Arthropod and plant diversity of maize agro-ecosystems in the Grassland and Savanna Biomes of South Africa

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Declaration

I declare that the work presented in this Masters dissertation is my own work, that it has not been submitted for any degree or examination at any other university, and that all the sources I have used or quoted have been acknowledged by complete reference.

Signature of the Student: MBotha …………………………   Date: 2014/03/11 ....

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Abstract

Maize (*Zea mays* L.) is the most important grain crop in the country. Approximately 12 million tons of maize grain is produced annually on approximately 2.5 million ha of land. However, increased farming intensity can lead to fragmentation of habitat and has a tendency to decrease the biodiversity of an area. Therefore, to ensure the continued functionality of agro-ecosystems, methods in agriculture must be assessed and adapted when necessary to ensure the persistence of biological diversity. Unfortunately, the effect of crop production on species diversity and composition in South Africa is still relatively unknown, and no baseline data exists with which to gauge the possibility of unknown extinction risks of important biological elements. The objectives of this study were to compare plant and arthropod diversity patterns and species turnover of maize agro-ecosystems between biomes (grassland and savanna) and along a maize field-field margin gradient (MAFFMAG). Surveys of maize agro-ecosystems were conducted in six provinces of South Africa, namely North-West, Mpumalanga, KwaZulu-Natal, Limpopo, Free State and the Eastern Cape. Repeated measures ANOVA revealed a significantly lower plant and arthropod species diversity and richness in maize fields compared to field margins. Non-metric multidimensional scaling revealed that arthropod species composition differed between biomes although not along MAFFMAGs, indicating that arthropod species composition is dependent on biome rather than distance from maize field. Floristic data revealed unique species compositions for maize fields and field margins and also for biomes. Furthermore, maize fields and field margins of grassland sites were more similar in plant species composition than the savanna localities, suggesting higher regional beta diversity for savanna regions. Spearman's rank order correlations revealed generally positive but weak or no relationships between plant and arthropod diversity. This study provides baseline data for identification, monitoring and conservation of priority species and will allow the future evaluation of ecosystem services provided by plants and associated arthropods, especially natural enemies of pests, in maize agro-ecosystems.

Keywords: Agro-ecosystems; arthropods; diversity; grassland; maize field; maize field-field margin gradient; plants; plant-arthropod diversity relationships; savanna.

Uittreksel

Mielies (*Zea mays* L.) word beskou as een van die belangrikste gewasse in Suid-Afrika, met ŉ jaarlikse opbrengs van ongeveer 12 miljoen ton wat op ongeveer 2,5 miljoen hektaar landbougrond geproduseer word. Sodanige landbou-aktiwiteite kan egter lei tot habitatfragmentering en het die neiging om biodiversiteit in landbou-ekostelsels te verlaag. Om die voortbestaan van biodiversiteit te verseker, moet daar dus oordeelkundig te werk gegaan word met die bestuur van landbou-aktiwiteite en moet metodes aangepas word waar nodig. Inligting aangaande die patrone van plant- en insekdiversiteit en spesiesamestellings in landbou-ekostelsels is egter nog beperk in Suid-Afrika. Om hierdie rede is die potensiële impak van landbou-aktiwiteite op hierdie ekologies belangrike organismes nog onbekend. Die doel van hierdie studie was dus om die diversiteitspatrone en spesiesamestellings van plante en insekte te vergelyk langs ŉ mielieland-bufferstrookgradiënt, eerstens tussen ses verskillende provinsies in en tweedens tussen twee verskillende biome (grasveld en savanna). Opnames is gedoen in die Noordwes-, Mpumalanga-, KwaZulu-Natal-, Limpopo-, Vrystaat- en Oos-Kaap provinsies van Suid-Afrika. Statistiese analises het aangedui dat plant- en insekdiversiteit beduidend laer was in mielielande as in die aangrensende natuurlike veld (bufferstrook). Verder is daar gevind dat die spesiesamestellings van beide plante en insekte nie afhang van die afstand vanaf die mielieland nie, maar wel van die bioom waarin hulle voorkom. Verder is daar gevind dat die spesiesamestellings van plante en insekte in mielielande relatief uniek is ten opsigte van elke bufferstrook. Die resultate dui ook daarop dat, wat plantegroei betref, die savannastreke tipies hoër beta-diversiteit gehad het as grasveld. Korrelasie-koeffisiënte het daarop gedui dat insekdiversiteit oor die algemeen nie sterk afhanklik was van plantdiversiteit nie. Die data wat deur hierdie studie genereer is, sal uiteindelik die identifisering, monitering en bewaring van belangrike en/of kwesbare plant-en insekspesies moontlik maak.

Sleutelwoorde: Grasveld; insekdiversiteit; insek-plantdiversiteit verhoudings; landbou-ekostelsels; mielielande; plantdiversiteit; savanna.

Chapter 1: Introduction

1.1 Introduction

South Africa is an immensely rich country in terms of species diversity and is considered to be one of the world's 17 mega-diverse countries (DEAT, 2005), being the third most biologically diverse country in the world (Crane, 2006). With a land surface area of 1.1 million km^2, South Africa covers approximately 1% of the total land area of the earth. However, it is estimated that the country hosts almost 10% of the world's plant species (Cowling *et al.*, 1989). The vegetation of Southern Africa is considered to have the highest species richness of any temperate flora in the world (Cowling *et al.*, 1989), with 19 581 indigenous vascular plant species, of which 60% are endemic (Germishuizen *et al.*, 2006).

Arthropods are considered to be one of the most successful groups of all living biota on earth and along with other invertebrates make up about 80% of the total number of species in the animal kingdom (Frost, 1959). However small in size, they play a major part in the ecosystems within which they live. Approximately 50 000 species of insects have already been recorded in South Africa but it is estimated that a further 50 000 exists that have not yet been described (DEAT, 2005). Also, 60 000 inland terrestrial and aquatic invertebrates have been described in the country of which 70% is endemic to South Africa (DEAT, 2005).

Biodiversity worldwide are increasingly coming under threat due to anthropogenic activities. As the human population expands, areas for habitation and food production must inevitably increase to meet the growing demand. As a result vast areas of land have been transformed for urban infrastructure and the production of food crops. The majority of land (86%) in South Africa is zoned for agriculture, of which 13% is used for cultivation of crops (DEAT, 2005). Maize (*Zea mays* L.) is the most important grain crop in the country and approximately 128 million tons of maize grain is produced annually on approximately 31 million hectares of land (Du Plessis, 2003). At the end of 2011, the area of farmland in South Africa used for maize production was 2.86 million hectares (Hannon, 2012).

This large scale transformation of natural vegetation poses a serious and growing threat to biodiversity (Darkoh, 2003; Wessels *et al.*, 2003). The most pressing issues include habitat destruction and fragmentation as well as the pollution of remaining adjacent natural habitat with agrochemicals such as fertilizers and pesticides (Pullin, 2002; Wardle *et al.*, 1999b).

Understanding what effect the anthropocene has on the complexity and interactions of ecosystems and its responses to disturbance is without doubt a daunting challenge. However, it is generally agreed that biodiversity plays a major role in the functioning of ecosystems and is generally considered to be an important aspect in both natural and agricultural ecosystems (Bond, 1989;

Wessels *et al.*, 2003; Duelli *et al.*, 1999; Altieri, 1999). Higher biodiversity may also results in stronger pest control within these systems (Gurr *et al*., 2012).Therefore it has become increasingly important to understand the effect of our activities on biodiversity as this may ultimately improve the management and conservation of our natural world. The assessment of potential risk posed by anthropogenic activities inevitably demands baseline data on the biodiversity of an area. Without the knowledge of historical and or current patterns it is virtually impossible to draw conclusions on current processes and temporal dynamics. This type of information is therefore crucial when deducing potential impacts of certain environmental features.

1.2 Aims and objectives

Since crop production is such a common feature in South Africa, it may be useful to understand the effects these activities may have on the biodiversity of the adjacent landscape. Ultimately this data may be used to indicate possible extinction risks of potentially important biological elements. Data of this nature may also be used to indicate where methods in agriculture have to be assessed and adapted to ensure the persistence of biological diversity, especially those species and habitats that are beneficial to crop protection. Unfortunately, knowledge of this nature is extremely limited in South Africa and almost no baseline data exists for the biodiversity of agro-ecosystems in the country. Therefore, the aims of this study were to:

- compare the diversity patterns of aboveground, plant-inhabiting arthropods and vegetation in maize fields and margins of two neighbouring biomes (grassland and savanna);
- test for a general relationship between plant diversity and arthropod diversity across the maize field-field margin gradient (MAFFMAG) and between biomes;
- test the Proches-Cowling hypothesis that overall differences in arthropod species assemblages are not as pronounced across biomes as those between plant species assemblages.

1.3 Hypotheses

In this study, the following hypotheses were tested:

- Diversity of plants and associated arthropods are higher in field margins than in maize fields.
- Diversity of plants and associated arthropods in the field margin increases with increasing distance away from maize fields. Therefore, the tension zone has lower plant and arthropod diversity than the natural area (explanation of zones included in chapter 4).
- A general positive relationship exists between plant and arthropod diversity. Therefore, arthropod species diversity increases in response to increased plant species diversity.

- The multi-layered vegetation structure of the savanna biome enables it to contain a higher plant and arthropod diversity than the grassland biome.
- Differences in arthropod species assemblages are not as pronounced across biomes as those between plant species assemblages.

Chapter 2: Literature review

2.1 Biodiversity and its importance in ecosystems

2.1.1 What is meant by biodiversity?

Biodiversity is a term frequently used in popular media and scientific papers. Yet it is often not accompanied by a satisfactory definition. The term has been loosely applied to depict the variability of living organisms in various contexts but is perhaps most commonly used as a synonym for species richness, which is the number of species present in a community or habitat (Begon *et al.*, 2008). However, biodiversity can be described at different levels of biological organisation that includes genetic diversity, species diversity and ecosystem diversity (Groombridge & Jenkins, 2002). Genetic diversity generally represents the variation of genetic material - the heritable variation - within and between populations of organisms of the same species (Groombridge, 1992). Species diversity on the other hand describes the variation of species in a community. Ecosystem diversity represents the variation in ecosystems or habitat, although the quantitative assessment of diversity at this level remains problematic (Groombridge, 1992).

Furthermore, species diversity may exist at different spatial scales (Hamilton, 2005). Firstly, variation can exist within a single homogenous habitat, termed point diversity or α-diversity. Furthermore, there can be variation between different habitats or communities, known as β-diversity. At an even larger scale, landscape or γ-diversity describes the variation between different landscapes (Hamilton, 2005).

Regardless of scale, communities are often described in terms of species composition and species richness. However, the usefulness of species richness as an index to compare communities is limited because an important aspect of species assemblages is omitted: some species are common and others are rare (Begon *et al.*, 2008). Therefore, more meaningful measures of biodiversity have been proposed that reflect both the species richness and relative abundance of individuals among species. Biodiversity may therefore be defined as the number of species present as well as the abundance of each of these species in a given system (Begon *et al.*, 2008).

Indices which are developed from information theory are often used to characterize the diversity of a sample by a single useful number. These indices may be divided into categories based on the aspect of the community they describe best (Magurran, 1988). Species richness indices focus mainly on the number of species in a sample while species abundance indices provide measures of the evenness/abundance of species in a community. Perhaps the most common indices used are those that incorporate richness and evenness into a single figure by measuring the proportional abundance of species. The latter are also known as heterogeneity indices, because they take both evenness and species richness into account (for example the Simpson and Shannon-Wiener

Diversity Indices). Simpson's Diversity Index is also referred to as a dominance measure, since it focuses mainly on the abundances of the most common species rather than species richness (Magurran, 1988).

2.1.2 The value of biodiversity in ecosystems

It is generally agreed that biodiversity is an important aspect in both natural and agricultural ecosystems and the conservation of global biotic diversity is therefore highly motivated (Bond, 1989). The diversity-stability hypothesis proposed by Elton (1958), predicts that higher biodiversity facilitates higher stability and function in a community or ecosystem. Ecosystem stability is often measured in terms of the resistance to change or resilience of a community (Hurd & Wolf, 1974). Theoretically, it makes sense that increased biodiversity facilitates greater resilience of an ecosystem. The greater the number of species and/or genotypes in a particular landscape, the higher the chances that the negative effects of sudden environmental changes can be absorbed by ecological resilience (Duelli *et al.*, 1999). Therefore, when environmental change takes place, it is likely that a more diverse community will contain the appropriate gene or trait that will enable its survival.

Although contradicted by some (Murdoch, 1975; Goodman, 1975; Murdoch *et al.*, 1972), recent studies indicate that diversity can generally be expected to give rise to ecosystem stability (McCann, 2000). This is not limited to species diversity but also functional diversity- based on physiological and morphological differences (Tilman *et al.*, 1997; Wardle *et al.*, 1999a). The diversity-stability hypothesis is supported by Tilman (1996), who found relationships between plant diversity and community stability in prairie grasslands. Haddad *et al.* (2011) also found that higher plant diversity increased the stability (lowered year-to-year variability) of arthropod communities in grasslands.

Modern commercial agriculture is dependent on monoculture production systems. It has been shown that insect pest outbreaks are often associated with the transformation of diverse ecosystems into monoculture crops (Pimentel, 1961; Altieri & Letourneau, 1982). A usable diversity-stability theory may therefore be very beneficial in alternative pest management strategies and in management of natural communities.

Other than increased ecosystem stability and function, biotic diversity may act as a source for new productive biota in agriculture (Wessels *et al.*, 2003). All agricultural plants and animals are genetically modified derivatives of one or more wild species and biodiversity may therefore act as a reservoir of potentially valuable plant and animal genes. Therefore, if species and genetic variation are destroyed, we may lose options for improving agricultural biota and practices. Furthermore, biodiversity has a scientific value in that it allows us to understand aspects such as evolution and adaptation; a cultural value in that it inspires and provides materials for the creation of art, music and literature; and an aesthetic value which urges us to preserve all rarities and facilitate public interest.

Perhaps one of the most common ways to express the value of biodiversity though, is its role in providing ecosystem services. Ecosystem services represent the benefits that ecological functions provide to human populations (Costanza *et al.*, 1997). These include provisioning services (food, fibre, fuel, biochemical, genetic resources, and fresh water), regulating services (flood, pest control, pollination, seed dispersal, erosion regulation, water purification, and climate and disease control), cultural services (spiritual and religious values, knowledge systems, education and inspiration, and recreational and aesthetic values) and supporting services (primary production, nutrient cycling, provision of habitat, production of atmospheric oxygen, and water cycling) (Cilliers *et al.*, 2012). The persistence of these services is, however, dependent on biodiversity as they are primarily biological. Vegetation cover in grassland can prevent soil erosion, replenish ground water and control flooding by enhancing infiltration and reducing water runoff (Altieri, 1999). Pollination by a variety of animal vectors is considered to be one of the most valuable ecosystem services for both natural and agricultural ecosystems by facilitating the reproduction of the majority of angiosperm plants. It is estimated that insects and other animals pollinate approximately 80% of angiosperms, which amounts to about 300,000 flower-visiting species (MEA, 2007).

The simplification of ecosystems for the purpose of agricultural production has led to the creation of artificial ecosystems in constant need of external inputs by humans to persist. These systems are becoming increasingly dependent on non-renewable resources, are resulting in the loss of biodiversity and land through soil erosion and rely heavily on chemical fertilizers and pesticides. As such, general concern has been raised about their long term sustainability (Altieri, 1999). Therefore, an urgent need has arisen for the development of agro-ecological technologies and systems that focus on the conservation-regeneration of biodiversity, soil, water and other resources to meet the growing array of socioeconomic and environmental challenges. A popular new movement is the conservation and enhancement of biodiversity in the farmed landscape as this may be beneficial for crop production in the long run (Pimentel *et al.*, 1997).

Vegetation other than crop plants may prevent soil erosion and act as wind breaks for crop fields (Nordstrom & Hotta, 2004). It may also serve as buffers to the movement of pollutants to adjacent terrestrial and aquatic habitats. This may be by drift retention of pesticides or by preventing the movement of surface water flow and particle movement (Marshall & Moonen, 2002). Increased plant diversity in agro-ecosystems may benefit crop production indirectly by providing alternative food sources, hiding places or overwintering sites for beneficial insects (Grez *et al.*, 2010).

2.1.3 Arthropods and their role in ecosystems

Among the living biota, arthropods take the lead in terms of species numbers (Schoonhoven *et al.*, 1998). If current classification methods are accurate, there are just over one million described species of arthropods worldwide, although realistic estimates of the total number of species may range between four and six million in total (Gullan & Cranston, 2005). The beetles (Coleoptera), flies (Diptera), wasps, ants and bees (Hymenoptera), butterflies and moths (Lepidoptera), and true bugs (Hemiptera) are considered to be the five major orders within the already described list of insects (Gullan & Cranston, 2005).

The majority of invertebrates live underground and it is estimated that only 1-2 % of all living invertebrate biomass can be found aboveground on the soil surface and on plants (Curry, 1976). Above-ground arthropods include a wide range of trophic groups such as sap-feeding hemipterans, leaf-feeding lepidopterans, beetles, dipterans, thrips, grasshoppers and other herbivores associated with the vegetation layer and groups such as surface-foraging termites, ants and litter-feeding isopods, millipedes and collembolans. They are in turn preyed upon by predatory carabids and staphylinid beetles, mites, spiders, omnivorous earwigs and parasitic wasps (Curry, 1976)

Contrary to the traditional viewpoint that insects are insignificant entities in nature or purely harmful pests, the sheer numbers of arthropods make them a highly significant component of the environment and in the lives of people. In many ecosystems, arthropods represent the most dominant herbivores. The consumption rates by grasshoppers in African savanna are similar to that of large ungulates and cattle (Andersen & Lonsdale*,* 1990). It has been shown that insects are accountable for 62% of the total leaf material consumed by herbivores in the savanna of the Nylsvley area in South Africa (Gandar, 1982). These arthropod herbivores may influence grassland and savanna productivity directly by consuming plant tissue and indirectly by altering the rate of plant growth (Curry, 1994).

Being prominent herbivores, arthropods are significant pests of food crops and cause major financial losses annually. Although weeds are considered to be the most important pest of maize, it is estimated that the total global potential loss due to arthropods and other animal pests are in the order of 16% (Oerke, 2006). Fortunately, predatory and parasitic insects have the potential to regulate populations of herbivorous insects and therefore play an important role in the control of pest populations in natural and agricultural ecosystems (Picker *et al.*, 2004). Some common beneficial organisms of agro-ecosystems include predatory carabid, coccinellid, and staphylinid beetles as well as predatory hemipterans, lacewings, predatory flies, ants, parasitic wasps, predatory mites and spiders (Stary & Pike*,* 1999). These beneficial arthropods can serve as a relatively low cost alternative pest management strategy without the target pests developing significant resistance and with minimal damage to human health and the environment (Stary & Pike, 1999).

Crop monocultures do however remain one of the most difficult environments in which to establish efficient biological control agents as they often lack adequate resources to sustain natural enemies and because of disturbances caused by agricultural practices (Altieri & Nicholls, 1999). The diversity of beneficials found in a cropping system is often linked to undisturbed natural areas (Stary & Pike, 1999) and therefore, possible ties between beneficial arthropods and natural plant communities must be identified and preserved to ensure effective biological control of pest species. It is generally accepted that higher biodiversity results in stronger pest control within a system, whether it be natural or agricultural (Gurr *et al.*, 2012).

Arthropods are responsible for many of the important ecosystem services provided by living biota. They are vital for nutrient recycling via the decomposition of plant and animal wastes, dispersal of fungi, the disposal of carrion and soil turnover (Gullan & Cranston, 2005). Low-level herbivory by canopy arthropods feeding on living plant material in forests, grasslands and deserts accelerates the rate of nutrient cycling in terrestrial ecosystems while having little impact on plant standing crops and their production. Arthropod detritivores also speed the rate of nutrient flux through soil by incorporating organic matter into the soil (Curry, 1994). It is estimated that the standing crop of faecal pellets from macro-arthropod detritivores such as millipedes may locally exceed annual litter-fall inputs (Seastedt & Crossley, 1984). Faecal matter of micro-arthropods such as mites and collembolans are often abundant in samples of humidified litter and decaying wood and make up a large fraction of what is commonly referred to as humus. These pellets accumulate to form aggregates that may decay slowly and represent a large reservoir of organic matter and nutrients (Seastedt & Crossley, 1984). By contributing organic components, soil invertebrates along with fungi and microbes facilitate soil formation. It is estimated that soil biota in the United States of America (USA) contribute 2.5 billion USD per year in topsoil value (Pimentel *et al.*, 1997). Many soil arthropods also play a role in the aeration of the soil (Curry, 1994).

Perhaps one of the most well-known and often cited benefits of arthropods is their role in plant propagation. This mainly consists of the vastly important task of plant pollination, especially of food crops and forage plants. These pollinators are becoming more and more valuable, especially since pollinator-dependent crops make up an increasingly important part of the human diet (Klein *et al.*, 2007; Aizen *et al.*, 2008). It is estimated that one third of our food supply relies directly on pollination by insects (Jolivet, 1998). In agro-ecosystems, bees, for example the honey bee (*Apis mellifera*) (Hymenoptera: Apidae) are regarded as the most important and economically valuable pollinator group (McGregor, 1976). These pollinators contribute not only to food security, but are also of great economic value. Estimates of the value of bee pollination services in the USA alone range up to 16 billion USD annually (Losey & Vaughan, 2006), while the value of non-bee pollination in the USA could be as much as 5-6 billion USD per year (Gullan & Cranston, 2005).

2.2 Agro-ecosystems

2.2.1 Introduction

At least 30% of the earth's surface has been transformed into agricultural land, with the subsequent alteration of the relative composition of the world's plant and animal populations, the replacement of the pre-existing wild by cultivated vegetation cover and drastic modification of much of the remaining area by grazing of domestic livestock (Tivy, 1990). In doing so, a particular type of man-made ecosystem is created namely the agricultural ecosystem or agro-ecosystem. The term agro-ecosystem refers to all the organisms, abiotic factors and the interactions among them that occur on land used for agriculture and adjacent areas that provide habitat to native wildlife (Mongillo & Zierdt-Warshaw, 2000). Therefore, agro-ecosystems represent unique systems that include populations of both native and introduced species. Agro-ecosystems differ from wild, unmanaged ecosystems in that they are often simpler, with less diversity in plant and animal species and with a less complex organization of its organic components (Tivy, 1990). Ultimately, the fundamental aspect of agro-ecosystems that sets them apart from their natural counterparts is of course the intervention of man and the specific human-determined function of harvest production (Swift & Anderson, 1993). This often results in the deliberate reduction in species richness in favour of productive biota.

The productive biota of agro-ecosystems comprises crop plants or livestock deliberately chosen by the farmer for the production of food, fibre and other products for consumption. These are the organisms that directly determine the diversity and complexity of the system. Besides productive biota, most agro-ecosystems rely on resource biota: organisms that are beneficial to the productivity of the system although they are not harvested themselves. These include organisms that manage soil fertility, facilitate plant propagation or serve as predators of harmful pests (Swift & Anderson, 1993). On the other hand, every agro-ecosystem has destructive biota which has a negative effect on the productivity of the system such as weeds, pest species and microbial pathogens (Swift & Anderson, 1993). These biotic components are in continuous interaction with the abiotic components of the agro-ecosystem, which include air, surface water and groundwater supplies as well as cultivated and uncultivated soil (Mongillo & Zierdt-Warshaw, 2000).

The living biota of agro-ecosystems are connected by trophic chains (Mongillo & Zierdt-Warshaw, 2000). These chains are often much simpler and shorter than in natural unmanaged ecosystems (Connor *et al.*, 2011). Each trophic level describes the layer within a food chain at which the different organisms in the system feed. Autotrophic green plants of crop fields and pastures are termed primary producers, and are responsible for the production of biomass through photosynthesis. The consumers of green plants are known as primary consumers (herbivores) while those organisms that feed on primary consumers are termed secondary consumers (carnivores). The organisms that consume waste and dead material in the system and therefore terminate trophic chains are known as decomposers or detritivores (Connor *et al.*, 2011).

These trophic chains result in more complex food webs when crop plants, weeds, arthropods, pathogens, nematodes, vertebrates and other organisms are linked by their feeding relationships (Cohen *et al.*, 1994). The interconnectedness of the components of these food webs means that the destruction of one group may have detrimental effects on other groups in the system (Altieri, 2000). There has been increasing concern regarding the drift of Bt-toxins from genetically modified Bt-maize through arthropod food chains (Gatehouse *et al.*, 2011). The Bt-toxin is intended for the control of specific phytophagous insect pests, but if these herbivores are consumed by predators or parasitoids, these beneficial insects may be killed as well (Altieri, 2000). However, due to the complexity of these food webs, the true effects of these toxins on the system are still poorly understood (chapter 2.4).

2.2.2 Cropping systems

Crop agriculture may be based on a variety of spatial designs that involves the nature of the crop structure. Whenever farmers focus on market production, high-input monocultures become predominant and as a result, monocultures have increased substantially on a global scale (Altieri, 2011). The term monoculture refers to the agricultural practice that involves the cultivation of a single plant species in an area year after year (Mongillo & Zierdt-Warshaw, 2000).

Large scale monoculture production has led to a number of inevitable negative consequences both for the environment and the agro-ecosystem. From an ecological perspective, monocultures may be viewed as constrained fundamental niches where plants are relatively free from interspecies competition but have constricted access to essential resources (Connor *et al.*, 2011). As mentioned previously (chapter 2.1), greater biodiversity may result in greater stability in ecosystems (Tilman *et al.*, 1997; King & Pimm, 1983; Frank & McNaughton, 1991). Therefore, unmodified wild ecosystems are frequently considered to be more stable than agro-ecosystems, being more resilient in the face of environmental fluctuations because of their greater species diversity and trophic complexity (Tivy, 1990).

The general tendency of monoculture production to be unsustainable has led many farmers to shift towards the more sustainable practice of polyculture, which involves simultaneous cultivation of multiple plant species in one area (Mongillo & Zierdt-Warshaw, 2000). This include monocultures with border plantings as well as intercropping systems such as mixed cropping or strip cropping (Ratnadass *et al.*, 2012; Altieri, 1983). Alternative spatial designs may ultimately lead to improved pest control and nutrient recycling, closed energy flows as well as water and soil conservation (Altieri, 2011).

2.2.3 General structure of crop fields

Regardless of the type of agriculture and cropping system, crop field agro-ecosystems consist of a number of basic components. Although the meaning of the terms surrounding the various components and structures of crop agro-ecosystems are extremely varied throughout the literature, definitions for some of the most important terms used in this study will be given following Greaves and Marshall (1987), Marshall (2005) and Marshall and Moonen (2002). These represent some of the most typical components of maize agro-ecosystems in South Africa, although some crop fields do not necessarily have all the features described while others may have additional features (a visual representation of the various components is given in fig. 2.1).

Crop edge: The outer few metres of the crop, sometimes also referred to as the crop 'headland'. It has the agricultural meaning of a turning space for machinery. The crop edge area may have the highest biodiversity of non-crop plants and insects of the crop itself due to its close proximity to the field margin. It is known that crop yields are often lower near the crop field margins (Sparkes *et al.*, 1998) and this may be due to increased competition with weeds (Cousens, 1985), increased damage by herbivores (Free & Williams, 1979) or increased soil disturbances such as compaction by agricultural machinery (Wilcox *et al.*, 2000).

Field boundary: This encompasses the physical barrier between the crop plants and the landscape that lies adjacent to the crop field. These barriers may include structures such as fences, walls or hedges.

Field boundary strip: This includes the area between the crop edge and the physical field boundary and usually contains features such as roads and watercourses such as streams, ditches or drains that accompany the field boundary. These areas may consist of grass or wildflower strips or it may be left uncultivated with naturally regenerated vegetation. In other cases it may be sterile strips maintained by herbicides.

Recent research suggests that the nature of this boundary strip may have significant effects on the nature of arthropod communities inside the crop field (Holland & Fahrig, 2000). The structure of vegetation may for instance affect the rate of arthropod dispersal. It was shown by Frampton *et al.* (1995) that the spread of beetle species was slower through a grassy bank than through a barley field. Tall vegetation such as hedges may also serve as barriers to insect dispersal. A study of hedge arthropods of crop fields in the United Kingdom revealed that small, flying insects accumulate in the sheltered zones near artificial windbreaks (Lewis, 1969). The boundary strip may also consist of plant stands that are used to attract insect pests to protect the target crop, a strategy known as trap cropping (Shelton & Badenes-Perez, 2006). This strategy has been used in push-pull systems to control maize stem borers (e.g. *Busseola fusca*) in maize fields by planting an attractant plant species such as Napier grass (*Pennisetum purpureum*) (Cook *et al.*, 2007; Van den Berg *et al.*, 2001).

Field margin: Marshall and Moonen (2002) define the field margin as "…the whole of the crop edge, any margin strip present and the semi-natural habitat associated with the boundary". For the purpose of this study, the field margin will also include any natural vegetation beyond the field boundary. Therefore, when using the term 'field margin', we refer to the whole area surrounding the crop field (outside the crop edge) that includes the field boundary strip and natural rangeland or pasture beyond that separates the various crop fields from one another.

These field margins are often viewed in a negative light by farmers as reservoirs for insect pests and weeds (Marshall & Arnold, 1995; Holland & Fahrig, 2000). However, this area along with the field boundary strip also have the potential to provide refuges and resources for beneficial arthropods and may play an essential role in biological pest control (Gurr *et al.*, 2012) as well as pollination of food crops (Lagerlöf *et al.*, 1992). The height and physical nature of the field margin vegetation seems to be an especially important factor (even more so than plant species composition) in enhancing arrival of beneficial insects into crop fields (Grez *et al.*, 2010).

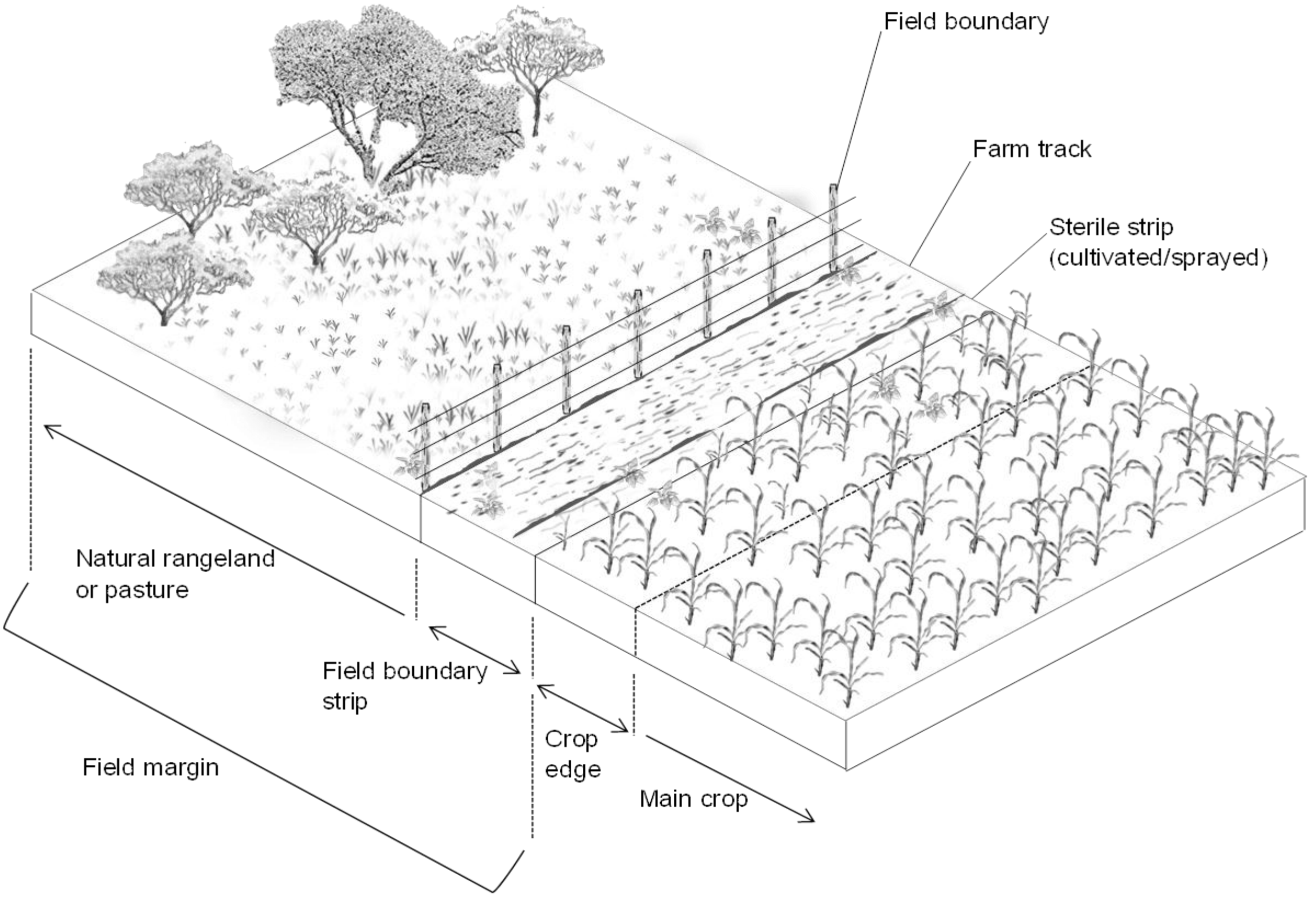

Fig 2.1: Typical structure of a maize agro-ecosystem sampling locality consisting of a maize field and margin (redrawn from Greaves and Marshall 1987). Within each transect, one plot was situated in the main crop, one in the crop edge area, and four in the field margin beyond the field boundary.

Unfortunately field margins are most vulnerable to agricultural operations which are likely to have a major negative impact on the flora of field margins through physical disturbance, fertilizer deposition and pesticide drift (Marshall & Arnold, 1995). As a consequence, margin vegetation near crop fields are often more weedy and native plants are generally more common farther from crop field edges (Clark *et al.*, 2005). This highlights the importance of sufficient size in field margins designed for conservation purposes.

The area between the cultivated crop and adjacent vegetation poses a unique situation as this is where the distinctly different communities of the crop monoculture and adjacent natural habitat meet. This may be viewed as a **transitional zone:** an area along which one community grades into another (Yahner, 1988) as a result of environmental gradients that can be natural or the result of a change in land-use (e.g. crop cultivation to natural rangeland). This transitional zone may therefore have characteristics of each of its adjacent ecosystems as well as its own unique fauna and flora. This led to the conclusion that they are in effect ecotones (Marshall, 1989). In the most basic sense, an ecotone is the ecological zone or boundary formed in an area where two or more ecosystems meet (Mongillo & Zierdt-Warshaw, 2000).

Recently, a distinction has been made between ecotones, ecoclines and edge effects (Dutoit *et al.*, 2007). Essentially, ecotones are always lower in species richness due to the harsh conditions of the transitional zone with which only a few species can cope. An ecocline on the other hand is a less stressed transition of one community into another and may have higher species richness than each of the adjacent communities due to species overlap (Maarel, 1990). If the transitional zone is characterized by an increase in species richness but not new species or properties, it is known as an edge effect (Dutoit *et al.*, 2007).

Habitat edges are important structures in the landscape as they have the potential to alter ecological processes from nutrient transport to the outcome of species interactions as well as species dispersal and community composition (Fagan *et al.*, 1999). It is well known that plant communities respond to habitat edges. Edges formed between forests and anthropogenic grasslands of China for example have plant communities of non-forest species on forest margins which invade the first few meters of the forest. These species are then replaced by secondary and finally primary forest species along the grassland-forest gradient (Lin & Cao, 2009).

At the crop field-field margin interface, plant communities may be altered by disturbances caused by agricultural management practices. Crop edges are often associated with an increased abundance of weeds (Wilson & Aebischer, 1995; Leeson *et al.*, 2005), which has the ability to grow in these high-disturbance areas. A study of the vegetation of crop field-field margin gradients in

England identified a relatively unique species composition for field boundaries compared to crop fields and extended field margins (Marshall, 1989). Although mostly weeds, there was limited spread of these species into the adjacent crop.

It has also been shown that arthropod communities respond to transitional zones. Forest-grass transition zones in Hungary revealed significantly unique species assemblages for forest interior, forest edge and grass sampling sites (Magura, 2002). Several studies revealed that many arthropod groups have a tendency to aggregate near crop field edges (Blackshaw & D'Arcy-Burt, 1997; Svensson *et al.*, 2000). Furthermore, habitat edges may have implications for simple vs. complex agricultural landscapes. As complex crop field systems often involve large numbers of smaller crop patches intercepted by hedges or uncultivated pastures, they have a higher edge to area ratio and may therefore influence the interaction of the biota in the system. It has been shown that complex landscapes increased the effectiveness of parasitoids in attacking armyworm larvae (*Pseudaletia unipuncta*) in maize fields (Marino & Landis, 1996). This was contributed to more alternative resources (such as alternative hosts, pollen sources and moderated microclimates) closer to field interiors.

2.3 Biodiversity in agro-ecosystems

2.3.1 Introduction

Despite the large shift of agriculture to monoculture production, agro-ecosystems are not invariably low in biodiversity from a global perspective. It has been illustrated by Perfecto and Vandermeer (2008) that many tropical agricultural systems have high levels of planned and associated biodiversity. Also, the species richness of all biotic components of traditional agro-ecosystems is comparable with that of many natural ecosystems (Altieri, 1999). It is estimated that some 200 000 species of plant and animals, apart from crops and livestock, are in some way involved in agricultural production (Tivy, 1990). Monocultures are traditionally thought of as areas completely devoid of life other than the crop plants. However, because of the high dispersal capacities of plants and arthropods, these systems are often found to be surprisingly rich in unintentional diversity. Crop fields may however differ in terms of how, where and at what rate they acquire new species (discussed below).

2.3.2 Colonization of introduced plants by arthropods

Crop fields have been compared to islands, where colonization by arthropods after crop establishment is influenced by the size of the field and the distance to an arthropod source. Annual and perennial crops also have different succession patterns and will therefore influence arthropod species composition in different ways (Gurr *et al.*, 2012). It is well known that spillover of species readily takes place between cultivated and uncultivated landscapes. It has been shown that many insect groups such as herbivore pests (Norris & Kogan, 2000), pollinators (Garibaldi *et al.*, 2011) and predators (Alomar *et al.*, 2002) often move from field margin vegetation into crop fields. Generally it seems that arthropods found on crops are more likely native individuals that have adapted to use a new potential host (the crop plant) rather than non-native introduced species (Strong *et al.*, 1984). It has been stated that many beneficial and pest insects of maize (which is phylogenetically part of the grass family) are African species that have moved to maize from related grasses (Annecke & Moran, 1982). The maize stem borer (*Busseola fusca*) is an example of a native grassland species that adopted maize as a new host plant (Annecke & Moran, 1982).

Although less well studied, the opposite is also true. Crop species have been shown to spill over into field margins as well (Blitzer *et al.*, 2012), sometimes with detrimental consequences to the natural habitat. McKone *et al.* (2001) showed that adult corn rootworm beetles (Chrysomelidae: *Diabrotica* spp.) originating from maize fields often colonized sunflower plants (Asteraceae: *Helianthus* spp.) in adjacent natural prairie grassland in southeast Minnesota. It was noted that the beetles fed extensively on these plants and may ultimately interfere with the successful reproduction of sunflowers. Also, it has been shown that spillover of an introduced coffee pest in Mauritius, the coffee berry moth (*Prophantis smaragdina*) (Lepidoptera: Crambidae), severely reduced the reproductive success of *Bertiera zaluzania,* which is a threatened endemic plant species in the region (Kaiser *et al.*, 2008).

It has been suggested that a major factor in the rate of colonization of new host plants by phytophagous insects is the taxonomic, phenological, biochemical and morphological match between the introduced crop and the indigenous flora (Strong *et al.*, 1984). Therefore, the more unusual the introduced plant, the lower the chances that local insects will colonize it.
Plant chemistry seems to be a major driver in this regard. It has been shown that host shifts of *Ophraella* spp. (Coleoptera: Chrysomelidae) are more likely between chemically similar plant hosts (Futuyma & McCafferty, 1990). Since some arthropods have been found to use visual stimuli above olfactory stimuli to find a host plant (Machial *et al.*, 2012; Stenberg and Ericson, 2007), plant structure may also play a major role in colonization rate. Therefore, an insect searching for a host plant may be more likely to choose plants of a similar physical shape.

Due to the high mobility of most arthropods, introduced plants are constantly visited by a variety of species. However, only a fraction of these arthropods will be able to establish. Therefore, a significant proportion of insects found on a crop plant may be there purely by chance, being migrants that found themselves on the wrong host plant. Therefore, the existing arthropod fauna on introduced plants such as crops may be described as a mixture of co-evolved, pre-adapted, opportunistic and accidental individuals that vary over space and time in complex ways as predicted by the nature of the vegetation and physical environment (Strong *et al.*, 1984).

2.3.3 Factors determining the biodiversity in agro-ecosystems

Environmental factors associated with the crop field influence the diversity, abundance and activity of arthropods in agro-ecosystems (Altieri & Nicholls, 1999). These factors include microclimate, availability of food (not only prey and hosts but also water, pollen and nectar), habitat requirements and intra-and interspecific competition, which are affected by the nature of the cropping system (e.g. the spatial and temporal arrangement of crops and the intensity of crop management). A few factors in particular have been reported to determine whether agro-ecosystems are rich or poor in species diversity. These include the type and diversity of the vegetation in and around the agro-ecosystem, the permanence of the crop, the type and intensity of management and the extent of isolation of the agro-ecosystem from the natural vegetation (Altieri & Nicholls, 1999).

Therefore, it can be argued that a greater diversity of plants in an agro-ecosystem or a particular cropping pattern could lead to a greater diversity of herbivorous arthropod species and a greater diversity of predators and parasitoids. Although this concept is notoriously difficult to test in the real agro-ecosystem environment, positive evidence has been provided by Denys and Tscharntke (2002); Schellhorn and Sork (1997) and Cardinale *et al.* (2003). Several hypotheses have been proposed to explain higher arthropod diversity in more diverse cropping systems, although different hypotheses may apply to different situations. These include the heterogeneity hypothesis, the predation hypothesis, the productivity hypothesis and the stability-temporal resource partitioning hypothesis (discussed in more detail in chapter 2.6).

The type of vegetation that occurs in the field margin may influence the movement of arthropods to and from crop fields. As indicated previously, tall companion plants in crop field borders have been shown to act as barriers to the movement of a variety of insect species (chapter 2.2). The type of vegetation in the field margin may influence the arthropod community composition in the agro-ecosystem. A study by Meek *et al.* (2002) illustrated that a sown ‘tussocky’ grass mix, a sown ‘grass and wildflower’ mix and naturally regenerated vegetation favoured different groups of arthropods and, overall, flowery treatments benefited more groups than the other vegetation types. This has mainly been attributed to increased food resources. Furthermore, the nature of the vegetation may influence the microclimate in the vicinity of the crop and may provide shelter in an otherwise exposed landscape. This could enable a greater number of organisms to persist inside the agro-ecosystem (Altieri, 1999).

As for the permanence of the crop, semi-perennial and perennial crops are considered to provide much more stable habitats than annual crops and may thus provide greater support for biodiversity (Stary & Pike, 1999). Annual monocultures, such as maize fields, on the other hand are considered to be the most difficult environments for biological diversity to persist as these systems often lack the necessary resources, are present only for part of the year and are managed by methods that often damage the natural vegetation and natural enemy populations in the system (Stary & Pike, 1999). This may cause problems for relatively immobile arthropod groups. It was shown by Ryszkowski (1979) that the numbers of relatively immobile invertebrate groups (Annelida: Enchytraeidae, Lumbricidae, and Arthropoda: Collembola, Elateridae and Acarina) are more severely affected in cultivated fields compared to the mobile arthropod groups such as Diptera, Heteroptera, Hymenoptera, Carabidae, Staphylinidae and Araneae.

Crop field margins may play a vital role in maintaining biodiversity in these ephemeral environments as they provide arthropod reservoirs that can colonize the crop during the growing season. In Switzerland it was shown by Pfiffner and Luka (2000) that five times more arthropod species (mostly staphylinids, carabids, spiders and chilopods) occurred in field margins than in arable fields during the winter months, indicating the importance of these field margins as overwintering sites for predatory arthropods. Diverse field margins may therefore serve as a source from where arthropods can move and increase their diversity annually in adjacent highly disturbed annual crops.

The position of the crop relative to natural vegetation may greatly influence the composition and diversity of non-intentional diversity in these systems (Altieri & Nicholls, 1999). It has been shown that crop plants near field margins tend to have more arthropod species on them. Clough *et al.* (2005) found a higher diversity of spider species near crop field edges compared to field interiors in western and central Germany and highlighted the importance of landscape heterogeneity in promoting spider diversity in agro-ecosystems. Therefore, smaller crop fields interspaced by uncultivated field margins may have greater unintentional diversity as the crop centres are closer to field margins and are therefore more accessible to living biota.

Of course, a major determinant of diversity in agro-ecosystems is the nature of the management practices used. In-field diversity may be influenced by management practices such as tillage, residue management and the application of agro-chemicals such as fertilizers and pesticides (Wardle *et al.*, 1999b). Unfortunately, these practices are often very damaging to the remaining natural habitats. It is therefore necessary to understand how and to what extent the activities associated with these systems affect plant and animal diversity before developing possible mitigation strategies to enhance biodiversity in and around agro-ecosystems.

2.4 Impacts of agricultural management practices on biodiversity

It is well known that the nature of agro-ecosystems does not favour the continued persistence of biodiversity (McLaughlin & Mineau, 1995; Matson *et al.*, 1997; Reidsma *et al.*, 2006). Habitats that are intensively managed tend to be simpler in structure compared to those that are left in a more natural state. Intensively managed habitats tend to be dominated by those few species that are able to tolerate the disturbance and are able to exploit the specific crop resource that dominate the habitat (Curry, 1994). Activities associated with agriculture such as the application of agrochemicals, irrigation as well as soil disturbance may have direct adverse effects on biodiversity inside the crop field and adjacent natural habitat through destroying individuals. Indirect adverse effects may result from the degradation of natural habitats as well as habitat fragmentation.

2.4.1 Fertilizers

Organic and inorganic fertilizers are commonly used in agriculture to increase crop yield. However, this may result in the application of additional nutrients to non-target areas such as field margins (Marshall & Moonen, 2002). Some evidence suggests that fertilizer drift can occur to at least 4 m outside crop fields and can range between 25 to 50% of the field applied rate in the first meter of a field margin (Tsiouris & Marshall, 1998). The addition of nutrients such as nitrogen and phosphorous is likely to result in the dominance of plant species with a high nutrient uptake requirement or tolerance (De Cauwer *et al.*, 2006), as well as the loss of species diversity (Marrs, 1993). It was found by Schmitz *et al.* (2013) for example that the abundance of common buttercup (*Ranunculus acris*) in field margin habitats decreased significantly in cases where fertilizer was applied. It was also observed that the effects of fertilizer application were additive since fertilizer effects were stronger in the second season.

It was shown by Kirchner (1977) that the combined effects of fertilizer application and irrigation had marked effects on plant and arthropod communities of shortgrass prairie. Although primary production increased with increased fertilizer application, plant species dominance (reduction in evenness) also increased at the cost of diversity. On the other hand, both arthropod diversity and biomass increased with fertilizer and irrigation treatments, possibly in response to higher plant productivity. Kleijn and Snoeijing (1997), who applied three levels of fertilizer to a low productive meadow and a high productive fallow arable field, found that fertilizer application caused a loss in plant species richness, particularly of low growing species, and an increase in biomass of the vegetation. They argued that the loss of non-tolerant species and domination by others may cause shifts in plant species communities and may have implications for field margin vegetation in the case of fertilizer drift. Therefore, nutrient enrichment may have a destabilizing effect in competitive systems (Rosenzweig, 1971).

Changes in feeding status of plants as a result of fertilization may influence the associated arthropod communities as well. It has been suggested by White (1974) that increased nitrogen concentrations in plants could increase the numbers of arthropod herbivore pests. Van den Berg and Van Rensburg (1991) observed that increased nitrogen application in sorghum fields resulted in increased infestation by the stem borers *Busseola fusca* (Lepidoptera: Noctuidae) and *Chilo partellus* (Lepidoptera: Crambidae). Furthermore, it was shown by Alasvand Zarasvand *et al.* (2013) that increased nitrogen fertilization resulted in increased soluble nitrogen concentrations in plants and that aphid (*Schizaphis graminum*) populations responded to these increases with significantly higher reproductive rate, doubling time and finite rate of increase. Increased plant productivity (usually expressed in terms of an increase in biomass) has been shown to influence arthropod communities in complex ways (Bishop *et al.*, 2010; Matis *et al.*, 2011; Siemann, 1998).

2.4.2 Pesticides

Pesticides are commonly used in many agro-ecosystems and the drift of agrochemicals, particularly insecticides and herbicides, may affect field margin flora and fauna along with crop field biodiversity (Marshall & Moonen, 2002). There has been increasing awareness of the possible negative impact of pesticide drift on vegetation in conservation areas as well as field-margin habitats adjacent to treated areas and several studies indicate that pesticide drift is a reality near sprayed crop fields (De Snoo & De Wit, 1998; Longley *et al.*, 1997; Kaiser, 2011). However, the extent to which plant and arthropod communities are affected and the range at which these effects occur is not yet clear.

As with fertilizers, the application of herbicides may also have a destabilizing effect on plant communities. Kleijn and Snoeijing (1997) reported that herbicide applications had similar effects on plant communities than fertilizer applications but that the effect of the latter was more severe. Herbicides also had a negative effect on biomass production of forbs and, interestingly, a positive effect on biomass production of grasses. It was stated however that the herbicide used was rather selective in its action and that the application of herbicides with a broader range of activity would probably have had a more severe effect on plant communities, including grasses.

The influence that herbicide application to crop edges may have on adjacent ditch-bank vegetation was investigated in the Netherlands by De Snoo and Van der Poll (1999). Along the unsprayed winter wheat crop the diversity and cover of dicotyledons increased, as did the floristic value of the vegetation. Several species were only found on the ditch banks next to the unsprayed cereal edges, such as *Papaver rhoeas*, *Ranunculus repens*, *Rumex crispus* and *Thlaspi arvense*. However, no effect was found on monocotyledons. Also, no significant effects were found in the ditch-bank vegetation adjacent to the sugar beet or potato crop that was spayed. These differences in effect on ditch-bank vegetation among the crops was contributed to differences in the spraying method, type of herbicides used and dosages employed.

Even though herbicides may not harm arthropods directly, changes in plant species composition may have an effect on the diversity and composition of arthropod communities as well (Siemann, 1998). It was found that the species richness of butterflies in field margins depended on the presence of flowering plants and that the application of herbicides significantly reduced flowering plant abundance and therefore, nectar sources. This in turn decreased the species richness of the butterflies (Feber *et al.*, 1996).

Large volumes of insecticides are commonly used in cropping systems to control pest outbreaks and limit pest damage. There has been increasing concern regarding the adverse effect insecticides may have on beneficial non-target arthropods (Cessna *et al.*, 2005). It was shown by De Snoo and De Wit (1998) that butterfly species numbers decreased 2 to 3 fold in insecticide sprayed edges of winter wheat and potato fields as opposed to unsprayed edges. Also, it was shown that the butterfly species *Pieris rapae* (Lepidoptera: Pieridae) and *P. brassicae* were susceptible to deltamethrin applied in field margins (Çilgi & Jepson, 1995).

Less well studied are the effects of insecticides on non-target herbivores in field margins. Bundschuh *et al.* (2012) monitored field margins that neighboured cereals, vineyards, and orchards and used grasslands as reference to determine if grasshopper nymphs (*Chorthippus* sp.) (Orthoptera: Acrididae) were affected by the insecticides dimethoate, pirimicarb, imidacloprid, lambda-cyhalothrin, and deltamethrin. Sensitivity to these toxins was proven in laboratory experiments and decreased grasshopper densities were also observed in field margins. Only field margins exceeding 9 m in width (stretching beyond the drift effect) rivalled grassland grasshopper densities and density decreases was attributed to the effects of insecticides on the grasshopper nymphs.

It has been shown however that the effect of pesticides on biota in field margins may depend on management practices in the field. A study by Badji *et al.* (2004) indicated that tillage, or the absence thereof, influenced the response of arthropods to deltamethrin. The authors observed a significant effect of cultivation practices on arthropod assemblages. The no-tillage cultivation system was able to buffer the negative impact of insecticides on arthropods, minimizing its effect. This did not occur in the conventional cultivation system where deltamethrin significantly decreased arthropod abundance in the maize canopy. The application technique of pesticides may influence the range at which these toxins affect the biota in field margins. It was found by De Snoo and De Wit (1998) that different spray nozzle designs resulted in large differences in the distance of pesticide deposition inside field margins.

In many cases, field design may mitigate adverse impacts of crop fields on natural habitats. As mentioned previously, field margin vegetation can be used as buffers to prevent pesticide drift. In this regard, the nature of the vegetation may play an important role. A drift model that was developed to simulate drift in a hedgerow–vineyard system indicated that the effectiveness of hedgerows as barriers to drift depended mainly on canopy density, vegetation height and wind speed (Otto *et al.*, 2009). The creation of unsprayed buffer zones in crop fields may also significantly reduce pesticide drift to crop field margins (Bundschuh *et al*., 2012). De Snoo and De Wit (1998) reported that the creation of a 3 m buffer zone decreased drift deposition in crop field ditches by a minimum of 95%.

The negative effect of pesticides on the environment, in combination with unguaranteed success in controlling arthropod pests, makes the merit of simply applying large amounts of insecticide questionable. In fact, it has been stated that while the application of insecticides increased tenfold since the 1940’s, crop losses due to insect pests doubled (Soule *et al.*, 1990). When biodiversity of beneficial insects are reduced, it may cause outbreaks of pests in crop fields (Fernandes *et al.*, 2010). It was found by Kfir and Van Hamburg (1983) that increases in insecticide application did not correlate with increased yield of cotton in South Africa. There was a tendency for yield to decrease with weekly applications and for secondary pesticide effects to increase, such as the stimulation of red spider mite populations as a result of predator suppression. Therefore, the pest control strategies that are currently being developed should be more environmentally sound and sustainable. These strategies should include the use of biological control methods in combination with chemical control, cultural control methods and host plant resistance. This strategy is commonly known as integrated pest management (IPM) (Tivy, 1990).

2.4.3 Bt-toxins

In addition to insecticide application, numerous plant varieties have been genetically modified so as to be resistant to insect pests. This often involves the insertion of genes form other organisms into the genome of the crop plants that code for insecticidal genes, therefore enabling the plant to produce these toxins themselves. Bt-maize (MON810), expressing the Cry1Ab protein with a gene form the bacterium *Bacillus thuringiensis* (Bt) has been planted in South Africa since 1998 (James, 2010) and targets the stem borers *Busseola fusca* (Lepidoptera: Noctuidae) and *Chilo partellus* (Lepidoptera: Crambidae). While the Cry 1Ab protein is toxic to lepidopterous stem borers and other Cry proteins are especially toxic to the insect orders Coleoptera, Hymenoptera and Diptera, they are apparently harmless to vertebrates and plants (Bravo *et al.*, 2007). However, there is increasing concern regarding the negative effect these toxins may have on non-target arthropods in the agricultural environment.

As mentioned previously (chapter 2.3), the living biota in agro-ecosystems are connected in complex food webs. Non-target arthropods may therefore be exposed to these insecticidal proteins via bitrophic or tritrophic interactions (Ferry, 2010). In bitrophic interactions, non-target arthropods may directly ingest the transgenic product by consuming GM plant material. Toxic plant material may also find its way into the natural ecosystem around the cultivated field where arthropods may be exposed to the toxins. Bt-toxins contained in plant material may find its way into the environment via root exudates, plant residues left in the field after harvest and pollen drift to adjacent field margins (Viktorov, 2011).

A study by Rosi-Marshall *et al.* (2007) on 12 headwater streams found maize plant by-products and pollen located 6 to 40 m from maize fields. Harvest residues containing corn leaves, fragments of stem, and ears ranged from 0.1 to 7.9 g per square meter of water surface and made up 17 to 22% of the total plant residues in the streams. If these maize residues contain Bt-toxins, it could create a potentially harmful environment for aquatic invertebrates in streams adjacent to Bt-maize fields. Furthermore, several studies indicated that Bt-toxins produced by GM plants are able to bind to soil particles when these plants are incorporated into the soil by tillage or as leaf litter (Palm *et al.*, 1996). Soil invertebrates such as Collembola and Carabidae may therefore be exposed to these toxins.

Furthermore, recent research indicates that plant material in the form of pollen grains has the potential to spread considerable distances form the mother plant. A study done by Fricke *et al.* (2004), in which Computational Fluid Dynamic (CFD) technology was used to estimate the distance travelled by genetically modified maize pollen, reported that the grains could travel as far as 815 m from the parent plant at maximum wind speeds of 40 $m.s^{-1}$. In the study by Rosi-Marshall *et al.* (2007) pollen drift of up to 2000 m were recorded. The concern is that this pollen, which may land on vegetation outside the field, will then be ingested by non-target phytophagous arthropods feeding on the vegetation. Laboratory studies have shown that Bt-pollen does in some cases have a negative effect on non-target organisms (Losey *et al.*, 1999; Mattila *et al.*, 2005; Lawo & Romeis, 2008), although the toxin concentrations are often not a realistic representation of those encountered in the field (Duan *et al.*, 2008).

Exposure of non-target Lepidoptera to insecticidal transgene products may occur through consumption of plant tissues or transgenic pollen. The Monarch butterfly (*Danaus plexippus*) is one such non-target lepidopteran that received special attention in this regard. Losey *et al.* (1999)

reported that the survival and consumption rates of Monarch larvae were significantly reduced when fed milkweed leaves dusted with Bt-pollen and concluded that Bt-crops could have profound implications for the conservation of the butterfly. However, field experiments that evaluated possible negative impacts of pollen on Monarch butterflies demonstrated that the wide-scale growing of Bt-maize did not pose a significant threat to the species (Gatehouse *et al.*, 2002). Rather, the primary threat to the monarch population is loss of crucial winter habitats in southern California and central Mexico (Gatehouse *et al.*, 2002), and also agricultural practices such as weed control (Zangerl *et al.*, 2001).

Alternatively, insecticidal proteins may be ingested in a more indirect way via tritrophic interactions. Natural enemies may for instance ingest transgene products via feeding on herbivorous arthropods that have themselves ingested the toxin from the GM plant (Ferry, 2010). Exposure of arthropod communities to Bt-toxins may be mediated by movement of individuals to and from GM maize fields. Bt-toxins may take up to several days to kill insects (Hagedorn, 1997) and poisoned individuals may have time to move out of the fields into the surrounding natural vegetation. It is possible that predatory arthropods may be exposed to the toxins when they subsequently prey on poisoned individuals. However, it seems that such tritrophic interactions are often dependent on the susceptibility of the herbivore to the plant produced toxins (Ferry, 2010). If the prey item is susceptible, the toxin is bound to receptors in the midgut epithelium and it may therefore lose its entomotoxicity. In non-target or resistant arthropods, the toxins do not bind and may therefore retain its biological activity (Ferry, 2010).

Lacewings (Neuroptera: Crysopidae) are important predators in many cropping systems. Studies indicated that larvae of the green lacewing, *Crysoperla carnea*, showed an increased mortality rate and slightly increased developmental time if they fed on prey that consumed Bt-maize (Hilbeck *et al.*, 1998). In this case it was also found that *C. carnea* that fed on prey that contained 100 mg/g Cry1Ab had a mortality rate of 78% compared to the control mortality rate of 26%. Once again, however, exposure to the amounts offered is unlikely occur under field conditions (Gatehouse *et al.*, 2002).

As a result of unrealistic conditions in laboratory experiments, an increasing number of studies are being conducted to test the effect of Bt-toxins on arthropod communities under field conditions in real agro-ecosystem environments. The drift of Bt-pollen was monitored by Hofmann *et al.* (2010) in the Ruhlsdorfer Bruch nature reserve (Brandenburg, Germany) in 2007 and 2008, which was surrounded with maize fields. One of these fields was planted with Bt-maize. The results of both seasons indicated that non-target organisms in the nature reserve were exposed to Bt-maize pollen, despite the presence of isolation distances between the maize fields and nature reserve.

With a buffer zone of 100 m, as much as 48% of the sampled pollen represented Bt-material. Even with buffer zones of 250 m and 500 m Bt-pollen was still in the order of 18%. This study confirmed that maize pollen drift in excess of 250 m is possible and therefore necessitates the need for larger buffer zones (according to their statistical analysis, at least 500 m).

It is clear that the drift of Bt-plant material to field margins is a reality. Despite this however, a considerable number of studies failed to indicate significant negative effects of Bt-toxins on non-target arthropods (Ferry, 2010). Review articles of Romeis *et al.* (2006) and Wolfenbarger *et al.* (2008) for example reported little evidence that non-target organisms that are not closely associated with target pests are negatively affected by Bt-toxins. It is therefore important to gain some perspective on the relative negative effects of different agricultural practices on arthropod populations. Despite the possible toxic effects on non-target arthropods, the alternative for Bt-maize is often the application of broad-spectrum pesticides, which may have a greater overall adverse impact on ecosystem health (Meissle & Lang, 2005). In fact, some GM crops may actually have the potential to increase biodiversity by enabling more environmentally sound farming practices (Ferry, 2010). Therefore, more detailed experiments and analyses are called for to assess whether genetically modified crops can be favoured in terms of environmental impact over previous destructive strategies (Gatehouse *et al.*, 2011).

2.4.4 Irrigation

The irrigation of crop fields may have a marked effect on both the plant and arthropod communities in agro-ecosystems. Applying large amounts of water to arid zones may alter the ecosystem (Soule *et al.*, 1990). Insect and weed species previously unable to withstand dry conditions may thrive in irrigated crop fields and become serious pests. It has been shown by Ghabbour (1977) that irrigation of rice fields in Egypt caused an increase in weed species as they recorded ten additional species for irrigated fields. As mentioned above, the combined effects of fertilization and irrigation also have an effect on the plant communities of shortgrass prairie (Kirchner, 1977). Plant productivity, measured in terms of biomass, increased with increased irrigation, and this may have an effect on the arthropod communities as well. Increased plant density associated with increased irrigation of grain sorghum (*Sorghum bicolor* L.) actually had a negative effect on the populations of greenbug (*Schizaphis graminum*) (Hemiptera: Aphididae) (Matis *et al.*, 2011). On the other hand, drought stressed plants may also have a negative effect on arthropod communities. It was shown by Michels and Undersander (1986) that greenbug reproduction on sorghum decreased as water stress increased.

Studies indicate that different arthropod groups react differently to increased moisture conditions (Lindberg *et al.*, 2002; Mackay *et al.*, 1986; Tsiafouli *et al.*, 2005) or the fluctuation thereof (Taylor *et al.*, 2004). Increased moisture may favour groups such as collembolans and mites, but have a negative effect on ants (Chikoski *et al.*, 2006). Moisture definitely affects the distribution and abundance of soil invertebrates (Curry, 1994). In temperate soils, the dominance of macro-invertebrates as opposed to mesofauna and microfauna decreases with decreasing soil moisture (Coleman & Sasson, 1980). Kirchner (1977) also showed that there was a significant shift toward more large arthropods in irrigated treatments of shortgrass prairie.

Some studies illustrate that irrigation may serve to increase arthropod numbers, abundance and biomass in crop fields. Frampton *et al.* (2000) found that spring drought had an overall negative impact on arthropod abundance, while that of irrigation was positive. However, this could be disadvantageous for the crop if these arthropods are pest species. It was found by Adabi *et al.* (2013) that poplar lace bug (*Monosteria unicostata*) (Hemiptera: Tingidae) infestations were significantly higher with increased irrigation of poplar trees (*Populous* spp.). Also, the density, number, dry mass and egg deposition of variegated leafhoppers (*Erythroneura variabilis*) (Hemiptera: Cicadellidae) increased on grapevines (*Vitis vinifera*, cv. Thompson Seedless) with increased irrigation (Daane & Williams, 2003). Interestingly, this study found that irrigation amounts above a certain critical level increased nymph densities, but did not have a marked adverse effect on grape yield. This indicates that it may be possible to manipulate irrigation amounts to control insect pests without compromising crop yield. Irrigation may benefit soil biota in agro-ecosystems. Soil pests such as the grass grub (*Costelytra zelandica*) (Coleoptera: Scarabaeidae) showed decreased mortalities as irrigation prevented soil temperatures from reaching the lethal range (East & Willoughby, 1980).

However, irrigation does not necessarily have a selective positive effect on certain functional groups such as herbivore pests and while irrigation may increase herbivore pest numbers it may also be beneficial for their predators and parasitoids. In the study of the grapevine leafhoppers, no functional group could be found that benefitted more than others (both pest species and predators benefitted) (Daane & Williams, 2003).

2.4.5 Soil disturbance

Agriculture can hardly function without soil disturbance caused by associated management practices. These agronomic practices such as tillage (no-till, minimum or conventional), tillage timing and mowing have complex effects on the physical, chemical and biological environment of the soil (Kladivko, 2001) and may therefore significantly affect biological elements and dispersal of beneficial organisms (Wardle *et al.*, 1999b). Compared to no-tillage systems, ploughing of fields may influence the importance of different decomposer groups in decomposition of organic matter and nutrient release (Hendrix *et al.*, 1986). The practice of tillage also has the potential to influence the species composition, diversity, biomass, density and evenness of the non-crop plant communities in cultivated fields. Santín-Montanyá *et al.* (2013) found that the abundance, diversity and evenness of weed communities in winter wheat of central Spain significantly increased in no-tillage systems compared to minimum and traditional tillage systems. Similarly, Menalled *et al.* (2001) found that weed biomass, density and diversity were highest in no-tillage, low-input organic systems of annual row crops in the USA.

Plant associated invertebrate communities of crop fields may also be affected by soil tillage practices, although not all species react in a similar fashion. In a study by Sharley *et al.* (2008) the effect of soil tillage on beneficial invertebrate communities was examined in vineyards of Australia. Spider, millipede, centipede and earwig numbers as well as Trichogrammatidae and other parasitoids decreased with increased levels of tillage while several families of beetle (e.g. Anthicidae, Byrrhidae, Nitidulidae and Staphylinidae) increased in abundance. This indicates that soil tillage has the potential to affect the species composition of arthropod communities and that it may have negative effects on beneficial species in crop fields. In general, the conversion of crop fields from conventional tillage systems to no-tillage systems seem to be beneficial for most soil fauna and micro-organisms due to increased soil moisture and smaller fluctuations in soil temperature (Kladivko, 2001). It seems that most invertebrate macrofauna are sensitive to soil tillage and may be absent or in low numbers in tilled fields (Kladivko, 2001). Therefore, tillage practices have the potential to decrease diversity in crop fields.

While soil tillage may affect plant and arthropod communities inside maize fields, dust produced by agricultural activities such as ploughing or traffic on dirt roads may have a negative impact on the surrounding field margin biota. It was shown in a study by Goossens and Buck (2009) that off-road driving was a significant source of dust in arid and semi-arid areas of Nevada, USA, although the amounts varied greatly with the type of soil and the characteristics of the top soil layer. The effects of dust production on arthropods are uncertain but it has been found to have a negative effect on vegetation.

Windblown dust has been shown to affect the physiological performance of desert shrubs. The physiological parameters of gas exchange for three species (*Atriplex canescens, Hymenoclea salsola* and *Larrea tridentata*) were measured at a Mojave Desert site, at which both undisturbed and heavily dusted individual shrubs occurred (Sharifi *et al.*, 1997). Maximum rates of net photosynthesis of dusted organs were reduced to 21% of those of control plants in resinous leaflets of *Larrea*, to 44% in resinous leaves and photosynthetic stems of *Hymenoclea*, and to 58% in non-resinous C_4 leaves of *Atriplex*, which have vesiculated trichomes. Dusted plants of all three species showed reduced maximum leaf conductance, transpiration and instantaneous water-use efficiency. Heavily dusted shrubs had smaller leaf areas and greater leaf-specific masses, suggesting that the short-term effects of reduced photosynthesis and decreased water-use efficiency may cause lowered primary production in desert plants exposed to dust during seasons when photosynthesis occurs. It is uncertain whether activities in maize fields are capable of producing this amount of dust but if plant productivity is affected, it may well affect arthropod diversity in complex ways (Siemann, 1998).

2.4.6 Livestock grazing

Agricultural land in the grassland and savanna biomes of South Africa that is not used for crop production is often utilized as grazing pastures for livestock (Mucina & Rutherford, 2006). Therefore, the biota of crop field margins may be subjected to the additional disturbances associated with this type of land use. Several studies have shown that abundance and composition of plant species are greatly affected by herbivore grazing (McNaughton, 1979; Milchunas *et al.*, 1988; Rutherford & Powrie, 2013). The responses of plant communities to grazing rely on a number of complex factors. The response of a single plant species may be influenced by abiotic environmental factors such as differences in soil. Therefore, grazing may have different effects on the same plant species in different regions (Tainton, 1999b).

Grazing does not influence all plant species in the same manner since some species may be more tolerant to defoliation than others (Wolfson, 1999). This may result in the elimination of sensitive species and the increase of more tolerant species. In general however, excessive grazing often result in the replacement of palatable, productive species with less palatable, less productive grasses and forbs (Tainton, 1999b) and a reduction in above-ground biomass (Wan *et al.*, 2011). Also, it has been found that grazing generally favours annual over perennial plants, short plants over tall plants and stoloniferous and rosette architecture over tussock architecture (Díaz *et al.*, 2007). Furthermore, heavy grazing may often, although not always, result in lower plant diversity (Rutherford & Powrie, 2013).

As with plants, grazing does not influence all arthropod groups in a similar fashion or to the same degree, but evidence suggests that it definitely has the potential to influence the species composition, diversity and interactions of plant associated arthropod communities as a whole. Grazing may affect arthropod communities via changes in floral composition and habitat structure and this is influenced by grazing intensity as determined by grazing regimes (Curry, 1994).

The dependence on certain floristic structures could cause some arthropod groups to decline if these structures are reduced by grazing. Many arthropod predators are more successful if the adult stages are supplied with alternative pollen or nectar supplies and may therefore be benefitted in landscapes with more flowering plants (Evans & Murdoch, 1968). It was shown by Morris (1967) that invertebrate species that are dependent on fruits and flowers such as seed weevils (e.g. *Apion loti*) (Coleoptera: Apionidae), bumblebees and a mirid (*Leptopterna ferrugata*) (Hemiptera: Miridiae), were much more numerous in exclosures where grazing was absent as opposed to grazed chalk grassland. This was contributed to increased flowers and fruits of the plant species *Lotus corniculatus* and *Campanula rotundifolia* in ungrazed grassland.

Furthermore, changes in the complexity of habitat structure caused by sheep grazing were shown to affect spider communities in moorland grassland (Cherrett, 1964). The authors found only seven spider species in grazed grassland as opposed to 14 in ungrazed sites and attributed this to the lack of complex vegetational structures in grazed moors that the spiders need to attach their webs to. These studies illustrate that grazed and ungrazed grassland may have very different faunas both in terms of quality and quantity.

The effect of grazing on plant and arthropod communities is also determined by grazing regime such as stocking rate and rotations. East and Pottinger (1983) distinguished between three different types of responses to stocking rate. Invertebrate species may either decrease with increasing stocking rate (type I), peak at intermediate levels of grazing (type II) or increase with increasing stocking rates (type III). They indicated that these responses were mainly due to the effect of defoliation and trampling on microclimate and living space.

A study by Hutchinson and King (1980) showed that stocking intensity of sheep had marked effects on the abundance and biomass of 16 groups of large invertebrates. Overall, the Hymenoptera (specifically ants) increased in number while most other groups decreased with increased stocking rate. Scarabaeid larvae were favoured by intermediate levels of grazing. These responses were mostly contributed to the alteration of living space, shelter and temperature. Ant species may be favoured by increased grazing as this creates bare soil patches where they often prefer to establish colonies (Pontin, 1963). Lenoir and Lennartsson (2010) illustrated that small spiders, carabids and ants (*Myrmica* spp.) were more abundant in continuous grazing than in late-grazing systems while larger spiders, carabids, and ants (*Formica* spp.) were more abundant in late-grazing systems in two Swedish semi-natural grasslands. Changes in temperature, food resources, vegetation structure, litter layer and competition have been proposed to explain these responses.

2.4.7 Habitat fragmentation

Land clearance for crop fields result in habitat loss and has a break-up effect on the landscape. Therefore, patches of natural vegetation are often completely separated from one another by a radically different vegetation type (the crop) which may influence the dispersal of individuals between habitat patches (Fahrig, 2007). This process is often termed habitat fragmentation and may be defined as “the dividing of an area of habitat into a number of smaller areas separated by stretches supporting a radically different community of organisms” (Allaby, 2009).

The effect of habitat fragmentation is two-fold in that it results in smaller habitat patches and also increased isolation of remnant patches. Therefore, the distinction must be made between the effects of habitat subdivision and habitat loss on communities (Lindenmayer & Fischer, 2006). Evidence suggests that habitat loss has a much greater negative effect on biodiversity than habitat fragmentation *per se* (Fahrig, 2003). Species diversity and richness may decrease with decreasing habitat area as was reported to be the case for insect communities in a review article by Debinski and Holt (2000). This may be due to larger resource concentrations and greater diversity of habitat in larger areas as well as increased extinction rates of smaller populations as a result of limited genetic diversity (Pullin, 2002). Also, smaller habitat fragments are characterized by increased edge effects (Ewers & Didham, 2006) and may have additional adverse impacts on biota in remnant patches (chapter 2.2).

Increased isolation may prevent exchange of individuals between habitat patches, which may disrupt gene flow and result in the loss of genetic diversity (Lange *et al.*, 2010). This may ultimately lead to the decline and extinction of isolated populations. It has been shown by Saccheri *et al.* (1998) that larval survival, adult longevity and egg-hatching rate of the Glanville fritillary butterfly (*Melitaea cinxia*) (Lepidoptera: Nymphalidae) were adversely affected by inbreeding and that extinction risk increased significantly with decreasing heterozygosity (an indication of inbreeding). Therefore, the effects of habitat fragmentation may have a detrimental effect on the functioning of the remaining natural habitat fragments and it often results in a continual loss of species even if habitat fragments are protected (Pullin, 2002). It has been shown that habitat fragmentation and the degradation it causes to habitat is a major cause of biodiversity and species richness loss (Wilcove *et al.*, 1998).

An increasing number of studies point to the potentially serious decline in populations of pollinators due to habitat fragmentation (Harris & Johnson, 2004). Pollinators may be negatively affected by smaller habitat fragments due to decreased nectar and pollen resources (Kearns & Inouye, 1997), decreased non-food resources (Spears, 1987) and reduced habitat diversity (Baz & Garcia-Boyero, 1995). Also, the degree of isolation experienced by flowering plant species has been shown to influence the pollinator species diversity and number of individuals (Wolf & Harrison, 2001) and also the species composition of pollinator species in habitat fragments (Rathcke, 1993).

Several field studies provided evidence that there may be considerable disruption of plant-pollinator relationships in fragmented habitats. Ågren (1996) indicated a positive relationship between plant population density and seed production in the self-incompatible herb *Lythrum salicaria* (Lythraceae), which is an indication of insufficient pollen transfer in smaller populations. Furthermore, small and fragmented populations of the tree species *Spondias mombin*

(Anacardiaceae) showed significant reductions in germination rate and fruit production compared to large fragment and continuous forest populations (Nason & Hamrick, 1997).

The effect of habitat fragmentation on communities is greatly affected by distance from other parches and organism size (Margules, 1991) as well as dispersal ability (Samways, 2005). In South Africa, Ingham and Samways (1996) found that most arthropod species are capable of transgressing borders of landscape elements. However, their results showed that the Blattodea, Hemiptera, and Diptera are generally restricted to remnant patches of vegetation and are highly affected by fragmentation while the Hymenoptera, Arachnida, and Orthoptera were generally more cosmopolitan and were distributed regardless of obvious landscape boundaries. Flightless arthropod species such as the bush cricket (*Metrioptera bicolor*) (Orthoptera: Tettigoniidae), are also vulnerable to extinction in small habitat patches (Kindvall, 1992). Therefore, habitat fragmentation may ultimately result in the selective extinction of species, depending on their dispersal ability but probably also on the taxa, habitats and regions considered (Samways, 2005).

2.5 Biota of grassland and savanna habitats

South Africa’s rich diversity is largely due to the wide range of climatic conditions and topographic variation in the country. This combination of topography and climate give rise to broad and relatively distinctive vegetation zones called biomes, each with characteristic plant and animal species (Mucina & Rutherford, 2006). Presently, nine terrestrial biomes are recognised in the region. These include the Desert, Forest, Fynbos, Grassland, Indian Ocean Coastal Belt, Nama-karoo, Savanna, Succulent Karoo and Thicket biomes. The largest part of South Africa consists of arid and semi-arid regions and most of the land area is therefore dominated by grassland and savanna (Low & Robelo, 1996).

2.5.1 The grassland biome

Grassland covers an estimated 21.3% of the land surface area in South Africa (Fairbanks *et al.*, 2000). The term ‘grassland’, as used by Mucina and Rutherford (2006), refers to a vegetation structure that is relatively simple, short and herbaceous and mostly consists of grasses (family Poaceae). Grass-like plants such as sedges of the family Cyperaceae and non-grass-like forbs are also characteristic of grassland vegetation (Coupland, 1979). Woody vegetation is rare or absent and, if present, usually consists of small to medium sized shrubs. The lack of woody vegetation is mostly maintained by the arid nature of natural grasslands (Coupland, 1979). Despite the seemingly simple vegetation structure of grassland, this biome houses a rich floristic community, with five centres of plant endemism that have been identified in the region. This includes the Barberton, Drakensberg Alpine, Lydenburg, Sekhukhune, Soutpansberg and Wolkberg areas (Schmidt *et al.*, 2007).

In drier regions such as grassland and savanna, insects are probably the most important invertebrate group due to their resistance to desiccation (Coupland, 1979). Compared to the multi-layered nature of habitats such as woodland, grasslands can be considered relatively simple in structure and it may therefore be argued that the range and species richness of invertebrates in these habitats are correspondingly lower (Curry, 1994). Nevertheless, there is ample evidence that grassland habitats can support large numbers of invertebrate species. A study done on the invertebrate species richness of a 12 acre tract of abandoned farmland in south-eastern Michigan, USA, revealed 1584 species which represent 179 families in fifteen orders (Evans & Murdoch, 1968).

Probably the most conspicuous insects in grassy habitats are the grasshoppers and other members of the order Orthoptera (Coupland, 1979) where they often play a significant role in the consumption of plant material (Andersen & Lonsdale, 1990). Also characteristic are the ants (Hymenoptera: Formicidae) and termites (Isoptera), which play significant roles in the modification of soil properties and the distribution of organic matter (Brian, 1978). Ants and termites may also be used in some cases as indicators of diversity and habitat disturbance in grassland habitats (Agosti, 2000).

Unfortunately, the grassland biome is also one of the most threatened in South Africa and it is estimated that 23% have been transformed for cultivation, 60% is irreversibly transformed and only 2% are currently protected (Fairbanks *et al.*, 2000). Maize, sunflower, sorghum and wheat are the most commonly cultivated crops in the grassland biome (Low & Robelo, 1996). Furthermore, overgrazing and soil erosion are common problems in South Africa's grasslands, especially in the Eastern Cape and Lesotho grasslands (Darkoh, 1987; Smits *et al.*, 1999).

Afforestation of the high rainfall areas of the eastern plateau with alien trees (e.g. *Pinus* and *Eucalyptus* species) is common (O'Connor & Bredenkamp, 1997) and the alteration of grasslands to alien tree plantations have been shown to have negative impacts on species diversity and the functioning of grassland ecosystems (Armstrong & Van Hensbergen, 1999). It is estimated that grassland in South Africa are being destroyed at a rate of over 200 square km per annum by commercial afforestation (Van Wyk, 1998). A number of alien woody species (such as *Solanum mauritianum*, *Acacia mearnsii*, *Acacia dealbata*, *Eucalyptus* spp., *Melia azedarach* and *Prunus persica*) have successfully invaded the grassland biome, especially near urban areas (O'Connor & Bredenkamp, 1997), which may cause further degradation to grassland habitats.

2.5.2 The savanna biome

The savanna biome is by far the largest in South Africa and occupies 32.8% of the land surface area (Mucina & Rutherford, 2006). Savannas are typically interactive grass and tree mixtures, being characterized by a grassy ground layer and a distinct upper layer of woody plants (Knoop &

Walker, 1985). Depending on the structure of the woody vegetation, savanna may be subdivided into “tree savanna," "shrub savanna," or "savanna woodland” (Scholes & Archer, 1997).

Because of their great structural complexity, trees have great niche diversification and may support more species than smaller plants such as shrubs and grasses (Lawton & Price, 1979; Strong & Levin, 1979). It has been demonstrated that savanna trees have the potential to house an incredible richness of arthropod species (Krüger & Mcgavin, 1998). Therefore, the presence of trees in savanna creates a multi-structured vegetation type, which may allow for more species per unit area than more simple structured habitats such as grassland (Schadek *et al.*, 2009). It has been illustrated in a study by Proches and Cowling (2006) that the savanna areas had a greater arthropod richness than grasslands. A follow-up study by the above authors also indicated that the arthropod communities of grassland and savanna are relatively distinct (Procheş & Cowling, 2007), although the reason for this is still poorly understood.

As with grassland, the savanna habitats of South Africa are negatively impacted by a variety of anthropogenic activities. This is a cause for concern as only about 5% are formally protected (Rebelo, 1997). Compared to other transformational land use practices, cultivation causes the greatest loss of savanna habitats in South Africa (Mucina & Rutherford, 2006). Furthermore, remaining savanna habitats near rural settlements are often characterized by a loss in woody vegetation as wood is a prominent source of energy for these poor communities (Shackleton *et al.*, 1994).

Most of the savanna vegetation types in South Africa are used as grazing pastures for livestock or game (Cousins, 1999). Even though grassy vegetation is resistant to grazing disturbances, overstocking can result in the degradation of plant communities. Palatable grasses such as *Panicum maximum* and *Anthephora pubescens* may be replaced with less palatable grasses like *Eragrostis pallens* and species of *Aristida* (Tainton, 1999a). The increase of selected species of woody vegetation, commonly known as “bush encroachment,” is a common phenomenon in South Africa’s savanna and results in the reduction of grazing capacity of natural rangelands (Smith *et al.*, 1999). Although the reasons for bush encroachment are multiple and complex, it has been stated that one of the main causes involves overgrazing of grasses (Vegten, 1984) as this influences the competitive relationships between grasses and woody vegetation. The Kalahari thornveld have for example been invaded by *Acacia mellifera* subsp. *detinens*, and many sweetveld areas have been invaded by *Dichrostachys cinerea* and other species of *Acacia* (Tainton, 1999a).

2.6 Plant-arthropod diversity relationships

2.6.1 Dependence of arthropod diversity on plant diversity

Most animal life, including arthropods, depend on green plants for food, shelter, oviposition sites and overwintering areas and it is therefore hardly surprising that intricate relationships exist between arthropods and plants (Schoonhoven *et al.*, 1998). As mentioned previously, insects are considered to be one of the most important pest species of crops but may also provide essential ecosystem services in natural and agricultural environments. For this reason, understanding the relationship between arthropods and plants has gained popularity in recent years as it may provide clarity concerning the causes of insect pest outbreaks and also aid in the enhancement of beneficial arthropods in the agro-ecosystem (Schoonhoven *et al.*, 1998).

By studying the interrelationships between plants and arthropods, the complexity thereof immediately becomes apparent. Arthropods associated with plants fill a variety of niches and occupy many different spaces on and around plants (Jolivet, 1998). Some decompose dead or dying plant matter around plants and others live under bark or in dead wood. They may also live on or inside roots, leaves, flowers and stems. Some produce galls or mines and may inhabit plant cavities. Some suck the sap of plant parts and others feed on nectar and pollen. This multitude of opportunities therefore enables a great variety of arthropods to be associated with plants.

It has been estimated that nearly half of all existing insect species feed on living plants, which means that more than 400 000 known herbivorous insect species are associated with approximately 300 000 vascular plant species (Schoonhoven *et al.*, 1998). In general, phytophagous arthropods may be described as being monophagous, oligophagous or polyphagous (Jolivet, 1998). Monophagous arthropods are specialists that feed exclusively on a single plant species. Oligophagous arthropods generally feed on a small group of plants that are usually, but not always, in the same family or genus. Polyphagous arthropods on the other hand are generalist feeders and feed on a wide variety of plants belonging to unrelated genera in different orders. It seems though that the majority of insect species are host-specific (Bernays & Graham, 1988), which is to say, they are specialized to feed on only one or a limited number of plant species (Jolivet, 1998).

As many arthropod herbivores are host-specific, it may also make them vegetation-specific (Procheş & Cowling, 2007). Therefore, it is tempting to conclude that a greater number of plant species will inevitably support a greater number of herbivore arthropod species and then also a greater richness of predators and parasitoids, either via direct (Jervis *et al.*, 1993) or indirect (Hunter & Price, 1992) mechanisms. In fact, decreased arthropod diversity and richness in agro-ecosystems is often attributed to reduced plant diversity (Tivy, 1990) and numerous models predict that plant diversity should increase arthropod diversity (Tilman, 1986.; Whittaker, 1970; Rosenzweig, 1995).

The diversity of bees in South Africa seems to be linked to plant diversity (Kuhlmann, 2009). Both plants and bees have their highest centres of diversity in the winter rainfall areas of western South Africa, which indicates that some form of relationship does exist between bee and plant diversity. Similarly Toft *et al.* (2001) found that the species richness of fungus gnats (Diptera: Mycetophilidae) and beetles (Coleoptera) correlated with vascular plant richness. However, an increasing number of studies indicate that these relationships are much more complex than previously believed and a number of factors (other than diversity *per se*) may have an effect on the number of arthropod species that occur on plants.

A study by Siemann *et al.* (1998) tested specifically whether increasing plant species richness and functional plant richness result in increased arthropod diversity. They found that increasing both the number of plant species and the number of functional groups significantly increased total arthropod species diversity. However, they also found high arthropod diversity in monocultures and generally weak statistical associations between plant and arthropod diversity. Furthermore, the diversity of herbivores was more strongly correlated with predator and parasitoid diversity than with plant diversity. The authors argued that local arthropod herbivore diversity may also be maintained by and, in turn, maintain a diversity of parasites and predators that prevent competitive exclusion, allowing a high diversity of herbivores to coexist, even in a monoculture. Therefore, arthropod diversity may in addition rely on factors such as interspecific interactions.

Caballero-López *et al.* (2010) indicated that the family richness of chewing and sucking herbivores as well as predators and parasitoids were closely associated with not only plant species richness but also the cover of grasses and legumes. They also found positive correlations between legume cover and flower consumers. Furthermore, Hawkins and Porter (2003) examined the extent to which plant and animal diversity is correlated by comparing the richness patterns of the 217 butterfly species resident in California to those of plants, including all 5,902 vascular plant species and the 552 host plant species of the caterpillars. They also examined the relationships between plant/butterfly richness and 20 environmental variables. Results showed that plant and butterfly diversities were positively correlated. However, multiple regression, path models, and spatial analysis indicated that once primary productivity and topographical variability were incorporated into models, neither measure of plant richness had any relationship with butterfly richness, not even in evaluations of strict monophage larvae. Therefore, it seems that plant diversity did not directly influence butterfly diversity but that environmental factors played a greater role in determining butterfly richness. On the other hand, a study by (Moolman *et al.*, 2013) showed that assemblages of stemborer species (of the genera *Busseola*, *Chilo* and *Sesamia*) are best determined by host plant assemblages rather than habitat. This host plant specificity has been ascribed to specific leaf surface odours or the internal structure of the plants, which favoured different stemborer species.

Koricheva *et al.* (2000) manipulated both plant species richness and plant functional groups and found that it only affected the richness of leafhoppers and wingless aphids, which are more sedentary and host specific. The richness of less specialized or mobile herbivores such as grasshoppers were not significantly affected. Therefore, the relationships of arthropods with plants may also be dependent on the biology of the arthropod species in question. Furthermore, it seems that herbivore diversity was once again affected to a greater extent by the diversity of their natural enemies than plant diversity.

Clearly, arthropod species diversity is not always a simple function of plant species diversity and many aspects thereof are still poorly understood. It is uncertain for instance whether plant diversity and richness affect arthropod communities directly or whether both groups simply respond to similar environmental factors (Proches & Cowling, 2006). Overall, it seems that direct effects do exist and involve factors associated with the characteristics of the host-plant and habitat (Curry, 1994). In general, habitats that are more heterogeneous have the potential to support more species, as these environments provide a greater variety of microhabitats, microclimates, and hiding places (Begon *et al.*, 2008). For plants, variations in the abiotic environment such as soil characteristics, temperature and precipitation may influence the species richness of an area (Visser *et al.*, 2012). Along with environmental factors, arthropod diversity may be influenced by the heterogeneity provided by plants. This heterogeneity may exist in the form of species diversity, but also in the form of structural diversity, variation in productivity and chemical variability.

2.6.2 Dependence of arthropod diversity on plant architecture

An important characteristic involving host plants that seems to play a role in determining arthropod diversity is plant architecture. Size (the spread of vegetation through different positions in space) and variety (in form and persistence) are considered to be two of the major factors involved in shaping arthropod communities (Strong *et al.*, 1984). The role of plant size is well illustrated in a study by Strong and Levin (1979). Insect associations of 215 genera of British plants and fungal parasites of 323 United States plant species indicated that trees tend to have more pest species than shrubs and shrubs more than herbs per unit area of geographical range. Greater size and morphological complexity has been proposed to explain these differences (larger, more complex hosts provide a greater diversity of niches). The rest of the variation in pest species diversity (20-60%) has been assigned to host-species range.

Furthermore, a study done by Stinson and Brown (1983) in an abandoned field undergoing secondary succession in Britain indicated that the number of different types of grass structure (a measure of architecture) accounted for 79% and 86% of the variance in leafhopper species richness and total abundance respectively. In a study concerning the plants and Homoptera on three old fields in southeast Michigan, it was shown that evenness and diversity of insects were equally correlated with plant structure (foliage height diversity) than with plant diversity and evenness (Murdoch *et al.*, 1972; Murdoch, 1975). Halaj *et al.* (2000) also indicated that the species richness of arthropod groups such as Araneae, Psocoptera, Collembola and Homoptera were affected by plant architecture as species richness increased with increased structural diversity of Douglas-fir branches.

Plant architecture may change dramatically in the course of a year, depending on the seasonal phenology of the individual plant species. This seasonal development of the host plant is considered to be one of the most important determinants of phytophagous arthropod diversity (Strong *et al.*, 1984). It has been illustrated by Niemelä *et al.* (1982) that the species richness of lepidopteran larvae on plants differed depending on seasonal phenology. In general, Lepidoptera species richness tended to peak earlier in the season for woody plants (especially for trees with a short shoot-growth period). Herbaceous plants on the other hand tended to peak much later in terms of Lepidoptera species richness. This has been contributed to the fact that woody plants have a much richer architecture earlier in the season, while herbaceous plants increase in structural complexity as the season progresses.

The physical structure of plants may have significant effects on the diversity of arthropods, not only because it provides more living spaces, but also because it has the potential to influence the microclimate of their living spaces. These microclimates vary greatly on different levels and parts of the plants and are also dependent on the nature of the plant architecture (Schoonhoven *et al.*, 1998). Photosynthetic and transpiration processes may have marked effects on the temperature and humidity of living space around the plant. Furthermore, vegetation cover reduces radiation on the ground level and also reduces wind speed. Different parts of the plant may also differ significantly in terms of microclimate so that arthropods living on different parts of the plant may experience significantly different environmental conditions (Schoonhoven *et al.*, 1998). This implies that species preferring different environmental conditions can live in close proximity to one another, enabling a greater diversity of arthropods to persist in a more structurally diverse habitat. Grasses that form tussocks may for example create favourable microclimates for more arthropod species as opposed to non-tussock forming species. It has been shown by Luff (1966) that diversity of beetle fauna tended to be higher in tussock grassland because more favourable temperatures and humidity exist within the tussocks and provide shelter from extreme climatic conditions throughout the year.

2.6.3 Dependence of arthropod diversity on plant productivity

It seems that animal diversity, or more specifically animal species richness, may also be related to plant productivity (Begon *et al.*, 2008). Three hypotheses have been proposed to explain why increased plant productivity in a system may facilitate an increase in arthropod diversity. Increased productivity may increase the abundance of rare resources, allowing extra arthropod species to persist ("the resource rarity hypothesis") (Abrams, 1995). Increased plant productivity may also allow rare herbivore species to become abundant enough to persist ("the consumer rarity hypothesis") (Abrams, 1995). Furthermore, increased plant productivity may allow the densities of resources to become abundant enough to allow coexistence of species that would otherwise have led to competitive exclusion ("the intraspecific density dependence hypothesis") (Abrams, 1995).

Therefore, increasing the productivity of a whole plant community may increase the diversity of arthropods associated with the plant layer. Siemann (1998) determined how grassland arthropod communities responded to independent manipulations of plant productivity compared to plant diversity and composition, employing fertilization on two different time scales. The experiment demonstrated that total species richness and abundance, as well as species richness and abundance of every trophic group (detritivores, herbivores, parasites, and predators), were significantly higher in plots that were fertilized and therefore had higher plant productivity. Another study by Davidson (1977) also indicated that increased plant productivity (facilitated by higher precipitation) increased the species richness of ants. This may be due to a greater range of seeds in more productive environments or an increased abundance of seeds, which may support extra consumers with narrow niches.

However, factors that increase the productivity of one plant species may not necessarily increase the productivity of another. As mentioned in chapter 2.4, the application of agrochemicals has the ability to influence the productivity of both crop plants and natural vegetation in positive and negative ways and affect arthropod communities. Therefore, this may lead to inconsistent responses of different arthropod groups associated with different plants (Altieri, 1999). Furthermore, increased productivity may not always have a positive effect on species richness and may even result in lower species richness in some cases (Begon *et al.*, 2008). Therefore, species richness may be highest at intermediate levels of productivity and coincides with the intermediate disturbance hypothesis (Huston, 1979) described in chapter 6.

2.6.4 Dependence of arthropod diversity on plant chemical composition and volatiles

Along with structural variability, there also exists a fair amount of chemical variability in the vegetation of any given habitat as each plant species and even individuals of a single species contain a unique mixture of chemical compounds that may have an effect on the arthropods associated with the vegetation layer (Schoonhoven *et al.*, 1998). It has been shown that host specialisation occurs more frequently in insects living on herbaceous plants than those on shrubs and trees (Futuyma, 1976), and this has been attributed to the fact that herbaceous plants generally have a greater range of chemical compositions than shrubs and trees (Schoonhoven *et* *al.*, 1998). This may in turn have an effect on the degree of association between plant and arthropod species.

Plant species diversity may increase chemical complexity directly in that each new species may contribute new chemical compounds and volatile substances and also indirectly by increasing structural complexity (Randlkofer *et al.*, 2010). Structural complexity may influence chemical composition by augmenting turbulence intensity and providing a variety of microclimates. Chemical complexity may then increase arthropod species diversity and richness as each new chemical compound, either within plant tissues or in the atmosphere, has the potential to attract a different arthropod species (Randlkofer *et al.*, 2010). On the other hand, chemical and structural complexity may not be directly related to plant species diversity, but rather to the diversity of chemical functional groups as closely related plant taxa may have similar chemical or structural characteristics (Randlkofer *et al.*, 2010).

The number of phytophagous arthropods in a given habitat may also be influenced by the efficiency of host plant location (Strong *et al.*, 1984). The relationship between plant and herbivore diversity may therefore not necessarily be linear because host choice is not always similar within a single species (Schoonhoven *et al.*, 1998). Different populations or even different individuals may have different host plant preferences so that some individuals may reject host plants, even though they belong to the host plant range of the species. This preference may be influenced by factors such as seasonality, temperature, developmental stage and sex (Schoonhoven *et al.*, 1998). Furthermore, herbivore loads may be lower in polycultures due to differences in the ability of herbivores to locate host plants in more diverse backgrounds (Siemann *et al.*, 1998). This may be influenced by the structural and chemical complexity of the vegetation (Randlkofer *et al.*, 2010).

Therefore, plant-arthropod diversity relationships may exist due to the host-specific nature of many arthropod species. Increasing the diversity of host plants may therefore increase the diversity of arthropod visitors. However, the lack of irrefutable evidence for linear relationships between plant and arthropod diversity is an indication that much more complex factors influence the arthropod diversity on plants other than plant diversity *per se*. The quality of food plants may be just as important and therefore, plant productivity could have additional effects on the arthropod communities associated with vegetation. Arthropods rely on plants, not only for food but also for shelter and the creation of the correct microclimate. In this regard, plant species composition and structural diversity may be just as important in shaping arthropod diversity.

2.6.5 Plant species composition as determinant of arthropod species composition

In addition to diversity relationships between plants and arthropods, the species composition of arthropod communities may be related to the species composition of plants. Schaffers *et al.* (2008) investigated the species composition of seven functionally different arthropod groups (epigaeic spiders, grasshoppers, ground beetles, weevils, hoppers, hoverflies, and bees) at 47 sites in the Netherlands, comprising a range of semi-natural grassland types and one heathland type to find the best predictor of arthropod species composition. The results demonstrated that local plant species composition was the most effective predictor of arthropod assemblage composition for all investigated groups, even more so than vegetation structure and environmental conditions. Furthermore, Symstad *et al.* (2000) illustrated that certain arthropod groups were associated with particular plant functional groups in a grassland experiment. The Homoptera and Coleoptera responded positively to the presence of forbs while the remainder of the Hemiptera group showed a decrease in species richness in response community composition dominated by C_4 grasses.

2.7 Biodiversity sampling techniques

2.7.1 Sampling arthropod diversity

Due to the overwhelming numbers of arthropods, acquiring absolute population estimates for a whole habitat is virtually impossible. Where the objective is to detect change in diversity or abundance, rather than absolute magnitude, absolute samples can be taken at regular intervals in the habitat, such as with the line transect method (Southwood & Henderson, 2000) (discussed below). However, the sampling of arthropods usually involve capturing and killing of individuals to facilitate identification to morphospecies level. Fortunately, with the exception of highly localised species, this removal of individuals does not seem to have a long lasting negative effect and arthropod communities seem to be able to recover relatively quickly (Samways, 1995). As discussed below, no single sampling technique is equally effective for all taxa. Therefore, the sampling technique used will depend on the desired purpose of the survey (Samways, 1995).

2.7.1.1 Sweepnet sampling

This method involves sweeping vegetation with a standard sized insect net and is probably one of the most common methods used for sampling insects from vegetation (Southwood & Henderson, 2000). Usually 48 or 50 successive sweeps are given that are synchronized with the pace of the collector (Whittaker, 1952). This method may be used with relative ease to sample invertebrates and it provides relative population estimates while providing a relatively large amount of information with minimal effort (Southwood & Henderson, 2000). However, this method is most effective in less dense vegetation and is known to catch mostly larger species while small, soft-bodied species tend to be damaged by this method (Nummelin & Zilihona, 2004). It has been stated by Hespenheide (1979) that sweepnet sampling may result in poor estimates of abundances of small insects and of faunal size classes.

2.7.1.2 Beating and chemical knock-down

The structural complexity of woody plants makes the collection of arthropods from their surfaces challenging. One method developed specifically for this type of vegetation involves holding a beating tray (usually a broad, cloth covered frame) under vegetation whilst beating the overhead branches with a stick, coaxing arthropods to fall into the tray (Southwood & Henderson, 2000). Individuals can then be collected from the tray by an aspirator or pooter. This method has proven to be effective for insects such as leaf beetles (Chrysomelidae), which have a tendency to fall from vegetation rather than fly away when disturbed (Richards & Waloff, 1961).

Very tall vegetation, such as tree canopies are commonly sampled by chemical knock-down methods, where vegetation is fumigated with insecticides and causes arthropods to fall from the tree, where they may be collected on trays (Southwood & Henderson, 2000). Alternatively, arthropods of row crops may be collected effectively by means of unrolling a length of oilcloth groundsheet between rows and shaking the plants over it (Southwood & Henderson, 2000). This method has proven to be successful for easily dislodged species such as certain Lepidoptera larvae (Turnipseed, 1974) but it has the disadvantage that it is time-consuming and may not be effective for flying insects. A technique involving the enclosure of an area of vegetation with a covered cylinder, fumigating the contents and collecting via suction sampler have been used in row crops such as soy-bean fields, although this method may also be rather time-consuming and costly (Southwood & Henderson, 2000).

2.7.1.3 Trap sampling

Pitfall trapping is a widely used method for sampling a variety of surface-dwelling, terrestrial arthropods (Southwood & Henderson, 2000). Setting up these traps usually involves burying open-topped plastic cups or bottles containing alcohol in the soil so that the rim of the containers are level with the soil surface. These traps have the advantage that they are low cost and easy to install and collect. However, they are limited to catching mainly ground-dwelling invertebrates. Their use is also limited in certain vegetation types and is dependent on insect activity (Thomas & Marshall, 1999). Furthermore, there is the added risk that the traps may be lost or carried away by animals, resulting in a loss of data.

Flight traps are another widely used technique to catch arthropods and works on the principle of random flight interception of insects on the wing (Duelli *et al.*, 1999). Window traps and malaise tents are often used for this purpose. Window traps seem to work better in open landscapes while malaise traps are used more often in forests (Duelli *et al.*, 1999). Yellow water pan traps may also be used to attract flower-visiting arthropods but can be used effectively for aphids and parasitoid wasps as well. Traps using colour have a major disadvantage in that the exact spectral properties have an influence on the fauna they attract. Since the human eye perceives colour differently from the insect eye, the many traps described in publications as all being yellow probably appear quite differently to insects (Duelli *et al.*, 1999). All of these traps are of course limited to flying arthropods and cannot be used for the sampling of a wide range of arthropod taxa.

2.7.1.4 Suction sampling

Suction sampling is a relatively fast method for sampling large areas of vegetation, although it is really only effective in dry, upright vegetation that is not more than 15 cm high (Southwood & Henderson, 2000). Therefore, it may be an effective method in grassy habitats, if not in dense woodlands. Suction in dense vegetation may selectively extract certain species and under-sample others (Elliott *et al.*, 2006). One of the most extensively used devices for sampling arthropods is the Dietrick vacuum (D-vac), which was the first commercially available suction machine used for the sampling of above-ground terrestrial invertebrates (Elliott *et al.*, 2006). Compared to other suction samplers, it has certain disadvantages in that it is bulky and heavy, making it tedious to manoeuvre in the field. Also, the velocity of air flow at the collection nozzle is relatively low, making it harder to catch larger arthropods. In this regard, care must be taken to move the nozzle vertically into the vegetation and down to the ground surface (Southwood & Henderson, 2000).

Comparisons of the D-vac method with others have revealed an efficiency of around 50-70% (Southwood & Henderson, 2000). It has been shown that the D-vac is not effective at sampling grassland Coleoptera. However, the D-vac method may still be used effectively if surveys only require that measures of diversity, evenness and species composition be relative. Furthermore, the D-vac method has a number of crucial advantages in that the large diameter sampling nozzle (33 cm) can enable the researcher to sample large areas rapidly. Also, the machine is available in a standard configuration so that different scientists repeating an experiment can expect similar results (Elliott *et al.*, 2006). Unlike pitfall traps the D-vac method is not as dependent on insect activity and is less prone to error (Thomas & Marshall, 1999).

It has been shown by Standen (2000) that the D-vac method is sufficient for estimating species richness of Hemiptera, most Diptera taxa, herbivorous Coleoptera and Linyphiidae in grassland, although not for all the Coleoptera and Araneae, which were better represented in pitfall traps. Furthermore, Buffington and Redak (1998) found that vacuum samplers caught significantly more individuals per unit effort than sweepnet methods for three out of six orders of arthropods in California coastal sage scrub. Significantly more individuals were caught using the suction sampler for two of the six orders. No significant differences could be found between the two methods for the remaining four orders. Also, a study in which the efficacy of the D-vac was compared to a “census-type” collection by means of plastic bags showed that the D-vac could accurately be used to collect Hemiptera insects from grain sorghum plants (Kruger *et al.*, 2008).

Therefore, although the D-vac method does not sample all arthropod taxa with equal efficiency, it may represent one of the best techniques for sampling a wide range of arthropod taxa in the vegetation cover and on the soil surface. In other words, it provides a quick and effective way to sample large areas.

2.7.2 Sampling plant diversity

The relative ease with which plants can be identified up to species level in the field means that collections are only necessary in the case of unidentifiable individuals. However, the selection of the correct sampling design is a vital part of any plant survey and will depend on the aims and objectives of the study (Kent & Coker, 1992). The time and resources available, as well as the type of habitat and methods of data analysis must also be taken into consideration (Knapp, 1983).

2.7.2.1 Quadrats

One of the most common methods by which plant communities can be sampled within a single sample plot is by means of the quadrat method. This involves the recording of vegetation in demarcated areas of equal size (usually square) and therefore provides a way to establish a standard area for examining vegetation (Kent & Coker, 1992). The appropriate size for the quadrats will depend on the type of vegetation, and methods for determining the optimal size of quadrats have been developed that are based on minimal area and species-area curves (Kent & Coker, 1992). However, this is only possible in homogenous plant communities and not where ecotones or edge communities are present. Quadrat size may also depend on the size of the plant species in the community. Bryophyte and lichen communities may only need quadrat sizes of 0.5 x 0.5m, whereas scrub and woodland shrub communities may need quadrats of 10 x 10m (Kent & Coker, 1992). Quadrats may be used to acquire presence/absence or abundance data that can be used to describe the species richness, diversity and evenness of plant communities and also other aspects such as density, frequency, cover, and biomass.

2.7.2.2 Fixed points

In some cases, plants are recorded at a single point, usually with the aid of metal pins with sharp tips attached to frames. All plants touching the pins are recorded and in addition to species composition, the % cover and % sward may be determined in this way (Barbour, 1999). Alternatively, distance methods may be used, where random or regular points are identified, and at each point the nearest individual are identified, its distance from the point measured and its basal area measured. The distance between plants may also be measured. Data acquired from this method may be converted to plant density data and may also reveal whether plants are randomly distributed or not (Barbour, 1999).

2.7.2.3 Transects

The position of plots in a field survey may be chosen via vegetation stratification or by choosing purely random positions (Kent & Coker, 1992). Alternatively, plots can be arranged at systematic or fixed intervals. Arranging plots in transects (lines along which samples of vegetation are taken) is a popular method, especially along gradients of change (e.g. environmental gradients) and is designed to describe maximum variation over the shortest distance in a minimum amount of time. Single transects can be laid out next to one another, in which case they are known as belt transects (Kent & Coker, 1992). At each plot along the transect plant characteristics may be surveyed using quadrates as described above.

Chapter 3: Study areas

3.1 Introduction

Study sites were selected in six of the major maize producing provinces of South Africa namely the Eastern Cape, Free State, KwaZulu-Natal, Limpopo, Mpumalanga and North-West (fig. 3.1). The sites were chosen to represent the grassland and savanna biomes and included commercial and subsistence farming, both irrigated and dry land, with maize fields ranging from 5000 m^2 to 500,000 m^2 in size (a summary of the general information and climate data of each study site is given in table 3.1 and 3.2). The study areas were not selected to present commercial and subsistence farms or certain farming practices specifically, but simply to include all types of maize producing systems to acquire baseline data for maize fields in general. In each province, two sites were selected for surveys (see chapter 4 for complete description of methods).

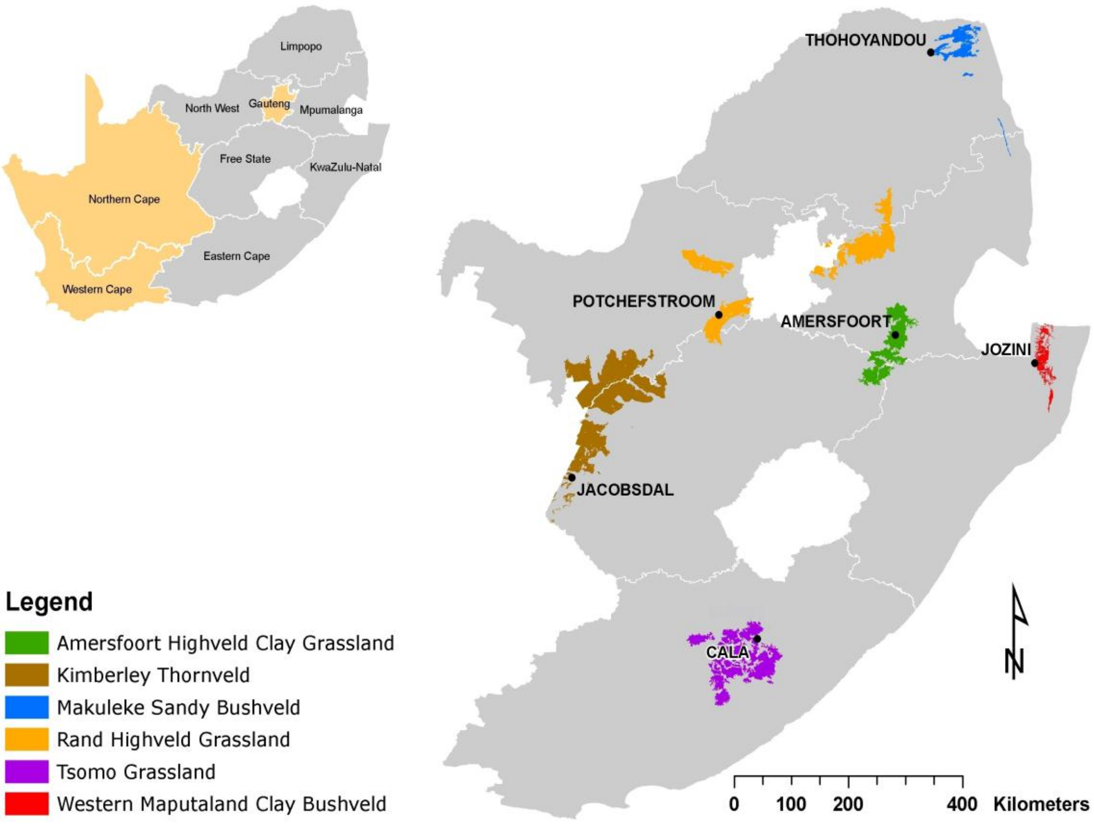

Figure 3.1: Nearest town and vegetation unit of each survey locality in the six major maize producing provinces of South Africa.

Table 3.1: Summary of general information regarding biome, farming type, presence or absence of irrigation regimes and width between rows of maize for all the localities.

	Biome	Farming type	Irrigation	Row width (cm)
Eastern Cape	Grassland	Commercial	Dry	100-150
Free State	Savanna	Commercial	Irrigation	75-100
KwaZulu-Natal	Savanna	Subsistence	Irrigation	80-100
Limpopo	Savanna	Subsistence	Irrigation	90-100
Mpumalanga	Grassland	Commercial	Dry	90-100
North-West	Grassland	Commercial	Dry	150-200

Table 3.2: Climate details for the vegetation units in which the six study sites were located (Mucina & Rutherford, 2006).

	Mean annual precipitation (mm)	Mean annual temperature (°C)	Mean frost days (<0°C)	Mean annual soil moisture stress (%)
Amersfoort Higveld Clay Grassland	694	14	42	74
Kimberly Thornveld	407	17.2	33	82
Makuleke Sandy Bushveld	489	21.7	1	81
Rand Highveld Grassland	654	15.8	28	76
Tsomo Grassland	609	15.2	28	76
Western Maputaland Clay Bushveld	597	21.8	0	78

3.2 Study sites

3.2.1 Potchefstroom

Surveys in this region were conducted during February and March (2010) in the Enselspoort and Rooipoortjie farms near Potchefstroom (26° 43'S, 27° 15’E, altitude 1407-1490 m a.s.l.), situated in the Mesic Highveld Grassland bioregion and Rand Highveld Grassland vegetation unit of the North-West province (fig. 3.2 C).

3.2.1.1 Maize cultivation

Maize represents one of the major summer crops in the North-West province and 2.87 million tons of maize were produced during the 2009/10 production season (DAFF, 2013). Maize in this region is mostly produced in high-input commercial production systems. Livestock grazing is also common in rangelands surrounding crop fields. Fences and small dirt roads formed anthropogenic boundaries between maize fields and field margins. Inter-row spacing in maize fields was exceptionally wide (2.0 m), to compensate for lower rainfall.

Figure 3.2: Visual representations of the maize fields and field margin vegetation of the six study sites in the vicinity of (A) Thohoyandou; (B) Amersfoort; (C) Potchefstroom; (D) Jozini; (E) Jacobsdal and (F) Cala.

3.2.1.2 Vegetation and landscape features

The topography is highly variable with sloping plains alternated by slightly elevated ridges (Mucina & Rutherford, 2006). The vegetation is typically wiry, sour grassland on the plains and low-growing, sour shrubland on the rocky outcrops and steeper slopes. Prominent grass species include those in the genera *Themeda, Eragrostis, Heteropogon* and *Elionurus*. A diverse array of herbs, commonly those of the Asteraceae (daisy family) is also typical of the area. Hills and ridges carry sparse woody vegetation with species such as *Protea caffra* subsp. *caffra, P. welwitschii, Acacia caffra* and *Celtis africana,* and shrubs dominated by the *Searsia* genus (Mucina & Rutherford, 2006).

3.2.1.3 Geology and soils

The area is characterized by quartzite ridges of the Witwatersrand Supergroup and the Pretoria Group as well as the Selons River Formation of the Rooiberg Group. Soils of various qualities can be found with shallow Glenrosa and Mispah typical of rocky ridges (Mucina & Rutherford, 2006).

3.2.1.4 Climate

The area is typically a warm-temperate region with seasonal summer rainfall and very dry winters. Mean annual precipitation is 654mm and slightly decreases towards the west. Frost is common in winter with a higher occurrence in the western regions (30-40 days) than in the east (10-35 days) (Mucina & Rutherford, 2006).

3.2.1.5 Conservation status

The Rand Highveld Grassland is endangered and only 1% is currently conserved in statutory reserves and private conservation areas (Mucina & Rutherford, 2006). Almost half of the natural vegetation has been transformed mainly by cultivation, plantations, urbanization and dams. Additionally, portions of the land area that are currently classified as grassland are in fact old fields that contain degraded ecosystems. Poor land management has also led to further degradation of the area. Invasive plant species such as *Acacia mearnsii* can be found scattered in about 7% of the unit (Mucina & Rutherford, 2006).

3.2.2 Amersfoort

Surveys for Mpumalanga were carried out in February 2010 in the Blomfontein and Maquabe farms near Amersfoort (26° 57'S, 29° 59'E, altitude 1689-1747 m a.s.l.), which is situated in the Mesic Highveld Grassland bioregion and Amersfoort Highveld Clay Grassland vegetation unit (fig. 3.2 B).

3.2.2.1 Maize cultivation

The Mpumalanga province represents the most significant maize producing area in South Africa, with 2.75 million tons produced in the 2009/10 production season (DAFF, 2013). This area also mainly represents high-input commercial farming systems. Similarly to the Potchefstroom sites, maize fields and field margins were separated by fences and dirt roads and livestock grazing were common in field margins. The spacing of crop rows was between 0.9-1.0 m.

3.2.2.2 Vegetation and landscape features

The area consists of low mountains, undulating grassland plains and scattered dolerite outcrops. The vegetation is mostly short grassland dominated by *Themeda triandra*, which is often severely grazed to form a short lawn (Mucina & Rutherford, 2006).

3.2.2.3 Geology and soils

The region is characterized by vertic clay soils derived from dolorite that is intrusive in the Karoo sediments of the Madzaringwe Formation in the north and the Volksrust formation and the Adelaide Subgroup in the south (Mucina &Rutherford, 2006).

3.2.2.4 Climate

The area is typically a summer rainfall area with most rainfall occurring in early summer (620 mm in the west to 830 mm in the east) and with a mean annual precipitation of 694 mm. Temperatures are generally higher in the east than in the west with a mean annual temperature of 14°C. Summers are mild and winters cold with a high frost incidence (Mucina & Rutherford, 2006).

3.2.2.5 Conservation status

The Amersfoort Highveld Clay Grassland vegetation unit is considered vulnerable, with at least 25% transformed, 22% thereof for cultivation (Mucina & Rutherford, 2006). No part of this unit is protected. *Acacia* species (silver and black wattle), and *Salix babylonica* are common invasive species invading drainage areas (Mucina & Rutherford, 2006).

3.2.3 Jozini

Surveys for KwaZulu-Natal were conducted during May (2010) in the Makhonyeni and Qokolwane communal areas of the Makhathini flats near Jozini (27° 26'S, 32° 09'E, altitude 72-112 m a.s.l.). These sites are situated in the Lowveld Bioregion and Western Maputaland Clay Bushveld vegetation unit (fig. 3.2 D).

3.2.3.1 Maize cultivation

KwaZulu-Natal had a maize production value of 524 thousand tons during the 2009/10 production season (DAFF, 2013) and mainly represents low-input subsistence farming systems. Furthermore, maize in this region is commonly cultivated year round under irrigation. Maize fields that were surveyed were commonly intercropped with pumpkins (*Cucurbita* species) and in some cases sweet potatoes (*Ipomoea batatas*). The distance of crop rows were similar to those of Amersfoort and fences and dirt roads were also present as field boundaries. Field margins were used for livestock grazing and also for the collection of wood for fuel and building materials.

3.2.3.2 Vegetation and landscape features

The topography comprises of gently undulating terrain, dominated by compound leaved short woodlands and wooded grasslands. Two large alluvial floodplains associated with the Mkuze and Phongolo Rivers characterize the area with Lowveld Riverine Forest and woodland dominating the alluvial soils and floodplains (Mucina & Rutherford, 2006). The area is characterized by fragmented bushveld habitats with small shrubs and trees such as *Dichrostachys cinerea* (Fabaceae) and *Acacia* species (Mimosaceae). Understory species are typically species of the Poaceae such as *Panicum maximum* and *Dactyloctenium australe* (Hofs *et al.*, 2008).

3.2.3.3 Geology and soils

Cretaceous shallow-marine and coastal sediments, siltstones and conglomerates of the Zululand Group and minor rhyolites of the Jozini Formation are characteristic of the area. Dominant soils of the unit include red sandy clay and red clay loam latosols (Hutton, Bainsvlei and Shortlands soil forms) as well as calcimorphic soils of the Valsrivier and Avalon soil forms (Mucina & Rutherford, 2006).

3.2.3.4 Climate

The area is characterized by summer rainfall and dry winters with a mean annual precipitation of 500-750mm. No incidence of frost occurs (Mucina & Rutherford, 2006).

3.2.3.5 Conservation status

The unit is considered vulnerable with 11% conserved in statutory reserves. A large portion has been transformed mainly by cultivation. Severe invasive plant infestations occur sporadically, commonly by *Opuntia* species (Mucina & Rutherford, 2006).

3.2.4 Thohoyandou

Surveys were conducted during November 2009 at Mutshenzheni and Tshiombo communal areas, situated in the Lowveld Bioregion and Makuleke Sandy Bushveld vegetation unit near Thohoyandou (22°47´S, 30°29`E, altitude 613-680 m a.s.l.) (fig. 3.2 A).

3.2.4.1 Maize cultivation

Maize fields in Limpopo are mostly subsistence farming systems. Maize is commonly cultivated under irrigation and more than one harvest per year may be produced in this way, although maize production is low, compared to the other provinces. Production values were at 210 thousand tons during the 2009/10 season (DAFF, 2013). In the surveyed fields, maize was commonly intercropped with pumpkins, sweet potatoes and peanuts (*Arachis hypogaea*). The distance between rows at this locality was approximately 1.0 m, although the pumpkin, sweet potato and peanut in some cases covered bare patches between rows. A small water canal at the Mutshenzheni locality served as boundary between crop fields and field margins, while dirt roads were present around the fields of the Tshiombo locality. Similarly to the Jozini localities, the field margins were commonly used for the collection of wood and as grazing pastures for livestock. Furthermore, the field margins were recently cleared and burned at the time of the survey.

3.2.4.2 Vegetation and Landscape features

The topography of the region varies from low mountains to irregular plains and hills. The deep sand areas of the bioregion is commonly dominated by a tree savanna with *Terminalia sericea, Burkea africana, Guibourtia conjugata* and *Peltophorum africana* representing typical tree species and with *Andropogon gayanus* and *Digitaria eriantha* commonly found in the moderate to dense ground layer. Tree species such as *Combretum apiculatum* and *Diplorhynchus condylocarpon* and ground layers of *Digitaria eriantha, Panicum maximum* and *Pogonarthria squarrosa* are typical of stony soils (Mucina & Rutherford, 2006).

3.2.4.3 Geology and soils

Most of the area has deep sands to shallow lithosols and is characterized by the Soutpansberg Group of sandstone with smaller amounts of conglomerate, shale and basalt. Karoo Supergroup rocks are also present (Mucina & Rutherford, 2006).

3.2.4.4 Climate

The area receives summer rainfall (typically 300-700 mm mean annual precipitation) with very dry winters. It is generally frost-free except at higher elevations. Mean monthly minimum and maximum temperatures are 8.5°C and 39.7°C respectively (Mucina & Rutherford, 2006).

3.2.4.5 Conservation status

The status of the Makuleke Sandy Bushvend bioregion is considered vulnerable with 27% transformed mostly due to cultivation. Currently, 32% of this bioregion is conserved in the Kruger National Park (Mucina & Rutherford, 2006).

3.2.5 Jacobsdal

Surveys were carried out in February, 2011 at two farms (Langhoek and Kempster) situated in the Jacobsdal area near Kimberley (29° 7'43.32"S 24°46'22.80"E, altitude 1138 m a.s.l.). The farms are located in the Free State province, close to the Northern Cape border (fig. 3.2 E). The study area represents the Kimberley Thornveld vegetation unit in the Eastern Kalahari Bushveld bioregion of the Savanna biome (Mucina & Rutherford, 2006).

3.2.5.1 Maize cultivation

The Free State is also a major maize producer in South Africa, and delivered 4.10 million tons of maize during the 2010/11 production year (DAFF, 2013). In the Northern Cape, maize production figures were much lower (538 000 tons in 2010/11) but are higher than expected for this dry region due to the irrigation of maize along the Orange and Vaal rivers. The maize fields used for the survey were also irrigated. Dirt roads and fences acted as boundaries between maize fields and surrounding vegetation and the field margins was used for livestock grazing (mostly sheep). The distance between rows of maize was 0.75m, which resulted in a very high plant stand and is common under center pivot irrigation systems.

3.2.5.2 Vegetation and landscape features

Slopes and elevated hills and ridges with plains are typical in this area. A tree layer with species such as *Acacia tortilis*, *A. karroo*, and *Boscia albitrunca* was common. The area also had a well-developed shrub layer, with species such as *Tarchonanthus camphoratus* and *A. mellifera* (Mucina & Rutherford, 2006).

3.2.5.3 Geology and soils

The area is situated on Andesitic lavas of the Allanridge Formation in the north and west and on fine grained sediments of the Karoo Supergroup in the south and east. Rock- and boulder covered slopes are common. The soil in this region is typically of the Hutton soil form and is sandy to loamy in nature (Mucina & Rutherford, 2006).

3.2.5.4 Climate

This region receives summer and autumn rainfall and has very dry winters. The mean annual precipitation is estimated at 300 mm in the southwest to 500 mm in the northeast. Frost is common in winter, particularly on bottomlands. The mean monthly maximum and minimum temperatures for Kimberley are 37.5 °C and -4.1 °C for January and July respectively (Mucina & Rutherford, 2006).

3.2.5.5 Conservation status

This vegetation unit is classified as least threatened at present. However, only 2% occur on statutorily conserved land in Vaalbos National Park and Sandveld, Bloemhof dam and S.A. Lombard nature reserves. An estimated 18% has been transformed mainly due to cultivation activities. Erosion is not considered a problem, although livestock grazing is common and may lead to bush encroachment of *Acacia mellifera* subsp. *detinens* (Mucina & Rutherford, 2006).

3.2.6 Cala

Surveys were conducted during March 2012 in the vicinity of the Skhangene and Ncora dam communal areas near Cala in the Eastern Cape (31°47’14.32”S, 27°44’35.53”E altitude 961 m a.s.l.), which is situated in the Tsomo Grassland vegetation unit of the Sub-escarpment Grassland Bioregion of the Grassland Biome (fig. 3.2 F).

3.2.6.1 Maize cultivation

Maize production values for the Eastern Cape were at 92 000 tons in the 2011/12 production year (DAFF, 2013). Maize in this region is commonly produced on subsistence farms, although the particular farms that were surveyed were commercial production systems. The maize fields in this region form part of the Ncora irrigation scheme, although the particular maize fields that were surveyed were not cultivated under irrigation. The inter-row spacing was 1.0 – 1.2 m, although bare patches and dwarfed plants were found in sections of the maize fields. This may have been due to moderate drought stress as well as nitrogen deficiency. Also, these maize fields were particularly weedy, likely as a result of the bare patches. As with most of the other sites, maize fields and field margins were separated by fences and dirt roads. Field margins were mainly used as grazing pastures for a variety of livestock (mainly cattle and sheep).

3.2.6.2 Vegetation and landscape features

The area is characterized by undulating lowland plains interrupted by mountains. The vegetation is typically grassland and open thornveld which are often overgrazed. Dominant grass species are typically those in the genera *Cymbopogon, Elionurus, Eragrostis, Aristida* and *Themeda* while dwarf shrubs such as species of *Euryops* are common. Typical forbs are those of the family Fabaceae (legume family) and Asteraceae (Mucina & Rutherford, 2006).

3.2.6.3 Geology and soils

The area is characterized by mudstones of the Tarkastad Subgroup (Karoo Supergroup) with relatively deep soils (Mucina & Rutherford, 2006).

3.2.6.4 Climate

The area typically receives its bulk rainfall in late summer, although it is not restricted to this period. Rainfall is generally higher in the east than the west with a mean annual precipitation of 430-790 mm. Frost incidence is variable and most common in the northwest (Mucina & Rutherford, 2006).

3.2.6.5 Conservation status

The status of Tsomo grassland is vulnerable and none is protected in statutory conservation areas. Only 1% is currently conserved in private reserves and 27% has been transformed, primarily for cultivation and rural settlements (Mucina & Rutherford, 2006). Overgrazing is a frequent problem with invasive species such as *Schkuhria pinnata* and *Tagetes minuta* increasing in disturbed areas. It has been stated that most of the Eastern Cape grasslands are of secondary nature due to long term overgrazing (Darkoh, 1987; Smits *et al.*, 1999). Erosion is also a serious problem, and is prominent along water bodies (Mucina & Rutherford, 2006).

Chapter 4: Material and methods

4.1 General method

In each of the six localities, two sites, approximately 5 km apart, were selected. At each of the two sites twelve sampling plots were placed (two transects with six plots per row) with rows approximately 250-500 m apart (fig. 4.2). Therefore a total of 24 plots were sampled at each of the six localities, consisting of four transects per locality (fig. 4.1). Plots were 25 m^2 (5 x 5 m) for arthropod sampling and 100 m^2 (10 x 10 m) for plant surveys. Each transect was placed along the maize field-field margin gradient to ensure that two plots were located in each of three treatments, namely the maize field, tension zone (adjacent land with a high level of anthropological disturbance) and natural area.

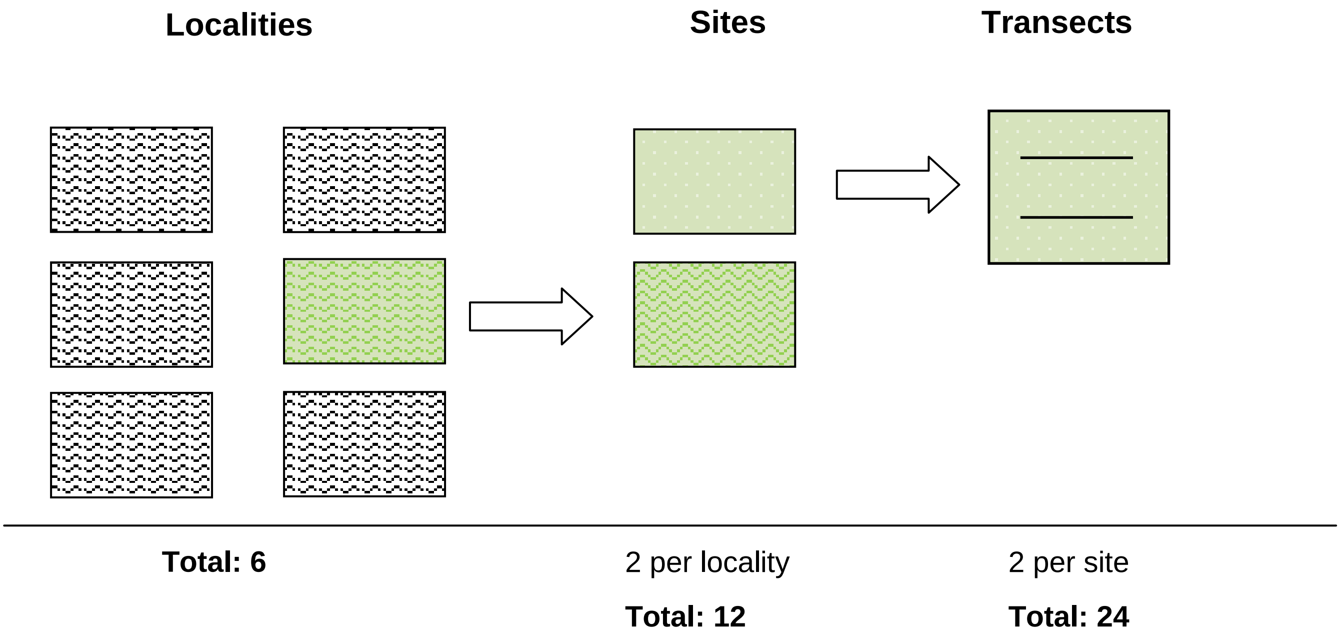

Figure 4.1: Six localities were chosen, one in each province. At each locality two sites were selected, each with two transects to cover the maize field-field margin gradient.

The **tension zone** will be used in this study as a hypothetical term to refer to the two sampling areas in the field margin closest to the maize fields. The purpose of naming the zone as such was to detect possible ecotone, ecocline or edge effects.

Plots were 100 m apart, with the first plot in the maize field, 150 m from the field margin. The second plot was in the maize 50 m from the field margin and the third and fourth plots 50 and 150 m from the maize field in the tension zone. Two plots were in the natural area, respectively 250 and 350 m from the maize field. The distances from the maize fields were chosen in accord with the known spreading distances of maize pollen from maize fields to adjacent field margins. Authors who determined sufficient separation distances to achieve minimal outcrossing between GM and non-GM maize recommended isolation distances of 20 m (Messeguer *et al.*, 2006), 25-50 m (Beckie & Hall, 2008), 50 m, (Devos *et al.*, 2009) and 135 m (Viljoen & Chetty 2011). Isolation distances in European countries have been set from 25m to 800m (Beckie & Hall, 2008). From these studies, along with those by Rosi-Marshall *et al.* (2007) and Hofmann *et al.* (2010), it seems that the critical zone for maize pollen deposition is in the first 150 m from maize fields. Although it is known that 98% of pollen grains remain within a 25 to 50 m radius from the source (Eastham & Sweet, 2002), low levels of pollen may still be found at or beyond 300 m from maize fields (Viljoen & Chetty, 2011). Sanvido *et al.* (2008) found the furthest point at which cross fertilisation between GM and non-GM maize occurred was 400 m. Although the sampled maize fields in our study did not contain Bt-varieties, the setup of the study will enable future studies on the possible negative impacts of Bt-maize on adjacent field margins.

4.2 Arthropod sampling

The target group for this survey included plant-dwelling arthropods that occur on plants during the reproductive stages of development. Other studies have shown that arthropod diversity during these plant growth stages and particularly on plant ears, capture different trophic levels and could be a good method to sample a comprehensive arthropod community (Eckert *et al.*, 2006). Dively (2005) also showed that arthropod biodiversity on maize in the period following anthesis is very high compared to the rest of the growing period. Therefore, surveys were scheduled to coincide with the regional flowering times of maize to ensure sufficient sampling of arthropods. This also ensured that all maize plants were at a similar growth stage when sampled.

An adapted D-vac method was used for arthropod collection. The D-vac suction machine was moved slowly over the surface of all plant material in each plot. Approximately seven swaths per plot were done, following a zigzag pattern with the D-vac nozzle. In cases where there was higher vegetation such as tall grass (e.g. maize plants), shrubs and trees inside the plots, these were also sampled by means of the D-vac by moving the machine over the branches/large leaves as well as the trunk/stem. Vegetation under dense shrubs and trees were also sampled as far as possible. No samples were taken of soil arthropods and this study is therefore based on above-ground arthropods that occur on plants. Soil-dwelling arthropods that occurred below plant debris or that were present at the lower parts of plants during the survey were also collected but the aim was not to use the D-vac to collect on the soil surface itself.

The material collected in each plot was placed in separate plastic bags and frozen to preserve the contents. The contents of each bag were then sorted in the laboratory to separate the arthropods from the plant material and other debris. The arthropods collected in each plot were placed in bottles containing 70% alcohol for preservation. Preserved arthropods were placed in Petri-dishes, inspected under a stereo microscope and classified up to morphospecies level (Picker *et al.*, 2004).

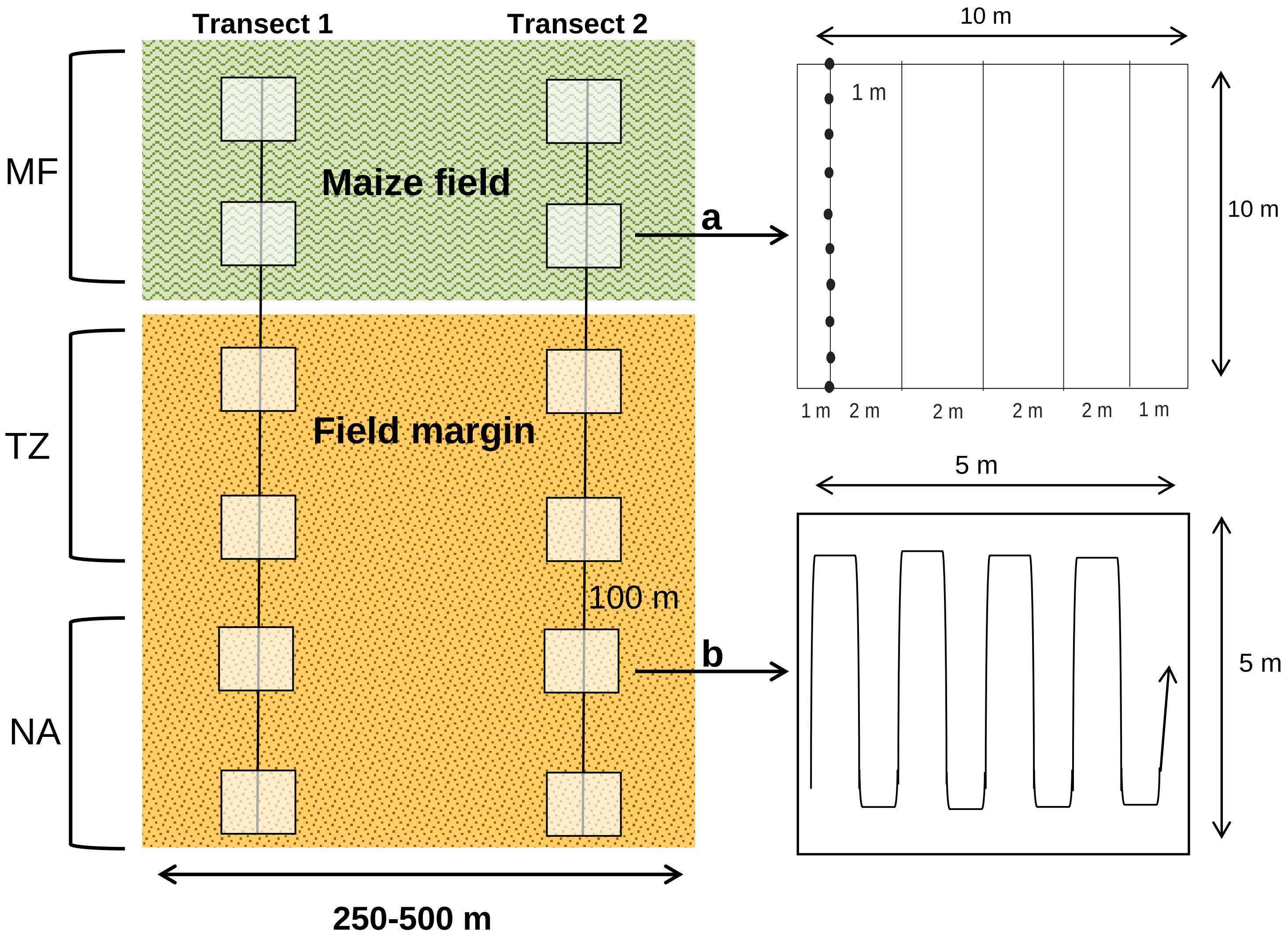

Figure 4.2: Transect layout for sampling plants and arthropods inside a maize field-field margin gradient. MF = maize field; TZ = tension zone; NA= natural area. For plants (a) five line transects were laid out along which plant species were recorded. For arthropods (b) samples were taken in a zigzag pattern as indicated.

4.3 Vegetation sampling

Inside each sampling plot five line transects were placed, with the first transect 1 m inside the sampling plot and the rest spaced 2 m apart (fig. 4.2). Along each 20 m line transect the nearest tree, shrub, forb and grass species, at intervals of 1 m was identified and recorded (100 point sampling approach). If no plant occurred within 0.5 m before or after the point a bare area was noted. Plants were identified up to species level and species names follow Germishuizen *et al*.

(2006). All voucher specimens were deposited in the A.P. Goossens Herbarium (PUC) and unknown specimens were identified by the Pretoria National Herbarium (PRE).

4.4 Data analysis

Species richness and species diversity indices were applied to express the diversity of plants and arthropods in each of the plots. These indices take both species richness and/or abundance into account (Begon *et al.*, 2008). Proportional abundance indices include both the species richness and the relative contribution (or abundance) of each species. Indices of this type can either stress the importance of species richness by weighting towards rare species (Shannon’s index) or emphasize dominance by regarding abundant species as more important (Simpson’s index) (Magurran, 2004). The following indices were used:

Species richness

Species richness is the number of species recorded (**S**) and does not take into account relative abundances. Species richness indices are a measure of species richness that includes the sum of individuals recorded for all the species in a specific sample plot.

Margalef’s Species Richness Index

$$\boxed{(d) = (S-1)/\ln N}$$

Where **S** is the number of species recorded and **N** is the total number of individuals in the sample.

Simpson’s Index of Diversity

$$\boxed{(\check{D}) = \Sigma\, [n_i\, (n_i - 1)/N\, (N - 1)] - 1}$$

Where **N** is the total number of individuals (all species) and $\mathbf{n_i}$ is the number of individuals for the i’th species.

Shannon-Wiener Diversity Index

$$\boxed{(H') = -\sum\, (p_i.\ln)\, p_i}$$

Where $\mathbf{p_i}$ is the relative abundance of the i’th species. This index provides a rough measure of diversity, which is much less biased by sample size than species richness.

Pielou’s Evenness Index

$$\boxed{(J') = H'/H'\max = H'/\ln S}$$

Where **H´** is the Shannon Wiener Diversity Index and **S** is species richness.

Index values were calculated with PRIMER 6 software (Clarke & Gorley, 2006). To test for significant differences in diversity, evenness and richness between localities, across MAFFMAGs and between biomes, One-way Repeated Measures Analysis of Variance (ANOVA) as well as Tukey's Honestly Significant Differences (HSD) and Bonferroni post-hoc tests were performed with STATISTICA 11 (StatSoft, 2013). The Tukey HSD post-hoc test was used for independent data sets, such as different localities. In the case of dependent data sets, such as measurements over distance, the more conservative Bonferroni test was performed.

The p-values were obtained for distance from maize field and for different localities as well as the interactions between these variables (distance x locality and distance x biome). Interaction effects are indications of the combined effects of factors on a dependent measure (Montgomery, 1997). A significant interaction between two variables in an ANOVA table is an indication that the effect of one of the variables differ depending on the level of the other variable and therefore that these two variables are affected differently by the specific treatment (Montgomery, 1997). The direction of the effect does not have to be different at different levels of a variable for a significant interaction to occur as long as the magnitude of an effect is greater at one level of a variable than at another (Montgomery, 1997).

Spearman's rank order correlations were used to test for general relationships between plant and arthropod diversity, determined with STATISTICA 11 (StatSoft, 2013). To illustrate how the different plots (maize field and natural veld) compared in terms of arthropod and plant species composition, Non-metric Multidimensional Scaling (NMDS), based on the Bray-Curtis Dissimilarity Index, was performed with PRIMER 6 software (Clarke & Gorley, 2006). This method provides a good way of visually representing the similarities between the species assemblages without attaching a specific meaning to the graph axes (Procheş & Cowling, 2007). The Similarity Percentage (SIMPER) method (Clarke, 1993) was applied to the data set in the PAST computer software package (Hammer *et al*., 2001) to determine which species were primarily responsible for distinctive grouping in the NMDS analyses. To determine the significance of these groupings, Analysis of Similarity (ANOSIM), a non-parametric test for significant differences, was performed with PAST software (Hammer *et al*., 2001).

Chapter 5: Descriptive data for plants and arthropods

5.1 Results for plants

A total of 15019 plants were counted and 846 species were recorded, with 151 species in the maize fields, 589 in the tension zone and 583 in the natural area. Also, 96 plant families were represented in the study. The ten best represented plant families of the total sample and respective zones are listed in table 5.1. Representation was determined by the number of species recorded for a given family. The Poaceae (grasses) was found to be the best represented family of the survey within all three treatments, which made up 15% of the total number of species. Also well represented were the Fabaceae and Asteraceae, which represented 12% and 11% of the total number of plant species respectively. This is consistent with plant lists of South Africa, where these three families along with the Mesembryanthemaceae and Iridaceae represent five of the largest plant families in South Africa (Klopper *et al.*, 2006). Also, the Convolvulaceae, Solanaceae and Oxalidaceae are known weed families (Bromilow, 2010) and were found to be most abundant relative to the treatment flora in the maize fields.

Table 5.1: Ten best represented plant families of 96 in total (according to the number of species in each family) for the total sample of treatments (Tot.), maize fields (MF), tension zones (TZ) and natural areas (NA), as well as the position of each family within the top ten in each treatment. Families with the same number of species were given similar ranking.

Family	Total	Position	MF	Position	TZ	Position	NA	Position
Poaceae	128	1	42	1	94	1	95	1
Fabaceae	101	2	13	3	71	2	71	2
Asteraceae	91	3	26	2	60	3	60	3
Cyperaceae	31	4	7	5	17	8	19	6
Acanthaceae	29	5	0	---	22	4	26	4
Euphorbiaceae	29	5	5	7	21	5	24	5
Rubiaceae	25	7	1	---	20	6	18	7
Apocynaceae	24	8	1	---	15	9	18	7
Malvaceae	24	8	5	7	20	6	17	9
Lamiaceae	20	10	1	---	14	10	13	10
Convolvulaceae	15	---	8	4	8	---	3	---
Solanaceae	12	---	7	5	6	---	6	---
Amaranthaceae	13	---	4	9	7	---	7	---
Oxalidaceae	5	---	4	9	2	---	2	---

Furthermore, the vegetation was classified into different growth forms according to the classifications by Germishuizen and Meyer (2003) (fig. 5.1). Overall, forbs represented the most numerous growth form of all sites (520 spp.), followed by graminoids (129 spp.), shrubs (124 spp.) and trees (73 spp.). The maize fields were found to be dominated by annual herbs, while perennial forbs were the most numerous in both the tension zone and natural area. As may be expected, the field margins were also characterized by woody vegetation, which was almost completely absent in the maize fields.

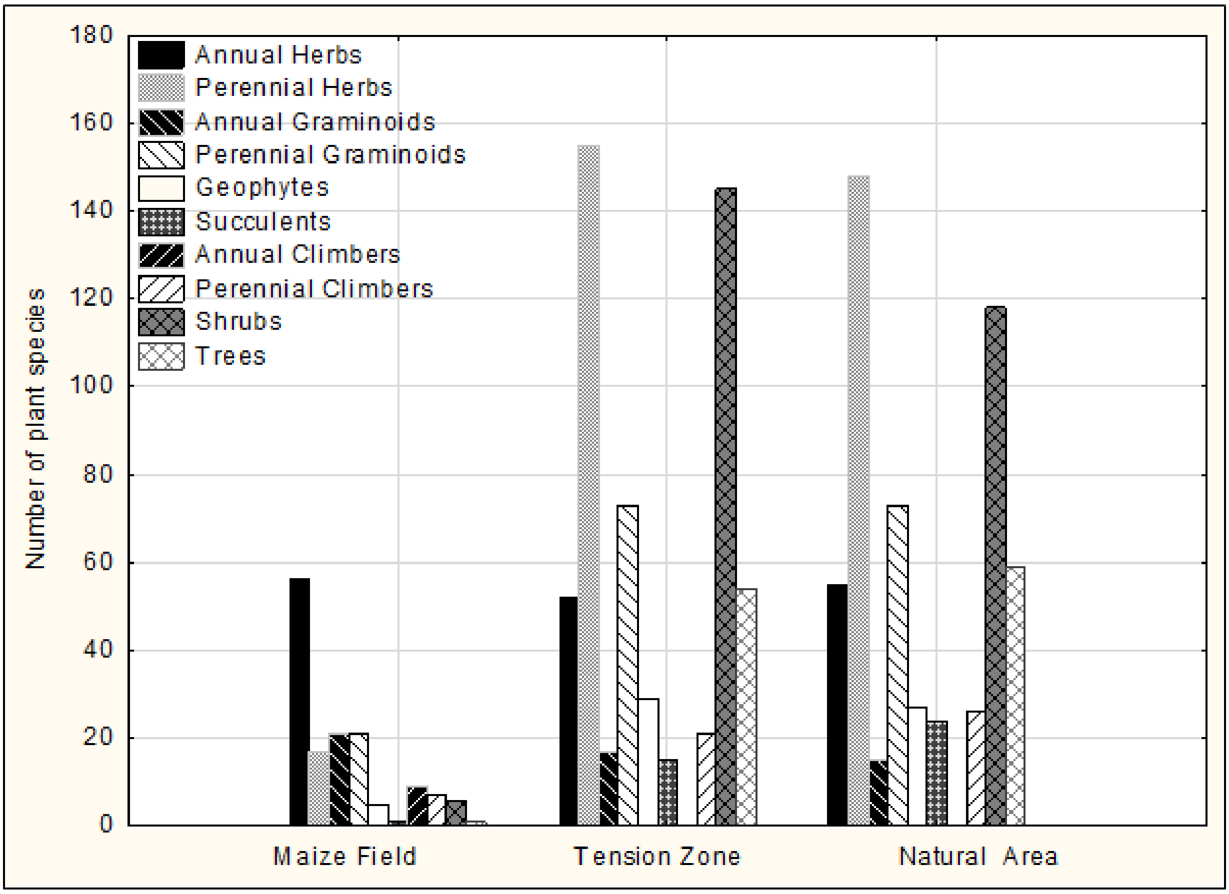

Figure 5.1: Combined species numbers per dominant growth form for the maize fields, tension zones and natural areas of all the study sites.

Of all the recorded plant species, 86 (10%) were noted as alien weeds. Most were found in the maize fields (64 spp.), while the field margins collectively contained 55 alien species (fig. 5.2). The largest proportion of alien species relative to the total number of species in each zone was found in the maize fields (42% of plant species were alien species, compared to 4% and 5% for the tension zone and natural area respectively). The twenty most common alien plant species were listed in table 5.2. *Digitaria sanguinalis* were the most frequently recorded, with 202 individuals found in the survey sites. Also frequent were common field weeds, *Richardia brasiliensis* and *Tagetes minuta*, with 197 and 112 individuals recorded respectively.

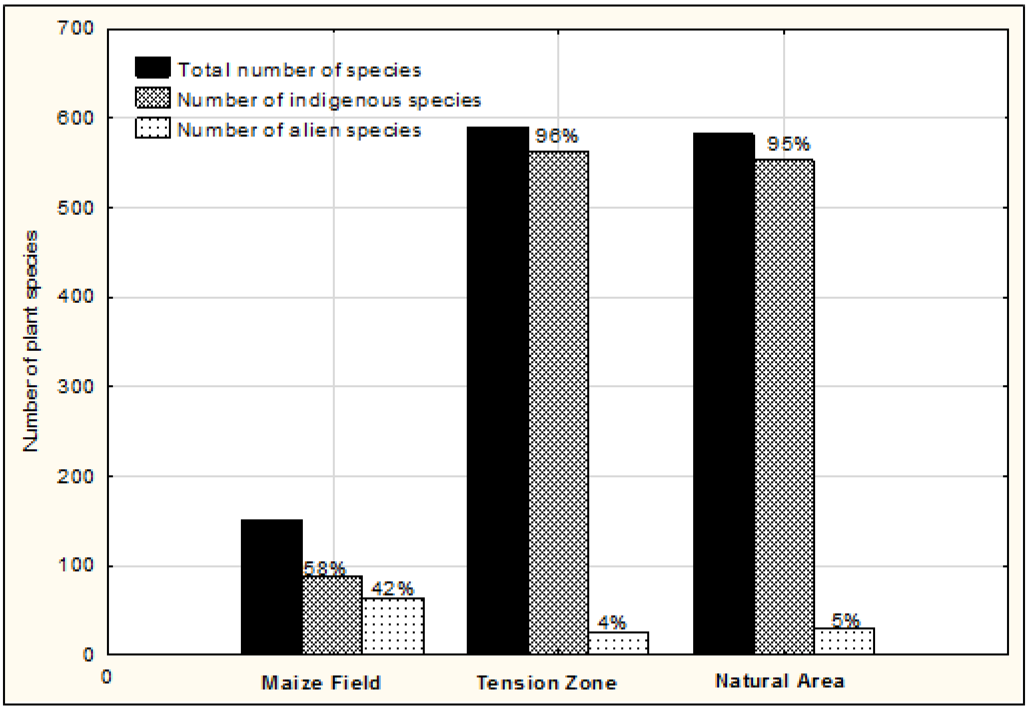

Figure 5.2: Comparison of the total number of plant species, number of indigenous and number of alien plant species for the maize fields, tension zones and natural areas of all sites.

Table 5.2: Twenty best represented alien plant species (excluding *Zea mays*) in the maize fields and field margins of all study sites.* Cultivated.

Alien plant species	Total no. individuals
Digitaria sanguinalis	202
Richardia brasiliensis	197
Tagetes minuta	112
Achyranthes aspera	80
Hibiscus trionum	73
Commelina benghalensis	71
Oxalis latifolia	70
Datura stramonium	69
Paspalum dilatatum	64
Bidens pilosa	59
*Ipomoea batatas**	51
*Cucurbita pepo**	49
Xanthium strumarium	49
Parthenium hysterophorus	45
Portulaca oleracea	44
Hypochaeris radicata	39
Centella asiatica	31
Eclipta prostrata	29
Chenopodium carinatum	26
Euphorbia heterophylla	26

5.2 Results for arthropods

A total of 1 689 arthropod morphospecies were recorded and 39 497 individuals were collected. This amounted to 576 morphospecies identified from the maize fields, 1031 from the tension zone and 1023 from the natural area. The arthropods collected for the study consisted of 23 identified orders with the most dominant ones being the Hemiptera (true bugs), Hymenoptera (bees, wasps and ants), Diptera (flies), Coleoptera (beetles), Araneae (spiders) and Orthoptera (crickets, grasshoppers, katydids and locusts) in order of significance (fig. 5.3). Also, 117 arthropod families were identified, of which the top ten best representatives are listed for the respective zones in table 5.3. Representation was determined according to the number of morphospecies in each family. In all the zones, the spiders (Araneae) made the most significant contribution, and represented 181 morphospecies (11%) to the total number of species in all study areas. Also, the leafhoppers (Hemiptera: Cicadellidae) and the short horned grasshoppers (Orthoptera: Acrididae) made large contributions, representing 7% and 5% of the total number of morphospecies respectively. Also, families such as the Braconid wasps (Hymenoptera: Braconidae), house flies (Diptera: Muscidae) and ladybugs (Coleoptera: Coccinellidae) were much more numerous in the maize fields than in the field margin while the stink bugs (Hemiptera: Pentatomidae) and short-horned grasshoppers (Orthoptera: Acrididae) were numerous in the field margin, but almost completely absent in the maize fields.

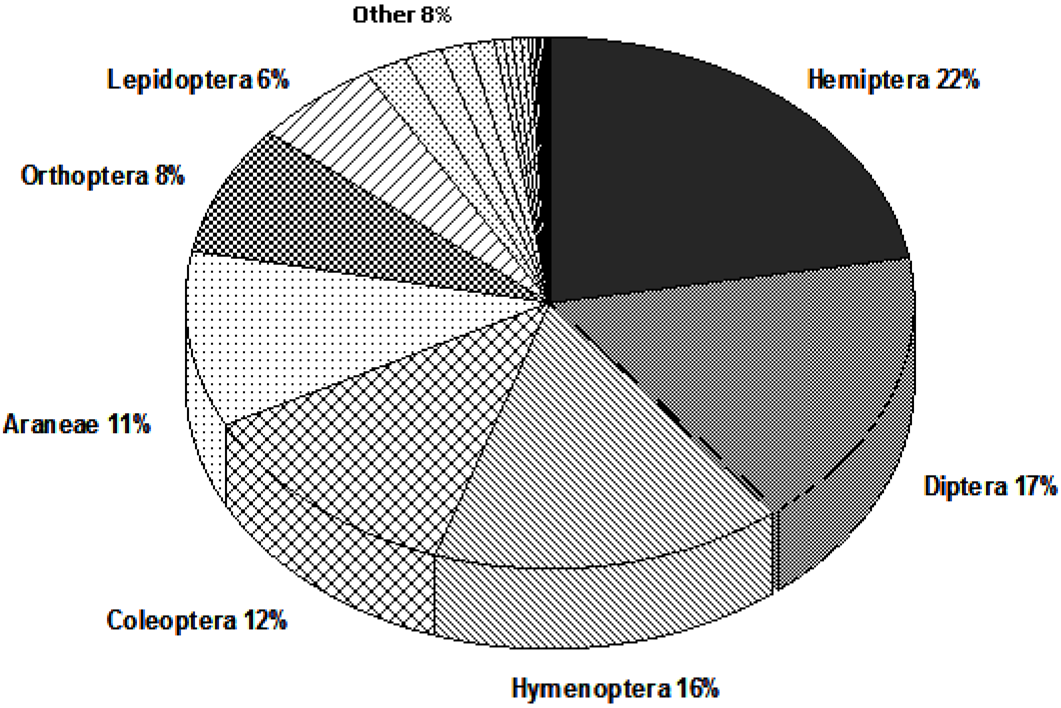

Figure 5.3: Contribution of arthropod orders towards the total diversity of arthropods collected in maize agro-ecosystems of South Africa.

Table 5.3: Ten best represented arthropod families of the 117 identified (according to the number of morphospecies in each family) of the total sample (Tot.), maize field (MF), tension zone (TZ) and natural area (NA), as well as the position of each family within the top ten in each sample. Families with the same number of species were given similar ranking.

Family	Total	Position	MF	Position	TZ	Position	NA	Position
Araneae	181	1	58	1	119	1	114	1
Cicadellidae	111	2	28	2	90	2	82	2
Acrididae	81	3	5	---	49	3	48	3
Chrysomelidae	70	4	19	4	37	5	40	5
Trichogrammatidae	69	5	28	2	40	4	47	4
Ichneumonidae	53	6	15	7	27	6	28	7
Pentatomidae	36	7	3	---	22	9	25	8
Braconidae	32	8	18	5	15	---	16	---
Formicidae	30	9	13	10	24	8	20	9
Curculionidae	29	10	8	---	12	---	17	---
Delphacidae	29	10	9	---	25	7	29	6
Culicidae	27	---	14	8	20	10	19	10
Muscidae	27	---	14	8	19	---	10	---
Coccinellidae	23	---	18	5	8	---	10	---

Chapter 6: Plant species diversity and composition of maize agro-ecosystems

6.1 Plant species diversity patterns along the MAFFMAG between localities

6.1.1 Results

Significant differences were recorded for the diversity indices at varying distances from the maize fields (table 6.1). Also refer to appendix A: table 11.1.1-11.1.5 for complete statistical values. Although the direction of the effect of distance is similar for all localities, some of the localities, such as Thohoyandou, had more pronounced effects (as indicated by the significant interactions). The majority of the localities displayed similar results in terms of H' (table 11.1.1). As predicted, most of the localities had lower H' values in maize fields than in field margins. An exception was found for the Jozini localities, which only had significantly higher plant diversity values at 50 m, but not further away from maize fields. However, no significant differences were found between the tension zone (50 and 150 m) and the natural area (250 and 350 m), which contradicts our original hypothesis that the tension zone should have lower diversity due to possible disturbances caused by agricultural activities (such as service roads, fence lines and herbicide drift).

For Pielou's Evenness (J'), the majority of the localities did not display significant differences in plant species evenness along the MAFFMAGs, with the exception of Jacobsdal and Cala (table 11.1.2). In these two localities, J' reacted in a similar fashion to H' with significant lower values in the maize field than in the field margin (tension zone and natural area). Margalef's Species Richness Index (d) indicated significant lower values between the maize fields and the natural vegetation in some localities, especially for Thohoyandou (table 11.1.3). However, the majority of the localities had no significant differences in d across the MAFFMAG, suggesting that d for plants is more or less constant across MAFFMAGs.

Analyses for Simpsons Diversity Index (Ď) revealed inconsistent results; with significant differences in plant diversity between the maize fields and field margins in Ermelo, Jacobsdal and Cala, to a lesser extent Potchefstroom, but not in Thohoyandou and Jozini (table 11.1.4). As with the other indices, no significant differences could be found for Ď between the tension zone and natural area in any of the localities.

Plant species richness (S) values differed significantly between most maize field and field margin plots, although not all localities followed similar patterns (table 11.1.5). In Thohoyandou, all field margin plots were significantly higher in terms of plant species richness than maize field plots. In Jacobsdal, richness tended to peak in the tension zone (50 and 150 m) and decrease again in the

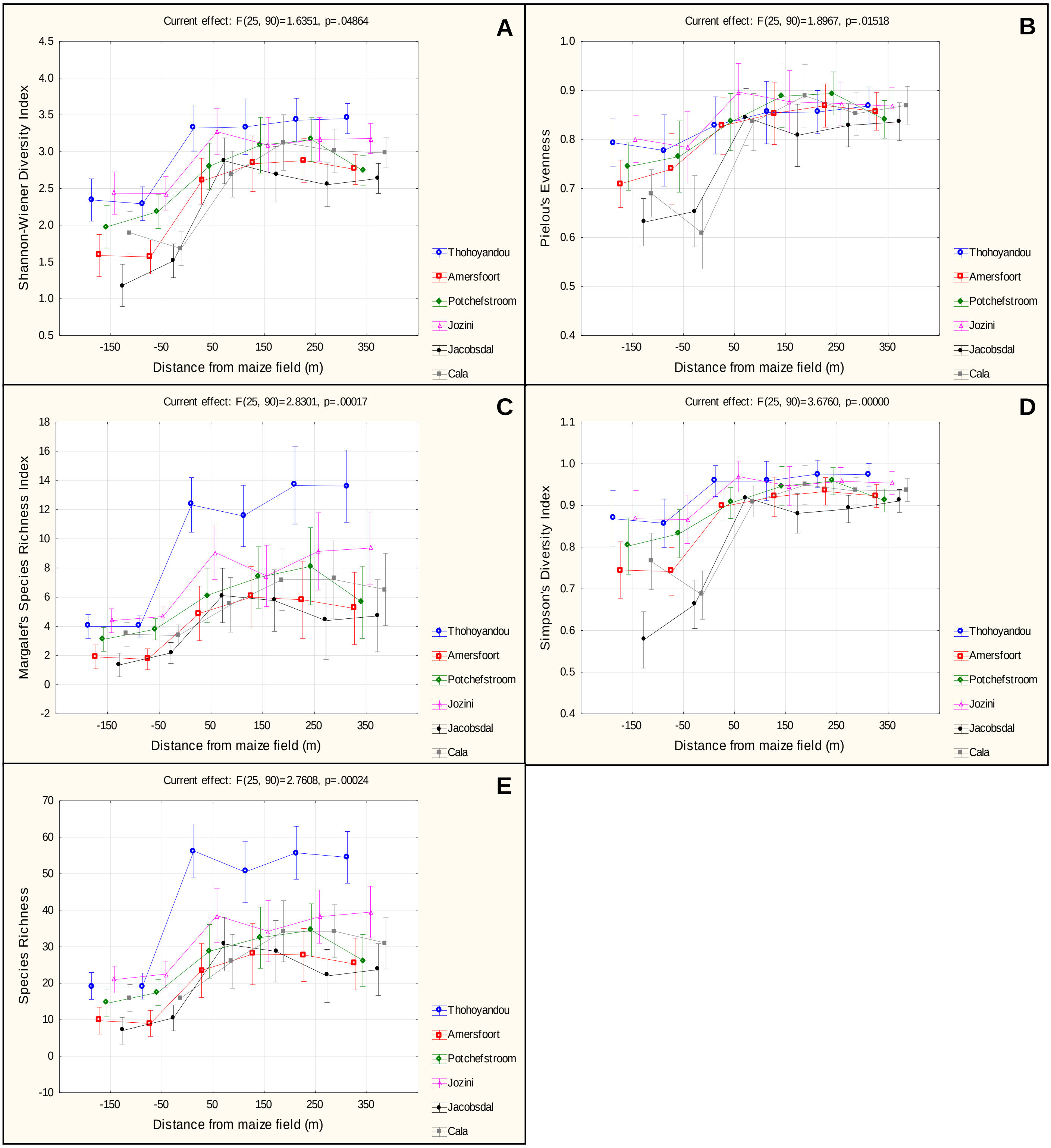

Figure 6.1: Diversity index values for plants along maize field-field edge gradients (MAFFMAG) of six localities in South Africa: (A) Shannon-Wiener Diversity Index; (B) Pielou's Evenness; (C) Margalef's Species Richness Index; (D) Simpson's Diversity Index and (E) Species Richness. Vertical bars denote 0.95 confidence intervals. The distances -150 and -50 m are located inside maize fields and 50-350 m in natural vegetation adjacent to fields.

natural area. On the other hand, in the grassland sites of Ermelo, Potchefstroom and Cala, plant species richness peaked at 150 and 250 m outside the maize fields and decreased again at 350 m. The Jozini localities had inconclusive results. The number of times each distance in the field margin showed significantly higher index values than that of the maize field was summarized in table 6.2 and the distance at which the most significant differences occurred are depicted in table 6.3 and fig. 6.2. From these results it was found that the most significant differences for plants occurred at 250 m, after which the index values decreased at 350 m outside the maize fields.

Table 6.1: P-values of Repeated Measures Analysis of Variance (ANOVA) for differences in plant diversity index values between distances from maize fields (-150, -50, 50, 150. 250, and 350 m), between six localities as well as interactions (between distance and locality). Values in red indicate significant differences (n=4; p<0.05). Refer to appendix A for complete statistical values.

Index	**Locality**	**Distance**	**Interaction**
Shannon-Wiener Diversity Index	0.000	0.000	0.049
Pielou's Evenness	0.001	0.000	0.015
Margalef's Species Richness	0.000	0.000	0.000
Simpson's Diversity Index	0.000	0.000	0.000
Species Richness	0.000	0.000	0.000

Table 6.2: Distances at which each locality showed significantly higher values in terms of plant diversity indices for the field margin than the maize field (there were four distances; All = 50, 150, 250 and 350). (THO) = Thohoyandou; (ERM) = Ermelo; (POT) = Potchefstroom; (JOZ) = Jozini; (JAC) = Jacobsdal; (CAL) = Cala.

	THO	ERM	POT	JOZ	JAC	CAL
H	All	All	50/150/250	50	All	All
J	None	300	None	None	All	All
Ď	None	All	150/250	None	All	All
d	All	None	250	50/250/350	50	None
S	All	150/250	150/250	50/250/350	50/150	150/250
Tot:	**12**	**11**	**8**	**7**	**15**	**14**

Table 6.3: Number of times each distance showed significantly higher plant diversity index values for the field margin than the maize field per locality (there were six localities).

	50	150	250	350
H	6	5	5	4
J	2	2	3	2
Ď	3	4	4	3
d	3	1	3	2
S	3	5	5	2
Tot:	**17**	**17**	**20**	**13**

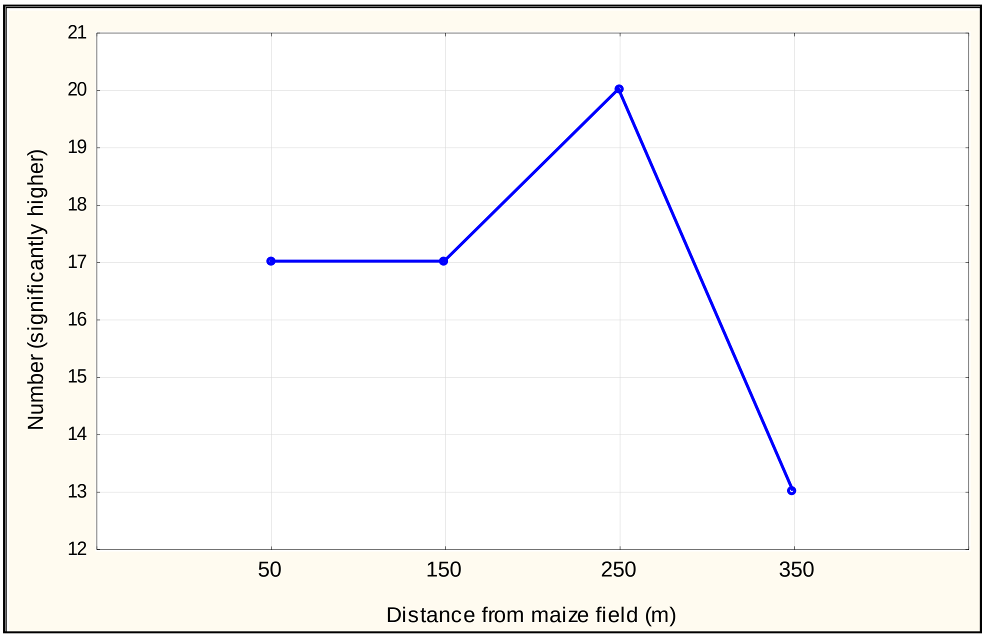

Figure 6.2: Number of times each distance showed significantly higher plant diversity index values for the field margin than the maize field per locality (there were six localities).

6.1.2 Discussion

Overall, the diversity and species richness indices of plants differed significantly between maize field and field margins (tension zone and natural area), with maize fields generally having lower plant diversity and richness. This was expected as disturbances associated with agricultural practices, such as the application of herbicides and disturbance of the soil by ploughing will inevitably (at least temporarily) reduce the number of non-crop plant species in a crop field (Altieri, 1999). Also, numerous studies have confirmed that plant diversity is lost with increased land management or land use intensity (Hamre *et al.*, 2010; Niedrist *et al.*, 2009; Marshall & Arnold, 1995). It was shown by Gabriel *et al.* (2006) that the highest plant species richness could be found in crop field edges, as opposed to crop centres and that organic fields had significantly higher plant species richness in both crop edges and centres than conventional fields. This has been attributed to the lack of herbicides and mineral fertilizers as well as a greater variability in crop rotations in organic fields. Furthermore, the maize plants themselves may also suppress non-crop plant diversity through growth and shading effects. It has been shown that plant species richness and evenness are strongly determined by community biomass and that crops have the ability to suppress weed growth in pea and barley fields in Argentina (Poggio & Ghersa, 2011). This is consistent with our findings of plant surveys in the Jacobsdal locality, which had a very high plant stand (0.75 m between rows and 2.5 m high) and revealed significantly lower in-field diversity than the other localities (fig. 6.1 A & D).

While marked differences were found in plant diversity and richness between maize fields and field margins, the tension zones and natural areas within the field margins were found to be relatively similar in terms of plant species diversity and richness. From these results and contrary to our original hypothesis, it seems that the tension zone of the field margin does not have lower plant diversity and richness than the natural area. This contradicts the notion that crop field margins are prone to disturbance and therefore tend to have low plant diversity because of their close proximity to agricultural activities (Marshall & Moonen, 2002). Therefore, it seems that agricultural practices do not have an overall negative impact on the vegetation in this case; at least not at the distances we sampled (plots closest to the maize fields were at least 50 m). Negative effects, if present, may be extremely localized, impacting only the very edge (10 m) between the tension zone and the maize field. It was proposed by Fridley *et al.* (2009) that agricultural influences on landscape-scale vegetation patterns in North Carolina are very close to agricultural activities (less than 50 m) as species composition and richness did not differ significantly beyond this point. Similar studies of vegetation responses to activities associated with crop fields indicated that changes in vegetation of field margins occurred within no more than 9 m from crop fields (Boutin & Jobin, 1998; Gove *et al.*, 2007). Also, it has been shown by Ma (2008) that plant species richness and evenness of buffer strips are scale dependent and therefore, studies conducted under different spatial scales may not yield similar results.

Shannon-Wiener Index values of Jozini and the species richness values of the grassland localities (Ermelo, Potchefstroom and Cala) showed significant peaks at intervals along the field margin (150-250 m in the case of the grassland localities and at 50 m for Jozini), followed again by a sudden decrease in plant diversity. Considering the combined effect of all the indices (fig. 6.2) it seems that the first plot of the natural area is most probable to have higher plant diversity and richness than the maize field. Although the exact reason for these patterns cannot be derived from this study, it may have been caused by the degrees of disturbance found in different positions of the field margin. Therefore, these findings may coincide with the intermediate disturbance hypothesis (Huston, 1979), which states that the highest diversity of a community can be found at intermediate levels of disturbance, with both exceptionally high and low levels of disturbance resulting in lower diversity levels. It has been shown that plant species distribution may be influenced by different types of land use (Wania *et al.*, 2006). Therefore, high levels of disturbance may be present close to the maize fields as a result of agricultural practices and furthest away from fields as a result of livestock grazing (Friedel, 1997) and resource harvesting by local communities (Shackleton *et al.*, 1994). At intermediate distances from the maize fields, the intensity of these disturbances may be at intermediate levels, allowing a higher plant diversity to persist in these positions.

Inconsistent results, as was found for Margalef's species richness and Simpson's diversity indices may have been caused by environmental heterogeneity between sampled localities. Localities may have varied in soil type, soil pH, water regime, elevation, climate and also landscape contexts (various habitats and land-use types) and these factors may have influenced the plant diversity of the sampled localities (Gabriel *et al.*, 2006). However, as these factors were not taken into account for this study, further research is required to determine their significance.

It is commonly stated that the species evenness of a community increases with increasing diversity and stability and decreasing anthropogenic disturbance (Gurr *et al.*, 2012; Chapin *et al.*, 2000; Matson *et al.*, 1997) and that communities that display higher evenness are generally healthier (Hillebrand *et al.*, 2008). It has been shown that the reduction of pest populations by natural enemies is more effective when enemy evenness is high (Crowder *et al.*, 2010), and that lower plant diversity compromises biological pest control in crops (Gurr *et al.*, 2012). Crop fields on the other hand, are considered to be low in species evenness, being dominated by a few hardy species able to withstand the high levels of disturbance (Curry, 1994). Although lower evenness was recorded for the maize fields, these results indicate that maize fields did not show significantly more dominance by plant species compared to field margins. This is unexpected as the evenness and species richness of communities are often said to be directly related to one another (DeBenedictis, 1973). However, Ma (2005) have shown that there was no clear correlations between plant species richness and evenness in small grain cereals and certain vegetables grown in Finland and that these two indices reacted differently to edaphic factors. In our findings, plant evenness also seemed to be unrelated to plant diversity and richness. This illustrates the importance of taking into account species evenness along with diversity and richness, especially since it has often been neglected in biodiversity studies (Bengtsson *et al.*, 2005).

However, our results do indicate significantly lower plant evenness in maize fields of the Jacobsdal and Cala localities, compared to their field margins. The exceptionally low plant species evenness in the Jacobsdal maize fields compared to the field margins may be the result of an exceptionally high maize plant stand, resulting in a virtually pure monoculture with little non-crop vegetation (Poggio & Ghersa, 2011; Weiner *et al.*, 2001). Plant evenness may however be affected by several factors such as fertilization and the application of herbicides (chapter 2.4). It has been shown that the application of herbicides has a destabilizing effect on plant communities (Kleijn & Snoeijing, 1997). Therefore, as the maize fields of Cala were treated with herbicides a month before the survey, this may have caused the plant species dominance (by crops) in these fields. Also, field margins had significantly higher values for Ď than maize fields for at least three of the localities. As Ď is an indication of the homogeneity of a population (Magurran, 1988), it seems that the plant communities are significantly more homogenous in a natural setting than in maize fields for the majority of the sampled localities.

6.2 Plant species diversity patterns along MAFFMAGs between biomes

6.2.1 Results

The mean diversity, evenness and richness index values of the two biomes all revealed significantly lower values for maize fields, compared to field margins, as was found for most of the separate localities (fig. 6.3 & appendix A: tables 11.2.1 – 11.2.5). Also, no significant differences could be found between the tension zone and natural area plots for any of the indices. The post hoc tests for Margalef's Species Richness Index revealed an overall significant difference in index values between biomes, although none of these differences were at similar distances along the MAFFMAG (in other words never 350 m with 350 m, but rather 350 m with, for instance, 150 m). However, a significant difference between biomes was found at similar distances for plant species richness (S). In this case, the savanna biome had significantly higher plant species richness than in the grassland at 50 m (table 11.2.5 C).

From the graphs it seems that the grassland and savanna biomes follow different trends along the MAFFMAG. Savanna diversity and richness peaked directly outside the maize field (50 m) after which it dropped back and stabilized in the natural area. On the other hand, grassland diversity and richness increased steadily up to 250 m and then decreased towards 350 m. However, these differences in response to distance are mostly not significant, as indicated by the non-significant interactions between biome and distance (table 6.4). Exceptions were found for Species Richness and Margalef's Species Richness Index, where interactions between biome and distance were significant. In these cases it seems that the direction of the effect of distance differs for the grassland and savanna biomes at 250-350m from the maize fields: Savanna plant species richness continues to increase while grassland plant species richness decreases (fig 6.3 C & E).

Table 6.4: P-values of Repeated Measures Analysis of Variance (ANOVA) for differences in plant diversity index values between distances from maize fields (-150, -50, 50, 150. 250, and 350 m), between two biomes (grassland and savanna) as well as interactions (between distance and biome). Values in red indicate significant differences (n=4; p<0.05). Refer to appendix A for complete statistical values.

Index	Biome	Distance	Interaction
Shannon-Wiener Diversity Index	0.111	0.000	0.075
Pielou's Evenness	0.668	0.000	0.270
Margalef's Species Richness	0.033	0.000	0.004
Simpson's Diversity Index	0.395	0.000	0.416
Species Richness	0.021	0.000	0.003

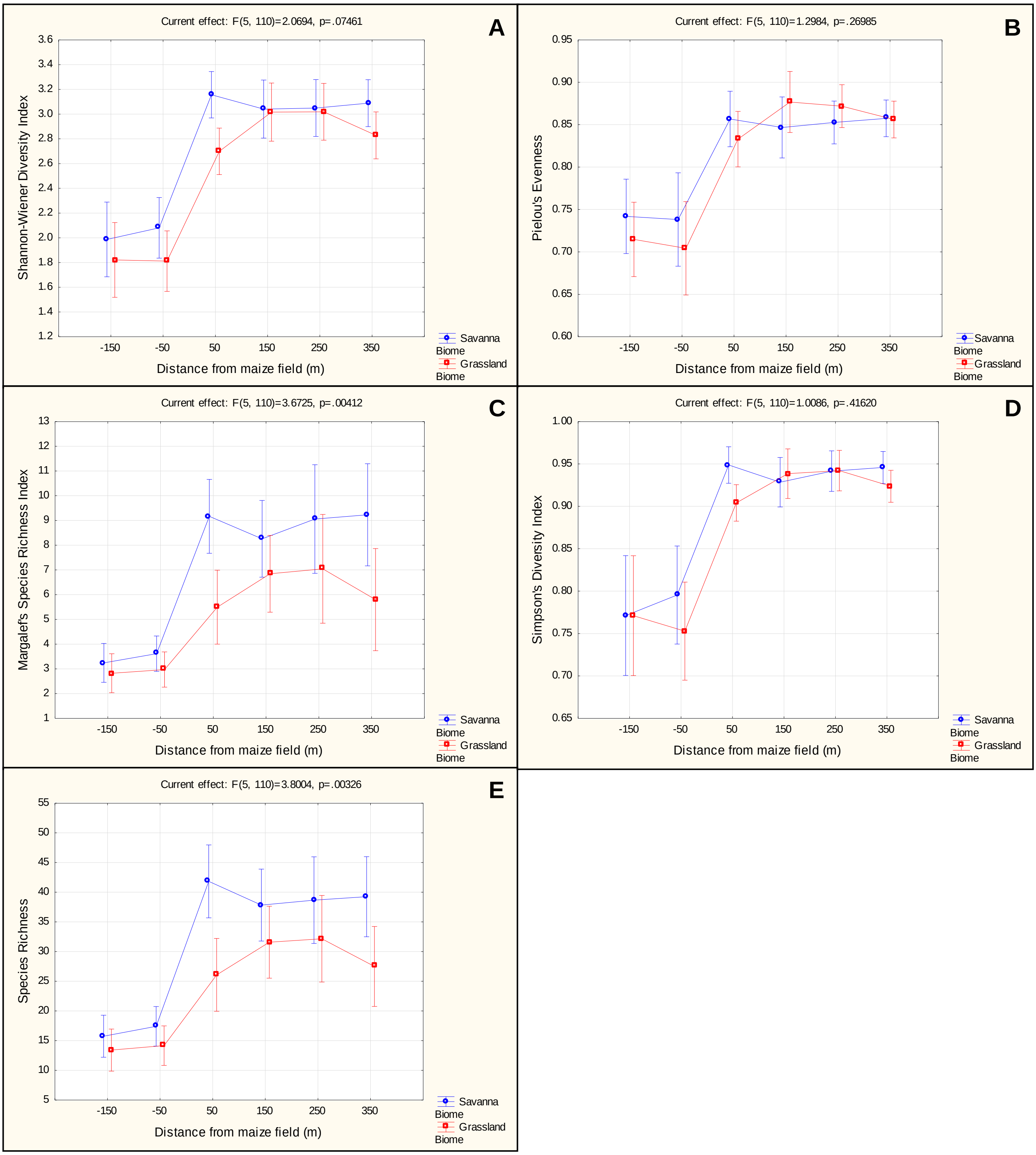

Figure 6.3: Diversity index values for plants along maize field-field edge gradients (MAFFMAG) of two biomes in South Africa: (A) Shannon-Wiener Diversity Index; (B) Pielou's Evenness; (C) Margalef's Species Richness Index; (D) Simpson's Diversity Index and (E) Species Richness. Vertical bars denote 0.95 confidence intervals. The distances -150 and -50 m are located inside maize fields and 50-350 m in natural vegetation adjacent to fields.

6.2.2 Discussion

Considering the results for each biome separately, no clear changes could be observed in plant species diversity and richness in the tension zone relative to the natural area, implying that disturbances associated with the maize fields did not have a detectable effect on the vegetation around maize fields at the distances that were sampled within biomes. This is also consistent with the results found for the separate localities. However, the difference between maize fields and field margins in terms of plant community evenness are more apparent in this case. This is consistent with results of Hillebrand et al. (2007) and Harpole and Tilman (2007), who indicated that plant species evenness can be reduced by factors associated with crop fields such as fertilization.

Furthermore, it seems that maize fields could have different effects on the vegetation of grassland and savanna at least in terms of plant species richness as the plant richness indices tended to peak at different intervals along the MAFFMAG. It is known that different vegetation types respond differently to disturbances, and therefore require unique management regimes (Tainton, 1999b). Therefore, the grassland localities could for example be more severely affected by livestock grazing than the savanna localities, which could have been a significant disturbance in the natural area. The exact cause for the trends displayed by the grassland vegetation is however unclear. As for the savanna vegetation, the peak in diversity at 50 m may have been caused by disturbances resulting in the co-dominance of savanna grassland and woody vegetation. The natural areas further away from the maize fields were probably associated with fewer disturbances, which may have resulted in the stabilization of savanna vegetation in this area. Therefore, this again coincides with the intermediate disturbance hypothesis (Huston, 1979). The overall tendency for savanna localities to have slightly higher plant diversity values may have been due to the multi-structured nature of this biome. As mentioned in chapter 2.5, this characteristic may allow for more species per unit area than one layered habitats such as grassland (Schadek *et al.*, 2009).

6.3 Plant species composition along MAFFMAGs between biomes

6.3.1 Results

All the NMDS analyses had stress values of ≤ 0.15, which is still sufficiently low to provide a useful two-dimensional picture (Clarke & Warwick, 2001). Overall, field margin plots showed distinct clustering based on biome. Therefore grassland and savanna field margin plots had distinct plant communities. However, there was no clustering based on the plots' location relative to maize field. Therefore, the tension zone did not have a unique plant species composition relative to the natural area. Maize field plots were also found to have a distinctive species composition relative to the field margin, with maize field plots from both biomes clustering together. This can be seen clearly in the analysis of all plots (fig. 6.4) as well as the analyses for each locality separately (fig. 6.5).

ANOSIM analyses (table 6.5) confirmed significant differences in species composition between maize fields and field margins and also between biomes at p<0.005 (Clarke, 1993). However, within the biomes, the tension zones and natural areas were never significantly different and therefore these results confirm the groupings found in the NMDS analysis. NMDS analysis excluding the maize plants themselves (fig. 6.4 B), formed a distinct cluster relative to the field margin plots, indicating that maize fields have several weed species in common across two biomes in South Africa. However, this cluster is clearly not as distinctive as for the plots with maize included, which illustrates that maize is mainly responsible for the tight clustering found in fig. 6.4 A (note that ANOSIM and SIMPER analyses were based on a dataset excluding maize). Although all maize field plots were distinctive from field margin plots, ANOSIM analyses revealed that the species composition of grassland and savanna maize fields are nevertheless significantly different at p<0.005. Furthermore, plant assemblages of the grassland biome seem to have a much tighter clustering, compared to the savanna plots (fig. 6.5), exceptions being the Jozini (tight cluster) and Cala localities (spread cluster).

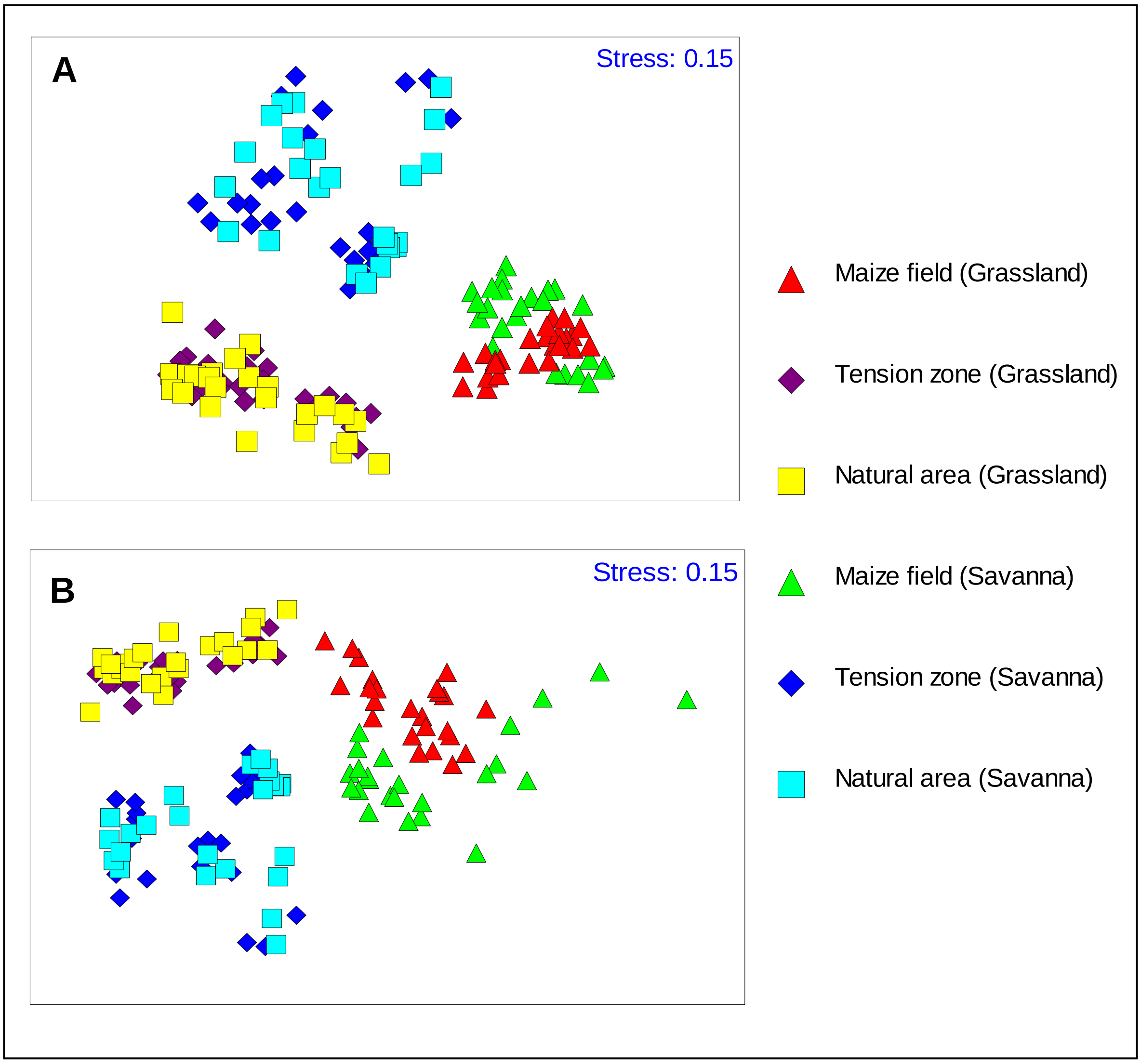

Figure 6.4: Non-metric multidimensional scaling analyses based on: (A) total plant species composition and (B) all plant species excluding *Zea mays* recorded at all sites.

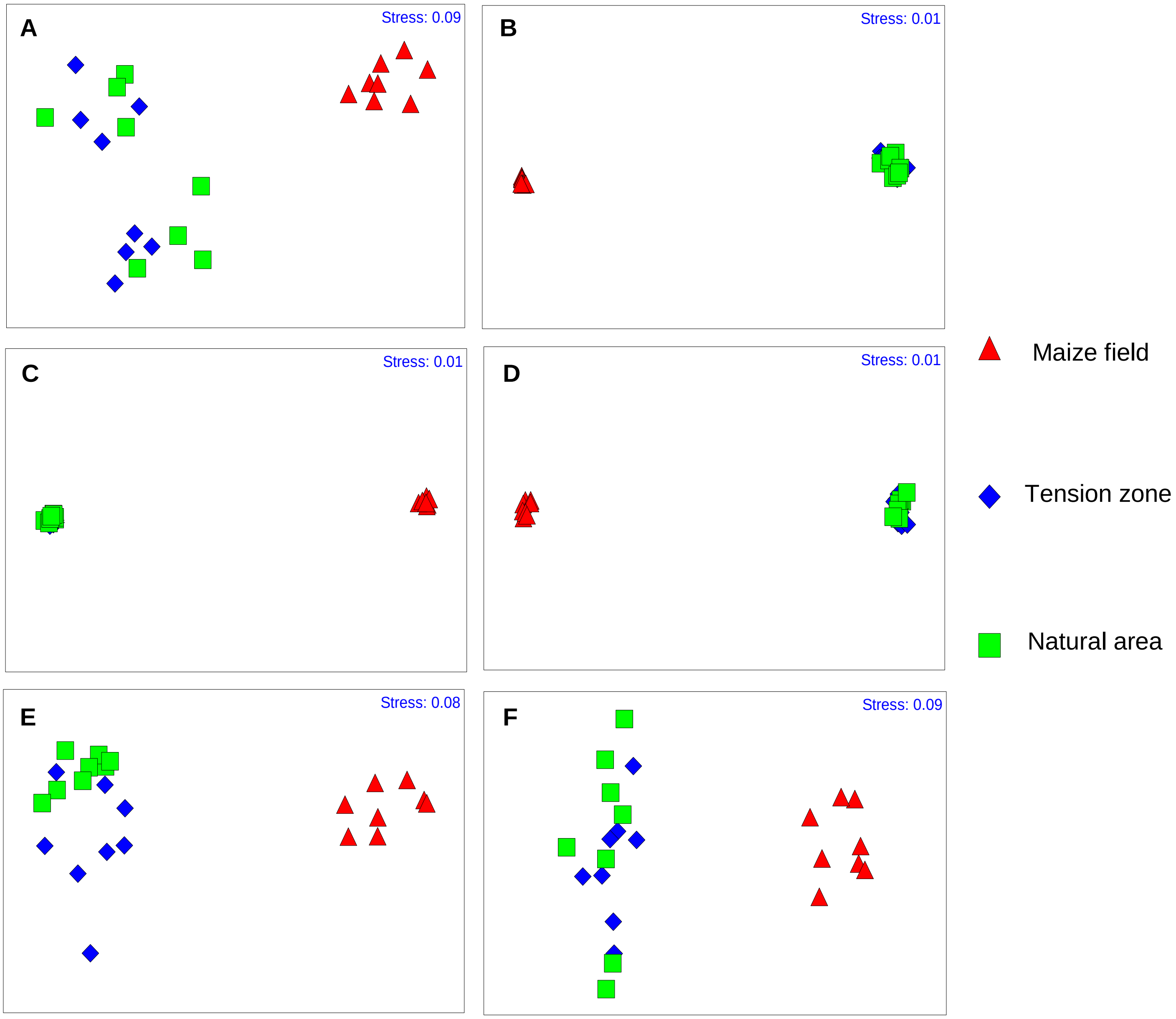

Figure 6.5: Non-metric multidimensional scaling analyses based on plant species composition for different localities: (A) Thohoyandou; (B) Ermelo; (C) Potchefstroom; (D) Jozini; (E) Jacobsdal; (F) Cala.

Table 6.5: Results for ANOSIM analysis indicating significance of separation between plant groups based on species composition. Values marked in red indicate significant separations at p<0.005 (p-values, uncorrected significance; permutiation N = 9999). (MG) = Maize field Grassland; (MS) = Maize field Savanna; (TG) = Tension zone Grassland; (TS) = Tension zone Savanna; (NG) = Natural area Grassland; (NS) = Natural area Savanna.

	MG	MS	NG	NS	TG
MS	0.0001	--	--	--	--
NG	0.0001	0.0001	--	--	--
NS	0.0001	0.0001	0.0001	--	--
TG	0.0001	0.0001	0.6583	0.0001	--
TS	0.0001	0.0001	0.0001	0.8084	0.0001

Comparisons of the maize fields, tension zones and natural areas between the grassland and savanna biomes in terms of their similarity in species composition by means of SIMPER analyses (appendix B: table 12.1) revealed that the maize fields of grassland and savanna were most similar in terms of species composition (dissimilarity: 91.4%), followed by the tension zones (dissimilarity: 97.63%) and finally the natural areas, which had the least similar species composition (dissimilarity: 98.3%). *Cyperus esculentus*, a grassland weed species, and *Digitaria sanguinalis*, a savanna weed species of maize fields, represented the most important species, contributing 11.87 and 5.14% respectively to the distinctive groupings found between grassland and savanna maize fields, with other species contributing less than 5%. *Themeda triandra* were the most important species of the grassland tension zone (contribution: 4.66%) while *Panicum maximum* was an important species of the savanna tension zones (contribution: 2.9%). Contribution of other species was less than 2.7%. The species determining the distinction between the grassland and savanna natural areas were also *T. triandra* (contribution: 3.68%) characteristic of the grassland and *P. maximum* (contribution: 2.88%) of the savanna (contribution of other species: 2.2%).

Comparisons between the maize fields, tension zones and natural areas within the grassland biome revealed that the smallest dissimilarity in species resided between the tension zone and natural area (dissimilarity: 79.95%), while the greatest dissimilarity in plant species composition was found between the maize fields and natural areas (dissimilarity: 98.82%). Comparisons between the maize fields and tension zones in the grassland biome revealed that *Cyperus esculentus* and *T. triandra* were the most important contributing species (8.12% and 7.18% respectively), with *C. esculentus* characteristic of the maize fields and *T. triandra* of the tension zone (contribution of other species: ≤ 3.6%). These two species were also most distinctive between the maize fields and natural areas of the grassland, with *C. esculentus* found exclusively in the maize field and *T. triandra* characteristic of the natural area. *Themeda triandra* and *Sporobolus africanus* contributed most to the distinction between the tension zone and natural area of the grassland biome (6.78% and 3.62% respectively), and were both characteristic of the tension zone (contribution of other species: ≤ 2.7%).

Between the maize field, tension zone and natural area within the savanna biome, the greatest similarity in plant species composition was again between the tension zone and natural area (dissimilarity: 89.61%). The greatest dissimilarity in plant species composition of the savanna was however between the maize fields and tension zones (dissimilarity: 98.76%), rather than between the maize fields and natural areas (as was found for the grassland biome). This also agrees with the findings that grassland and savanna diversity/richness tended to peak at different intervals along the MAFFMAG. Therefore, savanna diversity/richness was more likely to be significantly higher in the tension zone relative to the maize field, while grassland diversity/richness was more likely to be significantly higher in the natural area (6.2.1).

In the distinction between the savanna maize fields and tension zones, *P. maximum*, was the most prominent species in the tension zone with a contribution of 3.83% while *Digitaria sanguinalis* (contribution: 2.21%) were characteristic of the savanna maize fields (contribution of other species: ≤ 2.0%). These species were also the most significant contributors in the distinction between the savanna maize fields and natural areas, with *P. maximum* (contribution: 4.57%) characteristic of the natural areas while *D. sanguinalis* (contribution: 2.237%) were characteristic of the savanna maize fields (contribution of other species: ≤ 2.0%). The most important species distinguishing the savanna tension zone and natural area were mostly grasses, with *P. maximum* and *Urochloa mosambicensis* characteristic of the natural area (contribution: 4.70% and 2.28% respectively) and *Pentzia incana*, a non-grass species most common in the savanna tension zone (contribution of other species: ≤ 1.8%).

6.3.2 Discussion

Overall, the tension zones of the sampled field margins had a very similar plant species composition to the natural areas, which agrees with our findings on plant diversity and richness patterns in the field margins. Similar to the natural area, the tension zone also housed a minimal number of alien plant species (fig. 5.2). This seems to contradict the notion that natural vegetation adjacent to crop fields should change from weedy, annual species to non-weedy, perennial species with increased distance from crop fields. It has been shown by Boutin and Jobin (1998) and Boutin *et al.* (2008) that weeds, annuals and alien plant species were more numerous in disturbed sites compared to more natural sites in agro-ecosystems, with more weedy species closer to crop field edges than further away. However, they found these changes to occur within 9-25 m from the crop fields, which was 25 m closer to the crop field than our sampling.

As the tension zones and natural areas of the field margins did not seem to differ significantly in terms of plant species composition, diversity or richness, our findings do not support the ecotone, ecocline or edge effect hypotheses of crop fields. Piessens *et al.* (2006) found that the species composition of heathland vegetation adjacent to crop fields in Belgium differed from vegetation further away from field edges. In this case, dwarf shrubs characteristic of heathlands was mostly replaced by grass species towards the edge of crop fields. However, these edge effects seemed to be confined to the first 8 m outside the crop fields, which may explain why this study was unable to detect these changes along the MAFFMAG.

Furthermore, from the clustering of the maize field plots it can be concluded that the weed species composition of the sampled maize fields is very unique and few species are shared with the field margin. This is consistent with the results of Marshall (1989) who conducted a study on the plant communities in field margins of winter wheat and spring barley in lowland Britain. Their results indicated that most perennial plant species of field margins are not adapted to establish successfully in crops and that species similarities between crop fields and field margins were in the order of 30%. These patterns were contributed to low seed dispersal into crop fields and fewer opportunities for germination due to cultivation activities. Similar results have also been found on a farm in Essex UK, where 25% of species in the field margin coincided with crop fields (Marshall & Arnold, 1995). In our results, it was found that the field margin of the savanna shared only 6.23% of plant species with the maize field. These included species such as *Urochloa panicoides, Cynodon dactylon, Euphorbia inaequilatera, Setaria verticillata, Panicum maximum* and *Phyllanthus parvulus.* Also, the field margin of the grassland shared 9.09% of species with the maize field with shared species including *Commelina africana, Sporobolus africanus, Eragrostis gummiflua, Kyllinga erecta, Cynodon dactylon* and *Chloris virgata.*

The distinct species compositions of grassland and savanna maize fields may have been due to the tendency of weeds to spread into crop fields from the surrounding field margin (Leeson *et al.*, 2005). As grassland and savanna habitats may contain different pioneer species able to spread into maize fields, it can be expected that maize fields situated in different biomes will have different weed communities. However, considering the groupings of the NMDS analysis, more species are shared between maize fields than between grassland and savanna field margins. Therefore, field margins have greater beta diversity than maize fields. The plant species characteristic of the maize fields may be present in the field margins as well, although they are more abundant in the maize fields, probably due to more favourable conditions associated with this environment. Disturbances such as soil tillage, irrigation and the application of herbicides and fertilizers may cause unfavourable conditions for most non-crop vegetation, therefore eliminating competition for the few species that are able to tolerate these conditions (Curry, 1994). As the conditions of maize fields are more or less similar regardless of locality, this may result in a similar set of non-crop plant species, favoured by these specific conditions. This process is called biotic homogenisation (Olden & Poff, 2003).

The tendency of the grassland localities to have tighter clustering of their field margin plots indicates that the grassland localities have lower beta diversity (diversity between plots) than the savanna localities. Therefore, the grassland biome had relatively similar plant species in each plot, while each of the savanna plots had more unique plant species relative to the others. This is again possibly the result of the multi-structured nature of savanna, which may lead to a greater variation in species from plot to plot due to scattered woody plant species or may be scale dependant considering that savanna plots were sampled in 100m^2 and not the typical 400 m^2.

Chapter 7: Arthropod species diversity and composition of maize agro-ecosystems

7.1 Arthropod species diversity patterns along the MAFFMAGs between localities

7.1.1 Results

Table 7.1 displayed non-significant interactions between locality and distance for most diversity indices, indicating that all localities reacted in a relatively similar fashion to the distance from maize field in these cases. This was however not true for species richness and Margalef's Species Richness Index, which displayed significant interactions between locality and distance from maize field. Although the direction of the effect of distance is the same for all localities, more pronounced effects could be seen for Cala and to a lesser extent Jacobsdal.

The Shannon-Wiener Diversity Index (H') values indicated significantly lower arthropod diversity in maize fields than field margins, a tendency that was consistent across all localities, but this was true specifically at 50, 250 and 350 m from the maize field. A general decrease in H' values were observed at 150 m from maize fields (table 11.3.1). This observation is inconsistent with the results for plants, which tended to have a consistently high diversity across the whole field margin or increased diversity at 150 m (chapter 6).

Pielou's Evenness Index (J') revealed no significant differences between distances from maize fields at any of the localities (table 11.3.2). Also, evenness values for Cala were significantly lower than the other localities at all distances. Similarly, no significant differences were found for Simpson's Diversity Index (Ď) between distances (table 11.3.4). Since the Simpson's Diversity Index is an indication of the homogeneity of the population, with a value of 1 relating to complete homogeny (Begon *et al.*, 2008), arthropod populations do not seem to differ in terms of homogeneity across the sampled MAFFMAGs.

Margalef's Species Richness Index (d) showed inconsistent results for arthropod species (table 11.3.3). Most of the localities had no significant differences in terms of the Margalef Index across the MAFFMAG. However, significant differences were found in Jacobsdal and Cala. At these localities, field margins had significantly higher values than the maize fields. The Margalef Index for arthropods showed similar results to the species richness (S) (table 11.3.5).

The number of times each distance in the field margin showed significantly higher index values than that of the maize field was summarized in table 7.2, and the distance at which the most significant differences occurred are depicted in table 7.3 and fig. 7.2. It was found that the fewest significant differences for arthropods relative to the maize fields occurred at 150 m, with equal numbers of significantly different values at 50 m and in the whole natural area (250 and 350 m).

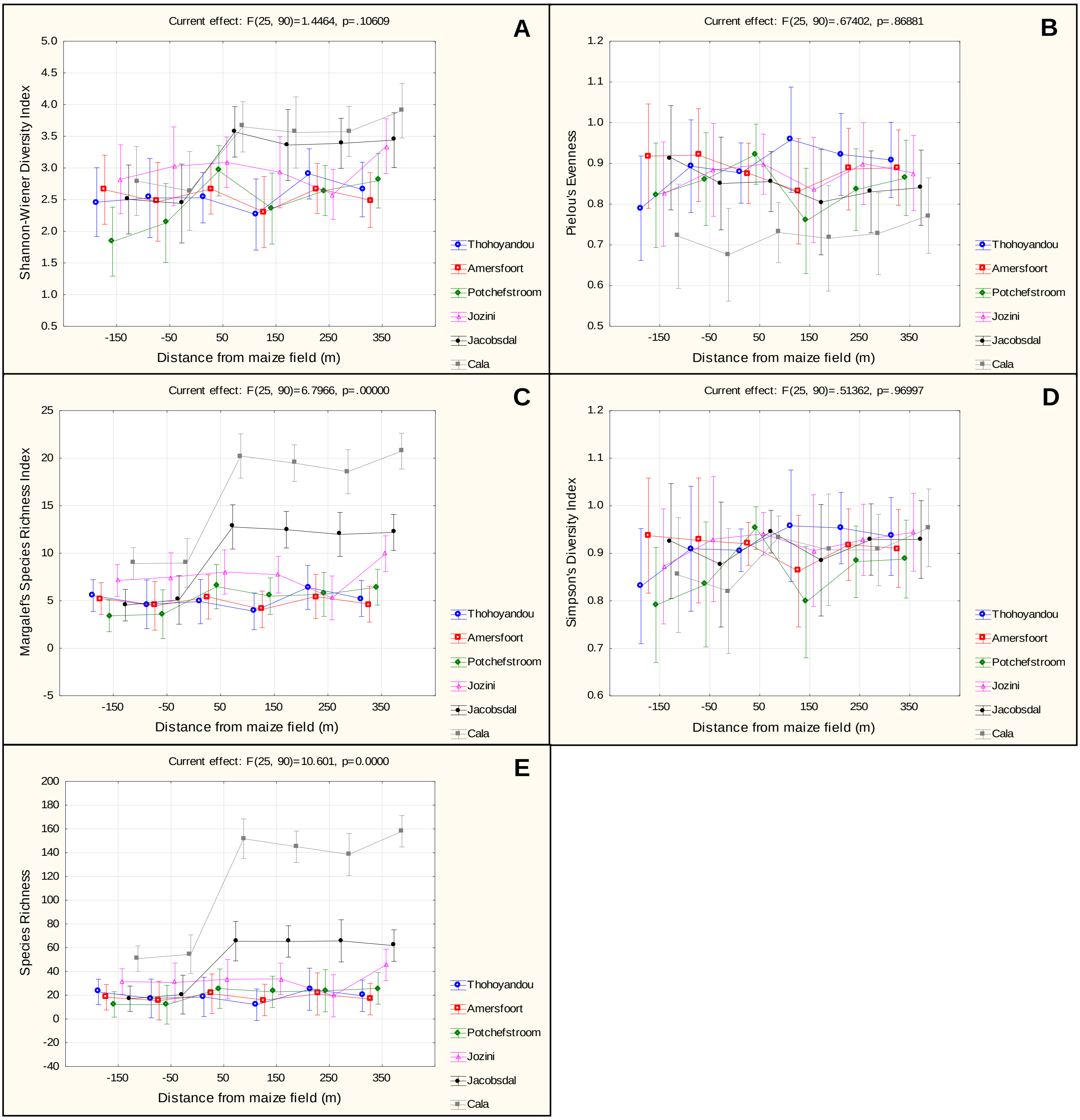

Figure 7.1: Diversity index values for arthropods along maize field-field edge gradients (MAFFMAG) at six localities in South Africa: (A) Shannon-Wiener Diversity Index; (B) Pielou's Evenness; (C) Margalef's Species Richness Index; (D) Simpson's Diversity Index and (E) Species Richness. Vertical bars denote 0.95 confidence intervals. The distances -150 and -50 m are located inside maize fields and 50-350 m in natural vegetation adjacent to fields.

Table 7.1: P-values of Repeated Measures Analysis of Variance (ANOVA) for differences in arthropod diversity index values between distances from maize fields (-150, -50, 50, 150. 250, and 350 m), between six localities as well as interactions (between distance and locality). Values in red indicate significant differences (n=4; p<0.05). Refer to appendix A for complete statistical values.

Index	**Locality**	**Distance**	**Interaction**
Shannon-Wiener Diversity Index	0.000	0.000	0.106
Pielou's Evenness	0.000	0.680	0.869
Margalef's Species Richness	0.000	0.000	0.000
Simpson's Diversity Index	0.061	0.127	0.970
Species Richness	0.000	0.000	0.000

Table 7.2: Distances at which each locality showed significantly higher values in terms of arthropod diversity indices for the field margin than the maize field (there were four distances; All = 50, 150, 250 and 350). (THO) = Thohoyandou; (ERM) = Ermelo; (POT) = Potchefstroom; (JOZ) = Jozini; (JAC) = Jacobsdal; (CAL) = Cala.

	THO	ERM	POT	JOZ	JAC	CAL
H	50/250/350	50/250/350	50/250/350	50/250/350	50/250/350	50/250/350
J	None	None	None	None	None	None
Ď	None	None	None	None	None	None
d	None	None	None	None	All	All
S	None	None	None	None	All	All
Tot:	**3**	**3**	**3**	**3**	**11**	**11**

Table 7.3: Number of times each distance showed significantly higher arthropod diversity index values for the field margin than the maize field per locality (there were six localities).

	50	150	250	350
H	6	0	6	6
J	0	0	0	0
Ď	0	0	0	0
d	2	2	2	2
S	2	2	2	2
Tot:	**10**	**4**	**10**	**10**

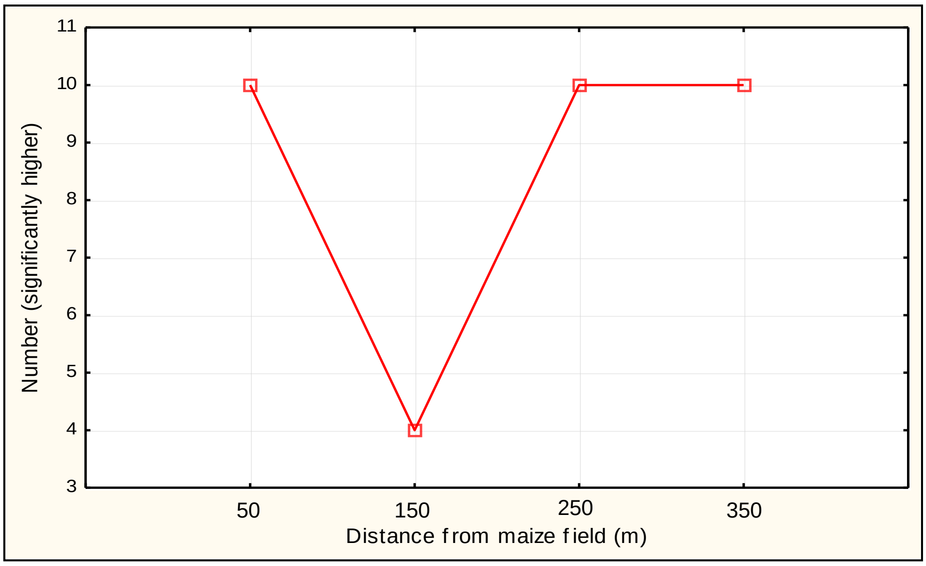

Figure 7.2: Number of times each distance showed significantly higher arthropod diversity/richness index values for the field margin than the maize field per locality (there were six localities).

7.1.2 Discussion

As expected, arthropod species diversity and richness were often found to be significantly higher in field margins compared to maize fields. This observation is supported by results of numerous studies comparing arthropod diversity of crop fields and natural vegetation. Szinicz (2005) studied the arthropod diversity along transects from tropical rainforest into agricultural habitats and found reduced arthropod diversity towards crop fields. They also found this arthropod diversity to be dependent on plant diversity, plant structure, plant species composition and plant productivity. However, they considered the largest factor to be the loss of microclimate towards the crop fields. Also, Thomas and Marshall (1999) found that arthropod diversity was lowest in crop fields, higher in crop edges and highest in field margins. They contributed these results to an increase in plant diversity, on which arthropods depend for resources. Similarly, Hendrickx *et al.* (2007) demonstrated that species richness of wild bees (Apoidea), carabid beetles (Carabidae), hoverflies (Syrphidae), true bugs (Heteroptera) and spiders (Araneae) decreased with increased farming intensity and was strongly affected by increased proximity to semi-natural habitat patches. As mentioned previously, arthropod diversity and richness can be influenced by factors such as microclimate, availability of food, habitat requirements, intra- and interspecific competition and other organisms (Altieri & Nicholls, 1999). Field margins are generally more heterogeneous in nature and as such provide opportunities for more arthropod species than crop fields (Ingham & Samways, 1996).

What is unexpected is that this pattern was not displayed for all localities regarding Margalef's Species Richness Index and arthropod species richness and was not displayed at all for Simpson's

Diversity Index. Since field margins did not display significantly higher arthropod species diversity and richness than maize fields in all these cases, it seems that maize fields are often much more species rich than previously thought. Due to the presence of weeds in maize fields, not all sampled maize fields were strict monocultures, probably resulting in these environments being able to support a greater variety of arthropod species that would otherwise not be associated with the maize plants (Perfecto & Vandermeer, 2008). However, as mentioned in chapter 2.3, the high mobility of many arthropod species means that numerous arthropods may be found in crop fields although they may not necessarily be able to persist in these environments (Strong *et al.*, 1984).

Although significant differences were found between maize field and field margin plots, the tension zones (50 and 150 m) rarely differed significantly from the natural areas (250 and 350 m) in terms of arthropod diversity and richness. This again contradicts the hypothesis that the tension zone should have lower arthropod diversity values compared to the natural area. As in the case of plant diversity and richness, negative effects on arthropods, if present, may be limited to the outer edge of the field. Similar studies conducted on arthropod diversity in crop fields and field margins, such as those by Thomas and Marshall (1999), Szinicz (2005) and Hendrickx *et al.* (2007) did not sample arthropods in field margin strips further than 25 m from crop fields and taking our results into account, it seems unlikely that any effects on arthropod diversity exists beyond 50 m from maize fields.

The findings that arthropod evenness and homogeneity were relatively similar in maize fields and field margins contradict hypotheses predicting that evenness or abundance of organisms at higher trophic levels should be dependent on plant species richness and diversity. Evidence that arthropod evenness and homogeneity decrease in monocultures as a result of lowered plant species richness have been provided by Pimentel (1961) and Root (1973). However, studies such as these were confined to a limited number of plant species in crop fields and few attempts have been made to confirm the merit of these hypotheses in natural systems. Furthermore, recent data indicate that arthropod evenness or abundance is not necessarily a simple function of plant species richness but may depend on complex interacting factors such as plant species composition, productivity, vegetation structure, nutritional value, soil characteristics and agricultural management (Siemann, 1998) (as discussed in chapter 2.6).

The cause of the overall lower arthropod species evenness for Cala is uncertain. However, it seems that the species that were particularly numerous in this area were mites of the family Oribatulidae, springtails (Entomobryoidea) and aphids (Hemiptera: Aphididae). The extreme abundance of the mites and springtails may have been due to a sampling bias. As for the aphids, specific conditions that prevailed during the specific season in which sampling was done may have caused a particularly large outbreak of these species and could have resulted in the low evenness observed in maize fields and field margins. It has been shown by Wains *et al.* (2010) that increases in aphid densities can be caused by factors such as higher temperatures, lower relative humidity, late planting of crops and susceptible plant varieties. If these factors were present, it may have caused aphid outbreaks at the time of sampling.

It seems that the overall effect regarding the diversity/richness indices (fig. 7.2) was that the natural area had a tendency to differ more frequently from the maize fields in terms of arthropod diversity/richness than the tension zone. In the tension zone, the plots located at the distance 150 m tended to have much lower diversity/richness values than the other field margin plots and were more frequently similar to maize fields in terms of arthropod species diversity and richness. The exact cause for these findings is unclear at this point, as it may have been caused by several factors that may or may not have been dependent on the presence of the maize fields. Since grazing by livestock was a common feature at these distances, it is possible that the arthropod communities were affected by such disturbances. It has been shown that vegetation associated insects are affected by livestock grazing in semi-arid grasslands of the United States and that at least some groups of insects (Coleoptera, Diptera and Hymenoptera) show a decrease in diversity and abundance in response to grazing activities (Debano, 2006).

Some of the inconsistent results found for arthropod diversity and richness responses to the MAFFMAG may have been caused by a sampling bias and it is likely that not all can be attributed to natural phenomena. Furthermore, the high mobility of most arthropods will inevitably complicate the detection of more permanent topological patterns in arthropod diversity. Therefore, while the activities associated with maize fields may cause mortalities in the field margin, these individuals may soon be replaced by others from the adjacent vegetation. Therefore, further monitoring of arthropod communities over time will be required to confirm the merit of these results.

7.2 Arthropod species diversity patterns along MAFFMAGs between biomes

7.2.1 Results

Comparisons of arthropod diversity and richness values between the grassland and savanna biomes generally revealed significant differences between maize fields and field margins, with lower diversity and richness inside maize fields than field margins (fig. 7.3). Furthermore, both biomes displayed a relatively similar trend along the MAFFMAG as indicated by the non-significant interactions between biome and distance, which was true for all diversity indices. Results for the Shannon-Wiener and Margalef indices as well as species richness were similar and values were generally found to differ significantly along the MAFFMAGs, with lower arthropod diversity and richness in maize fields than in field margins (table 11.4.1, 11.4.3 and 11.4.5). As with the results for plants, the tension zones and natural areas also did not differ significantly in terms of arthropod diversity and richness. However, the Shannon-Wiener Diversity Index displayed a tendency to decrease significantly at 150 m in both biomes.

Analyses for Pielou's Evenness, revealed no significant differences in arthropod species evenness between any of the plots along the MAFFMAG, a result that was observed for both biomes (table 11.4.2). Simpson's Diversity Index displayed similar results, with non-significant differences in values between maize fields and field margins. Overall, no significant differences could be found between the grassland and savanna biomes in terms of arthropod diversity and richness. Exceptions were found for Simpson's Diversity Index, which displayed significantly higher values in the savanna than in the grassland for most of the distances across the MAFFMAG.

Table 7.4: P-values of Repeated Measures Analysis of Variance (ANOVA) for differences in arthropod diversity index values between distances from maize fields (-150, -50, 50, 150. 250, and 350 m), between two biomes (grassland and savanna) as well as interactions (between distance and biome). Values in red indicate significant differences (n=4; p<0.05). Refer to appendix A for complete statistical values.

Index	Biome	Distance	Interaction
Shannon-Wiener Diversity Index	0.543	0.000	0.938
Pielou's Evenness	0.064	0.656	0.804
Margalef's Species Richness	0.487	0.000	0.657
Simpson's Diversity Index	0.039	0.096	0.880
Species Richness	0.232	0.000	0.187

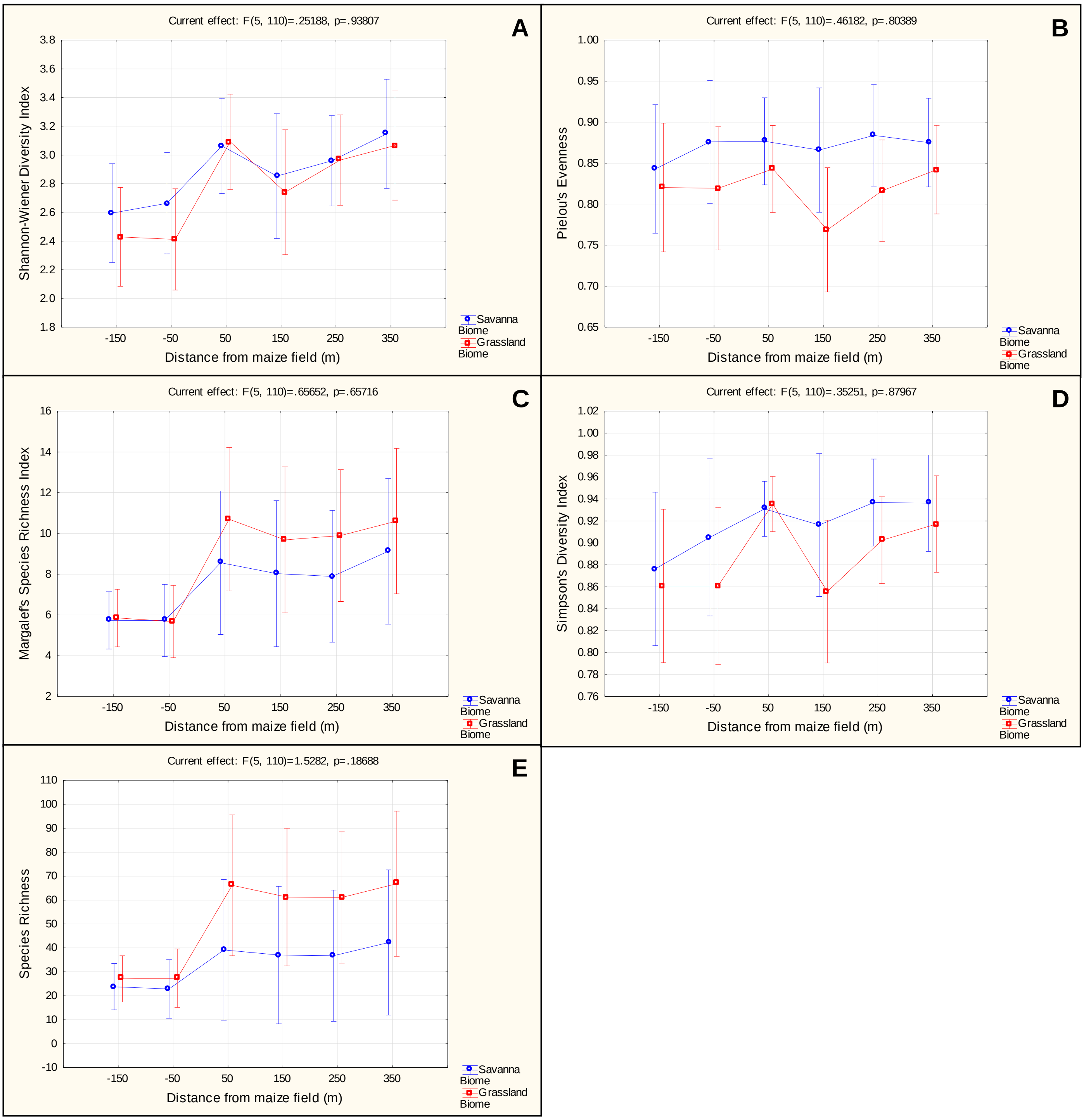

Figure 7.3: Diversity index values for arthropods along maize field-field edge gradients (MAFFMAG) of two biomes in South Africa: (A) Shannon-Wiener Diversity Index; (B) Pielou's Evenness; (C) Margalef's Species Richness Index; (D) Simpson's Diversity Index and (E) Species Richness. Vertical bars denote 0.95 confidence intervals. The distances -150 and -50 m are located inside maize fields and 50-350 m in natural vegetation adjacent to fields.

7.2.2 Discussion

The tendency for arthropod diversity and richness to be lower at 150 m, agrees with the results provided in 7.1.1 (fig. 7.1). Along with grazing pressure, this tendency may have been caused by arthropod migrations into maize fields during the flowering time of maize. As mentioned in chapter 4, it has been shown that arthropod biodiversity on maize in the period following anthesis is very high compared to the rest of the growing period (Dively, 2005). Consequently, there may have been a tendency for arthropods to congregate near field edges as these were likely high in food resources.

From these results, it seems that arthropod communities tend to follow a similar trend along MAFFMAGs across the grassland and savanna biomes of South Africa. Therefore, it may be said that savanna and grassland arthropod diversity/richness probably respond in a similar fashion to the presence of maize fields. Also, it seems that the arthropod communities in the savanna biome were more homogenous than those of the grassland biome, as the values for Simpson's Diversity Index were found to be significantly higher in the savanna biome than the grassland biome. As the savanna localities had slightly higher plant diversity and richness values (6.2.1), this may have caused the increased homogeneity of the arthropod communities as it has been shown by Murdoch *et al.* (1972) that increased plant diversity has the potential to increase the evenness (or homogeneity) of arthropod communities. Furthermore, savanna is characterized by an additional woody plant layer which Krüger and Mcgavin (1998) have shown to house a great variety of arthropod predators in savanna. Therefore, woody species may contain additional sources of predators as they may provide alternative nectar, pollen, hosts, and niches (Stamps & Linit, 1997). This may in turn aid in the suppression of pest populations and therefore prevent the dominance of arthropod pests.

7.3 Arthropod species composition along MAFFMAGs between biomes

7.3.1 Results

In the NMDS analysis based on all localities in two different biomes (fig. 7.4), the stress value of 0.22 is relatively high, which indicates that not too much reliance must be placed on the spacing of the plots of the particular ordination without cross-checking the results by means of other statistical analyses (Clarke & Warwick, 2001). Because these results were very similar to those of the analyses of the separate localities (with much lower stress values) this ordination can still be regarded as a good representation of the relationship between plots in terms of species composition. Furthermore, the results of ANOSIM analyses confirmed the significance of these groupings at $p<0.005$ (Clarke, 1993) (table 7.5).

NMDS and ANOSIM analyses both revealed distinctions in arthropod species composition between maize field and field margin plots, as was found for all localities (fig. 7.4) as well as for each separate locality (fig. 7.5). However, the tension zone and natural area did not represent separate clusters in any of the localities, indicating a similar arthropod species composition across the whole field margin. Furthermore, field margin plots of grassland and savanna were found to be significantly different in terms of species composition and cluster separately. Although maize field plots of the grassland and savanna appear to represent a single cluster (fig 7.4), ANOSIM analysis revealed that the arthropod species compositions of grassland and savanna maize field are nevertheless significantly different (p=0.001, table 7.5). It is also apparent that the overlap between the savanna maize plots with its field margins more prominent than those for the grassland biome (fig. 7.4, table 7.5).

Comparisons between biomes with SIMPER analyses revealed that the greatest similarity in arthropod species composition was between the natural areas of the grassland and savanna biomes (dissimilarity: 97.59%) (appendix B: table 12.2). The greatest dissimilarity was found between the tension zones of the grassland and savanna biomes (dissimilarity: 98.47%). Furthermore, distinctions between the grassland and savanna maize fields were mainly due to Aphididae morphospecies (MS) 1 and 2 (contributions of 7.48 and 5.18% respectively) that was characteristic of the grassland maize fields (contribution of other species: ≤2.2%). Distinctions between the tension zones of the grassland and savanna was mainly due to a mite species in the family Oribatulidae, MS 1 (contribution: 3.95%) which was characteristic of the grassland, and also a grasshopper species of the family Acrididae, MS 12 (contribution: 3.83%), also characteristic of the grassland tension zone (contribution of other species: ≤3.5%). The most important species that contributed to the distinction between the natural areas of the grassland and savanna were an ant species (Formicidae, MS 8) (contribution: 3.56%) that was more numerous in the savanna, and

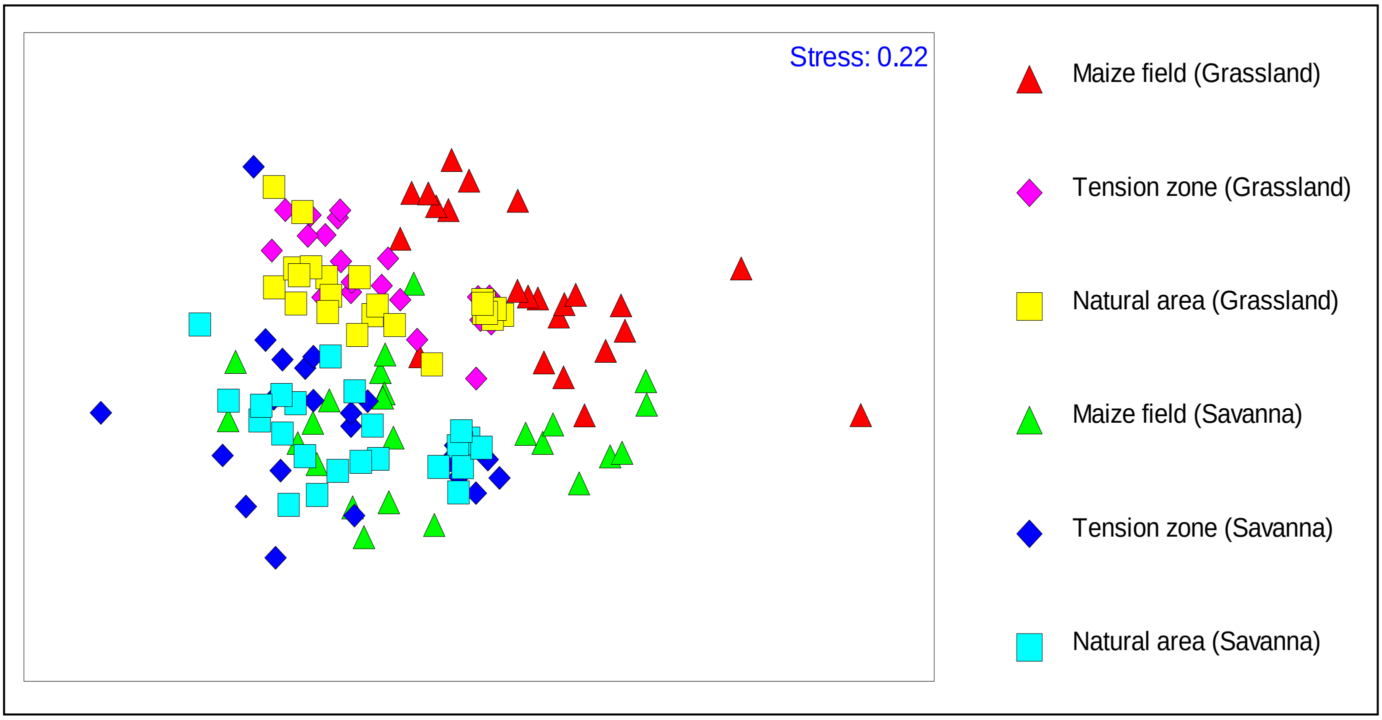

Figure 7.4: Non-metric multidimensional scaling analyses based on total arthropod species recorded at all sites defined according to zone and biome.

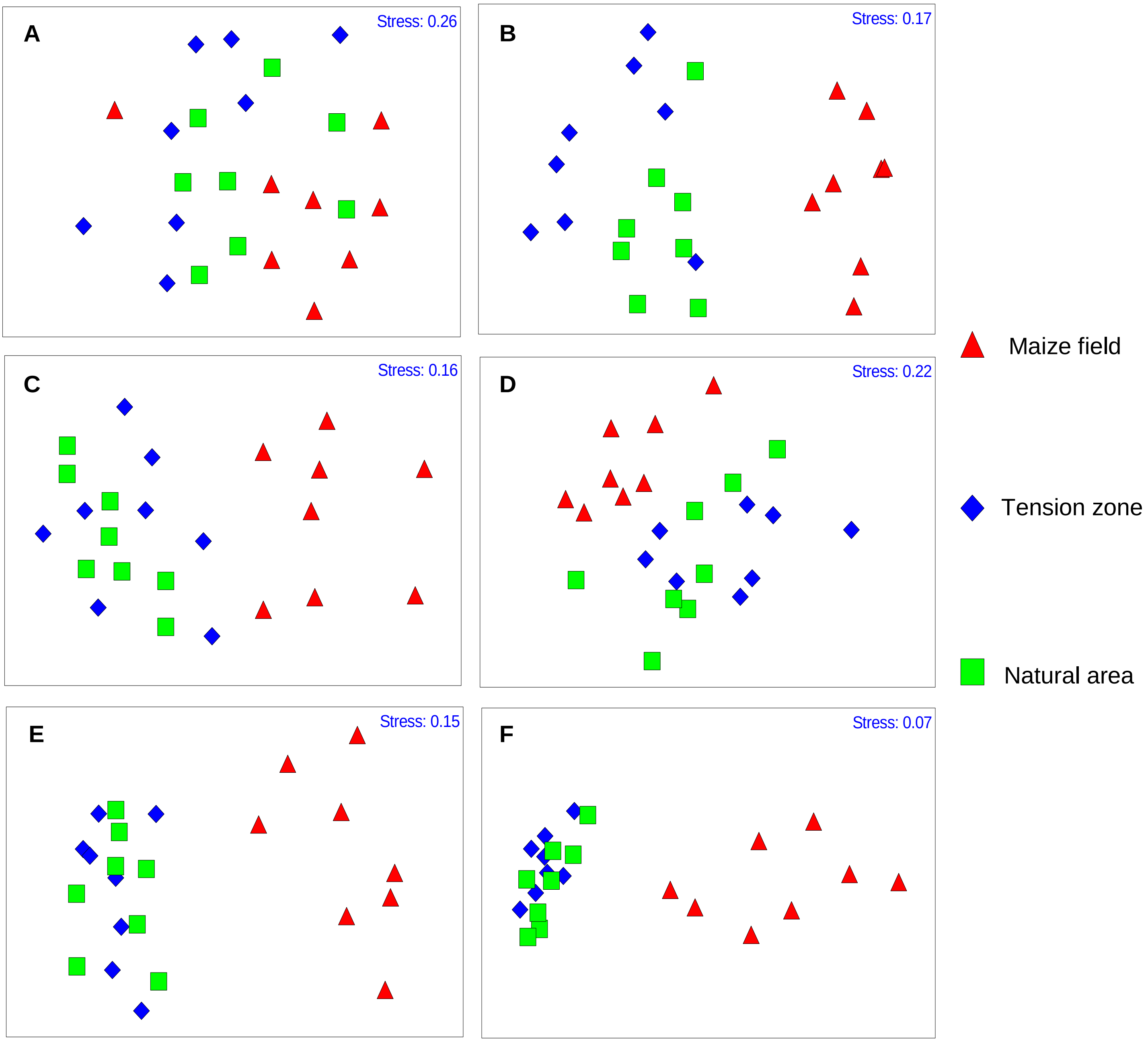

Figure 7.5: Non-metric multidimensional scaling analyses based on arthropod species composition for different localities: (A) Thohoyandou; (B) Ermelo; (C) Potchefstroom; (D) Jozini; (E) Jacobsdal; (F) Cala.

Table 7.5: Results for ANOSIM analysis indicating significance of separation between arthropod groups based on species composition. Values marked in red indicates significant separations at $p<0.005$ (p-values, uncorrected significance; permutation N = 9999). (MG) = Maize field Grassland; (MS) = Maize field Savanna; (TG) = Tension zone Grassland; (TS) = Tension zone Savanna; (NG) = Natural area Grassland; (NS) = Natural area Savanna.

	MG	MS	NG	NS	TG
MS	0.0001	--	--	--	--
NG	0.0001	0.0001	--	--	--
NS	0.0001	0.0013	0.0001	--	--
TG	0.0001	0.000	0.804	0.0001	--
TS	0.0001	0.0005	0.0001	0.8324	0.0001

also Oribatulidae MS 1 (contribution: 2.83%) characteristic of the grassland (contribution of other species: ≤2.7%).

Comparisons of the different treatments (maize field, tension zone and natural area) within the grassland biome revealed that the greatest similarity in arthropod morphospecies resided between the tension zone and natural area (dissimilarity: 91.63%). The greatest dissimilarity in arthropod species composition was found between the maize field and tension zone of the grassland biome (dissimilarity: 97.86%). The species that distinguished the maize fields from the tension zones in the grassland was mainly Aphididae MS 1 (contribution: 4.74%). Also important was the Oribatulidae MS 1, characteristic of the tension zone (contribution: 4.29%). Contribution of other species was ≤3.9%. These two morphospecies were also the most important in distinguishing the maize field from the natural area, along with Aphididae MS 2 with a contribution of 4.0% (contribution of other species: ≤3.0%) The distinction between the tension zone and natural area of the grassland was also due to Oribatulidae MS 1 and 2 that were characteristic of the tension zone and had contributions of 5.6 and 5.5% respectively (contribution of other species: ≤3.5%).

For the savanna, the greatest similarity in arthropod species composition was again found between the tension zone and natural area (dissimilarity: 94.06%), while the greatest dissimilarity in arthropod species composition was found between the tension zone and maize field. In the savanna biome, the most important species responsible for the distinction between the maize field and tension zone were a leafhopper morphospecies (Cicadellidae, MS 24) that was characteristic of the tension zone (contribution: 2.96%) and a gnat morphospecies (Sciaridae, MS 10) that was characteristic of both habitats but were more numerous in the tension zone (contribution: 2.45%). Also important was an ant morphospecies (Formicidae, MS 6) that was characteristic of the maize fields (contribution: 2.40%). Contribution of other species was ≤2.3%. Sciaridae MS 10 was also important in the distinction between the maize field and natural area of the savanna biome (contribution: 3.24%), along with Formicidae MS 15, which was also characteristic of the natural area (contribution: 2.9%). Contribution of other species was ≤2.6%. Distinctions between the natural area and tension zones of the savanna were mainly due to Cicadellidae MS 24 that was more numerous in the tension zone (contribution: 3.29%) and Sciaridae MS 10, that was characteristic of the natural area (contribution: 3.90%). Contribution of other species was ≤2.4%.

7.3.2 Discussion

From these results, it seems that the presence of maize fields did not have a detectable effect on the species composition of arthropods in field margins as the tension zone was found to have a very similar species composition to the natural area. This is consistent with the results of the diversity and richness of arthropods in the field margin. However, clear differences could be observed between the arthropod species compositions of the maize fields and field margins. Even within arthropod families, different species were characteristic of different environments. It was found for example that maize fields and field margins contained different species of ants (Formicidae) and aphids (Aphididae). This agrees with the notion that arthropod species may be characterised based on their preference of habitat (cultivated or natural) (Duelli & Obrist, 2003). Therefore, some species may be characterised as being crop field or cultural species, while others may be typical of an ecotone or undisturbed natural habitat (Duelli & Obrist, 2003). This is also consistent with the results of Kiss *et al.* (1997) who found that while almost twice as many predatory carabid beetles species occurred in field margins compared to crop fields, some are typical 'field species' that were unique to the crop fields either within certain periods of their lives or throughout their lifecycle. As maize fields represent unique environments, this may allow for only a few specialized species to persist, such as aphids (Aphididae), whose high fecundity allow them to successfully populate ephemeral habitats such as annual crops where others cannot (Wissinger, 1997).

Within each biome, the arthropod communities of maize fields and tension zones were least similar, which differs from the results for plants, where the most significant difference in plant species composition was found between the maize fields and natural areas. From this study the exact cause for this is unclear. However, a possible cause for this phenomenon may be the presence of rocky ridges or outcrops in the tension zones of Jacobsdal and Cala. Rocks provide unique and often challenging microclimates (Wilmer, 1982) and may therefore favour only specialised groups of arthropods. Also, it has been shown that characteristics such as habitat diversity and landscape structures such as woodlands, hedgerows or ditches may potentially regulate arthropod species composition (Schweiger *et al.*, 2005) and therefore, the unique characteristics provided by the slope, substrate (rocks) and possibly unique plant groups may have resulted in a more distinct arthropod species composition than the natural area.

Furthermore, the grassland and savanna had distinct arthropod communities. This was true not only for the field margins, but also for the maize fields. As was found by the authors Schaffers *et al.* (2008) and Symstad *et al.* (2000) arthropod species composition may be determined by plant species composition (chapter 2.6). As grassland and savanna had very distinct plant communities, this may also have resulted in distinct arthropod communities. As in the case of plants, distinctions between grassland and savanna maize field arthropod communities agree with findings that crop fields may be colonized by arthropods from the surrounding field margin (Norris & Kogan, 2000; Garibaldi *et al.*, 2011; Alomar *et al.*, 2002) (chapter 2.3). Since it has been shown that grassland and savanna field margins contained distinctive arthropod communities, it can be expected that maize fields will also have unique species associated with the particular biome in which the maize field is located.

The greater overlap in arthropod species between the maize field and field margin plots of the savanna biome indicates that more species are shared between the maize fields and field margins of this biome. Therefore, it seems that arthropod communities of the savanna biome may have a greater affinity for maize fields than the arthropod communities of the grassland localities. Vegetation structure is considered to be one of the major factors in shaping arthropod communities (Strong *et al.*, 1984). As maize plants are grass species it may be said that maize fields are in effect man-made grasslands. It could therefore be expected that grassland arthropods may have a greater affinity for maize fields than savanna arthropods, especially since maize fields rarely contain woody plant species. However, on closer inspection, a maize field also does not have the low-growing structure of grassland, but have much taller plant growth (± 1.5 -2.2 m) with bigger leaves and thicker stems. Therefore, the vegetation structure of a maize field may resemble a savanna or woodland habitat more closely than a grassland habitat, and attract more savanna arthropods than grassland arthropods. Alternatively, and perhaps more likely, most of the savanna maize fields (Thohoyandou and Jozini) were located on subsistence farms, and were often not strict monocultures (chapter 3). Since arthropods are often attracted to more diverse cropping systems (Stamps & Linit, 1997; Feber *et al.*, 1997), more arthropods could have been attracted to maize fields from field margins in the savanna than in the grassland.

Overall, it is clear that the clustering for arthropods is much less defined than for plants, and maize fields shared many more arthropod species than plant species. This is consistent with the results of Procheş and Cowling (2007), who contributed this phenomenon to the high mobility of most arthropod species. Since arthropods are able to move freely between habitats, it is expected that clustering of arthropod species will be less well defined than for plants.

Chapter 8: Plant-arthropod diversity relationships

8.1 Results

Comparison of the diversity values of all plots by means of Spearman’s Rank Order correlation analyses revealed a few significant, although generally weak, positive relationships between plant and arthropod diversity (table 8.1). Pielou’s Evenness Index (J’) values for plants were positively correlated with Margalef’s Species Richness Index (d) values and species richness (S) for arthropods. Also, the S values for plants were positively correlated with d values for arthropods. Therefore, increased plant species evenness and richness was correlated with increased arthropod richness and diversity. However, no other significant correlations could be found between plant and arthropod diversity.

Spearman’s Rank Order correlation analyses were also applied to determine whether relationships exist within the separate treatment zones (maize field, tension zone or natural area) with regard to distance from maize field. Again, few significant correlations could be found, and those that were significant were generally weak. Within the maize fields, there were significant positive correlations between S values for arthropods and S and d values for plants (table 8.2 A). Therefore, increases in plant species richness resulted in an increase in arthropod species richness in the maize fields. The most significant correlations were found in the tension zone, although these correlations were all negative (table 8.2 B). In this case, d values for plants were negatively correlated with the H’, d, and S values for arthropods. It was also found that the S values for plants were negatively correlated with the H’ and S values for arthropods, and that the H’ and Ď values for plants were negatively correlated with H’ for arthropods. Therefore, increased plant diversity and richness overall resulted in decreased arthropod diversity and richness in the tension zone. Very few significant correlations could be found between plant and arthropod diversity in the natural areas although Pielou’s evenness (J’) for plants was negatively correlated with Ď values for arthropods (table 8.2 C). Therefore, an increase in plant evenness (an indication of little disturbance) was correlated with a decrease in arthropod diversity.

Comparisons between plants and arthropod index values were also made between plots at similar distances from the maize fields (table 8.2 D). Mostly, correlations between plant and arthropod diversity were non-significant. However, significant positive relationships existed between the species richness for plants and arthropods at -150 m. Also, significant negative correlations existed between the H’ and S values for plants and J’ values for arthropods at -150 m. Therefore, although increased plant species richness resulted in increased arthropod species richness, increased plant species richness and diversity also resulted in decreased arthropod evenness at the plots deepest in the maize fields.

Table 8.1: Results for **Spearman Rank Order Correlations** indicating relationships between the index values for plants and arthropods. (H’) = Shannon-Wiener Diversity Index; (J’) = Pielou’s Evenness Index; (d) = Margalef’s Species Richness Index; (Ď) = Simpson’s Diversity Index; (S) = species richness. Values in red represent significant correlations at p<0.05.

	(H') Arthropods	(J') Arthropods	(d) Arthropods	(Ď) Arthropods	(S) Arthropods
(H') Plants	0.128	-0.001	0.158	0.088	0.150
(J') Plants	0.112	-0.095	0.169	0.005	0.173
(d) Plants	0.124	0.016	0.144	0.102	0.138
(Ď) Plants	0.107	-0.005	0.136	0.072	0.128
(S) Plants	0.150	0.028	0.165	0.125	0.154

Table 8.2: Results for **Spearman Rank Order Correlations** indicating relationships between plants and arthropods for: (A) the maize fields (MF); (B) the tension zone (TZ), (C) the natural area (NA) and (D) correlations between plant and arthropod indices for similar distances from the maize field. (H’) = Shannon-Wiener Diversity Index; (J’) = Pielou’s Evenness Index; (d) = Margalef’s Species Richness Index; (Ď) = Simpson’s Diversity Index; (S) = species richness. Values in red indicate significant correlations at p <0.05.

					A
	(H') Plants (MF)	(J') Plants (MF)	(d) Plants (MF)	(Ď) Plants (MF)	(S) Plants (MF)
(H') Arthropods (MF)	-0.007	-0.104	0.058	0.001	0.082
(J') Arthropods (MF)	-0.151	-0.068	-0.252	-0.104	-0.251
(d) Arthropods (MF)	0.107	-0.121	0.249	0.042	0.265
(Ď) Arthropods (MF)	-0.109	-0.082	-0.146	-0.063	-0.128
(S) Arthropods (MF)	0.139	-0.121	0.307	0.057	0.321

					B
	(H') Plants (TZ)	(J') Plants (TZ)	(d) Plants (TZ)	(Ď) Plants (TZ)	(S) Plants (TZ)
(H') Arthropods (TZ)	-0.312	-0.149	-0.365	-0.324	-0.334
(J') Arthropods (TZ)	-0.000	-0.115	0.030	-0.048	0.076
(d) Arthropods (TZ)	-0.192	0.012	-0.289	-0.180	-0.275
(Ď) Arthropods (TZ)	-0.140	-0.162	-0.148	-0.185	-0.098
(S) Arthropods (TZ)	-0.210	0.004	-0.301	-0.194	-0.294

					C
	(H') Plants (NA)	(J') Plants (NA)	(d) Plants (NA)	(Ď) Plants (NA)	(S) Plants (NA)
(H') Arthropods (NA)	-0.202	-0.257	-0.183	-0.269	-0.132
(J') Arthropods (NA)	0.148	-0.238	0.208	0.136	0.224
(d) Arthropods (NA)	-0.208	-0.169	-0.203	-0.267	-0.162
(Ď) Arthropods (NA)	0.005	-0.312	0.052	-0.046	0.095
(S) Arthropods (NA)	-0.201	-0.105	-0.210	-0.260	-0.177

		D
	(S) Plants (-150 m)	(H') Plants (-150 m)
(S) Arthropods (-150 m)	0.411	
(J') Arthropods (-150 m)	-0.497	-0.437

8.2 Discussion

Correlations between plants and arthropods of the entire dataset (table 8.1) indicate that the most important relationship existed between species richness (S) for plants and the Margalef Species Richness Index (d) for arthropods. In this case, arthropod species richness tended to increase with increasing plant species richness. Therefore, an increase in the variety of species within plant communties resulted in higher arthropod alpha diversity. This agrees with the results of Toft *et al.* (2001), Caballero-López *et al.* (2010), Hawkins and Porter (2003) and Siemann *et al.* (1998) who reported arthropod diversity to be positively correlated with plant diversity (discussed in chapter 2.6). Also, Haddad *et al.* (2009) illustrated in a decade long experiment of manipulated grassland plant species richness that arthropod species richness is positively correlated with plant species richness. Predator and parasitoid species richness also increased with increased herbivore diversity. They argued that the loss of plant species diversity is likely to result in the loss of arthropod species richness as well. However, Siemann *et al.* (1998) found the relationships of plants and arthropods to be generally weak, which was also the finding of this study. Siemann *et al.* (1998) attributed this to interspecific interactions of trophic groups. Also, the results in table 8.1 indicated that arthropod diversity and richness also tended to increase with increasing plant species evenness. This illustrates that less disturbed plant communities may lead to higher arthropod alpha diversity. These findings may be explained by the resource rarity hypothesis (chapter 2.6), which states that an increase in the abundance of rare resources will enable more consumers to exist in the habitat, and therefore increase their abundance (Abrams, 1995). Therefore, plant communities that tend to have fewer plant species (disturbed environment) will probably be able to support fewer arthropod species. Studies done by authors such as Murdoch *et al.* (1972) and Murdoch (1975) also found a positive correlation between plant species evenness and arthropod diversity. Furthermore, Wilsey and Potvin (2000) found that plant productivity and above-ground biomass of plant species were positively correlated with plant species evenness. These factors may therefore increase arthropod diversity and richness as well, since increased plant productivity and biomass (increased food resources and habitat) have been shown to increase arthropod diversity and richness (Siemann, 1998).

Comparisons of plant and arthropod diversity between plots at similar distances along the MAFFMAG (table 8.2 D) revealed that increased plant species diversity and richness resulted in increased arthropod species richness at -150 m within the maize field. Since the nature of crop fields often renders them impoverished in terms of arthropod habitat and food sources (Tivy, 1990), this is likely to decrease the diversity and richness of arthropod communities in these environments. On the other hand, increases in plant diversity inside crop fields, such as increases in weed species, is likely to result in increased arthropod species richness, as each new plant species potentially represents an extra resource that can be utilised by a new arthropod species. As mentioned in chapter 2.3, increased plant species diversity has been shown to increase arthropod diversity in agro-ecosystems (Denys & Tscharntke, 2002; Schellhorn & Sork, 1997; Cardinale *et al.*, 2003).

However, increased plant species richness at -150 m also resulted in increased arthropod species dominance. This was unexpected as it is commonly argued that increases in plant species richness should decrease the tendency for arthropod pests to become dominant (Gurr *et al.*, 2012). However, it is possible that an increase in plant species may be beneficial only to certain arthropod pests, such as aphids (Hemiptera: Aphididae), which may use the new plant cover as hosts and hiding places from predators. The efficiency of locating prey by predator may be compromised by increased plant density or patchiness in diverse agricultural systems (Sheehan, 1986). Also, it has been shown by Legrand and Barbosa (2003) that the efficiency of adult ladybirds (*Coccinella septempunctata* (Coleoptera, Coccinellidae) in predating pea aphids (*Acyrthosiphon pisumaphids*) (Hemiptera: Aphididae), was compromised by an increase in vegetational complexity. Also, a study by De Deyn *et al.* (2004) indicated that plant identity is more likely to influence nematode diversity than plant species diversity or richness *per se*. Therefore, some plant species have the potential to house more nematode species than others, and an increase in diversity of a specific plant group may cause an increase of already abundant taxa and a decrease of less abundant taxa. They also indicated that primary consumers and decomposers were more severely affected by differences in plant diversity and species composition than higher trophic groups such as carnivores and omnivores. It is possible that arthropods may react in a similar way in response to changes in plant species. However, from this study the exact cause of the negative relationships cannot be provided and further research is required to explain these results.

From these comparisons between plots at similar distances it seems that the significant positive relationship between plant and arthropod species richness, as was found at -150 m, was not found at any of the other distances either in the maize field or in the field margin. It is possible that the positive relationship between plant and arthropod species richness has a threshold point. As plant diversity increases, arthropod diversity also increase until a point is reached where further increases in plant diversity may not have further effects on arthropod diversity. If this is true, the plant diversity levels of the field margin are likely to be beyond this threshold.

Considering all the results for Spearman's Rank Order Correlations, it seems that the overall tendency is for arthropod species diversity, evenness and richness to be unrelated to plant diversity, evenness and richness. This contradicts our hypothesis that arthropod diversity ought to depend on plant diversity. However, as mentioned in chapter 2.6, arthropod diversity may not always be a simple function of plant diversity and may depend on a number of complex factors such as plant architecture (Stinson & Brown, 1983), plant productivity (Siemann, 1998) and the chemical complexity of the plant community (Randlkofer *et al.*, 2010). Also, it has been shown by Wenninger and Inouye (2008) that arthropod diversity may depend on moisture content as well as plant diversity, especially during dry periods. Therefore, irrigation patterns may have influenced arthropod diversity in and around maize fields. However, as these elements have not been considered in this study, further research will be required to confirm the effects of these factors. Alternatively, the lack of plant-arthropod diversity relationships may have been artificial results caused by difficulties in sampling highly mobile arthropods or the subjective process of classifying arthropods into morphospecies rather than true species. Possibly, relationships may also exist between plant and arthropod functional groups and will be tested in future studies.

Chapter 9: Summary, conclusions and recommendations

This study described for the first time the plant and arthropod species composition and diversity patterns along a maize field-field margin gradient (MAFFMAG) in two different biomes across South Africa. Overall, the results indicated that the patterns of arthropod diversity, richness and species composition followed similar trends for MAFFMAGs across South Africa. Furthermore, it seems that the grassland and savanna biomes followed different trends along the MAFFMAG in terms of plant species diversity and richness. Nevertheless, biodiversity was constantly found to be lower inside maize fields than in field margins, which confirms the first hypothesis that diversity of plants and associated arthropods should be higher in field margins than in maize fields. However, from the results it seems that the field margin diversity is not significantly affected by the presence of the maize fields, as the tension zone did not have significantly lower plant and arthropod diversity values than the natural area. This effect was consistent across localities and biomes and therefore, our second hypothesis, stating that the tension zone should have lower plant and arthropod diversity than the natural area, is rejected.

In addition to biodiversity patterns, this study also described the species assemblages of plants and arthropods in maize agro-ecosystems of South Africa. Overall, the species assemblage patterns for plants and arthropods was in accord with the results for the diversity patterns, with distinct communities in maize fields and field margins, but little difference in species composition between the tension zone and natural area in the field margin. Therefore, there seems to be no detectable effect of the presence of maize fields on either the diversity or species composition of plant and arthropod communities in the field margin.

These results indicate that crop field margins are not merely disturbed, non-functional ecosystems but are surprisingly rich in plant and arthropod diversity. Therefore, these sites may be of real conservation value in the agricultural landscape, especially since an increasing portion of arable land is being transformed into crop agro-ecosystems. In future it may be useful to survey sites closer to maize fields to determine the distance at which significant impacts on plant and arthropod communities do occur, if at all. Ultimately, this could aid in determining optimal sizes of field margins to be of conservation value.

This study also tested the dependence of arthropod species diversity on plant species diversity. Mostly, correlations between plant and arthropod diversity were not significant or generally weak. Therefore, these results indicate that arthropod diversity were overall not strongly dependent on plant diversity *per se*, but may be determined by other factors. The third hypothesis regarding a general positive relationship between plant and arthropod diversity is therefore also rejected. Furthermore, it was proposed that the multi-layered vegetation structure of the savanna biome should enable it to contain a higher plant and arthropod diversity than the grassland biome. However, comparisons between the grassland and savanna biomes revealed that no measurable difference could be found in terms of plant and arthropod species diversity, and therefore this hypothesis is also rejected.

Analyses on plant and arthropod species compositions across MAFFMAGs indicated that arthropod communities does seem to be defined by the biome in which they are found, if not as clearly as for plant communities. Plant species assemblages were however better defined than arthropod species assemblages, and this agrees with the Proches-Cowling hypothesis on arthropod assemblages across biomes.

This study provided baseline data on the plant and arthropod species associated with maize agro-ecosystems in South Africa within one specific time frame. However, it may be necessary to conduct further studies over time to identify and monitor priority species. Also, this study sought to describe the plant and arthropod diversity of maize fields in general and did not rely on specific characteristics associated with individual maize fields such as management practices, size, and environmental factors. Since these factors are likely to influence the distribution of plants and arthropods, further research in this regard is sensible. Further studies may determine the diversity patterns in commercial as opposed to subsistence farms, Bt- and non-Bt maize and irrigated opposed to non-irrigated fields. It may also be necessary to take into account other gradients that may be present such as slope, moisture and soil characteristics. One particular difficulty regarding this study and which may have caused artificial results involved the classification method of the arthropods. The classification into morphospecies is an extremely subjective process, and other methods for assessing arthropod diversity, for instance by using indicator species, may be a more useful and rapid monitoring technique.

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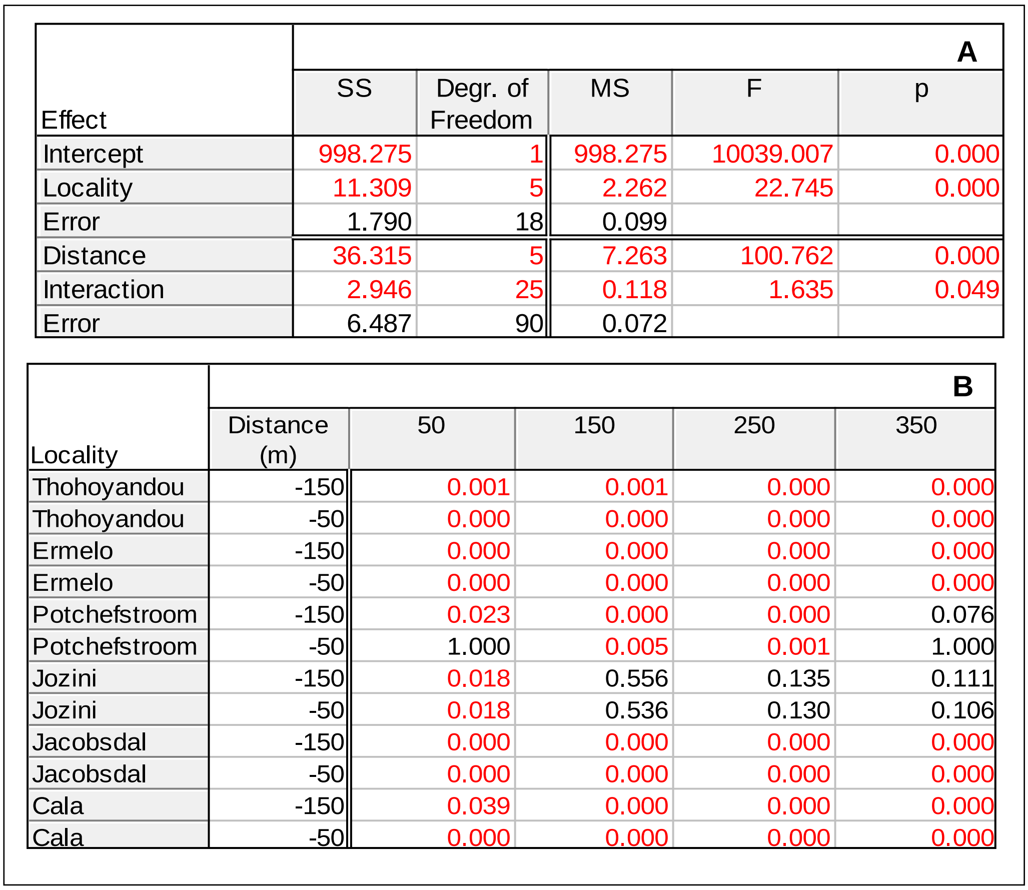
Appendix A

11.1. Tables for plant species diversity patterns along the MAFFMAG between localities

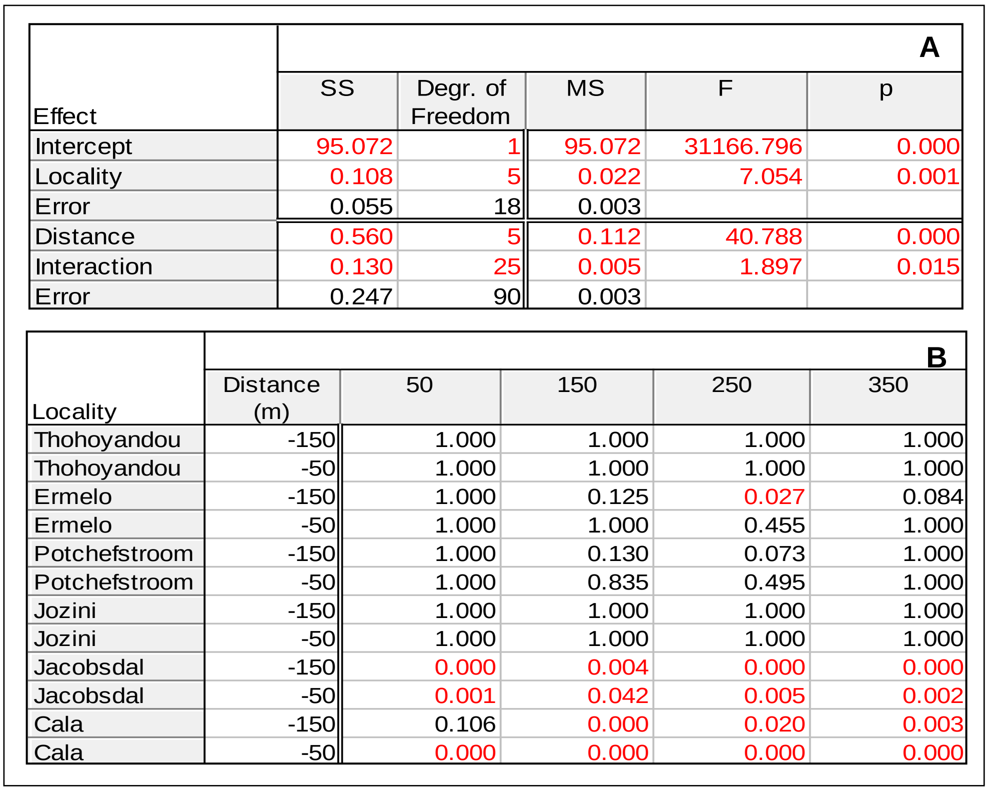
Table 11.1.1: Results of (A) Repeated Measures ANOVA and (B) summary of significant variation found in the Post-hoc test for the **Shannon-Wiener Diversity Index.** Values in red indicate significant differences in plant diversity between distances from maize fields and between six localities as well as interactions (locality x distance) (n=4; $p<0.05$). SS = sum of squares; MS = mean sum of squares; F = significance of F value; p = significance of p-value. -150, -50 m = maize field; 50, 150 m = tension zone; 250, 350 m = natural area.



					A
Effect	SS	Degr. of Freedom	MS	F	p
Intercept	998.275	1	998.275	10039.007	0.000
Locality	11.309	5	2.262	22.745	0.000
Error	1.790	18	0.099		
Distance	36.315	5	7.263	100.762	0.000
Interaction	2.946	25	0.118	1.635	0.049
Error	6.487	90	0.072		

					B
Locality	Distance (m)	50	150	250	350
Thohoyandou	-150	0.001	0.001	0.000	0.000
Thohoyandou	-50	0.000	0.000	0.000	0.000
Ermelo	-150	0.000	0.000	0.000	0.000
Ermelo	-50	0.000	0.000	0.000	0.000
Potchefstroom	-150	0.023	0.000	0.000	0.076
Potchefstroom	-50	1.000	0.005	0.001	1.000
Jozini	-150	0.018	0.556	0.135	0.111
Jozini	-50	0.018	0.536	0.130	0.106
Jacobsdal	-150	0.000	0.000	0.000	0.000
Jacobsdal	-50	0.000	0.000	0.000	0.000
Cala	-150	0.039	0.000	0.000	0.000
Cala	-50	0.000	0.000	0.000	0.000

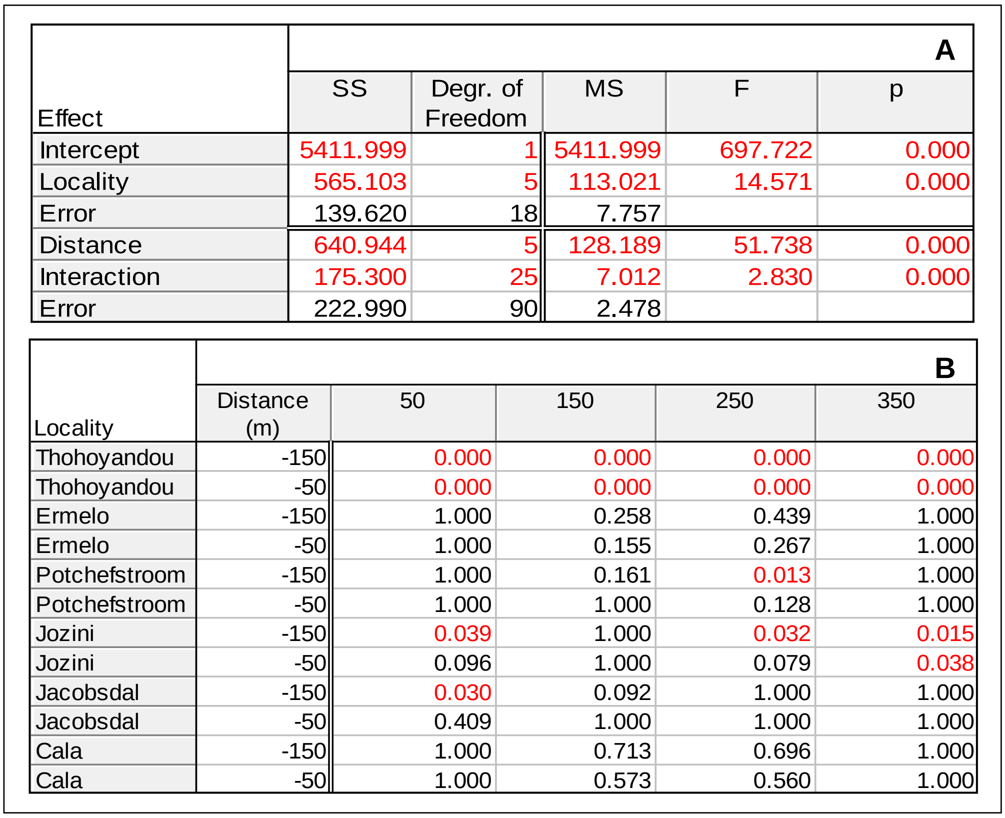
Table 11.1.2: Results of (A) Repeated Measures Analysis of Variance (ANOVA) and (B) summary of significant variation found in the Post-hoc test for **Pielou's Evenness**. Values in red indicate significant differences in plant diversity between distances from maize fields and between six localities as well as interactions (locality x distance) (n=4; p<0.05). SS = sum of squares; MS = mean sum of squares; F = significance of F value; p = significance of p-value. -150, -50 m = maize field; 50, 150 m = tension zone; 250, 350 m = natural area.



					A
Effect	SS	Degr. of Freedom	MS	F	p
Intercept	95.072	1	95.072	31166.796	0.000
Locality	0.108	5	0.022	7.054	0.001
Error	0.055	18	0.003		
Distance	0.560	5	0.112	40.788	0.000
Interaction	0.130	25	0.005	1.897	0.015
Error	0.247	90	0.003		

					B
Locality	Distance (m)	50	150	250	350
Thohoyandou	-150	1.000	1.000	1.000	1.000
Thohoyandou	-50	1.000	1.000	1.000	1.000
Ermelo	-150	1.000	0.125	0.027	0.084
Ermelo	-50	1.000	1.000	0.455	1.000
Potchefstroom	-150	1.000	0.130	0.073	1.000
Potchefstroom	-50	1.000	0.835	0.495	1.000
Jozini	-150	1.000	1.000	1.000	1.000
Jozini	-50	1.000	1.000	1.000	1.000
Jacobsdal	-150	0.000	0.004	0.000	0.000
Jacobsdal	-50	0.001	0.042	0.005	0.002
Cala	-150	0.106	0.000	0.020	0.003
Cala	-50	0.000	0.000	0.000	0.000

Table 11.1.3: Results of (A) Repeated Measures Analysis of Variance (ANOVA) and (B) summary of significant variation found in the Post-hoc test for **Margalef's Species Richness**. Values in red indicate significant differences in plant diversity between distances from maize fields and between six localities as well as interactions (locality x distance) (n=4; p<0.05). SS = sum of squares; MS = mean sum of squares; F = significance of F value; p = significance of p-value. -150, -50 m = maize field; 50, 150 m = tension zone; 250, 350 m = natural area.



					A
Effect	SS	Degr. of Freedom	MS	F	p
Intercept	5411.999	1	5411.999	697.722	0.000
Locality	565.103	5	113.021	14.571	0.000
Error	139.620	18	7.757		
Distance	640.944	5	128.189	51.738	0.000
Interaction	175.300	25	7.012	2.830	0.000
Error	222.990	90	2.478		

					B
Locality	Distance (m)	50	150	250	350
Thohoyandou	-150	0.000	0.000	0.000	0.000
Thohoyandou	-50	0.000	0.000	0.000	0.000
Ermelo	-150	1.000	0.258	0.439	1.000
Ermelo	-50	1.000	0.155	0.267	1.000
Potchefstroom	-150	1.000	0.161	0.013	1.000
Potchefstroom	-50	1.000	1.000	0.128	1.000
Jozini	-150	0.039	1.000	0.032	0.015
Jozini	-50	0.096	1.000	0.079	0.038
Jacobsdal	-150	0.030	0.092	1.000	1.000
Jacobsdal	-50	0.409	1.000	1.000	1.000
Cala	-150	1.000	0.713	0.696	1.000
Cala	-50	1.000	0.573	0.560	1.000

Table 11.1.4: Results of (A) Repeated Measures Analysis of Variance (ANOVA) and (B) summary of significant variation found in the Post-hoc test for **Simpson's Diversity Index**. Values in red indicate significant differences in plant diversity between distances from maize fields and between six localities as well as interactions (locality x distance) (n=4; p<0.05). SS = sum of squares; MS = mean sum of squares; F = significance of F value; p = significance of p-value. -150, -50m = maize field; 50, 150 m = tension zone; 250, 350 m = natural area.

					A
Effect	SS	Degr. of Freedom	MS	F	p
Intercept	111.595	1	111.595	65434.14	0.000
Locality	0.265	5	0.053	31.12	0.000
Error	0.031	18	0.002		
Distance	0.837	5	0.167	80.22	0.000
Interaction	0.192	25	0.008	3.68	0.000
Error	0.188	90	0.002		

				B
Distance (m)	50	150	250	350
-150	0.000	0.000	0.000	0.000
-50	0.000	0.000	0.000	0.000

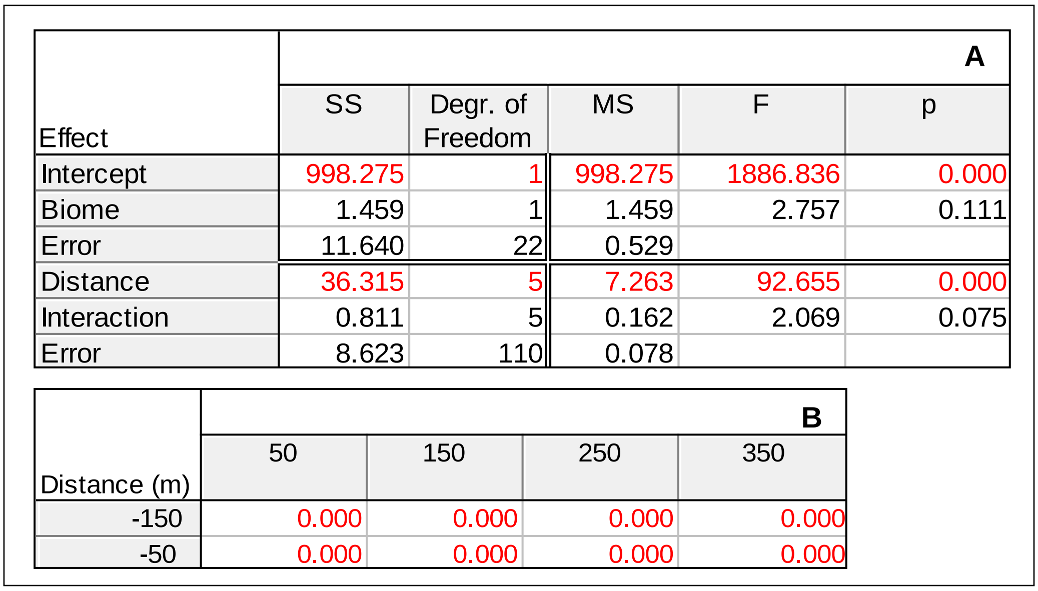
Table 11.1.5: Results of (A) Repeated Measures Analysis of Variance (ANOVA) and (B) summary of significant variation found in the Post-hoc test for **plant species richness**. Values in red indicate significant differences in plant richness between distances from maize fields and between six localities as well as interactions (locality x distance) (n=4; p<0.05). SS = sum of squares; MS = mean sum of squares; F = significance of F value; p = significance of p-value. -150, -50 m = maize field; 50, 150 m = tension zone; 250, 350 m = natural area.

					A
Effect	SS	Degr. of Freedom	MS	F	p
Intercept	112672.1	1	112672.1	1882.662	0.000
Locality	8459.0	5	1691.8	28.269	0.000
Error	1077.2	18	59.8		
Distance	11842.7	5	2368.5	69.351	0.000
Interaction	2357.2	25	94.3	2.761	0.000
Error	3073.7	90	34.2		

					B
Location	Distance (m)	50	150	250	350
Thohoyandou	-150	0.000	0.000	0.000	0.000
Thohoyandou	-50	0.000	0.000	0.000	0.000
Ermelo	-150	0.801	0.018	0.022	0.196
Ermelo	-50	0.444	0.009	0.011	0.104
Potchefstroom	-150	0.542	0.022	0.003	1.000
Potchefstroom	-50	1.000	0.296	0.054	1.000
Jozini	-150	0.035	1.000	0.043	0.014
Jozini	-50	0.129	1.000	0.159	0.054
Jacobsdal	-150	0.000	0.001	0.296	0.067
Jacobsdal	-50	0.003	0.018	1.000	1.000
Cala	-150	1.000	0.018	0.018	0.296
Cala	-50	1.000	0.018	0.018	0.296

11.2. Tables for plant species diversity patterns along MAFFMAGs between biomes

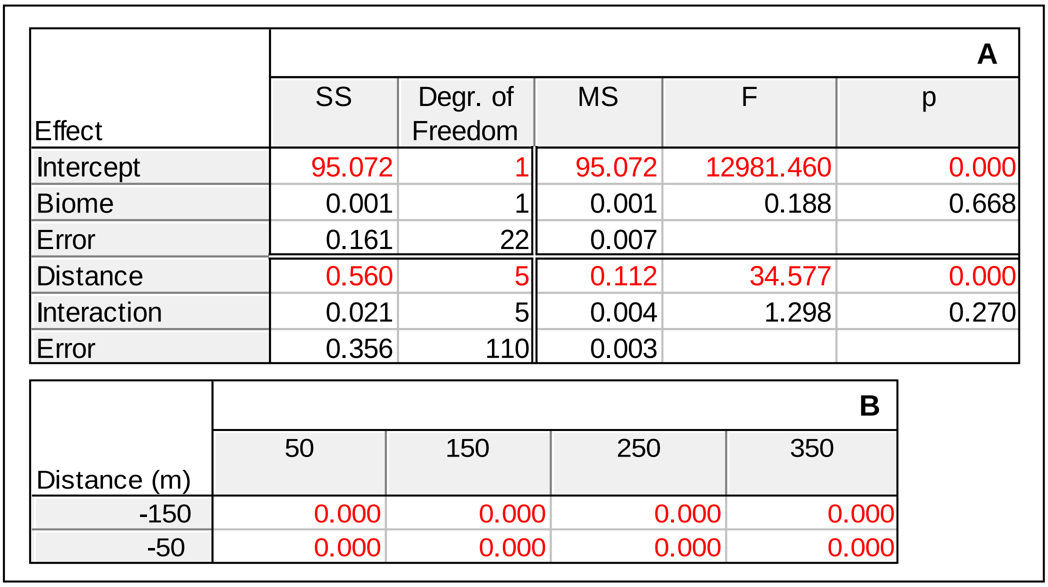
Table 11.2.1: Results of (A) Repeated Measures Analysis of Variance (ANOVA) and (B) summary of significant variation found in the Post-hoc test for the **Shannon-Wiener Diversity Index**. Values in red indicate significant differences in plant diversity between distances from maize fields and between biomes as well as interactions (biome x distance) (n=12; p<0.05). SS = sum of squares; MS = mean sum of squares; F = significance of F value; p = significance of p-value. -150, -50 m = maize field; 50, 150 m = tension zone; 250, 350 m = natural area.



					A
Effect	SS	Degr. of Freedom	MS	F	p
Intercept	998.275	1	998.275	1886.836	0.000
Biome	1.459	1	1.459	2.757	0.111
Error	11.640	22	0.529		
Distance	36.315	5	7.263	92.655	0.000
Interaction	0.811	5	0.162	2.069	0.075
Error	8.623	110	0.078		

				B
Distance (m)	50	150	250	350
-150	0.000	0.000	0.000	0.000
-50	0.000	0.000	0.000	0.000

Table 11.2.2: Results of (A) Repeated Measures Analysis of Variance (ANOVA) and (B) summary of significant variation found in the Post-hoc test for **Pielou's Evenness**. Values in red indicate significant differences in plant diversity between distances from maize fields and between biomes as well as interactions (biome x distance) (n=12; p<0.05). SS = sum of squares; MS = mean sum of squares; F = significance of F value; p = significance of p-value. -150, -50 m = maize field; 50, 150 m = tension zone; 250, 350 m = natural area.



					A
Effect	SS	Degr. of Freedom	MS	F	p
Intercept	95.072	1	95.072	12981.460	0.000
Biome	0.001	1	0.001	0.188	0.668
Error	0.161	22	0.007		
Distance	0.560	5	0.112	34.577	0.000
Interaction	0.021	5	0.004	1.298	0.270
Error	0.356	110	0.003		

				B
Distance (m)	50	150	250	350
-150	0.000	0.000	0.000	0.000
-50	0.000	0.000	0.000	0.000

Table 11.2.3: Results of (A) Repeated Measures Analysis of Variance (ANOVA) and (B) summary of significant variation found in the Post-hoc test for **Margalef's Species Richness Index**. Values in red indicate significant differences in plant diversity between distances from maize fields and between biomes as well as interactions (biome x distance) (n=12; p<0.05). SS = sum of squares; MS = mean sum of squares; F = significance of F value; p = significance of p-value. -150, -50 m = maize field; 50, 150 m = tension zone; 250, 350 m = natural area.

A

Effect	SS	Degr. of Freedom	MS	F	p
Intercept	5411.999	1	5411.999	208.720	0.000
Biome	134.274	1	134.274	5.178	0.033
Error	570.449	22	25.929		
Distance	640.944	5	128.189	41.313	0.000
Interaction	56.977	5	11.395	3.673	0.004
Error	341.314	110	3.103		

B

Biome	Distance (m)	50	150	250	350
Savanna	-150	0.000	0.000	0.000	0.000
Savanna	-50	0.000	0.000	0.000	0.000
Grassland	-150	0.021	0.000	0.000	0.004
Grassland	-50	0.044	0.000	0.000	0.010

Table 11.2.4: Results of (A) Repeated Measures Analysis of Variance (ANOVA) and (B) summary of significant variation found in the Post-hoc test for **Simpson's Diversity Index**. Values in red indicate significant differences in plant diversity between distances from maize fields and between biomes as well as interactions (biome x distance) (n=12; p<0.05). SS = sum of squares; MS = mean sum of squares; F = significance of F value; p = significance of p-value. -150, -50 m = maize field; 50, 150 m = tension zone; 250, 350 m = natural area.

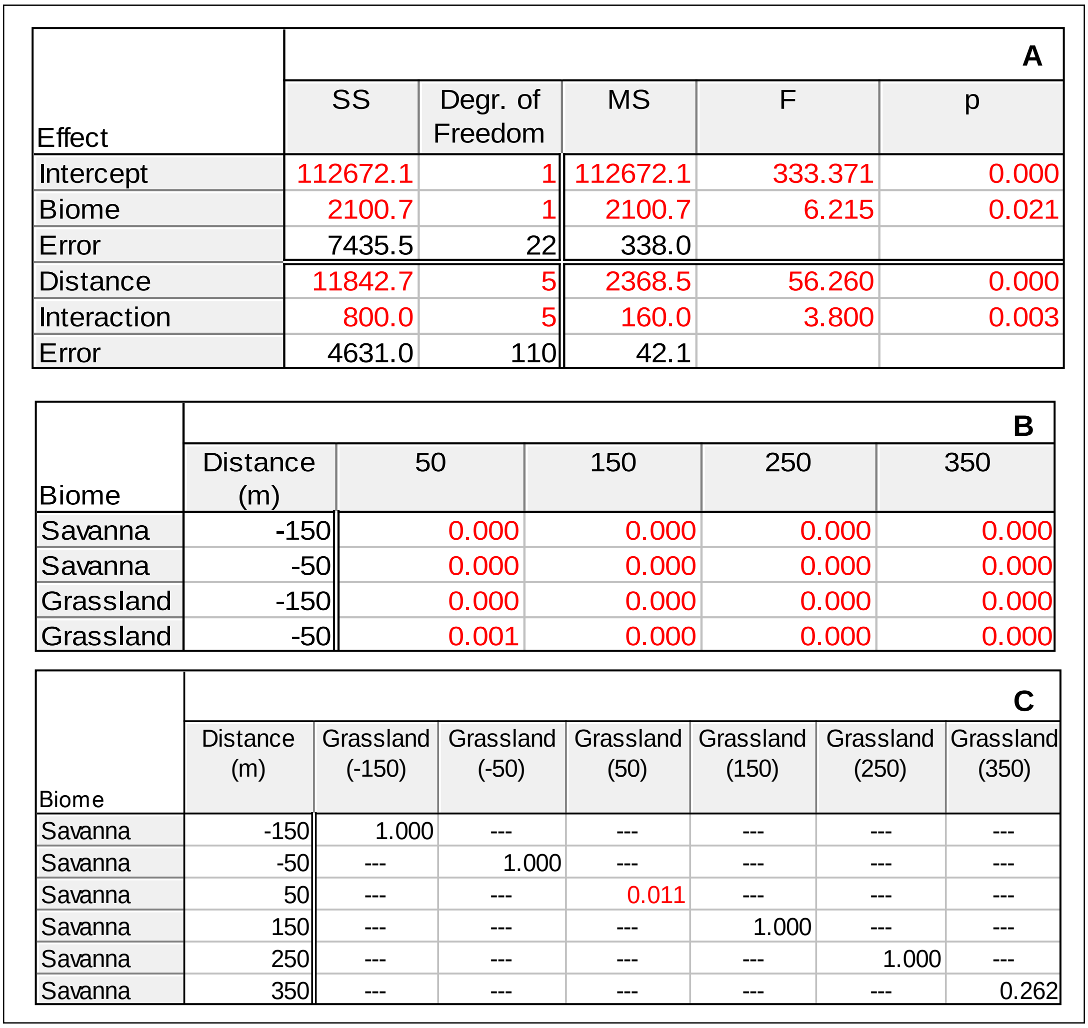
A

Effect	SS	Degr. of Freedom	MS	F	p
Intercept	111.595	1	111.595	8577.160	0.000
Biome	0.010	1	0.010	0.753	0.395
Error	0.286	22	0.013		
Distance	0.837	5	0.167	50.738	0.000
Interaction	0.017	5	0.003	1.009	0.416
Error	0.363	110	0.003		

B

Distance (m)	50	150	250	350
-150	0.000	0.000	0.000	0.000
-50	0.000	0.000	0.000	0.000

Table 11.2.5: Results of (A) Repeated Measures Analysis of Variance (ANOVA) and (B) summary of significant variation found in the Post-hoc test for **plant species richness**. Values in red indicate significant differences in plant richness between distances from maize fields and between biomes as well as interactions (biome x distance) (n=12; p<0.05). SS = sum of squares; MS = mean sum of squares; F = significance of F value; p = significance of p-value -150, -50 m = maize field; 50, 150 m = tension zone; 250, 350 m = natural area.



					A
Effect	SS	Degr. of Freedom	MS	F	p
Intercept	112672.1	1	112672.1	333.371	0.000
Biome	2100.7	1	2100.7	6.215	0.021
Error	7435.5	22	338.0		
Distance	11842.7	5	2368.5	56.260	0.000
Interaction	800.0	5	160.0	3.800	0.003
Error	4631.0	110	42.1		

					B
Biome	Distance (m)	50	150	250	350
Savanna	-150	0.000	0.000	0.000	0.000
Savanna	-50	0.000	0.000	0.000	0.000
Grassland	-150	0.000	0.000	0.000	0.000
Grassland	-50	0.001	0.000	0.000	0.000

							C
Biome	Distance (m)	Grassland (-150)	Grassland (-50)	Grassland (50)	Grassland (150)	Grassland (250)	Grassland (350)
Savanna	-150	1.000	---	---	---	---	---
Savanna	-50	---	1.000	---	---	---	---
Savanna	50	---	---	0.011	---	---	---
Savanna	150	---	---	---	1.000	---	---
Savanna	250	---	---	---	---	1.000	---
Savanna	350	---	---	---	---	---	0.262

11.3. Tables for arthropod species diversity patterns along the MAFFMAG between localities

Table 11.3.1: Results of (A) Repeated Measures Analysis of Variance (ANOVA) and (B) summary of significant variation found in the Post-hoc test for the **Shannon-Wiener Diversity Index.** Values in red indicate significant differences in arthropod diversity between distances from maize fields and between six localities as well as interactions (locality x distance) (n=4; p<0.05). SS = sum of squares; MS = mean sum of squares; F = significance of F value; p = significance of p-value. -150, -50 m = maize field; 50, 150 m = tension zone; 250, 350 m = natural area.

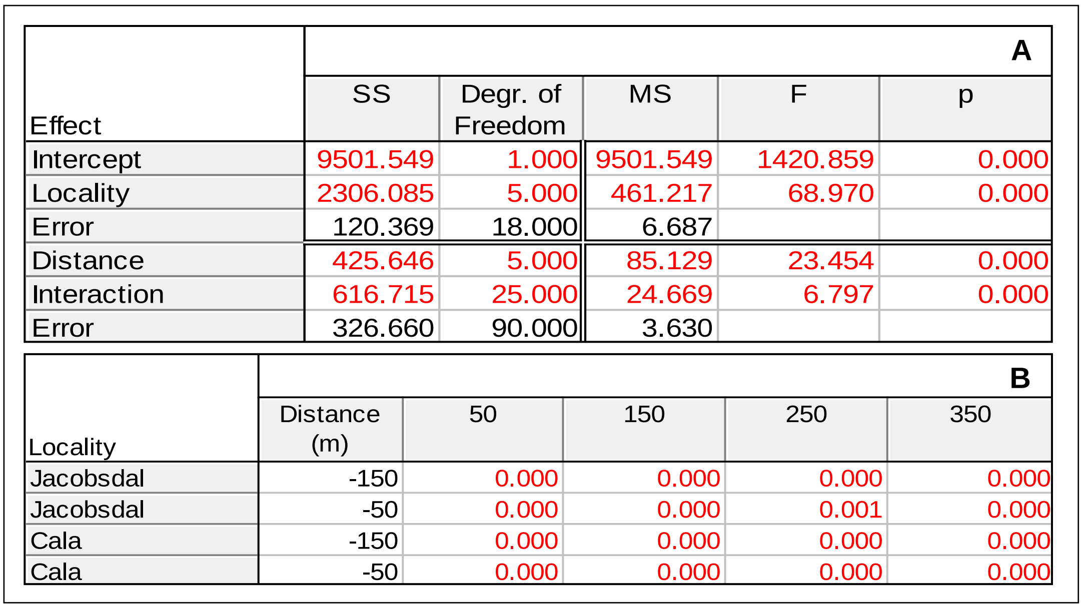
					A
Effect	SS	Degr. of Freedom	MS	F	p
Intercept	1154.816	1.000	1154.816	5924.948	0.000
Locality	16.130	5.000	3.226	16.551	0.000
Error	3.508	18.000	0.195		
Distance	8.230	5.000	1.646	7.075	0.000
Interaction	8.413	25.000	0.337	1.446	0.106
Error	20.939	90.000	0.233		

				B
Distance (m)	50	150	250	350
-150	0.002	0.659	0.026	0.001
-50	0.003	0.987	0.045	0.001

Table 11.3.2: Results of Repeated Measures Analysis of Variance (ANOVA) for **Pielou's Evenness Index**. Values in red indicate significant differences in arthropod diversity between distances from maize fields and between six localities as well as interactions (locality x distance) (n=4; p<0.05). SS = sum of squares; MS = mean sum of squares; F = significance of F value; p = significance of p-value. -150, -50 m = maize field; 50, 150 m = tension zone; 250, 350 m = natural area.

Effect	SS	Degr. of Freedom	MS	F	p
Intercept	102.625	1.000	102.625	9442.959	0.000
Locality	0.461	5.000	0.092	8.485	0.000
Error	0.196	18.000	0.011		
Distance	0.033	5.000	0.007	0.626	0.680
Interaction	0.178	25.000	0.007	0.674	0.869
Error	0.950	90.000	0.011		

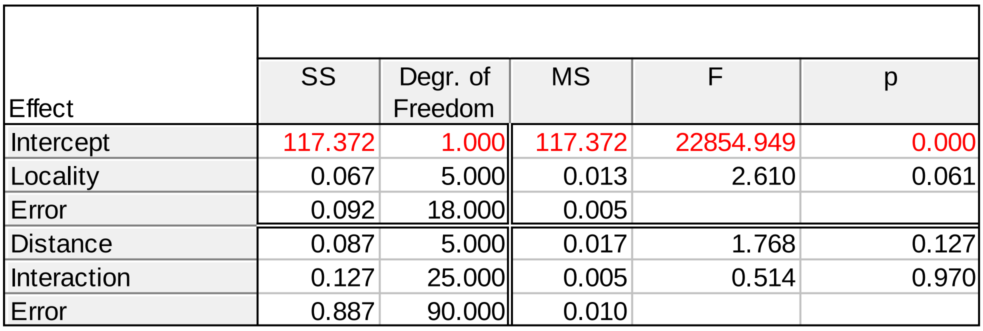
Table 11.3.3: Results of (A) Repeated Measures Analysis of Variance (ANOVA) and (B) summary of significant variation found in the Post-hoc test for **Margalef's Species Richness Index**. Values in red indicate significant differences in arthropod diversity between distances from maize fields and between six localities as well as interactions (locality x distance) (n=4; p<0.05). SS = sum of squares; MS = mean sum of squares; F = significance of F value; p = significance of p-value. -150, -50 m = maize field; 50, 150 m = tension zone; 250, 350 m = natural area.



					A
Effect	SS	Degr. of Freedom	MS	F	p
Intercept	9501.549	1.000	9501.549	1420.859	0.000
Locality	2306.085	5.000	461.217	68.970	0.000
Error	120.369	18.000	6.687		
Distance	425.646	5.000	85.129	23.454	0.000
Interaction	616.715	25.000	24.669	6.797	0.000
Error	326.660	90.000	3.630		

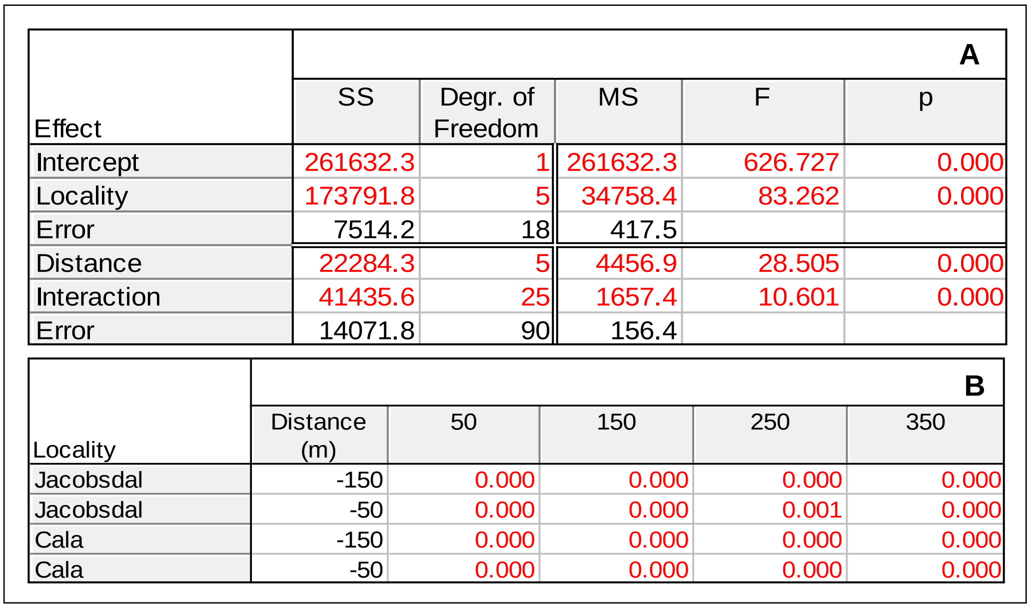
					B
Locality	Distance (m)	50	150	250	350
Jacobsdal	-150	0.000	0.000	0.000	0.000
Jacobsdal	-50	0.000	0.000	0.001	0.000
Cala	-150	0.000	0.000	0.000	0.000
Cala	-50	0.000	0.000	0.000	0.000

Table 11.3.4: Results of Repeated Measures Analysis of Variance (ANOVA) for **Simpson's Diversity Index**. Values in red indicate significant differences in arthropod diversity between distances from maize fields and between six localities as well as interactions (locality x distance) (n=4; p<0.05). SS = sum of squares; MS = mean sum of squares; F = significance of F value; p = significance of p-value. -150, -50 m = maize field; 50, 150 m = tension zone; 250, 350 m = natural area.



Effect	SS	Degr. of Freedom	MS	F	p
Intercept	117.372	1.000	117.372	22854.949	0.000
Locality	0.067	5.000	0.013	2.610	0.061
Error	0.092	18.000	0.005		
Distance	0.087	5.000	0.017	1.768	0.127
Interaction	0.127	25.000	0.005	0.514	0.970
Error	0.887	90.000	0.010		

Table 11.3.5: Results of (A) Repeated Measures Analysis of Variance (ANOVA) and (B) summary of significant variation found in the Post-hoc test for **arthropod species richness**. Values in red indicate significant differences in arthropod richness between distances from maize fields and between six localities as well as interactions (locality x distance) (n=4; p<0.05). SS = sum of squares; MS = mean sum of squares; F = significance of F value; p = significance of p-value. -150, -50 m = maize field; 50, 150 m = tension zone; 250, 350 m = natural area.

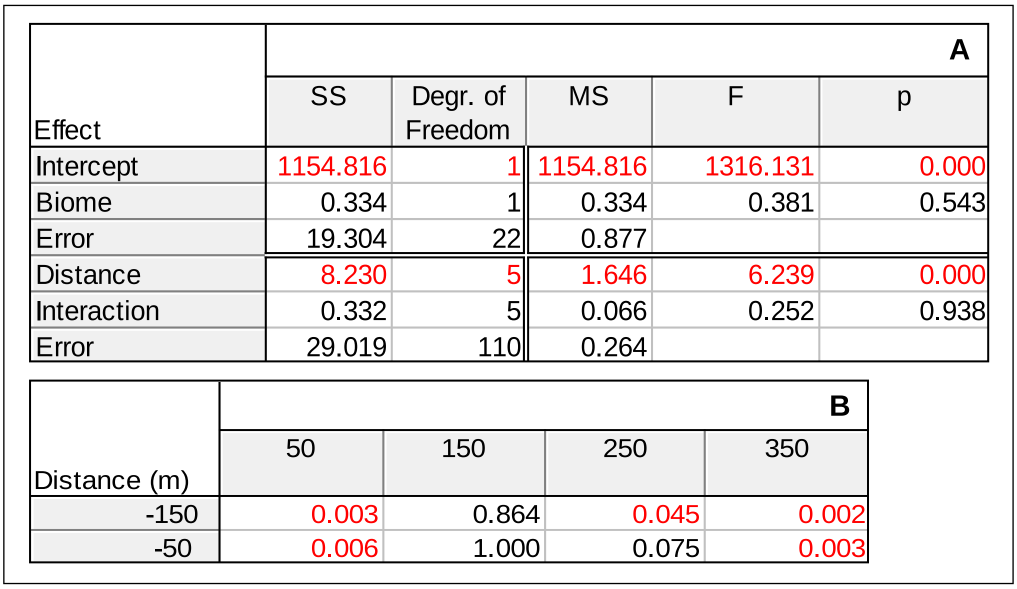


Effect	SS	Degr. of Freedom	MS	F	p
					A
Intercept	261632.3	1	261632.3	626.727	0.000
Locality	173791.8	5	34758.4	83.262	0.000
Error	7514.2	18	417.5		
Distance	22284.3	5	4456.9	28.505	0.000
Interaction	41435.6	25	1657.4	10.601	0.000
Error	14071.8	90	156.4		

Locality	Distance (m)	50	150	250	350
					B
Jacobsdal	-150	0.000	0.000	0.000	0.000
Jacobsdal	-50	0.000	0.000	0.001	0.000
Cala	-150	0.000	0.000	0.000	0.000
Cala	-50	0.000	0.000	0.000	0.000

11.4. Tables for arthropod species diversity patterns along the MAFFMAG between biomes

Table 11.4.1: Results of (A) Repeated Measures Analysis of Variance (ANOVA) and (B) summary of significant variation found in the Post-hoc test for the **Shannon-Wiener Diversity Index**. Values in red indicate significant differences in arthropod diversity between distances from maize fields and between biomes as well as interactions (biome x distance) (n=12; p<0.05). SS = sum of squares; MS = mean sum of squares; F = significance of F value; p = significance of p-value. -150, -50 m = maize field; 50, 150 m = tension zone; 250, 350 m = natural area.



Effect	SS	Degr. of Freedom	MS	F	p
					A
Intercept	1154.816	1	1154.816	1316.131	0.000
Biome	0.334	1	0.334	0.381	0.543
Error	19.304	22	0.877		
Distance	8.230	5	1.646	6.239	0.000
Interaction	0.332	5	0.066	0.252	0.938
Error	29.019	110	0.264		

Distance (m)	50	150	250	350
				B
-150	0.003	0.864	0.045	0.002
-50	0.006	1.000	0.075	0.003

Table 11.4.2: Results of Repeated Measures Analysis of Variance (ANOVA) for **Pielou's Evenness**. Values in red indicate significant differences in arthropod diversity between distances from maize fields and between biomes as well as interactions (biome x distance) (n=12; p<0.05). SS = sum of squares; MS = mean sum of squares; F = significance of F value; p = significance of p-value -150, -50 m = maize field; 50, 150 m = tension zone; 250, 350 m = natural area.

Effect	SS	Degr. of Freedom	MS	F	p
Intercept	102.625	1	102.625	4030.243	0.000
Biome	0.097	1	0.097	3.790	0.064
Error	0.560	22	0.025		
Distance	0.033	5	0.007	0.658	0.656
Interaction	0.023	5	0.005	0.462	0.804
Error	1.105	110	0.010		

Table 11.4.3: Results of (A) Repeated Measures Analysis of Variance (ANOVA) and (B) summary of significant variation found in the Post-hoc test for **Margalef's Species Richness Index**. Values in red indicate significant differences in arthropod diversity between distances from maize fields and between biomes as well as interactions (biome x distance) (n=12; p<0.05). SS = sum of squares; MS = mean sum of squares; F = significance of F value; p = significance of p-value -150, -50 m = maize field; 50, 150 m = tension zone; 250, 350 m = natural area.

					A
Effect	SS	Degr. of Freedom	MS	F	p
Intercept	9501.549	1	9501.549	88.106	0.000
Biome	53.914	1	53.914	0.500	0.487
Error	2372.541	22	107.843		
Distance	425.646	5	85.129	10.223	0.000
Interaction	27.336	5	5.467	0.657	0.657
Error	916.039	110	8.328		

				B
Distance (m)	50	150	250	350
-150	0.000	0.005	0.005	0.000
-50	0.000	0.003	0.003	0.000

Table 11.4.4: Results of (A) Repeated Measures Analysis of Variance (ANOVA) and (B) summary of significant variation found in the Post-hoc test for **Simpson's Diversity Index**. Values in red indicate significant differences in arthropod diversity between distances from maize fields and between biomes as well as interactions (biome x distance) (n=12; p<0.05). SS = sum of squares; MS = mean sum of squares; F = significance of F value; p = significance of p-value -150, -50 m = maize field; 50, 150 m = tension zone; 250, 350 m = natural area.

A

Effect	SS	Degr. of Freedom	MS	F	p
Intercept	117.372	1	117.372	19746.054	0.000
Biome	0.029	1	0.029	4.825	0.039
Error	0.131	22	0.006		
Distance	0.087	5	0.017	1.921	0.096
Interaction	0.016	5	0.003	0.353	0.880
Error	0.997	110	0.009		

B

Biome	Savanna	Grassland
Savanna		0.039
Grassland	0.039	

Table 11.4.5: Results of (A) Repeated Measures Analysis of Variance (ANOVA) and (B) summary of significant variation found in the Post-hoc test for **arthropod species richness**. Values in red indicate significant differences in arthropod richness between distances from maize fields and between biomes as well as interactions (biome x distance) (n=12; p<0.05). SS = sum of squares; MS = mean sum of squares; F = significance of F value; p = significance of p-value -150, -50 m = maize field; 50, 150 m = tension zone; 250, 350 m = natural area.

A

Effect	SS	Degr. of Freedom	MS	F	p
Intercept	261632.3	1	261632.3	33.930	0.000
Biome	11664.0	1	11664.0	1.513	0.232
Error	169642.1	22	7711.0		
Distance	22284.3	5	4456.9	9.446	0.000
Interaction	3605.2	5	721.0	1.528	0.187
Error	51902.1	110	471.8		

B

Distance	50	150	250	350
-150	0.000	0.004	0.004	0.000
-50	0.000	0.003	0.003	0.000

Appendix B

Table 12.1: Results for SIMPER analyses indicating the average dissimilarity, contribution of each species to the average dissimilarity, cumulative percent contribution and average abundance per plot for the ten most important plant species responsible for NMDS groupings. (MG) = Maize field Grassland; (MS) = Maize field Savanna; (TG) = Tension zone Grassland; (TS) = Tension zone Savanna; (NG) = Natural area Grassland; (NS) = Natural area Savanna.

MG vs. MS	Avg. dissim.	Contrib. %	Cumulative %	MG agv.abund.	MS avg.abund.
Cyperus esculentus	10.85	11.87	11.87	12.6	0.75
Digitaria sanguinalis	4.698	5.14	17.01	4.04	4.38
Cyperus rotundus	4.391	4.804	21.81	2.75	3.29
Tagetes minuta	3.571	3.907	25.72	4.21	0.333
Cynodon dactylon	3.491	3.819	29.54	3.25	1.33
Eleusine coracana	3.449	3.773	33.31	3	1.13
Corchorus schimperi	2.895	3.168	36.48	0	2.63
Oxalis latifolia	2.531	2.769	39.25	2.54	0.375
Hibiscus trionum	2.46	2.692	41.94	1.46	1.58
Datura stramonium	2.151	2.353	44.3	1.67	1.21
Total dissim.: 91.4					
TG vs. TS	Avg. dissim.	Contrib. %	Cumulative %	TG agv.abund.	TS avg.abund.
Themeda triandra	4.549	4.659	4.659	10.3	1.58
Panicum maximum	2.879	2.949	7.608	0	6.71
Pentzia incana	2.581	2.644	10.25	0	5.21
Helichrysum rugulosum	2.366	2.423	12.68	5.38	0
Sporobolus africanus	2.109	2.161	14.84	4.75	0.167
Hyparrhenia hirta	1.848	1.892	16.73	4.17	0
Eragrostis plana	1.703	1.744	18.47	3.83	0
Panicum coloratum	1.654	1.695	20.17	0.25	3.46
Richardia brasiliensis	1.539	1.576	21.74	3.54	0
Eragrostis curvula	1.51	1.547	23.29	2.79	1.04
Total dissim.: 97.63					

NG vs. NS	Avg. dissim.	Contrib. %	Cumulative %	NG agv.abund.	NS avg.abund.
Panicum maximum	3.612	3.681	3.681	0	8.5
Themeda triandra	2.821	2.875	6.556	6.21	1.63
Pentzia incana	2.131	2.171	8.727	0	4.54
Eragrostis curvula	1.992	2.03	10.76	3.71	1.5
Eragrostis plana	1.78	1.814	12.57	4.04	0
Urochloa mosambicensis	1.628	1.659	14.23	0	3.63
Helichrysum rugulosum	1.585	1.615	15.84	3.63	0
Aristida adscensionis	1.584	1.614	17.46	0	3.29
Tragus berteronianus	1.58	1.61	19.07	0	3.29
Enneapogon desvauxii	1.543	1.572	20.64	0	3.29
Total dissim.: 98.3					

MG vs. TG	Avg. dissim.	Contrib. %	Cumulative %	MG agv.abund.	TG avg.abund.
Cyperus esculentus	8.005	8.116	8.116	12.6	0.0417
Themeda triandra	7.085	7.183	15.3	0	10.3
Helichrysum rugulosum	3.585	3.635	18.93	0	5.38
Sporobolus africanus	3.244	3.289	22.22	0.583	4.75
Hyparrhenia hirta	2.837	2.877	25.1	0.167	4.17
Tagetes minuta	2.687	2.724	27.82	4.21	0
Eragrostis plana	2.593	2.629	30.45	0	3.83
Digitaria sanguinalis	2.564	2.6	33.05	4.04	0
Cynodon dactylon	2.466	2.501	35.55	3.25	1
Richardia brasiliensis	2.364	2.397	37.95	0.208	3.54
Total dissim.: 98.62					

MG vs. NG	Avg. dissim.	Contrib. %	Cumulative %	MG agv.abund.	NG avg.abund.
Cyperus esculentus	7.934	8.029	8.029	12.6	0
Themeda triandra	4.107	4.156	12.19	0	6.21
Eragrostis plana	2.66	2.692	14.88	0	4.04
Tagetes minuta	2.659	2.691	17.57	4.21	0
Cynodon dactylon	2.565	2.596	20.16	3.25	1.29
Digitaria sanguinalis	2.538	2.568	22.73	4.04	0
Eragrostis curvula	2.438	2.468	25.2	0.0833	3.71
Helichrysum rugulosum	2.363	2.391	27.59	0	3.63
Eleusine coracana	2.133	2.158	29.75	3	0
Heteropogon contortus	2.049	2.074	31.82	0	3.17
Total dissim: 98.82					

TG vs. NG	Avg. dissim.	Contrib. %	Cumulative %	TG agv.abund.	NG avg.abund.
Themeda triandra	5.424	6.785	6.785	10.3	6.21
Sporobolus africanus	2.893	3.619	10.4	4.75	2.83
Helichrysum rugulosum	2.802	3.504	13.91	5.38	3.63
Hyparrhenia hirta	2.721	3.403	17.31	4.17	2.33
Richardia brasiliensis	2.245	2.808	20.12	3.54	1.79
Eragrostis plana	2.169	2.712	22.83	3.83	4.04
Heteropogon contortus	2.159	2.701	25.53	2.5	3.17
Eragrostis curvula	2.037	2.548	28.08	2.79	3.71
Tristachya leucothrix	1.917	2.397	30.48	2.08	2.38
Eragrostis racemosa	1.65	2.063	32.54	1.88	2.42
Total dissim.: 79.95					

MS vs. TS	Avg. dissim.	Contrib. %	Cumulative %	MS agv.abund.	TS avg.abund.
Panicum maximum	3.782	3.829	3.829	1.79	6.71
Pentzia incana	3.222	3.263	7.092	0	5.21
Digitaria sanguinalis	2.18	2.207	9.299	4.38	0
Panicum coloratum	2.011	2.036	11.34	0	3.46
Dicrostachys cinerea	1.791	1.813	13.15	0	3.42
Acacia tortilis	1.758	1.78	14.93	0	3.21
Cyperus rotundus	1.665	1.686	16.62	3.29	0
Panicum schinzii	1.575	1.595	18.21	1.75	1.96
Corchorus schimperi	1.558	1.578	19.79	2.63	0
Urochloa mosambicensis	1.529	1.549	21.34	0.0833	2.79
Total dissim.: 98.76					

MS vs. NS	Avg. dissim.	Contrib. %	Cumulative %	MS agv.abund.	NS avg.abund.
Panicum maximum	4.499	4.567	4.567	1.79	8.5
Pentzia incana	2.648	2.688	7.256	0	4.54
Digitaria sanguinalis	2.204	2.237	9.493	4.38	0
Urochloa mosambicensis	2.015	2.046	11.54	0.0833	3.63
Tragus berteronianus	1.983	2.013	13.55	0.0417	3.29
Aristida adscensionis	1.982	2.012	15.56	0	3.29
Panicum schinzii	1.918	1.947	17.51	1.75	2.46
Enneapogon desvauxii	1.918	1.947	19.46	0	3.29
Galenia pubescens	1.779	1.806	21.26	0	3.04
Cyperus rotundus	1.684	1.71	22.97	3.29	0
Total dissim.: 98.51					

TS vs. NS	Avg. dissim.	Contrib. %	Cumulative %	TS agv.abund.	NS avg.abund.
Panicum maximum	4.209	4.696	4.696	6.71	8.5
Pentzia incana	3.474	3.876	8.573	5.21	4.54
Urochloa mosambicensis	2.038	2.275	10.85	2.79	3.63
Dicrostachys cinerea	1.62	1.807	12.65	3.42	2.63
Aristida adscensionis	1.579	1.762	14.42	1.08	3.29
Enneapogon desvauxii	1.567	1.748	16.16	1.17	3.29
Tragus berteronianus	1.559	1.74	17.9	1	3.29
Dichanthium annulatum	1.556	1.736	19.64	2.5	1.92
Panicum coloratum	1.504	1.679	21.32	3.46	1
Panicum schinzii	1.497	1.671	22.99	1.96	2.46
Total dissim.: 89.61					

Table 12.2: Results for SIMPER analyses indicating the average dissimilarity, contribution of each species to the average dissimilarity, cumulative percent contribution and average abundance per plot for the ten most important arthropod taxa responsible for NMDS groupings. (MG) = Maize field Grassland; (MS) = Maize field Savanna; (TG) = Tension zone Grassland; (TS) = Tension zone Savanna; (NG) = Natural area Grassland; (NS) = Natural area Savanna.

MG vs. MS	Avg. dissim.	Contrib. %	Cumulative %	MG agv.abund.	MS avg.abund.
AphididaeMS1	7.312	7.482	7.482	15.4	1.58
AphididaeMS2	5.059	5.177	12.66	14.8	0.292
EntomobryoideaMS1	2.195	2.246	14.9	7.63	1.21
MelyridaeMS1	1.823	1.865	16.77	0.542	1
AphididaeMS3	1.764	1.805	18.58	0	2.13
AnthicidaeMS3	1.752	1.793	20.37	0.583	0.958
AphididaeMS5	1.738	1.779	22.15	1.75	0.0833
FormicidaeMS15	1.691	1.731	23.88	0	1.88
TipulidaeMS2	1.525	1.56	25.44	1.08	0
FormicidaeMS6	1.435	1.468	26.91	0	1.63
Total dissim.: 97.93					

TG vs. TS	Avg. dissim.	Contrib. %	Cumulative %	TG agv.abund.	TS avg.abund.
OribatulidaeMS1	3.887	3.947	3.947	81.2	0.0417
AcrididaeMS12	3.767	3.825	7.772	3.63	1.79
OribatulidaeMS2	3.475	3.529	11.3	75.1	0
CicadellidaeMS8	3.006	3.053	14.35	6.79	0.333
EntomobryoideaMS1	2.051	2.083	16.44	40.5	0.125
FormicidaeMS8	1.887	1.916	18.35	2.25	0.292
CicadellidaeMS24	1.803	1.831	20.18	0	3.33
CicadellidaeMS31	1.429	1.451	21.64	0.75	4.08
CecidomyiidaeMS1	1.398	1.419	23.06	14.8	1.25
AcrididaeMS13	1.18	1.198	24.25	1.21	0
Total dissim.: 98.47					

NG vs. NS	Avg. dissim.	Contrib. %	Cumulative %	NG agv.abund.	NS avg.abund.
FormicidaeMS8	3.478	3.564	3.564	3	4.04
OribatulidaeMS1	2.758	2.826	6.39	44.8	0.208
OribatulidaeMS2	2.673	2.739	9.129	58.5	0
EntomobryoideaMS1	2.105	2.157	11.29	29.5	0.167
AcrididaeMS3	1.824	1.869	13.16	1.96	0.0417
CicadellidaeMS8	1.541	1.579	14.73	6.42	0.583
SciaridaeMS10	1.5	1.537	16.27	0	6.75
FormicidaeMS5	1.307	1.34	17.61	0.0833	3.25
FormicidaeMS15	1.3	1.332	18.94	0.167	2.29
TingidaeMS6	1.259	1.29	20.23	1.63	0.0417
Total dissim.: 97.59					

MG vs. TG	Avg. dissim.	Contrib. %	Cumulative %	MG agv.abund.	TG avg.abund.
AphididaeMS1	4.638	4.739	4.739	15.4	0.333
OribatulidaeMS1	4.198	4.289	9.028	3.63	81.2
AphididaeMS2	3.808	3.891	12.92	14.8	7.38
AcrididaeMS12	3.686	3.767	16.69	0	3.63
OribatulidaeMS2	3.453	3.528	20.22	0.125	75.1
CicadellidaeMS8	3.208	3.279	23.49	0.125	6.79
EntomobryoideaMS1	2.929	2.993	26.49	7.63	40.5
FormicidaeMS8	2.031	2.076	28.56	0	2.25
AcrididaeMS13	1.333	1.362	29.92	0	1.21
CicadellidaeMS23	1.27	1.298	31.22	0.0833	2.08
Total dissim.: 97.86					

MG vs. NG	Avg. dissim.	Contrib. %	Cumulative %	MG agv.abund.	NG avg.abund.
AphididaeMS1	4.65	4.76	4.76	15.4	0.208
AphididaeMS2	3.995	4.089	8.849	14.8	8.42
OribatulidaeMS1	3.049	3.122	11.97	3.63	44.8
EntomobryoideaMS1	2.978	3.048	15.02	7.63	29.5
OribatulidaeMS2	2.672	2.736	17.76	0.125	58.5
FormicidaeMS8	2.264	2.317	20.07	0	3
AcrididaeMS3	2.143	2.193	22.27	0	1.96
CicadellidaeMS8	1.616	1.655	23.92	0.125	6.42
DelphacidaenymphMS12	1.41	1.444	25.36	7.04	20.3
TingidaeMS6	1.39	1.423	26.79	0	1.63
Total dissim.: 97.68					

TG vs. NG	Avg. dissim.	Contrib. %	Cumulative %	TG agv.abund.	NG avg.abund.
OribatulidaeMS1	5.143	5.613	5.613	81.2	44.8
OribatulidaeMS2	5.045	5.506	11.12	75.1	58.5
EntomobryoideaMS1	3.158	3.447	14.57	40.5	29.5
AcrididaeMS12	2.961	3.231	17.8	3.63	0.875
CicadellidaeMS8	2.928	3.196	20.99	6.79	6.42
FormicidaeMS8	2.826	3.084	24.08	2.25	3
AcrididaeMS3	1.661	1.813	25.89	0.417	1.96
FormicidaeMS9	1.632	1.781	27.67	15.5	14.1
CecidomyiidaeMS1	1.431	1.562	29.23	14.8	19.1
CicadellidaenymphMS25	1.202	1.312	30.54	4.5	25.8
Total dissim.: 91.63					

MS vs. TS	Avg. dissim.	Contrib. %	Cumulative %	MS agv.abund.	TS avg.abund.
CicadellidaeMS24	2.87	2.956	2.956	0.5	3.33
SciaridaeMS10	2.374	2.446	5.402	1.67	2.83
FormicidaeMS6	2.327	2.397	7.799	1.63	0.875
FormicidaeMS5	2.243	2.311	10.11	1.38	1.42
FormicidaeMS15	2.027	2.088	12.2	1.88	1.21
CicadellidaeMS31	1.935	1.994	14.19	0	4.08
AphididaeMS3	1.624	1.673	15.86	2.13	0
AraneaeMS1	1.618	1.667	17.53	0.125	1.92
AphididaeMS1	1.348	1.389	18.92	1.58	0
FormicidaeMS9	1.291	1.33	20.25	1.88	0.167
Total dissim.: 97.07					

MS vs. NS	Avg. dissim.	Contrib. %	Cumulative %	MS agv.abund.	NS avg.abund.
SciaridaeMS10	3.124	3.242	3.242	1.67	6.75
FormicidaeMS15	2.803	2.908	6.15	1.88	2.29
FormicidaeMS5	2.553	2.649	8.799	1.38	3.25
FormicidaeMS8	2.528	2.623	11.42	0	4.04
FormicidaeMS6	1.733	1.798	13.22	1.63	0.458
AphididaeMS3	1.695	1.759	14.98	2.13	0.125
DipteraMS57	1.653	1.715	16.69	0.417	2
AlydidaeMS5	1.647	1.709	18.4	0.5	1.21
CicadellidaeMS24	1.567	1.626	20.03	0.5	1.96
CaeculidaeMS1	1.487	1.543	21.57	0	3.5
Total dissim.: 96.38					

TS vs. NS	Avg. dissim.	Contrib. %	Cumulative %	TS agv.abund.	NS avg.abund.
CicadellidaeMS24	3.096	3.292	3.292	3.33	1.96
SciaridaeMS10	2.902	3.085	6.377	2.83	6.75
FormicidaeMS8	2.292	2.437	8.814	0.292	4.04
FormicidaeMS5	2.26	2.402	11.22	1.42	3.25
FormicidaeMS15	1.773	1.885	13.1	1.21	2.29
CicadellidaeMS31	1.704	1.811	14.91	4.08	0
CaeculidaeMS1	1.622	1.725	16.64	1.13	3.5
DipteraMS57	1.602	1.703	18.34	0.5	2
AraneaeMS1	1.576	1.676	20.02	1.92	1.5
CicadellidaenymphMS23	1.316	1.399	21.42	2.71	1.13
Total dissim.: 94.06					