9707 (±1952)	3000 (±917)	9600 (±3747)	4800 (±1386)	800 (±306)
		Full Access	11700 (±6235)	4000 (±1681)	3600 (±1058)	13000 (±2088)	6800 (±2706)	1067 (±702)
		No Access	17100 (±5011)	8533 (±192)	3000 (±1249)	11400 (±917)	5067 (±2596)	800 (±503)
2	Grass	Top Access	0 (±0)	4960 (±514)	3000 (±1587)	13200 (±1929)	2533 (±1638)	533 (±240)
		Full Access	0 (±0)	6187 (±1384)	2200 (±800)	9200 (±4854)	1600 (±693)	867 (±133)
		No Access	0 (±0)	3893 (±417)	1000 (±200)	6600 (±1510)	1467 (±667)	1067 (±570)
	Clover	Top Access	0 (±0)	3787 (±615)	2400 (±1039)	6400 (±3470)	400 (±400)	400 (±115)
		Full Access	0 (±0)	4000 (±775)	2200 (±693)	14200 (±8190)	2400 (±1091)	867 (±416)
		No Access	900 (±900)	4907 (±1558)	600 (±0)	5400 (±2750)	533 (±353)	667 (±291)
3	Grass	Top Access	3600 (±900)	5280 (±666)	2000 (±1114)	8200 (±2088)	1200 (±400)	1200 (±643)
		Full Access	7200 (±3923)	6880 (±1208)	3800 (±1400)	6600 (±2615)	1067 (±481)	933 (±133)
		No Access	7200 (±900)	6720 (±2331)	1200 (±917)	8800 (±3143)	2400 (±1222)	1400 (±721)
	Clover	Top Access	4500 (±2381	5387 (±1399)	1000 (±529)	13800 (±5242)	3067 (±581)	933 (±353)
		Full Access	1800 (±1800)	5120 (±213)	2800 (±1217)	2800 (±872)	1867 (±533)	867 (±406)
		No Access	2700 (±2700)	4533 (±1102)	1600 (±872)	10800 (±7660)	2133 (±706)	800 (±611)

Appendix XIX The mean transformed invertebrate population data recorded from the post-transplantation Little Burrow mesocosms, for time series (1,2,3), foliage type (Ryegrass, White Grass) and mode of access (top, full, no). Statistical differences, as determined by ANOVA, for each invertebrate group for time series, foliage and mode of access variables without variable interactions are denoted by the symbols, with the probability values displayed at the base of the table (Section 5C.3.1).

Data Type (Transformation)	Variable		Mean Transformed Values of Invertebrate Populations (m^{-2})								
			Mesostigmata	Prostigmata	Oribatida	Entomobryomorpha	Poduromorpha	Symphypleona	Other Invertebrates	Total Collembola	Total Acari
Abundance (√)	Time Series	1	26.3*	102~	34.4†	59.7	41.6ˆ	27.4	33.8	80.7	112.5*
		2	0.8*	75~	23.4†	51.8	22.5ˆ	25.6	38.5	64.4	79.2*
		3	14.6*	82.7~	22†	48.9	29.8ˆ	28.2	37.9	66.7	88.4*
Biomass (LOG_{10})	Time Series	1	8.19*	8.866•	7.73	9.19	7.63°	6.18	-	-	-
		2	0.44*	8.384•	7.26	8.85	5.67°	6.38	-	-	-
		3	5.82*	8.574•	5.97	8.66	7.38°	5.81	-	-	-
Abundance (√)	Foliage	Ryegrass	15.1	91.8	28.7	54.5	28.7	28.4	37.2	70.8	99
		White Clover	12.7	81.3	24.5	52.5	34	25.7	36.4	70.4	87.7
Biomass (LOG_{10})	Foliage	Ryegrass	5.27	8.691	7.2	8.99	6.83	6.2	-	-	-
		White Clover	4.36	8.525	6.76	8.81	6.96	6.04	-	-	-
Abundance (√)	Mode of Access	Top	16.1	91.6	28.5	61.2	30.9	27	35.7	76.2	98.8
		Full	10.6	77.3	27.1	49.5	33.3	29.2	39.4	69.6	84.9
		No	15	90.8	24.2	49.7	29.8	25.1	35.2	66	96.4
Biomass (LOG_{10})	Mode of Access	Top	5.46	8.743	7.32	9.21	6.52	6.2	-	-	-
		Full	3.54	8.366	6.98	8.73	7.14	6.4	-	-	-
		No	5.44	8.715	6.65	8.76	7.02	5.77	-	-	-

*P<0.001 ~P=0.005 †P=0.014 •P=0.050 ˆP=0.004 ° P=0.023

Appendix XX The mean transformed invertebrate population data, recorded from the post-transplantation Little Burrow mesocosms, for time series (1, 2, 3) and mode of access (top, full, no) variable interactions. Statistical differences (determined by ANOVA) between the variable interactions are depicted by symbols, with the probability values at the base of the table, (pp.163).

Data Type (Transformation)	Time Series	Transformed Values of Invertebrate Populations (m^{-2}) within each mode of access																	
		Mesostigmata			Prostigmata			Oribatida			Entomobryomorpha			Poduromorpha			Symphypleona		
		Top	Full	No	Top	Full	No	Top	Full	No	Top	Full	No	Top	Full	No	Top	Full	No
Abundance (√)	1	32.8	19	27.2	120.5•	67.5•	118•	38.4	25.3	39.4	70.7	53.7	54.6	43.3	43.7	37.9	31.4	29	21.8
	2	0	0	2.4	73.4•	78.4•	73•	27.8	26.3	16.1	54.4	58.1	43	18.2	30.1	19.3	20.7	28.7	27.8
	3	15.5	12.7	15.6	80.8•	85.8•	81.5•	19.3	29.7	17	58.4	36.7	51.5	31.3	26.2	32	28.8	29.8	26
Biomass (LOG_{10})	1	9.39	6.11	9.08	9.332†	7.97†	9.297†	8.32	6.52	8.34	9.51	9	9.06	8.18	6.9	7.81	6.78	5.76	6.01
	2	0	0	1.32	8.354†	8.467†	8.331†	7.57	7.57	6.63	8.95	9.07	8.54	3.89	7.38	5.73	5.98	6.66	6.48
	3	7	4.52	5.93	8.542†	8.662†	8.519†	6.07	6.84	4.98	9.17	8.12	8.69	7.49	7.14	7.51	5.83	8.77	4.81

•P=0.009, †P=0.010

Appendix XXI The mean (√) transformed invertebrate abundance data, recorded from the post-transplantation Little Burrow mesocosms, for time series (1, 2, 3) x mode of access (top, full, no) variable interactions. Significant differences (determined by ANOVA) are depicted by *, with the probability value below (pp.163).

Data Type (Transformation)	Time Series	Transformed Values of Invertebrate Populations (m^{-2}) within each mode of access								
		Other Invertebrates			Total Collembola			Total Acari		
		Top	Full	No	Top	Full	No	Top	Full	No
Abundance (√)	1	33	37.9	30.6	90.5	80.1	71.6	131.6*	77.9*	128.2*
	2	37.6	41.9	36	64.2	72.5	56.4	79.3*	83.3*	75.1*
	3	36.3	38.4	39.1	74.1	56	69.9	85.5*	93.6*	86*

*P=0.007

Appendix XXII The mean (√) transformed invertebrate abundance data, recorded from the post-transplantation Little Burrow mesocosms, for time series (1, 2), mode of access (top, full, no) and foliage species (White Clover, Ryegrass) variables. Significant differences (determined by ANOVA) are depicted by *, with the probability value below (pp.163).

Statistical Analysis	Variation Source	Soil Moisture Content (%)						
		Species		Mode of Access			Time Series	
		Clover	Ryegrass	Full Access	No Access	Top Access	1	2
ANOVA analysis	Foliage Species	38.2	46.5	-	-	-	-	-
	Mode of Access	-	-	48.4	39.4	39.2	-	-
	Time Series	-	-	-	-	-	32	52.7
Probability Value		P<0.001		P=0.010			P<0.001	

Appendix XXIII Little Burrows Experiment: The ANOVA analysis for the isotopic results of the foliage removed from the mesocosms, for vegetation type (top), time (middle, top), mode of access (middle, bottom) and time x vegetation type (bottom) variables (pp.165).

Analytical Component	Species		Significant Difference P=value
	Clover	Grass	
Total C	32.51	39.63	<0.001
^{15}N	0.4742	0.5194	0.001
^{13}C	1.08376	1.08158	0.007
DM	0.454	1.052	<0.001
N_mg	12.5	26.3	<0.001
C_mg	144	414	<0.001
^{15}N_mg	0.0387	0.0941	0.001

Analytical Component	Time Phase		Significant Difference P=value
	1	2	
Total N	3.09	2.39	<0.001
Total C	38.21	33.93	0.01
^{13}C	1.08	1.08	0.027
DM	0.53	0.98	<0.001
N_mg	16.2	22.7	0.029
C_mg	209	349	<0.001
^{15}N_mg	0.02	0.11	<0.001

Analytical Component	Mode of Access			Significant Difference P=value
	Full Access	No Access	Top Access	
^{15}N	0.4743	0.4915	0.5247	0.008

Analytical Component	Foliage Species	Time Phase		Significant Difference P=value
		1	2	
^{13}C	Clover	1.084	1.084	0.005
	Grass	1.083	1.080	
^{15}N_mg	Clover	0.006	0.072	<0.001
	Grass	0.036	0.152	

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