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THE EFFECT OF MAIZE CULTIVATION ON INVERTEBRATE BIODIVERSITY

By

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Authors Declaration

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

Papers:

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Poster; Rothamsted Research Student Symposium, March 2014, Competitive maize cultivation at reduced environmental impact

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1. Summary

Agriculture is being challenged to provide food, and increasingly fuel, for an expanding global population (Werling *et al*., 2014). Row crop agriculture threatens long-term food security through conversion of natural and semi-natural habitats to arable land (Clay *et al*., 2014; Wodika and Baer, 2015). Land use change from natural to agricultural is well known to reduce genetic diversity, enhancing atmospheric gas emissions, accelerating soil erosion and reducing water quality (Tiemann *et al*., 2015; Clay *et al*., 2014). Biodiversity loss is an important consequence of agricultural intensification and can lead to reductions in agroecosystem functions and services (Bardgett and Van der Putten, 2014; Tiemann *et al*., 2015; DeFries *et al*., 2004; Tsiafouli *et al*., 2015).

This thesis investigates contrasting maize cultivation techniques to understand how these changes in agricultural practice affect above-below ground invertebrate interactions. Positive impacts of above-ground biodiversity on below-ground communities and processes have primarily been observed in natural systems (Caruso *et al*., 2012; Scherber *et al*., 2010; Tiemann *et al*., 2015). However, these theories can be applied to agricultural systems to increase inter-species interactions between plants and invertebrates (Briones and Bol, 2003; Tiemann *et al*., 2015; Wodika and Baer, 2015). This study uses literature surrounding grassland above- and below-ground interactions to understand why arthropod communities in conventional maize cultivation systems exhibit poor biodiversity (Wardle *et al*., 1999; Saviozzi *et al*., 2001; Firbank *et al*., 2003; Groom *et al*., 2008; Scherber *et al*., 2010).

1.1. Hypotheses, aims and objectives

In this thesis, the effect of different maize cultivation techniques on invertebrate biodiversity was assessed. The goal was to gain an accurate understanding of the effects of maize cultivation and ground cover management practices on above- and below-ground invertebrate biodiversity, functionality and resource use.

H_1= reduction in physical disturbance would increase the biodiversity of below-ground invertebrates

H_1= reduction in physical disturbance would increase the biodiversity of above-ground invertebrates

H_1= Increasing non-crop richness increases below-ground invertebrate biodiversity

H_1= Increasing non-crop richness increases above-ground invertebrate biodiversity

H_1= Increasing non-crop cover increases below-ground invertebrate biodiversity

H_1= Increasing non-crop cover increases above-ground invertebrate biodiversity

H_1= Above- and below-ground invertebrates derive carbon from dominant vegetation

1.2. General conclusions

The findings from this thesis highlight that grassland communities have a greater richness than maize cultivation systems. Conventional maize cultivation was found to have fewer taxonomic groups than the more stable grassland system. Functional niches within each system were comprised of different taxa. The below-ground invertebrate communities within each system consumed carbon that was derived from the dominant vegetation, although the isotopic signature of the maize community was diluted. This work was used to inform a more detailed field study regarding the effects of different maize cultivation techniques on invertebrate biodiversity in which soil preparation and ground cover management was altered.

Reduced disturbance and increases in non-crop vegetation in the different maize cultivation systems was shown to improve invertebrate diversity and change community composition. Changes in above- and below-ground community composition were found to be strongly linked to changes in vegetation richness and litter. This linkage via changes in ground cover management between the above- and below-ground communities demonstrates that although both were influenced by changes in vegetation richness, variation in litter composition was the predominant driver of β-diversity. However, for the first time it has been shown that the above- and below-ground communities responded differently to increases in the cover of litter. The above-ground β-diversity was found to increase with greater litter cover, but differences in below-ground β-diversity reduced with increases in litter.

Overall, above-ground communities were found to be more disturbed than the below-ground communities; for the first time this has been identified as a link between the size

distributions of the above- and below-ground invertebrates, where smaller biomass taxa at greater densities were able to respond quickly to disturbance. This showed that below-ground invertebrate communities were better able to recover from disturbance events and retain important ecosystem services. This thesis has used innovative statistical techniques which has shown that the size distribution of predators within the above- and below-ground communities link the respective food webs, with the smaller bodied generalist predators being better able to feed in both the below-ground mainly detrital food web and the above-ground mainly herbivorous food web.

Chapter 2

Literature review

2. Background

2.1. Maize cultivation in temperate regions

Increased crop production is required in order to feed the world's rapidly growing population (Cassman, 1999; Edgerton, 2009; Werling *et al.,* 2014). However, this must be balanced with maintaining ecosystem services, the functionality and resilience of biodiversity (Delaplane *et al*., 2000). It has been understood for many years that all agricultural management practices, such as in the production of maize (*Zea mays* L.), affect both above- and below-ground biodiversity (Stockdale *et al.,* 2006; Bardgett and Van der Putten, 2014). To what degree crop production affects invertebrate biodiversity depends on crop type, soil and climate (Tilman *et al*., 2011; Birkhofer *et al*., 2011), but little is known about how the above- and below-ground communities are linked.

Agricultural management practices have both direct and indirect effects on biodiversity (Hawes *et al*., 2010; Overstreet *et al*., 2010; Van Capelle *et al*., 2012; Birkhofer *et al*., 2011). Direct effects of agricultural activities specifically on soil biota were summarised by Overstreet *et al*. (2010); these include bodily damage from soil preparation, habitat destruction and modification, reduction of plant pests with biocides, and modification of nutrient availability. Indirect effects of agricultural activities include soil compaction, reduction of soil organic matter, reduction of complexity and diversity of carbon inputs, disturbance of trophic interactions from selective pressure on target and non-target organisms, and toxicity from residual and breakdown products of biocides (Overstreet *et al*., 2010; Van Capelle *et al*., 2012; Birkhofer *et al*., 2011).

Maize is an increasingly important crop with over 184,000 ha grown annually in the UK (DEFRA, 2015). Maize is a multifunctional crop being used both for animal and human consumption, and is becoming increasingly important as a feed for biogas generation (Hochholdinger and Tuberosa, 2009; Adams, 1989; Banse *et al*., 2008). It is the latter use which is currently driving the increase in land under maize cultivation (Rosegrant, 2008; Alignier and Baudry, 2015). Maize cultivation is well known for providing a poor farmland habitat; the Defra Farm Scale Evaluation showed that of maize, barley and oilseed rape, maize had the worst farmland biodiversity profile, being lowest in both flora and fauna (Firbank *et al*., 2003).

There are a number of negative environmental and ecological impacts associated with maize cultivation including soil erosion, sediment loss and poor biodiversity (Firbank *et*

al., 2003; Nakamoto and Tsukamoto, 2006; Hartwig and Ammon, 2002; Groom *et al*., 2008). This is due to maize being sensitive to weed competition, especially in the early stages of growth, and therefore requiring intensive soil preparation and high application rates of herbicides to reduce early competition (Altieri, 1999; Holzschuh *et al*., 2007; Batary *et al*., 2010). The application of herbicides leads to low botanical diversity, which is well known to reduce the diversity of both above- and below-ground invertebrate communities through reductions in diversity of plant derived inputs (Wardle *et al*., 1999; Birkhofer *et al*., 2011). Bardgett and Wardle (2003) hypothesised several mechanisms by which herbivores can indirectly affect decomposer organisms and soil processes through altering the quantity and quality of resources entering the soil, which also varies with depth in the soil profile (Doblas-Miranda *et al*., 2009). However, little is understood about how above- and below-ground invertebrate communities interact within conventional maize systems, which undergo large amounts of soil disturbance, have low weed diversity and a poor litter layer with little residue left in the field post-harvest (Firbank *et al*., 2003; Holzschuh *et al*., 2007; Batary *et al*., 2010; Nakamoto and Tsukamoto, 2006). The above practices are known to affect invertebrate trophic structure, complexity and diversity (Groom *et al*., 2008; Overstreet *et al*., 2010, Van Capelle *et al*., 2012; Wardle *et al*., 1999; Birkhofer *et al*., 2011; Bardgett and Van der Putten, 2014) and ultimately the ecosystems services these communities facilitate (Stockdale *et al*., 2006; Tsiafouli *et al*., 2015).

Maize is harvested between September and December in Europe, but for the most common commercial varieties the harvest is carried out during late September/early October, depending on favourable meteorological conditions (Firbank *et al*., 2003). Conventional maize cultivation requires the soil to be prepared by ploughing and tilling, with the crop being planted in straight rows, leaving approximately 50-70% of the field uncultivated (Hartwig and Ammon, 2002; Nakamoto and Tsukamoto, 2006; Firbank *et al*., 2003). The large proportion of bare ground leaves the soil surface exposed to soil erosion, surface runoff, and nitrate leaching (Feil *et al*., 1997). This is exacerbated by the high rates of N fertilizer applied in conventional cultivation (Hartwig and Ammon, 2002; Briones and Bol, 2003). In addition, maize crops are treated with a comprehensive herbicide programme to reduce early competition of weeds with maize (Hartwig and Ammon, 2002; Feil *et al*., 1997). The application of herbicides reduces food availability and habitat quality for invertebrates and higher species that feed on them, such as mammals and birds (Wilson *et al*. 1999). Continuous monoculture cropping of maize leads to a reduction in soil nutrient availability, and reduction in soil organic matter recycling (Groom *et al*., 2008; Aune *et al.,*

2012). All of the above factors are known to directly and indirectly affect the invertebrate community dynamics within maize cultivation (Overstreet *et al*., 2010).

Wilson *et al.,* (1999) identified that reductions in diversity and abundance of plants in intensively managed arable systems is a result of the combination of frequent tillage, improved seed-cleaning technologies, herbicidal weed control and increasingly competitive nitrogen-responsive crops. These are all characteristic traits within modern maize production systems and have negative direct and indirect impacts on food resources for invertebrates and higher biodiversity (Overstreet *et al*., 2010).

2.2. Maize cultivation at reduce environmental impact

Maize cultivation practices to reduce negative environmental impacts have been developed since the 1980s (Pywell *et al*., 2005; Nakamoto and Tsukamoto, 2006; Briones and Bol, 2003). These include conservation tillage systems, integrated weed management, use of intercrops, and biological pest control, with a major focus on providing crops with specific nutrients to meet demand rather than haphazardly applying fertilisers, pesticides or herbicides (Hartwig and Ammon, 2002). Through improved soil quality reducing seed bed preparation and drilling time, these management practices have added benefits of reducing costs associated with chemical inputs and contractors to carry out works (Finke *et al*., 1999).

There are a number of EU and UK based policy measures to encourage farmers to move away from conventional monocropping systems (Cortigiani and Tantari, 2015). These include Ecological Focus Areas (EFA), which aim to improve the cover of nitrogen fixing crops. Under this scheme's crop diversification rules the nitrogen fixing crops have to be in the ground for the same period as the crop. There are also measures to utilise catch crops or cover crops; these must consist of a sown mix of at least 2 different cover crop types; these can be either cereal or non-cereal and must establish quickly, achieve good ground cover and utilise available nutrients (Cortigiani and Tantari, 2015). Rye (*Secale cereal* L.), vetch (*Vicia*), *Phacelia*, Barley (*Hordeum vulgare* L.), mustard (*Brassica*), oats (*Avena sativa* L.) and Lucerne (*Medicago sativa* L.) are considered suitable cover crops but the scheme does not include crops that are usually grazed except grass that is under-sown in a previous crop. The minimum area of catch/cover crops that can count as part of an EFA is 0.01 hectares. Wild-bird seed mixes and nectar sources are also supported under the EFA

scheme and can be planted during the fallow period. These should not be harvestable and contain at least two crops that support wildlife and pollinators.

Simple alteration of management practices can have benefits for biodiversity in maize cultivation. For example, DEFRA project AR0412 (2004) found that by delaying the application of herbicides there was enough resource available to support a wider range of Carabids, Hymenoptera, Parasitoids and Diptera as well as reduced densities of aphids and other pests due to higher densities of predators, whilst not significantly impacting on maize yields or quality.

Differing cultivation techniques such as intercropping between the rows of maize with ryegrass (*Lolium perenne* L.) or legumes promotes rainfall infiltration, reduces fossil fuel consumption, provides soil stabilisation and reduces run-off and diffuse pollution (Hartwig and Ammon, 2002; Pywell *et al*., 2005; Nakamoto and Tsukamoto, 2006). These benefits in turn reduce the amount of N fertilization required and maintain the farmland biological community over winter, providing resources for higher species (Finke *et al*., 1999). Wardle *et al*. (1999) demonstrate that an above-ground change in plant species composition has an effect on below-ground soil invertebrate trophic relationships at the functional group level. Sabais *et al*. (2010) found that increases in plant diversity which can be found in intercrop cultivation systems, positively affect the diversity and density of Entomobryomorpha, Poduromorpha and Symphypleona, both below-ground and in the litter layer. This is supported by a study by Eisenhauer *et al*. (2010) that found positive effects on earthworm density and diversity in agricultural grasslands with greater plant species diversity. A study conducted by Wilson *et al.* (1999) showed that increases in weed biomass within the inter-row in strawberry crops improved predatory *Carabidae* abundance, which in turn reduced pest species which helped maintain crop yield. Despite this little is known about the effects of intercropping management practices on above- and below-ground invertebrate diversity.

Studies investigating the effect of inter cropping wheat (*Triticum aestivum* L.) with white clover (*Trifolium repens* L.), which was found to support larger populations of earthworms (Lumbricidae) than conventional wheat monocropping systems (Schmidt *et al*., 2001). Studies have also been conducted using leguminous intercrops within maize cultivation; results from these studies indicate that leguminous intercrops compete less with maize for nitrogen than grass intercrops (Feil *et al*., 1997). Nakamoto and Tsukamoto (2006) found that maize plants benefitted from the additional nitrogen released by white clover

intercrops. However nitrogen availability in the system may be reduced by the presence of non-leguminous weeds within the intercrop. Nakamoto and Tsukamoto (2006) also identified that with adequate control of intercrops, such as mowing or spraying with a weak herbicide solution, crop yield could be as high as that in conventional cropping systems with the advantages of improving biodiversity. In contrast, Liedgens *et al*. (2004) found that intercropping reduced maize yield as a result of competition, especially for water and nitrogen. The incorporation of grasses or leguminous species in-between the rows of maize has the potential to promote soil biological functions by improving organic matter and soil quality with the added benefit of alleviating fodder problems by providing an additional forage crop (Rabary *et al*., 2008). Intercrops can provide a valuable winter feed for livestock, allowing animals to graze when the maize has been removed and prior to the next season's planting (Rabary *et al*., 2008). This can reduce competition by intercrops in the early stages of maize growth and, through livestock excretion, return N to the soil for the next growing season. In addition, intercrops such as ryegrass can be mechanically harvested, providing a considerable hay or haylage yield in spring (Rabary *et al*., 2008).

2.3. Maize cultivation techniques

2.3.1. Conventional maize cultivation

Agricultural intensification has led to dramatic losses in biodiversity over the past 50 years (Culman *et al.,* 2010). Arable cultivation techniques need to modify natural environments to maximise crop yield (Van Capelle *et al*., 2012). This is achieved in maize cultivation by a variety of methods depending on geoclimatic conditions (Nakamoto and Tsukamoto, 2006). Physical disturbance of the soil caused by tillage is a crucial factor in determining soil biotic activity and species diversity in agroecosystems (Altieri, 1999). Arable soils reflect a significant decrease of individual numbers and species diversity with an increase in tillage intensity (Van Capelle *et al*., 2012; Caruso *et al*., 2012) with Oribatid mite populations being significantly reduced by ploughing and tilling (Coleman *et al*., 2004; Caruso *et al*., 2012). This is due to some organisms depending on far-reaching and connected networks of soil pores. For example, earthworms due to their restricted burrowing activity are adversely affected by ploughless tillage in loamy soils (Van Capelle *et al*., 2012). Van Capelle *et al*., (2012) found that total mite densities were highest where the largest amount of organic matter was provided, which is supported by Caruso *et al*. (2012). Van Capelle *et al*., (2012) concluded that mites, like Collembola, are less sensitive to mechanical injury and soil inversion exerted by ploughing. Therefore different soil

organisms are disturbed differently by ploughing and/or tilling, indicating that to understand how maize cultivation affects invertebrate biodiversity a community approach must be used.

There is a lack of knowledge about the length of time above- and below-ground invertebrate communities' recover from intensive tillage (Adl *et al*., 2006). Adl *et al*. (2006) study determined the time frame for significant changes in species richness and abundance to be detected in no-till fields ranging for 0-25 years. This provided an outlining time scale required for recovery of biodiversity in agroecosystems (Adl *et al*., 2006). Adl *et al*. (2006) highlighted that there was an increasing microbial biomass with age in no-tillage. The most important observation of Adl *et al*. (2006) was an increase in species diversity and increased dominance of Oribatids with age in no-tillage. The diversity of species in any given soil sample was found to be greatest in a 25–26 year no-till field and least in the conventionally tilled fields (Adl *et al*., 2006). Significant shifts in diversity and functional composition were only observed in the 8–9 and 25–26 year sites, suggesting that species richness recovered slowly (Adl *et al*., 2006). However, patterns of response between taxonomic groups differed showing that some populations are resilient to tillage and recover quickly whereas others take much longer, which is supported by Van Capelle *et al*. (2012).

2.3.2. Conservation tillage for maize cultivation

Conservation agriculture is defined as any management system that includes the following principles; first, a serious reduction in soil movement with the ultimate goal to eliminate it completely except for the disturbance caused when sowing; second, the preservation of a permanent or semi-permanent organic cover, i.e. standing crop or a layer of stubble, on the soil and third, the rotation of economically viable crops (Fuentes *et al*., 2010). Minimum tillage is conventionally carried out at < 20 cm depth. This reflects FAO (2009) recommendations for food production by reducing soil disturbance. Additional benefits of reducing tillage include increased rainfall infiltration by concentrating rainfall to the root zone (Rockström *et al*., 2009), reduction in soil erosion (Tabaglio *et al*., 2009), enhanced soil biological activity (Blackshaw and Kerry, 2008) and a reduction in labour and fossil fuel usage (Aune *et al*., 2012), in turn, reducing the carbon footprint of maize production. Other studies highlighted by Aune *et al*., (2012) showed that a reduction in tillage improved soil organic matter and increased nitrogen available for crops. A study by Feil *et al*. (1997) also showed that by sowing maize in winter cover crop residues, killed by frost

or herbicides, in conjunction with minimum tillage, is an effective means of controlling soil erosion and run-off , however, maize produced lower silage yields than under conventional plough based tillage system. Tabaglio *et al*. (2009) showed that four years of no-tillage on a silt loam under continuous maize significantly increased soil organic carbon, total N, C/N, exchangeable K and water aggregate stability; however, Blackshaw and Kerry (2008) showed that there could be a build-up of soil dwelling pests.

In the UK, specific to maize cultivation, voluntary measures have been developed to reduce erosion and diffuse pollution under the Soil Protection Review (DEFRA, 2010). These include:

1. Under sowing the maize
2. Sowing other crops 10 days after harvest
3. Sowing cover crops over winter periods

Reducing the environmental impact of maize cultivation practices has primarily focused on reducing soil erosion, diffuse pollution and improving soil fertility (DEFRA, 2010). These practices can also benefit the soil fauna and in turn nutrient cycling (Bardgett and Van der Putten 2014) within maize systems. Aune *et al*. (2012) found that a reduction in tillage can both reduce soil degradation and improve production. Where Overstreet *et al*. (2010) found that response to tillage operations by any given population of soil invertebrates depends on their vertical distribution in the soil profile, ability to disperse and their response to soil compaction and disturbance, all of which ultimately impacts organic matter decomposition rates.

2.3.3. Intercropping maize cultivation

Intercrops or living mulches are cover crops (Kramberger *et al*., 2009) that are maintained as a living ground cover throughout the growing season of the main crop, and are distinguished from cover crops that are killed using herbicides or machines before the main crop is planted (DEFRA, 2010). Intercropping in arable cultivation systems is a well-established technique for non-commercial agricultural production. For example, for several centuries the Native Americans grew maize in a ‘three sisters’ method with squash and beans (Mt Pleasant *et al*., 2006). In the ‘three sisters’ the maize is planted first to avoid being outcompeted by the squash and the beans (Mt Pleasant *et al*., 2006). The beans are then planted to use the maize as climbing posts and the squash is used as a live mulch to

reduce weed competition and reduce surface run-off and aid infiltration (Mt Pleasant *et al*., 2006).

Intercropping mimics natural ecological processes more closely than conventional arable systems. Mimicking natural ecological processes improves the sustainability of agro-ecosystems by promoting ecological dynamics (Altieri, 1999) such as organic matter recycling (Gardi and Jeffrey, 2009) and bio-control of pests (Wilson *et al.,* 1999). More modern intercropping techniques include alley crops, live mulches or intercrops of leguminous species to aid in N-fixation (Nakamoto and Tsukamoto, 2006). The use of inter-row crops such as clover or ryegrass with maize cultivation promotes rainfall infiltration, reduces fossil fuel consumption, provides soil stabilisation, and reduces run-off and diffuse pollution (Nakamoto and Tsukamoto, 2006; Liedgens *et al*., 2004; Briones and Bol, 2003). Increased biological N-fixation by intercrops, in turn, reduces the amount of N fertilization required and maintains the farmland biological community over winter, providing resources for many species (Liedgens *et al*., 2004). When cultivating maize in intercrop systems, the intercrop requires either mechanical or chemical control to avoid outcompeting the maize crop in the early stages (Liedgens *et al*., 2004; Nakamoto and Tsukamoto, 2006).

The benefits of living soil surface plant cover are:

(i) Plant nitrogen uptake during late autumn and winter may prevent soil nitrate from being leached, because nitrate levels are normally lower in planted soils than in bare soil

(ii) Plant cover intercepts falling raindrops, dissipating energy before striking and dislodging soil particles

(iii) High plant density decreases surface water flow rates

(iv) Plant roots prevent soil from being carried away by surface runoff

(v) Soil is less susceptible to structural damage by wheel traffic

(vi) Weed control between the maize rows is improved, and the development of herbicide-resistant weed populations is prevented

(Liedgens *et al*., 2004)

Intercrops also supply organic carbon and nitrogen to the soil from root exudates and dead plant parts throughout the growing season. After the maize harvest, the grass strips regrow

and remove mineral N from the soil, reducing soil erosion and nitrate leaching during the winter (Feil *et al*., 1997).

Maize yield and quality may also be improved through the increased opportunities for natural pest and disease management that intercrop species can provide (Nakamoto and Tsukamoto, 2006). Liedgens *et al*. (2004) found that the intercrop strips with ryegrass were less affected by maize smut (*Ustilugo muydis*), aphids (*Rhopulosiphon muidis*), and European corn borers (*Ostriniu nubilulis*) when compared to traditional maize cultivation. In addition, Garibay *et al*. (1997) found that intercrop grass strips harboured many predatory insects and spiders aiding in the control of pests. When selecting an intercrop, plant species or species mix it is important to assess the competitive potential of the inter crop to outcompete weed species and the crop (Liedgens *et al*., 2004). Both grass and leguminous species have been shown to have this competitive ability (Liedgens *et al*., 2004). The use of intercrops in protecting the cultivated crop can reduce the amount of herbicides, fungicides and molluscicides needed during the maize growing season which in turn reduces labour and fuel costs at the same time as reducing production costs. However, Nakamoto and Tsukamoto (2006) found that weeds, such as *Digitaria adscendens* (Kunth), grow at a similar rate to the intercrop until the end of July. Thereafter, the biomass of weeds exceeded that of the intercrop demonstrating that there is still a requirement for some weed control in intercropping systems. Nakamoto and Tsukamoto (2006) also identified that maize biomass was higher in the without intercrop than in the white clover intercrops suggesting that white clover and weeds were both competing with the maize. Intercrops also have important implications for the use of providing refuges for arthropods and bio-control (Khan *et al*., 2009). For example, where there is a naturally abundant invertebrate pest, seeding of specific vegetative species could be implemented as controls to attract and/or act as refuges for predatory populations. These techniques of integrated pest management have been shown to be successful in a number of push-pull systems in different geo-climatic regions (Khan *et al*., 2009).

2.4. Measuring biodiversity in agroecosystems

Biological diversity is comprehensively defined by the Convention of Biological Diversity as "The variability among living organisms from all sources, including, *inter alia*, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems" (CBD, 2001). Hubbell (2008) defines biodiversity as being synonymous with species

richness and relative species abundance in space and time. Biological diversity provides economical, aesthetic benefits as well as contributing to the furthering of scientific and ethical knowledge (Vié *et al*., 2008). Biodiversity provides a range of ecosystem services within agriculture which would be expensive to anthropogenically replace (Gardi and Jeffery, 2009); such as recycling of nutrients, control of local microclimate, regulation of local hydrological processes, regulation of the abundance of undesirable organisms, and detoxification of noxious chemicals (Giller, 1996; Costanza, 1997; Altieri, 1999; Hines *et al*., 2015).

Altieri (1999) separated the components of biodiversity in agroecosystems into three functional groups. Firstly, productive biota: crops, trees and animals chosen by farmers which play a determining role in the diversity and complexity of the agroecosystem - these vary depending on the management inputs and crop spatio-temporal arrangements (Altieri, 1999). Secondly, resource biota: organisms that contribute to productivity through pollination, biological control, decomposition - characterised by species that colonize the agroecosystem from surrounding environments and that will thrive in the agroecosystem depending on its management and structure (Altieri, 1999). Thirdly, destructive biota: weeds, insect pests, microbial pathogens, etc. - which farmers aim at reducing through management of productive biota (Altieri, 1999).

To adequately measure biodiversity it is imperative to understand what aspects of biodiversity need to be measured (Altieri, 1999). Pattern diversity was pioneered by Whittaker (1975), describing scales at which to measure diversity and the variation in the diversity of samples taken within a homogenous habitat. *Alpha diversity* refers to the number of species within a sample or habitat area. *β-diversity* refers to the difference in species composition between two adjacent areas, and is defined by Whittaker (1975) as the ratio of *Gamma diversity* over *Alpha diversity*. *Gamma diversity* describes regional differences in species composition (Whittaker, 1975; Crawley, 1997; Carson and Schnitzer, 2008).

Literature shows that it is difficult to achieve representative samples of species numbers and abundance (Blackshaw, 1987; Kent and Cooker, 1992; Whittaker, 1975; Crawley, 1997; Carson and Schnitzer, 2008; Southwood and Henderson, 2000). This is confounded by identification of species varying with the skill of the assessor when identifying morphological features, and their ability to collect and transfer data accurately (Kent and

Cooker, 1992). Taxonomy was first founded by Linnaeus (1758) (cited in Carson and Schnitzer, 2008) when applying a binomial nomenclature to species, by giving them a generic and a specific name. Hey (2006) listed 24 different suggestions on defining a species, finding the most commonly used to be the biological species concept based on reproductive isolation. However, there are often disagreements and revisions to species taxonomy, which makes it difficult to apply an accurate measure of species to determine diversity. Darwin's (1859) theory of evolution by natural selection is based on morphological characteristics, on which a majority of invertebrate diversity assessments still rely, which can be costly and time-consuming (Black *et al*., 2003).

2.4.1. Measuring below-ground invertebrate diversity in agroecosystems

Below-ground invertebrates are often sampled using soil corers to remove undisturbed cores (Southwood and Henderson, 2000). This soil fauna sampling methods can be used to measure both soil meso- and macrofauna. However, due to the number of soil organisms per sampling unit and their heterogeneous distribution at field scale (Bardgett and Van der Putten, 2014) a large number of samples are required to accurately estimate populations, which can be labour intensive (Southwood and Henderson, 2000; Black *et al*., 2003).

Soil organisms are most commonly extracted using behavioural or dynamic methods such as Berlese-Tullgren funnels (Southwood and Henderson, 2000; Crotty *et al*., 2014). Berlese-Tullgren funnels have been used in entomology for over 100 years (Southwood and Henderson, 2000). The use of a lamp or heating element to create a heat gradient forces soil dwelling invertebrates to migrate in to an extraction pot commonly filled with 70% ethanol in order to preserve the invertebrates (Southwood and Henderson, 2000). However, further analysis such as using stable isotopes at natural abundace to trace nutrient flows must be considered when choosing the preservative as using 70% ethanol may skew results (Crotty, 2011). The target group of invertebrates extracted from the soil core depends on the size of mesh in the Berlese-Tullgren funnel (Swift *et al*., 1979).

The main disadvantage of using behavioural or dynamic methods is that extraction time and efficiency will vary depending on the organisms present and soil conditions such as moisture content (Southwood and Henderson, 2000, Crotty, 2011). For example, mite extraction time is irregular, though there is normally a flush after 12 days (Crotty, 2011) which is correlated with moisture content reaching approximately 20%, triggering geotaxis (Southwood and Henderson, 2000).

Earthworm population estimates can be obtained by inserting a plastic frame (40x40 cm) on the soil and driven into the ground to a depth of 1 cm to retain the chemical expellant in the sampling area (Pelosi *et al.,* 2009). Commercial 'hot' mustard is thoroughly mixed with water to obtain a solution at a concentration of 15 g l^{-1} (Pelosi *et al.,* 2009). Mustard solution is then poured into the plastic sampling frame at a rate of initially 1.5L and after 10 minutes a further 1.5L. Sampling is normally replicated approximately 5 times depending on sampling area size. Emerging earthworms are retrieved during a 20 minute period after the expellant application and mature worms are identified to species level and assigned to ecological group (e.g. Endogeic, Anecic and Epigeic) (Pelosi *et al*., 2009). Different expellant efficiencies have been tested by Pelosi *et al*., (2009) finding that of formaldehyde, allyl isothiocyanate (AITC) and mustard powder the first two were the most efficient, however, formaldehyde is carcinogenic and AITC is used as a bio-pesticide so if further study of organisms present is required it is not optimal to use AITC. Other methods of sampling earthworms are based on extraction of soil cores similar to soil arthropod extraction methods discussed earlier, followed by hand sorting (Briones *et al.,* 2002, Smith *et al*., 2008). However, hand sorting can be time consuming and return low observation rates. Schmidt (2001) found that electrical pulses using the Thielemanns' octet method was a good alternative to using formalin extraction in field, although soil conditions such as moisture and temperature can restrict the timing of sampling.

2.4.2. Measuring above-ground arthropod diversity in agroecosystems

There are a range of monitoring methods that have been developed over many years to determine the effects and impacts on populations of invertebrates in arable systems. The most widely used of these methods include pitfall traps, suction sampling (D-Vac) and sweep net sampling (Southwood and Henderson, 2000).

Mommertz *et al*. (1992) compared sampling methods for above-ground invertebrates. The two most efficient methods were D-Vac sampling and pitfall traps. Pitfall traps were found to be much more efficient at capturing larger bodied organisms such as Carabidae, Staphylinidae, and Lycosidae. Although pitfall traps do not give a true density estimate unlike D-vac sampling, the organisms that they efficiently collect, especially Carabidae, are well known for being sensitive indicators of environmental change (Brooks *et al*., 2012). Despite pitfall traps not providing absolute density estimation they are effective in collecting mobile arthropods, providing a good estimate of population densities (Pekár,

2002; Brooks, *et al*., 2012), although this can be biased as larger organisms are often more active.

There is not a uniform design of pitfall traps (Barber, 1931; Querner and Bruckner, 2011). Traps differ from research team to team since the traps are made of material available and are modified according to previous experience (Pekár, 2002; Southwood and Henderson, 2000). Generally, the trap consists of a steep sided plastic cup dug in the ground, filled with a preservative to inhibit predation and organism escape (Southwood and Henderson, 2000). Pitfall traps are often sheltered from rainfall by a metal plate or up-turned plant pot. The cheap and simple design of pitfall traps makes them a very popular technique to assess mobile surface dwelling invertebrate populations (Pekár, 2002; Brooks, *et al*., 2005). In addition, pitfall traps are left *in-situ* for a standardised period of time where the observer does not need to be present; this reduces labour cost associated with other population density measures such as D-Vac or sweep-netting (Southwood and Henderson, 2000).

A number of different preservatives and preservative concentrations are used in pitfall traps (Pekár, 2002; Southwood and Henderson, 2000). The presence of preservative and detergent in traps is very important to conserve the caught material in good condition and to allow safe identification (Querner and Bruckner, 2011). Typically a few drops of detergent are added to the preservative to reduce the surface tension (Pekár, 2002). The particular preservative and detergent used is dependent on further analysis required, for example if $\delta^{13}C$ or $\delta^{15}N$ analysis is required then the preservative used cannot contain carbon or nitrogen as this will skew the results, or at least introduce a correction factor that must be used (Tiunov, 2007; Crotty *et al*., 2014). In this case the alternative preservative is saturated salt solution (Crotty *et al*., 2014).

2.4.3. Linking above- and below-ground invertebrate diversity

There are a range of methods for assessing biodiversity; these include indices and rapid assessments techniques looking at specific indicator taxonomic or functional groups (Altieri, 1999; Brooks *et al*., 2005). Indicator taxa, guilds, structural characteristics, functional groups, habitat or environmental factors offer a more cost-effective, rapid, but less accurate proxy for the measure of population diversity (Elzinga *et al*., 2001). Bio-indicators are practical measures of biological activity that reflect aspects of the functioning of food webs (Elzinga *et al*., 2001).

Büchs (2003) found a number of limitations with the application of bio-indicators for biodiversity assessment including the lack of consensus on how to use bio-indicators and the lack of an indicator for biodiversity as a whole, meaning that each aspect of biodiversity needs its own indicator with very specific and well defined features and agreements on the mode of application. Büchs (2003) showed that invertebrates were more suitable than vegetation for showing a difference in the effects of agricultural land conversion. For example, spiders (Araneae) and beetles (Coleoptera) showed clear responses to changes in abiotic conditions (Brooks *et al*., 2005; Büchs, 2003). As such, in central Europe *Carabus auratus* can be assumed as a species which indicates an acceptable standard of an agro-ecosystem with regards to predator activity (Büchs, 2003).

Carabids are suitable for use as above-ground bio-indicators as they are a species-rich group of insects that occur in the majority of terrestrial ecosystems, being taxonomically tractable and for which there is well documented, reliable biological information available (Büchs, 2003; Brooks, *et al*., 2005). Carabids provide important agricultural ecosystem services through feeding on numerous economically damaging pest species and the regulation of weed seeds in arable fields (Büchs, 2003; Brooks, *et al*., 2005). The UK Environmental Change Network uses the density of *Pterostichus madidus* as an environmental change indicator (Morecroft *et al*., 2009; Brooks, *et al*., 2005). It is well documented that *P. madidus* has leg-colour morphs which are sensitive to changes in local climatic condition (Morecroft *et al*., 2009; Brooks, *et al*., 2005).

Although links between the above- and below-ground components of soils are recognised, only a few studies have included the effects of changes in above-ground plant species composition on the below-ground soil food web (Neilson *et al*., 2002; Scherber *et al*., 2010; Burgio *et al*., 2015) and bio-indicators of these changes (Sauberer, 2004). Below-ground invertebrates have been proposed as potential bio-indicators, with most studies concentrating on the dominant two groups of micro-arthropods, Collembola and Acari. These are often highly abundant in a wide range of soil types and habitats while being relatively easy to extract from soil, (Neilson *et al*., 2002; Burgio *et al*., 2015; Sauberer, 2004; Black *et al*., 2003; Caruso *et al*., 2012) and with well documented ecological literature.

Comparisons between above- and below-ground biodiversity often use Shannon diversity and β-diversity as comparative statistics (Scherber *et al*., 2010; Li *et al*., 2015). To

disentangle the linkages between the plant – soil – invertebrate continuum and how these influence each other *β*-diversity of the focus community is often correlated with experimental factors and changes in community dynamics (Li *et al*., 2015). Linking above- and below-ground communities can be achieved by regressing community dissimilarities indices (Scherber *et al*., 2010). Multivariate analysis of variance tests can then be used to determine the effects of influencing soil or plant dynamics on these communities (Li *et al*., 2015).

Shannon diversity has been used in a number of studies to link above- and below-ground communities (Antoninka *et al*., 2009; Li *et al*., 2015). Shannon diversity reflects both evenness and richness of species, without favouring either dominant or rare species (Li *et al*., 2015). The Shannon diversity index provides a comparable index that incorporates both the abundance and richness of organisms within a community (Antoninka *et al*., 2009; Southwood and Henderson, 2000). The Shannon index was originally designed for use in information theory but was quickly adopted in ecology to describe the diversity of communities (Southwood and Henderson, 2000). Shannon diversity is commonly used at high taxonomic resolution, such as species level, but has been increasingly used to describe communities at lower taxonomic resolutions (Biaggini *et al*., 2007). This is particularly applicable to below-ground communities where higher taxonomic resolution is often time consuming and costly (Marshall *et al*., 2006). The Shannon diversity index has been shown to be a reliable method for describing the diversity of communities between agro-ecosystems, at the order level (Biaggini *et al*., 2007). Shannon diversity as a measure of community diversity has been shown to be as accurate as using Carabidae as bio-indicators to distinguishing different agricultural systems (Biaggini *et al*., 2007).

2.5. Invertebrate food webs using indirect stable isotope techniques

The use of stable isotopes at natural abundance in terrestrial ecology is a relatively new application of a widely used technique. Stable isotopes at natural abundance have been used to elucidate soil feeding ecology at a rapid rate, providing a robust standardised methodology for comparing food webs (Briones *et al*., 1999; Parnell *et al*., 2013; Jackson *et al*., 2009; Crotty *et al*., 2014, Brose and Scheu, 2014; Ferlian and Scheu, 2014) with a high precision and accuracy in the range of 0.2–0.5‰ (Tiunov, 2007). Before the widespread application of natural abundance stable isotope analysis more traditional ecological methods were used to elucidate soil food webs. These included techniques such as invertebrate abundance and biomass (Elton, 1927) as well as functional group

divergences (Neilson *et al*., 2002; Hines *et al*., 2015). Stable isotopes at natural abundance techniques have advantages when applied to below-ground ecology, as unlike above-ground ecology, feeding observations are notoriously difficult due to the opaque nature of the soil habitat (Bardgett and Van der Putten, 2014; Pausch *et al*., 2015).

Maraun *et al*. (2011) reviewed over 300 papers from the previous 15 years and highlighted that many biogeochemical processes are accompanied by changes in the ratio between stable isotopes of carbon and nitrogen ($^{12}C/^{13}C$ and $^{14}N/^{15}N$). It is this change in isotopic ratio that allows stable isotope natural abundance of C and N to be used to compare different ecosystem components and for different ecosystems to be distinguished by their isotopic composition (Pausch *et al*., 2015; Crotty *et al*., 2014). Stable isotope analysis is equally useful for evaluating ecological processes (West *et al*., 2006). The isotopic composition of soil and vegetation can be indicative of fundamental ecosystem properties such as the openness and intensity of biogeochemical cycles, water availability, and limiting chemical elements (Tiunov, 2007; Pausch *et al*., 2015).

Isotope fractionation in trophic chains is defined by Tiunov (2007) as the difference in the isotopic signature between the consumer and food. The measurement of isotopic signatures of different feeding groups reflects the isotopic composition of their basal feeding resource (Ferlian and Scheu, 2014). Natural abundance stable isotope techniques are widely used to determine trophic relationships, which requires a significant difference in stable isotope content between consumers and potential food sources (Ward *et al*., 2010). Since trophic fractionation of ^{13}C is insignificant, the carbon isotope is often used to evaluate the main food sources (Tiunov, 2007). By analysing C and N simultaneously this allows taxa or functional groups to be allocated a basal resource using $^{12}C/^{13}C$, and trophic position using $^{14}N/^{15}N$ (Tiunov, 2007; Phillips *et al*., 2014).

Tiunov (2007) summarised that the isotopic composition of natural materials varies within relatively narrow ranges and is commonly expressed in ‰ difference by comparison with the international standard:

$$\delta^n E = [(Rsample - Rstandard)/Rstandard] x 1000$$

Where E is the element (e.g., C or N), n is the weight of the heavier (and rarer) isotope, and R is the ratio of heavy to light isotopes. Atmospheric N_2 is the standard for nitrogen, while

Vienna PeeDee belemnite (VPDB) is the standard for carbon. The standard carbon and nitrogen Rstandard equals 1.1237×10^{-2} and 3.6764×10^{-3}, respectively (Tiunov, 2007).

The application of natural abundance stable isotopes to elucidate food webs has been more extensively used in marine ecology than terrestrial ecological research (Crotty *et al*., 2012; Brose and Scheu, 2014; Tiunov, 2007; Phillips *et al*., 2014; Jennings *et al*., 1997) and is more widely used in agro-ecological research than in conventional ecological assessments (Brose and Scheu, 2014). Colombini *et al*. (2011) used stable isotopes of $\delta^{13}C$ and $\delta^{15}N$ in plants at natural abundance to trace macro-invertebrates of marine and terrestrial origins. Colombini *et al*. (2011) employed hierarchical cluster analysis to group species with similar values and utilised multi-source mixing models to analyse the contribution of carbon of marine origin to the diets, to calculate trophic levels and to estimate the diets of certain species. However there is currently a trend to move towards Bayesian apportioning of dietary sources (Stock and Semmens, 2013; Parnell *et al*., 2013; Jackson *et al*., 2009).

Whole communities and/or individual taxa apportioning of resource use with Bayesian statistical procedures has revolutionised the use of stable isotope information (Stock and Semmens, 2013). The use of Bayesian mixed models over more traditional mass balance approaches has allowed the uncertainty in isotopic variation of a resource to be incorporated into the model. Bayesian credibility intervals are better able to account for variation and uncertainty and the inclusion of prior information which makes this a superior analytical method (Parnell *et al*., 2013).

2.5.1. Vegetation as a tracer for invertebrate basal feeding resources

Plants provide the primary carbon source for above- and below-ground communities (Hirsch *et al*., 2009; Hines *et al*., 2015). Natural abundance stable isotope techniques are useful for understanding primary carbon sources that arthropods feed on in close spatial proximity (Tiunov, 2007; Ferlian and Scheu, 2014). Studies using vegetation of contrasting isotopic composition, such as intercropping, can provide insights into the primary feeding resources of arthropod communities (Briones and Bol, 2003). The contrasting isotopic signatures of C3 compared with C4 plants and their derivatives can be traced through the above- and below-ground food web (Pausch *et al*., 2015).

C3 and C4 plants and all carbon forms produced from them have significantly different carbon isotopes; which has opened up wide research opportunities (Tiunov, 2007). A

change from C3 vegetation to C4 vegetation, or vice versa, can be used as a natural ^{13}C-labelling technique (Werth *et al*., 2010). Using $\delta^{13}C$ stable isotope analysis in this way can help to unravel the complexity of interactions within soil food webs (Crotty *et al*., 2014; Pausch *et al*., 2015). The concurrent growth of C4 maize and C3 intercrops can be used to elucidate the proportions of basal resource for the above- and below-ground invertebrate communities and individual taxa or functional group (Briones and Bol, 2003).

This difference in vegetative isotopic composition occurs during photosynthesis. In a C3 plant, such as perennial ryegrass, CO_2 is initially fixed into a 3-C compound called 3-phosphoglyceric acid (3-PGA), a reaction catalysed by rubisco. Most plants are C3 plants and have a $\delta^{13}C$ of approximately -24‰ (Staddon, 2004). During photosynthesis in a C4 plant, such as maize, CO_2 is initially fixed into a 4-C compound (malic or aspartic acids), a reaction catalysed by PEP carboxylase and has a $\delta^{13}C$ isotopic ratio of approximately -11‰ (Staddon, 2004). The difference in $\delta^{13}C$ signatures of biological material occurs as a result of differing discrimination against ^{13}C in different biochemical pathways (Staddon, 2004). This can be used to distinguish between different carbon sources for soil fauna and elucidate soil fauna feeding preferences and niche partitioning (Staddon, 2004; Parnell *et al*., 2013; Pausch *et al*., 2015). For example, the differences in $\delta^{13}C$ allow feeding preferences of root feeders to be assigned to C3 or C4 plants and their derivatives by determining if they feed on solely one plant type or a mix of C3 and C4 plants. Albers *et al*. (2006) investigated the stable isotope composition of soil fauna under a C4-plant (maize) growing in an arable field with C3-plant derived organic matter, showing that 40-50% Collembolan body carbon within a growing season was root-derived.

2.5.2. Invertebrate isotopic composition for allocating trophic position

Unlike carbon isotopes, nitrogen isotopes are considerably fractionated through trophic chains. This makes Nitrogen less convenient for ascribing basal feeding resources, but allows their use as an integral index of many ecological processes by ascribing trophic positioning (Schmidt *et al*., 2004; Ferlian and Scheu, 2014). For example, the changes in $\delta^{15}N$ during plant residue degradation are much more pronounced compared to $\delta^{13}C$ (Tiunov, 2007). Soil microorganisms substantially fractionate the isotopes during nitrogen assimilation (Pausch *et al*., 2015). The biochemical reactions of the nitrogen cycle such as nitrification and ammonification can be accompanied by changes in $\delta^{15}N$ in the tens of ppm range (Tiunov, 2007). The accumulation of heavy nitrogen in food chains is due to the discrimination of the heavy isotope in the synthesis of excreted nitrogen metabolites.

However, many details of the fractionation mechanisms and factors of its intensity remain unclear (Abd El-Wakeil, 2009; Tiunov, 2007).

The most extensive analysis of 134 published experiments evaluated the mean $\delta^{15}N$ elevated per trophic level as 2.54 ± 0.11‰ (Tiunov, 2007). Different studies have used different values as trophic level cut off points and a general consensus is to use an approximate change in value of 3‰. However, more recent research by Maraun *et al*. (2011) showed that, on average, animal tissues are elevated in $\delta^{15}N$ compared with their food source by about 3.4‰ per trophic level, corroborating early research by DeNiro and Epstein (1981). Utilising the natural enrichment of $\delta^{15}N$ Schneider *et al.* (2004) suggested that high $^{15}N/^{14}N$ ratios measured in *Hypochthonius rufulus* indicated that they predominantly feed on an invertebrate diet, presumably nematodes or other small and slow moving soil invertebrates which these slow moving mites are able to catch.

Similarities in the isotopic signature of $\delta^{13}C$ and $\delta^{15}N$ of taxa can be used to indicate similarity of trophic niches even if taxa have different activity patterns (Colombini *et al*., 2011). Abd El-Wakeil (2009) showed differences in $\delta^{15}N$ between most flying and flightless invertebrate species, with flying species showing higher nitrogen isotopic ratios than the flightless species. As such, $\delta^{15}N$ can be used to determine movement and dispersal of species relatively quickly, with little prior ecological knowledge needed. Abd El-Wakeil (2009) identified that the greater deviation of $\delta^{15}N$ values for invertebrates at one study site compared with another could be due to the differences in vegetation composition, soil organic matter content and greater numbers of predators. Abd El-Wakeil's (2009) study confirmed the importance of investigating invertebrate trophic structure at a local scale, highlighting issues when drawing landscape scale conclusions as the difference influencing the trophic structures of communities vary based on both community composition and resource availability.

Colombini *et al*., (2011) showed that elevated levels of N availability can lead to increased rates of N-cycling and that this increase in turn results in $\delta^{15}N$ enhancement of the soil pool. Plants accessing the soil nutrient pool can then become elevated in ^{15}N over time. Schmidt *et al*. (2004) found that in earthworm communities, litter-feeding is indicated by low $\delta^{15}N$ values which might be associated with high body fat contents, while feeding on $\delta^{15}N$ elevated soil organic matter is associated with low body fat contents.

Neilson *et al*., (2002) showed that even subtle changes in trophic relationships within an ecosystem can be detected using stable isotopes, providing a relatively cheap, robust and accurate technique. Neilson *et al*. (2002) also found that changes in above-ground management which alters plant species composition are propagated through the soil food web and were manifested as changes in $\delta^{13}C$ and $\delta^{15}N$. More recent studies by Klarner *et al*. (2013) showed that Mesostigmata occupy high trophic positions in the soil food web due to the broad range of $\delta^{13}C$ and $\delta^{15}N$ signatures, which supports the view that Mesostigmata are generalist predators - feeding on a variety of prey from different trophic levels and functional groups. These studies show that natural abundance stable isotope techniques provide an insight into how management practices can affect both trophic partitioning and resource use in above- and below-ground invertebrate food webs.

Chapter 3

Common Materials and Methods

3. Materials and methods

The work described in this thesis determines the effect of contrasting maize cultivation techniques on above- and below-ground invertebrate biodiversity. A substantial component of this work distinguishes between the different feeding interactions and networks co-existing within and between the above- and below-ground invertebrate communities. A range of methods have been utilised and adapted to meet these objectives. The field sites, common methods and statistical procedures are described below, with more detailed descriptions where appropriate within individual chapters.

3.1. Site description

Field trials were established in a conventionally ploughed maize crop at two study sites (Appendix Plate 12.2.1). Both field trial sites were established in April 2012; the first study site was near Bow, Devon, and the second near Copys Green, Norfolk (Plate 3.1 Bow and 3.2 Fakenham). The two field sites had been under conventional maize cultivation for the previous 10 years. The Bow site received annual inputs of slurry from the resident dairy herd, whilst the Fakenham site had historically received inorganic fertiliser. At Bow the dairy herds were fed on pastures during the summer and ensiled maize during the winter.

The study sites were selected for the freely draining, slightly acidic loam soil of the Dystric Cambisol soil type (Driessen, 2001) in Devon and the shallow well drained calcareous coarse loamy and sandy soils of the Calcaric Leptosols soil type in Norfolk (Driessen, 2001); both were typical of land under maize cultivation. One topsoil sample (0-15 cm) was collected using a soil corer from a random location in each block at both sites in autumn 2012 before the field experiment commenced; these topsoil samples were analysed for pH, extractable and water soluble P, extractable K and Mg, total N, P, K, Mg and S, organic carbon content (by wet chemistry oxidation method) and particle size distribution (Appendix Table 12.2.1), as only one sample was taken per block these result may not be representative of field conditions when scaled up, however these results do indicate a baseline for the field experiment.

Twelve study plots were delineated from the rest of the field, each 10 m wide and 60 m in length with 2 m of uncultivated area between each study plot. The different cultivation regimes were established in a randomised triplicate block design at each site (Plate 3.1 and 3.2). Maize yields were measured in October of each field trial year (Appendix Table 13.2.2).

Plate 3.1 Field trial plot plan for Bow, Devon. Twelve plots were delineated from the rest of the field, with different cultivation methods applied to one plot within each block.

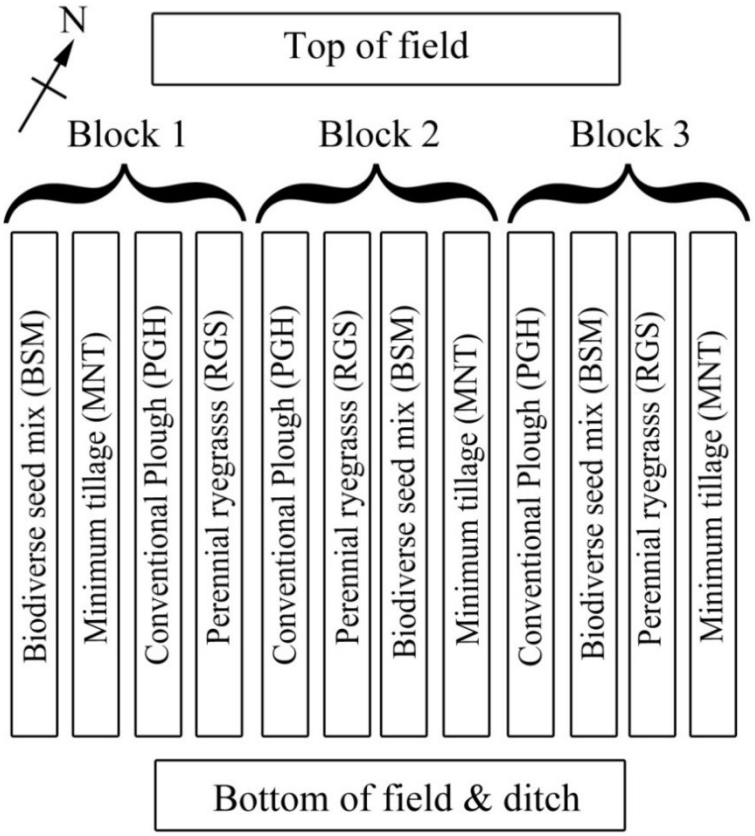
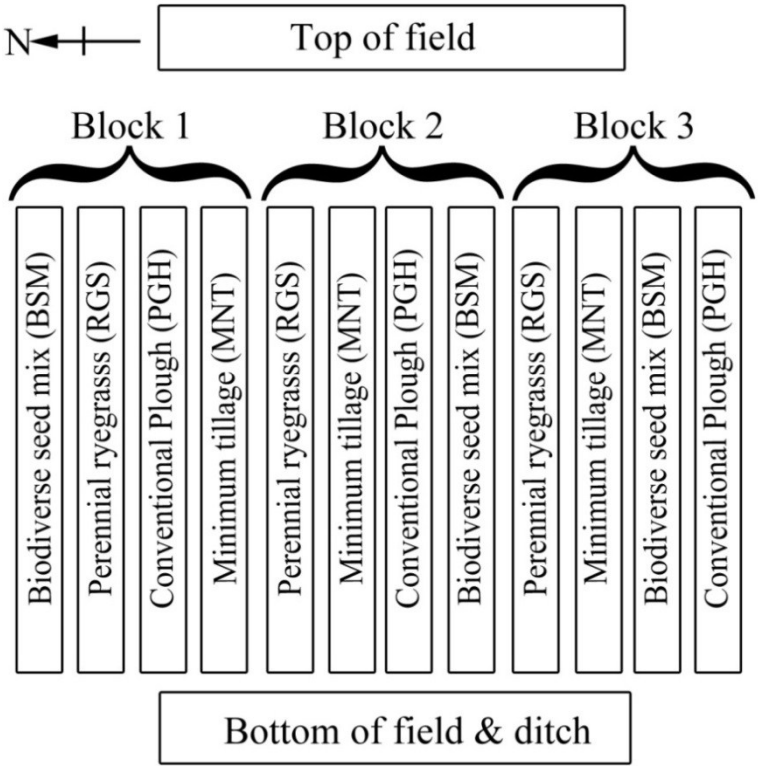


Plate 3.2 Field trial plot plan Fakenham, Norfolk



3.2. Description of soil cultivation and ground cover management

The field trial consisted of four different maize cultivation methods:

1. Conventional plough-based cultivation, where the soil was ploughed to a depth >20 cm, tilled (PGH).
2. Strip tillage under sown with perennial ryegrass at a rate of 35kg ha^{-1}, where only the crop row area was ploughed and the maize drilled directly into this area (RGS).
3. Strip tillage under sown with a biodiverse seed mix, where only the crop row area was ploughed and the maize drilled directly into this area (BSM). The seed mix was sown at a rate of 15 kg/ha^{-1} with *Medicago lupulina* L. 20%, *Onobrychis viciifolia* L. 25%, *Trifolium hybridum* L. 20%, *Trifolium incarnatum* subsp. *Incarnatum* L. 20%, *Lotus corniculatus* L. 10% and *Malva moschata* L. 5%.
4. Non-inversion cultivation, the soil was tilled (MNT)

At the two sites herbicides and fertilisers were applied in keeping with conventional agronomic practice. At both sites in 2013 pre-emergence application of herbicides were 4.5 l ha^{-1} Stomp® (a.i Pendimethalin) to all cultivation techniques, an additional 3.5 l ha^{-1} of Hoedown® (a.i Glyphosate) pre-emergence and 1 l ha^{-1} Touchdown® (a.i Glyphosate) post-drilling was applied to the ryegrass plots and 150ml ha^{-1} Reglone® (a.i Diquat) to the two strip tillage into ground cover cultivation techniques. Post-emergence, at the two leaf stage, Callisto® (a.i Mesotrione) at a rate of 1 l ha^{-1} was applied to all cultivation methods except the BSM cultivation method where 0.5 l ha^{-1} Callisto® was applied. In 2014, to reduce inter-crop competition and improve yields additional herbicides were applied, 5 l ha^{-1} Wing P® (a.i Pendimethalin) was applied to all cultivation methods. An additional 1 l ha^{-1} Touchdown® (a.i Glyphosate) was applied to all cultivation methods except BSM where Touchdown® was applied at a half rate of 0.5 l ha^{-1}. Post-emergence in 2014, Callisto® was applied at a rate of 2 l ha^{-1} to all cultivation methods. At both sites 150 kg ha^{-1} of ammonium nitrate (a.i nitrogen) was applied to all cultivation techniques in 2013 and 2014. However, in 2014, additional 175 kg ha^{-1} potash was applied to all cultivation techniques.

3.3. Sampling timeline and procedures

Below-ground macrofauna, mesofauna and earthworms were sampled pre-cultivation at both sites, in each year (Plate 3.3). Additional below-ground mesofauna samples were collected during cultivation and post-harvest at Bow (Plate 3.3). Above-ground invertebrates were sampled for six weeks during cultivation at both sites in each field trial

year. Each pitfall trap was filled with saturated salt solution to preserve above-ground invertebrates; traps were collected and replaced each week (Plate 3.3).

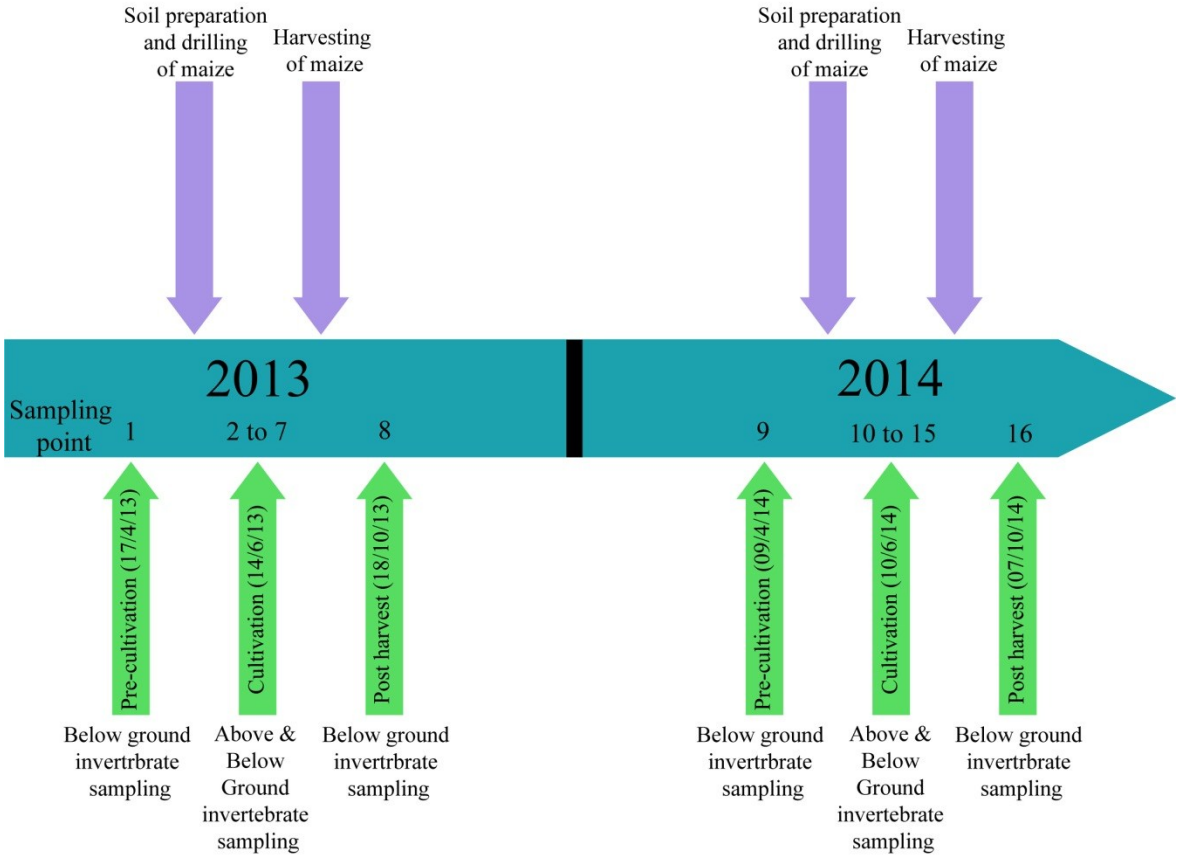


Plate 3.3 Timeline of major cultivation and invertebrate sampling events. Sampling dates are in brackets formatted as (dd/mm/yy).

All below-ground invertebrate sampling was carried out on the complete randomised block field experiment (Plate 3.2 and 3.3). Below-ground invertebrate soil core samples (10 cm depth by 8 cm diameter - mesofauna; 10 cm depth by 6 cm diameter - macrofauna) were collected from all plots at Bow and Fakenham at times specified in Plate 3.3. Two sets of eight cores were taken per plot from all four cultivation methods; one set for mesofauna extraction and one set for macrofauna extraction. Four cores from both the meso- and macro-fauna sampling were taken from the mid-line of the crop row and four collected from the mid-line of the strip crop row, except in the case of the June 'cultivation' sampling period where eight cores were only taken from the inter-row area. Pseudo-replication was accounted for by pooling invertebrates from the row or inter-row area of each plot.

Below-ground mesofauna were extracted from soil cores over a temperature gradient using modified Berlese-Tullgren funnels for 14 days (Crotty, 2011; Section 4.2.1; Figure 3.4a). Below-ground macrofauna were extracted using Blasdale dry heat extractors for a period of 48 hours (Blasdale, 1974; Plate 3.4c). All below-ground invertebrates were extracted into saturated salt solution and stored at 4 °C before identification (Section 3.4).

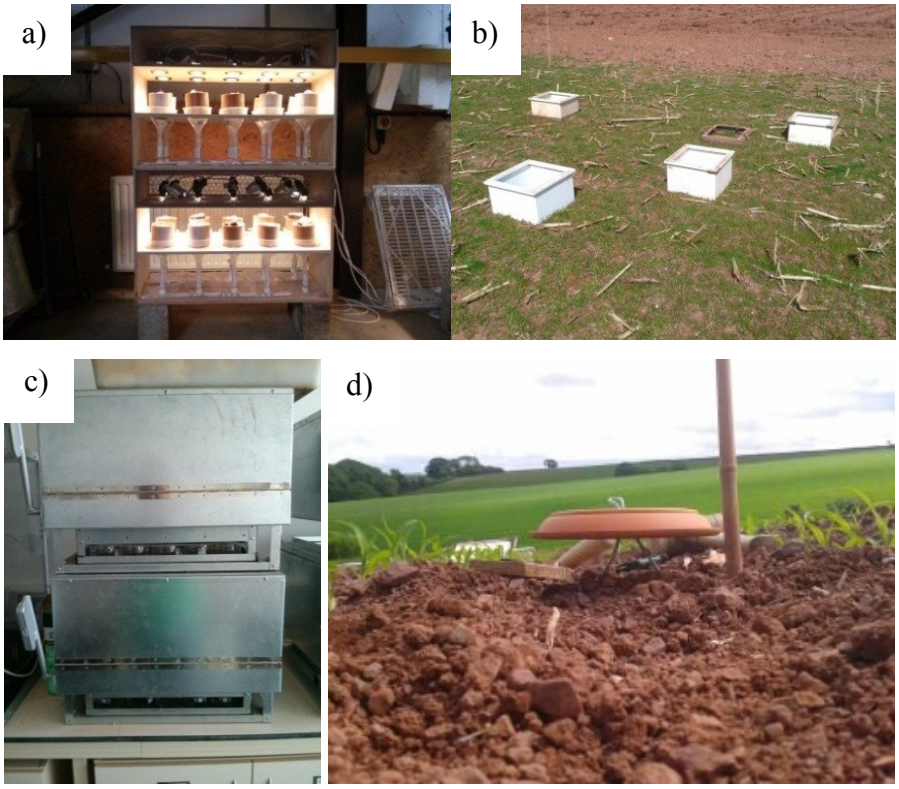


Plate 3.4 Invertebrate collection and extraction apparatus: a) Berlese-Tullgren funnels with 20W halogen bulb for the extraction of soil mesofauna; b) *in-situ* mustard extractions of earthworms - white boxes demarcated the extraction area that mustard solution was poured into to agitate earthworms; c) Blasdale dry heat extractors for the extraction of soil macrofauna; d) Pitfall trap, rain cover and demarcation cane for the collection of surface active invertebrates

Earthworm sampling coincided with invertebrate soil core sampling in April 2013 and 2014 at both sites. Sampling was carried out by inserting a plastic frame (40 by 40 cm) into the soil, at a depth of 1 cm to retain the chemical expellant in the sampling area in both the row and inter-row areas (Plate 3.4b). Commercial 'hot' mustard was thoroughly mixed with water to obtain a solution at a concentration of 15 g l^{-1} (Pelosi *et al*., 2009). The mustard solution was poured into the plastic sampling frame at a rate of 1.5 liters followed by 1.5 liters 10 minutes later. Emerging earthworms were retrieved over a 20 minute period after the first expellant application, washed with distilled water and placed in a

labelled container with moist tissue, air vent and mesh covering the air vent to prevent escape. For each of the cultivation plots sampling was pseudo-replicated four times; twice on the crop row area and twice in the intercrop areas with results pooled per plot and by row or inter-row area. Mustard extraction preferentially extracts aneric earthworms (Bartlett *et al*., 2006), however given time and cost constraints this was considered an appropriate method for assessing earthworm communities.

Pitfall traps (10 cm depth by 6.5 cm diameter) were used to collect above-ground invertebrates (Barber, 1931) from the intercrop area of all four cultivation methods (Plate 3.4d). Eight pitfall traps were installed on each plot for six weeks during June/July 2013 and 2014 (Plate 3.3). Traps were collected and replaced once a week. Pitfall trap locations were demarcated with a 2 m cane with a safety cap. The pitfall traps were plastic cups with steep sides, which were contained in a plastic sheath to aid installation, removal and to reduce soil disturbance. Rain covers were placed over the top of the traps. Traps contained 20 g of salt and, once installed, pitfall traps were filled with 50 ml water, providing an oversaturated salt solution for invertebrates to be destructively sampled. Once a pitfall trap was removed it was covered with a water-tight lid and transported to the laboratory for specimen identification (Section 3.4).

3.4. Specimen identification

Once extracted, below-ground invertebrates were pooled as distinct row and inter-row area samples for each plot, and identified to family level (sub-order for Acari) under a stereo light microscope using identification keys (Crotty, 2011; Dindal, 1990; Hopkin, 2007; Krantz and Walter, 2009). Above-ground invertebrates that were collected using pitfall traps were pooled per plot and identified to family level using identification keys (Crotty, 2011; Dindal, 1990; Hopkin, 2007; Krantz and Walter, 2009; Tilling, 1987; Unwin, 1984). Mature worms were identified to genus level using Sims and Gerard (1999), juvenile earthworms were not identified to genus level but were noted as juveniles.

3.5. Stable isotope analysis

Identified specimens were weighed into tin capsules using a Mettler Toledo MX5 microbalance (precision to 0.1 mg) and were analysed using a Carlo Erba NA2000 analyser (CE Instruments, Wigan, UK) linked to a SerCon 20-22 isotope ratio mass spectrometer (SerCon Ltd, Crewe, UK). The precision range was 800 - 1800 μg C, and 40 -

80 µg N, with an analytical precision for atom% measurements of ±6x10^{-4} for ^{13}C and ±4x10^{-4} for ^{15}N. For isotopic ratio calculation see Section 2.6.

3.6. Statistical analysis

All statistical analysis and graphics have been produced using RStudio (Racine, 2012); an integrated development environment for R (R core development team, 2008). Taxonomic richness was calculated using the function 'specnumber' in R-package 'vegan' (Oksanen *et al*., 2007) which finds the number of taxa.

Below-ground invertebrate population density was calculated by multiplying the number of invertebrates observed by the number of soil cores (or extraction area for earthworms). The multiplying factor for each type of soil core (meso- or macro-fauna) or extraction area for earthworms was based on the number of replications per plot and the diameter of the soil cores/extraction area using the calculation:

$$Area = \pi * r * r$$

The area that the pseudo-replicated soil cores accounted for was used to calculate the multiplication factor.

Shannon diversity indices were calculated as:

$$H' = \sum_{i=1}^{S} P_i \, log_b P_i$$

Where p_i was the proportional abundance of species and *i* and *b* was the base of the logarithm, which in this case was 10. Pielou's evenness was calculated as

$$J = H'/\log_{10}(S)$$

Where *H'* was Shannon diversity and *S* was richness.

Plots of means and standard error calculation were derived from the R-package 'sciplot' (Morales, 2011). R-package 'car' was used to test for normality of variates and residuals resulting from models. Where normalisation of data was required the Box-Cox power transformations (Box and Cox, 1964) was used unless otherwise stated. R-package 'doBy'

(Højsgaard, 2006) has been used to generate summary statistic tables. R-package 'ggplot2' has been used to create scatter plots. R-package 'agricolae' (De Mendiburu, 2009) has been used to calculate Tukey HSD post-hoc significance groups. Significance intervals are denoted as <0.05(*), <0.01(**), <0.001(***) unless otherwise stated.

R-package 'vegan' (Oksanen *et al*., 2007) has been used to assess community and functional similarities using Euclidean distance algorithm unless otherwise stated. Non-metric multidimensional scaling (NMDS) (Faith *et al*., 1987) and 'envfit' (Oksanen *et al*., 2007) were used to identify how taxonomic and functional community composition correlated with experimental variates, and to assess how changes in vegetation influenced invertebrate community composition. The Euclidian distance algorithm was used to calculate taxa similarity scores for NMDS, which is analogous to PCA and PCoA (Kent and Coker, 1992). Non-metric Multidimensional Scaling (NMDS) is commonly regarded as the most robust unconstrained ordination method in community ecology (Minchin, 1987; Kent and Coker, 1992). NMDS uses transformation if the data values are larger than common abundance class scales; the function performs a Wisconsin double standardisation. If the values are very large, the function also performs square root transformation which is common with count data, especially below-ground invertebrate population densities (Oksanen *et al*., 2007).

Chapter 4

An exploratory study to Compare below-ground biodiversity in two contrasting agricultural systems

4. An exploratory study to Comparison Compare of below-ground biodiversity in two contrasting agricultural systems

4.1. Introduction

Soil represents one of the most important and diverse reservoirs of biodiversity (Gardi *et al*., 2009; Giller, 1996; Tabaglio *et al*., 2009; Bardgett and Van der Putten, 2014). Few studies have investigated below-ground biodiversity under contrasting agricultural land uses in close spatial proximity (Benefer *et al*., 2010). This study compares the differences in below-ground invertebrate diversity, community and functional composition between neighbouring conventionally ploughed maize and permanent pasture fields. Assessing the below-ground invertebrate diversity, community and resource use (Briones and Bol, 2003) in close spatial proximity offers the opportunity to understand compositional and functional differences of soil communities under contrasting agricultural systems.

Little is known about the community structure of below-ground invertebrates within maize cultivation systems. In contrast, there is extensive literature considering linkages between temperate grassland vegetation and below-ground invertebrate community diversity which highlights that grassland makes an important contribution to biodiversity within the agricultural landscape (Isselstein *et al*., 2005; Crotty *et al*., 2014; Wilson *et al*., 1999; Bardgett and Cook, 1998). Grasslands are considered to be one of the most species-rich habitats in the world in terms of vegetation (Wilson *et al*., 1999; Crotty *et al*., 2014; Bardgett and Cook, 1998), and the diversity of vegetation promotes feeding activity of soil fauna via alterations of both microclimate and resource availability (Birkhofer *et al*., 2011).

Saviozzi *et al*. (2001) compared the changes in soil quality after 45 years of continuous production of maize with an adjacent poplar forest and native grassland. They showed that long-term intensive maize cultivation caused a marked decline in all measured soil quality parameters leading to a decrease in habitat quality for below-ground invertebrates. It is suggested that the decline in habitat quality for below-ground invertebrates in turn impacted above-ground invertebrate biodiversity and ecosystem functionality (Saviozzi *et al*., 2001; Hooper *et al*., 2000; Tilman, 1996), which is dependent on the strength and stability of interactions between the above- and below-ground communities (Bardgett and Cook, 1998). Werling *et al*. (2014) quantified ecological processes including plant primary productivity, consumption of methane by soil bacteria, consumption of insect pest eggs by arthropod natural enemies, pollination and colonisation by pest aphids. They concluded

that although maize fields produced an order of magnitude more above-ground biomass than perennial grass systems, all other beneficial ecosystem processes measured were greater in grassland (Werling *et al*., 2014). Conventional maize cultivation systems have poor ground flora cover and diversity (Brooks *et al*., 2012). Fewer plants to create barriers affect the surface predators by improving the dispersal ability across the soil surface. However, reduced ground cover in maize cultivation systems also increases predation rates of invertebrates in comparison to grasslands (Landis *et al*., 2000).

Stable isotope ratio analysis of the below-ground invertebrate community offers a sound analytical basis to assess resource use of invertebrate communities under different dominant vegetation (Crotty *et al*., 2014). Whole community stable isotope analysis can be used to assign basal feeding resources as the isotopic signature of the dominant food sources will be reflected in the invertebrate community; little fractionation occurs when the basal resource is consumed and as the derived carbon flows through the invertebrate food web (Tollenaar *et al*., 1994; Gregorich *et al*., 2001; Tiunov, 2007; Crotty *et al*., 2014). Contrasting carbon isotopic signals from the dominant vegetation (C3 vs. C4) in the two cropping systems offers an opportunity to identify basal feeding resource for the invertebrate community within each system (Tiunov, 2007). Crotty *et al*. (2014) found differences in the functionality of below-ground communities between a temperate grassland and a woodland concluding that these were due to the difference in carbon inputs from the dominant vegetation. These results highlight that similar taxonomic groups within each system utilised different resources (Klarner *et al*., 2014).

4.1.1. Hypothesis, aims and objectives

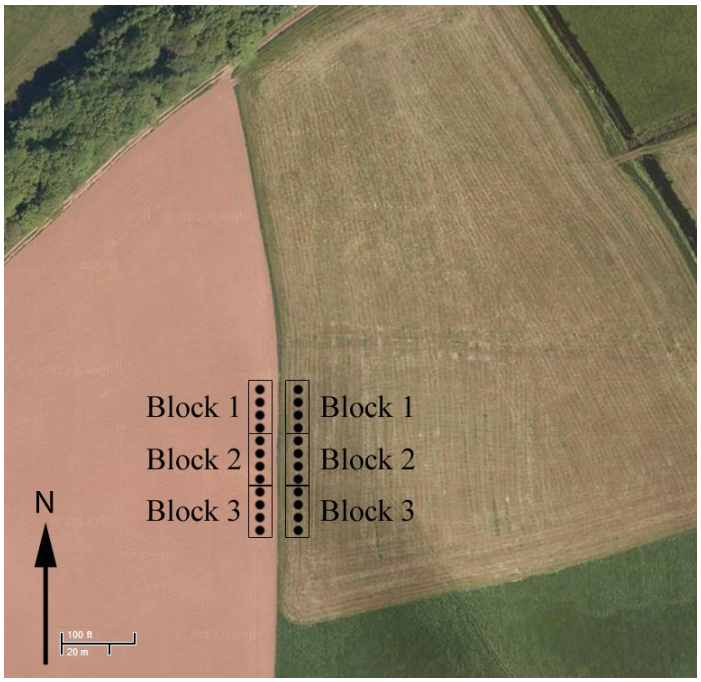
An exploratory study was undertaken to understand the diversity, functional and isotopic composition of below-ground communities under different agricultural systems. The goal was to understand what communities the two contrasting agriculture systems supported, if these communities were functionally different and if the communities derived carbon from the dominant vegetation in each system.

H_1=Below-ground diversity is dependent on cropping system
H_1=Below-ground community composition is dependent on cropping system
H_1=Below-ground inverebrate isotopic composition reflects that of the domient vegation in a cropping system

4.2. Methods

4.2.1. Study site and sampling method

The field trial site at Bow was used for this investigation (see Section 3.1). The grassland selected for comparison was dominated by perennial ryegrass (*Lolium perenne* L.), and was adjacent to the maize field (Plate 4.1). Both were on the same soil type (Section 3.1) and had been under their respective land use for over 10 years. 36 m transects was established in each cropping system, 2 m from the field boundary, i.e. 4 m apart (Plate 4.1). Transects were delineated into three blocks in each field measuring 8.6 m in length and 75 cm width and four soil cores were collected from each block with a minimum distance of 2 m between cores (Plate 4.1). Soil cores (10 cm by 8 cm diameter) were collected in October 2012, four weeks before the maize crop was harvested. Soil cores collected from the maize field were sampled from the mid-line of the maize crop row (Smith *et al*., 2008).



Plates 4.1 Field locations, three 8.6 m blocks (denoted by boxes) were established in each field over 36 m transects. Twelve soil cores were taken from the maize (right) and grassland (left) systems; each soil core is denoted with a black circle. Below-ground invertebrates were extracted from each of the soil cores, identified and counted. Base map from Google Earth (2012).

Soil cores were placed on Berlese-Tullgren funnels with a mesh size of 2 mm (Burkard Manufacturing Co. Ltd, Rickmansworth, UK). A temperature gradient of approximately 14°C stimulated the downward movement of organisms through the gauze to a receiver

vial at the base of the funnel. The receiver vial was filled with saturated salt solution to avoid contamination or the need for correction factors for stable isotope analysis (Tiunov, 2007; Crotty *et al*., 2014), to preserve invertebrates and to inhibit in-vial predation during the extraction period. The soil cores remained on Berlese-Tullgren funnels for five days. After the five days, cores were crumbled and hand sorted for any remaining macrofauna (> 2 mm). Once soil fauna had been extracted they were identified under a stereo light microscope on a per core basis (Section 3.4).

4.2.2. Stable isotope analysis

Post extraction, the invertebrates were sorted into groups of < 2 mm, > 2 mm and earthworms for each habitat. This was required to obtain a sufficient biomass of (≥ 90 µg) for stable isotope analysis of $^{13}C/^{12}C$ and $^{15}N/^{14}N$ (Tiunov, 2007; Crotty *et al*., 2014).

4.2.3. Statistical analysis

The counts of invertebrates were summed for the four soil cores collected in each block to reduce biasing results due to heterogeneous distribution of soil invertebrates (Ekschmitt and Griffiths, 1998). The counts of all taxonomic and functional groups from each block were multiplied by 49.5 to give an estimate of abundance per m^2.

Analysis of variance (Chambers *et al*., 1992 from Fisher, 1946) was used to test for significant differences between agro-systems and below-ground diversity indices, where agro-system and block were fixed factors once data had been normalised if required (Section 3.6). Diversity indices for taxonomic richness, abundance m^{-2}, evenness and Shannon diversity were used to test for difference in below-ground invertebrate biodiversity between cropping systems (please see section 3.6 for detailed calculations).

The abundances of the different taxonomic groups on a per block basis were allocated to functional groups based on literature (Table 4.1). Functional group abundances were used to determine whether all functional groups were present in both cropping systems, and if so, whether they were comprised of similar taxonomic groups. Functional and taxonomic abundances were analysed using analysis of variance and Tukey HSD test (Section 3.6) where cropping system and block were fixed factors.

Analysis of variance was also used to test for significant differences in the isotopic composition of the two invertebrate communities with cropping system as the fixed factor.

Post-hoc Tukey HSD tests (Yandell, 1997) were applied to identify honest significant differences between cropping system.

Similarity percentage analysis (Clarke, 1993; Oksanen *et al*., 2007) was used to discriminate between arthropods that contributed to the greatest difference in community composition between cropping systems using the abundance data matrices. The 'simper' functions in R-package 'vegan' performs pairwise comparisons of groups of sampling units and finds the average contributions of each species to the average overall Bray-Curtis dissimilarity (Oksanen *et al*., 2007). The 'simper' function displays the most important species for each cropping system. β-diversity was calculated from below-ground abundance matrices using the function 'betadiver' to account for dispersion in R-package 'vegan' (Oksanen *et al*., 2007). Correlations with habitat were computed using R-package 'vegan' (Oksanen *et al*., 2007) and the function 'envfit'. β-diversity was calculated as

$$w = (b + c)/(2a + b + c)$$

a was the number of shared taxa between cultivation methods, and *b* and *c* were the numbers of unique taxa not shared between cultivation methods.

4.3. Results

4.3.1. Diversity and community composition

The grassland community had a significantly greater taxonomic richness compared with the maize field (P =0.022, Figure 4.1). There were no significant differences in abundance, evenness or Shannon diversity of the below-ground communities between the two cropping systems (P >0.05, Figure 4.1).

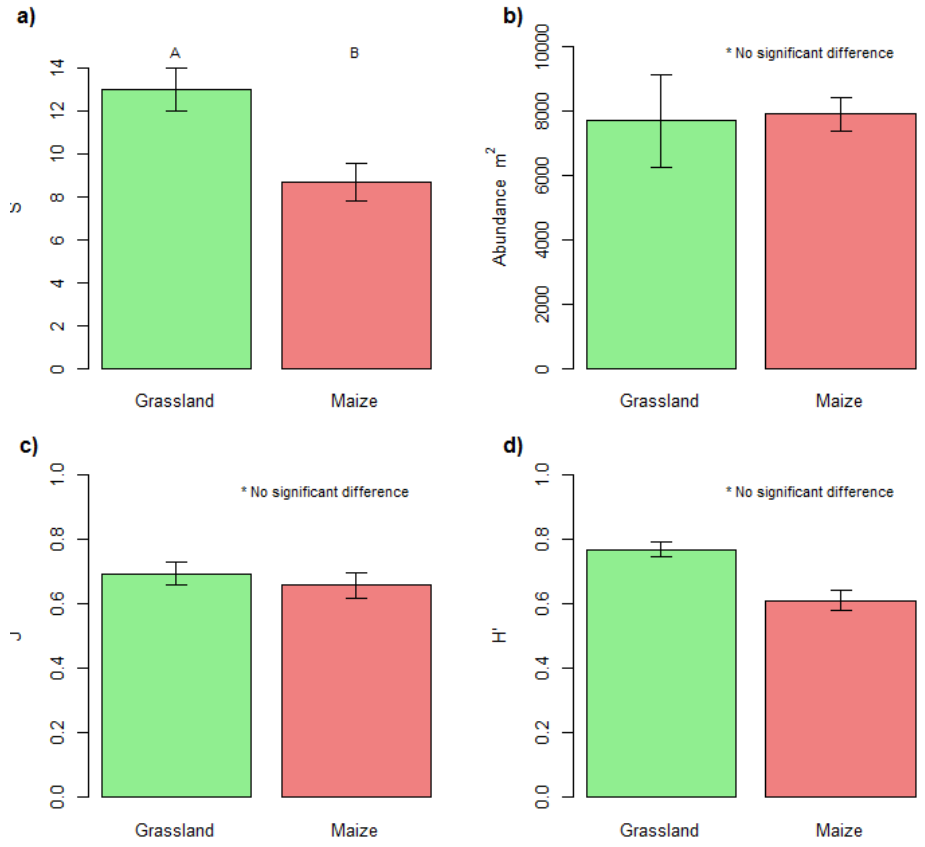


Figure 4.1 Below-ground invertebrate community mean (± s.e.) a) taxonomic richness; b) abundance; c) evenness; d) Shannon diversity in the grassland ( ) and maize ( ) cropping systems. Below-ground invertebrates were extracted from soil cores collected in the two cropping systems (n =12). Letters denote Tukey HSD levels, where different letters denote significant differences between groups.

The invertebrate orders with the greatest abundance in both cropping systems were Acari; Psoroptidae and Gamasida, and Collembola; Entomobryomorpha and Poduromorpha (Table 4.1). There was a significant difference in the abundance of Entomobryomorpha and Poduromorpha between cropping system but not between Psoroptidae and Gamasida. Entomobryomorpha had the greatest mean abundance in the maize system whereas Poduromorpha had the greatest mean abundance in the grassland system (Table 4.1). Although Acari; Uropodidae and Oribatida were not found to be significantly different between the two cropping systems they did show a similar response to difference in cropping system as Entomobryomorpha and Poduromorpha, where there were greater abundance of Oribatida in the maize systems and greater numbers of Uropodidae in the grassland system (Figure 4.2, Table 4.1). The greatest contributors to the difference in community composition between the cropping systems were Poduromorpha (29%), Entomobryomorpha (26%), and Gamasida (18%) accounting for 72% of the difference.

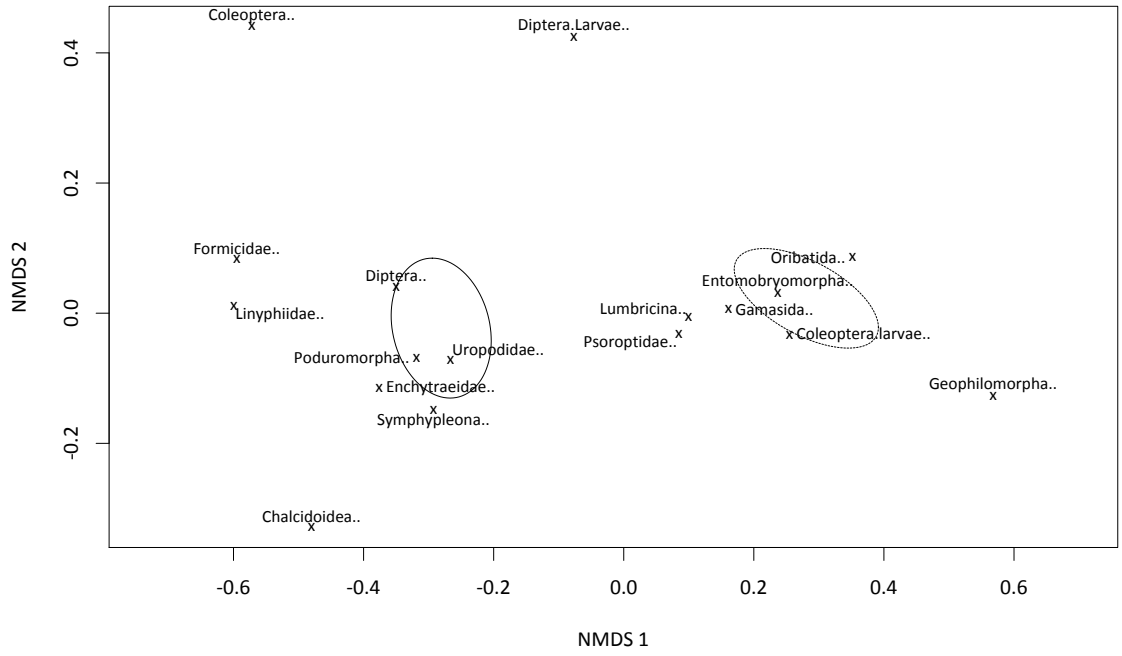


Figure 4.2 Relationship between two-dimensional non-metric multidimensional scaling (NMDS) of the Wisconsin squared root transformed below-ground invertebrate community count data (n =24) using β-diversity dissimularity to detect differences between the maize (dotted line) and grassland (solid line) cropping systems (ellispse ± standard error from centroids).

Although no significant difference was found in the mean density of Psoroptidae or Gamasida between the two cropping systems (Table 4.1), the β-diversity scores of these taxa, or the difference in abundances between cropping systems (Whittaker, 1975), indicate that Gamasida were more associated with the maize cropping system. However, Psoroptidae were not associated with either cropping system (Figure 4.2). Uropodidae were more associated with the grassland system (Figure 4.2). Interestingly, Gamasida are known predators, however, Uropodidae include both fungivores and predators, indicating a different predatory structure in the grassland system to the maize system. Entomobryomorpha and Oribatida were associated with the maize cultivation systems (Figure 4.2). The predators associated with the maize cropping system were Coleoptera larvae and Geophilomorpha (Figure 4.2). In contrast, the predators associated with the grassland system were Linyphiidae, Formicidae and Coleoptera indicating greater predatory richness and thus greater top-down stability than found within the maize cultivation system (Peckarsky *et al*., 2014).

4.3.2. Isotopic composition of mesofauna communities

The isotopic signatures of the below-ground invertebrate communities were significantly different depending on if recovered from the maize and grassland systems (Figure 4.3). The maize invertebrate community $\delta^{13}C$ composition was found to be more elevated in comparison with the grassland invertebrate community $\delta^{13}C$ composition. This was probably due to the community deriving a proportion of diet from the more elevated maize vegetation, whereas in the grassland the maize derived feeding resource was absent resulting in a more depleted $\delta^{13}C$ community signature (Figure 4.3).

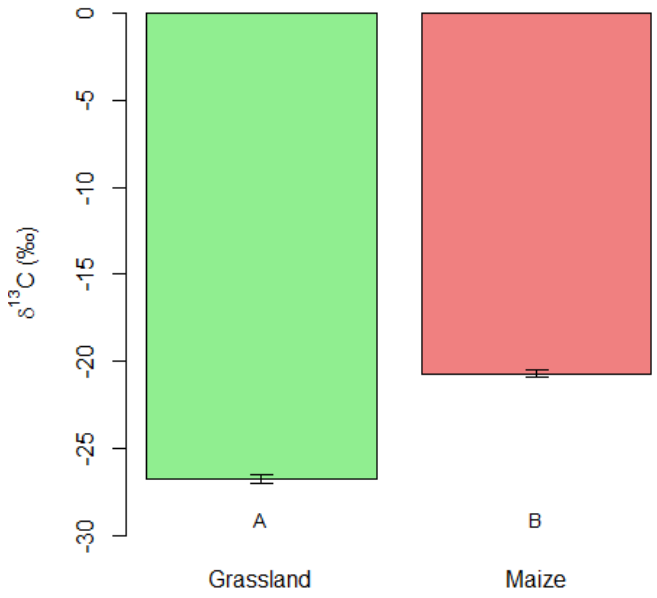


Figure 4.3 Mean (± s.e.) $\delta^{13}C$ signature of the below-ground invertebrate communities (n =12) from the grassland ( ) and the maize ( ) cropping systems. Letters denote Tukey HSD significance levels, the different letter show that there was a significant difference in the plant resources the two communities consumed.

4.4. Discussion

The below-ground community in the grassland was found to be significantly richer than that of the maize system (Figure 4.1). Grasslands are more stable and less disturbed, with a higher abundance and diversity of vegetative inputs (Roger-Estrade *et al*., 2010; Finke *et al*., 1999; Faget *et al*., 2012; Firbank *et al*., 2003; Scherber *et al*., 2010) which provides more suitable habitats for invertebrates (Birkhofer *et al*., 2011). In contrast, the soil habitat in the conventional maize cultivation undergoes annual disturbance by ploughing and tillage.

Ploughing is detrimental to soil biodiversity, damaging organisms, destroying hyphae linkages, and reducing resource availability and connectivity (Roger-Estrade *et al*., 2010). There is evidence to suggest that in the grassland, due to a lesser degree of disturbance, there was a greater abundance of Uropodidae and Poduromorpha whereas in the maize system Entomobryomorpha and Oribatida were greater in abundance. The lesser degree of disturbance in the grassland system may be favouring Poduromorpha and Uropodidae due to the greater stability in the fungal community. In contrast, in the maize cultivation system, which had undergone annual disturbance for a number of years, there was disruption of fungal hyphae, and therefore the fungal community which maybe favouring more generalist detritivores such as Oribatida and Entomobryomorpha. It has been shown that Entomobryomorpha and Oribatida can be tolerant to stresses such as oil pollution in river systems, which may play a key role in their ubiquitous diversity and resilience to disturbances (Okiwelu, 2011).

There was a more complex predator taxonomic assemblage in the grassland, where three predatory taxa (Coleoptera, Linyphiidae and Formicidae) were recovered compared with only one predatory taxa (Geophilomorpha) in the maize system. Coleoptera, Linyphiidae and Geophilomorpha are important within agricultural systems as controllers of pests (Farinós *et al*., 2008; Sileshi *et al*., 2006). Sileshi *et al*. (2006) found that Geophilomorpha densities increase in maize cultivation systems if remaining fallow for a number of years. However this study shows that there may be short term effects where populations increase in density over the course of the growing season through the winter, when in the following cultivation year there is disturbance to the population through ploughing, causing their numbers to reduce, and allowing other predators to colonise. Understanding the effects of taxa absence and redundancy in multi-trophic food webs are complicated by the idiosyncrasy of the predator effects on lower trophic levels (Schneider *et al*., 2012). The redundancy of taxa in multi-trophic food webs can have direct or indirect effects which may increase, decrease or not affect ecosystem functioning (Hassel and May, 1986; Schneider *et al*. 2012). It is also noteworthy that where there were fewer macro-predators within the maize system the number of micro-predators increased.This suggests that although larger predators were displaced or disturbed in the maize cultivation system the smaller bodied, often more abundant, micro-predators were still able to facilitate bio-control of soil dwelling plant pests.

There were no Enchytraeidae recovered from the maize system though they were present in the grassland system (Table 4.1). Enchytraeidae are recognized as important and beneficial components in agro-systems as their feeding activity enhances decomposition and mineralization of organic matter which results in improved soil fertility (Swift et al., 1998; Lavelle, 1997; Wardle, 1995). The absence of Enchytraeidae in the maize is more likely due to poor organic matter content rather than direct disturbance by ploughing within the maize system (Swift *et al*., 1998). Diptera were the only omnivorous taxa encountered within either cropping systems and were absent from the maize system. This suggests a more stable biotic community as omnivory acts as a stabilising effect in ecosystems and as the degree of omnivory within a system increases it in turn stabilises wider community dynamics (Fagan, 1997).

Although there were differences in the abundances of taxonomic and functional groups between the two cropping systems, overall, there was similar abundance of soil fauna in the two cropping systems suggesting the two populations were not resource limited (Figure 4.1). This may indicate that soil type may be an influencing factor in determining the overall abundance of the soil invertebrate communities independent of cropping systems. However, the maize system was greater in the abundance of taxa and functional groups that generally have shorter life histories. This indicates that the maize system community was in a disturbed state with a 'basal' soil invertebrate community (Turnbull *et al*., 2014) that was more tolerant to disturbances and able to continue important ecosystem processes such as the recycling of organic matter (Gardi *et al*., 2009; Turnbull *et al*., 2014). The increases and reductions in density of Entomobryomorpha and Poduromorpha as well as Oribatida and Uropodidae may suggest changes in community composition with time after disturbance from tillage interventions. These changes in composition could also be related to difference in resource quality, quantity and better established fungal communities in the grassland system (Table 4.1). However, overall the total numbers of the fungivorous functional group were similar in the two cropping systems indicating that although there was a difference in community composition the functionality of ecosystem services would remain stable (Bardgett and Cook, 1998). Interestingly, Entomobryomorpha are generally larger than Poduromorpha and are often found higher up in the soil layers making these taxa better able to disperse to exploit resources and avoid disturbance, however research has shown that Poduromorpha can swarm (Fountain *et al*., 2007) which may explain the greater variation in the abundance of Poduromorpha compared with Entomobryomorpha.

The difference in the isotopic signatures of the two invertebrate communities can be attributed to the availability of C4 derived vegetative resource within the maize system. However, the isotopic signature of the below-ground invertebrate community recovered from the maize system was above that of what was expected from literature (Tiunov, 2007) could be caused by a number of factors i.e. soil management through ploughing, and the release of stored C3 carbon overriding that of the C4 soil signal (Gregorich *et al*., 2001; Lobe *et al*., 2005). The greater than expected below-ground invertebrate community isotope signature could also be due to increased weed biomass at time of sampling (Tollenaar *et al*., 1994) of which a proportion of the community would be deriving their diet (Parnell *et al*., 2013). It could also be speculated that there may be differences in $\delta^{13}C$ in Phospholipid Fatty Acid (PLFA) composition and fractionation by the different family groups present in each system (Pausch *et al*., 2015; Hines *et al*., 2015; Börjesson *et al*., 2015). The more depleted signal could also be due to the decomposer community, which account for a significant proportion of the population in the maize field, consuming the microbial community which isotopic signature is often associated with plant litter and detritus (Hyodo *et al*., 2010; Hyodo*,* 2015). However, plant decomposition is known to increase $\delta^{13}C$ signature, as during plant decomposition the variation of $\delta^{13}C$ in structural polysaccharides results from the incorporation of new carbon into leaf litter through microbial decomposers. Fungi, in particular, show important fractionation effects for stable isotopes of C and N causing depletion of heavier isotopes relative to source (Henn and Chapela, 2001).

4.5. Conclusions

The differences in the isotopic signatures of the below-ground communities in the maize and grassland systems reflected the dominant vegetation of the system that the arthropods were collected from (Gregorich *et al*., 2001; Lobe *et al*., 2005; Hyodo *et al*., 2010; Crotty *et al*., 2014). These results show that this is a suitable method for tracing resource use through invertebrate food webs (Tiunov, 2007).

Taxonomic richness and basal feeding resources of the below-ground communities were dependent on cropping system. The greater richness in the grassland system was due to less frequent disturbances (Werling *et al*. 2014) and greater abundance of feeding resources that could be derived from vegetation and annual organic matter inputs from the dairy herd (Birkhofer *et al*., 2011).

This study adds to the well-established knowledge that reduced disturbance favours bacteria and fungi (Hendrix *et al*., 1986; Fu *et al*., 2000). The greater abundance of the less mobile Poduromorpha in the grassland system indicates that there was a more stable fungal community (Nakamoto and Tsukamoto, 2006), in contrast the maize system was greater in the abundances of Entomobryomorpha which are better able to disperse to avoid disturbances and exploit resources.

Chapter 5

The effect of maize cultivation on below-ground invertebrate diversity

5. The effect of maize cultivation on below-ground invertebrate diversity

5.1. Introduction

The soil ecosystem is often described as the 'poor man's rainforest' (Giller, 1996). Like the rainforest, the soil ecosystem has high species diversity comprised of many trophic levels, is vertically and horizontally stratified and is essential for biogeochemical cycling (Giller, 1996; Bardgett and Van der Putten, 2014; Wardle 2006). The soil ecosystem has these characteristics because, like the rainforest, it is a stable system that has constant inputs and does not naturally undergo dramatic perturbations but instead alters steadily over time (Giller, 1996). This stability allows species to diversify and maintain high populations, with a number of taxa in the system being able to occupy the same biogeochemical niche, making the system resilient to perturbation (Bardgett and Van der Putten, 2014; Wardle, 2006). However, anthropogenic manipulation of the soil by agricultural practices disturbs the stability of the soil ecosystem which has both direct and indirect effects on the diversity of below-ground invertebrates, and in some cases can inhibit the functionality of biogeochemical processes (Adl *et al*., 2006; Bardgett and Cook, 1998; Bardgett and Van der Putten, 2014).

Maintaining the stability of biogeochemical processes in agricultural systems is important for supporting the functionality of ecosystem services. Globally organic matter recycling economic value is estimated to be around $760 billion dollars a year (Constanza, 1997; Gardi and Jeffery, 2009; Pimentel *et al*., 1997). Collembola play an important role in the decomposition of organic matter (Altieri, 1999) and represent an important below-ground invertebrate group in arable soils (Van Capelle *et al*., 2012). They and other below ground taxa participate in decomposition processes by increasing nutrient mobilisation and catalysing microbial activity by grazing on bacteria and fungi (Cole *et al*., 2006). However, within arable soils seasonal patterns in soil invertebrate communities are highly complex, varying with crop type and management from year to year (Hawes *et al*., 2009; Stockdale *et al*., 2006; Bardgett and Van der Putten, 2014) making it difficult to predict the effect of changes in agricultural management practices on these important functional groups. This highlights the importance of temporal sampling in below-ground invertebrate community studies to gain an accurate understanding of how these functional groups are affected by changes in maize cultivation practice.

Two of the maize cultivation methods in this study utilise strip cropping techniques. An important component of strip cropping is to maintain soil biodiversity, sustain soil

function, improve soil quality and reduce runoff (Bardgett and Van der Putten, 2014). Little is known about the effect of intercrops on below-ground organisms within maize cultivation. However, it is hypothesised that a reduction in disturbance and an increase in non-crop vegetation would improve below-ground biodiversity (Scherber *et al*., 2010). A study where wheat (*Triticum aestivum* L.) was sown into an existing stand of white clover (*Trifolium repens* L.) was shown to support larger populations of Lumbricidae than in conventional wheat monoculture systems (Schmidt *et al*., 2003). The organic matter supplied by strip crops contained residues derived from dead plant parts and organic materials released from living roots (Briones and Bol, 2003). This can aid in promoting below-ground invertebrate communities and enhance their ecosystem functions such as nutrient cycling, soil structure preservation, and pest population control; all of which result in improved soil productivity and ecosystem functioning (Bardgett and Van der Putten, 2014).

Nakamoto and Tsukamoto (2006) found that under maize strip cropping systems there were correlations among fungi, nematodes, and Collembola, suggesting that the fungal pathway of decomposition was stimulated. Nakamoto and Tsukamoto (2006) also concluded that the greater input of organic matter from strip crops increased populations of below-ground invertebrates and by reducing water loss through the soil surface, improved ground cover, creating an overall better habitat for soil organisms, however pore space was not found to increase suggesting that although the overall habitat quality improved there was no significant increase in habitat complexity. Although environmental benefits such as the protection of soil organisms and a decrease in soil erosion and pollution have been reported from incorporating strip cropping systems (Nakamoto and Tsukamoto, 2006), there are practical limitations to adoption. There is conflicting evidence of the effects of strip crops on maize growth and yield (Nakamoto and Tsukamoto, 2006; Liedgens *et al*., 2004). Reductions in maize yield as a result of strip crops have been attributed to competition, especially for water and nitrogen (Liedgens *et al*., 2004). The study by Liedgens *et al*. (2004) showed that an Italian ryegrass strip crop, into which maize was directly sown, reduced the maize growth, biomass production and grain yield over three growing seasons. However, Nakamoto and Tsukamoto's (2006) study showed that in strip cropping systems where the intercrop of white clover was suppressed, yields of maize were equal to those obtained in conventional systems. The effects of how the strip crops interact with the below-ground invertebrate community is an important component of this study.

5.1.1. Hypothesis, aims and objectives

This chapter quantifies and compares the effects of different maize cultivation methods on below-ground invertebrate diversity and community assemblages. The goal was to assess how changes in cultivation and ground cover management practice affects below-ground invertebrate communities, if the community responses were similar at the two field trial sites and to understand how responses change over time.

H_1= A reduction in physical disturbance increases below-ground invertebrate biodiversity

H_1= An increase in non-crop richness increases below-ground invertebrate biodiversity

H_1= Increases in non-crop cover increases below-ground invertebrate biodiversity

5.2. Materials and methods

Soil invertebrates were collected using three different methods (Section 3.3). Earthworms, macrofauna and mesofauna were collected before the maize was drilled in 2013 and 2014 from both sites (Plate 3.3). Soil mesofauna were collected more frequently from the Bow site (Plate 3.3), as such, firstly the difference in experimental factors were investigated using count data from all three sampling methods at the pre-cultivation sampling point. Secondly mesofauna data from the Bow site was analysed separately to understand how the diversity and community composition changed at the different sampling points over the two years. The mesofauna data from the two separate sites was also analysed in more detail to understand how the diversity and community structure was affected by different cultivation factors and changes in ground cover management practices.

5.2.1. Statistical analysis

Soil invertebrate densities were summed per plot to remove pseudo-replication of collecting multiple samples from each plot. Earthworm densities were multiplied by 6.25 to give an estimate of abundance per m^{-2}, Macrofauna densities were multiplied by 75 to give an estimate of abundance per m^{-2}. Mesofauna densities were multiplied by 49.5 to give an estimate of abundance per m^{-2}.

Shannon diversity, richness, abundance and evenness were calculated as described in section 3.6 on a per plot bases. Analysis of variance was used to test for significant differences between experimental factors (Section 3.6). Analysis of variance in taxonomic

richness, abundance, evenness and Shannon diversity of earthworms, macrofauna and mesofauna was carried out on results from both sites at the pre-cultivation sampling point for both field trial years. Additional mesofauna samples were collected at Bow after the maize had been drilled and once the maize crop had been harvested; this information was further analysed separately to the data collected from the Fakenham site to understand how diversity changed over the course of the cultivation season.

Non-metric multidimensional scaling (NMDS) (Faith *et al*., 1987) and 'envfit' (Oksanen *et al*., 2007) were used to identify how below-ground mesofauna community composition correlated with experimental variates. Initially NMDS was used to disentangle differences in community composition between sites using count data from the pre-cultivation sampling points in 2013 and 2014. As there were differences in the composition of communities between sites the count data for each site was analysed separately to understand the factors driving differences in community composition among the different cultivation methods over the two cultivation seasons. For full descriptions of statistical procedures see Section 3.6.

5.3. Results

5.3.1. Macrofauna diversity

Overall, there were significant differences in the richness and abundance of macrofauna among the cultivation methods (Table 5.1a, Figure 5.1a and b). The BSM (strip tillage into a biodiverse seed mix) cultivation method was found to be significantly richer and more abundant in macrofauna compared with PGH (conventional cultivation)(*P.adjusted* = 0.006 and 0.003 respectively). There were also significant interaction differences between cultivation methods and sites (Table 5.1a). At Bow, both RGS (strip tillage into ryegrass) and BSM supported significantly more abundant communities of macrofauna compared with PGH (*P.adjusted* = 0.009 and 0.001 respectively). However, there were no significant differences in the abundance of macrofauna amongst the cultivation methods at Fakenham (*P.adjusted* > 0.05). There was however a difference in the abundance of macrofauna collected from PGH at Fakenham compared with PGH at Bow (*P.adjusted* = 0.030), this was due to no macrofauna being recovered from the PGH cultivation method at Bow (Appendix Table 12.3.1). The richness of macrofauna at Bow was also greater in BSM and RGS compared with PGH (*P.adjusted* = 0.002 and 0.02 respectively), however this was not found to be the case at Fakenham (*P.adjusted* > 0.05). There were also differences in the richness of macrofauna under PGH at Bow compared with BSM and MNT (minimum

tillage)at Fakenham (*P.adjusted* = 0.010 and 0.005 respectively), as with abundance which was due to no macrofauna being recovered for the PGH cultivation method at Bow. These results suggest that although the response of macrofauna was not consistent at either site there were benefits to biodiversity through a reduction in disturbance and an increase in non-crop vegetation.

MAcrofaun were significantly more diversity (*P.adjusted* = 0.013) in with the row areas with the communities also being more evenly distributed (*P.adjusted*= 0.016) compared to the inter-row areas. However, there were no significant differences in the evenness and diversity of macrofauna between the row and inter-row areas of the different cultivation methods (Table 5.1a, *P.adjusted* > 0.450), indicating a general trend independent of cultivation method for the row areas to support more diverse macrofauna communities.

5.3.2. Earthworm diversity

There were significant differences in the richness, abundance, evenness and Shannon diversity of earthworms collected at the pre-cultivation sampling points from the different cultivation methods (Table 5.1b, Figure 5.1c and d). Earthworm taxonomic richness was found to be significantly greater under BSM compared with RGS but was not significantly greater than PGH or MNT (Figure 5.1c). In addition, PGH and BSM supported significantly more abundant earthworm communities compared to RGS (Figure 5.1d). However, no significant differences were found in the abundance of earthworms recovered from MNT, PGH or BSM (Figure 5.1d).

There were also significant differences between the richness, abundance, evenness and diversity of earthworms between the two sites (Table 5.1b). In addition, there were significant interaction effects between cultivation method and site (Table 5.1b). Overall the Fakenham site was greater in earthworm richness, abundance, diversity and evenness compared to Bow (*P.adjusted* < 0.005). The richness of earthworms was lower in RGS compared with MNT (*P.adjusted*= 0.013) and lower in PGH compared with MNT (*P.adjusted*= 0.007) at Fakenham. However, this was not found to be the case at Bow (*P.adjusted* > 0.05). A similar trend between sites and cultivation methods was observed for the abundance of earthworms with all cultivation methods at Fakenham being more abundant than Bow (*P.adjusted*< 0.05). In addition, earthworms were significantly more abundant under BSM compared with MNT at Fakenham (*P.adjusted*< 0.001).

Table 5.1 Analysis of the variance in a) macrofauna, b) earthworm c) mesofauna richness, abundance evenness and Shannon diversity for the pre-cultivation sampling points (Plate 3.3) in both field trial years at both sites.

a) Macrofauna		**Richness**		**Abundance**		**Evenness**		**Diversity**	
	df	**F-Value**	***P*-Value**	**F-Value**	***P*-Value**	**F-Value**	***P*-Value**	**F-Value**	***P*-Value**
Site	1	1.94	0.168	2.47	0.120	0.08	0.772	0.06	0.807
Cultivation method	3	4.22	0.043 *	4.00	0.049 *	0.28	0.596	0.28	0.597
Row or inter-row	1	2.63	0.109	2.08	0.153	6.48	0.013 *	6.81	0.011 *
Year	1	2.53	0.116	2.87	0.094	1.01	0.318	0.94	0.335
Block	2	2.29	0.134	1.62	0.207	4.43	0.038 *	4.30	0.041 *
Site*Cultivation method	3	0.42	0.519	0.37	0.544	0.19	0.666	0.20	0.655
Site*Row or inter-row	1	3.72	0.057	4.77	0.032 *	0.10	0.756	0.08	0.776
Cultivation method*Row or inter-row	3	0.60	0.442	0.61	0.435	0.19	0.668	0.19	0.660
Site*Year	1	0.23	0.630	0.25	0.620	1.01	0.318	0.94	0.335
Cultivation method*Year	3	0.62	0.433	0.53	0.469	1.29	0.260	1.31	0.257
Row or inter-row*Year	1	0.43	0.516	0.66	0.418	0.16	0.688	0.19	0.663
Site*Cultivation method*Row or inter-row	3	0.09	0.759	0.15	0.699	0.29	0.594	0.29	0.592
Site*Cultivation method*Year	3	0.64	0.425	0.76	0.385	0.10	0.755	0.11	0.746
Site*Row or inter-row*Year	1	0.08	0.777	0.00	0.976	0.16	0.688	0.19	0.663
Cultivation method*Row or inter-row*Year	3	0.14	0.705	0.04	0.848	1.07	0.304	1.11	0.296
Site*Cultivation method*Row or inter-row	3	0.01	0.931	0.01	0.943	0.17	0.679	0.17	0.679

b) Earthworms		**Richness**		**Abundance**		**Evenness**		**Diversity**	
	df	**F-Value**	***P*-Value**	**F-Value**	***P*-Value**	**F-Value**	***P*-Value**	**F-Value**	***P*-Value**
Site	1	92.41	0.000 ***	167.27	0.000 ***	42.18	0.000 ***	44.56	0.000 ***
Cultivation method	3	4.44	0.007 **	4.07	0.010 *	3.49	0.021 *	4.73	0.005 **
Row or inter-row	1	0.00	0.978	0.42	0.517	0.01	0.921	0.00	0.972
Year	1	46.39	0.000 ***	60.03	0.000 ***	13.50	0.001 ***	17.77	0.000 ***
Block	2	0.61	0.545	2.62	0.081	0.37	0.691	0.87	0.424
Site*Cultivation method	3	5.18	0.003 **	7.18	0.000 ***	4.65	0.005 **	5.02	0.004 **
Site*Row or inter-row	1	0.05	0.832	0.42	0.521	0.59	0.446	0.32	0.571
Cultivation method*Row or inter-row	3	1.70	0.176	1.77	0.162	0.71	0.551	0.95	0.423
Site*Year	1	12.34	0.001 ***	9.24	0.003 **	7.32	0.009 **	5.09	0.028 *
Cultivation method*Year	3	0.88	0.458	0.23	0.875	1.30	0.284	1.68	0.180
Row or inter-row*Year	1	0.00	0.982	0.12	0.727	0.17	0.681	0.17	0.679
Site*Cultivation method*Row or inter-row	3	0.64	0.592	0.50	0.681	0.55	0.648	0.26	0.852
Site*Cultivation method*Year	3	0.69	0.562	1.31	0.280	1.36	0.264	0.81	0.492
Site*Row or inter-row*Year	1	0.05	0.829	0.12	0.731	0.03	0.861	0.00	0.968
Cultivation method*Row or inter-row*Year	3	1.06	0.371	1.11	0.354	0.57	0.635	0.45	0.719
Site*Cultivation method*Row or inter-row	3	1.30	0.282	1.73	0.170	2.13	0.106	1.41	0.247

c) Mesofauna		**Richness**		**Abundance**		**Evenness**		**Diversity**	
	df	**F-Value**	***P*-Value**	**F-Value**	***P*-Value**	**F-Value**	***P*-Value**	**F-Value**	***P*-Value**
Site	1	0.50	0.481	5.13	0.027 *	0.49	0.486	0.04	0.834
Cultivation method	3	7.98	0.000 ***	10.20	0.000 ***	1.95	0.131	1.33	0.274
Row or inter-row	1	0.00	0.998	0.20	0.655	0.02	0.882	0.07	0.792
Year	1	21.60	0.000 ***	87.89	0.000 ***	14.94	0.000 ***	0.40	0.529
Block	2	3.88	0.026 *	1.44	0.244	0.34	0.713	1.13	0.329
Site*Cultivation method	3	1.45	0.236	1.88	0.143	2.11	0.108	2.28	0.088
Site*Row or inter-row	1	0.33	0.568	0.04	0.852	0.01	0.939	0.10	0.752
Cultivation method*Row or inter-row	3	1.44	0.240	1.49	0.225	0.33	0.803	0.35	0.788
Site*Year	1	1.63	0.207	4.02	0.049 *	0.36	0.548	1.93	0.170
Cultivation method*Year	3	2.60	0.060	5.96	0.001 **	2.89	0.042 *	1.74	0.169
Row or inter-row*Year	1	3.67	0.060	9.60	0.003 **	7.24	0.009 **	0.19	0.665
Site*Cultivation method*Row or inter-row	3	0.29	0.835	0.76	0.523	1.33	0.274	0.74	0.530
Site*Cultivation method*Year	3	1.27	0.293	1.40	0.250	0.80	0.499	0.17	0.916
Site*Row or inter-row*Year	1	1.75	0.190	2.44	0.123	0.04	0.838	2.55	0.115
Cultivation method*Row or inter-row*Year	3	2.14	0.105	1.14	0.339	0.71	0.551	1.47	0.232
Site*Cultivation method*Row or inter-row	3	0.11	0.956	0.21	0.891	0.22	0.880	0.03	0.992

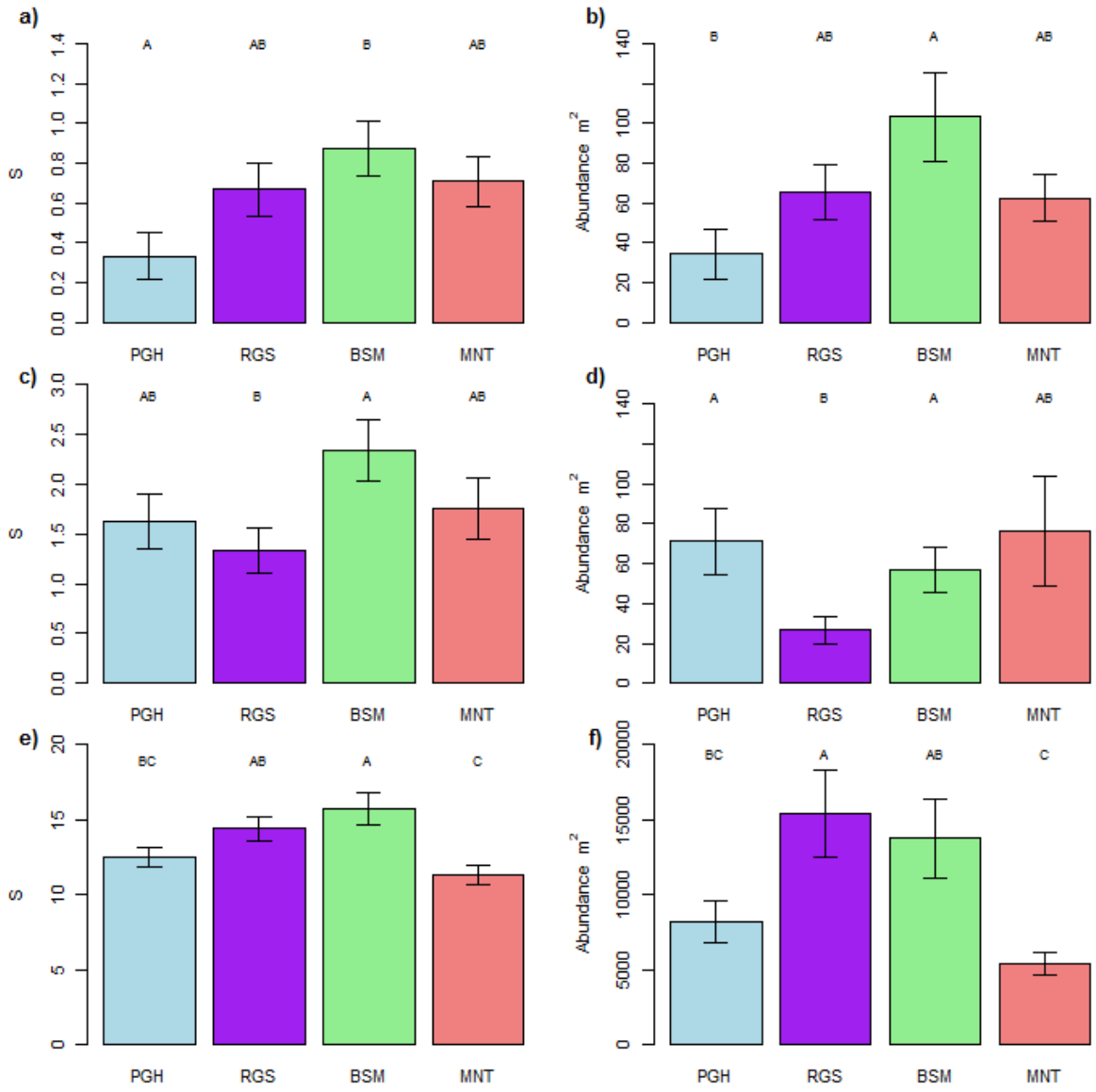


Figure 5.1 Below-ground invertebrate count data, collected from both sites at the pre-cultivation sampling points in 2013 and 2014, was used to calculate a) macrofauna richness b) macrofauna abundance c) earthworm richness d) earthworm abundance e) mesofauna richness f) mesofauna abundance for each cultivation method (PGH, RGS, BSM, MNT). Letters denote Tukey HSD significance levels, solid bars denote mean values and error bars denote standard error.

5.3.3. Mesofauna diversity

Overall, there were significant differences in the richness and abundance of mesofauna recovered from the different cultivation methods at the pre-cultivation sampling points in 2013 and 2014 (Table 5.1c, Figure 5.1e and f). However, there was no significant difference in the evenness or diversity of communities among cultivation methods (Table 5.1c). Mesofauna richness under BSM was significantly greater than PGH and MNT

(Figure 5.1e), indicating a positive effect of reduced disturbance and increased non-crop vegetation cover. Mesofauna richness under RGS was also significantly greater than MNT, but was not significantly greater than mesofauna richness under PGH (Figure 5.1e), indicating that although disturbance positively affected mesofauna richness non-crop richness had a greater affect.

The abundance of mesofauna was greater under RGS compared with PGH and MNT, but was not significantly different to the abundance of mesofauna recovered from BSM (Figure 5.1f). The abundance of mesofauna recovered from BSM was greater than MNT but was not significantly different to PGH (Figure 5.1f). Increase in the abundance but not the richness of mesofauna under RGS indicates that only few taxa were benefiting from the changes in cultivation practice.

5.3.3.1. Temporal and spatial diversity

There were differences in the abundance of mesofauna between sites at the pre-cultivation sampling point (Table 5.1c, Figure 5.1e and f). In addition, samples were collected more frequently at Bow (three samples during the cultivation season) compared with Fakenham (one sample during the cultivation season). As such, the two sites have been further analysed separately to understand the within year temporal dynamics of below-ground mesofauna, and how these communities responded to contrasting maize cultivation and ground cover management practices. The data used to test for difference between sampling times was the inter-row area mesofauna count data from Bow. The inter-row areas were used only as during the summer sampling point taxa were only collected from this area (Figure 5.2). As there was no difference in the biodiversity of mesofauna between the row and inter-row areas of individual cultivation methods (Figure 5.3) analysis of only the samples collected from the inter-row area was a good reflection of the response of invertebrate biodiversity at different sampling points during the two cultivation years.

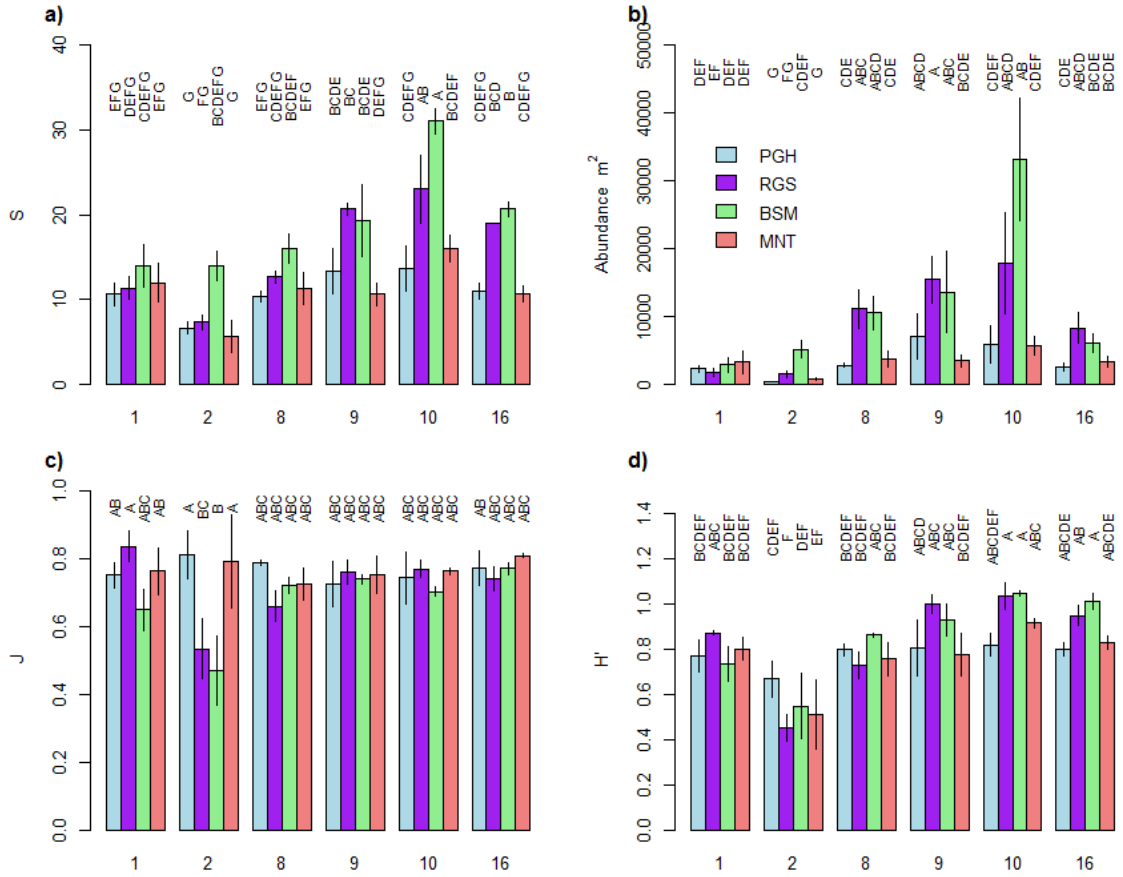


Figure 5.2 Below-ground mesofauna count data from Bow was used to calculate the mean (± s.e.) a) taxonomic richness b) abundance c) evenness and d) Shannon diversity for each cultivation method and sampling point over the two cultivation seasons. Sampling points on denoted along the x-axis numbers representing different times during the two field trial years; 1: Pre-cultivation 2013, 2: Cultivation 2013, 8: Post-harvest 2013, 9: Pre-cultivation 2014, 10: Cultivation 2014, 16: Post-harvest 2014. The different cultivation methods are denoted by colour (PGH, RGS, BSM, and MNT). Letters denote Tukey HSD level codes where different letters denote significantly different groups (P <0.05)

At Bow there was a significant difference in below-ground mesofauna richness among the cultivation methods (Figure 5.2a) which varied depending on sampling time during the cultivation year. There were no differences in the richness of below-ground mesofauna between cultivation methods sampled from the different points over the 2013 cultivation year (Figure 5.2a). At the start of the second field trial year, before cultivation had taken place, there were no significant differences between the strip tillage (RGS and BSM) and more conventional (PGH and MNT) cultivation methods (Figure 5.2a). During cultivation in 2014 the strip tillage cultivation methods were significantly richer in below-ground invertebrates compared with the PGH (Figure 5.2a). Post-harvest 2014 there was a significantly greater richness of below-ground invertebrates in BSM compared with PGH

(Figure 5.2a). Overall, this shows that there was variation in the richness of the communities in the second year; however, the strip tillage cultivation techniques did generally support richer mesofauna communities.

Similar to richness, mesofauna abundance was not significantly different among cultivation methods at the initial sampling point, pre-cultivation 2013 (Figure 5.2b). However, during cultivation in 2013 BSM was significantly greater in abundance of mesofauna compared with the PGH and MNT but not RGS (Figure 5.2b), suggesting that non-crop richness promoted mesofauna abundance. However, once the maize was harvested in 2013 there were no significant differences in the abundance of soil mesofauna among the cultivation methods (Figure 5.2b). In 2014, at the initial pre-cultivation sampling RGS was significantly more abundant in mesofauna than MNT (Figure 5.2b). In 2014, during cultivation BSM was significantly greater in abundance of mesofauna compared with MNT and PGH (Figure 5.2b). Similar to 2013, there were no differences in the abundances of below-ground mesofauna between cultivation methods at the final post-harvest sampling point in 2014 (Figure 5.2b).

There were only significant differences in the evenness of soil mesofauna at the cultivation sampling point in 2013, where the strip tillage cultivation method communities (BSM and RGS) were less evenly distributed compared with the more conventional cultivation methods (PGH and MNT) (Figure 5.2c). There were no significant differences in below-ground mesofauna Shannon diversity between cultivation methods at the different sampling points (Figure 5.2d). However, there were significant differences in the Shannon diversity of mesofauna within cultivation methods at the different sampling points, for example Shannon diversity of below-ground mesofauna significantly reduced in RGS from the initial pre-cultivation sampling point to the cultivation sampling point in 2013, however, a similar trend was not observed in 2014 (Figure 5.2d).

The row and inter-row sampling areas at Bow were not found to be significantly different in the evenness or Shannon diversity of mesofauna (Figure 5.3c and d). Overall, there were no significant differences in the richness or abundance of mesofauna between the row and inter-row areas within each cultivation method (Figure 5.3a and b). There were, however, differences in the richness and abundance of mesofauna recovered from the row and inter-row areas of the different cultivation methods (Figure 5.3a and b). For example, there were significantly fewer invertebrate taxa recovered from the inter-row area of MNT and PGH

compared with the inter-row area of RGS (Figure 5.3a and b). In addition, there were significant greater abundances of invertebrates in the inter-row area of BSM than the row areas of PGH and MNT (Figure 5.3b).

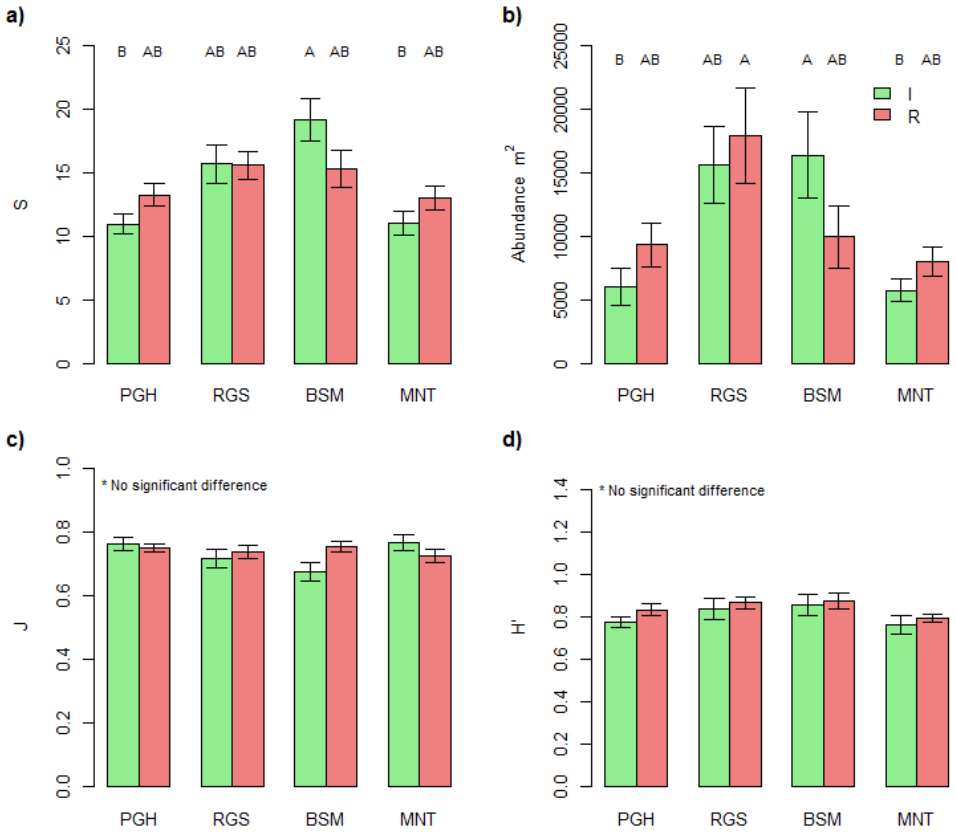


Figure 5.3 Below-ground mesofauna count data from Bow was used to calculate the mean (± s.e.) a) taxonomic richness b) abundance c) evenness d) Shannon diversity for the row (R;) and inter-row (I;) areas of each cultivation method. Letters denote Tukey HSD level codes where different letters denote significantly different groups (P <0.05)

Mesofauna diversity was also assesed for temporal responses to different maize cultivation systems at Fakenham using the pre-cultivation count data. Overall, there were no significant differences in Shannon diversity of below-ground invertebrate communities at Fakenham between the two years (Figure 5.4d). However, there were significant differences in the richness and abundance of the below-ground mesofauna communities (Figure 5.4a and b). Significant differences in the richness of below-ground invertebrate communities were found only in the BSM cultivation method at Fakenham, with no significant increase in the richness of below-ground communties in PGH, MNT or RGS (Figure 5.4a). The abundance of the below-ground community did not significantly increase in the PGH and MNT cultivation methods between field trial years, however, there were significant increases within BSM and RGS (Figure 5.4b). There were no

significant differences in the eveness of the below-ground invertebrate communities between 2013 and 2014 (Figure 5.4c), however the communities encountered in the strip tillage techniques in 2014 were significantly less evenly distributed between taxonomic groups than MNT in 2013.

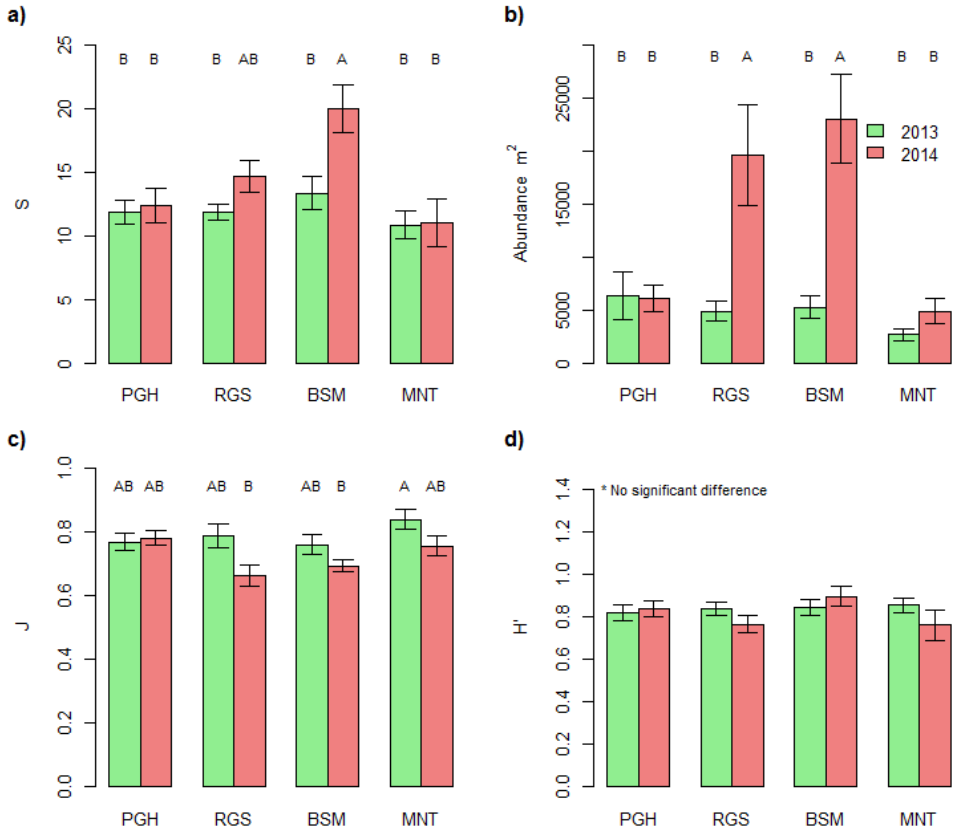


Figure 5.4 Below-ground mesofauna count data from Fakenham was used to calculate the mean (± s.e.) a) taxonomic richness b) abundance c) evenness d) Shannon diversity for each cultivation method before cultivation in 2013 ( ) and 2014 ( ). Letters denote Tukey HSD level codes, where different letters denote significantly different groups (P <0.05)

5.3.4. Mesofauna community composition

It is important not just to understand how differing maize cultivation techniques affect below-ground mesofauna diversity, but also how they affect community composition. There is strong evidence to suggest that changes in soil preparation and ground cover management practices had an influence on mesofauna diversity (Table 5.1); as such, the community composition of mesofauna at the two sites has been analysed separately to highlight any effects at individual sites and to identify consistent patterns in community response to changes in cultivation practice.

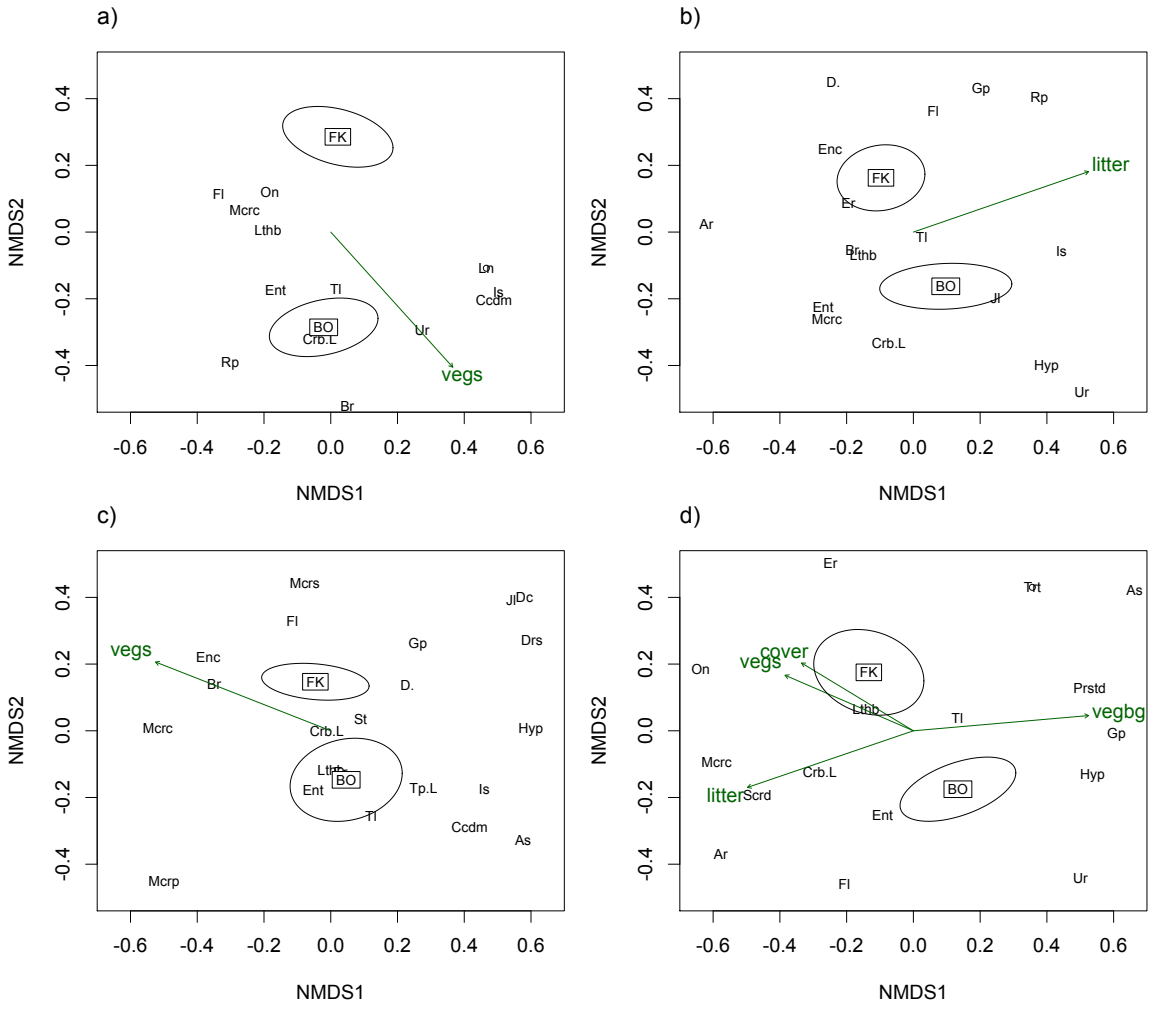


Figure 5.5 Relationship between two-dimensional non-metric multidimensional scaling (NMDS) of the Wisconsin squared root transformation mesofauna community composition of a) conventional plough (PGH), b) strip tillage under sown with ryegrass (RGS), c) strip tillage under sown with a biodiverse seed mix (BSM), d) minimum tillage (MNT). The below-ground mesofauna community euclidean dissimilarity matrix was calculated using the pre-cultivation count data from both sites in 2013 and 2014 which was correlated with changes in vegetation (green arrows where P <0.05) and field sites (represented by ellipse (± s.e.) from centroids), to understand how the vegetation afftected the communties at the different sites (vegs = vegeation species richness, cover =cover by vegeation, vegbg =cover by bare ground, litter =cover by litter). Taxa abbreviations are denoted in Appendix 12.3.2.

The communty composition of below-ground mesofauna collected from the two sites during the pre-cultivation sampling in 2013 and 2014 were significantly different from each other, this was a consistent difference that was noted when the communties from the two sites under the different cultivation mehtods were investigated separately (Figure 5.5a to d). There were also differences in which vegetative dynamics influenced the below-

ground mesofauna community at each site, which also varied with cultivation method (Figure 5.5).

The below-ground invertebrate PGH community at Bow correlated with greater vegetative species richness than Fakenham, which may have influenced the difference observed in communty compoisition between the two sites (Figure 5.5a) and although not measured could be linked to isolation of field sites from surrounding natural vegeation (Altieri, 1999). The PGH community at Bow was more associated with Collembola; Hypogastruridae and Poduridae, whereas Fakenham was associated with Macrochelidae and Earthworms (Figure 5.5a); which maybe linked to the historical management of the site where at Bow there was a history of organic matter being applied annually whereas at Fakenham inorgainc fertiliser was used.

The RGS below-ground mesofauna community composition was significantly influenced by changes in litter composition. However, these changes in litter composition were more associated with Fakenham (Figure 5.5b). The Fakenham RGS below-ground community was associated with Earthworms and Entomobryidae, whereas the Bow RGS community was more associated with Folsomia and Sciaridae larvae (Figure 5.5b).

The BSM cultivation methods had the greatest similarity in below-ground community composition between the two sites (Figure 5.5c), however the communities were still significantly different from each other. The BSM community at Bow was associated with Geophilomorpha, whereas Fakenham was more associated with Entomobryidae (Figure 5.5c). At both sites BSM below-ground invertebrate community composition was significantly affected by in vegetation richness (Figure 5.5c), although the Fakenham communty was more sensitive to increases in vegeation richness.

The below-ground mesofauna communities within MNT were significantly different between field sites (Figure 5.5d). The Fakenham MNT community was more associated with Lithobiidae, whereas Bow was more associated with Entomobryidae and Uropodina (Figure 5.5d). The community composition of below-ground invertebrates within MNT was significantly affected by all measured vegetative variates (Figure 5.5d). However, the Fakenham site was more associated with greater vegeation richness and cover compared with MNT at Bow.

These results show consistent differences in the response of community composition at the two sites under different cultivation techniques, which maybe linked to differences in soil organic carbon (Appendix Table 12.2.1), isolation from surrounding vegetation (Altieri, 1999) and historical site management (Section 3.1). Due to the difference in response of communties at the two sites, further anaysis has been preformed on mesofauna count data from the two sites separately to understand common drivers of community composition under the different maize cultivation techniques.

5.3.4.1. Bow

The count data of below-ground mesofauna collected at the pre-cultivation, cultivation and post-harvest sampling points from Bow in 2013 and 2014 (Plate 3.3) was used to test for differences in the communties amongst cultivation methods, sampling years, sampling times, row and inter-row areas and the associated changes in vegetation (Figure 5.6). As there was no vegetation survey carried out in October 2013, this below-ground mesofauna data set was excluded from analysis.

There were significant differences in the community composition of BSM and PGH, RGS and PGH, BSM and MNT, and RGS and MNT at Bow but there were no significant differences in below-ground community composition between RGS and BSM or PGH and MNT (Figure5.6a). These results indicate that soil preparation had a greater effect on mesofauna community composition than vegetation richness. Taxa associated with strip tillage cultivation methods and the associated increases in vegetative cover included Drosophila, Lithobiidae, Pseudosinella and Julidae, whereas fewer taxa were characteristic of conventional maize cultivation methods (PGH and MNT); one of the few examples being Tullbergiidae (Figure 5.6a). These results suggest that reduced disturbance and increases in non-crop vegetation benefited omnivores, predators and detritivores.

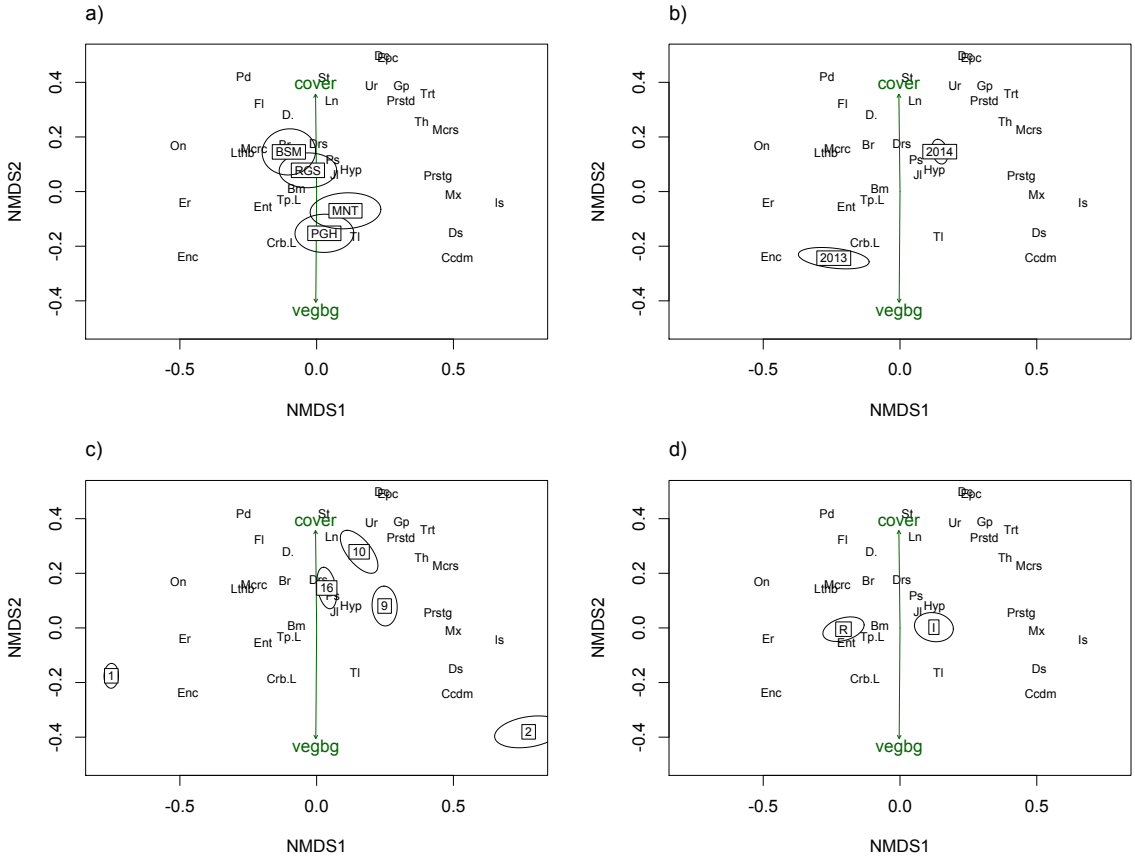


Figure 5.6 Relationship between two-dimensional NMDS of Wisconsin squared root transformation mesofauna community composition of a) cultivation method b) field trial year c) sampling period and d) the row or inter-row sampling areas. The Bow below-ground mesofauna community count data euclidian disssimilarity matrix was correlated with changes in vegetative variates (green arrows where P <0.05, vegs = vegetation species richness, cover =cover by vegetation, vegbg =cover by bare ground, litter =cover by litter) . Ellipse (± s.e.) from centroids represent the communities associated with the different factors. Taxa abbreviations are denoted in appendices 12.3.2.

At Bow there was a significant difference in the taxonomic communities associated with the two field trial years (Figure 5.6b). Taxa associated with 2013 include Carabidae larvae, Entomobryidae and Enchytraeidae, whereas Hypogastruridae, Pseudosinella and Julidae were more associated with 2014 and the greater percentage cover by vegetation (Figure 5.6b). The communities associated with different sampling points during the two cultivation years (Figure 5.6c) indicate that there was much more variation among the communities collected at the different samplng points in 2013 compared with 2014 (Figure 5.6b and c). There were significant differences in the communities associated with the row or inter-row areas at Bow (Figure 5.6d) where the row areas were more associated with

Entomobryidae, Tipulidae larvae and Bembidion, and the inter-row areas with Hypogastruridae and Julidae (Figure 5.6d).

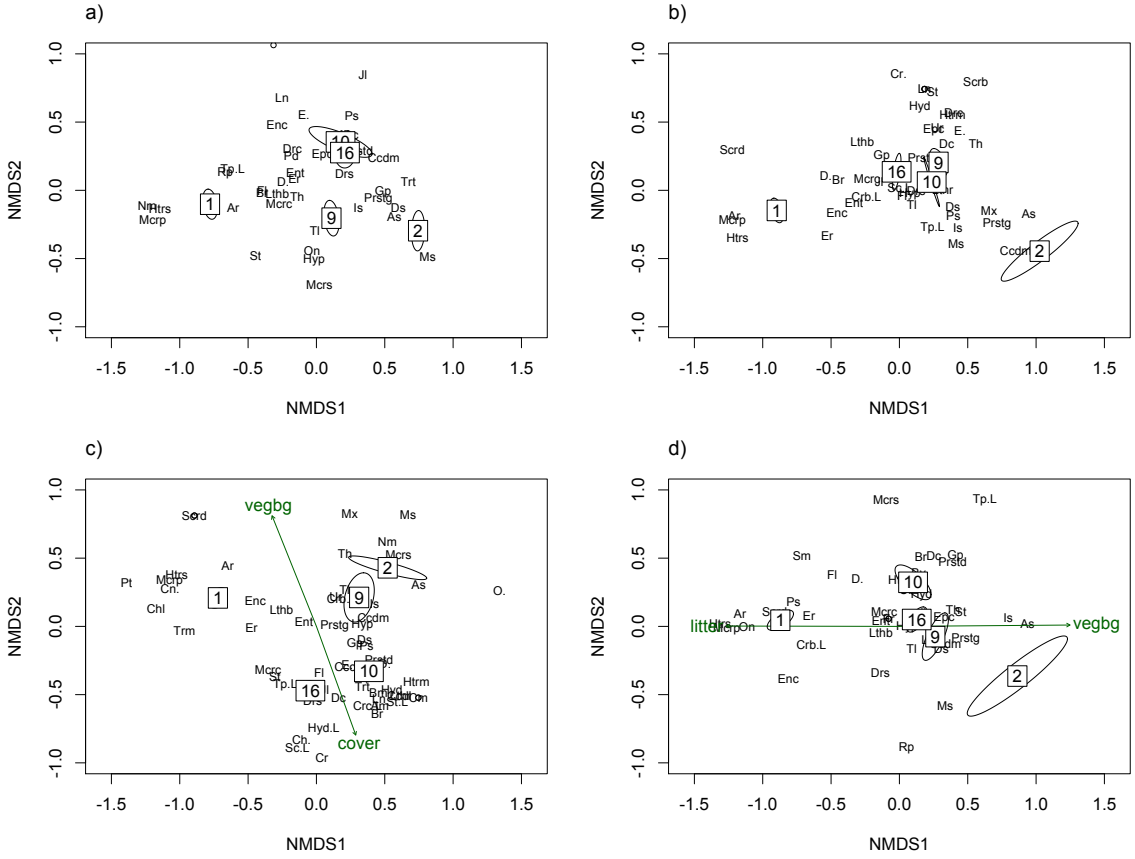


Figure 5.7 Relationship between two-dimensional NMDS of Wisconsin squared root transformation mesofauna community composition of a) conventional plough (PGH), b) strip tillage under sown with ryegrass (RGS), c) strip tillage under sown with a biodiverse seed mix (BSM), d) minimum tillage (MNT), at the different sampling points. The Bow below-ground mesofauna community count data euclidian disssimilarity matrix was correlated with changes in vegetative variates (green arrows where $P < 0.05$, vegs = vegetation species richness, cover =cover by vegetation, vegbg =cover by bare ground, litter =cover by litter). Ellipse (± s.e.) from centroids represent the communities associated with the different factors. Taxa abbreviations are denoted in appendices 12.3.2.

Individual cultivation methods below-ground mesofauna community composition changed among the different sampling times at Bow (Figure 5.7). Overall, there was less variation in community composition in 2014 compared with 2013 for all cultivation methods (Figure 5.7). The conventional cultivation method community composition was not significantly influenced by vegetation dynamics, but the mesofauna community composition did change

over the course of the experiment (Figure 5.7a), indicating that changes in composition were independent of vegetation. In 2013, the below-ground mesofauna community was initially associated with Raphignathae, Arrihopalitida, Hetrostigmata and Macropylinae; however during cultivation the community was more associated with Mesostigmata and Desmonomata (Figure 5.7a). In 2014 there was a significant difference in the community composition at the pre-cultivation sampling time but no significant difference was found between the cultivation and post-harvest sampling times (Figure 5.7a). The PGH community in 2014 pre-cultivation was associated with Brachypyline and Tullbergiidae.

Temporal changes in the RGS community (Figure 5.7b) indicate that, as with PGH, there were significant differences in the below-ground community composition (Figure 5.7b). In 2013 the pre-cultivation community which was associated with Hetrostigmata, Macropylinae and Brachypyline, whereas during cultivation in 2013 (Figure 5.7b) the community was more associated with Psoroptidae and Cecidomyiidae. In 2014 the RGS community at the different sampling times was much more closely related compared with 2013; however there was no overlap between sampling periods, indicating that although the communities were more similar, they remained significantly different (Figure 5.7b). The RGS 2014 pre-cultivation sampling below-ground community was associated with Dicyrtomidae, during cultivation the RGS community was associated with Prostigmata and post-harvest the community was associated with Geophilidae and Lithobiidae (Figure 5.7b).

Percentage cover by vegetation and bare ground had a significant influence on the below-ground invertebrate community composition within BSM (Figure 5.7c). Similar to RGS and PGH, there was a temporal change in the below-ground community composition in BSM (Figure 5.7c). The initial pre-cultivation community was similar to that found in RGS and PGH and was comprised of taxa such as Arrihopalitidae, Hetrostigmata and Macropyline, and during cultivation the community was more associated with taxa such as Thysanoptera, Macropyline and Psoroptidae (Figure 5.7c). BSM pre-cultivation 2014 was associated with taxa such as Carabidae larvae (Figure 5.7c). During cultivation and post-harvest 2014 the community was much more similar in composition compared with pre-cultivation 2014, with post-harvest being more associated with Drosophila and *Folsomia* (Figure 5.7c).

Below-ground invertebrate community composition in MNT was significantly influenced by percentage cover of litter and bare ground (Figure 5.7d). As with PGH, RGS and BSM the MNT temporal community assemblage in 2013 was separated along axis 1 and the temporal shifts in below-ground community composition in 2014 were separated along axis 2 (Figure 5.7d). Initial pre-cultivation sampling in MNT showed a high degree of similarity community composition to the other cultivation methods; all being associated with Arrihopalitidae, Hetrostigmata and Macropyline (Figure 5.7d). Once cultivation had taken place there was a change in the below-ground community composition within MNT (Figure 5.6d) which was more associated with Mesostigmata (Figure 5.7d).

5.3.4.2. Fakenham

In contrast with the differences observed in the community composition of below-ground invertebrates between cultivation methods at Bow (Figure 5.6a), at Fakenham (Figure 5.8a) there were no significant differences between RGS, BSM and PGH or RGS, MNT and PGH (Figure 5.8a). However, community composition of the MNT and BSM were significantly different (Figure 5.8a). The below-ground community composition of MNT at Fakenham was associated with Macropyline and Lithobiidae, whereas BSM was more associated with Staphylinidae and Hypogastruridae (Figure 5.8a), suggesting that there were benefits to biometrically larger predators and fungivores from greater non-crop vegetation richness and may indicate a stimulation of the fungal pathway (Nakamoto and Tsukamoto, 2006).

At Fakenham there was a clear separation in the below-ground invertebrate community composition between the two field trial years (Figure 5.8b), following a similar trend observed at Bow (Figure 5.6b). The difference in taxonomic community composition in 2013 at Fakenham was more associated with Brachypyline and Macrochelidae whereas 2014 was more associated with Isotoma, Folsomia and Julidae (Figure 5.6b), indicating a strengthening of the fungal pathway in 2014 (Nakamoto and Tsukamoto, 2006).

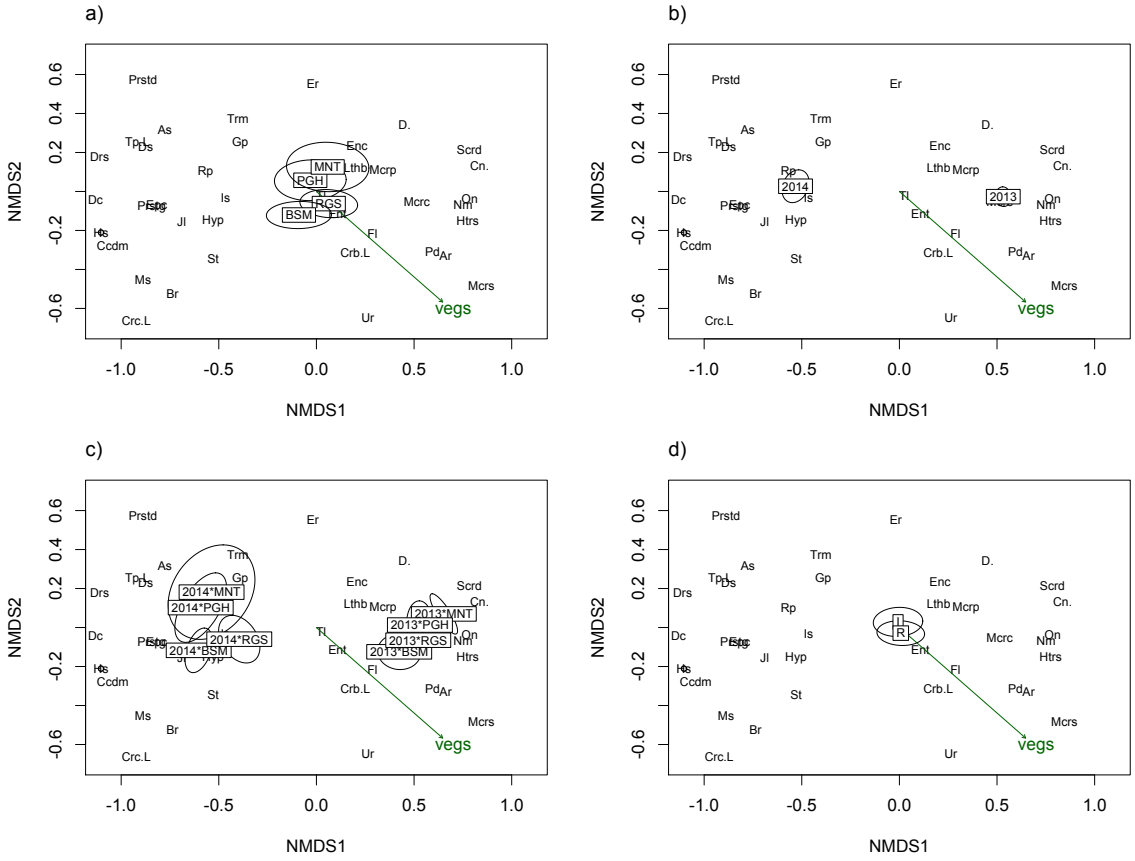


Figure 5.8 Relationship between two-dimensional NMDS of Wisconsin squared root transformation mesofauna community composition of a) cultivation method b) field trial year c) interaction between field trial year and cultivation method d) spatial communities between rows (R) and inter-row (I) areas at Fakenham. The Fakenham below-ground mesofauna community count data euclidian disssimilarity matrix was correlated with changes in vegetative variates (green arrows where P <0.05). Ellipse (± s.e.) from centroids represent the communities associated with the different factors. Taxa abbreviations are denoted in appendices 12.3.2.

There were significant differences between the below-ground mesofauna community composition of cultivation methods at Fakenham in 2013 and 2014 (Figure 5.8c). In 2013 MNT was significantly different in community composition to the other three cultivation methods (Figure 5.8c). In 2014, the community compositions of the four cultivation methods were not significantly different from each other (Figure 5.8c). In contrast with Bow (Figure 5.6d) there was no significant difference in the community composition between the row or inter- row areas at Fakenham (Figure 5.8d). As there were difference in community composition of below-ground mesofauna between 2013 and 2014 in all cultivation methods at Fakenham (Figure 5.8c), analysis of all the communities together masked the effect of changes in vegetation on the communities under the different

cultivation techniques. As such the variation in vegetation between the two years was assessed for the effect on mesofauna community composition under the different cultivation methods (Figure 5.9).

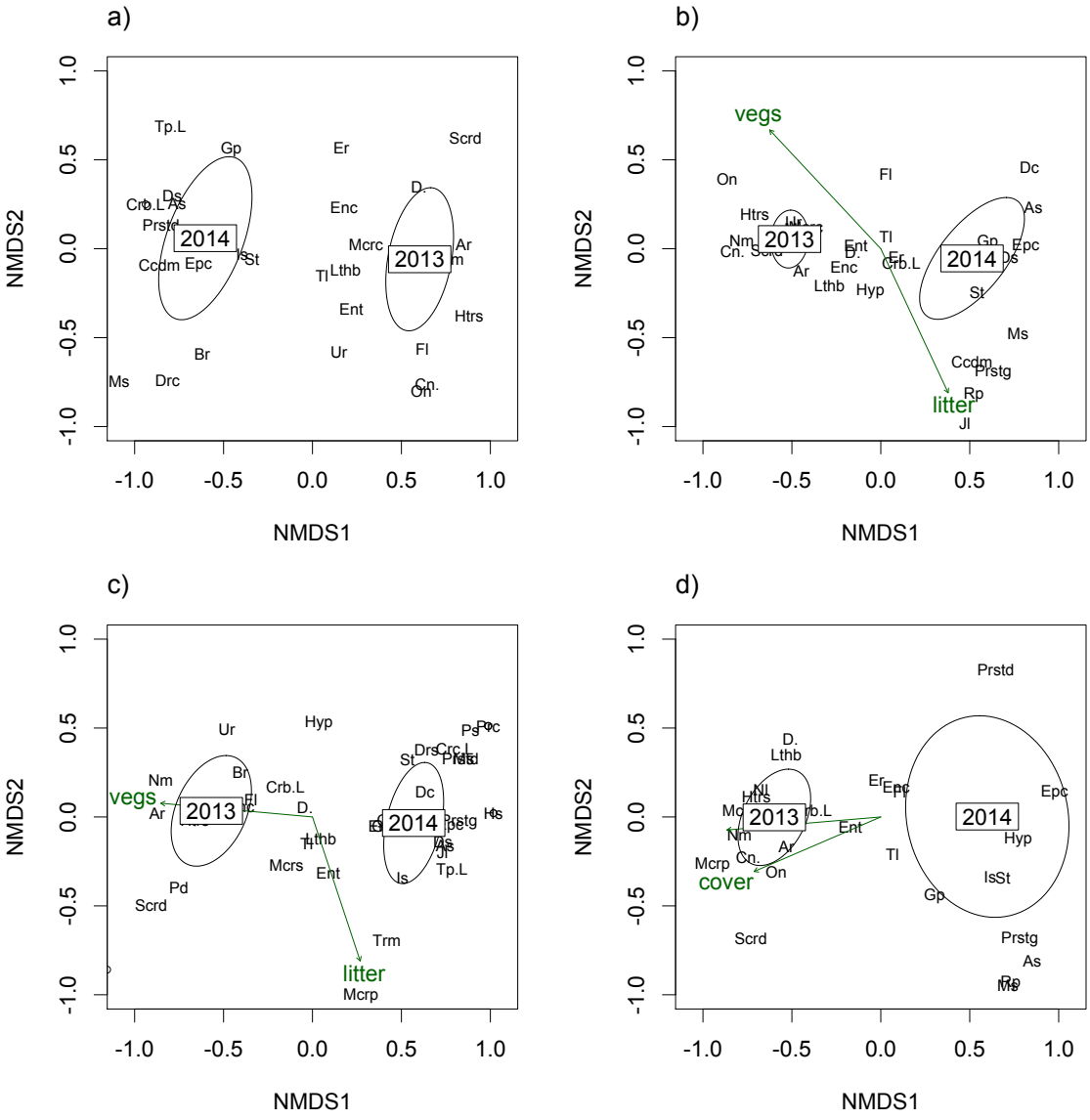


Figure 5.9 Relationship between two-dimensional NMDS of Wisconsin squared root transformation mesofauna community composition of a) conventional plough (PGH), b) strip tillage under sown with ryegrass (RGS), c) strip tillage under sown with a biodiverse seed mix (BSM), d) minimum tillage (MNT) at Fakenham in 2013 ( ) and 2014 ( ). The Fakenham below-ground mesofauna community count data euclidian disssimilarity matrix was correlated with changes in vegetative variates (green arrows where P <0.05). Ellipse (± s.e.) from centroids represent the communities associated with the two cultivation years. Taxa abbreviations are denoted in appendices 12.3.2.

Below-ground invertebrate community composition at Fakenham changed between field trial years (Figure 5.8 and 5.9). The communities in PGH did change between field trial years but were not found to be associated with changes in vegetation composition (Figure 5.9a). The change in mesofauna community composition under RGS at Fakenham was associated with greater litter in 2014 (Figure 5.9b). The change in BSM below-ground invertebrate community composition from 2013 to 2014 was associated with changes in plant species richness (Figure 5.9c). The MNT invertebrate community in 2013 was influenced by vegetation richness and percentage cover (Figure 5.9d). The increase in cover by litter in 2014 was caused by the greater application rates of herbicides to improve crop yield from 2013. The associated increases in litter in BSM and RGS promoted greater densities of Macropyline and Trombidiformes in BSM and greater densities of Raphignathae and Anystides in RGS, indicating a strengthening of the fungal feeding pathway and the associated predators.

5.4. Discussion

Overall there were significant improvements to below-ground meso- and macro-fauna biodiversity through a reduction in tillage and an increase in plant species richness (Figure 5.1). Although there was no significant improvement in the richness or abundance of earthworms under strip tillage cultivations methods, greater mean richness of earthworms was found under strip tillage into a biodiverse seed mix ground cover. This study shows that changes in plant species richness had a greater effect on below-ground community composition than increases in cover by vegetation possibly due to associated enhancement of the soil microflora community, especially the fungal feeding channel (Nakamoto and Tsukamoto, 2006). These results show that overall the inclusion of additional plant species within a maize cultivation system supports invertebrate biodiversity and associated ecosystem functions (Bardgett and van der Putten, 2014).

5.4.1. Diversity and community composition

Increases in below-ground invertebrate biodiversity were similar to that found by Nakamoto and Tsukamoto (2006) (Figure 5.1). However, reductions in crop yield were similar to those reported by Liedgens *et al*. (2004) (Appendix Table 12.2.6). Biodiversity gains within row crop agricultural systems must be balanced with yield penalties to farmers to encourage changes in management practices to enhance ecosystem services.

Reducing the area disturbed during soil preparation and increasing the vegetative cover significantly improved the abundance and diversity of mesofauna. However, in the first field trial year the evenness of mesofauna communities at Bow were significantly lower under the two strip tillage cultivation methods (Figure 5.2c). Despite soil preparation affecting the evenness of the communities in 2013, there were no significant differences in the evenness of communities among the different cultivation methods in 2014 (Figure 5.2c). Initially, the strip tillage communities were less evenly distributed compared with the more conventional cultivation methods (Figure 5.2c). This suggests that only some taxonomic groups benefitted from increases in the richness of the non-crop vegetation and reduced disturbance. However, as there were no differences in the evenness of communities among cultivation methods in 2014, it would appear that initially cultivation favoured some taxa over others. However, as the experiment developed there was a more even distribution of populations within the communities after soil preparation in 2014. These results indicate that the taxa in the strip tillage communities that benefited from the reduction in disturbance and greater resource availability in 2014 were more resilient to disturbance compared with the community in 2013.

It is well known that anthropogenic manipulation of the soil by agricultural production disturbs the stability of the soil ecosystem, which has direct and indirect effects on the diversity of invertebrates and can inhibit biogeochemical processes (Stockdale *et al*., 2006; Tilman, 1996). The organic matter supplied by the intercrops in the strip tillage cultivation methods contained residues derived from dead plant parts and organic materials released from living roots (Nakamoto and Tsukamoto, 2006). The improved diversity and quantity of these resources under strip tillage cultivation sustain soil organisms and enhance ecosystem services such as nutrient cycling and soil structure preservation, which can result in improved soil productivity and ecosystem functioning (Bardgett and Van der Putten, 2014).

Interestingly there were no significant differences between the conventional and minimum tillage cultivation methods below-ground diversity or community composition (Figure 5.1, Figure 5.6, and Figure 5.8). These are similar to results reported by Cortet *et al*. (2007) but are in contrast to the more traditional view that minimum tillage is beneficial for soil biodiversity (Chen, 2001; Doran, 1980). The similar proportions of bare ground, due to low vegetative cover and diversity within conventional plough and minimum tillage maize cultivation systems, resulted in poor below-ground invertebrate biodiversity, which may be

exacerbated by the poor ability of maize to supporting invertebrates (Firbank *et al*., 2003). Where there was greater cover by vegetation there were significantly different invertebrate communities which had greater diversity, this trend was consistent at both sites (Figure 5.6a and 5.9a). Where vegetation cover was increased (Figure 5.6a and Figure 5.8a), within the strip tillage cultivations, there was an increase in the abundance of Collembola, which are important grazers of fungi (Van Capelle *et al*., 2012). These increases in Collembola abundance suggest that under strip tillage cultivation methods there was a stimulation of the fungal feeding pathway (Nakamoto and Tsukamoto, 2006). Through increases in the richness and abundance of Entomobryomorpha and Poduromorpha there can be an increase in the agro-system resilience of soil biogeochemical processes to disturbances (Bardgett and Van der Putten, 2014).

5.4.2. Temporal effects on diversity and community composition

The increase in richness and abundance of mesofauna in the more conventional cultivation methods between 2013 and 2014 may have been exacerbated through the dispersal of populations from strip tillage cultivations to the more conventional cultivations (Figure 5.6 and 5.9). Overall, increases in below-ground biodiversity in the two strip tillage cultivation techniques can be attributed to the increased diversity of plant-derived resources entering the soil ecosystem, supporting and promoting below-ground invertebrate richness and abundance (Bardgett and Van der Putten, 2014). It is also evident that there was a significant increase in richness and abundance of below-ground invertebrates in the strip tillage into an understory of ryegrass compared with the more conventional cultivation methods (Figure 5.2 and 5.5); this could be due to invasion by other taxa, population growth of existing taxa, or a combination of the two. The successional change in the below-ground mesofauna community composition and diversity during the maize cultivation season and between the two maize cultivation years shows that agricultural systems can be manipulated over both the short and long term to benefit below-ground invertebrate biodiversity (Figure 5.3; Wardle *et al*., 1999).

The increased cover by litter in 2014 was caused by increasing the application rates of herbicides to improve maize yields by reducing early intercrop competition (Section 3.1, Appendix Table 12.2.2, Figure 5.7, Figure 5.9). Increases in cover by litter combined with developmental effects of the experiment, i.e. not ploughing the strips for two years, were found to influence below-ground community composition (Figure 5.7 and 5.10) similar to increases in plant residues reported by Scheunemann *et al*. (2015). These developmental

effects during the experiment could be attributed to the significant increases in below-ground invertebrate richness and abundance in the strip tillage cultivation methods over that of the more conventional cultivation methods (Table 5.1). In addition under the two strip tillage cultivation techniques where there was greater litter composition there were greater densities of Oribatida and Prostigmata; these are secondary decomposers (Crotty *et al*., 2014) that are known to consume fungi which results suggest were stimulated under the greater availability of litter (Figure 5.7). This indicates that there are intrinsic links between the quantity of litter, the fungal community and the mesofauna community (Cortet *et al*., 2003).

Increases in the densities of herbivores, their predators Carabidae and Staphylinidae, and the larvae of these Coleoptera families (Figure 5.6a, 5.9a) were associated with increases in native vegetation in the strip tillage cultivation techniques. The increase in predators may have beneficial top-down effects on the decomposer communities, whilst increases in herbivore densities may have bottom-up effects on generalist predators. Bottom-up and top-down effects are well documented in the literature as affecting above- and below-ground invertebrate communities (Scheu, 2001; Hawes *et al*., 2009), and have been proposed as a mechanism for improving bio-control within agricultural systems (Scheu, 2001). The presence of litter also improved the abundance of predators which suggests that bio-control benefits may be achieved through cultivating maize using litter mulch rather than a live intercrop.

The cover of non-crop vegetation significantly increased the community complexity of below-ground invertebrates (Figure 5.5 and 5.8). This effect was observed in both RGS and BSM cultivation techniques, indicating that the community composition was driven by both density and diversity of vegetative resources entering the soil system from non-crop vegetation. In combination with the temporal development of the communities between the two field trial years the response of below-ground invertebrate community composition and diversity was initially influenced by the diversity, and subsequently the quantity of plant derived resources entering the soil system. This highlights that both vegetation composition and quality are important for supporting below-ground invertebrate biodiversity.

At both sites there was an increase in the numbers of detrital feeding taxa as well as predators under the two strip tillage cultivation methods (Figure 5.6b, 5.8b). This indicates

that there was a stimulation of the fungal feeding pathway similar to that shown by Nakamoto and Tsukamoto (2006). Through a reduction in the area disturbed and maintenance of a non-crop vegetative cover as found with the two strip tillage cultivation methods this stimulation was found to be exacerbated indicating that the reductions in disturbance and greater non-crop resource supported the fungal communities which supported the mesofauna that feed on them (Van Capelle *et al*., 2012). Further analysis of the functional group responses to changes in vegetation will highlight if these changes in detrital fauna were in response to increases in non-crop vegetation and their derivatives (Chapter 7)

5.4.3. Spatial effects on diversity and community composition

Natural variation in local taxonomic pools that the communities were recruited from may explain the differences (Figure 5.6 and 5.9) in community composition between the two field sites. Similar studies have found that community composition changes over spatial scales (Baur *et al*., 1996; Tsiafouli *et al*., 2015). Although the abundance of below-ground invertebrates in MNT between the two sites (Table 5.1) was significantly different, there were no significant differences found between cultivation method and the richness, evenness or diversity of below-ground meso-fauna between the two sites (Baur *et al*., 1996). This shows that below-ground invertebrate diversity, despite differences in community composition, show consistency to changes in maize cultivation practice independent of the soil's chemical and physical properties. These results also provide supporting evidence for the trends found in Chapter 4 where although the cultivation systems were different on the same soil type the two systems supported similar abundances of soil fauna, however this chapter shows that similar cultivation techniques support similar richness, evenness and diversity of communities but at different abundances of mesofauna on different soil types.

Similarities in diversity between the row and inter-row areas (Figure 5.3, 5.5) support findings by Smith *et al*. (2008). However, differences in the community composition between the row and inter-row areas at Bow may be linked with the overall differences in community composition between the two sites; at Bow the community was better able to respond to increases in vegetation richness and cover in the row or inter-row areas driving the difference in community composition between these two areas (Baur *et al*., 1996; Tsiafouli *et al*., 2015).

5.5. Conclusions

Changes in maize cultivation practice by reducing the area disturbed and increasing non-crop vegetation can improve below-ground invertebrate biodiversity over the short (during the cultivation years) and long term (over multiple cultivation years).

This chapter adds to the established body of work that shows physical disturbance has a negative impact on below-ground invertebrate diversity (Stockdale *et al*., 2006; Tilman, 1996; Nakamoto and Tsukamoto, 2006; Bardgett and Van der Putten, 2014), even where there are increases in plant resource availability.

However, plant inputs were found to promote differences in community composition over the cultivation season. Balancing these below-ground biodiversity benefits, and reducing soil disturbance must be carefully managed within agroecosystems to reduce negative environmental impacts whilst maintaining crop yield, ultimately providing a viable alternative for farmers.

Through increases in the cover of vegetation and litter there were significant increases in the abundances of below-ground mesofauna, especially fungivores and predators (Nakamoto and Tsukamoto, 2006). This could offer a possible mechanism for improving below-ground biodiversity within maize cultivation systems without the negative competition effects on maize from non-crop vegetation. This could be achieved by artificially increasing the amount of litter within conventional maize systems by supplementing with litter mulches, which offers opportunities for further research.

Chapter 6

Effects of Maize Cultivation on Above-ground Invertebrates

6. Effects of Maize Cultivation on Above-ground Invertebrates

6.1. Introduction

Above-ground invertebrates are an important biological component of agroecosystems and offer a way of assessing wider biodiversity (Firbank *et al*., 2003). Invertebrates show remarkably consistent and sensitive responses to changes in vegetative diversity (Brooks *et al*., 2005). The loss of above-ground invertebrate biodiversity from agro-systems has been shown to affect ecosystem services such as primary productivity, nutrient cycling, and bio-control (Scherber *et al*., 2010).

Inherently low plant species richness has been shown to directly cause losses to above-ground invertebrate diversity, biomass and functionality (Hawes *et al*., 2010). In addition, low plant diversity has been shown to alter mutualistic interactions such as pollination or mycorrhizal association (Scherber *et al*., 2010). Changes in plant species richness also affect higher trophic levels; however this effect is dampened with increasing trophic level (Scherber *et al*., 2010). As vegetation species richness increases there are generally positive effects on the diversity and community composition of above-ground invertebrates (Scherber *et al*., 2010; Hawes *et al*., 2010). In support of the relationship between plant and above-ground invertebrate species richness, the diversity-stability hypothesis states that loss of plant diversity can impair the ability of an ecosystem to dampen the effect of disturbances on its functioning (Proulx *et al*., 2010). It is well known that species-rich vegetative communities are more resilient to environmental perturbations and contribute to ecological functioning in various ways, increasing ecosystem stability and invertebrate specialisation (Proulx *et al*., 2010).

Increases in non-crop vegetation in genetically modified herbicide-tolerant maize has been shown to correlate with increases in the abundance of Collembola, Carabids, Staphylinidae and some Linyphiidae, relative to conventional maize due to greater weed diversity later in the cropping season (Brooks *et al*., 2005). However, Scherber *et al*.'s (2010) study found that above-ground herbivores responded more strongly to changes in plant diversity than predators or omnivores. Scherber *et al*. (2010) also showed that the density and richness of predators was independent of vegetation structure with stronger links between increasing density of fungivorous Collembola. These factors affect both arable and natural invertebrate communities, their food web structure and stability (Albers *et al*., 2006; Birkhofer *et al*., 2012; Crotty *et al*., 2014).

Within arable food webs there are two main interactions between above-ground invertebrate groups; one between omnivores, generalist predators and detritivores, which are positively associated with monocotyledons, and one between omnivores, parasitoids, sap feeders and leaf chewers, which have a stronger association with dicotyledons (Hawes *et al*. 2010). Hawes *et al*. (2010) concluded that although management has an influence on within-field arable biodiversity, crop type and sowing season have an overriding effect on the composition of plant and above-ground invertebrate communities.

Although pitfall trapping has been shown to be a cost effective method for sampling above ground invertebrates it is biased by collecting large numbers of individuals with greater activity. These differences in the densities of taxa collected may also be exacerbated by comparing population from habitats with contrasting vegetation structural and complexity which may impede the activity or reduced the dispersal efficiency of some arthropod taxa. Pitfall traps are however the most time and cost effective methods for assessing above ground arthropod diversity and can be comparable to a number of other studies that have applied this method.

6.1.1. Hypotheses aims and objectives

This chapter quantifies and compares the effects of different maize cultivation methods on above-ground invertebrate diversity and community structure. The goal was to assess how changes in cultivation and ground cover management practices in maize systems affects above-ground invertebrate communities, if the community responses are similar at the two field sites and how community responses change over time.

H_1= A reduction in physical disturbance increases the above-ground biodiversity invertebrates

H_1= An increase in non-crop richness increases above-ground invertebrate biodiversity

H_1= An increase in non-crop cover increases above-ground inverebrate biodiversity

6.2. Materials and Methods

Above-ground invertebrates were collected using pitfall traps (10 cm depth by 6.5 cm diameter) at both sites (Plate 3.1 to 3.3); traps were set out for six weeks from the start of

June in 2013 and 2014 (Plate 3.3). Eight pitfall traps were located in each plot. Above-ground invertebrates were sampled at the same time at both field sites (Plate 3.3), as such, count data from the two sites was analysed together to test for the effect that maize cultivation method, site and sampling time had on above-ground invertebrate biodiversity. The two sites were found to be different in community composition, as such, further analysis of the response of the communities to cultivation and temporal differences at the two sites were analysed separately.

6.2.1. Statistical analysis

The above-ground invertebrate counts were summed based on the eight pitfall traps per plot to remove pseudo-replication. Shannon diversity, richness, activity/density and evenness were calculated for each plot as described in section 3.6. If required, above-ground invertebrate diversity calculations were Box-Cox transformed in order to conform to normality assumptions (Box and Cox, 1964). Analysis of variance and Tukey HSD post hoc significance tests were used to identify significant differences between factors. Factors included field site, cultivation method, sampling week and sampling year and all possible interactions, block was used as the fixed factor.

Non-metric multidimensional scaling (NMDS) (Faith *et al*., 1987) and 'envfit' (Oksanen *et al*., 2007) were used to identify how above-ground invertebrate counts correlated with experimental factors and assess how changes in vegetation influenced above-ground invertebrate community composition. The above-ground invertebrate Bray-Curtis dissimilarity matrix was Wisconsin square root transformed to accommodate the large number of Acari and Collembola collected (Faith *et al*., 1987). For a full description of statistical procedures see section 3.6.

6.3. Results

6.3.1. Diversity

Overall, the richness, activity/density, evenness and Shannon diversity of above-ground invertebrate communities, collected from the both sites, were significantly different among cultivation methods (Table 6.1, Figure 6.1). The two strip tillage cultivation methods (RGS and BSM) were significantly greater in above-ground invertebrate richness compared with the more conventional cultivation methods (PGH and MNT) (Figure 6.1a), suggesting that reduced disturbance benefited above-ground invertebrates. The BSM cultivation method was also significantly greater in above-ground invertebrate richness compared with RGS

(Figure 6.1a) which indicates that the richness of non-crop vegetation also benefited above-ground invertebrates. However, there was no significant difference between PGH and MNT (Figure 6.1a), indicating that the tilling process affected invertebrate richness to a greater degree than ploughing.

The two strip tillage cultivation methods (RGS and BSM) were also significantly greater in above-ground invertebrate activity/density compared with the more conventional cultivation methods (PGH and MNT) (Figure 6.1b). However, there was no significant difference in activity/density between BSM and RGS or PGH and MNT (Figure 6.1b). The evenness of the BSM community was significantly greater than the PGH, MNT or RGS communities (Figure 6.1c). The strip tillage cultivation methods BSM and RGS were significantly greater in Shannon diversity compared to the more conventional cultivation methods. There was also a significant difference between the two strip tillage cultivation methods, with BSM being greater in Shannon diversity compared with RGS (Figure 6.1d). There was no significant difference in Shannon diversity between PGH and MNT (Figure 6.1d).

Table 6.1 Above-ground invertebrate richness, activity/density, and evenness and Shannon diversity analysis of variance summary. The above-ground invertebrate count data from both sites and both field trial years was used to calculate richness, activity/density, evenness and Shannon Diversity.

		Richness		**Density**		**Evenness**		**Diversity**	
	df	**F-Value**	***P*-value**	**F-Value**	***P*-value**	**F-Value**	***P*-value**	**F-Value**	***P*-value**
Site	1	1.70	0.195	7.76	0.006 **	0.2415	0.624	0.5413	0.463
Cultivation method	3	39.62	0.000 ***	21.13	0.000 ***	9.7658	0.000 ***	42.0864	0.000 ***
Year	1	37.93	0.000 ***	92.59	0.000 ***	213.6887	0.000 ***	62.977	0.000 ***
Period	5	18.54	0.000 ***	40.30	0.000 ***	31.7594	0.000 ***	10.5172	0.000 ***
Block	2	6.92	0.001 **	0.88	0.418	4.0757	0.018 *	9.2352	0.000 ***
Site*Cultivation method	3	1.75	0.158	3.54	0.016 *	8.286	0.000 ***	5.6154	0.001 **
Site*Year	1	23.27	0.000 ***	52.29	0.000 ***	3.3436	0.069	0.578	0.448
Cultivation method*Year	3	4.97	0.002 **	4.18	0.007 **	9.8336	0.000 ***	11.4155	0.000 ***
Site*Period	5	0.97	0.437	15.99	0.000 ***	3.1713	0.009 **	3.6668	0.003 **
Cultivation method*Period	15	1.30	0.208	2.13	0.010 *	2.0453	0.014 *	1.9334	0.022 *
Year*Period	5	20.18	0.000 ***	57.64	0.000 ***	18.26	0.000 ***	9.2057	0.000 ***
Site*Cultivation method*Year	3	0.61	0.611	5.91	0.001 ***	2.5128	0.060	4.9122	0.003 **
Site*Cultivation method*Period	15	1.43	0.136	2.45	0.003 **	2.9759	0.000 ***	2.1837	0.008 **
Site*Year*Period	5	9.29	0.000 ***	18.41	0.000 ***	22.2137	0.000 ***	24.9255	0.000 ***
Cultivation method*Year*Period	15	0.33	0.991	1.69	0.056	1.3176	0.195	0.7838	0.695
Site*Cultivation method*Year*Period	15	0.61	0.861	0.95	0.509	1.7508	0.045 *	1.8829	0.027 *

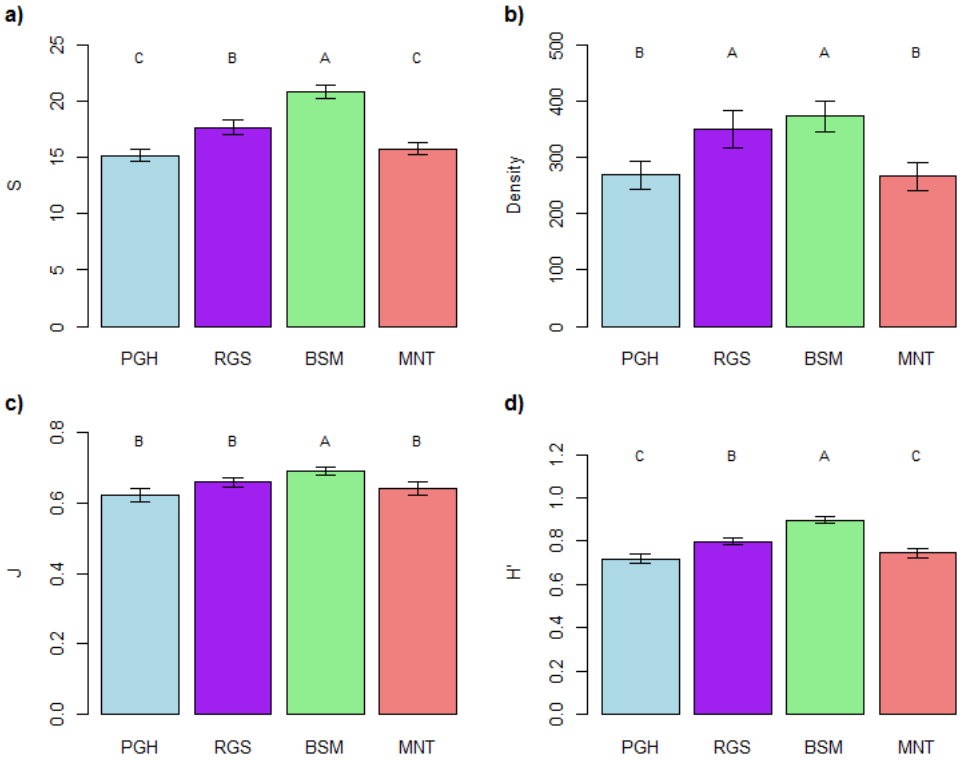


Figure 6.1 Above-ground invertebrate count data form both sites and all sampling times was used to calculate the mean (± s.e.) a) taxonomic richness b) activity/density c) evenness d) Shannon diversity for each cultivation method (PGH , RGS , BSM , MNT). Tukey HSD post-hoc tests were used to test for true significant difference between cultivation methods. Different letters denote Tukey HSD significant differences (P <0.05) between cultivation methods for each index.

To understand if the invertebrate communities at the two sites responded similarly to changes in ground cover and soil management practices the calculated diversity indices (richness, activity/density, evenness and Shannon diversity) of communities recovered from the two sites were analysed for interaction effects (Table 6.1). Independent of cultivation method, above-ground invertebrates were significantly more active/dense at Fakenham compared to Bow (Table 6.1, *P.adjusted*= 0.005). The activity/density, evenness and Shannon diversity of above-ground invertebrates were also significantly different depending on cultivation method (Table 6.1), which also varied depending on sites (Figure 6.2).

At Bow, the BSM cultivation method was significantly richer in above-ground invertebrates than PGH, RGS and MNT (Figure 6.2a). In contrast, at Fakenham, BSM was significantly richer than PGH and MNT but not RGS (Figure 6.2a). There were also significant differences between activity/densities of invertebrates between PGH, MNT and

BSM at Bow (Figure 6.2b). BSM was significantly greater in above-ground invertebrate activity/density compared with the more conventional cultivation methods (Figure 6.2b). However, there was no significant difference in the activity/densities of above-ground invertebrates among the different cultivation methods at Fakenham (Figure 6.2b). These results suggest site specific community responses by above-ground invertebrates to changes in maize cultivation practice.

There were significant differences in the evenness of the above-ground invertebrate communities between cultivation methods at Fakenham but not at Bow (Table 6.1 and Figure 6.2c). At Fakenham the BSM community was found to be significantly more evenly distributed than the PGH community (Figure 6.2c). At Bow, RGS and BSM were significantly greater in Shannon diversity than PGH (Figure 6.3). BSM was also significantly more diverse than MNT, but there was no significant difference in Shannon diversity between RGS and MNT (Figure 6.3d). There were also significant differences between PGH, MNT, RGS and BSM at Fakenham. At Fakenham BSM was found to be significantly greater in Shannon diversity compared with the other three cultivation methods, however there was no significant difference between PGH, MNT and RGS (Figure 6.2d).

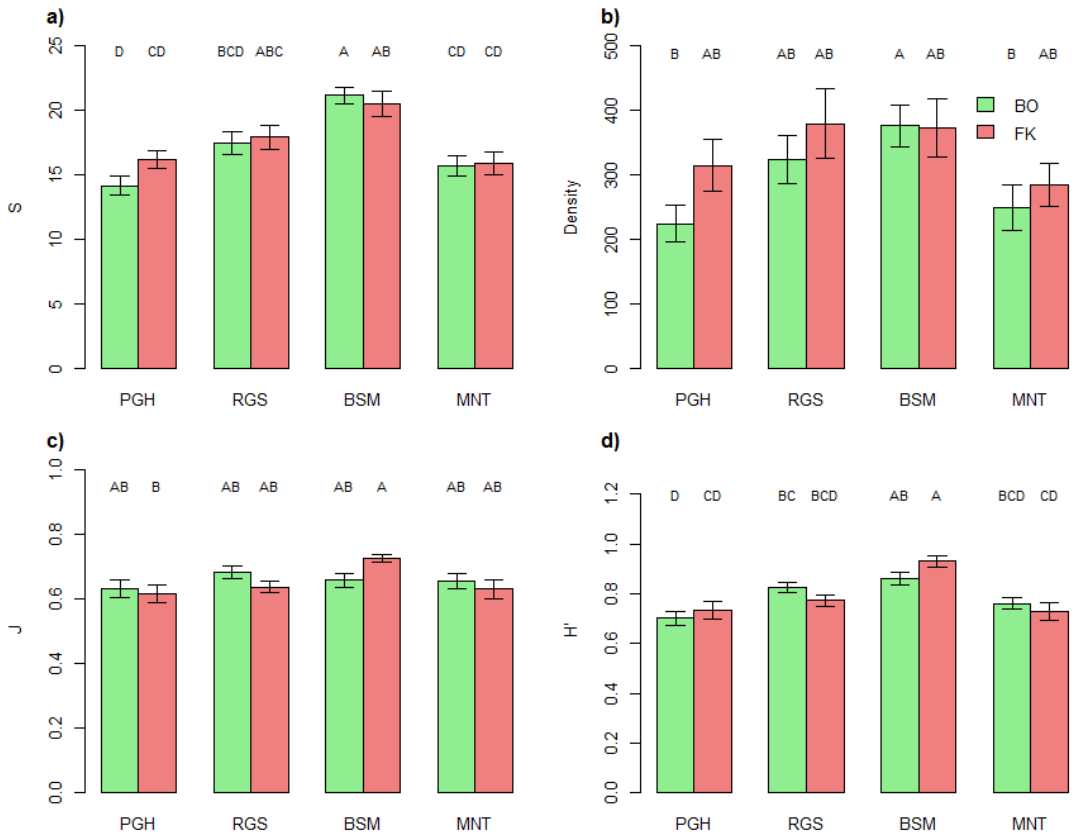


Figure 6.2 Above-ground invertebrate count data form all sampling times was used to calculate the mean (± s.e.) a) taxonomic richness b) activity/density c) evenness d) Shannon diversity for each cultivation method at the two sites (Bow (BO) , Fakenham (FK)). Taxonomic richness, activity/density, evenness and Shannon Diversity were Box-Cox transformed to ensure normality before analysis of variance and Tukey HSD post-hoc tests were used to test for true significant difference between cultivation methods. Different letters denote Tukey HSD significant differences (P <0.05) between cultivation methods for each index.

The above-ground invertebrate count data from the two sites was analysed together to identify if there was any general trends in how the richness, activity /density, evenness or Shannon diversity changed between sampling years. There was a significant difference in all four calculated diversity indices of above-ground invertebrates between the two field trial years (Table 6.1). There were also differences in how these indices varied under the different cultivation techniques (Table 6.1, Figure 6.3).

The richness of above-ground invertebrates increased from 2013 to 2014, however, there were no significant increases in richness in PGH, BSM or MNT (Figure 6.3a). There were no significant differences in the activity/density between the more conventional cultivation methods or BSM in either year; however there was a significantly greater activity/density of above-ground invertebrates in RGS in 2014 compared with 2013 (Figure 6.3c). Above-ground invertebrate evenness significantly decreased in PGH, RGS and MNT from 2013 to 2014, however, there was not a significant reduction in the evenness of BSM community between cultivation years (Figure 6.3c). There was a significant reduction in Shannon diversity of above-ground invertebrates between the two years in the more conventional cultivation methods (Table 6.1 and Figure 6.3d), however, there were no significant reductions in above-ground invertebrate Shannon diversity in the strip tillage cultivation methods (RGS and BSM) (Figure 6.3d), suggesting these cultivation methods were better able to support and maintain greater above-ground invertebrate biodiversity.

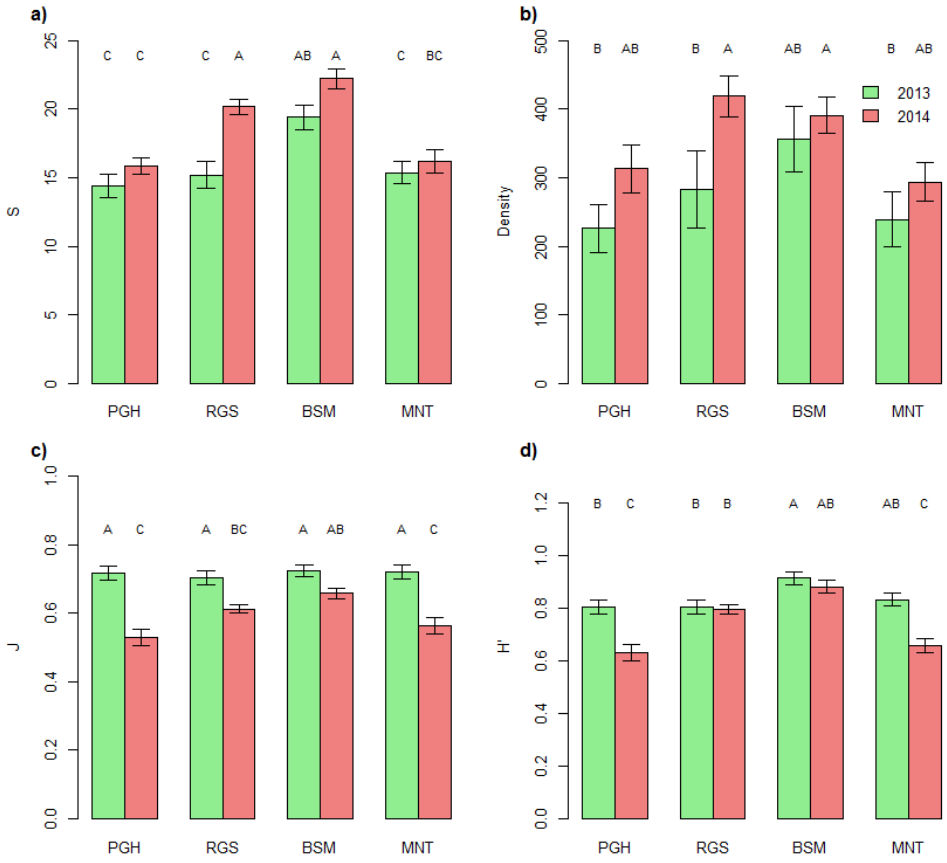


Figure 6.3 Above-ground invertebrate count data form both sites was used to calculate the mean (± s.e.) a) taxonomic richness b) activity/density c) evenness d) Shannon diversity for each cultivation method for each cultivation year (2013 , 2014). Taxonomic richness, activity/density, evenness and Shannon Diversity were Box-Cox transformed to ensure normality before analysis of variance and Tukey HSD post-hoc tests were used to test for true significant difference between cultivation methods. Different letters denote Tukey HSD significant differences (P <0.05) between cultivation methods for each index.

6.3.2. Community composition

As with below-ground responses to changes in cultivation practice, it is of critical importance to understand the effects of cultivation practice on above-ground communities. Although the activity/density of above-ground invertebrates was greater in RGS compared with PGH and MNT, there were no significant differences in community composition (Figure 6.4a). However, the community composition of BSM was significantly different (Figure 6.4a) compared to the communities recovered from more conventional cultivation methods (PGH and MNT). The differences in above-ground invertebrate community composition were associated with increases in cover by litter and vegetation richness (Figure 6.4a).

Over the two field trial years there was a significant difference in above-ground invertebrate community composition (Figure 6.4b). In 2013, the RGS community composition was significantly different to the other three cultivation methods, however in 2014, BSM was found to be significantly different in above-ground invertebrate community composition to the other three cultivation methods (Figure 6.4b).

There was a greater degree of variation in the community composition of above-ground invertebrates at Bow compared with Fakenham (Figure 6.4c). At Fakenham the above-ground invertebrate communities were found to be particularly sensitive to changes in the richness of vegetation and cover of litter. Vegetation richness at Fakenham was associated with greater numbers of Carabidae larvae, adult *Bembidion* spp. and adult *Cortcaria* spp., whereas Bow correlated with lower vegetation richness and associated with Cocclinidae (Figure 6.4d). At Fakenham there was no significant difference in community composition among cultivation methods (Figure 6.4d). However at Bow, the RGS and BSM communities were significantly different compared to PGH and MNT; the strip tillage cultivation techniques were associated with greater densities of Cocclinidae (Figure 6.4d).

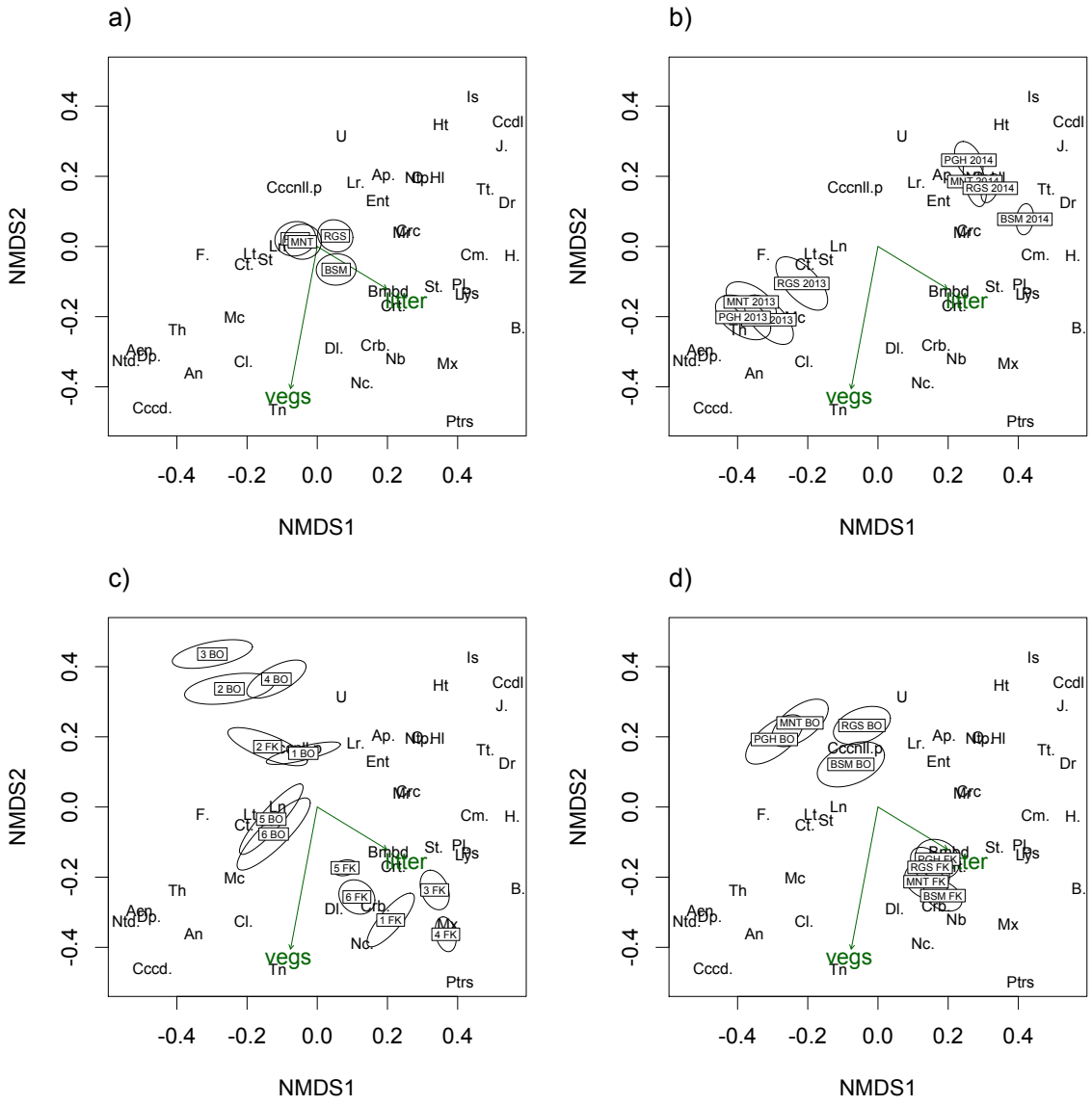


Figure 6.4 Relationship between two-dimensional NMDS of the Wisconsin squared root transformed above-ground community composition of a) among cultivation methods, b) among cultivation years and methods, c) among sampling weeks at the two sites, d) among cultivation methods at the two field sites. The above-ground invertebrate community euclidean dissimilarity matrix was calculated from the count data was correlated with changes in vegetation (green arrows where $P < 0.05$) and experimental factors (represented by ellipse (± s.e.) from centroids). Taxa abbreviations are denoted in Appendix 12.4.2.

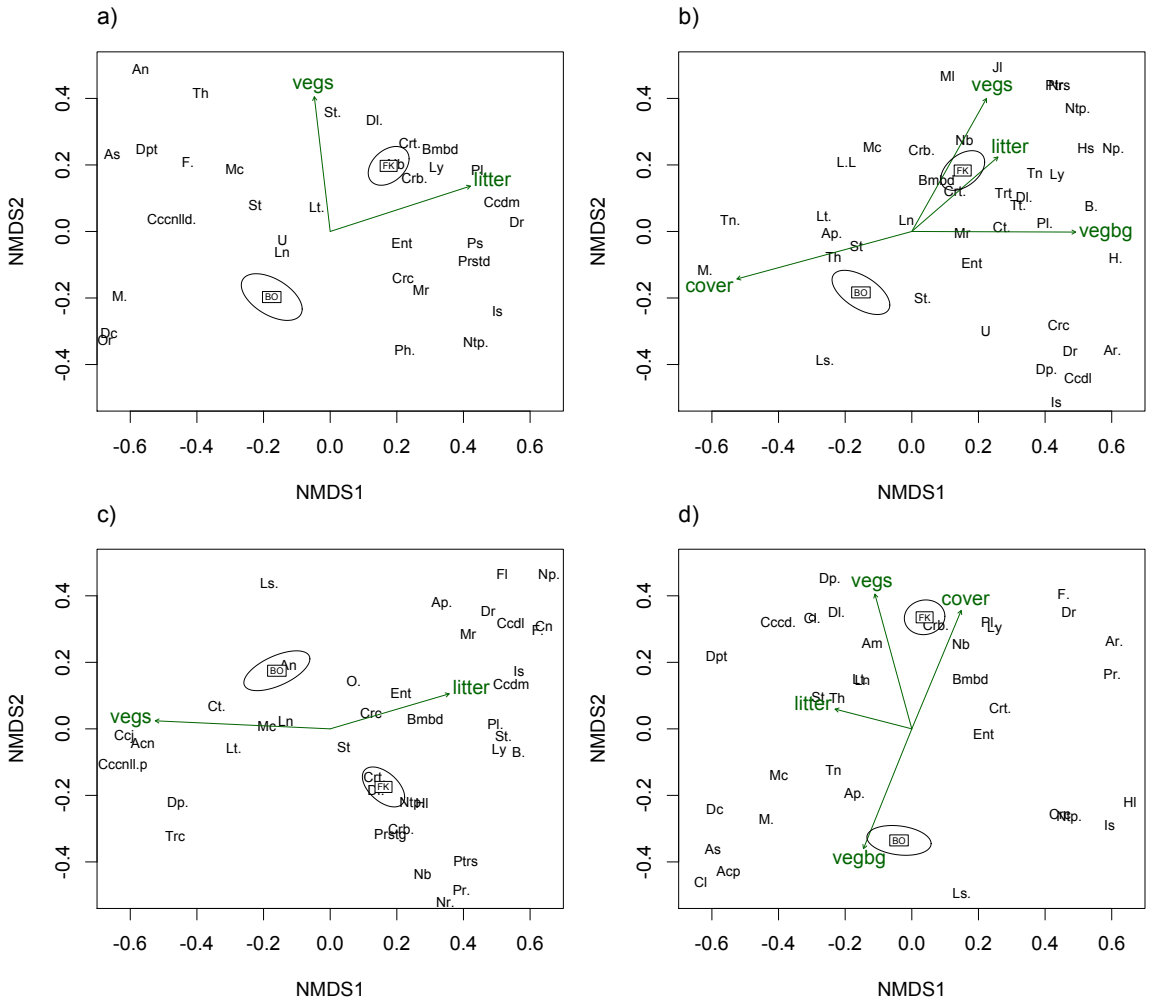


Figure 6.5 Relationship between two-dimensional NMDS of the Wisconsin squared root transformed above-ground community composition of a) conventional plough (PGH), b) strip tillage under sown with ryegrass (RGS), c) strip tillage under sown with a biodiverse seed mix (BSM), d) minimum tillage (MNT). The above-ground invertebrate community euclidean dissimilarity matrix calculated from count data was correlated with changes in vegetation (green arrows where P <0.05) and experimental factors (represented by ellipse (± s.e.) from centroids), to understand how the vegetation afftected the communties at the different sites. Taxa abbreviations are denoted in Appendix 12.4.2.

The percentage cover by bare ground and cover by litter are intuitively negative co-variates, as where there was an increase in cover it was predominantly by vegetation rather than litter (Appendix Figure 12.1.1). Although the diversity of the communities did not vary between sites (Figure 6.2) there were differences in the composition of communities at the two sites (Figure 6.5). There is evidence to suggest that the two distinct communities were driven by the difference in vegetation composition at the two sites (Figure 6.5). Therefore the temporal changes in community composition have been assessed for each site separately (Figure 6.6 and Figure 6.7).

At Bow different vegetative variates had differing degrees of influence on the above-ground invertebrate community composition under the contrasting maize cultivation techniques (Figure 6.5 and Figure 6.6). No significant influence was found by changes in vegetation or litter on the composition of above-ground invertebrates within PGH, but there were differences in invertebrate community composition between the two years (Figure 6.6a).The above-ground invertebrate community composition of RGS and BSM was significantly influenced by all of the measured changes in vegetation composition (Figure 6.6b and c). In 2013, the RGS community correlated with greater cover by vegetation, however litter, plant species richness and bare ground had a stronger influence on above-ground invertebrate community composition in 2014 (Figure 6.6b), which was influenced by the increased application rates of herbicides (Section 3.2) to improve maize yield (Appendix Table 12.2.2). The BSM community composition correlated with greater vegetation richness in 2013, but in 2014 was more associated with the increases in litter and cover (Figure 6.6c), again affected by the increased application rates of herbicides to reduce early completion with the maize crop. The percentage cover by vegetation significantly affected the MNT above-ground invertebrate community composition (Figure 6.6d). In 2013 there was greater cover by litter, however in 2014 there was greater cover by bare ground but also greater vegetation richness (Figure 6.6d).

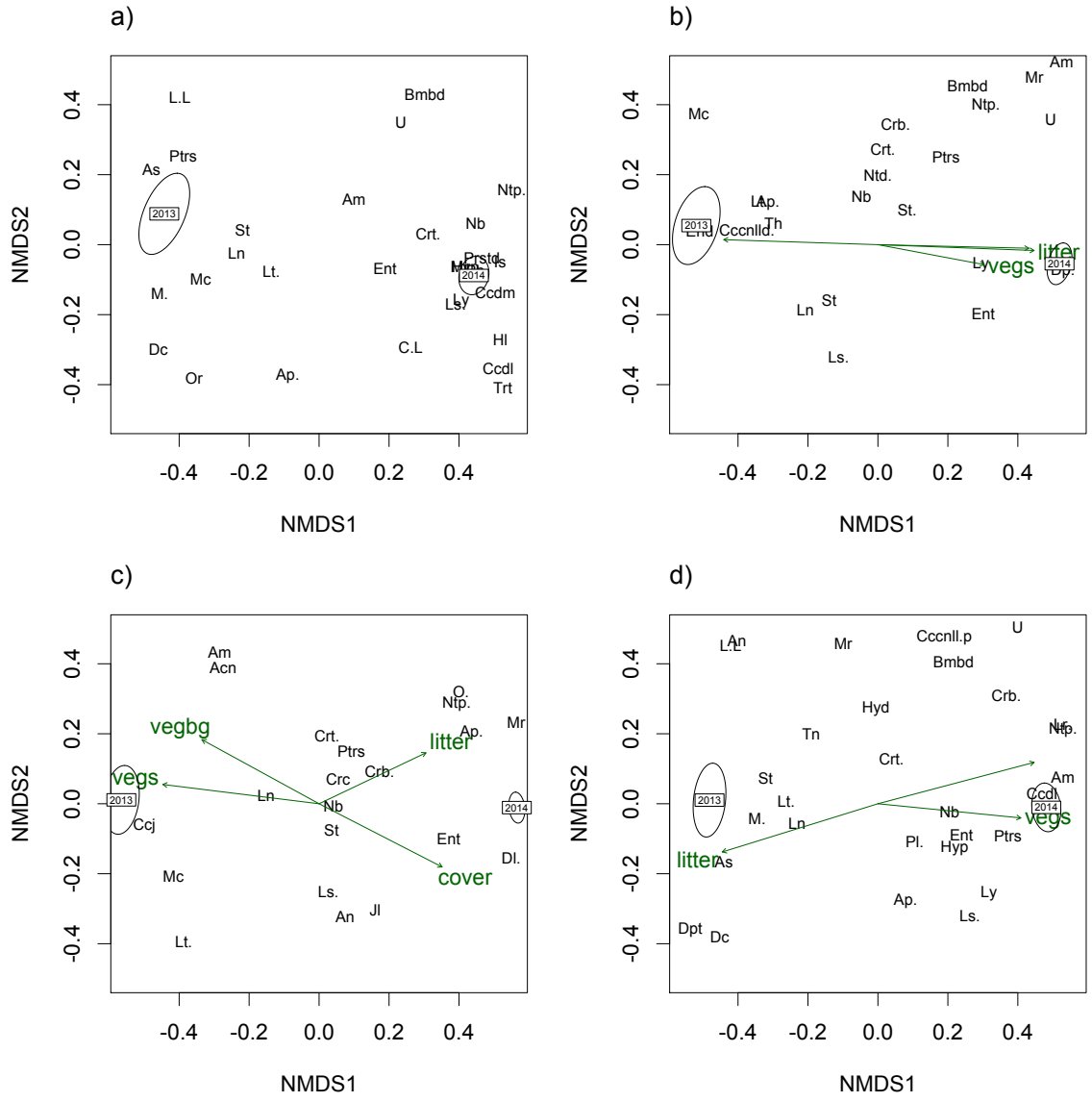


Figure 6.6 Relationship between two-dimensional NMDS of the Wisconsin squared root transformed above-ground community composition of a) conventional plough (PGH), b) strip tillage under sown with ryegrass (RGS), c) strip tillage under sown with a biodiverse seed mix (BSM), d) minimum tillage (MNT) at Bow. The above-ground invertebrate community euclidean dissimilarity matrix was calculated from the count data for each year and correlated with changes in vegetation (green arrows where P <0.05) and experimental factors (represented by ellipse (± s.e.) from centroids), to understand how the vegetation afftected the communties in the two cultivation years. Taxa abbreviations are denoted in Appendix 12.4.2.

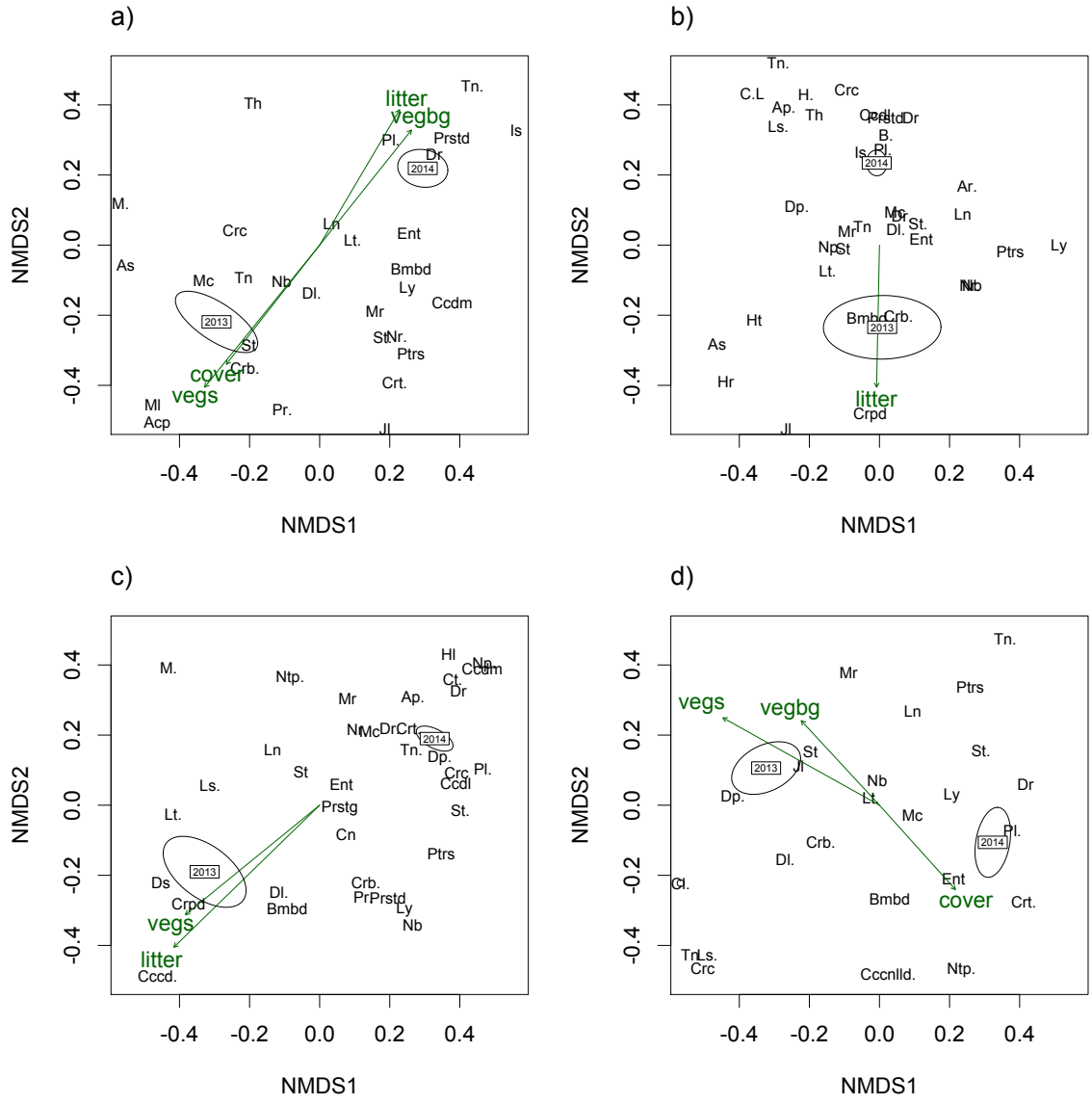


Figure 6.7 Relationship between two-dimensional NMDS of Wisconsin squared root transformation above-ground community composition of a) conventional plough (PGH), b) strip tillage under sown with ryegrass (RGS), c) strip tillage under sown with a biodiverse seed mix (BSM), d) minimum tillage (MNT) at Fakenham. The above-ground invertebrate community euclidean dissimilarity matrix was calculated from the count data for each year and correlated with changes in vegetation (green arrows where P <0.05) and experimental factors (represented by ellipse (± s.e.) from centroids), to understand how the vegetation afftected the communties in the two cultivation years. Taxa abbreviations are denoted in Appendix 12.4.2.

As with Bow, the above-ground invertebrate communities were affected by different vegetation variates within the different cultivation methods at Fakenham (Figure 6.5 and Figure 6.7). PGH above-ground invertebrate community composition was significantly affected by increases in percentage cover by vegetation and vegetation species richness in

2013, which was found to be negatively correlated to percentage cover by litter and bare ground (Figure 6.7a). RGS above-ground invertebrate community composition was significantly affected by increases in percentage cover by litter (Figure 6.7b). Percentage cover by litter and vegetative species richness significantly influenced the above-ground invertebrate community composition within BSM (Figure 6.7c). At Fakenham the MNT above-ground invertebrate community composition was significantly influenced by percentage bare ground and vegetative species richness, which were negatively correlated with percentage cover by vegetation (Figure 6.8d).

6.4. Discussion

Inherently low plant species richness, as found in conventional maize cultivation, has been shown to cause losses to above-ground invertebrates, which in turn influences the diversity and composition of communities (Scherber *et al*., 2012; Proulx *et al*., 2010; Firbank *et al*., 2003; Hirsch *et al*., 2009). These results support the diversity-stability hypothesis (Proulx *et al*., 2010), showing that where there were increases in vegetative richness there was an increase in the richness, activity/density and diversity of above-ground invertebrates (Figure 6.1). Increases in vegetative richness and percentage cover by vegetation in the strip tillage cultivation methods (RGS and BSM) supported both a greater diversity and different community assemblages of above-ground invertebrates compared with conventional cultivation methods (Figure 6.5a, Figure 6.6, Figure 6.1a b d and Figure 6.4a).

Where there were increases in vegetative richness and cover there were significant increases in above-ground invertebrate diversity (Figure 6.4, Appendix 12.1). For example, within BSM, where there was significantly greater vegetative richness, the above-ground invertebrate community was significantly more evenly distributed and had a greater Shannon diversity compared with the more conventional cultivation methods (PGH and MNT) (Figure 6.1c,d). Scherber *et al*. (2012) found that changes in vegetation richness affect herbivores and neighbouring trophic levels, causing bottom-up affects on higher trophic levels. These results support this hypothesis; that as vegetative species richness increases, there were positive effects on the diversity and community composition of above-ground invertebrates (Figure 6.4a and Figure 6.5 a, c).

Other studies have also shown that increases in vegetation positively affects above- and below-ground invertebrate biodiversity in both natural and agricultural systems (Wardle *et*

al., 1999; Sabais *et al*., 2010; Briones and Bol, 2003; Caruso *et al*., 2012; Wilson *et al*. 1999; Hawes *et al*., 2010). The diversity-stability hypothesis states losses of plant diversity can impair the ability of an ecosystem to dampen the effect of environmental perturbations on its functioning (Proulx *et al*., 2010). In PGH and MNT there were significantly less diverse communities with reduced community complexity than the strip tillage cultivation methods (Figure 6.5). Where non-crop vegetation richness and percentage cover were increased, it can be speculated that the resistance and resilience of the communities was improved (Figure 6.1c), which is similar to findings by Wardle *et al*. (1999); Sabais *et al*. (2010); Briones *et al*. (2003); Caruso *et al*. (2012); Wilson *et al*. (1999). These results and supporting literature show that reducing physical disturbance and increasing vegetative richness and their associated derivatives supports above-ground invertebrate diversity, which improves and protects the functioning of important ecosystem services (Tiemann *et al*., 2015).

The differences in response of the above-ground invertebrate communities to similar increases in vegetative dynamics between sites (Figure 6.1a to d, Figure 6.4 and 6.5) can be attributed to differences in the community composition of the local invertebrate taxa pools (Baur *et al*., 1996; Tsiafouli *et al*., 2015; Caruso *et al*., 2008). Differences in the existing invertebrate communities between the sites before the experiments were established was due to differences in the local taxonomic pools from which the invertebrates could be recruited (Altieri, 1999). Although not measured in this study, differences in surrounding vegetation are known to have a significant influence on invertebrate community composition (Altieri, 1999). Altieri (1999) found that with increasing habitat complexity in surrounding areas of experimental sites effected the composition of invertebrates recovered at different field site locations. It was this difference in community composition at the two sites which resulted in different community level responses to changes in vegetation dynamics found within this experiment, which is supported by similar findings from Baur *et al*. (1996) and Tsiafouli *et al*. (2015). The difference in community composition and their response to vegetation richness and cover has important implications for the use of intercrops in providing refuges and bio-control. For example, where there is a naturally abundant invertebrate pest, seeding of specific vegetative species could be implemented to control the pests by attracting and/or providing refuges to specific predatory populations as found within push-pull systems (Khan *et al*., 2009). These results indicate that within push-pull systems, knowledge of local invertebrate communities would be important for selecting vegetation

to attract abundant predators rather than predators of low abundance, suggesting that generic planting prescriptions may not always be an effective integrated pest management tool.

Over the two field trial years BSM maintained a greater above-ground invertebrate richness (Figure 6.3a) indicating that increased vegetative richness and a reduction in disturbance supported more stable communities (Proulx *et al*., 2010). Variation in the diversity and community composition of above-ground invertebrates showed that agro-ecosystem invertebrate communities were temporally dynamic in both shorter (between weeks) and longer terms (between years) (Figure 6.4c). The reduction in richness and density in the more conventional (PGH and MNT) and not in the strip tillage cultivation methods indicates that the intercrop was acting as both the overwinter feed resource and as a refuge from physical disturbance during soil preparation (Figure 6.3); these findings are similar to Landis *et al*. (2000) and Wilson *et al*. (1999). Reductions in the evenness and diversity in all cultivation methods between field trial years demonstrates that there were increases in the density of few above-ground invertebrate taxa, which altered the community composition, reducing overall Shannon diversity (Figure 6.1, Figure 6.3).

6.5. Conclusions

The diversity of above-ground invertebrates responded similarly at the two sites. However, the structure of the communities at the two sites responded differently, which was linked to the differences in vegetation composition (Altieri, 1999; Tsiafouli *et al*., 2015).

Different ground cover management and soil preparation practices affect above-ground invertebrate diversity and community composition (Hawes *et al*., 2010). A reduction in disturbance and sowing of non-crop plants provided refuges and increased the availability of food for above-ground invertebrates (Scherber *et al*., 2010); this increased richness and activity/density of invertebrates from the first to the second field trial year, possibly favouring taxa that bred over autumn or overwintered as adults or larvae (Hawes *et al*., 2010).

Strip tilling maize into an intercrop of either ryegrass or a biodiverse seed mix limits the erosion of ecosystem services facilitated by above-ground invertebrate biodiversity (Tiemann *et al*., 2015). It is of intrinsic importance within maize cultivation to limit the

erosion of biodiversity, as unlike most arable crops that are cultivated in rotation, maize is commonly grown year after year in the same field for multiple seasons (Aune *et al*., 2012).

Chapter 7

Linking above- and below-ground invertebrate communities

7. Linking above- and below-ground invertebrate communities

7.1. Introduction

Above- and below-ground relationships are regulatory forces within terrestrial landscapes (Bardgett *et al*., 2005; Li *et al*., 2015), and are intrinsically linked (Scheu, 2001). These linkages, like above- and below-ground communities, are known to vary both spatially and temporally (Bardgett and Van der Putten, 2014). Despite this knowledge, the numbers of simultaneous studies of local above- and below-ground biodiversity are still too limited to reveal any general patterns or theoretical links between these two communities (De Deyn and Van der Putten 2005; Li *et al*., 2015). Furthermore, little is known about the consequences of changes in community dynamics on above- and below-ground interactions or ecosystem services (De Deyn and Van der Putten, 2005). This chapter explores the relationship between above- and below-ground invertebrate community composition and functionality and how these are affected under contrasting maize cultivation practices.

Plants and their derivatives provide the primary food source for above- and below-ground arthropod communities (Hirsch *et al*., 2009). The concept of feedback has often been used to explain plant-invertebrate community dynamics (Hawes *et al*., 2009; Scherber *et al*., 2010). The invasiveness of plants in grasslands is related to the ability of invading species to promote positive feedback, whereas negative feedback contributes to rarity (Bardgett *et al*., 2005). In the current study, the differences in vegetation diversity within the different maize cultivation techniques will be used to test above- and below-ground linkages. De Deyn and Van der Putten (2005) found that, although context dependent, higher trophic levels in the above- and below-ground habitats increase in abundance with plant diversity. De Deyn and Van der Putten (2005) concluded that changes in resource availability and consumption by lower trophic levels affect the next trophic level. This occurs because local biodiversity within a trophic level is driven both bottom-up (competition for resources) and top-down (control by predators or pathogens) (Prather *et al*. 2013; Landis *et al*., 2008); it is this that is hypothesised to link the above- and below-ground invertebrate communities.

Diversity has been thought to be a prerequisite for the maintenance of stability, resistance and resilience of ecosystem services (De Deyn and Van der Putten, 2005). Theoretical studies of how biodiversity relates to ecosystem stability are embedded in food-web modelling (Bagdassarian *et al*., 2007). However, approaches differ according to the above- or below-ground focus of the studies. Below-ground, detritus-based models focus on

nutrient and energy flow, whereas above-ground primary productivity driven models concentrate on bottom-up and top-down control effects in food chains (Bagdassarian *et al*., 2007). A more efficient approach is to link the above- and below-ground through a dynamic approach, which incorporates functional diversity (De Deyn and Van der Putten, 2005). It is also important to understand the changes in functional composition and how these act as important drivers of ecosystem services (Bardgett *et al*., 2005; Prather *et al*., 2013). Studies that have investigated above- and below-ground invertebrate community interactions have shown links between functional diversity which stabilises productivity by enhancing resource use through reducing fluctuations in top-down control (De Deyn and Van der Putten, 2005), but little is known about these forces within maize cultivation systems.

In natural terrestrial ecosystems most above-ground primary production enters the below-ground system without being consumed by herbivores, and thus fluxes of energy and matter through below-ground (detrital) food webs are larger than through above-ground (grazing) food webs (Hyodo *et al*., 2010). Through the use of meta-analysis of global data, Freschet *et al*. (2013) quantified the relative roles of plant litters from roots and shoots to the composition of labile organic matter. Freschet *et al*. (2013) showed that below-ground, litter is a driver of ecosystem organic matter dynamics, and that the relative inputs of litter strongly control the overall quality of the litter entering the decomposition system. In addition, above- and below-ground herbivores can also enhance decomposer activity and, consequently, nutrient availability to the plants by selectively consuming different plant species (De Deyn and Van der Putten, 2005).

Spatial scales of changes in above- and below-ground invertebrate diversity are important for understanding the nature of relationships between plant and soil communities and the functional role of linkages between above- and below-ground invertebrate diversity (Bardgett *et al*., 2005). It has been found that there is often a decoupling of the composition of above- and below-ground invertebrate communities over spatial scales (Eisenhauer *et al*. 2011; Baur *et al*., 1996; Tsiafouli *et al*., 2015). Globally, diversity peaks towards the Equator for large above-ground organisms but not for small (mainly below-ground) organisms, suggesting that there are size-related biodiversity gradients in global above-below ground linkages (De Deyn and Van der Putten 2005). At local scales, it is understood that above- and below-ground invertebrate interactions drive ecosystem

properties, however, it is unclear how these local interactions scale-up to regional or global scales (De Deyn and Van der Putten, 2005).

Consideration of temporal scale is crucial to our understanding of above–below ground relationships and their significance for ecosystem properties (Bardgett *et al*., 2005). Relationships between above- and below-ground communities operate over a hierarchy of temporal scales, ranging from days to millennia, with differing consequences for ecosystem structure and function (Bardgett *et al*., 2005). The effects of above-ground communities on below-ground interactions, and *vice versa*, are not easily predicted and a major challenge is to unravel their context dependency (Bardgett and Van der Putten, 2014). These are related to abiotic factors that interact with the biotic factors to drive ecosystem properties and the time scales in which these operate (Bardgett *et al*., 2005). For example, changes in below-ground communities during succession feedback have been found to affect plant communities through a variety of mechanisms (Bardgett *et al*., 2005). One of these mechanisms is the build-up in the abundance, activity and complexity of soil food webs, which positively feeds back to the plant community through improvements in rates of nutrient recycling (Bardgett *et al*., 2005). It is understood that this build-up of below-ground communities becomes more efficient in nutrient cycling as succession proceeds, leading to greater retention of nutrients in the system (Bardgett *et al*., 2005, Prather *et al*. 2013). However, the numbers of species interacting and their interdependency depends strongly on the spatial and temporal scale considered (De Deyn and Van der Putten 2005).

7.1.1. Hypotheses, aims and objectives

This chapter further instigates the responses of above- and below-ground community composition to changes in vegetation dynamics over temporal scales. This chapter also investigates how functional composition was affected by different maize cultivation techniques. The goal was to identify linkages between above- and below-ground community and functional composition in response to cultivation practice.

H_1= Increases in vegetation cover drive above-ground community composition

H_1= Increases in vegetation cover drive below-ground community composition

H_1= Increases in vegetation cover drive above-ground functional composition

H_1= Increases in vegetation cover drive below-ground functional composition

7.2. Material and methods

7.2.1. β-diversity

β-diversity can be used as a measure of the similarity of assemblages between sites, cultivation methods and changes over time (Koleff *et al*., 2003). This application of β-diversity is often termed differentiation diversity and is synonymous with measuring the extent of change in community composition. β-diversity was calculated based on the counts of above- and below-ground invertebrates collected at Bow during summer 'cultivation' sampling points in both field trial years. The function 'betadiver' in R-package 'vegan' was used to compute β-diversity (Section 4.2.3). Correlations with experimental and vegetative factors were computed using R-package 'vegan' function 'envfit' (Section 4.2.3).

7.2.2. Functional composition

Invertebrates recovered from Fakenham and Bow, at all sampling times, were allocated to functional groups based on ecological knowledge (Table 7.1). The distribution of functional density did not conform to normality assumptions. Invertebrate abundance was $\log_{10}$ transformed and found to be negatively distributed. To ensure analysis of data was robust, data was analysed using negative binomial general linear regression analysis to correct for dispersion before analysis of variance. Analysis of variance was used to determine experimental factor (site, year, cultivation method etc.) effects on functional density. Tukey HSD post-hoc tests were used to identify significant differences between cultivation methods. Non-metric multidimensional scaling in the R-package 'vegan' was used to test for effects of experimental factors and vegetative variates on above- and below-ground invertebrate functional composition.

7.3. Results

7.3.1. $\boldsymbol{\beta}$-diversity

Above- and below-ground invertebrate β-diversity, calculated from the Bow field site summer cultivation count data, was significant between 2013 and 2014 (Figure 7.1, r^2= 0.21, P =0.001 0.01, r^2= 0.17, P = 0.01 respectively). The β-diversity of the above-ground invertebrates were also significantly different among cultivation methods (r^2= 0.06, P = 0.01 respectively). However, this was not the case for below-ground β-diversity (r^2= 0.16, P = 0.102). Whilst these results are statistically significant the r^2 values for both the above- and below-ground $\boldsymbol{\beta}$-diversity were very low indicating that a large amount of variation remains unexplained. Although the below-ground community composition was

not significantly different among cultivation methods it did explain a similar proportion to the observed difference in community composition between the two field trial years. As such, the change in community composition between field trial years and cultivation methods has been looked at in more detail (Figure 7.1).

Table 7.1 Functional groups to which above- and below-ground invertebrate taxa were assigned

Abbreviation	Functional Group	Reference
BA	Bacterivores	Crotty, 2011
CFP	Colony forming predators	Brewitt *et al*., 2015
CP	Predatory centipede	Ferlian and Scheu, 2015
D	Detritivores	Brussaard, 1998
E	Engineers	Brussaard, 1998
F	Fungivores	Crotty, 2011
LAP	Large arachnid predators	Birkhofer *et al*., 2015
MP	Micro-predators	Crotty, 2011
O	Omnivores	Hyodo *et al*., 2010
PA	Parasitoids	Birkhofer *et al*., 2015
PBL	Predatory beetle larvae	Crotty, 2011
PC	Plant chewers	Walling, 2000
PO	Pollinators	Hoehn, 2008
PS	Plant suckers	Walling, 2000
PB	Predatory beetles	Birkhofer *et al*., 2015

In 2013 the below-ground community composition of BSM was significantly different to the other three cultivation methods, which were not significantly different from each other (Figure 7.1a). However, in 2014 there was a greater similarity in community composition among the cultivation methods (Figure 7.1a). The cover of litter and richness of vegetation increased in 2014; which influenced the increase in similarity between the below-ground communities in the different cultivation methods (Figure 7.1a). The increase in vegetation richness had a greater influence on below-ground β-diversity compared with litter (r^2= 0.02, r^2= 0.04 respectively).

Above-ground invertebrate β-diversity in 2013 was not different between the four cultivation methods (Figure 7.1b). However, in 2014 BSM-PGH, BSM-MNT and RGS-PGH β-diversity were significantly different from each other (Figure 7.1b). Despite these differences between cultivation methods there were no significant differences between the β-diversity of PGH and MNT or RGS and BSM (Figure 7.1b). Increases in vegetation richness in 2014 had a significant effect on above-ground invertebrate β-diversity (Figure

7.1b). These increases in percentage cover by litter were found to be driving the increase in dissimilarity of community composition between cultivation methods (Figure 7.1b).

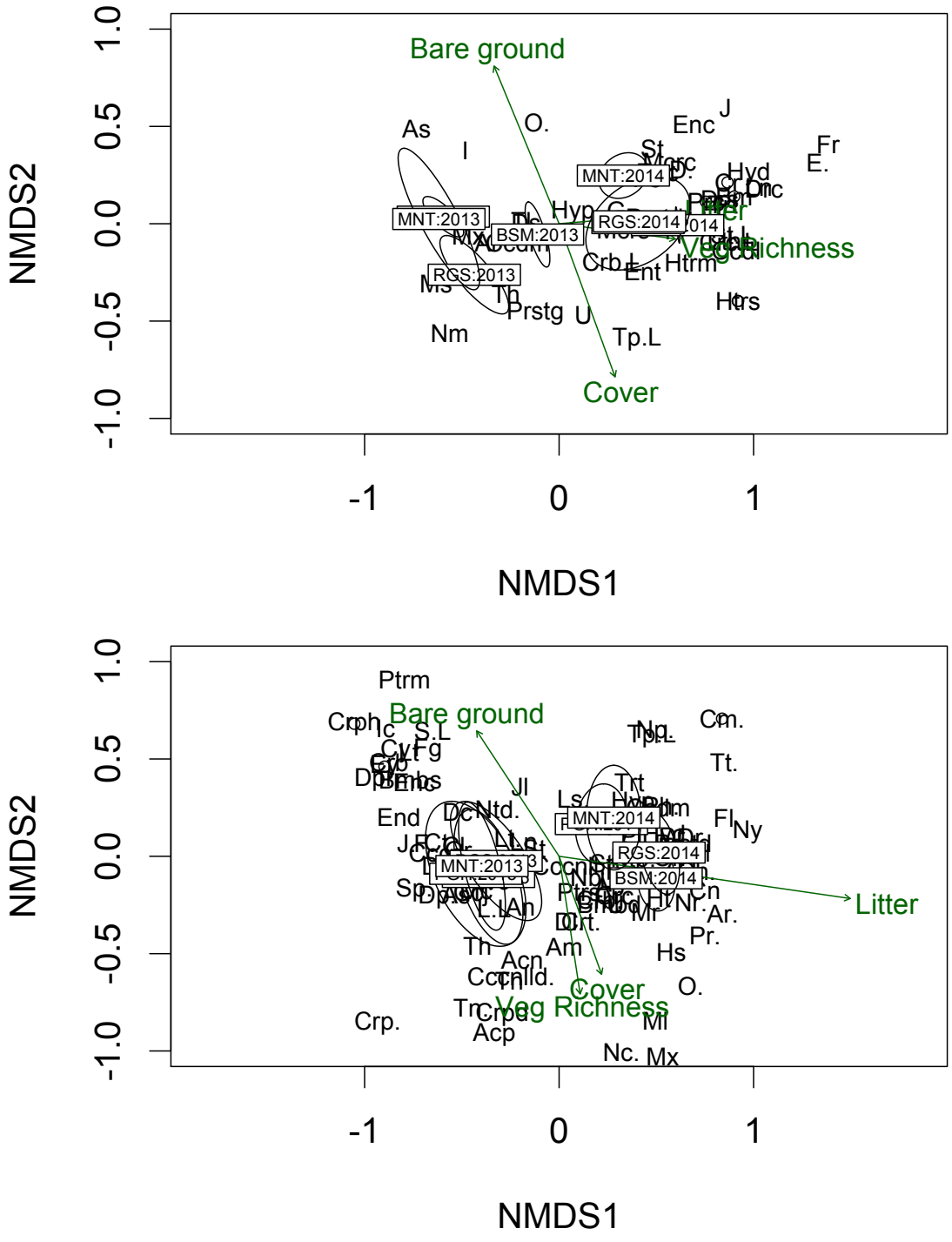


Figure 7.1 Relationship between two-dimensional NMDS of Wisconsin squared root transformation community composition of a) below-ground, b) above-ground. The above- and below-ground invertebrate community β-diversity dissimularity matrix was correlated with changes in vegetation (green arrows where P <0.05) and communty composition of cultivation methods and year (represented by ellipse (± s.e.) from centroids), to understand how the vegetation affected the communties in the different communties. Appendices table

12.4.1 contains abbreviations for the below-ground taxa and appendices table 12.4.2 contains abbreviations for the above-ground taxa.

7.3.2. Functional composition

The count data of above- and below-ground taxa recovered from the different cultivation methods at the two sites in 2013 and 2014 were allocated to different functional groups based on literature (Table 7.1). Significant differences in the counts of above- and below-ground functional groups were then tested for significant differences depending on site collected from, cultivation methods and cultivation year (Table 7.2). The density of above-ground functional groups varied among cultivation methods and years (Table 7.2). There were also differences in the density of functional groups at the different sites which also varied depending on field trial year (Table 7.2). Above-ground functional density also varied depending on field site and cultivation method (Table 7.2).

Vegetation beta-diversity was found to have a significant influence on the functional composition of above- and below-ground invertebrate communities. Vegetation β-diversity positively correlated with below-ground functional diversity ($F_{1, 22}$ 12.32, P =0.001, r^2=0.32). Above-ground, increasing vegetation β-diversity also significantly affected functional diversity ($F_{1, 22}$ 13.06, P =0.001, r^2=0.34). However a majority of variation in the functional composition remained unexplained and may be due to other factors having a strong influence on functional composition.

There were differences in the densities of below-ground functional groups depending on field site, cultivation method and year (Table 7.2). Although the overall density of functional groups was greater at Bow compared with Fakenham there was no significant difference in the density of functional groups between site (P >0.05) there were however overall difference in the densities of the different functional groups independent of site (Figure 7.2).

Both the above- and below-ground communities had greater mean densities of predatory beetle larvae (PBL) in the strip tillage cultivation methods (Figure 7.2a, b). Above-ground BSM had greater mean densities of Parasitoids (PA) and phloem feeding taxa (PS) (Figure 7.3b). Below-ground there were greater densities of fungivores (F) found within BSM compared with PGH (Figure 7.2a). Although there were no overall significant differences in the densities of functional groups there were differences between the densities of the

functional groups within the different cultivation methods. Overall, below-ground fungivores (F) were greater in density in the two strip tillage cultivation. Interestingly, fungivores in PGH and MNT were not significantly greater in density of bacterivores, however in the strip tillage cultivation methods they were, indicating a stimulation of the fungal pathway (Figure 7.2a; Nakamoto and Tsukamoto, 2006). Above-ground there were no significant differences in the densities of fungivores and bacterivores, however there were significant differences in the density of fungivores compared with the other functional groups (Figure 7.2b).

Table 7.2 Above- and below-ground invertebrate taxa count data was allocated to functional groups (Table 7.1). The variation in functional group counts were then tested for significant differences between site, cultivation method and sampling year and interactions between them.

	Below-ground			Above-ground			
Functional group density	**df**	***F*-Value**	***P*-Value**		**df**	***F*-Value**	***P*-Value**	
Site	27	62.62	0.000	***	29	45.42	0.000	***
Cultivation method	39	2.45	0.000	***	45	2.18	0.000	***
Year	13	6.65	0.000	***	15	17.38	0.000	***
Block	35	1.56	0.022	*	30	0.55	0.978	
Site*Cultivation method	30	0.79	0.784		43	1.47	0.027	*
Site*Year	9	0.90	0.525		15	6.07	0.000	***
Cultivation method*Year	30	0.62	0.949		41	1.44	0.035	*

Although it is important to understand the differences in the densities of functional groups under different cultivation methods, it is also critically important to understand the relationships between functional groups and how these change with vegetation dynamics. The above- and below-ground functional composition varied with changes in vegetation composition among cultivation methods (Figure 7.3a and b). The BSM below-ground functional community was associated with greater numbers of predatory beetle larvae (PBL), micro predators (MP), detritivores (D) and predatory beetles (PB), indicating an increase in detritivores and thier predators. Above-ground there were significant differences between the functional composition of the two strip tillage cultivation techniques (RGS and BSM) and the two more conventional cultivation techniques (PGH and MNT) (Figure 7.3b). There were also significant differences between the above-ground functional composition of RGS and BSM but no significant difference in functional composition between MNT and PGH (Figure 7.3b). The BSM functional composition was associated with greater vegetative richness, whereas RGS was associated with increased percentage cover by litter (Figure 7.3b). The increase in vegetation richness in BSM was

associated with increases in detritivores (D), predatory beetle larvae (PBL) and parasitoids (PA), as with below-ground this indicates an increase in detritivores and their predators, although parasitoids are often more associated with increases in herbivore densities (Hawes *et al*., 2010). In contrast, MNT and PGH were associated with greater percentage cover by bare ground and greater densities of predatory centipedes (CP) (Figure 7.3b).

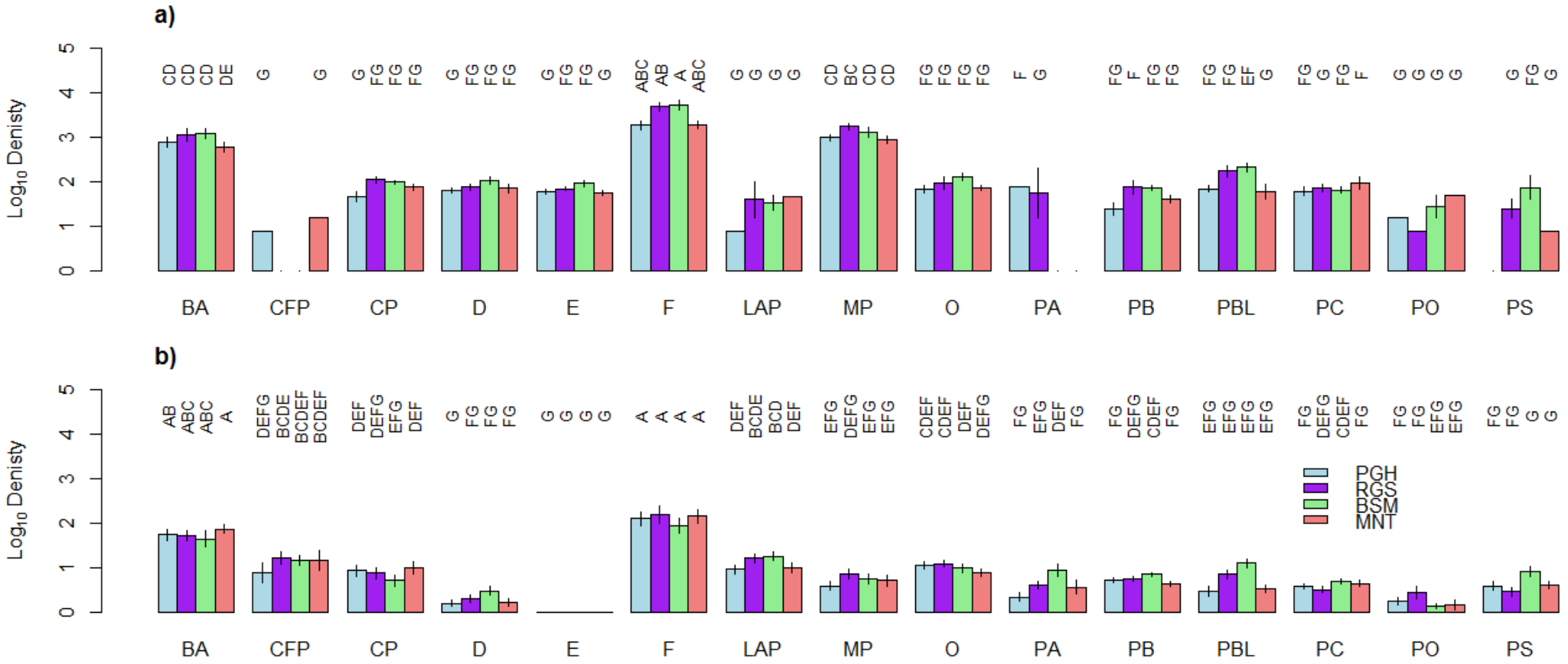


Figure 7.2 Below-ground (a) and above-ground (b) invertebrate functional groups count data form both sites and all sampling times were summed and used to calculate the mean log_{10}denity (± s.e.) of each functional group (Table 7.1) from the four different cultivation techniques (PGH , RGS , BSM , MNT). Functional group densities were Box-Cox transformed to ensure normality before analysis of variance and Tukey HSD post-hoc tests were used to test for true significant differences between cultivation methods. Different letters denote Tukey HSD significant differences (P <0.05).

There were changes in functional composition between the two experiment years (Figure 7.3c and d) with the second field trial year being associated with greater vegetation richness and ground cover by litter. In 2014, the below-ground functional composition was associated with greater densities of micro-predators (MP), predatory beetle larvae (PBL) , detritivores (D), predatory beetles (PB), eco-system engineers (E) and colony forming predators (CFP), whereas 2103 was more associated with bacterivores (BA) and fungivores (F) (Figure 7.4c). In 2014, the above-ground functional composition was associated with greater percentage cover by litter and increases in the density of omnivores (O) which are indicators of stability (Fagan, 1997), but in 2013 functional community was associated with greater densities of micro-predators (MP) (Figure 7.3d).

There were significant interaction differences between cultivation method, field trial years and the functional community composition of below-ground invertebrates (Figure 7.3e). In 2013, there were significant differences in the above-ground functional composition between the four cultivation methods (Figure 7.3e). The above-ground BSM functional community was associated with greater vegetation richness and greater densities of micro-predators (MP), whereas PGH and MNT in 2013 were more associated with a bacterivorous (BA) community. In 2014, there was a greater similarity amongst the functional composition of below-ground invertebrates. In 2014 there were increases in the densities of predatory beetles (PB), detritivores (D) and centipede predators (CP) suggesting successional convergence of below-ground functional communities in response to increased litter (Walker *et al*., 2010).

The above-ground functional composition within individual cultivation methods over the two field trial years was significantly different (Figure 7.3f). In 2013, the strip tillage cultivation methods were significantly different in functional composition compared to the more conventional cultivation methods, which were not significantly different from each other (Figure 7.3f). The two strip tillage cultivation methods were associated with greater vegetation richness cover which supported greater densities of detritivores (D), micro-predators (MP) and parasitoids (PA). In contrast, under PGH and MNT greater densities of bacterivores (BA) were recovered (Figure 7.3f). In 2014 however, there was a high degree of overlap between the above-ground trophic composition between PGH and MNT which was associated with increases in percentage bare ground and fungivores (F). However, in 2014 RGS and BSM were associated with increases in cover by litter and increases in the density of omnivores (O) which often indicate of greater stability (Fagan, 1997).

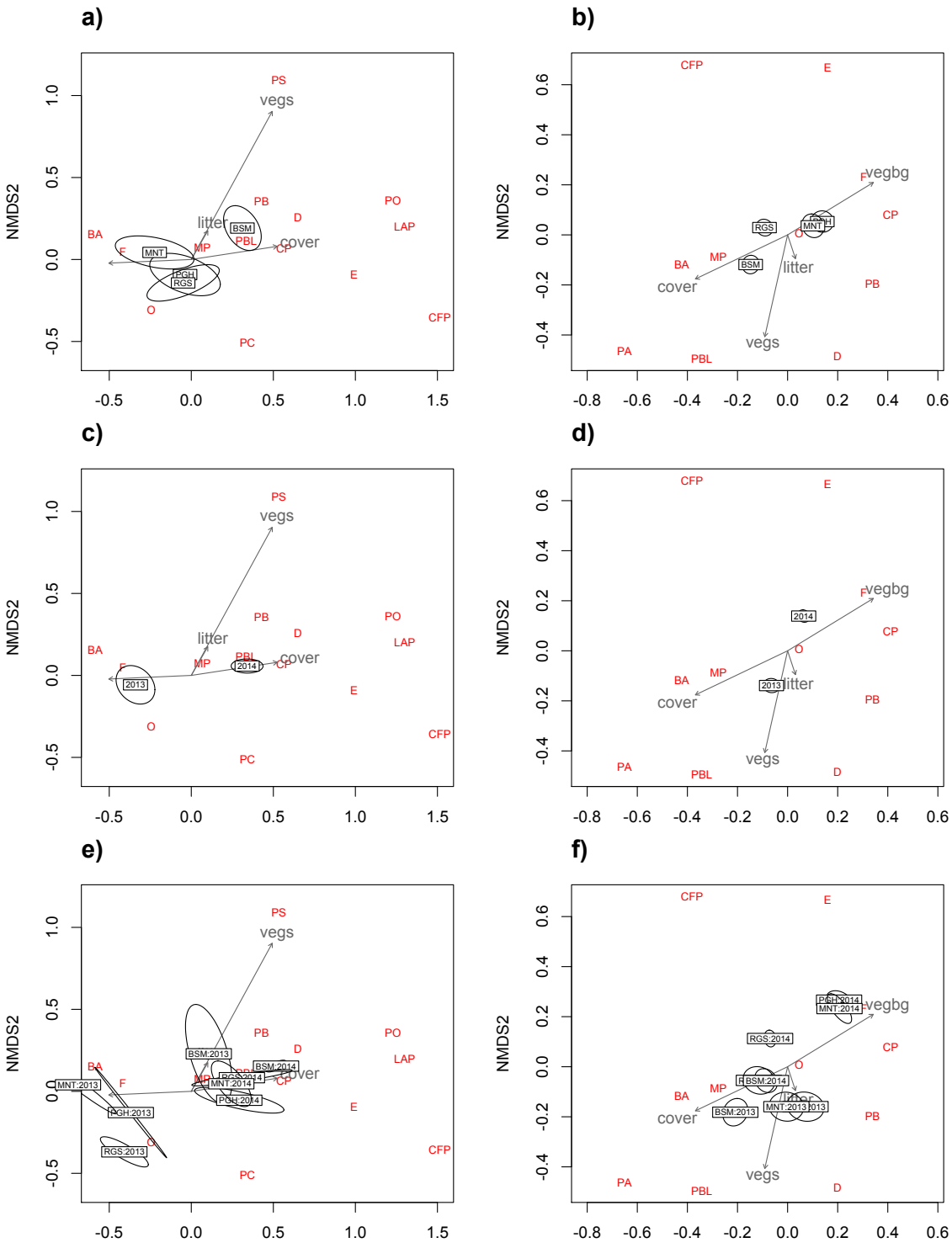


Figure 7.3 Relationship between two-dimensional NMDS Wisconsin squared root transformed functional (Table 7.1) composition used to test for differences in a) below- and b) above-ground functional composition between cultivation methods, c) below- d) above-ground functional composition between field trial years, e) below- f) above-ground functional composition between field trial years and cultivation methods. Invertebrate functional community euclidean dissimilarity matrix was calculated from functional group

count data and correlated with changes in vegetation (grey arrows where $P < 0.05$) and experimental factors (represented by ellipse (± s.e.) from centroids).

7.4. Discussion

7.4.1. *β*-diversity

This is the first study to examine simultaneous changes in above- and below-ground arthropod community composition under contrasting maize cultivation techniques. The composition of arthropod communities changed depending on cultivation method and field trial year (Figure 7.1). Differences in the responses of above- and below-ground invertebrate communities to changes in vegetation show that there was an idiosyncratic response of the two communities to changes in resource availability (De Deyn and Van der Putten, 2005), which may be linked to species specific responses above-ground and more general community responses below-ground (Hawes *et al*., 2010; Scherber *et al*., 2010).

Below-ground, the dissimilarity in arthropod community composition among cultivation methods reduced from 2013 to 2014, but above-ground there was an increase in the dissimilarity of the arthropod communities (Figure 7.1). These differences in response of the above- and below-ground communities to changes in vegetation (Hawes *et al*., 2010; Scherber *et al*., 2010) and successional dynamics (Walker *et al*., 2010) can be attributed to the above-ground invertebrate community's greater dispersal efficiency making this community more effective at exploiting plant species specific relationships. The below-ground community was both restricted in dispersal ability by habitat and morphology (Mitchell, 1970). Greater dispersal efficiency of individuals in the above-ground community allowed these taxa to exploit spatial changes in resource availability quicker than that of the below-ground community, altering community composition (Baur *et al*., 1996; Tsiafouli *et al*., 2015). In contrast, below-ground, existing taxa were able to exploit resources quickly competitively excluding immigrants (Vandegehuchte *et al*., 2015).

The above-ground community was influenced by all measured changes in vegetation, whereas the below-ground was influenced by changes in vegetation richness which positively co-varied with increases in percentage cover by litter (Figure 7.1). However, it is evident that below-ground increases in vegetation richness and cover by litter reduced the differences in community composition among cultivation methods. In contrast, the differences in above-ground arthropod community composition among cultivation methods increased. These results highlight that percentage cover by litter was a key driver of the

above-ground arthropod community composition, but below-ground community composition was more influenced by the diversity of vegetative resources and their derivatives (Figure 7.1), similar to findings by Hirsch *et al*. (2009).

The observed differences in the response of the above- and below-ground community composition could be attributed to increases in vegetation richness and litter improving organic matter quality and quantity (Hättenschwiler *et al*., 2005). Below-ground, increases in the diversity of plant resource available to the invertebrate community, through increases in vegetation richness, provided sufficient resources to increase the abundance of existing populations that were common to all cultivation methods (Hättenschwiler *et al*., 2005). This competitively excluded migrants, in agreement with the intermediate disturbance hypothesis (McCabe and Gotelli, 2000; Huston, 1979; Ottosson *et al*., 2014). In contrast, above-ground, increases in percentage cover by litter and vegetation richness attracted specialists and their predators to the strip tillage cultivation methods, increasing the dissimilarity in community composition compared with the more conventional cultivation methods. These results demonstrate a decoupling of the above- and below-ground arthropod communities, where below-ground were limited by dispersal ability and responded differently to increases in vegetative resource availability (Auclerc *et al*., 2009). The observed decoupling of the response of the above- and below-ground community may also be affected by changes in micro-environmental conditions under strip cropping into a ground cover of either ryegrass or biodiverse seed mix (Nakamoto and Tsukamoto, 2006). Collembola and Acari are known to be sensitive to changes in micro-environmental conditions such as changes in the cover by vegetation (Lindo and Visser, 2004; Chen, 2014).

These differences in the response of the above- and below-ground communities could explain the increases in similarity of communities between cultivation methods; where there were increases in vegetation richness the abundance of Collembola and Acari were increased to account for a similar proportion of the community as the communities under the more conventional cultivation methods. Although not measured, it should also be considered that through the increase in vegetation richness in 2014, below-ground, there may have been a change in the fungal to bacteria ratio in the strip tillage cultivation methods more akin to that found in the more conventional cultivation techniques, again reducing the difference in community composition between cultivation methods.

7.4.2. Functional density

Differences in density of functional groups between cultivation methods can be attributed to the quantity and quality of resources available for both the above- and below-ground communities as a general trend was found for decomposer and predatory groups to be greater in mean density under strip tillage with a biodiverse seed mix (Table 7.2, Figure 7.1). In the first field trial year all cultivation methods started with an invertebrate community that was a remnant from the previous maize crop, a 'baseline' community. During the cultivation season, once the maize cultivation techniques had been established, there were increases in the densities of invertebrates and their functional groups, especially in the strip tillage into ground cover management techniques (Figure 7.3a and b). The increase in functional density was linked with increases in the diversity and quantity of vegetative resources available within the cultivation system. This is coupled with decreases in the physical disturbance by ploughing and the increased availability of refuges made the strip tillage cultivation techniques better able to maintain more dense populations supporting ecosystem services (Stockdale *et al*., 2006; Bardgett and Van der Putten, 2015)

The strip tillage into a biodiverse seed mix ground cover was significantly different in above- and below-ground functional composition to the other three cultivation methods (Figure 7.3a and b). The greater mean density of parasitoids and detritivores above-ground, and micro-predators and predatory beetle larvae below-ground indicating that by increasing the vegetative diversity within maize cultivation systems there can be increases in the density of detritivores and predators (Nakamoto and Tsukamoto, 2006). These ecosystem functions facilitated by the invertebrate community are important for recycling of nutrients and pest control (Prather *et al*., 2013; Landis *et al*., 2008; Bardgett *et al*., 2005) and have been shown to link above- and below-ground communities (Bardgett and Cook, 1998; Scheu, 2001).

Below-ground functional density and composition was found to be driven by increases in quantity and quality of vegetative resources and their derivatives entering the system. In contrast the above-ground functional community was more influenced by the direct plant resources within the system (Figure 7.3). These results support the finding by Bardgett *et al*. (1998) that there are complex interactions between the above- and below-ground communities with a certain amount of decoupling. Bardgett *et al*. (1998) also noted that the directions and magnitude of these effects are often unpredictable because several

mechanisms are often involved, and because of the inherently complex nature of the soil food-web.

7.5. Conclusions

Changes in the above- and below-ground invertebrate communities showed a certain amount of decoupling in response to differences in vegetation composition (Bardgett *et al*., 1998). These types of changes are temporally linked to shifts in the ratio of bacteria to fungi over short periods (Bardgett *et al*., 2005; Pausch *et al*., 2015), which are influenced by ploughing or tillage (Hendrix *et al*., 1986; Adl *et al*., 2006).

Independent of spatio-temporal differences, the below-ground invertebrate β-diversity and functional structure was influenced by the diversity and quantity of resources within the cultivation system (Bardgett *et al*., 1998). In contrast, above-ground β-diversity and functional structure were influenced by the diversity and availability of plant resources (Hawes *et al*., 2009).

Increases in the mean densities of predators and detritivores indicate a strengthening of top-down and bottom-up forces within the strip tillage cultivation systems (Prather *et al*., 2013; De Deyn and Van der Putten, 2005; Nakamoto and Tsukamoto, 2006). This shows that ecosystem functionality was greatly increased through reduced disturbance and increases in non-crop resources (Peckarsky *et al*., 2014).

Chapter 8

Invertebrate food webs; a stable isotope approach

8. Invertebrate food webs; A stable isotope approach

8.1. Introduction

Ecosystems contain many species that are connected by their feeding interactions across multiple trophic levels (Elton, 1927; Brose and Scheu, 2014). These interactions make complex food webs (Brose and Scheu, 2014; Allesina *et al*., 2008). Food webs have been analysed using descriptions of trophic links or energy and mass flow among food web compartments (Pausch *et al*., 2015; de Ruiter *et al*., 1995; Thiele-Bruhn *et al*., 2012; Huddson *et al*., 2012; Reuman *et al*., 2008). These networks of complex interaction are similar across both marine and terrestrial habitats and can be explained by general physical principles (Brose and Scheu, 2014; Pacella *et al*., 2013).

The relationship between consumer and resource body masses constrain feeding interactions in arthropod food webs (Turnbull *et al*., 2014). These biometric constraints influence the number of interactions, the trophic position of an individual and how individuals interact (Brose and Scheu, 2014; Reuman *et al*., 2008). However, disentangling trophic interactions in the soil has posed a challenge for decades due to the complexity of below-ground food webs, especially due to the difficulty in observing small sized organisms in an opaque habitat (Coleman *et al*., 2004; Ferlian and Scheu, 2014; Hines *et al*., 2015).

Plants provide the primary carbon source for above- and below-ground communities (Hirsch *et al*., 2009). Differences in photosynthetic pathways give rise to different $\delta^{13}C$ signatures in plant tissues and exudates (Briones *et al*. 2003, Section 2.6) when these plant tissues are consumed the carbon is incorporated into the consumer's body tissue with little fractionation. The majority of arable plant species are C3, which is typical in the UK (Pyankov, 2010). In contrast, maize is a C4 photosynthetic plant, which offers the opportunity to trace $\delta^{13}C$ through the invertebrate food chain to identify invertebrate trophic structure and resource use (Ponsard *et al*. 2000). Stable isotope techniques provide an indirect basis on which to link the above- and below-ground invertebrate communities (Neilson *et al*. 2002; Hyodo, 2015), and to construct food webs that investigate invertebrate carbon use (Crotty *et al.* 2012, Ruf *et al.* 2006; Crotty *et al.* 2014).

Stable isotopes at natural abundance can be used to understand patterns of trophic levels, major energy pathways, functional groups and the width of ecological niches (Brose and Scheu, 2014; Tiunov, 2007; Schmidt *et al*., 2004). Stable isotope techniques have shown

that food web dynamics are predominantly driven by carbon inputs from plants (Pausch *et al*., 2015; Crotty *et al*., 2014; Hirsch *et al*., 2009). The two main sources of carbon inputs to the soil in arable systems are litter; this is the slowly decomposing plant material and rhizodeposits (Pausch *et al*., 2015). In conventional maize cultivation systems, ploughing and tillage annually incorporates vegetation, litter and soil which are thoroughly mixed (Firbank *et al*., 2003; Nakamoto and Tsukamoto, 2006; Hartwig and Ammon, 2002). Furthermore, in temperate regions, when maize is harvested, the field is often left fallow over winter periods. This shifts carbon cycling to be more dependent on root-derived carbon rather than above-ground litter (Drigo *et al*., 2010). Pausch *et al*. (2015) found that from the rhizosphere and bulk soil, a larger proportion of the maize-fixed C4 carbon was transferred to saprotrophic fungi than bacteria. Despite the low soil abundance of saprotrophic fungi, Pausch *et al*. (2015) showed that there was a much higher ^{13}C incorporation and turnover rate than bacteria under conventional maize systems concluding that this was due to the fungi translocating plant derivatives further into the bulk soil. However, ploughing is known to destroy fungi hyphal linkages which may impede the rate at which maize derived carbon is incorporated into the soil and ultimately the above- and below-ground food webs (Stockdale *et al*., 2006).

The applications of stable isotopes in terrestrial ecology was comprehensively reviewed by Staddon (2004), who used $\delta^{13}C$ to understand soil carbon cycling and soil trophic relationships. Unlike carbon isotopes, nitrogen isotopes are fractionated during transmission through trophic chains. This makes nitrogen less convenient for ascribing basal feeding resources, but allows it to be used as an integrating index of many ecological processes by ascribing trophic positioning (Staddon 2004; Albers *et al*. 2006; Tiunov 2007). For example the changes in $\delta^{15}N$ during plant residue degradation are much more pronounced compared to $\delta^{13}C$ (Tiunov, 2007). The biochemical reactions of the nitrogen cycle such as nitrification and ammonification can be accompanied by changes in $\delta^{15}N$ in the tens of ppm range (Tiunov, 2007). The accumulation of heavy nitrogen in food chains is due to the discrimination of the heavy isotope in the synthesis of excreted nitrogen metabolites (Staddon, 2004).

Sample preparation often limits the resolution of stable isotope approaches especially for small bodied, highly abundant taxa such as Collembola and Acari. It can be time consuming to gather sufficient biomass for analysis, and leads to a large sample size being required when investigating mesofauna (Crotty *et al*., 2014). If sample biomass is

insufficient grouping can occur based on ecological knowledge but this can mask the subtleties of the underlying difference in arthropod trophic position and/or primary feeding resource (Jennings *et al*., 1997).

8.1.1. Hypothesis, aims and objectives

This chapter quantifies the isotopic composition of invertebrates under contrasting maize cultivation techniques. The primary goal was to understand how different ground cover management practices influence the resource use and trophic structure of above- and below-ground invertebrate communities. The secondary goal was to understand if the resources used by the invertebrate communities in the conventional cultivation technique (PGH) changed between sampling times during the cultivation season.

H_1=Invertebrate isotopic signatures reflect that of the dominant vegetation in cropping systems
H_1=Invertebrate isotopic signatures change over the cropping season

8.2. Materials and methods

Once specimens had been collected (Section 5.2 and 6.2) and identified (Section 3.4) they were separated into functional groups based on ecological information (Table 7.1) and if collected from above- or below-ground (Appendix Table 12.5.1).

To obtain a sufficient invertebrate biomass for stable isotopic analysis, a group mass of ≥ 90 µg was required. This limited the taxonomic and functional resolution of analysis due to the low invertebrate abundance characteristic of conventional maize systems. This, therefore, resulted in compromises based on ecological knowledge regarding the groupings (Appendix Table 12.5.1). Invertebrates were dried at 60 ºC for 24 hours and weighed using a microbalance (MX5 Mettler, Toledo). If sufficient group biomass was obtained whole invertebrates were analysed using an elemental analyser (Carlo Erba NA2000,CE Instruments, Wigan, UK) linked to an isotope ratio mass spectrometer (20-22 SerCon Ltd, Crewe, UK) to determine invertebrate whole body isotopic ratios of carbon and nitrogen relative to standards. Isotopic ratio calculations were based on Tiunov (2007) and can be found in Section 2.6.

Analysis of variance and Tukey HSD post hoc tests were used to identify significant differences between sites, sampling times, and maize cultivation techniques (full details

Section 3.6). Mean invertebrate isotopic composition (± s.e.) was used to construct isoplots in R-package 'ggplot2' (Wickham, 2009) (Section 3.6). Isoplots were used to understand both the trophic structure and the carbon resource use with a conventional maize cultivation system at different sampling times. The definition of trophic grouping was based on the literature estimate of trophic level enhancement of ca. 3.4 ‰ δ^{15}N (Tiunov, 2007; Albers *et al*., 2006).

8.3. Results

The isotopic composition of invertebrates and their functional groups varied significantly between the two sites (Table 9.1). There were significant differences in δ^{15}N of the above- and below-ground functional groups collected from the two sites but not in δ^{13}C indicating that although the different functional groups were trophically different they were consuming similar resources at the two sites (Table 9.1).

Cultivation method had a significant effect on the isotopic composition of above- and below-ground invertebrates (Table 9.1). In addition, the above-, but not, the below-ground communities were significantly different in δ^{15}N composition between cultivation methods (Table 9.1). This suggests that below-ground there were significant differences in resources the communities used among the different cultivation methods, which may also be affecting trophic structuring under the different cultivation techniques (Table 9.1). There were significant interaction effects on the below-ground δ^{15}N of functional groups depending on which cultivation method and which sampling point they were collected from (Table 9.1). This indicates that over the course of the experiment there were changes in proportions of available resources used by the below-ground community within the different maize cultivation techniques.

Table 8.1 Above- and below-ground invertebrate community $\delta^{13}C$ and $\delta^{15}N$ composition. Differences in the isotopic composition of invertebrates was analysed using analysis of variance and tested for significant differences between sites, functional groups, cultivation methods and sampling periods as well as interaction between these factors.

	Below-ground					Above-ground				
		$\delta^{15}N$		$\delta^{15}C$			$\delta^{15}N$		$\delta^{15}C$	
	df	F-value	*P*-value	F-value	*P*-value	df	F-value	*P*-value	F-value	*P*-value
Site	1	2.36	0.131	4.23	0.045 *	1	11.53	0.001 ***	10.74	0.001 **
Functional group	12	13.05	0.000 ***	9.10	0.000 ***	14	16.33	0.000 ***	4.72	0.000 ***
Cultivation method	3	0.75	0.528	4.26	0.009 **	3	3.93	0.009 **	4.52	0.004 **
Period	5	9.94	0.000 ***	8.95	0.000 ***	1	0.02	0.901	2.51	0.114
Site*Functional group	6	3.82	0.003 **	0.58	0.744	11	5.30	0.000 ***	1.71	0.072
Site*Cultivation method	3	3.51	0.022 *	2.11	0.111	3	0.33	0.806	0.04	0.988
Functional group*Cultivation method	23	5.12	0.000 ***	1.58	0.087	32	2.27	0.000 ***	0.49	0.991
Functional group*Period	1	0.67	0.417	0.12	0.734	6	1.49	0.183	1.10	0.360
Cultivation method*Period	24	3.08	0.000 ***	2.66	0.002 **	1	0.95	0.330	0.02	0.879
Site*Functional group*Cultivation method	5	4.90	0.001 ***	2.26	0.062	13	0.80	0.662	0.76	0.704
Functional group*Cultivation method*Period	3	4.45	0.007 **	2.58	0.063	4	1.50	0.204	0.05	0.995

8.3.1. Above- and below-ground invertebrate resource use

Soil and maize were significantly different from each other in isotopic composition (Figure 8.1). There were also significant differences between soil, maize and vegetation; however there was no significant difference in the isotopic signature of litter compared with soil (Figure 8.1). These results suggest that the soil, maize and weed vegetation can be used as tracers of carbon and ultimately resources used by invertebrate communities.

There were a number of invertebrate taxonomic groups that were not significantly different in $\delta^{13}C$ isotopic composition to either the maize or soil and non-crop vegetation indicating that these taxa consumed carbon from both C3 and C4 derived resources. However, Enchytraeidae, Predatory mites, Earthworms, Geophilidae, Julidae, Lepidoptera Larvae and Entomobryidae were significantly different in $\delta^{13}C$ isotopic composition to C3 vegetation suggesting that these taxa consumed soil, litter and maize derived carbon. A majority of the above taxa are well known feed within detrital pathways (Table 7.1), however, Lepidoptera larvae were also found to be consuming carbon from C3 and C4 pathways indicating an generalist feeding behaviours of these herbivores.

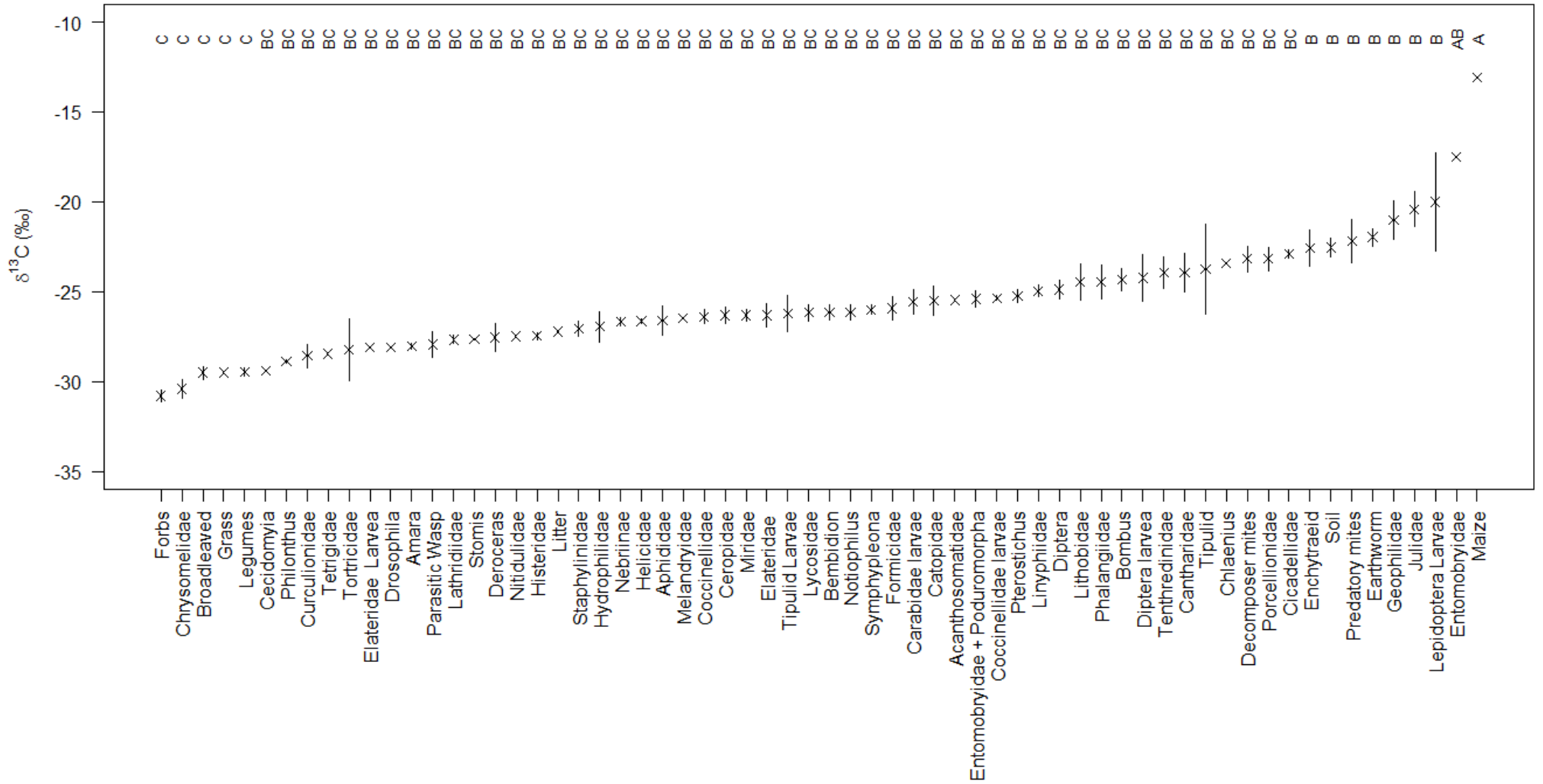


Figure 8.1 Mean (± s.e.) $\delta^{13}C$ composition of each invertebrate taxonomic group. Isotopic signatures with the same letter are not significantly different.

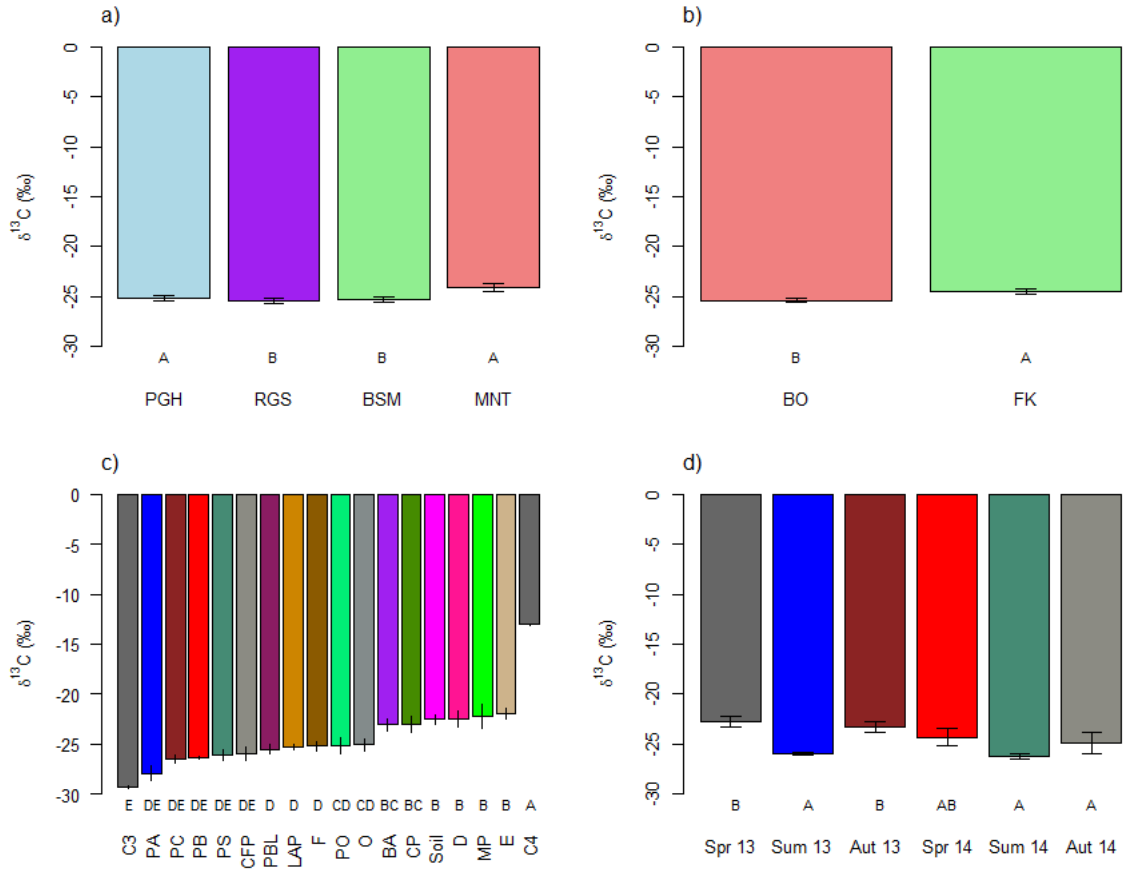


Figure 8.2 Above- and below-ground invertebrate community mean $\delta^{13}C$ (± s.e.) composition a) in each cultivation method b) at each site c) for each functional group d) at each sampling point. $\delta^{13}C$ values with the same Tukey HSD letters are not significantly different. Functional group abbreviations can be found in Table 7.1.

The above- and below-ground communities in PGH and MNT had significantly different isotopic signatures to RGS and BSM, which exhibit a more depleted $\delta^{13}C$ signature (Figure 8.2a), indicating that taxa in RGS and BSM were feeding on C3 derived resources. The two field trial sites had significantly different community $\delta^{13}C$ signatures; the Bow community signature was more depleted compared to Fakenham (Figure 8.2b), which was probably due to differences in historical management and surrounding vegetation at the two sites. There were differences in $\delta^{13}C$ composition of the functional groups, indicating significant differences in resource use between the functional groups (Figure 8.2c). There were significant differences in the $\delta^{13}C$ isotopic composition of maize and colony forming predators, predatory beetles', bacterivores', predatory beetle larvae, predatory centipedes', detritivores' and fungivores' indicating that these functional groups did not obtain their carbon from C4 maize, but were utilising the other available resources (Figure 8.2c). There

were significant differences between sampling times and whole community isotopic composition (Table 9.1 and Figure 8.2d), the community recovered during the summer sampling periods was significantly more depleted in $\delta^{13}C$ in comparison to the spring and autumn sampling points in 2013 (Figure 8.2d), indicating that during the summer sampling a majority of resource the invertebrate community exploited was not derived from maize.

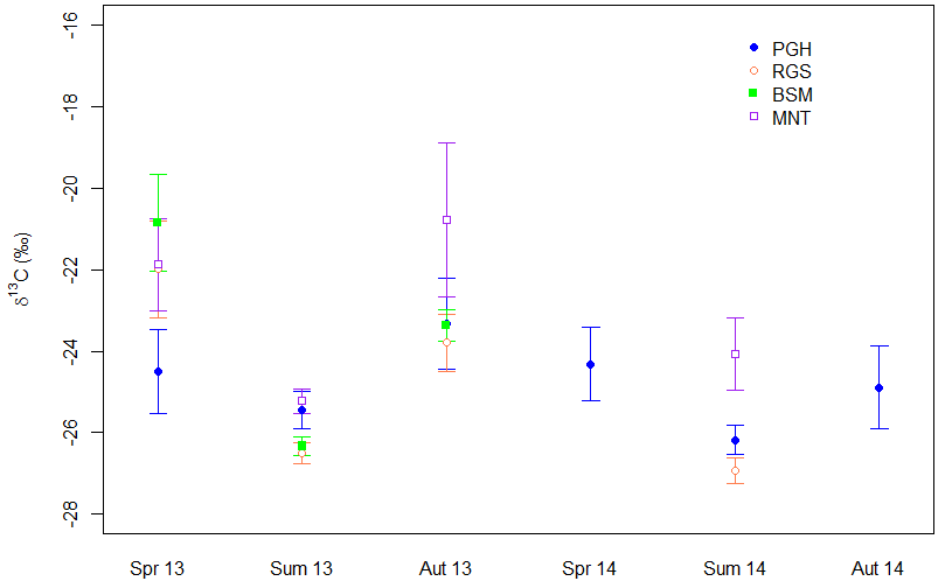


Figure 8.3 Above- and below-ground invertebrate community mean $\delta^{13}C$ (± s.e.) signatures from the different cultivation methods (PGH , RGS , BSM , MNT) at the different sampling times. Along the x-axis sampling points are denoted as Spr 13 and 14 is Spring pre-cultivation sampling in 2013 and 2014, Sum 13 and 14 is summer sampling during cultivation in 2013 and 2014 and Aut 13 and 14 are the post maize harvest sampling point in 2013 and 2014.

The relationship between cultivation method and seasonal fluctuation in the whole community $\delta^{13}C$ composition is an import indicator of communities switching feeding resources (Figure 8.3). At the initial pre-cultivation sampling (spring 2013) before the maize was drilled the isotopic composition of the invertebrate communities showed no significant differences between RGS, BSM and MNT. Surprisingly, due to the predominance of maize derived litter and low C3 plant cover, the PGH community was significantly more depleted compared with the other three communities (Figure 8.3). Once cultivation had taken place and the maize had been drilled there were significant differences in the whole community isotopic composition between cultivation methods (Figure 8.3). The invertebrate communities collected from the strip tillage cultivation methods (RGS and BSM) were significantly more depleted compared with the two more

conventional cultivation methods (PGH and MNT) at this sampling time, indicating that taxa in the strip tillage cultivation techniques consumed a greater proportion of C3 derived carbon. Post-harvest (Autumn 2013) the isotopic signature of the invertebrate communities recovered from the different cultivation methods were significantly more elevated $\delta^{13}C$ signature in comparison to the during cultivation communities (Figure 8.3). In 2014 there was a similar trend for the pre-cultivation and post-harvest sampling point to be more elevated in $\delta^{13}C$ compared with the cultivation sampling point. Interestingly, the isotopic signature of the MNT community sampled during the cultivation sampling point in 2014 was significantly more depleted compared with PGH which may be due to difference in soil preparation during cultivation (Figure 8.3). These results highlight that there were temporal changes in the resources used by invertebrate communities during a cultivation season.

8.3.2. Above- and below-ground invertebrate trophic structure

There were significant differences between invertebrate taxonomic groups and their trophic position (Figure 8.4). Using Tiunov (2007), trophic separation of ca. 3.4‰ $\delta^{15}N$ per trophic level there are approximately four trophic levels independent of cultivation method or field trial site (Figure 8.4).

Trophic level one contained grasses, legumes, maize and a number of herbivorous and Omnivorous taxa (Figure 8.1). The second trophic level contained soil as a source of carbon, within this trophic group there was a combination of Fungivorous, bacterivorous and predator taxa indicating that this trophic level contained predatory taxa feeding on trophic level one and primary and secondary decomposers (Figure 8.4). Trophic level 3 contained taxa that were predominantly predatory, although Tenthredinidae, which are often considered pollinators, had the greatest mean $\delta^{15}N$ signature. However, Tenthredinidae are a diverse family, with some Genus being known to predate on other taxa (Willemstein, 1987), because of this there may be a high degree of specialisation at the Genus level which was not detected due to mass limitations. Despite this, there is evidence to suggest due to the large variation in $\delta^{15}N$ signature of Tenthredinidae that there were in fact both pollinators and predators within this group (Figure 8.4).

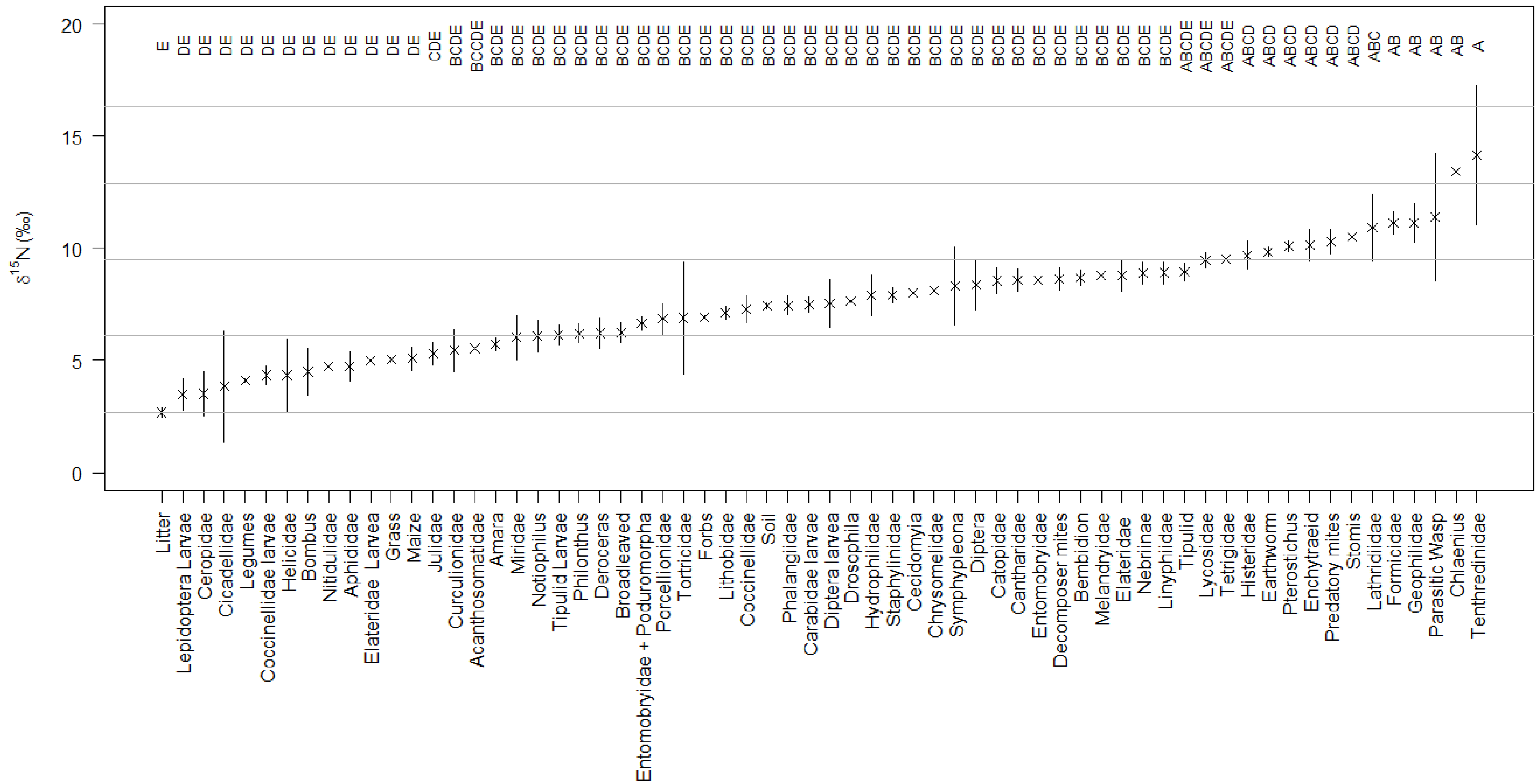


Figure 8.4 Mean $\delta^{15}N$ (± s.e.) signature of each taxonomic group (denoted by number). Isotopic signatures with the same letter are not significantly different. Lines represent trophic levels increasing by 3.4‰ $\delta^{15}N$ per trophic level (Tiunov, 2007) from the lowest mean observed isotopic signature.

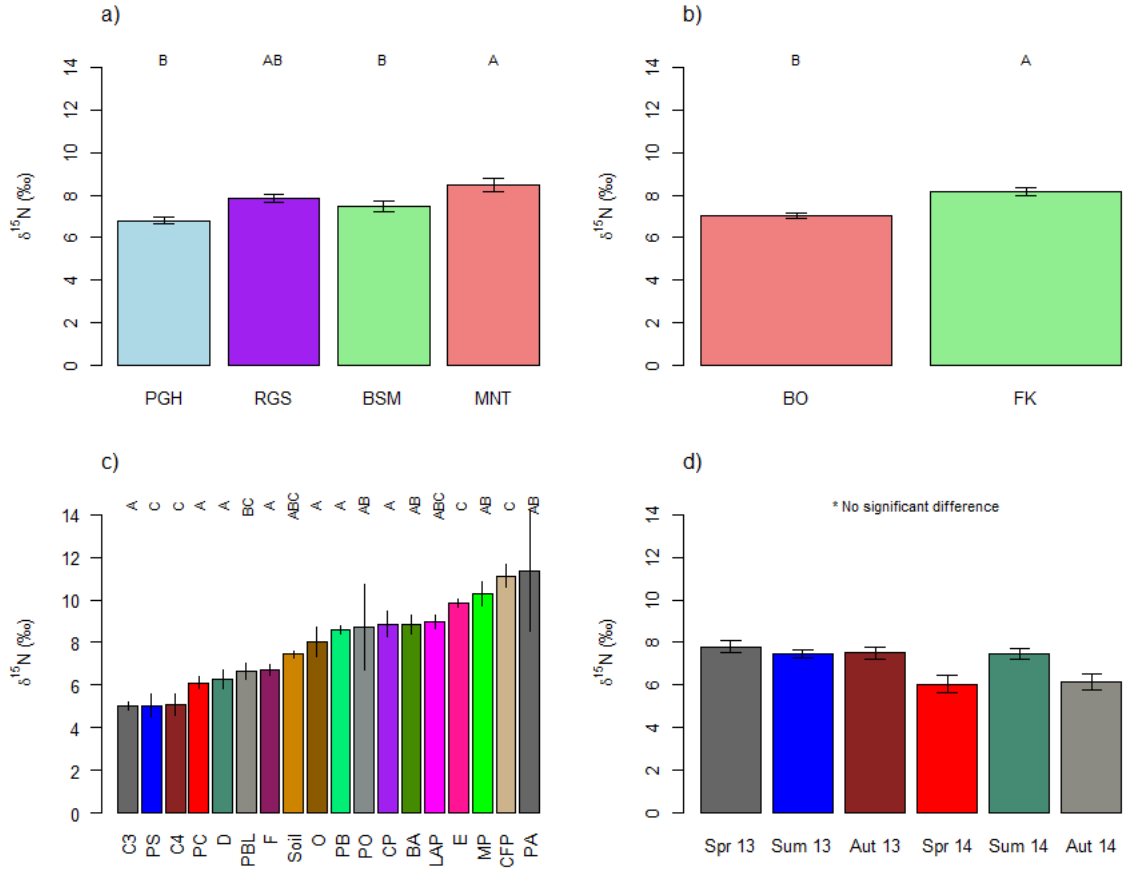


Figure 8.5 Above- and below-ground invertebrate community mean (± s.e.) $\delta^{15}N$ signatures from a) each cultivation method b) each site c) each functional group d) each sampling point. Community isotopic signatures were calculated from the isotopic signatures of invertebrates within the communities. Isotopic signatures with the same Tukey HSD letters are not significantly different. Functional groups abbreviations can be found in Table 7.1.

The mean $\delta^{15}N$ signature of the MNT invertebrate community was significantly elevated compared with PGH and BSM, but not significantly different RGS (Figure 8.5a). Bow had a significantly lower $\delta^{15}N$ whole community signature compared with Fakenham indicating that there were fewer predators, more consumers or a more even distribution between predators and consumers at the Bow site (Figure 8.5b). $\delta^{15}N$ isotopic composition of functional groups, irrespective of cultivation method, demonstrates that plant suckers, plant chewers and detritivores had low $\delta^{15}N$ signature indicating that these were primary consumers, whereas parasitoids, colony forming predators and micro-predators had high $\delta^{15}N$ signature indicating that these were predators (Figure 8.5c).

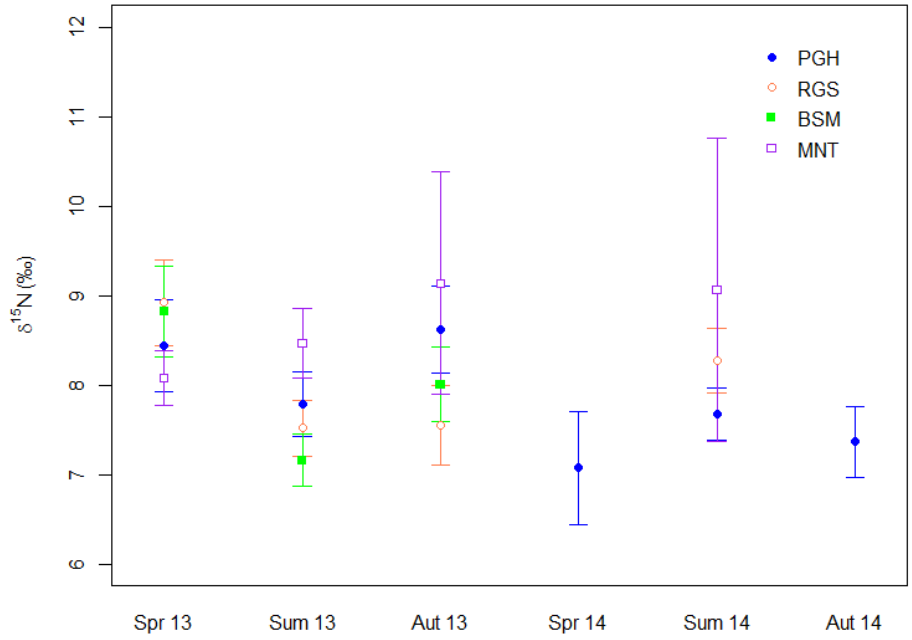


Figure 8.6 Above- and below-ground invertebrate community mean $\delta^{15}N$ (± s.e.) signatures from the different cultivation methods (PGH , RGS , BSM , MNT) and sampling times. Along the x-axis sampling points are denoted as Spr 13 and 14 is Spring pre-cultivation sampling in 2013 and 2014, Sum 13 and 14 is summer sampling during cultivation in 2013 and 2014 and Aut 13 and 14 are the post maize harvest sampling point in 2013 and 2014.

There were significant differences among the trophic compositions of the communities when all cultivation methods were pooled, but no significant difference between sampling times when cultivation methods were pooled (Figure 8.5d). However, the $\delta^{15}N$ signatures of the different invertebrate communities recovered from the different cultivation methods during different sampling times fluctuated (Figure 8.6). At the initial pre-cultivation sampling point (Spring 2013) the RGS invertebrate community had significantly greater $\delta^{15}N$ signature than MNT, indicating that there were more predators present within the RGS community than the MNT community (Figure 8.6). During cultivation (Summer 2013) there were significant differences between RGS, BSM and MNT, where MNT was found to have a significantly greater whole community $\delta^{15}N$ signature, than RGS or BSM (Figure 8.6). There were no significant differences in $\delta^{15}N$ invertebrate isotopic composition of PGH for any of the sampling points over the course of the two year field experiment (Figure 8.6).

8.3.3. Above- and below-ground invertebrate trophic positioning and resource use within conventional maize cultivation

Due to the variation in the isotopic composition of the invertebrate communities between sites and cultivation methods (Figure 8.2 and 9.5) only the invertebrate isotopic compositions of the Bow PGH community were used to evaluate how the isotopic composition of taxa changed at the different sampling points (Figure 8.7 to 9.13).

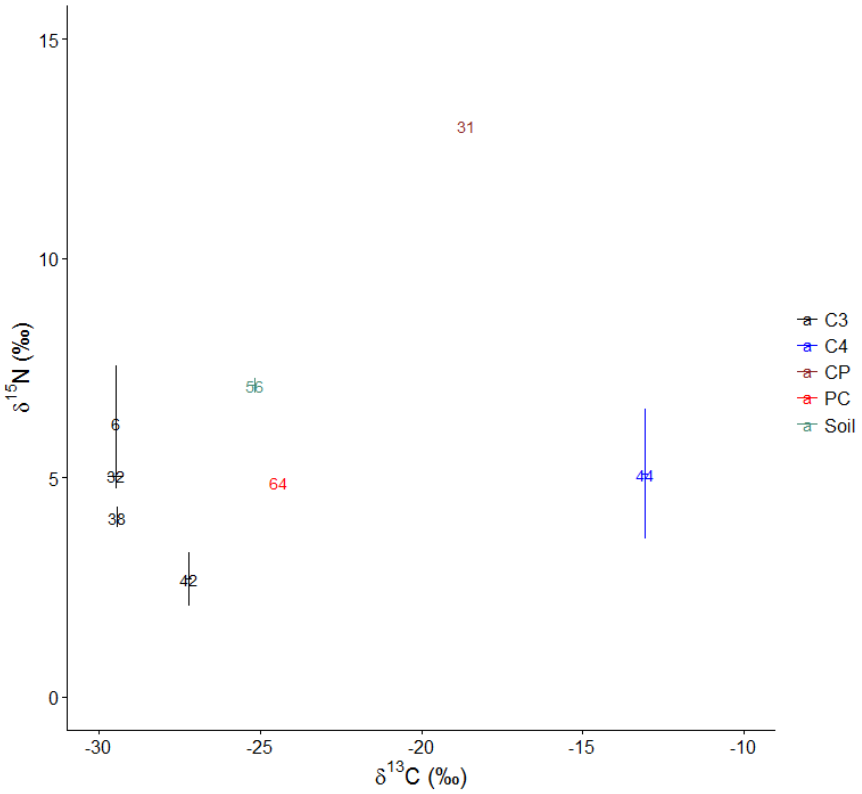


Figure 8.7 Mean (± s.e.) isotopic composition of above- and below-ground invertebrates collected in spring 2013, pre-cultivation, before the maize was drilled in the conventional plough cultivation techniques (PGH). Numbers represent taxonomic groups, and colours represent functional groups. Taxonomic and functional abbreviations are given in Appendix Table 12.5.1. The isotopic composition of invertebrate taxonomic groups collected from Bow was used to calculate mean (± s.e.).

The isotopic compositions of taxonomic groups collected pre-cultivation 2013 within PGH showed that a majority of taxa collected were consuming C3 derived carbon as reflected by their isotopic composition (Figure 8.7). There were differences between below-ground Tipulidae larvae, which are herbivores and were found to be consuming carbon from C3 derived resources, and Geophilidae which had a more elevated $\delta^{13}C$ and elevated $\delta^{15}N$

signature indicating predating on taxa that were feeding on a greater proportion of maize derived carbon (Figure 8.7).

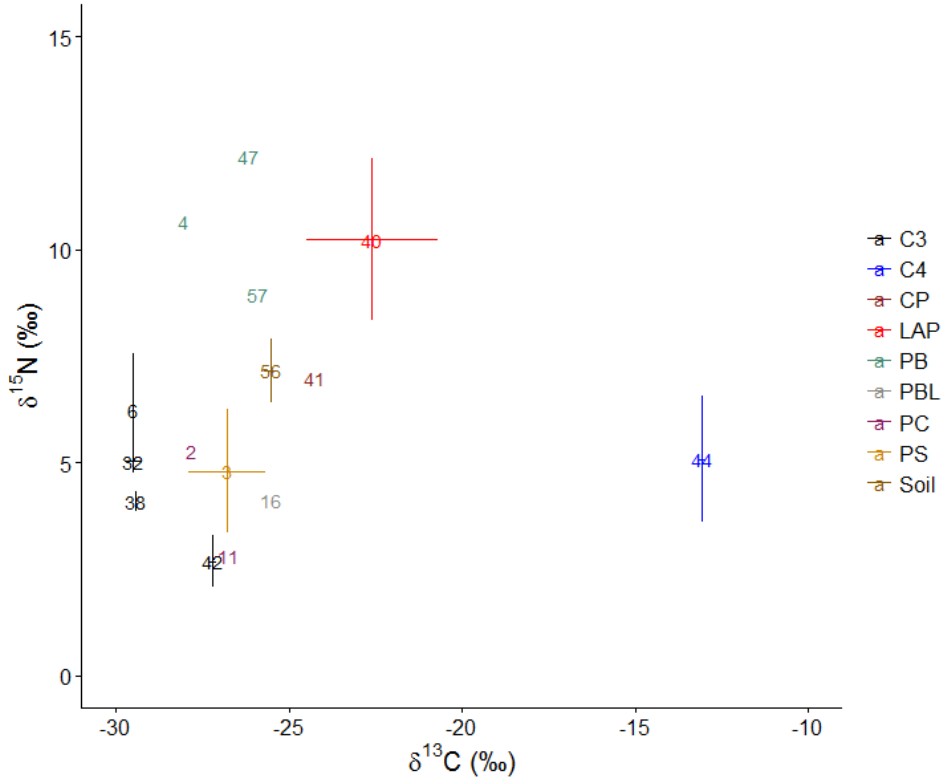


Figure 8.8 Mean (± s.e.) isotopic composition of above- and below-ground invertebrates collected in summer 2013, after maize had been drilled in the conventional cultivation techniques (PGH). Numbers represent taxonomic groups, and colours represent functional groups. Taxonomic and functional abbreviations are given in Appendix Table 12.5.1. The isotopic composition of invertebrate taxonomic groups collected from Bow was used to calculate mean (± s.e.).

After the maize was drilled (Summer 2013), taxonomic groups were found to be feeding from predominantly C3 derived resources under conventional maize cultivation. $\delta^{15}N$ composition indicates three trophic levels; the first trophic level contained herbivores (Amara, Cercopidae and Chrysomelidae larvae (Figure 8.8)). The second trophic level contained Lithobiidae and Staphylinidae which are known predators (Figure 8.8). This second trophic group also contained Linyphiidae, however due to the large variation in $\delta^{15}N$ Linyphiidae could be either feeding in the 2nd trophic level i.e. consuming taxa from trophic level one, two and three or could be exhibiting elevated $\delta^{15}N$ because of intraguild predation (Figure 8.8). In the third trophic level were the predatory adult Carabidae *Bembidion* spp. and *Nebriinae* spp., though like Linyphiidae these could maybe more

elevated in $\delta^{15}N$ relative to the second trophic level due to intraguild predation or through consuming both herbivores and/or predators in trophic level two (Figure 8.8).

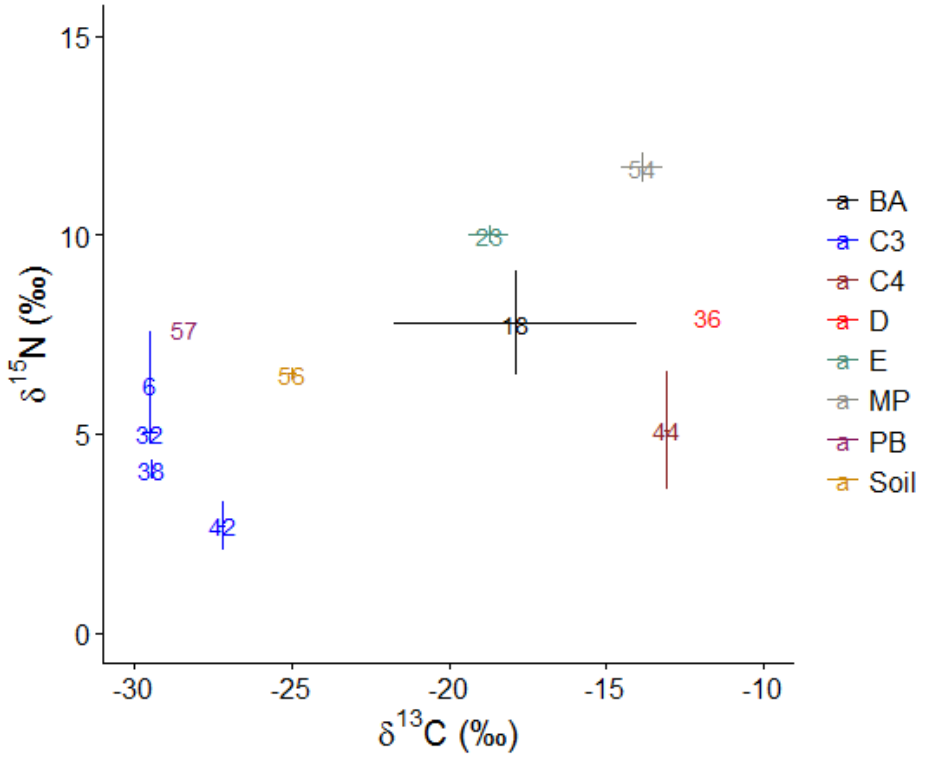


Figure 8.9 Mean (± s.e.) isotopic composition of above- and below-ground invertebrates sampled in autumn 2013, after the maize had been harvested, from the conventional cultivation technique (PGH). Numbers represent taxonomic groups, and colours represent functional groups. Taxonomic and functional abbreviations are given in Appendix Table 12.5.1. The isotopic composition of invertebrate taxonomic groups collected from Bow was used to calculate mean (± s.e.).

There were differences in the resources that taxonomic and functional groups were found to consume under conventional maize cultivation during the post-harvest sampling time in 2013 (Figure 8.9). At the more elevated end of the isotopic spectrum there were a number of taxonomic and functional groups associated with the below-ground detrital food web. For example, decomposer mites, detrital feeding Julidae, micro-predators and earthworms (Figure 8.9) were found to be deriving a significant proportion of their diet from the maize derived resources, as reflected by their isotopic composition. At the more depleted end of the $\delta^{13}C$ spectrum there were Staphylinidae, which were associated with the above-ground herbivorous food web, with a $\delta^{13}C$ similar to that of non-crop vegetation, but with elevated $\delta^{15}N$ above ryegrass reflecting that these were predators (Figure 8.9). The trophic structures of the herbivore and detrital communities were trophically stratified where

Staphylinidae, which are predators, were found to occupy approximately the same trophic level as Julidae, which are not predators. This suggests that, although Staphylinidae are directly feeding on herbivores, Julidae were feeding on maize derived plant matter that has been mediated by bacteria and fungi, increasing the basal $\delta^{15}N$ signal of the detrital community and, therefore, any consumption by higher trophic levels (Figure 8.9).

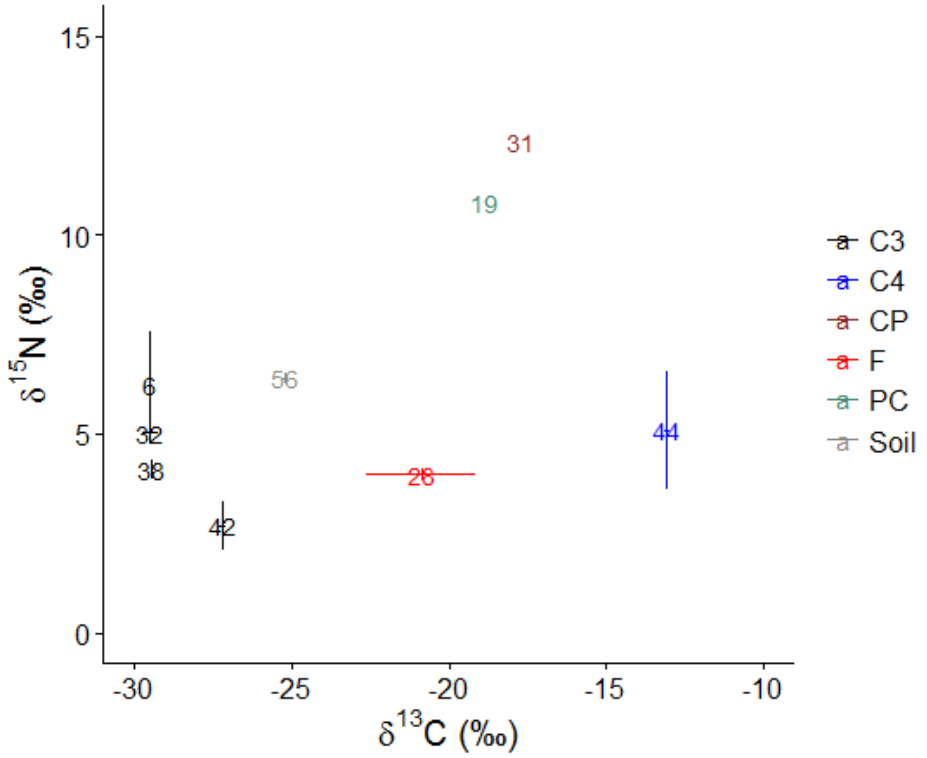


Figure 8.10 Mean (± s.e.) isotopic composition of above- and below-ground invertebrates sampled in Spring 2014, before the maize was drilled, from the conventional cultivation techniques (PGH). Numbers represent taxonomic groups, and colours represent functional groups. Taxonomic and functional abbreviations are given in Appendix Table 12.5.1. The isotopic composition of invertebrate taxonomic groups collected from Bow was used to calculate mean (± s.e.).

At the pre-cultivation (Spring) sampling point in 2014, the isotopic composition of Geophilidae again reflected feeding within the C4 feeding channel (Figure 8.10). In contrast, *Deroceras* spp. appeared to be feeding within the same feeding channel although these have been documented as being herbivorous (Bohan *et al*., 2000), but may indicate a certain amount of omnivory (Figure 8.10). The Entomobryidae and Poduromorpha combined taxonomic group (due to mass limitations of the stable isotope approach), indicated that this group appeared to fit between the herbivorous and detrital food web. This could be due to either a wider resource spectrum feeding on fungi that are deriving

carbon from soil, weeds and maize derived resources (Figure 8.10) or could be due to seasonal changes in fungi to bacteria ratio, where Collembola could be feeding on microflora that are better adapted to utilising more recalcitrant maize derived carbon (Bardgett, 2005; Pausch *et al*., 2015; Hyodo, 2015). This could also be influenced by the greater abundances of Entomobryidae (mean density 20.91 ± 7.10 s.e.) compared with Poduromorpha (mean density 0.33 ± 0.33 s.e.).

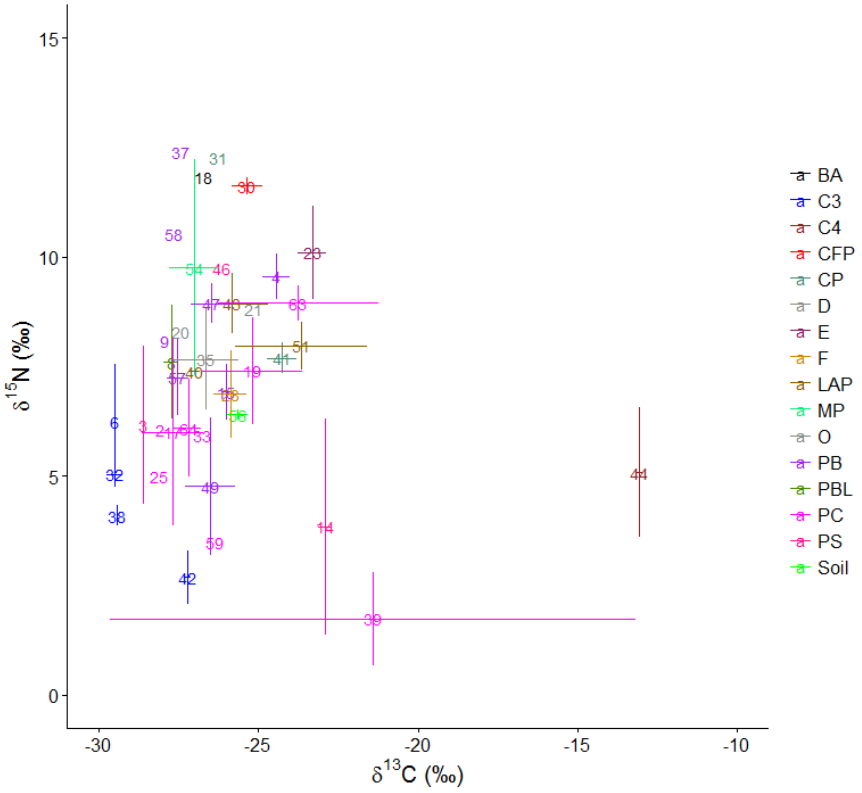


Figure 8.11 Mean (± s.e.) isotopic composition of above- and below-ground invertebrates sampled in summer 2014, after maize had been drilled, from the conventional cultivation technique (PGH). Numbers represent taxonomic groups, and colours represent trophic groups. Taxonomic and functional abbreviations are given in Appendix Table 12.5.1. The isotopic composition of invertebrate taxonomic groups collected from Bow was used to calculate mean (± s.e.).

At the cultivation (Summer 2014) sampling point, approximatly a month after drilling, the isotopic composition of the invertebrate communtiy was more associated with weed and soil derived carbon rather than maize derived carbon (Figure 8.11). The exception to this was Lepidoptera larvae which had a higher degree of variation along the $\delta^{13}C$ axis; this shows that they had a broad spectrum of primary feeding resources suggesting that Lepidoptera larvae were generalist rather than selective herbivores (Figure 8.11).

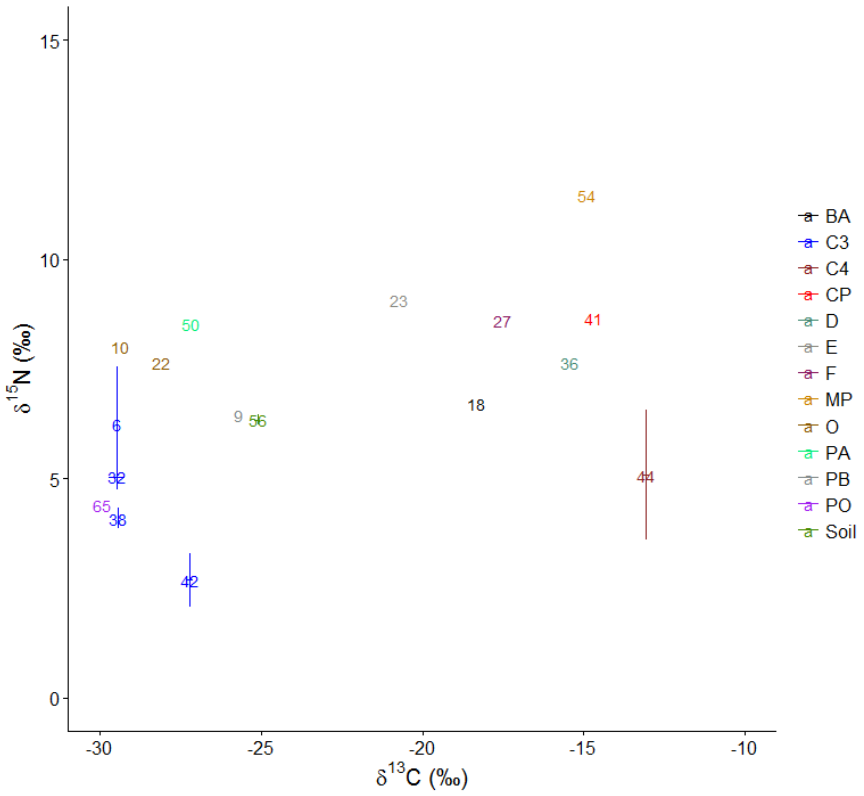


Figure 8.12 Mean (± s.e.) isotopic composition of above- and below-ground invertebrates sampled in autumn 2014, after harvest, from the conventional cultivation techniques (PGH). Numbers represent taxonomic groups, and colours represent functional groups. Taxonomic and functional abbreviations are given in Appendix Table 12.5.1. The isotopic composition of invertebrate taxonomic groups collected from Bow was used to calculate mean (± s.e.).

After the maize had been harvested (Autumn 2014) there was an isotopic separation between functional groups, the taxonomic groups that comprise the functional groups and the resources these different taxonomic groups used (Figure 8.12). The micro-predators, fungivores, detritivores, predatory centipedes and bacterivores had an elevated $\delta^{13}C$ similar to that of maize indicating that these detrital functional groups were feeding on predominantly maize derived resources (Figure 8.12). At the more depleted end of the $\delta^{13}C$ axis was occupied by omnivores, predatory beetles, parasitoids and pollinators indicating that these functional groups were feeding on carbon derived from weeds, in the herbivorous feeding channel (Figure 8.12). The detrital feeding channel had two predatory groups, firstly the micro-predators mainly comprising predatory mites, which were trophically elevated compared with the fungivores, detritivores and bacterivores indicating that the micro-predators predated these groups. On the other hand, the Geophilidae were not trophically elevated compared with the fungivores, detritivores and bacterivores

indicating that the trophic group the predatory centipedes were feeding on was not sampled (e.g. Nematodes). Although grouping was required to accommodate biomass-resolution trade-offs, grouping taxa can mask trophic separation and positioning. Trophic enhancement in the C3, mainly herbivorous, feeding channel indicates that the prey of the parasitoids was pollinators and that the prey of predatory beetles was not sampled.

8.4. Discussion

8.4.1. Resource availability

The soil at Bow was found to have a signature associated with depleted $\delta^{13}C$ which can be partially attributed to the previous management of the field. The field had been under continuous maize for ten years before the experiment was established. However, there was an annual input of separated slurry from the resident dairy herd which grazed for a majority of the year on C3 grasses (Figure 8.7); this depleted the $\delta^{13}C$ signature of the soil. In addition, the field was ploughed to a depth > 20 cm, which is known to deplete the bulk $\delta^{13}C$ signature of the soil (Balesdent *et al*., 1990; Gregorich *et al*., 2001; Lobe *et al*., 2005). Annual ploughing would also contribute to the depleted signature of soil at Fakenham; however, there was not a history of applying organic amendments to this field.

Overall, the more depleted isotopic signature of the invertebrate communities in the strip tillage cultivation method compared with the more conventional cultivation methods can be attributed to the increase in richness and percentage cover by C3 vegetation. This provides a greater abundance of C3 resource for invertebrates to consume. This depleted signature of the strip tillage invertebrate communities may suggest preferential consumption of C3 vegetation over C4 vegetation (Heidorn and Jones, 1984). Implications for management from these results indicate that to support above- and below-ground invertebrate biodiversity in maize cultivation systems C3 organic matter should be incorporated as a food source; this could be achieved by ploughing in a live strip crop, using litter mulches or applying slurry dry matter; these three management options open up opportunities for further research in to how the diversity and stability of invertebrates and their food webs would be affected.

Changes in the resource use of the invertebrate communities' at the different sampling times could be due to a number of factors. Firstly, during the summer sampling, the maize had only just been drilled so was storing carbon from photosynthesis in plant tissue resulting in little carbon 'leaking out' as exudates. However, post-harvest, once the crop

had been cut, any stored carbon in the remaining residuals (i.e. shoot and root) would be flushed into the soil system providing more elevated carbon for the detrital community to consume (Börjesson *et al*., 2015); these results are supported by analysis from the second sampling year which showed a similar pattern of changes in invertebrate whole community $\delta^{13}C$ to 2013 (Figure 8.3).

The compartmentalisation of resource use (herbivore against detrital) supports a number of well-developed hypotheses regarding feeding pathways within invertebrate communities (de Ruiter *et al*., 1995; Crotty *et al*., 2014; Pausch *et al*., 2015; Hyodo, 2015). Pausch *et al*. (2015) showed that fungi are important for distributing maize derived carbon through the soil matrix. Only at the post-harvest sampling point was maize derived carbon detected in the below-ground decomposer community (Figure 8.9 and Figure 8.12). The destruction of fungal hyphae linkages during ploughing (Bardgett and Van der Putten 2014) disrupts the use of maize derived carbon (Pausch *et al*., 2015). Through the growing season these hyphae re-establish and are better able to exploit maize derived carbon, and it is only once these linkages are re-established that there is a maize signal detected in the invertebrate detrital community. Initially, only the predatory Geophilidae exhibit the maize derived isotopic signal, which may be due to isotopic turn over lag (Pausch *et al*., 2015). To further understand these temporal dynamics more detailed analysis using Bayesian mixed modelling to apportion resource use over temporal scales will be used (Chapter 10).

There were clear differences between the above- and below-ground invertebrate community isotopic compositions (Table 9.1 and Figure 8.13). The below-ground food web was dominated by groups that were detritivores and their predators, whereas the above-ground food web was dominated by groups that were herbivorous and their predators; these results are similar to those found by Eisenhauer *et al*. (2010). Predators were found to feed in either the herbivore or detrital feeding channels dependent on sampling period, but were found to consume prey from different feeding channels. This highlights the opportunistic feeding nature of predatory groups (Ferlian and Scheu, 2014). This is reinforced by the variation in the diets of Geophilidae (below-ground) (± s.e. 1.04) and *Nebriinae* spp. (above-ground) (± s.e. 0.24), where *Nebriinae* spp. had much less variation in $\delta^{13}C$ (Appendix Table 12.5.1), indicating that below-ground predators were much more generalist than above-ground predators.

There was also a high degree of variation in the carbon that the Collembola consumed at the different sampling points throughout the experiment. These changes indicate variation in resource use which could be due to feeding on fungi that are deriving carbon from soil, weeds and maize resources (Figure 8.10). The variation in resource use was exacerbated by ploughing and tillage, which redistributed plant residues, soil organic matter and destroyed fungal hyphae, which has been shown to subsequently change the microbial community composition (Fu *et al*., 2000). Although not measured, literature has shown that these changes induced by ploughing or tillage reduce the ratio of fungi to bacteria (Bardgett, 2005; Pausch *et al*., 2015). As such, Collembola were feeding on fungi, which only used maize carbon after hyphae re-established.

8.4.2. Trophic Structure

The communities recovered from the conventional maize cultivation methods did not vary in $\delta^{15}N$ between sampling times over the cultivation season (Figure 8.6), suggesting that the PGH cultivation method was trophically stable throughout the course of the experiment. The trophic stability of the conventional cultivation techniques may be due to the site history. The field had been under conventional maize cultivation for a number of years prior to the experiment, and although regularly disturbed by ploughing the invertebrate community was found to be comprised of taxa that were more resistant and resilient to disturbances (Figure 8.2). These results suggest that there was a community comprised of taxa that could recover from disturbance, and were resilient enough to maintain trophic stability.

The below-ground detrital food chain conformed to the difference of ca. 3.4 ‰ $\delta^{15}N$ between decomposers and their soil dwelling predators in conventional maize systems (Figure 8.4). Evidence that the herbivore food chain displayed a higher degree of intra-guild predation compared with the detrital food chain comes from the elevated $\delta^{15}N$ signature of predators indicating two predatory trophic levels (Figure 8.4). Groups such as adult *Bembidion* spp. and *Nebriinae* spp. appeared to be feeding on herbivores, primary predators and within their own trophic and functional group, this is evident from the large amount of variation in $\delta^{15}N$ for these taxonomic groups (Appendix Table 12.5.1).

Maize derived carbon in the conventional plough systems was consumed mainly by detrital feeding taxa, and therefore subsequently the predators of these groups reflected the isotopic signature of the detritivores that they were feeding on (Pausch *et al*., 2015).

Predatory taxa included predatory mites and soil dwelling centipedes (Geophilidae) at the pre-cultivation and post-harvest sampling times (Figure 8.12). However, during the summer sampling periods where there was an increase in weeds in the conventional maize systems the decomposer feeding channel switched to feed on C3 derived resources (Figure 8.11). Van Soest (1994) found that maize derived carbon was less palatable for herbivores which may also be true for decomposers which require maize derived carbon to be mediated by microflora. Evidence for this comes from the elevation in $\delta^{15}N$ of the decomposer feeding channel in comparison with the herbivore feeding channel (Pausch *et al*., 2015). These results suggest that below-ground, the decomposition of maize residues was mediated by microflora (Pausch *et al*., 2015; Hyodo, 2015). Although the microbial assemblages were not evaluated in this study, it can hypothesise that they would be acting in the isotopic space in the C4 pathway equivalent to that which herbivores occupy in the C3 pathway, approximately 3.4 ‰ $\delta^{15}N$ below the primary decomposer organisms (Tiunov *et al*., 2007; Crotty *et al*., 2012; Pausch *et al*., 2015). Additional supporting evidence was found where Staphylinidae were directly feeding on herbivores and Julidae were feeding on maize derived plant matter. Although the two taxonomic groups had similar $\delta^{15}N$ signatures they had different functions. These results indicate that Julidae were consuming maize derived carbon that had been mediated by bacteria, fungi or nematodes which increased the $\delta^{15}N$ signature of carbon consumed within the detrital community which was then further increased as these resources were consumed by invertebrates and were transferred through the food web (Figure 8.9).

A major constraint to this work is based around the critical mass required for isotopic analysis, and because maize cultivation is well known for its poor biodiversity exhibited in both richness and abundance it was problematic to obtain critical mass for analysis of the below-ground invertebrate food web at a high enough resolution to conclude taxa level isotopic positioning for each sampling time. As such diverse groups such as decomposer mites and Collembola had to be pooled, this reduces the resolution at which meaningful conclusions can be drawn from these pooled groups.

8.5. Conclusions

Only a small proportion of maize was found to be consumed by invertebrate communities. When and where maize derived carbon was consumed by invertebrates it was found to be mediated by the microflora community (Crotty *et al*., 2014; Pausch *et al*., 2015; Bardgett and Cook, 1998; Pausch *et al*., 2015; Hyodo, 2015).

When maize derived carbon was available for the detrital community to consume, after being mediated by fungi (Pausch *et al*., 2015), there were distinctive feeding pathways in the conventional maize system. The two distinctive feeding channels were predominantly herbivorous and detritovores (Hunt *et al*., 1987; de Ruiter *et al*., 1995; Pausch *et al*., 2015; Moore *et al*., 2004; Crotty *et al*., 2014).

These results suggest that to improve ecosystem services facilitated by invertebrate biodiversity, supporting the detrital community by providing greater availability of C3 resources could improve ecosystem functionality. However, this must be balanced with yield penalties to farmers, but does open up options for further research into manipulating strip cropping maize cultivation practices.

Chapter 9

Temporal dynamics of resource use in conventional maize invertebrate communities; A Bayesian approach

9. Temporal dynamics in invertebrate community resource partitioning; A Bayesian approach

9.1. Introduction

Food webs are examples of complex systems in nature (Allesina *et al*., 2008). Elton (1927) first described food webs as the resource-consumer trophic interactions within a community (Huddson *et al*., 2012). Classically food webs were based on pyramid of numbers which displayed the total abundance or biomass at each trophic level (Huddson *et al*., 2012). However, ecologists are increasingly focusing on explaining the structure of communities by enriching traditional food web data with additional information, especially in relation to taxa body sizes or isotopic composition. Increasing the amount of information used has provided new insights into how trophic niches are partitioned (Huddson *et al*., 2012).

A consumer's tissues are ultimately derived from the dietary sources they consume; as such it is possible to use stable isotope mixing models to derive the assimilated diet of anindividual, or a group of individuals, given the isotopic ratios of the consumers' tissues and food sources (Phillips, 2012). This has been further developed to incorporate Bayesian methods and stable isotope mixing models (BSIMS) which has revolutionised ecological research (Jackson *et al*., 2009). BSIMS improve isotope analysis over traditional mass balance methods by explicitly taking into account uncertainty in resource isotopic signatures, categorical and/or continuous covariates, and prior information (Stock and Semmens, 2010). These advances in the field of ecology include the inference of diet selection, clarifying resource use and nutrient flow (Stock and Semmens, 2010; Allesina *et al*., 2008). Stable isotope mixing models (Parnell *et al*., 2013) offer a robust statistical framework in the form of MixSIAR (Stock and Semmens, 2010) for estimating the contribution of multiple sources (such as prey) to consumers (Ward *et al*., 2010). Despite recent advances and a move away from mass balance approaches, the integration of stable isotope Bayesian mixing models with whole food web networks has not been utilised to its full potential (Pacella *et al*., 2013).

Bayesian stable isotope mixing models can provide insights into consumer-resource relationships that would otherwise be difficult to quantify (Jackson *et al*., 2009). Bayesian stable isotope mixing models (BSIMS) have been developed that allow flexible model specification in a rigorous statistical framework to incorporate uncertainties, concentration dependence, and a larger number of contributing sources (Jackson *et al*., 2009; Stock and

Semmens, 2010). Most studies focus on the dietary contributions of prey items directly consumed (Pacella *et al*., 2013). However, in this study the importance of the invertebrate consumers was based on three different basal resources namely soil, weeds and maize. Stable isotope mixing models can be a useful in unravelling trophic relationships in food webs and understanding the causes and consequences of variation in diets (Phillips, 2012). Furthermore, stable isotope mixing models can estimate the assimilated diet of individuals, populations or communities (Phillips, 2012). Bayesian stable isotope mixing model frameworks are capable of including any number of sources (Benetti *et al*., 2014; Jackson *et al*., 2009), which makes this a suitable method for assessing differences in the proportions of diet at different trophic levels and between the above- and below-ground communities.

A critical assumption of BSIMS is that all food sources are included in the analysis (Jackson *et al*., 2009; Stock and Semmens, 2010; Rossberg, 2013). Excluding a food source will bias the apparent proportions of the other sources that were included in the analysis, and may yield a diet with apparent food source proportions inconsistent with the observed isotopic composition of the consumer (Parnell *et al*., 2012; Phillips, 2012). BSIMS estimates the probability distributions (mean, standard deviation and credibility intervals ranging from 2.5% to 97.5%) of each source to a consumer's isotopic composition, accounting for uncertainty associated with multiple sources and tissue-diet discrimination factors (Stock and Semmens, 2010). Within this chapter the 97.5th credibility interval was used to determine food web linkages for primary consumer taxa and their predators to identify proportions of contribution to invertebrate community diet from available resources within conventional maize cultivation systems.

The number of trophic levels within food webs can estimate the connectedness of taxa, where the higher trophic levels are more stable due to wider prey spectrums (Hudson *et al*., 2013). Generally, the larger a species is, the more available prey taxa there are (Cohen *et al*., 2003). However, prey species are often shared by other consumers, therefore the larger the taxa or functional group, the higher in the food web it may feed, despite there being less energy available due to ecological efficiencies (Jonsson *et al*., 2005). Integrating food web, body mass and numerical abundances of arthropod populations provides an integrated approach to investigating these efficiencies (Huddson *et al*., 2012; Turnbull *et al*., 2014).

9.1.1. Hypotheses, Aims and objectives

This chapter uses recent advances in MixSIAR's Bayesian framework to apportion feeding resource, understand the trophic structure and inform food web linkages of above- and below-ground invertebrate communities under conventional maize cultivation. The goal of this chapter was to identify if the Bayesian credibility intervals could be used to inform food web linkages and if this technique could be used to better understand the linkages between the above- and below-ground invertebrate food webs.

H_1=Bayesian credibility intervals provide a more accurate interpretation of food webs links compared with mass balance approaches

9.2. Materials and Methods

MixSIAR Bayesian mixing models were used to apportion basal feeding resources of the whole invertebrate community within the conventional maize cultivation methods at Bow. Mean (± s.e.) above- and below-ground invertebrate taxa isotopic signatures were used for BSIMs analysis (Appendix Table 12.6.1).

Hierarchical analysis was performed to understand the changes in community basal feeding resources between different sampling points to apportion temporal shifts in basal feeding resources for the whole community. Further analysis of the higher trophic levels within conventional maize cultivation was carried out using primary invertebrate consumer feeding groups (Figure 8.4) as sources to apportion feeding resources to predatory taxa within the conventional maize cultivation. Secondary predators were also separated from the primary predators, which were then used as a potential food source of the secondary predators to identify linkages between higher level predation. Trophic levels were separated based on fractionation of $^{14}N/^{15}N$ at about 3.4‰ (Tiunov, 2007). A limitation of this method is that intraguild predation cannot be accurately modelled as the isotopic composition of secondary predators would indicate high probability and proportion of intraguild predation. Therefore it has not been considered within this model framework.

Bayesian mixed modelling of invertebrate isotopic data has been conducted using MixSIAR V1.0 (Stock and Semmens, 2013) in R v 3.0.2 (R Development Core Team, 2008). The MixSIAR GUI is a graphical user interface (GUI) that allows analysis of stable isotope data using the MixSIAR model framework. Mean (± s.e.) of carbon sources (weeds, maize and soils) were used to apportion basal feeding resources. Light isotopes are

lost during the conversion of source proteins into consumer tissues (Parnell *et al*., 2013), as such trophic enrichment factors (TEF) are normally adjusted based on literature values (Stock and Semmens, 2010). However, as there is sparse information regarding the trophic enrichment factors (TEF) of invertebrates in maize systems the TEFs were set to 0‰ for $\delta^{13}C$ and 3.4‰ for $\delta^{15}N$.

Markov Chain Monte Carlo methods (MCMC) were used to estimate the probability density functions of invertebrate source consumption rates. MCMC estimates the entire distribution for each invertebrate and each source (Stock and Semmens, 2010). From this estimated "posterior distribution" mean, standard deviation, and Bayesian credible intervals were calculated. "Chain Length" depends on the number of data points and complexity of covariates and the number of isotopes in the model. Initially a short "Chain Length" was used to identify if the model was functioning correctly (Stock and Semmens, 2010). Once diagnostics showed that the chains did not converge, the chain length was increased until convergence occurred. "Burn-in" is the first section of the chain that is discarded, as it can be heavily influenced by the initial values which are not representative of the true posterior distribution (Stock and Semmens, 2010). Initially "Burn-in" was set at half of the "Chain Length". Finally, the chains were "Thinned" to reduce auto-correlation (thinning by 25 means every 25^{th} value in the chain is used). MCMC parameters after optimisation were set at "Number of chains" = 3, "Chain length"= 20000, "Burn-in"=10000 and "Thin" = 25. MixSIAR includes process and residual errors, and these account for the estimated uncertainty in source and discrimination values (process error) and unknown sources of error (residual error). After MCMC optimisation it was concluded that a 'normal' MCMC was suitable for both consumer and predator food webs.

BSIMS summary statistical values > 0.5 at the 97.5% confidence interval were used as indicators of food web linkages. Linkages where then combined with isotopic, elemental and allometric information to inform node properties for the analysis using R-package 'Cheddar' (Hudson *et al*., 2013) in RStudio (Racine, 2012). The 'Cheddar' functions 'PlotWebByLevel', 'PlotNPS' and 'TrophicLevels' to calculate trophic levels (Hudson *et al*. 2013). Chain averaged trophic Level was used to calculate the mean position of each taxonomic group for every chain in the food web, which is synonymous with 'trophic height' described by Jonsson *et al.* (2005). As the trophic height of a taxonomic group increases the resource supply rate could either increase or decrease with increasing consumer body size or trophic height. For example, the larger a taxa is, the more available

prey taxa there are. On the other hand, prey taxa are in general shared by other consumers, so the larger a taxa is the higher in the food web it may feed, with possibly less energy available due to ecological efficiencies (Jonsson *et al*., 2005).

9.3. Results

9.3.1. Resource use over temporal scales

There was strong evidence to suggest changes in the diversity and community composition of above- and below-ground communities collected during the two cultivation seasons (Figure 6.3; Figure 6.4; Figure 5.7). There were also differences in the isotopic signature of the whole invertebrate community depending on sampling time (Figure 8.2), as such the different sampling times during the two year field trial were analysed separately to understand temporal changes in resource use (Figure 9.3). The consumption of the three feeding resources by the invertebrate communities changed over the course of the experiment (Figure 9.3). At the initial sampling point, pre-cultivation 2013 (Figure 9.3a) the majority of the carbon consumed by the below-ground invertebrate community was derived from soil resources with only a small proportion being derived from C3 or C4 vegetation. A similar pattern of whole invertebrate community basal resource consumption was found during the 2013 cultivation sampling period (Figure 9.3b). However, once the maize crop had been harvested (Autumn 2013) there was a change in the proportion of the invertebrate community consumption of the three basal resources (Figure 9.3c). Post-harvest 2013 (Figure 9.3c) there was a significant proportion of the community feeding on resources derived from the maize and soil with only a small proportion derived from C3 weeds. In the second field trial year, initially at the pre-cultivation sampling point a large proportion of carbon consumed by below-ground invertebrates was derived from maize, with the proportions of resource consumed remaining similar to that observed during the post-harvest 2013 sampling point. This suggests that maize derived carbon supports the below-ground community over winter (Figure 9.3d). During cultivation in 2014, as with 2013, a majority of resources consumed by the below-ground invertebrate community was derived from soil (Figure 9.3f). The post-harvest sampling point in 2014, unlike post-harvest 2013, showed similar amounts of C3 and C4 carbon were consumed by the below-ground invertebrate community (Figure 9.3f). The two year cyclical change in resource use (Figure 9.3) was due to changes in nitrogen amendments. Before the field experiment was established there was an annual input of separated slurry dry matter applied to the field. This gave a strong C3 organic matter signal for invertebrates to feed upon, which initially masked the C4 signal at the pre-cultivation sampling point in 2013. During the experiment

inorganic fertilizers were applied. This meant that the invertebrate detrital community was not able to derive resource from additional organic matter applied and became more reliant on the resource available.

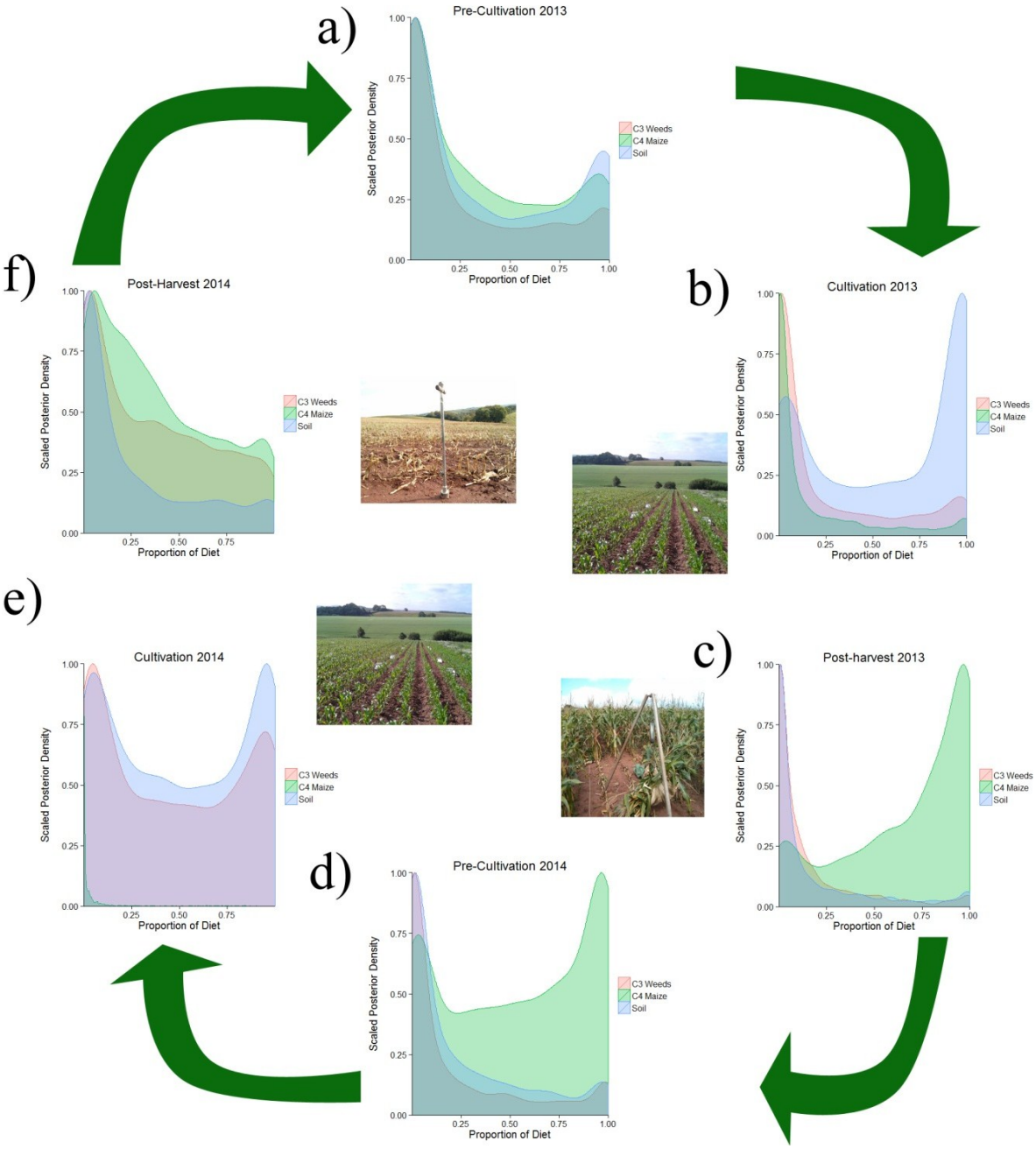


Figure 9.1 Below-ground invertebrate community resource assimilation from soil ( ), C3 weeds ( ), and C4 maize ( ) from each sampling point during the two year field trial. Posterior density plots represent the proportion of diet and the scaled posterior density of each community at a) pre-cultivation 2013, b) during cultivation, c) post-harvest 2013 d) pre-cultivation 2013, e) during cultivation, f) post-harvest 2013.

9.3.2. Resource use in conventional maize systems

Overall, there were differences in the resources taxonomic groups consumed (Figure 9.2, Chapter 9). The distribution of above-ground isotopic signatures shows the community predominantly consumed C3 derived carbon (Figure 9.2a). However below-ground, a greater number of taxa reflected a C4 isotopic signature (Figure 9.2b), suggesting that below-ground invertebrates consumed a wider range of resources under conventional maize cultivation.

The isotopic compositions of the resources that invertebrates were deriving resources from were different (Figure 9.2c). Maize and soil had very different isotopic signatures (Figure 9.2c, 10.3a), as did maize and the weeds sampled (Figure 9.1c, 10.3a). However, the weeds and litter were similar in isotopic composition, as such the mean isotopic composition of C3 weeds was averaged to provide one isotopic source of 'C3 weeds' for the BSIMS model (Figure 9.3a); this was required to reduce the noise and improve model performance (Jackson *et al*., 2009). There was a strong correlation between the isotopic signature of C3 weeds and soil; however there was a much weaker correlation between C4 maize with soil and C3 weeds (Figure 9.2a, -0.75 and 0.64 respectively). Despite this, the isotopic distribution (Figure 9.3a) shows that the differences between C3 weeds and soil were isotopically skewed in different directions with C3 weeds being negatively skewed and soil being positively skewed (Figure 9.3a). Therefore, the three sources of carbon with the conventional maize cultivation system were viable for apportioning the relative contribution of feeding resource to invertebrate isotopic composition.

The invertebrate community under conventional maize cultivation consumed more soil and C3 derived carbon than maize derived carbon (Figure 9.3b). There were differences in the taxonomic and functional groups and the proportions of resources they consumed. For example there were significant differences in the isotopic composition of detritivores e.g. Julidae (Figure 9.3d) which fed on C4 derived carbon whereas Aphididae (Figure 9.3c) feed on predominantly C3 weed derived carbon.

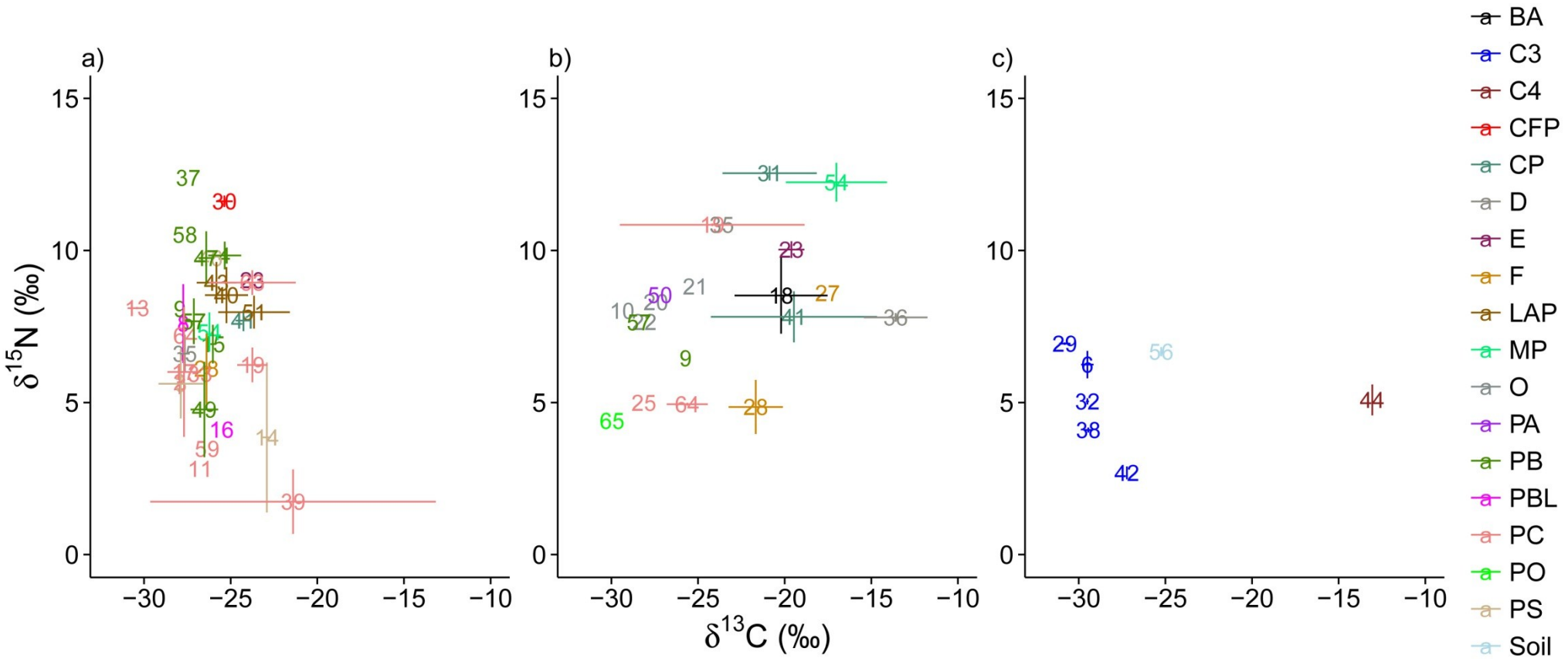


Figure 9.2 Mean (± s.e.) isotopic composition for each invertebrate taxonomic groups collected using a) pitfall traps; b) soil core and heat extraction techniques and c) soil and vegetation including legumes and ryegrass to ensure all available resource were analysed following Jackson *et al*. (2009). Invertebrate taxonomic groups are represented by numbers (abbreviations appendix table 12.5.1) and functional groups (represented by colour, abbreviations Table 7.1). Isotopic composition of invertebrates was pooled for all sampling points from the PGH cultivation technique at Bow.

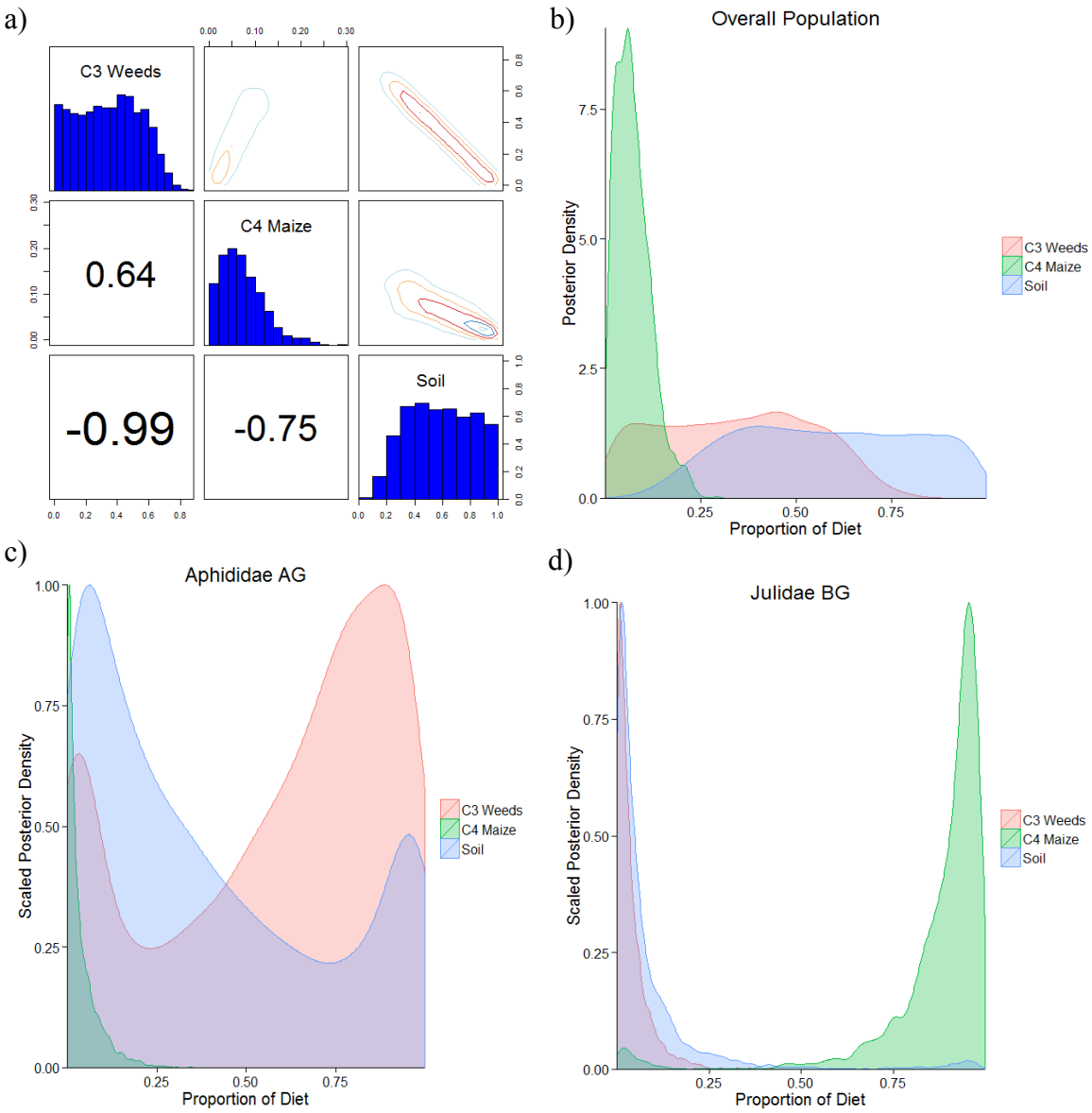


Figure 9.3 MixSIAR Bayesian mixed model output. Graph a) is the correlation between the $\delta^{13}C$ values of the basal feeding resources, the upper-diagonal are contour plots, the diagonal shows histograms, and the lower-diagonal shows the correlations between the different basal resources. Graph b) posterior plot of the proportion of diet of the whole invertebrate community for all sampling points, graph c) posterior plot of the proportion of diet for above-ground Aphididae and graph d) posterior plot of the proportion of diet of below-ground Julidae. The isotopic data used was from specimens collected at Bow from the PGH cultivation techniques.

9.3.3. Food webs

The 97.5th credibility interval of the Bayesian model out-puts for each trophic level based on ecological and isotopic knowledge were used to separate out consumers and predators.

Information regarding the proportions of consumption was used to inform food web linkages. The structure and length of linkages are important in understanding invertebrate food web dynamics (Figure 9.4).

There were four trophic levels within conventional maize cultivation at the Bow site (Figure 9.4a). These trophic levels consisted of a basal resource level of C4 maize, C3 weeds and soil, which were consumed by invertebrates in trophic level two which were in turn consumed by trophic level three, where invertebrates in trophic level four were consuming taxa that were present both in trophic level two and trophic level three and predating within trophic level four (Figure 9.4a). The below-ground food web was dominated by smaller taxa which had narrower prey source ranges leading to few chain averaged trophic levels (Figure 9.4b). In contrast, the above-ground food web was dominated by larger taxa with wider prey spectrums (Figure 9.4c). However, biomass and abundance of individuals does not vary systematically with trophic height, as variations in numerical abundance are generally more closely associated with variations in body mass than with variations in trophic height (Jackson *et al*., 2009).

Food webs use the averaged trophic level chain length to estimate the connectedness of taxa (Figure 9.4). Taxa with higher chain averaged trophic levels are more stable than those with lower chain averaged trophic levels as they have a greater prey spectrum (Figure 9.4). Above- and below-ground conventional maize cultivation invertebrate food webs had a maximum of eight averaged trophic chain lengths (Figure 9.4a). The above-ground *Bembidion* spp. and below-ground predatory mites had the longest chain averaged trophic levels (Figure 9.4a), which suggest that these taxa were the most stable within the above- and below-ground systems due to a wider prey spectrum than other predators such as Lycosidae and Linyphiidae (Figure 9.4b). Separation of the above- and below-ground food webs shows that below-ground predatory mites and Geophilidae had the greatest chain averaged trophic level indicating that these were stable predators below-ground. In contrast, the above-ground community had four stable predatory groups *Bembidion* spp., Formicidae, Linyphiidae, Lycosidae and *Nebriinae* spp. indicating greater predatory food web stability within the above-ground food web compared to the below-ground food web.

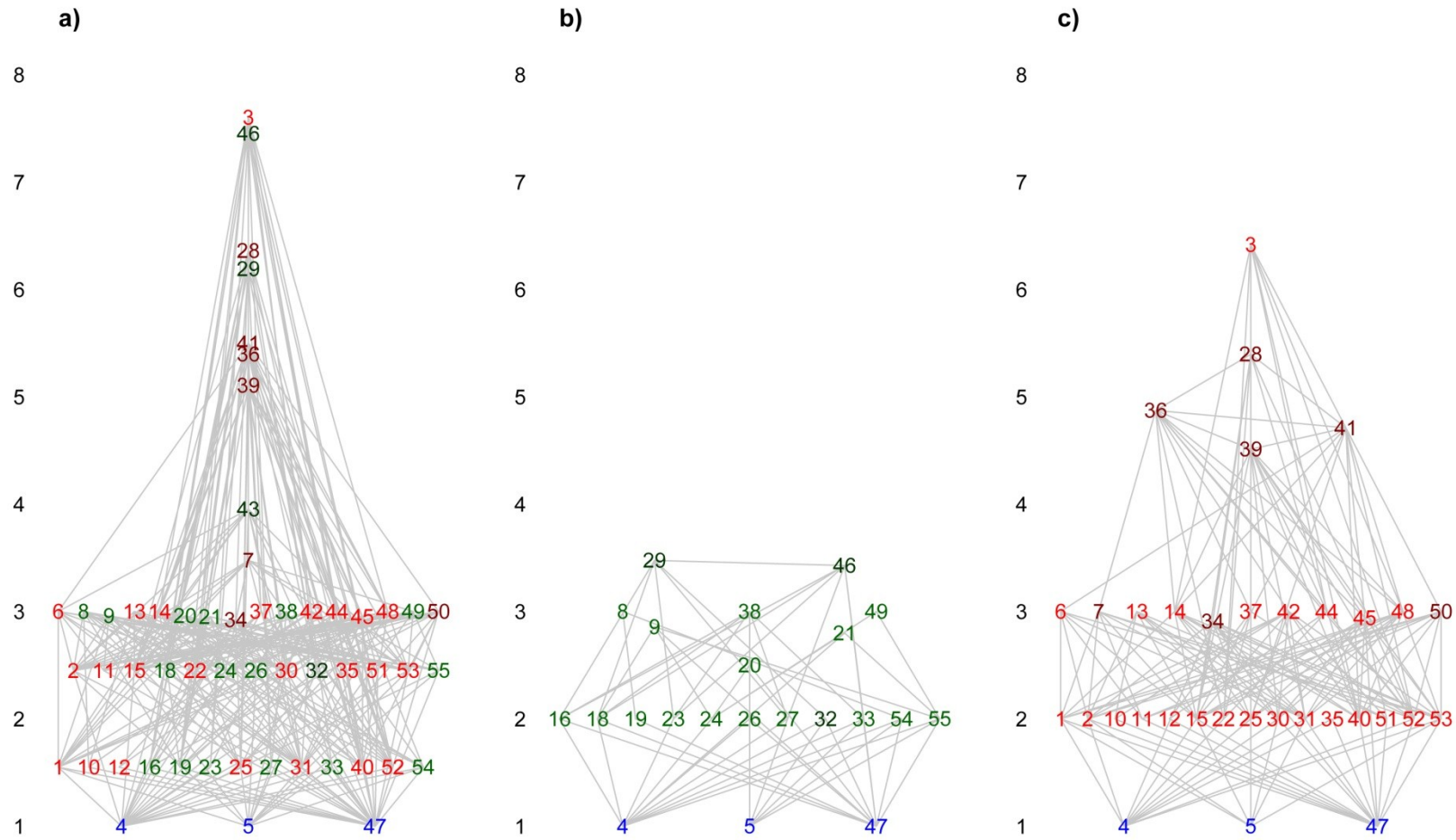


Figure 9.4 Conventional maize cultivation Bayesian informed invertebrate food webs. Graph a) is the combined above- and below-ground invertebrate food webs, b) is the below-ground invertebrate food web, and c) is the above-ground invertebrate food web. Bayesian credibility intervals were used to inform the strengths and numbers of food web linkages using the R-package 'Cheddar'. Below-ground parasitic wasps were omitted from separate food web analysis as no food web linkages were found. Taxa numerical abbreviations are noted in appendix Table 12.6.1.

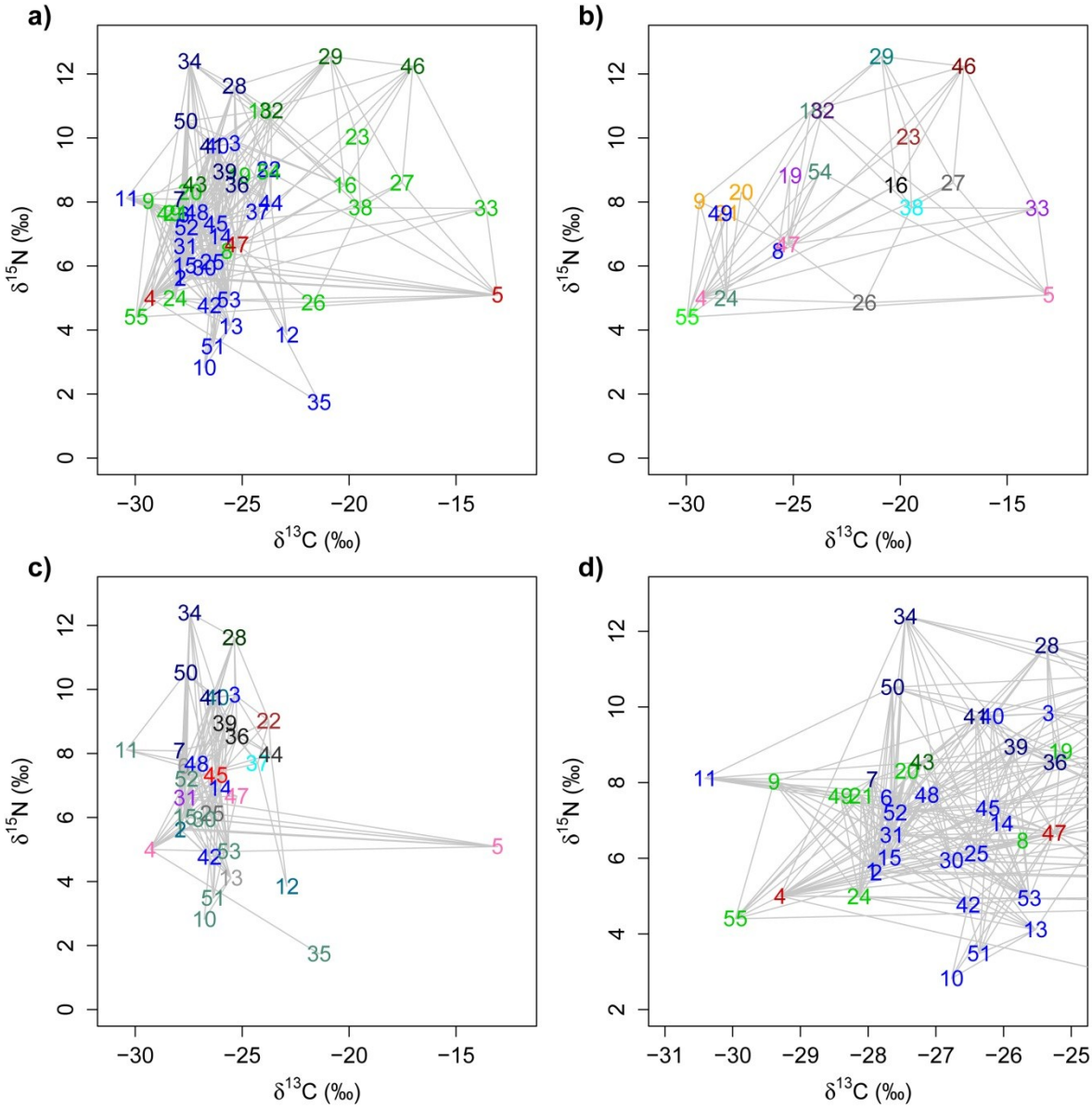


Figure 9.5 Mean isotopic composition of above- and below-ground invertebrate within conventional maize cultivation systems. Food web linkage strength and number were calculated from Bayesian credibility intervals using the R-package 'Cheddar'. Numerical abbreviation are noted in appendix Table 12.6.1, Graph a) Isoplot with informed food web linkages of the above- ( ) and below- ( ) ground communities, b) Isoplot with informed food web linkages for the below-ground invertebrate community, colours denote functional group, c) Isoplot with informed food web linkages for the above-ground community, colours denote functional group; plant suckers( ), predatory beetle larvae ( ), large arachnid predators ( ), predatory beetles( ), omnivores( ), bacterivores( ), plant chewers( ) detritivores( ), earthworms( ), fungivores( ), predatory centipedes( ), micro-predators( ), pollinators( ) and carbon sources ( ) d) Restricted isoplot of the C3 basal feeding resources (red) with informed food web linkages for the above- ( ) and below-ground ( ) invertebrate communities.

Using the Bayesian proportions of resource use to inform food web linkages has shown that there were a number of links between the detrital and herbivore feeding channels (Figure 9.5b), that were not observed in Chapter 9. There were increases in depleted $\delta^{13}C$ body content of predators within the detrital feeding channel, which is hypothesised to be related to the relative consumption of prey from the herbivorous, predominately C3, feeding channel. There is also evidence that a number of herbivorous taxa and their predators fed within the C4 derived detrital feeding channel (Figure 9.1).

Separation of the above- (Figure 9.5c) and below-ground isotopic compositions (Figure 9.5b) shows clear differences in the isotopic space occupied by these spatially distinct communities. The below-ground community consumed carbon from both C3 and C4 derived resources (Figure 9.5). It is also evident that below-ground there were two isotopically distinct feeding channels; a herbivorous feeding channel and a detrital feeding channel. Entomobryidae and Poduromorpha linked the detrital and herbivorous feeding channels presumably through the consumption of fungi that were acquiring carbon from both C3 and C4 derived resources (Figure 9.5). In contrast, the above-ground food web was nested within C3 isotopic space, indicating that a majority of the feeding resources being consumed were not derived from maize. There were, however, a number of food chain linkages that connect the primary consumer trophic levels to maize demonstrating that some prey were utilising carbon derived from the maize crop.

When the more elevated C4 community was excluded from the Bayesian informed food web linkage isotopic composition plots (Figure 9.5d), there is evidence to suggest that there was separation in the herbivorous feeding channels. The herbivorous feeding channel was separated by a greater proportion of invertebrates consuming either vegetative or soil derived resources. However, there were a number of linkages between these two feeding channels (Figure 9.5d). The above-ground community (Figure 9.5 d) did not show a clear separation between the soil and C3 plant derived carbon with several taxonomic groups deriving carbon from both resources (Figure 9.5 d). However, the larger arachnid predators; Linyphiidae and Lycosidae, isotopic composition reflected that of initially deriving carbon from soil, C3 weeds and C4 maize resources which can be attributed to these predatory taxa being generalist feeders consuming a wide range of prey that were feeding in both the soil and plant derived feeding channels. In addition, changes from

larvae to adult, i.e. Diptera, significantly shifted the resources which the two life stages of the taxonomic group consumed (Scheu, 2001; Abd El-Wakeil, 2009).

Food web connectivity can be further applied to incorporated biometric relationships found within conventional maize cultivation systems (Figure 9.6). This information can be used to understand the connectedness of food webs and their relative stabilities (Hudson *et al*., 2013). The invertebrates collected from both the above- and below-ground communities under conventional cultivation were analysed for isotopic composition, density and individual biomass to inform allometric food webs. The Bayesian informed food web linkages between the two communities show that overall the above- and below-ground community can be considered relativity stable when analysed together (slope = -0.75). When considering below-ground community (Figure 9.6b) connectedness and stability of linkages it is evident that the below-ground community was significantly more stable than that of the above-ground (Figure 9.6c; Slope = -0.67, Figure 9.6a; Slope = -0.57, respectively). These observations are well supported by the literature (Neary *et al*., 1999; Baur *et al*., 1996; Tsiafouli *et al*., 2015), often being attributed to both the greater numbers and reduced dispersal efficiency of the below-ground invertebrates.

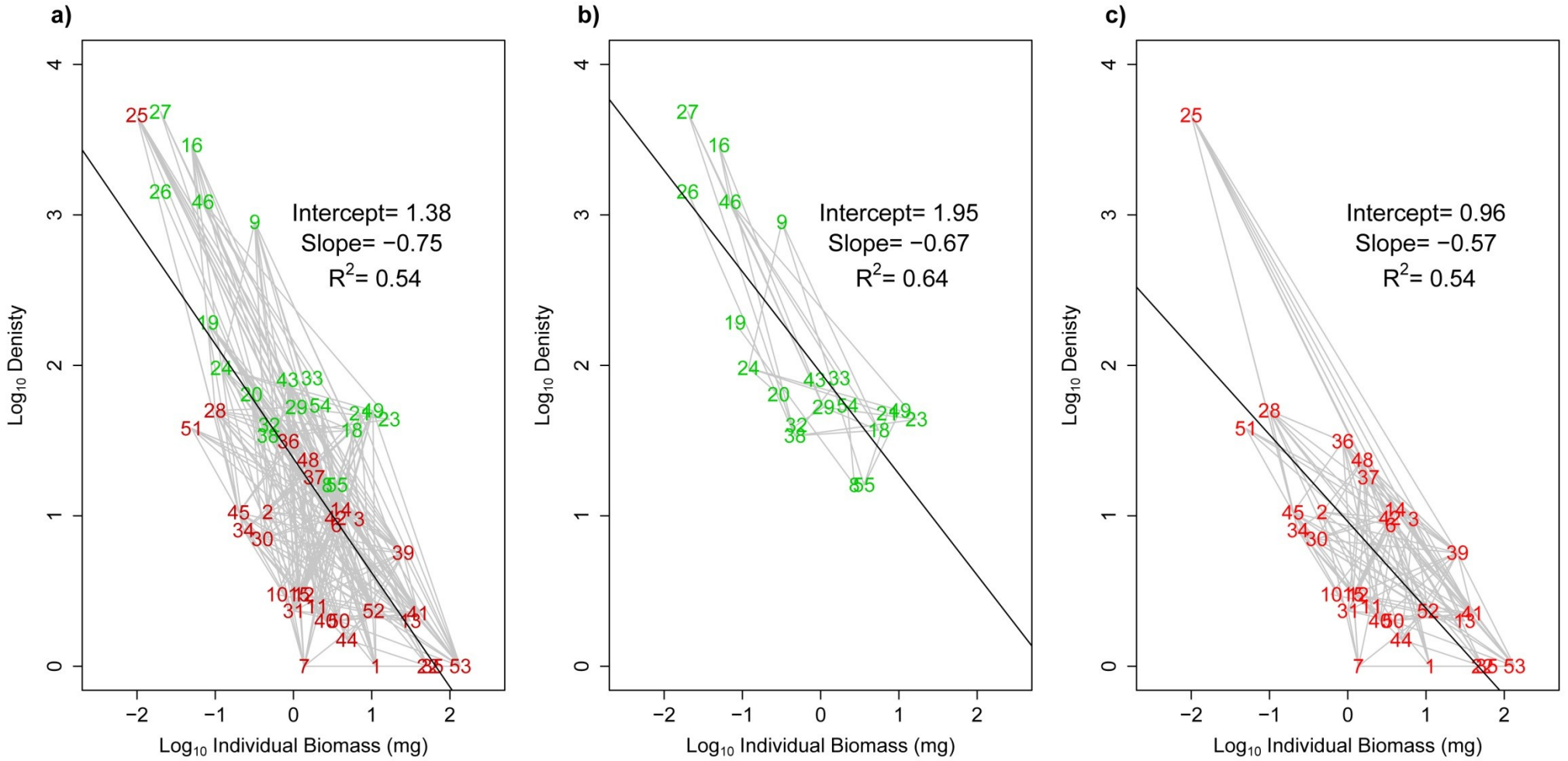


Figure 9.6 Allometric analysis of food web stability for a) above- and below- b) below- and c) above-, ground invertebrates using the Bayesian informed food web linkages. Colours denote above- ( ) or below-ground ( ) community. Taxonomic groups are numerical denoted with abbreviation in appendix Table 12.6.1

9.4. Discussion

9.4.1. Changes in resource use over time

The MixSIAR modelling framework provides a robust measure of temporal changes in community diet preferences (Figure 9.3). The application of the Bayesian framework to individual sampling times during the course of the experiment highlighted that there were changes in the dominant feeding resource of the community. There was only a strong C4 signal in the post-harvest sampling points indicating that there is a 'flush' of carbon to the soil system once the crop has been removed from the field (Börjesson *et al*., 2015). However, this may also be due to the re-establishment of fungal hyphae post-harvest which were able to distribute maize derived carbon through the soil matrix (Pausch *et al*., 2015; Börjesson *et al*., 2015). This indicates that in heavily disturbed agroecosystems the above- and below-ground invertebrate food webs are strongly linked to temporal shifts in the bacteria to fungi ratio as shown by Bardgett *et al*. (2005) and Pausch *et al*. (2015) in systems that are low in plant diversity. The implication of these results show that to support resistant and resilient invertebrate biodiversity in arable systems soil disturbance should be minimised.

9.4.2. Food webs

The application of this Bayesian informed credibility intervals to determine food web linkages has yielded important insights into the links between the above- and below-ground food webs within conventional maize cultivation systems (Figure 9.4). Although there would appear to be a clear isotopic separation between the below-ground detrital and the above-ground herbivorous feeding channels using conventional stable isotope mass balance approaches (Figure 9.1a and b). there were actually a number of food web links occurring between the different isotopic channels (Figure 9.4). Within the two respective feeding channels the top predators had relatively long food chain lengths (Figure 9.4a). This has shown that Adult *Bembidion* spp. had a wider prey spectrum than grouped Carabidae larvae which had a comparatively low number of food chain links. Fewer food chain links make populations more susceptible to fluctuations in prey populations compared with more generalist predators such as *Bembidion* spp. (Figure 9.4b). Although grouping the Carabidae larvae may have masked the greater number of trophic linkages of some Carabidae genera over others grouping was required to obtain sufficient biomass for isotope analysis; in addition Carabidae larvae are difficult to identify to genera (Lindroth *et al*., 1985)

Separation of the above- and below-ground community food webs has shown that there were a greater number of predatory groups above- (Figure 9.4b) than below-ground (Figure 9.4a), these above-ground predators had a greater numbers of linkages indicating wider prey sources and greater stability. This is commonly linked to the biomass of predators (Turnbull *et al*., 2014) where above-ground predators were found to have a greater mass than below-ground predators (Figure 9.6; Rickers *et al*. 2014; Peckarsky *et al*. 2014). However, the isotopic composition of below-ground predators indicates that they consumed carbon originating from a wider range of basal resources. This could suggest that above-ground predators were more specific whereas below-ground predators were more generalist, which may be linked to differences in body size distribution (Ferlian and Scheu, 2014). This offers an explanation as to why below-ground predatory mites had greater trophic chain links than above-ground predatory mites. When the above- and below-ground habitat compartments that taxa inhabit are considered it is intuitive that below-ground, where the physical environment is more restrictive, that generalism is an ecological advantage. In contrast, above-ground where and when specific prey were not abundant it is much easier to disperse to areas of greater prey availability in this case specialism may be an advantage to avoid competition. This is supported by the similar $\delta^{15}N$ of predators that have been found in the detrital and herbivourus food webs, where the detrital food web $\delta^{15}N$ was elevated due to the mediation of carbon by microflora (Hyodo, 2015), however within the herbivorous feeding channel high $\delta^{15}N$ of predators may be due to dispersial ability (Abd El-Wakeil, 2009).

Through incorporating the Bayesian informed food web linkages with the isotopic community data, it is evident that there was a greater amount of feeding within the two seemingly separated feeding channels (Figure 9.5b). It is evident that the higher trophic levels showed less of an isotopic distinctness between the two feeding channels where there is evidence to suggest that the predatory taxa from both feeding channels converge at higher trophic levels, due to at least consuming a small proportion of resources from both the feeding channels (Abd El-Wakeil, 2009; Albers *et al*., 2006). This provides evidence to suggest that the predatory groups converged with similar carbon isotopic signal, possibly due to feeding on a wider range or resource, which was especially evident for the below-ground Geophilomorpha (Abd El-Wakeil, 2009).

Bayesian statistical methods for apportioning feeding resources cannot utilise isotopic signature to model intraguild predation. Invertebrate groups that do display intraguild predation may have elevated $\delta^{15}N$ relative to the rest of the community (Rickers *et al*. 2014). However, as Bayesian modelling frameworks function on the relative difference in isotopic composition to apportion feeding resource, as the taxonomic group isotopic signature of the resource is the same as the consumer the Bayesian modelling framework will assume total consumption within the group. Therefore, a resulting credibility interval provides a false positive result to determine food web linkages but does offer an opportunity for further research to utilise compound specific isotope, Phospholipids fatty acid (PLFA) or gut content analysis techniques to further clarify intraguild predation (McNabb *et al*., 2001; Pond *et al*., 2006; Rickers *et al*., 2014; Ferlian and Scheu, 2014).

9.5. Conclusions

There were greater numbers of taxonomic groups that consumed maize derived carbon in the below-ground community compared with the above-ground community. The proportion of maize derived resources changed with seasonal variation, which was linked to the re-establishment of fungal communities after ploughing (Pausch *et al*., 2015).

BSIMS revealed there were greater numbers of linkages between the predators that feed in both the above- and below-ground food webs. Although it is known that the above- and below-ground food webs are linked through predation (Scheu, 2001; Scherber *et al*., 2010) for the first time it has been shown that the strength of these links are dependent on the biometric distribution of invertebrates within communities.

The MixSIAR model framework provides a robust interpretation of basal feeding resource and predator prey consumption to determine food web linkages (Rossberg, 2013). However, coupling these statistical techniques with isotopic information, the Bayesian model framework incorporated into the food web model is incapable of modelling intraguild predation, providing an opportunity for further research using PLFA or gut contents analysis (Ferlian and Scheu, 2014).

Chapter 10

General Conclusions

10. General conclusions

This chapter draws together conclusions from the experimental chapters to distil wider conclusions and inform the direction of further work to reduce the ecological degradation caused by conventional maize cultivation systems.

Overall, there were no significant benefits to invertebrate biodiversity or maize yield by cultivating maize using minimum tillage rather than conventional ploughing (Table 10.1). There were however, benefits to invertebrate biodiversity and community composition by cultivating maize in the strip tillage areas and leaving an understory of either a biodiverse seed mix or ryegrass in the un-tilled areas (Table 10.1). This shows that although agriculture has repeatedly been identified as one of the largest contributors to the loss of biodiversity (Bardgett and Van der Putten, 2014; Clay *et al*., 2014; Wodika and Baer, 2015; Tiemann *et al*., 2015; DeFries *et al*., 2004; Tsiafouli *et al*., 2015), especially maize cultivation (Firbank *et al*., 2003; Nakamoto and Tsukamoto, 2006; Hartwig and Ammon, 2002), simple changes in management practice can improve above- and below-ground invertebrate biodiversity.

Although there can be improvements to invertebrate biodiversity in maize cultivation systems, this work has also shown that these gains must be balanced with the yield penalty to farmers (Appendix Table 12.2.2). In both field trial years, there were reductions in the yield of maize in both of the strip tillage into ground cover cultivation methods (Table 10.1). However, in the second field trial year, through the increased application rates of herbicides (Section 3.2) to the strip tillage cultivation methods, maize yields were significantly improved (Appendix Table 12.2.2), without significant impacting invertebrate biodiversity (Table 5.1 and Figure 6.3). This therefore shows that further work should investigate how to control inter-crops to facilitate biodiversity gains and maximise maize yields.

Table 10.1 Summary of the effects of contrasting maize cultivation techniques on invertebrate biodiversity and maize yield. Table contains (+) were there was a positive effect, (-) where there were negative affect and (NC) where there was no change over that observed in the conventional maize cultivation technique.

			Strip tillage into ryegrass inter-crop	Strip tillage ground into a biodiverse seed mix inter-crop	Minimum tillage	
Above-ground		Richness	+	+	NC	Figure 6.1a
		Density	+	+	NC	Figure 6.1b
		Evenness	NC	+	NC	Figure 6.1c
		Diversity	+	+	NC	Figure 6.1d
		Community composition	+	+	NC	Figure 6.5a
		Beta-Diversity	+	+	NC	Figure 7.2b
Below-ground	Earthworm	Richness	NC	+	NC	Figure 5.1c
		Density	NC	+	NC	Figure 5.1d
		Evenness	NC	NC	NC	Table 5.1b
		Diversity	NC	NC	NC	Table 5.1b
	Macrofauna	Richness	NC	NC	NC	Figure 5.1a
		Density	-	NC	NC	Figure 5.1b
		Evenness	NC	NC	NC	Table 5.1a
		Diversity	NC	NC	NC	Table 5.1a
	Mesofauna	Richness	+	+	NC	Table 5.1c
		Density	+	+	NC	Table 5.1c
		Evenness	NC	+	NC	Table 5.1c
		Diversity	NC	NC	NC	Table 5.1c
		Community composition	NC	+	NC	Figure 5.7a & Figure 5.9a
		Beta-Diversity	NC	+	NC	Figure 7.2a
Yield (t ha-1)			-	-	NC	Appendix Table 12.2.2

10.1. Reductions in physical disturbance and increases in non-crop vegetation improve above- and below-ground invertebrate biodiversity

This thesis shows conclusively that above- and below-ground invertebrate food webs are linked through the physical disturbance and vegetative diversity within maize cropping systems. These results are supported by a number of other studies in both natural and agricultural systems that show reduced disturbance and greater diversity of vegetation supports more diverse above- and below-ground invertebrate communities (Adl *et al*.,

2006; Caruso *et al*., 2008; Hawes *et al*., 2009; Scherber *et al*., 2010; Bardgett and Van der Putten, 2014; Hines *et al*., 2015). However, these results regarding invertebrate biodiversity are in contradiction to studies investigating above- and below-ground linkages between plants and bacteria (Postma-Blaauw *et al*., 2010; Li *et al*., 2015), suggesting that plant-invertebrate and plant-microbe interactions may be decoupled. Li *et al*. (2015) showed that it was only in well-established communities where vegetation and β-diversity coupled after long sessional time periods. However, due to annual disturbance from ploughing within conventional maize cropping systems the successional time periods are relatively short suggesting that conventional maize system communities are more reliant on resource richness rather than the physical stability of the macro-environment (Postma-Blaauw *et al*., 2010). In conjunction with ploughing and tillage impacting the successional development of soil microflora communities, the development of below-ground arthropod communities is also impeded (Li *et al*., 2015). This offers a rationale as to why the below-ground invertebrate communities were found to be more strongly linked to changes in disturbance, resource availability and invertebrate population recovery rates than above-ground (Wardle *et al*., 1995; Scherber *et al*., 2010), which were better able to avoid disturbances, and benefit from refuges. These results have implications for the functionality and resistance of ecosystem services facilitated by below-ground invertebrates in row crop agricultural systems, specifically reduced soil disturbance and incorporation of greater ground cover by vegetation could better support these functions, particularly as below-ground microflora and mesofauna are crucial from the recycling of organic matter, retention of nutrients and carbon sequestration (Finke *et al*., 1999; Liedgens *et al*., 2004; Gardi and Jeffery, 2009; Bardgett and Cook, 1998)

There is strong evidence to suggest that under the more conventional cultivation methods (PGH and MNT) communities were at a 'baseline' being dominated by *r*-selected taxa (Larsen, 2007). However, where there was a reduction in disturbance and the provision of additional plant resources and refuges for invertebrates to exploit (Klein, 1988), as within the strip tillage into ground cover management practices (BSM and RGS), there were increases in the density and richness of invertebrates. This indicates that the community increased in complexity, with the communities in the strip tillage into ground cover management practices containing more *K*-selected taxa. These results highlight that the community composition and the life histories of taxa within the community are equally important when assessing the resilience of communities to changes in agro-management practices.

Overall, invertebrate communities under the different maize cultivation techniques were more strongly influenced by the richness of sown plants (BSM) rather than cover of sown plants (RGS). These findings regarding the differences in either the quantity (cover) or quality (richness) of sown non-crop resources are supported by Bardgett and Van der Putten (2014). Although greater plant species richness in maize cultivation systems were found to support more abundant, diverse, complex communities, it was also shown that implementing relatively low levels of vegetative richness also benefited arthropod communities. It should therefore be hypothesised that to increase the rate at which beneficial ecosystem services are facilitated by the below-ground community there should be increases in non-crop vegetative cover, as found within the strip tillage into a ground cover of ryegrass. There is also evidence to suggest that by maintaining relatively low vegetative diversity there could be benefits in reduced environmental impacts (Appendix Figure 12.2.1). In addition to the reductions in run-off and sediment loss, there is evidence to suggest that there would be a strengthening of the relationship between the generalist predators and detritivores in ryegrass strip tillage systems. The strengthened generalist predator densities due to more abundant detritivores may enable greater populations of predators to be more suppressive of dramatic increases in pest numbers (Scheu, 2001), through larger populations of generalist predators (De Ruiter *et al*., 2005). Despite these linkages, work by Scherber *et al*. (2010) showed that these effects for both the above- and below-ground invertebrate communities would be dampened at higher trophic levels indicating that there would be less of an improvement in the bio-control of pests.

Below-ground invertebrates are linked to the above-ground communities by mediating changes in plant performance which consequently affects above-ground herbivores influencing bottom-up trophic cascades (Scheu, 2001; Johnson *et al*., 2011). Above- and below-ground feedbacks are also influenced by generalist predators (Wardle, 2005). The generalist predator pathway is considered to be particularly important in natural and agricultural systems (Scheu, 2001; Johnson *et al*., 2011; Hines *et al*., 2015). However, management strategies in arable systems that support detritivore populations could switch generalist predators' prey from detritivores to herbivores; this would improve top-down control by predators through the increased density of prey, which may also help control herbivores in arable systems through a strengthening of trophic linkages.

In the two more conventional maize cultivation methods (PGH and MNT) there were reductions in density and richness of above-ground invertebrates over the two cultivation seasons, which further impeded important ecosystem function and ultimately the rate and resilience of these services (Turnbull *et al*., 2014). In contrast, where there was a non-crop refuge, that was not tilled, and greater native vegetation for above- and below-ground invertebrates to consume there was an increase in richness and abundance of invertebrates from the first to the second field trial year. This demonstrates that by implementing strip tillage over multiple cropping seasons it is possible to reduce the impact on invertebrate biodiversity and the erosion of the ecosystem services (Giller, 1997; Gardi and Jeffery, 2009). This is of intrinsic importance within maize cultivation as unlike most arable crops that are cultivated in rotation, maize is commonly grown year after year in the same field for multiple seasons (Aune *et al*., 2012; Hartwig and Ammon, 2002; Nakamoto and Tsukamoto, 2006), which has a detrimental effect on above- and below-ground invertebrate biodiversity.

10.2. Above-ground invertebrate food webs are less stable than below-ground invertebrate food webs

Differences in the isotopic signatures of the below-ground communities recovered from the grassland and maize systems were similar to those found by Crotty *et al*. (2013) when comparing resource use by invertebrate communities in grasslands and woodlands. These consistent results indicate that similar taxonomic groups in different habitats are able to consume different resources. The resources invertebrate communities use are derived predominantly from the dominant vegetation, either in the form of plant matter, degraded residues and/or litter within each habitat (Hirsch *et al*., 2009), these resources before being consumed by detrital invertebrates are often mediated by the microflora community (Pausch *et al*., 2015; Börjesson *et al*., 2015). This adds to the growing body of evidence to suggest an intrinsic interconnectedness between plants-bacteria-invertebrates suggesting that to improve the ecosystem functionality within arable systems through reductions in disturbance and increases in non-crop vegetation richness and cover could better support these linkages.

Under the conventional maize cultivation system there was a temporal shift in the diets of invertebrates within the community (Chapter 9). Blagodatskaya *et al*. (2011) found under changes in C3 to C4 vegetation where there was mediation of maize derived carbon by the microflora community indicated by elevated $\delta^{15}N$ of invertebrates that were feeding within

the detrital feeding channel (Pausch *et al*., 2015; Hyodo, 2015). The detrital community performs two major functions: the mineralisation of essential plant nutrients and the formation of soil organic matter (Swift *et al*., 1979). The detrital feeding channel was found to predominantly consume maize derived carbon during pre-cultivation and post-harvest under conventional maize cultivation (Chapter 8 and 9). The temporal shift in isotopic composition of invertebrate taxa indicates that during cultivation only a small proportion of maize derived carbon was consumed by the microflora community (Kramer *et al*., 2012; Börjesson *et al*., 2015), which was then reflected by the invertebrate community (Hyodo, 2015). The lack of maize derived carbon being mineralised or incorporated into soil organic matter led to a more depleted soil carbon isotope signature than expected. This low incorporation of C4 carbon into the bulk soil could be due to the temporal abundance of fungal consumers, which were disturbed by cultivation and only recovered later in the cropping season (Pausch *et al*., 2015; Börjesson *et al*., 2015). During the maize growth phase of cultivation under PGH, only a small proportion of maize derived carbon was being consumed by invertebrates (Börjesson *et al*., 2015). This can be attributed to the low amount of C4 carbon entering the soil system for microflora to consume, which could be due to the maize being in a rapid growth phase and storing carbon within plant tissue rather than losses through exudates (Newell, 1984), and may be why other studies have observed low proportions of C4 carbon within the soil (Dungait *et al*., 2013).

Changes in which resources were consumed over relatively short temporal scales (within the cultivation season) shows that when considering actions to improve biodiversity, the below-ground communities within maize systems must be considered as an important component in the decomposer network. By focusing future research on supporting the detrital feeding channel there is an opportunity to understand the transformation, transmission and translocation of nutrients within agro-systems. It is through better understanding of these complex nutrient flow pathways that agro-environment management plans should aim to improve the rate at which ecosystem services occur (Gardi and Jeffery, 2009), leading to improved yield (Stockdale *et al*., 2006) or improved carbon storage capacity (Dungait *et al*., 2013).

Coupling Bayesian informed credibility intervals and network analysis has shown that, due to greater abundance of biometrically smaller taxa, the below-ground food web had greater stability than the above-ground. It should also be noted that the above-ground community

had a greater dispersal efficiency and higher degree of predator specialisation in comparison to the below-ground community. In contrast, below-ground where there were restrictions, both morphologically and by habitat structure, predators exhibit more generalist isotopic signatures providing uniform top down pressures on the below-ground community (Scheu, 2001; Barbosa and Castellanos, 2005; Peckarsky *et al*., 2014). Links between the above- and below-ground communities, and the generalism of predators, were found to be size dependent. For example, Staphylinidae were found using both the above- and below-ground sampling methods and exhibited generalist feeding patterns (Figure 9.4). The allometric distribution of the Staphylinidae allowed them to feed in both above- and below-ground habitat compartments (Figure 9.5 and 9.6). This is the first experimental evidence to show that the top down linkages between the above- and below-ground habitats may be size related. Scheu (2001) showed that of the generalist predators Araneae, Staphylinidae and Carabidae are among the most important within agricultural systems. As such these predators are often viewed as predators of the above-ground system, which are subsidised by resources from the decomposer system. However, when the prey from the below-ground system predominates, the opposite view may be more appropriate. Scheu (2001) highlighted that when herbivores are scarce, as in well managed conventional maize cultivation systems, the below-ground decomposer prey supports generalist predators which may strengthen trophic cascade above-ground reducing plant damage by herbivores. This body of work adds to the growing evidence to suggest that the above- and below-ground invertebrate communities are intrinsically linked and that these links between the two systems are more complex than previously thought.

10.3. Further work

This thesis provides a framework from which to further measure the effects of contrasting maize cultivation techniques on above- and below-ground biodiversity in temperate regions. This work highlights that when considering agro-management practices the below-ground community must be considered as a significant proportion of invertebrates that facilitate important ecosystem services reside within the soil system for part or all of their life histories (Giller, 1996).

Implementing MixSIAR Bayesian mixing model credibility intervals (Stock and Semmens, 2010) in conjunction with food web analysis (Hudson *et al*., 2013) provides a robust repeatable method for assessing invertebrate food webs (Chapter 9). All future analysis should be performed within these model frameworks to provide comparable community

information between habitats and geo-climatic regions. This would increase our understanding of complex community dynamics within the soil and between the above- and below-ground communities improving our conceptualisation of ecosystem processes. However, the BSIM and 'Cheddar' model frameworks do not provide insights into intraguild predation. The adaption of compound specific mass spectroscopy and PLFA analysis with BSIMS informed food web models may yield valuable insights into the proportion of intraguild predation exhibited at higher trophic levels. Incorporating intraguild predation may provide solutions in the future for defining smart bio-control techniques through supporting both generalist and specialist predators. In addition, calculations by De Ruiter *et al*. (2005) should be incorporated into the 'Cheddar' model framework as this would give valuable insights into the strengths and relative importance of food web linkages with regards to nutrient transfer and storage in both natural and agricultural systems.

Evidence for the strengthening of bottom-up and top-down force in maize cultivation systems through reduced disturbance and increases in vegetation cover and richness generate interesting testable theories regarding the longevity of these linkages. This thesis suggests that experimentally manipulating the numbers of detritivores in the above- and below-ground food webs may have legacy effects on the ability of predator populations to control increases in herbivore numbers. This could be examined by carrying out laboratory and field experiments where the number of above- and below-ground detritivores could be artificially increased for a period of time and then a combination of above- and below-ground herbivores could be added whilst consistently monitoring predator numbers. This would enable the strengths of these relationships and the longevity of the effects to be disentangled.

To provide a viable cultivation alternative to farmers there must be further research into balancing invertebrate biodiversity gains with maintaining maize yields. This could be achieved through a number of strategies. The strip crop could be rotavated and incorporated into the soil before drilling. Although this practice would increase the area disturbed, there may be sufficient diversity of invertebrates to tolerate these disturbances and recover, especially if the strip crop was ryegrass. Rotavating the strip crop would allow the vegetation to recover over the cultivation season, providing greater vegetative cover and increased root biomass to aid with soil stability, reduce rain splash, run-off, sediment loss and improve invertebrate biodiversity over the often fallow winter season.

Alternatively biodiversity benefits, especially to the detrital community, maybe gained from applying litter mulch immediately before the soil is ploughed. However, any policies that implement changes in management practice should be considered in light of the fact that additional use of machinery within the field will ultimately increase fuel usage and soil compaction, which may result in reduced pore space, leading to an overall reduction in habitat quality for important below-ground decomposers (Nakamoto and Tsukamoto, 2006). Balancing the yield penalties to farmers as well as ecological and environmental benefits from strip cropping maize must be researched as the current practice for cultivating maize is unsustainable due to the risk of soil erosion and sediment loss from conventional maize cropping systems.

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Appendices

12. Appendix

12.1. Effects of maize cultivation on vegetation dynamics

12.1.1. Introduction

This appendix describes procedures for in situ botanical recording during 2013 and 2014 field trial years as part of Work Package 2 in the Competitive Maize Cultivation with Reduced Environmental Impact project. The sampling strategy and data collation was designed by Nigel Crichley at ADAS.

12.1.1.1. Objectives

The overall objective of this work package was to quantify the effects of contrasting cultivation and ground cover management practices on vegetativebiodiversity.

12.1.2. Material and methods

12.1.2.1. Quadrat locations

Visual assessment of the non-crop vegetation was carried on three occasions in 2013 and 2014. Visual assessments were carried out in May, late June/ early July and October/November to coincide with arthropod sampling. The row and inter-row areas were sampled separately within each plot. Six vegetation samples were located within each of the row and inter-row areas within plots with quadrat (1.0 m x 0.25 m) placed at random locations, parallel to the rows of maize. Mean percentage cover by litter, percentage cover by bare ground and vegetation richness (number of plants 0.25 m^2)was calculated for each plot.

12.1.2.2. Statistical analysis

All statistical analysis was conducted using Rstudio (Racine, 2012). The overall difference in vegetation between sites, cultivation methods, row or inter-row areas and cultivation years were tested using Euclidian algorithm was used to calculate a distance matrix before analysis of dissimilarity between factors was tested on 999 permutations. Analysis of variance was used to identify significant difference between factors and vegetative variates. Tukey HSD tests were applied to identify true significant differences between factor levels using R-package ‘agricolae’. For full descriptions of statistical procedures please see Section 3.6.

Table 12.1.1 Percentage by weight of species sown in the strip tillage with biodiverse seed mix cultivation method at a rate of 15 kg/ha.

Species Binomial	Common name	Percentage by weight
Medicago lupulina L.	Black medick	20
Onobrychis viciifolia L.	Sainfoin	25
Trifolium hybridum L.	Alsike clover	20
Trifolium incarnatum L. subsp. Incarnatum	Crimson clover	20
Lotus corniculatus L.	Bird's-foot trefoil	10
Malva moschata L.	Musk mallow	5

12.1.3. Results

12.1.3.1. Both experimental sites

Table 12.1.2 Vegetation richness, percentage cover by litter, percentage cover by bare-ground and percentage cover by vegetation information collected from both sites and all sampling times except post-harvest 2013 was used test for difference in factors. The Euclidian algorithm was used to calculate a distance matrix before analysis of dissimilarity between factors was tested on 999 permutations. The vegetation Euclidian distance matrix was used to test for significant differences between the two sites, all four cultivation methods, the row or inter-row areas, the two cultivation years, and all interactions between these factors, whilst block was used as the fixed factor strata.

		Litter		Bare ground		Cover		Vegetation Richness	
	Df	F-Model	P-Value	F-Model	P-Value	F-Model	P-Value	F-Model	P-Value
Site	1	6.57	0.012 *	3.67	0.058	1.86	0.175	4.66	0.033 *
Cultivation method	3	44.44	0.000 ***	75.33	0.000 ***	161.37	0.000 ***	66.00	0.000 ***
Row or Inter Row	1	3.14	0.079	6.02	0.016 *	1.47	0.228	2.26	0.136
Year	1	0.07	0.791	0.14	0.706	4.24	0.042 *	41.41	0.000 ***
Block	1	0.71	0.403	0.29	0.594	0.01	0.941	0.12	0.729
Site*Cultivation method	3	8.71	0.000 ***	0.83	0.480	2.37	0.074	3.05	0.032 *
Site*Row or Inter Row	1	0.84	0.362	0.27	0.604	0.11	0.745	0.06	0.812
Cultivation method*Row or Inter Row	3	3.33	0.022 *	6.20	0.001 ***	2.95	0.036 *	2.41	0.071
Site*Year	1	0.17	0.684	0.23	0.636	0.58	0.449	36.84	0.000 ***
Cultivation method*Year	3	17.09	0.000 ***	1.65	0.183	3.19	0.026 *	10.09	0.000 ***
Row or Inter Row*Year	1	1.43	0.234	12.67	0.001 ***	5.52	0.021 *	0.31	0.576
Site*Cultivation method*Row or Inter Row	3	4.43	0.006 **	1.37	0.256	0.88	0.456	1.93	0.130
Site*Cultivation method*Year	3	5.35	0.002 **	0.65	0.587	2.21	0.090	10.01	0.000 ***
Site*Row or Inter Row*Year	1	3.37	0.069	2.52	0.115	4.63	0.034 *	2.30	0.132
Cultivation method*Row or Inter Row*Year	3	1.55	0.207	2.48	0.065	1.23	0.304	0.20	0.899
Site*Cultivation method*Row or Inter Row*Year	3	1.65	0.181	2.14	0.100	2.74	0.047 *	0.87	0.461

The richness and percentage cover of litter was significantly different between the two field trial sites and cultivation methods which varied over the two field trial years (Table 12.1.2). There were significant differences in the percentages cover of vegetation and bare ground between the row and inter-row areas varied over the two field trial years (Table 12.1.2). There were significant differences in the cover of vegetation between the row and inter-row areas, which varied depending on cultivation method and field trial site (Table 12.1.2).

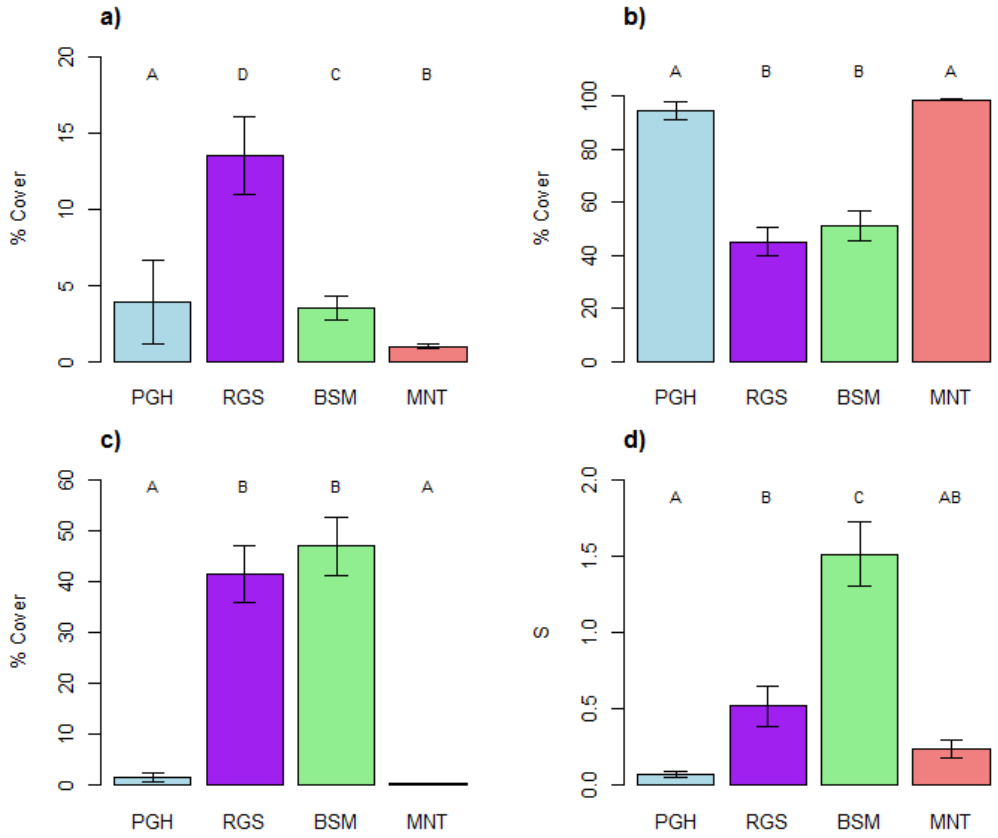


Figure 12.1.1 Vegetation composition data from both field sites was used to calculate the mean (± s.e.) a) percentage cover by litter, b) percentage cover by bare ground c) percentage cover by vegetation and d) vegetation richness for each cultivation method (PGH , RGS , BSM , MNT). Letters denote Tukey HSD significance groups where different letters denote significantly different groups; Tukey HSD tests were calculated based on Box-Cox transformed values

The percentage cover by litter was significantly greater in RGS compared with the other three cultivation methods (Figure 12.3.1a). The strip tillage cultivation methods were significantly lower in the percentage cover by bare ground (Figure 12.3.1d), where percentage cover by vegetation in the strip tillage techniques was also greater (Figure 12.3.1c). Vegetation richness was significantly greater in BSM when compared with the other three cultivation methods (Figure 12.3.1d).

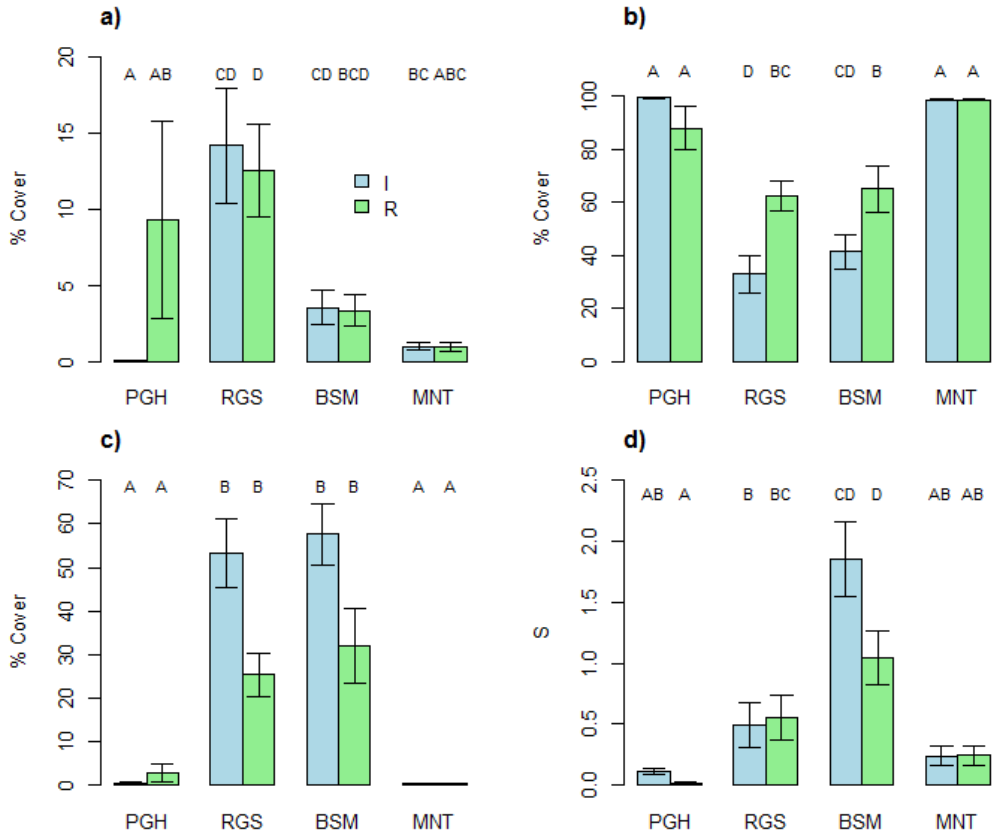


Figure 12.1.2 Vegetation composition data from both field sites was used to test for difference in a) percentage cover by litter, b) percentage cover by bare ground c) percentage cover by vegetation and d) vegetation richness between the row (R) or inter-row (I) areas. Bars represent mean values (± s.e.) and letters represent Tukey HSD significance groups, where different letters denote significantly different groups.

There were no significant differences in the percentage cover by litter between the row and inter-row areas of each cultivation method (Figure 12.3.2). The strip tillage cultivation methods had significantly less bare ground in the inter-row areas compared with the row areas, where as the conventional cultivation methods had similar coverage by bare ground (Figure 12.3.2b). The percentage cover by vegetation between row and inter-row areas was significantly different in the strip tillage treatments with the inter-row area being significantly greater in coverage by vegetation than the row areas; however, as with cover by bare ground, there were no significant differences between the row and inter-row areas in the more conventional cultivation methods (Figure 12.23.2c). There was no significant difference in the vegetation species richness between the row and inter-row areas of any cultivation method **(**Figure 12.3.2d).

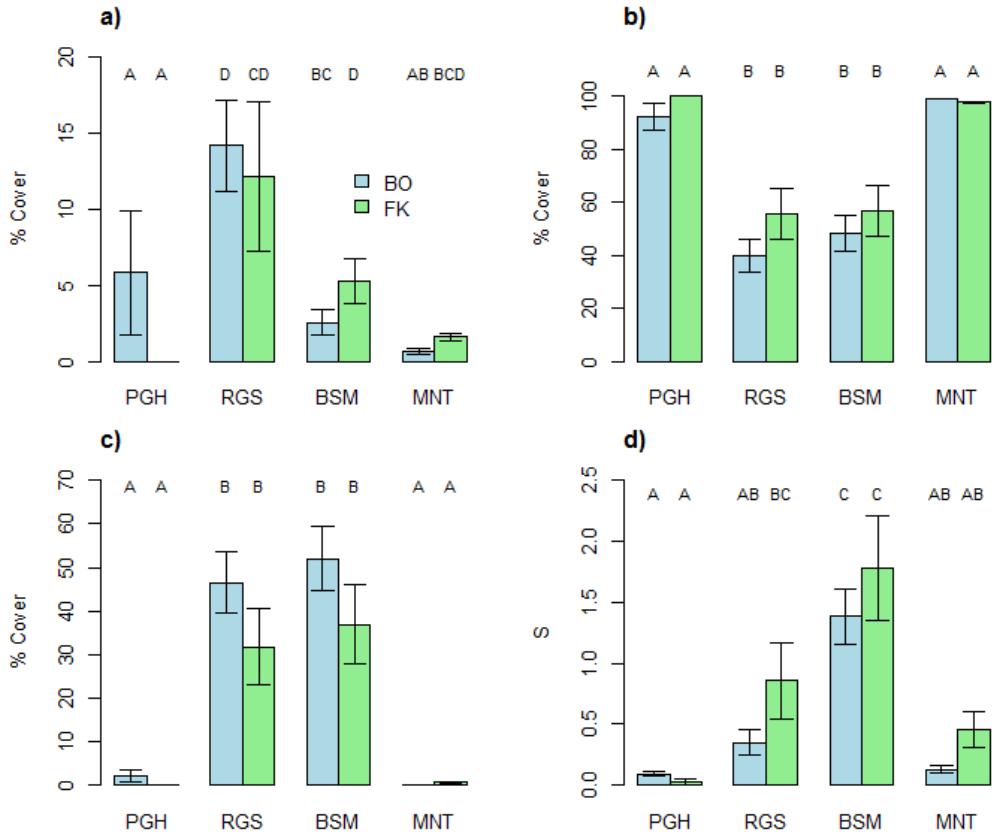


Figure 12.1.3 Vegetation composition data from both row and inter-row areas was used to test for difference in a) percentage cover by litter, b) percentage cover by bare ground c) percentage cover by vegetation and d) vegetation richness between the sites (Fakenham , Bow). Bars represent mean values (± s.e.) and letters represent Tukey HSD significance groups, where different letters denote significantly different groups.

There were significant differences between the vegetation composition and cover between the two field trial sites (Table 12.1.2). There was significantly less coverage by litter at the Bow site in BSM (Figure 12.3.3a). There were no significant differences in coverage by bare ground, percentage cover by vegetation or vegetative richness between the field trial two sites (Figure 12.3.3b to d).

There was a significant increase in the percentage cover by litter in RGS between field trial year one and two (Figure 12.3.4a). There were no significant differences in the percentage cover by bare ground or vegetation in any of the cultivation methods between field trial years (Figure 12.3.4 b and c). There were however changes in the vegetation richness between field trial years in the two strip tillage cultivation methods where both where significantly reduced in the second field trial year.

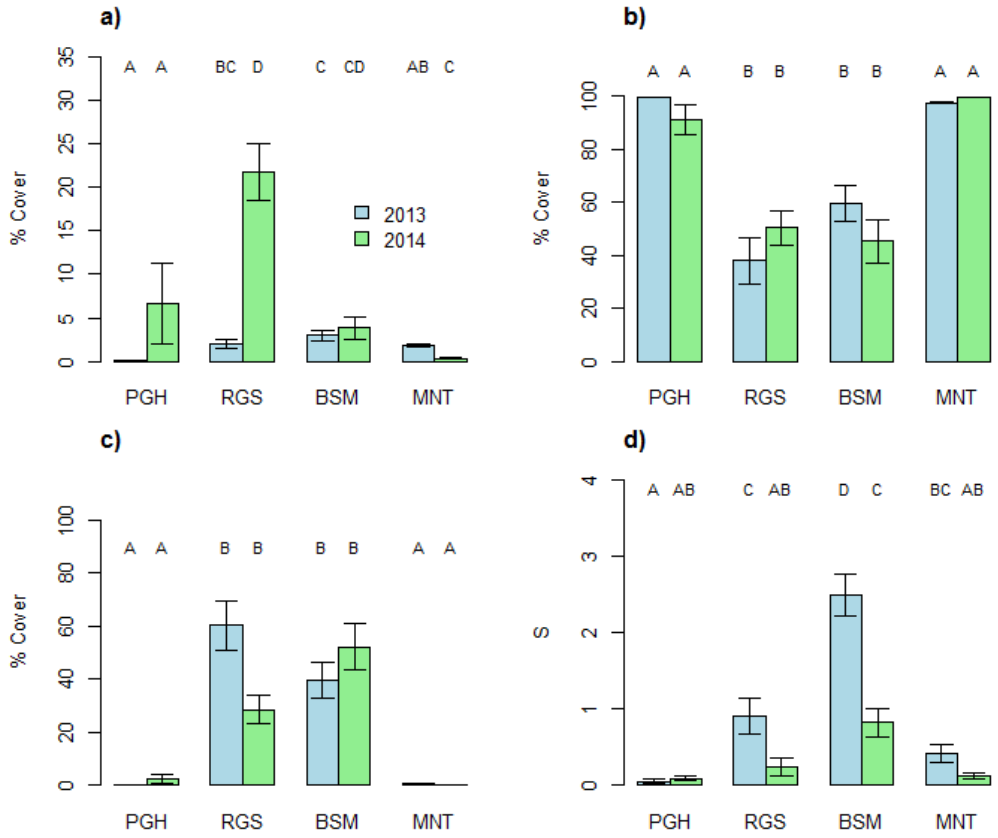


Figure 12.1.4 Vegetation composition data from both sites was used to test for difference in a) percentage cover by litter, b) percentage cover by bare ground c) percentage cover by vegetation and d) vegetation richness between the two cultivation seasons (2013 , Fakenham). Bars represent mean values (± s.e.) and letters represent Tukey HSD significance groups, where different letters denote significantly different groups.

12.1.4. Discussion and Conclusions

There were changes in vegetation composition between the two field trial sites over the course of the experiment. To attempt to improve maize yields in the second field trial year additional herbicides were applied and although this increased maize yield it also had a significant impact on the richness of vegetation in the two strip tillage cultivation methods. Changes in ground cover management had a significant effect on overall invertebrate biodiversity, where increases in the cover and richness of vegetation positively affected both above- and below-ground invertebrate biodiversity.

12.2. Materials and methods appendices

Plate 12.2.1 Outline map of the United Kingdom showing the two field experiment sites. The Bow, Devon site is denoted by a circle and the Fakenham, Norfolk site by a circle.

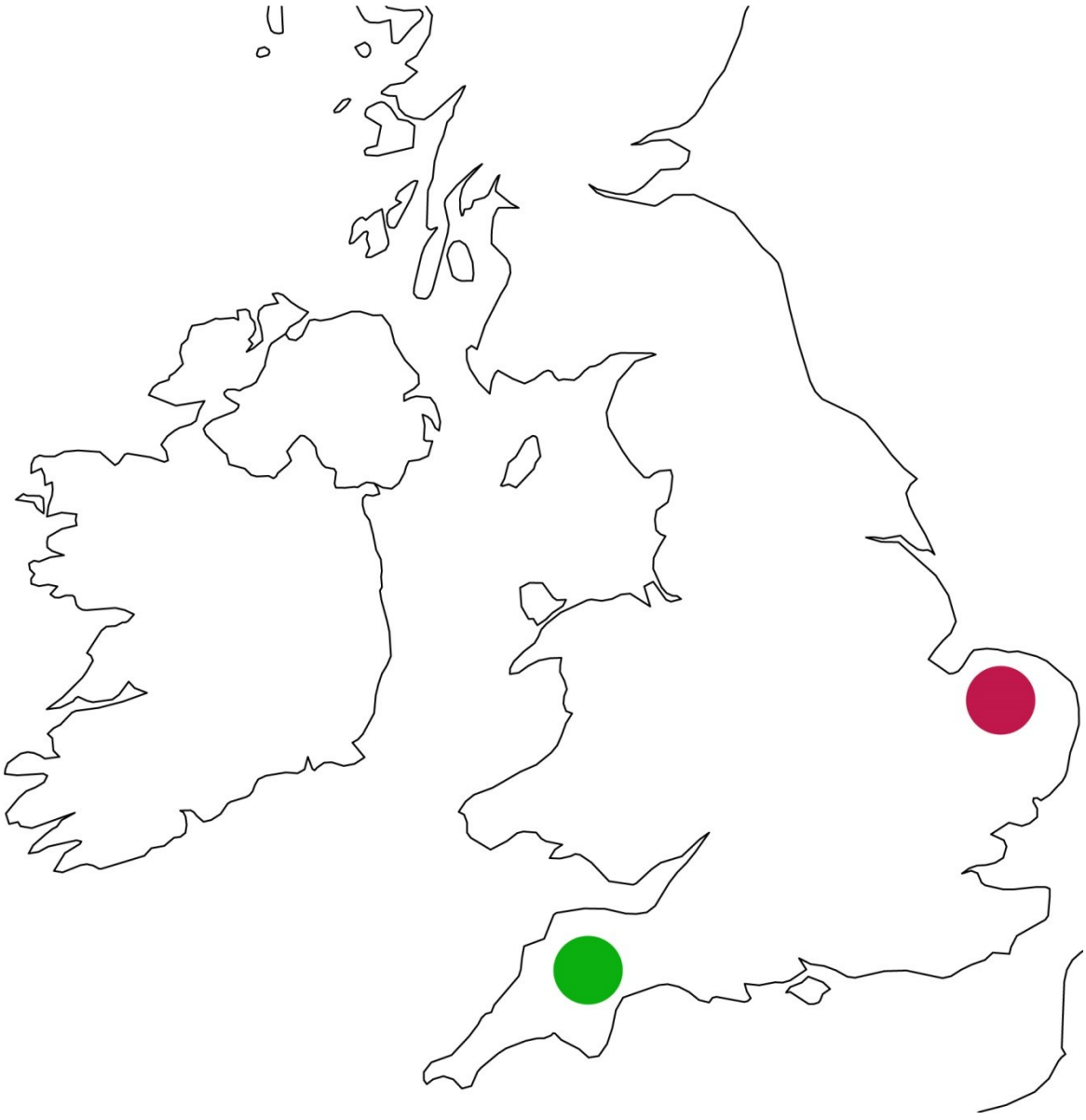


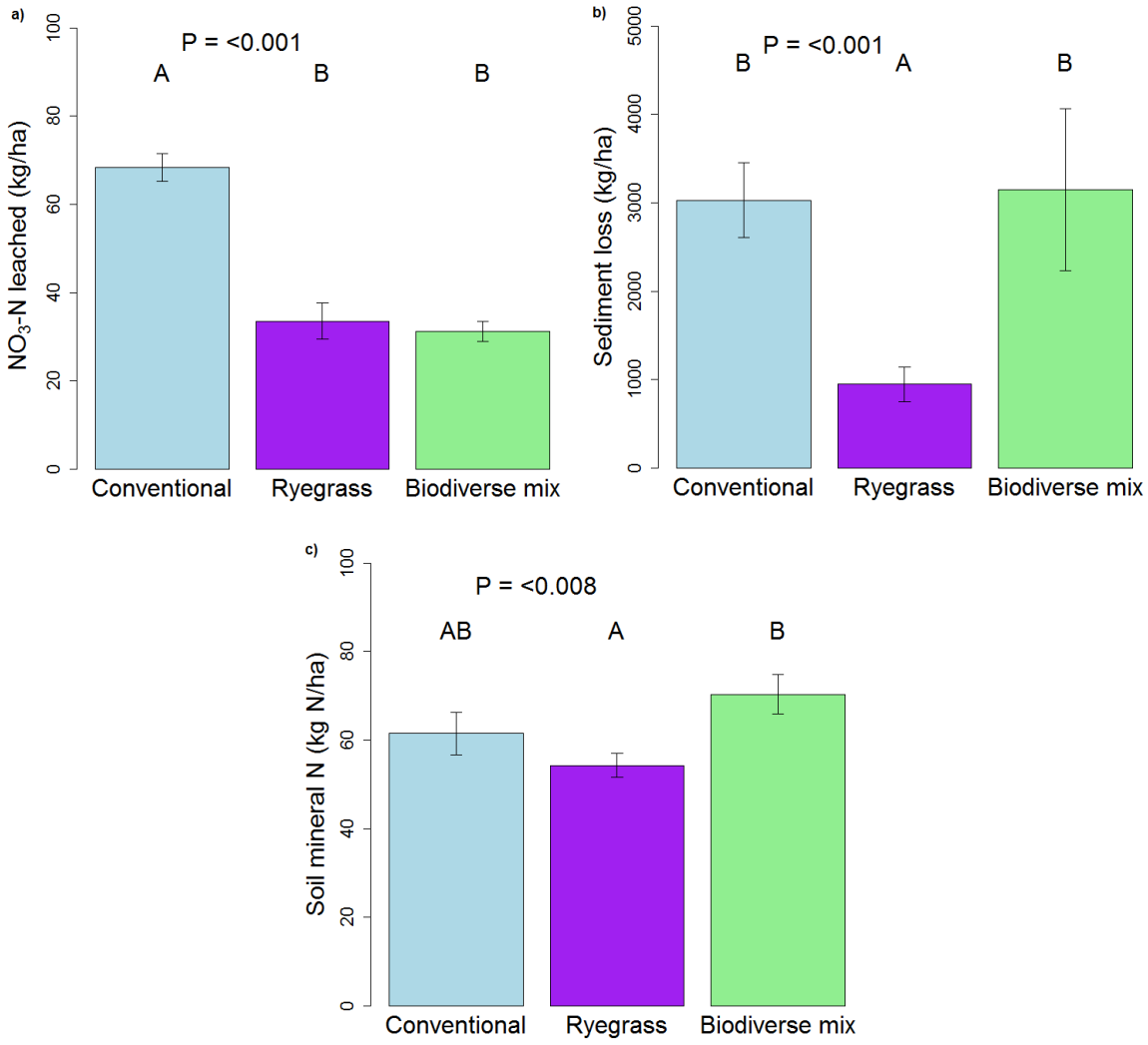
Table 12.2.1 Soil physiochemical properties, meteorological information and slope of the two field trial sites (Bow, Devon and Fakenham, Norfolk)

	Bow		Fakenham	
	Mean (s.e.)		Mean (s.e.)	
pH	7.37	(0.03)	7.97	(0.03)
Available P (mg/l)	75.67	(3.67)	45	(2.08)
P Index	5		4	
Available K (mg/l)	242.33	(7.09)	142.33	(1.33)
K index	3		2	
Available Mg (mg/l)	120.67	(7.97)	48.33	(0.88)
Mg Index	2		1	
Sand %	51		66	
Silt %	28		19	
Clay %	21		15	
Available sulphate (mg/l)	25.93	(1.07)	20.17	(0.39)
Total Nitrogen	0.27	(0.01)	0.22	(0.01)
Soil organic matter (%w/w)	1.26	(0.05)	1.74	(0.12)
Textural class	Sandy clay loam		Sandy loam	
Slope (%)	10		2.5	
Total daily rainfall (mm)	2.92	(0.21)	2.15	(0.16)
Max Air Temperature (°C)	14.07	(0.22)	14.45	(0.24)
Min Air Temperature (°C)	7.21	(0.18)	6.80	(0.18)

Table 12.2.2 Mean dry matter yield (t/ha) (± s.e.) (n=3) at Bow and Fakenham for both cultivation seasons. Letters denote Tukey HSD level codes where different letters denote significantly different groups. Dry matter yield (t/ha) data was Box-Cox transformed to ensure normality before Tukey HSD test were carried out. Sampling strategy and data collation was carried out by Kate Smith (ADAS).

Cultivation method	Year	Mean dry matter yield (t/ha) (± s.e.)		Tukey HSD
PGH	2013	11.16	(1.31)	BC
	2014	11.27	(0.96)	BC
RGS	2013	1.21	(0.16)	A
	2014	8.28	(1.10)	B
BSM	2013	1.21	(0.08)	A
	2014	8.08	(0.30)	B
MNT	2013	9.65	(0.48)	BC
	2014	12.62	(0.29)	C

Figure 12.2.1 Mean (± s.e.) of the a) nitrate leached; b) sediment lost and c) soil mineral nitrogen from the conventional plough, strip tillage with ryegrass and strip tillage with a biodiverse seed. *P*-value based on Box-Cox transformed data from both field trial sites over the two cultivation seasons. Letters denote Tukey HSD differences, where different letters denoted significantly different groups. Sampling strategy and data collation was carried out by Kate Smith (ADAS).



12.3. The effect of maize cultivation on below-ground invertebrate biodiversity

Table 12.3.1 Mean (± s.e.) mesofauna, macrofauna and earthworm richness, abundance, evenness and Shannon diversity for each site, cultivation method, row or inter-row area and experimental year.

					Meso-invertebrates				Macro-invertebrates				Earthworms			
Site	Culitvatiom method	Row or Inter-row	Experimental year	df	Richness (s)	Abundace (m^2) (s.e)	Pielou's Evenness (J) (s.e)	Shannon divetsity (H') (s.e)	Richness (s) (s.e)	Abundace (m^2) (s.e)	Pielou's Evenness (J) (s.e)	Shannon divetsity (H') (s.e)	Richness (s) (s.e)	Abundace (m^2) (s.e)	Pielou's Evenness (J) (s.e)	Shannon divetsity (H') (s.e)
BO	PGH	I	2013	3 11	(1.33)	4633 (1133.70)	0.75 (0.04)	0.77 (0.07)	1 (0.33)	50 (25.00)	0.00 (0.00)	0.00 (0.00)	0 (0.00)	0 (0.00)	0.00 (0.00)	0.00 (0.00)
			2014	3 13	(2.73)	14333 (6880.91)	0.72 (0.07)	0.81 (0.12)	1 (0.33)	50 (25.00)	0.00 (0.00)	0.00 (0.00)	2 (1.00)	40 (27.32)	0.12 (0.12)	0.16 (0.16)
		R	2013	3 11	(0.00)	4733 (820.74)	0.79 (0.03)	0.82 (0.04)	1 (0.58)	75 (43.30)	0.33 (0.33)	0.10 (0.10)	0 (0.00)	0 (0.00)	0.00 (0.00)	0.00 (0.00)
			2014	3 16	(1.86)	16933 (4735.89)	0.75 (0.01)	0.91 (0.04)	1 (0.33)	175 (25.00)	0.33 (0.33)	0.10 (0.10)	1 (0.88)	23 (11.60)	0.14 (0.14)	0.15 (0.15)
	RGS	I	2013	3 11	(1.33)	3617 (1192.45)	0.84 (0.04)	0.87 (0.01)	0 (0.33)	25 (25.00)	0.00 (0.00)	0.00 (0.00)	0 (0.33)	2 (2.08)	0.00 (0.00)	0.00 (0.00)
			2014	3 21	(0.67)	31183 (6820.15)	0.76 (0.04)	1.00 (0.04)	1 (0.33)	50 (25.00)	0.00 (0.00)	0.00 (0.00)	2 (0.58)	29 (16.67)	0.28 (0.14)	0.25 (0.13)
		R	2013	3 12	(1.53)	3600 (251.66)	0.83 (0.03)	0.89 (0.07)	0 (0.33)	25 (25.00)	0.00 (0.00)	0.00 (0.00)	1 (0.67)	4 (4.17)	0.14 (0.14)	0.10 (0.10)
			2014	3 18	(0.88)	36117 (3363.08)	0.68 (0.02)	0.85 (0.03)	1 (0.58)	100 (50.00)	0.33 (0.33)	0.10 (0.10)	1 (0.88)	25 (21.95)	0.11 (0.11)	0.12 (0.12)
	BSM	I	2013	3 14	(2.52)	5883 (2078.13)	0.65 (0.06)	0.73 (0.08)	0 (0.00)	0 (0.00)	0.00 (0.00)	0.00 (0.00)	0 (0.33)	4 (4.17)	0.00 (0.00)	0.00 (0.00)
			2014	3 19	(4.26)	27383 (12047.21)	0.74 (0.01)	0.93 (0.07)	0 (0.00)	0 (0.00)	0.00 (0.00)	0.00 (0.00)	3 (0.33)	52 (24.56)	0.38 (0.02)	0.36 (0.05)
		R	2013	3 11	(0.88)	3517 (348.01)	0.77 (0.04)	0.81 (0.06)	0 (0.00)	0 (0.00)	0.00 (0.00)	0.00 (0.00)	0 (0.33)	2 (2.08)	0.00 (0.00)	0.00 (0.00)
			2014	3 15	(4.10)	16700 (8070.47)	0.72 (0.01)	0.80 (0.10)	0 (0.00)	0 (0.00)	0.00 (0.00)	0.00 (0.00)	3 (0.88)	40 (22.05)	0.27 (0.14)	0.34 (0.17)
	MNT	I	2013	3 12	(2.31)	6583 (3181.50)	0.76 (0.07)	0.80 (0.05)	1 (0.00)	150 (43.30)	0.00 (0.00)	0.00 (0.00)	0 (0.00)	0 (0.00)	0.00 (0.00)	0.00 (0.00)
			2014	3 11	(1.33)	7050 (1757.84)	0.75 (0.05)	0.78 (0.10)	1 (0.00)	75 (0.00)	0.00 (0.00)	0.00 (0.00)	0 (0.33)	4 (4.17)	0.00 (0.00)	0.00 (0.00)
		R	2013	3 10	(1.86)	3150 (1159.02)	0.79 (0.03)	0.79 (0.07)	1 (0.67)	50 (50.00)	0.33 (0.33)	0.10 (0.10)	0 (0.00)	0 (0.00)	0.00 (0.00)	0.00 (0.00)
			2014	3 14	(0.67)	11433 (1198.73)	0.66 (0.02)	0.74 (0.03)	0 (0.33)	25 (25.00)	0.00 (0.00)	0.00 (0.00)	2 (0.33)	25 (6.25)	0.27 (0.13)	0.18 (0.09)
FK	PGH	I	2013	3 13	(0.88)	8800 (4175.62)	0.78 (0.04)	0.88 (0.05)	0 (0.33)	25 (25.00)	0.00 (0.00)	0.00 (0.00)	2 (0.33)	58 (5.51)	0.28 (0.14)	0.19 (0.10)
			2014	3 10	(0.88)	4033 (1044.16)	0.81 (0.04)	0.80 (0.05)	1 (0.33)	250 (108.97)	0.22 (0.22)	0.07 (0.07)	3 (0.33)	131 (42.54)	0.28 (0.03)	0.27 (0.05)
		R	2013	3 10	(1.20)	3933 (1628.48)	0.76 (0.05)	0.76 (0.04)	0 (0.33)	25 (25.00)	0.00 (0.00)	0.00 (0.00)	2 (0.33)	152 (31.53)	0.34 (0.03)	0.29 (0.07)
			2014	3 15	(1.15)	8200 (1589.29)	0.75 (0.02)	0.88 (0.05)	1 (0.33)	175 (50.00)	0.31 (0.31)	0.09 (0.09)	3 (0.58)	165 (77.42)	0.24 (0.05)	0.27 (0.09)
	RGS	I	2013	3 11	(0.33)	5733 (732.76)	0.78 (0.07)	0.82 (0.07)	1 (0.33)	50 (25.00)	0.00 (0.00)	0.00 (0.00)	2 (0.67)	25 (15.73)	0.14 (0.14)	0.15 (0.15)
			2014	3 14	(2.08)	20217 (8189.75)	0.67 (0.05)	0.76 (0.07)	0 (0.33)	25 (25.00)	0.00 (0.00)	0.00 (0.00)	2 (0.58)	48 (22.05)	0.20 (0.10)	0.18 (0.09)
		R	2013	3 12	(1.33)	4033 (1718.61)	0.80 (0.04)	0.86 (0.01)	1 (0.00)	100 (25.00)	0.00 (0.00)	0.00 (0.00)	1 (0.33)	6 (3.61)	0.00 (0.00)	0.00 (0.00)
			2014	3 15	(1.86)	18950 (6698.01)	0.66 (0.06)	0.77 (0.06)	1 (0.33)	125 (25.00)	0.33 (0.33)	0.10 (0.10)	2 (0.58)	75 (25.26)	0.20 (0.10)	0.17 (0.09)
	BSM	I	2013	3 14	(1.15)	7183 (724.76)	0.75 (0.04)	0.86 (0.08)	1 (0.33)	50 (25.00)	0.00 (0.00)	0.00 (0.00)	3 (0.33)	52 (7.51)	0.35 (0.05)	0.33 (0.03)
			2014	3 20	(1.76)	22317 (2290.62)	0.71 (0.02)	0.93 (0.02)	0 (0.33)	25 (25.00)	0.00 (0.00)	0.00 (0.00)	4 (0.88)	123 (35.60)	0.39 (0.01)	0.56 (0.07)
		R	2013	3 13	(2.60)	3317 (1112.93)	0.78 (0.06)	0.83 (0.04)	1 (0.33)	75 (43.30)	0.00 (0.00)	0.00 (0.00)	3 (0.33)	60 (24.03)	0.33 (0.08)	0.31 (0.07)
			2014	3 20	(3.76)	23733 (9102.40)	0.68 (0.03)	0.87 (0.10)	1 (0.58)	125 (66.14)	0.33 (0.33)	0.10 (0.10)	3 (0.58)	121 (41.04)	0.35 (0.04)	0.36 (0.04)
	MNT	I	2013	3 12	(1.20)	3033 (922.11)	0.79 (0.02)	0.86 (0.02)	0 (0.00)	0 (0.00)	0.00 (0.00)	0.00 (0.00)	3 (0.33)	60 (18.16)	0.36 (0.03)	0.35 (0.07)
			2014	3 9	(3.38)	2500 (1201.39)	0.78 (0.05)	0.72 (0.12)	0 (0.33)	25 (25.00)	0.00 (0.00)	0.00 (0.00)	3 (0.33)	113 (23.66)	0.35 (0.05)	0.32 (0.03)
		R	2013	3 9	(1.45)	2283 (713.17)	0.89 (0.05)	0.86 (0.08)	1 (0.58)	100 (50.00)	0.33 (0.33)	0.10 (0.10)	3 (0.00)	108 (43.05)	0.37 (0.02)	0.40 (0.02)
			2014	3 13	(1.76)	7250 (305.51)	0.73 (0.04)	0.80 (0.09)	1 (0.00)	100 (25.00)	0.00 (0.00)	0.00 (0.00)	4 (0.88)	300 (177.70)	0.28 (0.02)	0.35 (0.10)

12.4. Above- and below-ground taxonomic abbreviations used for multivariate analysis

Table 12.4.1 Taxonomic groups and abbreviations of below-ground mesofauna collected using Berlese-Tullgren funnels. Invertebrates that were collected from both sites and all sampling times were allocated to taxonomic groups.

Taxa		Abbreviation	Taxa		Abbreviation
Carabidae	Amara	Am	Hymenoptera larvae		Hym.L
Symphypleona	Arrhopalitidae	Ar	Poduromorpha	Hypogastruridae	Hyp
Sarcoptiformes	Psoroptidae	As	Entomobryomorpha	Isotomidae	Is
Hymenoptera	Pompilidae	A.	Julida	Julidae	Jl
Carabidae	Bembidion	Bm	Coleoptera	Latridiidae	Lthr
Oribatida	Brachypylina	Br	Coleoptera	Leiodidae	Ld
Byturidae	Byturus	By	Araneae	Linyphiidae	Ln
Diplura	Campodeidae	Cm	Lithobiomorpha	Lithobiidae	Lthb
Cantharidae	Larvae	Cn.	Mesostigmata	Macrochelidae	Mcrc
Carabidae	Larvae	Crb.L	Oribatida	Macropyline	Mcrp
Diptera	Cecidomyiidae	Ccdm	Hemiptera	Aphididae	Mcrs
Hemiptera	Cercopidae Nymph	Cr.	Mesostigmata		Ms
Hymenoptera	Chalcidoidea	Chl	Oribatida	Mixmonoata	Mx
Coleoptera	Chrysomelidae	Chr	Neelipleona	Neelidae	Nl
Coleoptera	Chrysomelidae Larvae	Ch.	Nematoda		Nm
Hemiptera	Cicadellidae	Ccdl	Coleoptera	Ochthebius	O.
Coleoptera	Coccinellidae	Ccc	Poduromorpha	Onychiuridae	On
Coleoptera	Coccinellidae Larvae	Cc.	Mesostigmata	Parasitidae	Prstd
Coleoptera	Curculionidae	Cr	Poduromorpha	Poduridae	Pd
Coleoptera	Curculionidae Larvae	Crc.L	Isopoda	Porcellionidae	Prc
Gastropoda	Agriolimacidae	Drc	Trombidiformes	Anystides	Prstg
Oribatida	Desmonomata	Ds	Entomobryomorpha	Pseudosinella	Ps
Symphypleona	Dicyrtomidae	Dc	Diptera	Ptychopteridae	Pt
Diptera larvea		D.	Mesostigmata	Raphignathae	Rp
Diptera	Drosophilidae	Drs	Coleoptera	Scarabaeidae	Scrb
Megadrilacea	Lumbricidae	Er	Diptera	Sciaridae	Scrd
Coleoptera	Elateridae Larave	E.	Diptera	Sciaridae Larvae	Sc.L
Haplotaxida	Enchytraeid	Enc	Symphypleona	Sminthurididae	Sm
Entomobryomorpha	Entomobryidae	Ent	Coleoptera	Staphylinidae	St
Mesostigmata	Epicriioidea	Epc	Coleoptera	Staphylinidae Larvae	St.L
Trombidiformes	Eupodides	Epd	Hymenoptera	Tenthredinidae Larvae	Tn.L
Entomobryomorpha	Folsomia	Fl	Thysanoptera	Thripidae	Th
Hymenoptera	Formicidae	Fr	Diptera	Tipulidae Larvae	Tp.L
Geophilomorpha	Geophilidae	Gp	Diptera	Tipulidae	Tp
Gastropoda	Helicidae	Hl	Lepidoptera	Tortricidae	Trt
Entomobryomorpha	Heteromurus	Htrm	Diptera	Trichoceridae	Trc
Mesostigmata	Hetrostigmata	Htrs	Trombidiformes		Trm
Coleoptera	Histeridae	Hs	Poduromorpha	Tullbergiidae	Tl
Coleoptera	Hydrophilidae	Hyd	Oribatida	Uropodina	Ur
Coleoptera	Hydrophilidae Larvae	Hyd.L			

Table 12.4.2 Taxonomic groups and abbreviations of above-ground invertebrates collected using pitfall traps. Invertebrates that were collected from both sites in 2013 and 2014 were allocated to taxonomic groups.

Taxa		Abbreviation	Taxa		Abbreviation
Hemiptera	Acanthosomatidae	Acn	Coleoptera	Hydrophilidae	Hyd
Hymenoptera	Pompilidae	Acp	Poduromorpha	Hypogastruroidea	Hyp
Carabidae	Amara	Am	Hymenoptera	Ichneumonidae	Ic
Phthiraptera	Linognathidae	An	Entomobryomorpha	Isotomia	Is
Hemiptera	Lygaeidae	Ar.	Julida	Julidae	Jl
Sarcoptiformes	Psoroptidae	As	Megadrilacea	Lumbricidae Juvenille	J.
Hymenoptera	Ichneumonidae	Ap.	Hymenoptera	Formicidae	Ls.
Carabidae	Bembidion	Bmbd	Coleoptera	Latridiidae	Lt
Hymenoptera	Apidae	Bmbs	Lepidoptera Larvae		L.L
Hymenoptera	Braconidae	Br	Araneae	Linyphiidae	Ln
Coleoptera	Byturidae	B.	Lithobiomorpha	Lithobiidae	Lt.
Psocoptera	Calopsocidae	Cl	Carabidae	Loricera	Lr.
Coleoptera	Coccinellidae	Cl.	Araneae	Lycosidae	Ly
Diplura	Campodeidae	Cm.	Mesostigmata	Macrochelidae	Mc
Coleoptera	Cantharidae	Cn	Coleoptera	Melandryidae	Ml
Carabidae		Crb	Hemiptera	Miridae	Mr
Carabidae	Larvae	Crb.	Oribatida	Mixmonoata	Mx
Diptera	Cecidomyia	Ccdm	Hemiptera	Aphididae	M.
Hymenoptera	Ceraphronidae	Crph	Hemiptera	Nabidae	Nb.
Hemiptera	Cercopidae	Crpd	Coleoptera	Leiodidae	Nr.
Hemiptera	Cercopidae Nymph	Crp.	Carabidae	Nebriinae	Nb
Carabidae	Chlaenius	Ch.	Diptera	Tipulidae	Np.
Hemiptera	Cicadellidae	Ccdl	Coleoptera	Silphidae	Nc.
Coleoptera	Coccidula	Cccd.	Coleoptera	Nitidulidae	Ntd.
Coleoptera	Coccinellidae puncata	Cccnll.p	Carabidae	Notiophilus	Ntp.
Coleoptera	Coccinellidae Larvae	Cccnlld.	Lepidoptera	Nymphalidae	Ny
Coleoptera	Latridiidae	Crt.	Coleoptera	Hydraenidae	O.
Coleoptera	Cryptophagidae	Cry	Entomobryomorpha	Oncopoduridae	On
Siphonaptera	Pulicidae	Ct.	Oribatida		Or
Coleoptera	Cucujidae	Ccj	Mesostigmata	Parasitidae	Prstd
Coleoptera	Curculionidae	Crc	Coleoptera	Chrysomelidae	Ph.
Coleoptera	Curculionidae Larvae	C.L	Opiliones	Phalangiidae	Pl.
Hymenoptera	Cynipidae	Cy	Hymenoptera	Sphecidae	Pd.
Coleoptera	Elateridae	Dl.	Isopoda	Porcellionidae	Pr.
Hemiptera	Delphacidae	Dl	Hymenoptera	Proctotrupidae	Prc
Gastropoda	Agriolimacidae	Dr.	Trombidiformes	Anystides	Prstg
Oribatida	Desmonomata	Ds	Pseudoscorpionida	Chernetidae	Ps
Hymenoptera	Diapriidae	Dpr	Hymenoptera	Pteromalidae	Ptrm
Symphypleona	Dicyrtomidae	Dc	Carabidae	Pterostichus	Ptrs
Diptera		Dpt	Coleoptera	Leiodidae	Pt.
Diptera Larvea		Dp.	Coleoptera	Alexiidae	Sp.
Diptera	Drosophila	Dr	Lepidoptera	Sphingidae	Sp
Megadrilacea	Lumbricidae	Er	Staphylinidae Larvae		S.L
Hymenoptera	Encyrtidae	Enc	Staphylinidae		St
Coleoptera	Endomychidae	End	Carabidae	Stomis	St.
Entomobryomorpha	Entomobryidae	Ent	Hymenoptera	Tenthredinidae	Tn
Hymenoptera	Euytomidae	Ey	Hymenoptera	Tenthredinidae Larvae	Tn.
Hymenoptera	Figitidae	Fg	Orthoptera	Tetrigidae	Tt.
Entomobryomorpha	Folsomia	Fl	Thysanoptera	Thripidae	Th
Diplura	Campodeidae	F.	Diptera	Tipulidae Larvae	Tp.L
Coleoptera	Staphylinidae Gabius	G.	Lepidoptera	Tortricidae	Trt
Coleoptera	Coccinellidae	H.	Lepidoptera	Tortricidae Larvae	Tr.L
Carabidae	Harpalus	Hr	Hymenoptera	Torymidae	Try
Gastropoda	Helicidae	Hl	Carabidae	Trechinae	Trc
Entomobryomorpha	Heteromurus	Ht	Carabidae	Trichocellus	Tr.
Coleoptera	Histeridae	Hs	Oribatida	Uropodina	Ur

12.5. Conventional maize invertebrate food webs; A stable isotope approach appendices

Table 12.5.1 Mean (± s.e.) isotopic composition of above- and below-ground invertebrate taxa collected from both sites and all cultivation methods. Invertebrate taxonomic groups were assigned numerical abbreviations and allocated to functional groups.

Taxa Group	Trophic Group	Taxa Number	n	Mean $\delta^{15}N$ (s.e.)	Mean $\delta^{15}C$ (s.e.)	Taxa Group	Trophic Group	Taxa Number	n	Mean $\delta^{15}N$ (s.e.)	Mean $\delta^{15}C$ (s.e.)
Acanthosomatidae	PC	1	1	-25.47 NA	5.54 NA	Histeridae	PB	34	12	-27.37 (0.17)	9.43 (0.49)
Amara	PC	2	21	-28.00 (0.13)	5.89 (0.27)	Hydrophilidae	D	35	5	-26.95 (0.85)	7.89 (0.92)
Aphididae	PS	3	12	-26.71 (0.74)	4.59 (0.60)	Julidae	D	36	15	-20.64 (0.94)	5.28 (0.47)
Bembidion	PB	4	15	-26.34 (0.39)	8.76 (0.31)	Lathridiidae	PB	37	3	-27.63 (0.14)	10.53 (0.94)
Bombus	PO	5	4	-24.64 (0.55)	4.37 (0.73)	Legumes	C3	38	3	-29.45 (0.66)	4.10 (0.23)
Broadleaved	C3	6	3	-29.50 (1.04)	6.25 (1.32)	Lepidoptera Larvae	PC	39	11	-22.74 (2.08)	3.48 (0.62)
Cantharidae	PB	7	6	-24.85 (0.90)	8.28 (0.46)	Linyphiidae	LAP	40	34	-24.97 (0.33)	8.89 (0.43)
Carabidae larvae	PBL	8	20	-25.66 (0.67)	7.29 (0.40)	Lithobidae	CP	41	14	-24.59 (0.87)	7.16 (0.26)
Catopidae	PB	9	10	-25.55 (0.64)	9.29 (0.68)	Litter	C3	42	3	-27.22 (0.12)	2.69 (0.61)
Cecidomyia	O	10	1	-29.39 NA	8.02 NA	Lycosidae	LAP	43	16	-26.12 (0.39)	9.36 (0.31)
Ceropidae	PC	11	8	-26.16 (0.29)	4.46 (0.76)	Maize	C4	44	3	-13.06 (0.10)	5.09 (1.48)
Chlaenius	PB	12	1	-23.41 NA	13.42 NA	Melandryidae	D	45	1	-26.45 NA	8.78 NA
Chrysomelidae	PC	13	2	-30.41 (0.55)	8.11 (0.04)	Miridae	PS	46	6	-26.32 (0.35)	6.02 (1.00)
Cicadellidae	PS	14	2	-22.91 (0.23)	3.85 (2.47)	Nebriinae	PB	47	26	-26.74 (0.24)	8.74 (0.45)
Coccinellidae	PB	15	4	-26.41 (0.39)	7.29 (0.58)	Nitidulidae	PB	48	1	-27.49 NA	4.72 NA
Coccinellidae larvae	PBL	16	10	-25.61 (0.24)	4.77 (0.44)	Notiophilus	PB	49	10	-26.33 (0.36)	6.68 (0.74)
Curculionidae	PC	17	6	-28.57 (0.51)	4.96 (0.92)	Parasitic Wasp	PA	50	2	-27.94 (0.74)	11.38 (2.84)
Decomposer mites	BA	18	33	-23.31 (0.59)	8.23 (0.50)	Phalangiidae	LAP	51	4	-24.46 (0.97)	7.46 (0.41)
Deroceras	PC	19	18	-27.55 (0.76)	6.22 (0.67)	Philonthus	PB	52	2	-28.89 (0.12)	6.21 (0.41)
Diptera	O	20	12	-24.57 (0.58)	8.62 (1.00)	Porcellionidae	D	53	6	-22.87 (0.61)	6.99 (0.57)
Diptera larvea	O	21	7	-25.23 (1.47)	8.05 (1.02)	Predatory mites	MP	54	22	-22.30 (1.05)	10.21 (0.59)
Drosophila	O	22	1	-28.10 NA	7.65 NA	Pterostichus	PB	55	22	-25.22 (0.32)	9.59 (0.60)
Earthworm	E	23	29	-21.96 (0.49)	9.68 (0.26)	Soil	Soil	56	87	-22.17 (0.48)	7.53 (0.13)
Elateridae	PC	24	7	-26.11 (0.57)	8.80 (0.61)	Staphylinidae	PB	57	34	-26.96 (0.40)	7.94 (0.32)
Elateridae Larvea	PC	25	1	-28.13 NA	4.99 NA	Stomis	PB	58	1	-27.64 NA	10.52 NA
Enchytraeid	BA	26	5	-22.59 (1.01)	10.14 (0.71)	Symphypleona	PC	59	5	-26.00 (0.24)	8.31 (1.75)
Entomobryidae	F	27	1	-17.52 NA	8.60 NA	Tenthredinidae	PO	60	5	-24.92 (1.08)	14.10 (1.74)
Entomobryidae + Poduromorpha	F	28	40	-25.58 (0.40)	6.56 (0.25)	Tenthredinidae larvae	PC	61	3	-28.63 (1.42)	3.99 (1.50)
Forbs	C3	29	3	-30.81 (0.93)	6.94 (0.12)	Tetrigidae	PC	62	1	-28.46 NA	9.51 NA
Formicidae	CFP	30	4	-25.92 (0.66)	11.12 (0.51)	Tipulid	PC	63	4	-21.29 (3.03)	9.35 (0.50)
Geophilidae	CP	31	10	-20.65 (1.04)	10.95 (0.79)	Tipulid Larvae	PC	64	12	-25.65 (1.20)	7.03 (0.72)
Grass	C3	32	3	-29.50 (0.24)	5.04 (0.29)	Tortricidae	PO	65	2	-28.22 (1.74)	6.90 (2.50)
Helicidae	PC	33	2	-26.64 (0.13)	4.35 (1.59)						

12.6. Conventional maize cultivation invertebrate food webs; A Bayesian approach appendices

Table 12.6.1 Above- (AG) and below-ground (BG) invertebrate food web properties calculated from the invertebrates collected from the conventional plough cultivation method at Bow. Bayesian credibility intervals were used to inform food web linkages and strengths. Taxonomic groups were assigned to functional groups and numerically abbreviated.

Family	Assigned Number	Trophic Group (Abbreviation)		df	Log_{10} Density	Log_{10} Individual Biomass	$\delta^{13}C$ (s.e.)		$\delta^{15}N$ (s.e.)		Shortest Trophic Level	Longest Trophic Level	Trophic Level Chain Averaged
Amara AG	1	Plant chewer	(PC)	2	0	1.05	-27.95	-0.1	5.67	-0.28	2	2	2
Aphididae AG	2	Plant sucker	(PS)	5	1.03	-0.33	-27.88	-1.44	5.62	-1.28	2	2	2
Bembidion AG	3	Predatory beetle	(PB)	4	0.98	0.84	-25.34	-0.95	9.83	-0.46	3	11	8
C3 Weeds	4	Basal source	(Source)	15	NA	NA	-29.3	-0.79	5	-0.93	1	1	1
C4 Maize	5	Basal source	(Source)	3	NA	NA	-13.06	-0.09	5.09	-1.28	1	1	1
Carabidae larvae AG	6	Beetle larvae	(PBL)	3	0.94	0.55	-27.73	-0.21	7.6	-1.13	3	3	3
Catopidae AG	7	Predatory beetle	(PB)	3	0	0.14	-27.94	0	8.08	0	3	4	3
Catopidae BG	8	Predatory beetle	(PB)	1	0	0.43	-25.72	0	6.46	0	3	3	3
Cecidomyia BG	9	Omnivore	(O)	1	1.75	-0.49	-29.39	0	8.02	0	2	3	3
Cercopidae AG	10	Plant chewer	(PC)	1	0.48	-0.21	-26.77	0	2.82	0	2	2	2
Chrysomelidae AG	11	Plant chewer	(PC)	1	0.4	0.3	-30.41	-0.39	8.11	-0.03	2	2	2
Cicadellidae AG	12	Plant sucker	(PS)	2	0.48	0.13	-22.91	-0.17	3.85	-1.75	2	2	2
Coccinellidae larvae AG	13	Beetle larvae	(PBL)	2	1.04	0.61	-25.53	0	4.11	0	3	3	3
Coccinellidae AG	14	Predatory beetle	(PB)	3	0.3	1.49	-26.03	-0.13	6.92	-0.55	3	3	3
Curculionidae AG	15	Plant chewer	(PC)	1	0.48	0.07	-27.69	-0.68	6.01	-1.51	2	2	2
Decomposer mites BG	16	Bacterivore	(BA)	2	2.1	-1.3	-20.21	-2.69	8.52	-1.26	2	2	2
Deroceras AG	17	Plant chewer	(PC)	4	1.87	1.65	-23.74	-0.76	6.24	-0.5	2	2	2
Diptera Larvae BG	19	Omnivore	(D)	2	0.9	-0.54	-25.16	0	8.82	0	2	2	2
Diptera BG	20	Omnivore	(O)	1	1.38	-1.1	-27.43	0	8.3	0	2	3	3
Drosophila BG	21	Omnivore	(O)	1	0.48	0.85	-28.1	0	7.65	0	2	3	3
Earthworm AG	22	Engineers	(E)	1	0	1.72	-23.75	0	9.02	0	2	2	2
Earthworm BG	23	Engineers	(E)	1	0.11	1.23	-19.61	-0.99	10	-0.36	2	2	2
Elateridae Larvae BG	24	Plant chewer	(PC)	7	1.08	-0.92	-28.13	0	4.99	0	2	2	2
Entomobryidae & Poduromorpha AG	25	Fungivore	(F)	1	3.15	-1.7	-26.4	-0.08	6.12	-0.82	2	2	2
Entomobryidae & Poduromorpha BG	26	Fungivore	(F)	1	2.21	-1.7	-21.67	-1.76	4.85	-1	2	2	2
Entomobryidae BG	27	Fungivore	(F)	2	2.46	-2	-17.52	0	8.6	0	2	2	2
Formicidea AG	28	Colony forming predators	(CFP)	5	1.7	-1	-25.36	-0.42	11.6	-0.17	3	10	6
Geophilidae BG	29	Chilopoda	(CP)	3	0.12	0.04	-20.87	-2.36	12.5	-0.21	3	10	6
Helicidae AG	30	Plant chewer	(PC)	3	0.85	-0.4	-26.77	0	5.94	0	2	2	2
Hydrophilidae AG	31	Detritivore	(D)	3	0.37	0	-27.65	-0.25	6.61	-0.54	2	2	2
Hydrophilidae BG	32	Detritivore	(D)	3	0.7	-0.31	-23.63	0	10.9	0	2	2	2
Julidae BG	33	Detritivore	(D)	1	0.48	0.24	-13.59	-1.3	7.8	-0.1	2	2	2
Lathridiidae AG	34	Predatory beetle	(PB)	3	0.9	-0.64	-27.45	0	12.4	0	2	3	3
Lepidoptera Larvae AG	35	Plant chewer	(PC)	1	0	1.78	-21.4	-5.83	1.74	-0.75	2	2	2
Linyphiidae AG	36	Large aracnid predatory	(LAP)	2	1.49	-0.07	-25.24	-1.39	8.53	-1.03	3	10	5
Lithobiidae AG	37	Chilopoda	(CP)	1	1.26	0.26	-24.27	-0.39	7.69	-0.3	3	3	3
Lithobiidae BG	38	Chilopoda	(CP)	3	0.6	-0.33	-19.47	-3.39	7.82	-0.6	3	3	3
Lycosidae AG	39	Large aracnid predatory	(LAP)	2	0.75	1.4	-25.82	-0.99	8.94	-0.59	3	10	5
Miridae AG	40	Plant sucker	(PS)	5	0.3	0.41	-26.17	0	9.75	0	2	2	2
Nebriinae AG	41	Predatory beetle	(PB)	3	0.35	1.59	-26.41	-0.45	9.75	-0.88	3	10	6
Notiophilus AG	42	Predatory beetle	(PB)	2	0.99	0.54	-26.52	-0.69	4.77	-1.36	3	3	3
Parasitic Wasp BG	43	Parasitode	(PA)	3	0.7	-0.08	-27.2	0	8.54	0	3	5	4
Phalangiidae AG	44	Large aracnid predatory	(LAP)	3	0.18	0.68	-23.65	-1.46	7.97	-0.38	3	3	3
Predatory mites AG	45	Micro-predator	(MP)	3	1.02	-0.7	-26.23	-0.04	7.32	-0.46	2	3	3
Predatory mites BG	46	Micro-predator	(MP)	1	1.75	-1.15	-17.02	-3.26	12.2	-0.71	2	11	7
Soil	47	Basal source	(Source)	4	NA	NA	-25.25	-0.19	6.67	-0.43	1	1	1
Staphylinidae AG	48	Predatory beetle	(PB)	3	1.37	0.19	-27.13	-0.47	7.67	-0.75	3	3	3
Staphylinidae BG	49	Predatory beetle	(PB)	1	0	1.02	-28.41	0	7.64	0	3	3	3
Stomis AG	50	Predatory beetle	(PB)	2	0.3	0.58	-27.64	0	10.5	0	3	3	3
Symphypleona AG	51	Plant chewer	(PC)	2	1.58	-1.3	-26.36	0	3.48	0	2	2	2
Tipulidae AG	52	Plant chewer	(PC)	5	0	2.13	-27.6	0	7.2	0	2	2	2
Tipulidae Larvae AG	53	Plant chewer	(PC)	33	0.18	0.34	-25.62	-0.84	4.94	-0.03	2	2	2
Tipulidae Larvae BG	54	Plant chewer	(PC)	4	0.37	1.02	-23.75	-2.17	8.94	-0.35	2	2	2
Tortricidae BG	55	Pollinator	(PO)	1	0	0.56	-29.96	0	4.4	0	2	2	2

Table 12.6.2 Mean, standard deviation and 97.5% credibility intervals of above- and below-ground invertebrate BSIM using isotopic information on arthropods that were collected from the conventional cultivation techniques at Bow. The 97.5% credibility intervals that were > 0.5 were used to inform trophic links. Entom and Poduro are abbreviations of Entomobryomorpha and Poduromorpha.

Consumer	Resource	Mean	SD	97.5%
Bembidion AG	Diptera Larvae BG	0.233	0.379	1.00
Formicidae AG	Diptera Larvae BG	0.217	0.371	1.00
Linyphiidae AG	Diptera Larvae BG	0.236	0.38	1.00
Geophilidae BG	Earthworm BG	0.279	0.389	1.00
Predatory mites BG	Entomobryidae BG	0.146	0.331	1.00
Lycosidae AG	Miridae AG	0.236	0.374	1.00
Nebriinae AG	Miridae AG	0.292	0.404	1.00
Deroceras AG	Soil	0.696	0.29	1.00
Deroceras BG	Soil	0.761	0.256	1.00
Diptera Larvae BG	Soil	0.757	0.266	1.00
Hydrophilidae BG	Soil	0.731	0.269	1.00
Miridae AG	Soil	0.69	0.292	1.00
Tipulidae AG	Soil	0.72	0.281	1.00
Tipulidae Larvae BG	Soil	0.682	0.302	1.00
Lithobiidae AG	Earthworm AG	0.189	0.348	1.00
Phalangiidae AG	Earthworm AG	0.186	0.349	1.00
Predatory mites BG	Earthworm BG	0.212	0.38	1.00
Chrysomelidae AG	C3 Weeds	0.807	0.259	1.00
Diptera BG	Soil	0.496	0.336	1.00
Earthworm AG	Soil	0.716	0.278	1.00
Entom and Podur AG	Soil	0.602	0.32	1.00
Helicidae AG	Soil	0.552	0.328	1.00
Hydrophilidae AG	Soil	0.424	0.332	1.00
Lathridiidae AG	Soil	0.566	0.333	1.00
Catopidae AG	Tipulidae Larvae AG	0.128	0.294	1.00
Tortricidae BG	C3 Weeds	0.81	0.249	1.00
Cicadellidae AG	Soil	0.597	0.31	1.00
Curculionidae AG	Soil	0.413	0.331	1.00
Symphypleona AG	Soil	0.567	0.329	1.00
Tipulidae Larvae AG	Soil	0.45	0.339	1.00
Carabidae larvae AG	Amara AG	0.126	0.296	1.00
Staphylinidae BG	Amara AG	0.118	0.287	1.00
Notiophilus AG	Helicidae AG	0.131	0.297	1.00
Staphylinidae BG	Tipulidae Larvae AG	0.126	0.291	1.00
Cecidomyia BG	C3 Weeds	0.727	0.302	1.00
Aphididae AG	Soil	0.379	0.329	1.00
Catopidae AG	Amara AG	0.116	0.284	1.00
Drosophila BG	Amara AG	0.119	0.288	1.00
Predatory mites BG	Deroceras BG	0.18	0.338	1.00
Carabidae larvae AG	Hydrophilidae AG	0.111	0.275	1.00
Drosophila BG	Hydrophilidae AG	0.119	0.284	1.00

Coccinellidae larvae AG	Symphypleona AG	0.158	0.321	1.00
Carabidae larvae AG	Tipulidae Larvae AG	0.127	0.292	1.00
Drosophila BG	Tipulidae Larvae AG	0.131	0.297	1.00
Drosophila BG	Soil	0.377	0.327	1.00
Staphylinidae BG	Soil	0.34	0.327	1.00
Cecidomyia BG	Chrysomelidae AG	0.27	0.36	1.00
Lathridiidae AG	Miridae AG	0.142	0.295	1.00
Julidae BG	C4 Maize	0.875	0.134	0.99
Lithobiidae BG	Earthworm BG	0.139	0.305	0.99
Carabidae larvae AG	Elateridae Larvae BG	0.107	0.272	0.99
Amara AG	Soil	0.36	0.321	0.99
Predatory mites BG	Decomposer mites BG	0.17	0.328	0.99
Staphylinidae BG	Elateridae Larvae BG	0.111	0.279	0.99
Staphylinidae AG	Helicidae AG	0.096	0.256	0.99
Staphylinidae BG	C3 Weeds	0.631	0.323	0.99
Elateridae Larvae BG	Soil	0.328	0.315	0.99
Entom and Podur BG	Soil	0.501	0.293	0.99
Diptera BG	Helicidae AG	0.096	0.253	0.99
Stomis AG	Hydrophilidae AG	0.094	0.257	0.99
Geophilidae BG	Deroceras BG	0.146	0.303	0.99
Catopidae AG	Elateridae Larvae BG	0.103	0.264	0.99
Catopidae BG	Entomo and Podur AG	0.104	0.261	0.99
Coccinellidae AG	Miridae AG	0.111	0.261	0.99
Catopidae AG	C3 Weeds	0.561	0.329	0.99
Elateridae Larvae BG	C3 Weeds	0.639	0.311	0.99
Drosophila BG	Elateridae Larvae BG	0.108	0.275	0.99
Predatory mites AG	Entomo and Podur AG	0.099	0.256	0.99
Staphylinidae BG	Hydrophilidae AG	0.097	0.259	0.99
Predatory mites AG	Miridae AG	0.109	0.262	0.99
Stomis AG	Tipulidae Larvae AG	0.085	0.244	0.99
Aphididae AG	C3 Weeds	0.588	0.322	0.99
Drosophila BG	C3 Weeds	0.591	0.321	0.99
Catopidae AG	Hydrophilidae AG	0.105	0.267	0.99
Amara AG	C3 Weeds	0.607	0.315	0.99
Geophilidae BG	Soil	0.482	0.268	0.99
Lepidoptera Larvae AG	Soil	0.439	0.288	0.99
Cecidomyia BG	Soil	0.251	0.301	0.99
Curculionidae AG	C3 Weeds	0.552	0.322	0.99
Hydrophilidae AG	C3 Weeds	0.54	0.322	0.98
Notiophilus AG	Ceropidae AG	0.088	0.24	0.98
Stomis AG	Curculionidae AG	0.115	0.272	0.98
Coccinellidae AG	Entomo and Podur AG	0.1	0.257	0.98
Carabidae larvae AG	C3 Weeds	0.533	0.32	0.98
Tipulidae Larvae AG	C3 Weeds	0.515	0.327	0.98
Geophilidae BG	Decomposer mites BG	0.151	0.3	0.98
Lathridiidae AG	Deroceras BG	0.103	0.258	0.98
Stomis AG	C3 Weeds	0.47	0.328	0.98
Diptera BG	C3 Weeds	0.469	0.322	0.98
Stomis AG	Deroceras BG	0.106	0.254	0.98

Coccinellidae larvae AG	Entomo and Podur AG	0.095	0.246	0.97
Chrysomelidae AG	Soil	0.176	0.255	0.97
Stomis AG	Amara AG	0.066	0.212	0.97
Lathridiidae AG	Curculionidae AG	0.112	0.261	0.97
Decomposer mites BG	Soil	0.421	0.252	0.97
Parasitic Wasp BG	Helicidae AG	0.076	0.223	0.97
Staphylinidae AG	Hydrophilidae AG	0.097	0.246	0.97
Parasitic Wasp BG	C3 Weeds	0.426	0.319	0.97
Whole community	Soil	0.617	0.201	0.96
Ceropidae AG	C3 Weeds	0.459	0.31	0.96
Diptera BG	Tipulidae Larvae AG	0.12	0.27	0.96
Diptera BG	Hydrophilidae AG	0.096	0.241	0.96
Tortricidae BG	Soil	0.172	0.246	0.96
Lathridiidae AG	C3 Weeds	0.401	0.318	0.96
Staphylinidae AG	Tipulidae Larvae AG	0.125	0.27	0.96
Staphylinidae AG	C3 Weeds	0.432	0.315	0.95
Lithobidae BG	Entomobryidae BG	0.254	0.368	0.95
Earthworm BG	Soil	0.38	0.237	0.95
Helicidae AG	C3 Weeds	0.405	0.306	0.95
Notiophilus AG	C3 Weeds	0.388	0.303	0.95
Lithobidae BG	Soil	0.362	0.237	0.95
Parasitic Wasp BG	Hydrophilidae AG	0.094	0.24	0.95
Notiophilus AG	Hydrophilidae AG	0.081	0.223	0.94
Lithobidae AG	Hydrophilidae BG	0.1	0.245	0.94
Catopidae BG	Miridae AG	0.075	0.211	0.94
Phalangiidae AG	Hydrophilidae BG	0.099	0.245	0.94
Parasitic Wasp BG	Tipulidae Larvae AG	0.109	0.254	0.94
Cecidomyia BG	Curculionidae AG	0.075	0.219	0.94
Catopidae BG	Symphypleona AG	0.076	0.216	0.94
Geophilidae BG	Tipulidae AG	0.064	0.206	0.93
Symphypleona AG	C3 Weeds	0.38	0.299	0.93
Formicidea AG	Deroceras BG	0.079	0.219	0.93
Parasitic Wasp BG	Miridae AG	0.083	0.219	0.93
Lycosidae AG	Entomo and Podur AG	0.071	0.212	0.93
Formicidae AG	Hydrophilidae BG	0.116	0.253	0.93
Formicidea AG	Miridae AG	0.095	0.234	0.92
Lathridiidae AG	Hydrophilidae AG	0.078	0.221	0.92
Predatory mites BG	Julidae BG	0.105	0.253	0.92
Coccinellidae larvae AG	Ceropidae AG	0.093	0.239	0.92
Lithobiidae BG	Decomposer mites BG	0.098	0.237	0.92
Cecidomyia BG	Aphididae AG	0.072	0.209	0.91
Coccinellidae larvae AG	Tipulidae Larvae BG	0.072	0.21	0.91
Cecidomyia BG	Hydrophilidae AG	0.058	0.191	0.91
Phalangiidae AG	Deroceras AG	0.062	0.197	0.90
Catopidae BG	Helicidae AG	0.076	0.216	0.90
Lithobiidae BG	Tipulidae AG	0.061	0.196	0.90
Catopidae BG	Tipulidae Larvae BG	0.064	0.197	0.90
Entom and Podur AG	C3 Weeds	0.348	0.288	0.90
Stomis AG	Tipulidae AG	0.06	0.193	0.90

Nebriinae AG	Diptera Larvae BG	0.079	0.212	0.90
Lathridiidae AG	Tipulidae Larvae AG	0.077	0.216	0.90
Predatory mites BG	C4 Maize	0.675	0.153	0.89
Predatory mites AG	C3 Weeds	0.3	0.276	0.89
Lycosidae AG	Diptera Larvae BG	0.084	0.218	0.89
Drosophila BG	Curculionidae AG	0.06	0.189	0.88
Nebriinae AG	Entomo and Podur AG	0.058	0.193	0.88
Bembidion AG	Miridae AG	0.084	0.217	0.88
Lathridiidae AG	Tipulidae AG	0.056	0.184	0.88
Predatory mites BG	Tipulidae AG	0.051	0.189	0.88
Predatory mites AG	Helicidae AG	0.069	0.202	0.88
Notiophilus AG	Tipulidae Larvae AG	0.078	0.209	0.87
Nebriinae AG	C3 Weeds	0.28	0.274	0.87
Notiophilus AG	Tipulidae Larvae BG	0.052	0.183	0.87
Lithobiidae BG	Julidae BG	0.117	0.244	0.86
Coccinellidae AG	Helicidae AG	0.077	0.212	0.86
Coccinellidae AG	C3 Weeds	0.28	0.272	0.86
Entomobryidae BG	C4 Maize	0.63	0.15	0.85
Catopidae BG	C3 Weeds	0.253	0.261	0.85
Parasitic Wasp BG	Entomo and Podur AG	0.055	0.185	0.85
Carabidae larvae AG	Curculionidae AG	0.058	0.187	0.85
Tipulidae Larvae BG	C3 Weeds	0.263	0.265	0.85
Stomis AG	Aphididae AG	0.06	0.191	0.85
Catopidae AG	Curculionidae AG	0.062	0.19	0.85
Parasitic Wasp BG	Curculionidae AG	0.064	0.193	0.85
Cecidomyia BG	Tipulidae AG	0.057	0.188	0.85
Cecidomyia BG	Tortricidae BG	0.086	0.223	0.85
Lithobiidae AG	Deroceras AG	0.062	0.192	0.84
Staphylinidae BG	Curculionidae AG	0.063	0.192	0.84
Miridae AG	C3 Weeds	0.264	0.26	0.84
Bembidion AG	Tipulidae AG	0.056	0.182	0.84
Stomis AG	Elateridae Larvae BG	0.045	0.172	0.84
Notiophilus AG	Amara AG	0.074	0.203	0.83
Coccinellidae larvae AG	C3 Weeds	0.267	0.264	0.82
Linyphiidae AG	Miridae AG	0.07	0.19	0.82
Lycosidae AG	C3 Weeds	0.234	0.247	0.81
Diptera BG	Entomo and Podur AG	0.058	0.187	0.81
Phalangiidae AG	Diptera Larvae BG	0.061	0.184	0.81
Lathridiidae AG	Decomposer mites BG	0.047	0.171	0.80
Coccinellidae larvae AG	Helicidae AG	0.062	0.19	0.80
Staphylinidae AG	Entomo and Podur AG	0.057	0.181	0.79
Lathridiidae AG	Entomo and Podur AG	0.047	0.171	0.79
Notiophilus AG	Entomo and Podur AG	0.055	0.18	0.79
Lithobiidae AG	Diptera Larvae BG	0.059	0.178	0.78
Catopidae AG	Chrysomelidae AG	0.097	0.21	0.77
Diptera BG	Amara AG	0.062	0.183	0.77
Notiophilus AG	Elateridae Larvae BG	0.064	0.186	0.77
Entomobryidae BG	Soil	0.248	0.184	0.76
Stomis AG	Chrysomelidae AG	0.094	0.21	0.76

Linyphiidae AG	C3 Weeds	0.192	0.225	0.76
Bembidion AG	C3 Weeds	0.181	0.217	0.76
Diptera Larvae BG	C3 Weeds	0.187	0.221	0.75
Bembidion AG	Hydrophilidae BG	0.079	0.2	0.75
Lithobiidae BG	Entom and Poduro BG	0.044	0.168	0.75
Staphylinidae BG	Chrysomelidae AG	0.098	0.213	0.75
Drosophila BG	Chrysomelidae AG	0.091	0.204	0.74
Predatory mites AG	Diptera Larvae BG	0.064	0.181	0.74
Formicidea AG	C3 Weeds	0.168	0.208	0.74
Coccinellidae AG	Diptera Larvae BG	0.066	0.182	0.74
Formicidea AG	Decomposer mites BG	0.049	0.164	0.74
Diptera BG	Miridae AG	0.067	0.185	0.73
Staphylinidae AG	Amara AG	0.058	0.172	0.73
Bembidion AG	Earthworm AG	0.064	0.181	0.73
Predatory mites BG	Soil	0.217	0.179	0.73
Phalangiidae AG	Tipulidae AG	0.053	0.17	0.72
Staphylinidae AG	Miridae AG	0.064	0.18	0.72
Carabidae larvae AG	Chrysomelidae AG	0.092	0.201	0.72
Lithobiidae BG	C4 Maize	0.475	0.158	0.71
Lithobiidae AG	C3 Weeds	0.174	0.204	0.70
Earthworm BG	C4 Maize	0.462	0.158	0.70
Lithobiidae BG	Deroceras BG	0.057	0.173	0.70
Linyphiidae AG	Earthworm AG	0.065	0.181	0.70
Stomis AG	Decomposer mites BG	0.043	0.159	0.70
Linyphiidae AG	Deroceras AG	0.047	0.161	0.70
Diptera BG	Curculionidae AG	0.052	0.167	0.69
Parasitic Wasp BG	Amara AG	0.054	0.168	0.69
Staphylinidae BG	Aphididae AG	0.047	0.157	0.69
Coccinellidae AG	Tipulidae Larvae BG	0.048	0.162	0.68
Notiophilus AG	Symphypleona AG	0.045	0.162	0.68
Deroceras AG	C3 Weeds	0.186	0.21	0.68
Lithobiidae AG	Tipulidae AG	0.049	0.161	0.68
Lycosidae AG	Helicidae AG	0.047	0.16	0.68
Linyphiidae AG	Hydrophilidae BG	0.065	0.177	0.67
Formicidea AG	Tipulidae AG	0.049	0.164	0.67
Cecidomyia BG	Amara AG	0.044	0.159	0.67
Predatory mites AG	Symphypleona AG	0.047	0.162	0.67
Predatory mites AG	Tipulidae Larvae BG	0.047	0.16	0.67
Parasitic Wasp BG	Tipulidae AG	0.047	0.161	0.67
Linyphiidae AG	Tipulidae AG	0.046	0.158	0.66
Tipulidae AG	C3 Weeds	0.169	0.2	0.66
Deroceras BG	C3 Weeds	0.151	0.187	0.66
Phalangiidae AG	C3 Weeds	0.176	0.199	0.66
Staphylinidae AG	Curculionidae AG	0.049	0.161	0.66
Coccinellidae AG	Symphypleona AG	0.044	0.156	0.66
Earthworm AG	C3 Weeds	0.17	0.194	0.65
Decomposer mites BG	C4 Maize	0.41	0.157	0.65
Lathridiidae AG	Aphididae AG	0.041	0.152	0.65
Carabidae larvae AG	Aphididae AG	0.046	0.159	0.65

Cicadellidae AG	C3 Weeds	0.215	0.21	0.65
Nebriinae AG	Tipulidae AG	0.041	0.149	0.65
Stomis AG	Miridae AG	0.049	0.164	0.64
Lithobiidae AG	Cicadellidae AG	0.044	0.151	0.64
Formicidea AG	Earthworm AG	0.053	0.161	0.64
Predatory mites AG	Hydrophilidae AG	0.049	0.154	0.64
Coccinellidae AG	Curculionidae AG	0.047	0.159	0.64
Nebriinae AG	Deroceras BG	0.048	0.157	0.64
Hydrophilidae BG	C3 Weeds	0.155	0.186	0.64
Whole community	C3 Weeds	0.316	0.171	0.63
Bembidion AG	Deroceras BG	0.049	0.157	0.63
Notiophilus AG	Curculionidae AG	0.047	0.156	0.62
Staphylinidae AG	Elateridae Larvae BG	0.047	0.148	0.62
Drosophila BG	Aphididae AG	0.046	0.155	0.62
Catopidae BG	Hydrophilidae AG	0.047	0.152	0.62
Cecidomyia BG	Tipulidae Larvae AG	0.045	0.158	0.62
Catopidae BG	Diptera Larvae BG	0.05	0.153	0.61
Phalangiidae AG	Cicadellidae AG	0.042	0.147	0.61
Geophilidae BG	C4 Maize	0.353	0.163	0.61
Coccinellidae AG	Tipulidae Larvae AG	0.049	0.149	0.61
Geophilidae BG	Entomobryidae BG	0.055	0.153	0.60
Catopidae BG	Tipulidae Larvae AG	0.044	0.145	0.59
Lepidoptera Larvae AG	C3 Weeds	0.232	0.188	0.59
Geophilidae BG	Hydrophilidae BG	0.046	0.154	0.59
Predatory mites AG	Tipulidae Larvae AG	0.048	0.145	0.58
Lycosidae AG	Curculionidae AG	0.042	0.144	0.58
Coccinellidae AG	Hydrophilidae AG	0.046	0.148	0.58
Formicidea AG	Curculionidae AG	0.043	0.147	0.58
Lycosidae AG	Tipulidae AG	0.041	0.15	0.58
Entom and Podur BG	C3 Weeds	0.209	0.184	0.57
Diptera BG	Aphididae AG	0.043	0.147	0.57
Lepidoptera Larvae AG	C4 Maize	0.328	0.153	0.57
Predatory mites AG	Curculionidae AG	0.045	0.147	0.57
Parasitic Wasp BG	Chrysomelidae AG	0.054	0.145	0.57
Nebriinae AG	Curculionidae AG	0.042	0.147	0.57
Coccinellidae larvae AG	Curculionidae AG	0.043	0.146	0.56
Drosophila BG	Tortricidae BG	0.043	0.136	0.56
Catopidae AG	Aphididae AG	0.044	0.148	0.56
Diptera BG	Elateridae Larvae BG	0.041	0.134	0.55
Cecidomyia BG	Deroceras BG	0.046	0.147	0.55
Parasitic Wasp BG	Aphididae AG	0.041	0.145	0.55
Staphylinidae AG	Aphididae AG	0.042	0.145	0.55
Catopidae BG	Cercopidae AG	0.039	0.139	0.54
Entom and Podur BG	C4 Maize	0.29	0.156	0.54
Cecidomyia BG	Elateridae Larvae BG	0.038	0.146	0.54
Catopidae AG	Tipulidae AG	0.035	0.136	0.54
Lycosidae AG	Tipulidae Larvae AG	0.043	0.137	0.53
Coccinellidae larvae AG	Aphididae AG	0.039	0.14	0.53
Lycosidae AG	Hydrophilidae AG	0.038	0.133	0.52

Diptera BG	Tipulidae AG	0.037	0.138	0.52
Catopidae AG	Tortricidae BG	0.04	0.127	0.52
Staphylinidae AG	Chrysomelidae AG	0.049	0.135	0.52
Coccinellidae AG	Amara AG	0.038	0.128	0.52
Geophilidae BG	C3 Weeds	0.165	0.157	0.51
Catopidae BG	Aphididae AG	0.04	0.138	0.51
Notiophilus AG	Aphididae AG	0.041	0.142	0.50
Coccinellidae larvae AG	Elateridae Larvae BG	0.037	0.133	0.50
Bembidion AG	Decomposer mites BG	0.04	0.138	0.50
Carabidae larvae AG	Tortricidae BG	0.04	0.125	0.50
Lathridiidae AG	Helicidae AG	0.034	0.142	0.50
Coccinellidae larvae AG	Hydrophilidae AG	0.036	0.129	0.50
Whole community	C4 Maize	0.067	0.042	0.16