Arthropod and plant diversity in maize agro-ecosystems of South Africa

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It all starts here ™

PREFACE

Studying the diversity of living organisms is truly a humbling experience. Nowhere is this complexity more apparent than in two of the largest and most ecologically important groups of organisms in terrestrial ecosystems, vascular plants and their associated invertebrates. It is estimated that at least half of all recorded macroscopic species worldwide are plants and the arthropods that feed on them. All we can hope to accomplish with this work is to present a mere snapshot in time and space of the dynamic plant and invertebrate communities living at the crop-rangeland interface, an immensely complex system governed by both anthropogenic and natural factors. Nevertheless, with this and on-going future research we may systematically build a more complete picture of anthropogenic impacts on the natural habitat and in doing so, ensure a more sustainable and diverse agricultural landscape.

Naturally, this study would not have been possible without several individuals and organisations which I would like to thank for their exceptional contributions towards the completion of this thesis. Firstly, I want to thank my supervisors, Prof. Stefan Siebert and Prof. Johnnie van den Berg for their inspiration, guidance and tireless dedication to this work. I also thank our statistician, Dr. Suria Ellis for conducting the majority of our statistical analyses as well as her valuable advice and assistance throughout this project. Also, a special thanks to Dr. Niels Dreber (University of Göttingen, Germany), Dr. Frances Siebert (North-West University) and Prof. Braam van Wyk (University of Pretoria) for valuable discussions on the topic of plant functional traits and assistance with statistical analyses.

Of course, a fundamental aspect of this study was the identification of an overwhelming number of collected specimens. As such, the Pretoria National Herbarium (PRE) is acknowledged for assistance in the identification of unknown plant specimens as well as the Biosystematic division of the Agricultural Research Council (ARC) and the Ditsong Museum in Pretoria for assistance in the identification of arthropod predators. A special thanks to Prof. Ansie Dippenaar-Schoeman and her team for the tedious task of identifying the myriad of spider specimens to species level.

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Finally, the financial assistance of the National Research Foundation (NRF) towards this research is hereby acknowledged. Opinions expressed and conclusions arrived at, are those of the author and are not necessarily to be attributed to the NRF. Additional financial support was provided by GenØk-Centre of Biosafety, Norway, Norad project GLO-3450.

Declaration

I, Monique Botha, declare that the work presented in this PhD thesis 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.

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ABSTRACT

Agricultural intensification in the twentieth century has led to rapid biodiversity decreases on farmland. In sub-Saharan Africa, where rapid population increases and high direct dependence on natural resources coincide, biodiversity loss due to land-use change is of particular concern. Stock-grazing and dryland crop agriculture are two prominent and growing land-uses in the Grassland and Savanna Biomes of South Africa. Maize (*Zea mays* L.) represents the most important grain crop, with an approximate annual production of 128 million tons of maize grain on approximately 31 million hectares of land. Understanding what effect farmland management regimes have on the complexity and interactions of biota in remnant semi-natural ecosystems is a necessary step towards a sustainable future for biodiversity in agro-ecosystems. However, there has not been a considerable effort to understand the effects of these agricultural disturbances on species, structural, or functional diversity in South Africa's grassy biomes. The research project described in this thesis aimed to address the knowledge gap regarding biodiversity of maize agro-ecosystems in the Grassland and Savanna Biomes of South Africa by providing insight into the observational patterns of taxonomic and functional diversity, compositional structure and diversity relationships of two major groups of biota (vascular plants and plant-associated arthropods) in relation to an agricultural disturbance gradient at regional and local scales. Surveys were conducted in six provinces of South Africa, namely North-West, Mpumalanga, KwaZulu-Natal, Limpopo, Free State and the Eastern Cape. The transformation of semi-natural grassland and savanna into maize fields resulted in severely decreased species diversity, functional diversity and abundance as well as marked changes in species composition of plants and arthropods. However, there was no evidence for reduced levels of species diversity, functional diversity or trait abundance of plants and arthropods at medium disturbance intensity marginal vegetation (30-100 m from the maize field edges) compared to low-disturbance intensity rangelands. The pattern was consistent across the Grassland and Savanna Biomes. This suggests that the possible disturbance effects of maize fields do not have considerable negative effects on either the diversity or species assemblages of plant and arthropod communities at ≥30 m from the area of active cultivation. Uncultivated semi-natural vegetation of the Grassland and Savanna Biomes had distinct arthropod assemblages although these distinctions were better explained by geographical position than by plant features such as tree and grass cover. There was also evidence for positive relationships between low-growing (>2m) plant species and arthropod richness, diversity and abundance in maize fields and in uncultivated vegetation. The patterns recorded in this study suggest that crop field margins ≥ 30 m from the site of active cultivation are valuable conservation sites for the continued persistence of beneficial species and functional diversity of non-crop plants and arthropods within the agricultural environment.

Key terms: agricultural disturbance gradient; alpha-diversity; beta-diversity; corn (*Zea mays*); functional diversity; Grassland; insects; plant-arthropod diversity relationships; Savanna

OPSOMMING

’n Toename in intensiewe kommersiële landbou-bestuurspraktyke in die twintigste eeu het gelei tot 'n verlies aan biodiversiteit in landbou-ekostelsels. Hierdie grootskaalse verlies aan biodiversiteit is veral prominent in sub-Sahara-Afrika as gevolg van die gekombineerde effekte van eksponensiële bevolkingsgroei en direkte afhanklikheid van natuurlike hulpbronne. Die Grasveld en Savanna Biome van Suid-Afrika word merendeels benut vir veeproduksie en gewasverbouing. Mielies (*Zea mays* L.) word beskou as die belangrikste graangewas, met ’n jaarlikse opbrengs van ongeveer 12 miljoen ton wat op ongeveer 2,5 miljoen hektaar landbougrond geproduseer word. Om ’n volhoubare toekoms vir biodiversiteit in landbou-ekosisteme te verseker, is dit noodsaaklik om kennis te dra van die effek van landbou-bestuurspraktyke op die kompleksiteit en interaksies van biota in oorblywende natuurlike habitatte. Tot dusver is daar is egter nog geen betekenisvolle poging aangewend om die gevolge van landbou-versteurings vir spesie-, en funksionele diversiteit in Suid-Afrika te bestudeer nie. Die navorsingsprojek wat uiteengesit is in hierdie proefskrif was gemik daarop om hierdie gaping in die literatuur aan te spreek deur inligting te verskaf aangaande die diversiteitspatrone (spesie asook funksioneel) en spesiesamestellings van plante en insekte langs ’n 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. Resultate het daarop gedui dat die getal individue, spesiediversiteit en funksionele diversiteit van plante en insekte beduidend laer was in mielielande as in die aangrensende onbewerkte natuurlike veld, en dat die spesiesamestelling ook aansienlik verskil het tussen hierdie twee habitatte. Daar was egter geen aanduiding dat die teenwoordigheid van mielielande ’n beduidende negatiewe effek gehad het op die getal individue, spesiediversiteit of funksionele diversiteit van plante en insekte in die bufferstrook (30-100 m vanaf die mielielande) nie. Beide die Grasveld en Savanna Biome het dieselfde patrone getoon. Hierdie resultate dui daarop dat die effek van versteurings geassosieer met die landbouaktiwiteite waarskynlik nader as 30 m van die lande voorkom. Verder is daar ook gevind dat die onbewerkte natuurlike plantegroei van die Grasveld en Savanna Biome verskil het ten opsigte van hulle insek spesiesamestelling, alhoewel hierdie onderskeid merendeels toegeskryf kon word aan geografiese ligging, eerder as deur bioom-spesifieke eienskappe (persentasie gras en boom bedekking). Die resultate het ook daarop gewys dat positiewe verhoudings bestaan tussen die getal individue, spesierykheid en diversiteit van laag-groeiende plante (> 2 m) en insekte in mielielande en in die omringende onbewerkte natuurlike plantegroei. Hierdie studie dui op die belang van onbewerke bufferstroke langs mielielande vir die bewaring van voordelige plant en insekdiversiteit in hoogs-versteurde landbou-ekosisteme.

Sleutelterme: alfa diversiteit; beta diversiteit; funksionele diversiteit; geleedpotiges; Grasveld; insek-plantdiversiteit verhoudings; landbou versteuringsgradiënt; mielielande; Savanna

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CHAPTER 1: INTRODUCTION AND LITERATURE REVIEW

1.1 Introduction

The large-scale transformation of natural vegetation into farmland poses a serious and growing threat to biodiversity on a global scale (Darkoh, 2003; Wessels *et al.*, 2003). As the human population expands, areas for habitation and food production must increase to meet the growing demand. Management regimes of crop agriculture over thousands of years have gradually changed the composition of landscapes, creating complex patchworks of man-made habitats and semi-natural remnant vegetation that together support a wide range of plant and animal species (Altieri, 1999; Perfecto & Vandermeer, 2008). In the second half of the twentieth century however, agricultural intensification has resulted in a rapid decrease in the diversity of fauna and flora on farmland (Baessler & Klotz, 2006; Benton *et al.*, 2002; 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).

In sub-Saharan Africa, where rapid population increases and high direct dependence on natural resources coincide, biodiversity loss due to land-use change is of particular concern (Sanderson *et al.*, 2002). Approximately 11 million hectares of land in South Africa are currently utilised for commercial pivot (irrigated) and non-pivot (dryland) annual crops and a further 20 40530 hectares have been transformed for subsistence crop cultivation (DEA, 2016). South Africa's grasslands have been classified as one of the most transformed and critically endangered biomes following the degree of habitat loss, fragmentation and estimated future threats (Reyers *et al.*, 2001). It is estimated that 23% have been transformed for cultivation and only 2% are currently protected (Fairbanks *et al.*, 2000). Most of the savanna vegetation types in South Africa are used as grazing pastures for livestock or game (Cousins, 1999), although crop cultivation causes the greatest loss of savanna habitats in South Africa (Mucina & Rutherford, 2006). An estimated 11% of South Africa's savannas are transformed for crop cultivation and only about 5% are formally protected (Fairbanks *et al.*, 2000). With grassland and savanna being two of the most agriculturally productive biomes in South Africa, stock-grazing and dryland crop agriculture are two prominent and growing land-uses in the country (Mucina & Rutherford, 2006; Nazare, 2005; Neke & Du Plessis, 2004). Maize (*Zea mays* L.) represents the most important grain crop, with an approximate annual production of 128 million tons of maize grain on approximately 31 million hectares of land (Du Plessis, 2003). As a result, a larger proportion of South Africa's biodiversity is currently found on farmland than in conservation areas (Wessels *et al.*, 2003).

Remnant patches of naturally regenerated vegetation adjacent to crop fields probably provide important refuges for a wide range of biota of farmland (Fitzgibbon, 1997; Lagerlöf *et al.*, 1992; Rand *et al.*, 2006;

Vickery *et al.*, 1998), and these habitats may represent a key element in sustaining biodiversity in agro-ecosystems (Wilson *et al.*, 1999). Biodiversity plays a major role in the functioning of natural and agricultural ecosystems (Altieri, 1999; Bond, 1989; Duelli *et al.*, 1999; Wessels *et al.*, 2003). Higher biodiversity may also improve the efficiency of pest control in food crops (Gurr *et al.*, 2012). This supports the merit to conserve biodiversity in agro-ecosystems and highlights the need to adapt current farm management so as to prevent further degradation of these important natural habitats.

Understanding what effect farmland management regimes have on the complexity and interactions of biota in remnant semi-natural ecosystems presents a daunting but necessary step towards a sustainable future for biodiversity in agro-ecosystems (Settele *et al.*, 2010). As such, the assessment of potential risks posed by anthropogenic activities 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 the effects that current processes have on temporal dynamics. This type of information is crucial when deducing potential impacts of certain environmental features. Considering the rapid transformation and degradation of South Africa's grassy biomes into croplands, there is a need to develop conservation strategies for the remaining semi-natural habitats. However, this realisation has not been accompanied by a considerable effort to understand the effects of these agricultural disturbances on species, structural, or functional diversity (Neke & Du Plessis, 2004).

There is a fair amount of information on the impact of livestock grazing on diversity and trait composition of natural and semi-natural grassland and pasture in South Africa (e.g. Fabricius *et al.*, 2003; Geldenhuys, 2013; Rutherford *et al.*, 2012; Seymour & Dean, 1999; Uys, 2006). Similar research in crop agro-ecosystems are scarce, which reflects the overall tendency for ecologists to avoid highly disturbed agricultural areas (Robertson, 2000). South African studies that have focused on the effect of crop agriculture on plant (O'Connor, 2005; Siebert, 2011; Walters *et al.*, 2006; Wessels *et al.*, 2003), and arthropod (Gaigher *et al.*, 2016; Witt & Samways, 2004) species diversity were usually limited to specific geographical areas or were concerned with only one aspect of diversity (e,g, species richness). Very few studies to date sought to test the effects of crop agriculture on trait groups and functional diversity (e.g. Kemper *et al.*, 1999). Even in well-studied agricultural habitats such as Europe, there is a tendency for biodiversity studies to focus on specific key invertebrate groups or species and often ignore the patterns of complete invertebrate diversity in agro-ecosystems (Meissle *et al.*, 2012). Also, difficulty in disentangling the various effects of complex and interacting agriculture related factors on non-crop biota has led to the increased popularity of manipulative (experimental) studies, where the individual effects of these factors can be controlled more effectively (Lepš & Šmilauer, 2003).

However, manipulative studies are inevitably limited in space and time and for larger spatial scales it becomes necessary to rely on observational studies. The importance of non-manipulative studies cannot be ignored as they provide information on real-world dynamics of biota in 'natural experiments' that is virtually impossible to recreate at similar spatial scales in manipulative experiments (Lepš & Šmilauer, 2003). In general, these two approaches can be used effectively in combination, where observational studies are utilised for hypothesis generation and manipulative experiments for hypothesis testing (Lepš & Šmilauer, 2003).

1.2 Aims, objectives and hypotheses

The primary aim of this study was to address the knowledge gap regarding biodiversity of maize agro-ecosystems in the Grassland and Savanna Biomes of South Africa by providing insight into the observational patterns of taxonomic and functional diversity, compositional structure and diversity relationships of two major groups of biota (vascular plants and plant-associated arthropods) in relation to a gradient of agricultural disturbance at regional and local scales. It has to be acknowledged that the confounding effects of various agriculture-associated disturbances can never be fully separated in observational studies such as presented in this work. However, the aim was primarily to provide a real-world description of the community patterns associated with the study areas at the time of sampling, and not to disentangle the effects of specific agriculture-related disturbances. The hypotheses generated from these findings may be tested in future manipulative studies at smaller spatial scales.

The specific objectives were to:

- compare the taxonomic diversity, functional diversity and composition patterns of aboveground, plant-inhabiting arthropods and vascular plants between maize fields and adjacent natural vegetation at various distances from the actively cultivated area, which were perceived as different levels of agricultural disturbance intensity;
- compare the results of all the above-mentioned elements between the Grassland and Savanna Biomes of South Africa;
- test for correlations between plant and arthropod diversity and species composition in maize fields and adjacent natural vegetation.

The following hypotheses were tested:

- It is known that the disturbances associated with agricultural transformation may have a lasting negative effect on the biota in adjacent uncultivated vegetation (Bundschuh *et al.*, 2012; de Snoo & van der Poll, 1999; de Snoo & de Wit, 1998; Marshall & Moonen, 2002). From this, the first hypothesis states that taxonomic and functional diversity of plants and associated arthropods in uncultivated semi-natural vegetation will decrease with decreasing distance to maize fields across the Grassland and Savanna Biomes. Therefore, with increased agricultural management intensity, the biota in marginal habits in close proximity to the actively cultivated area will show a negative response to agricultural activities, irrespective of biome.

- To compensate for species loss and to maintain ecosystem functioning in disturbed areas, disturbance-intolerant species are often replaced by disturbance-tolerant species (Liira *et al.*, 2008; Siebert, 2011; Yachi & Loreau, 1999). Also, grassland and savanna are distinguished mainly on their unique plant species assemblages (Mucina & Rutherford, 2006). Therefore, the second hypothesis states that maize field and marginal vegetation in close proximity to the actively cultivated area will be replaced by a unique set of species and or functional types that are presumably better adapted to tolerate agriculture-associated disturbance, and that these disturbance-tolerant types will differ between grassland and savanna habitats.
- Numerous models predict increased consumer diversity in response to increased plant diversity (Rosenzweig, 1995; Tilman, 1986; Whittaker, 1970). Supporting this, empirical evidence suggests that a diverse vegetation background generally increases beneficial arthropod diversity (Finch & Collier, 2000; Gurr *et al.*, 2016), although the nature of these relationships may be more pronounced for certain families or functional guilds (Koricheva *et al.*, 2000). Therefore, the third hypothesis states that a general positive relationship exists between overall plant and arthropod diversity in both maize fields and adjacent natural vegetation, but that the strength of these relationships will be dependent on specific plant families and arthropod guilds.

1.3 General outline of the thesis

In the remainder of this chapter (1.4) a review of the literature is given that touches on the most important aspects discussed in this study. Chapter 2 presents the general survey methods used to compile data for plant and arthropod species and applies to all the following chapters in this thesis. In chapters 3-8 the results and subject-specific discussions and conclusions of the various elements composing this thesis will be presented. A general layout of the results chapters presented in this study is provided in Figure 1.1. Chapter 3 represents the first results chapter, where the total plant and arthropod datasets are considered to provide information regarding the overall patterns of species diversity and composition along the maize field-field margin gradient between the two biomes. In chapter 4, species composition of all arthropod species and selected trophic groups is related to the Grassland and Savanna Biomes in natural vegetation adjacent to maize fields to assess whether arthropod assemblages fit these two biomes. Chapter 5 describes the overall diversity and compositional relationships between plants and arthropods for all species and for prominent arthropod guilds and plant family groups. Chapter 6 describes the abundance patterns of plant functional types and selected plant traits as well as the functional diversity of plant communities along the maize field-field margin gradient between the two biomes. Chapter 7 provides a more in-detail description of the diversity and composition patterns of selected insect predator groups (classified to species level) in relation to maize field, marginal and rangeland vegetation. The overall synthesis, conclusions and future research recommendations are given in chapter 8.

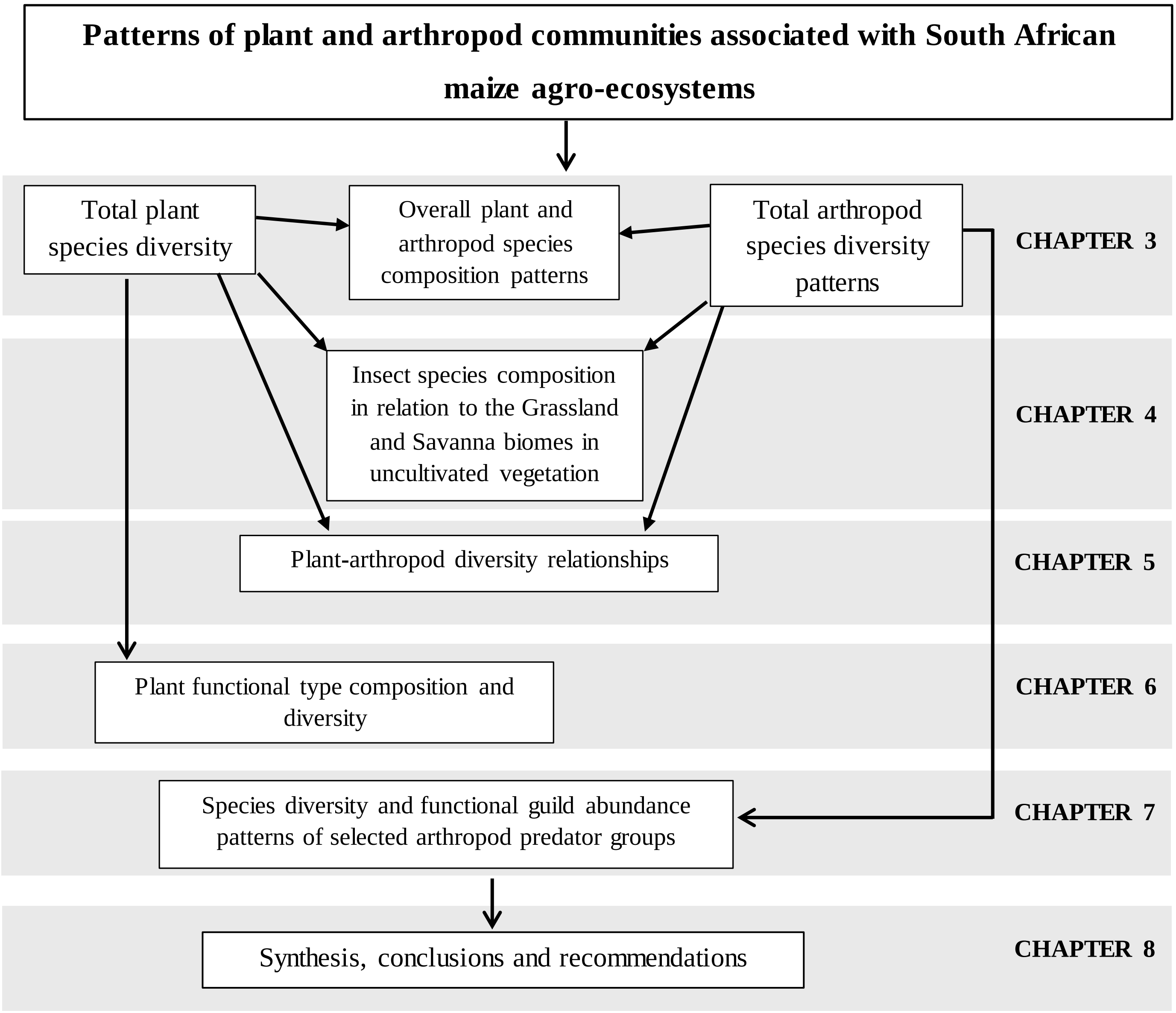

Figure 1.1: Layout of results chapters summarizing the various elements considered in this study.

1.4 Literature review

1.4.1 Quantifying biodiversity

Biodiversity is a term frequently used in popular media and scientific papers. Yet it is often not accompanied by an all-encompassing definition. The term has been loosely applied to depict the variability of living organisms in various contexts. The concept of biodiversity is in fact very complex and may be described at different levels of biological organisation. This includes genetic diversity, species diversity, functional 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 describes the variation of taxonomic species in a community (Begon *et al.*, 2008). Functional diversity is concerned with the variety of functional traits, which is theoretically linked to the diversity of functions performed by individuals in the community (Díaz & Cabido, 2001; Petchey & Gaston, 2006). Ecosystem diversity represents the variation in ecosystems or habitat, although the quantitative assessment of diversity at this level remains problematic (Groombridge, 1992). Biodiversity may also be described at different spatial scales (Hamilton, 2005). Variation can exist within a single homogenous habitat, which is termed point diversity or alpha (α) diversity. There can also be variation between different habitats or communities, known as beta (β) diversity. At a larger scale, landscape or gamma (γ) diversity describes the variation between different landscapes (Hamilton, 2005).

The diversity of communities is often expressed in terms of species richness (S), i.e. the number of species present in a community or habitat (e.g. Marc & Canard, 1997; Proches & Cowling, 2006). However, the usefulness of species richness as a measure of biodiversity 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). Measures of biodiversity that reflect both species richness and relative abundance of individuals among species are therefore more informative. As such, biodiversity may then be defined as the number of species present and how well each of these species is represented (in terms of abundance) in a given system (Begon *et al.*, 2008).

Indices developed from information theory are 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, such as Margalef's species richness index (d), focus mainly on the number of species in a sample. Meanwhile, species abundance indices, such as Pielou's evenness (J'), provide measures of the evenness (proportion) of species in a community. Perhaps the most popular 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, as they take both evenness and species richness into account (i.e. the Simpson and Shannon-Wiener diversity indices). Simpson's Diversity Index (Ď) 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). The Shannon-Wiener diversity index (H') on the other hand, tends to weigh towards species richness (Magurran 1988).

1.4.2 Biodiversity value

It is generally agreed that biodiversity is an important aspect in both natural and agricultural ecosystems and the conservation of global biotic diversity is favourable (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 resistance to change or resilience of a community (Hurd & Wolf, 1974). 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 set that will enable its survival (Walker & Salt, 2012).

Although the diversity-stability link is highly debated, both in specific contexts and generally, some recent studies suggest that biological diversity may be expected to give rise to ecosystem stability (Hautier *et al.*, 2015; Venail *et al.*, 2015). This is not limited to species diversity but is also linked (in particular) to 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 confirmed positive 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 invariably dependent on monoculture production systems. However, the transformation of diverse natural habitats into species-poor crop production systems has negative consequences both for the natural environment and the agro-ecosystem (Altieri & Letourneau, 1982; Pimentel, 1961). General concern has been raised about their long term sustainability (Altieri, 1999). 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). A usable diversity-stability theory may be beneficial in alternative pest management strategies and in management of natural communities associated with agricultural production systems.

Perhaps one of the most common ways to express the value of biodiversity 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 control, pest control, pollination, seed dispersal, erosion regulation, water purification, climate control and disease control), cultural services (spiritual and religious values, education, 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).

Vegetation cover in grassland may 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 agricultural ecosystems by facilitating the reproduction of the majority of angiosperm plants. It is estimated that animals (primarily insects) pollinate approximately 80% of angiosperms, which amounts to about 300,000 flower-visiting species (MA, 2007). Non-crop vegetation 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 through drift retention or by preventing the movement of surface water flow and particle movement (Marshall & Moonen, 2002). Increased plant diversity in agro-ecosystems may also benefit crop production indirectly by providing alternative food sources, hiding places or overwintering sites for beneficial insects (Grez *et al.*, 2010).

1.4.3 The role of arthropod diversity

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) represent the five major orders within the already described list of insects (Gullan & Cranston, 2005). Above-ground arthropods include a wide range of trophic groups such as sap-feeding hemipterans, leaf-feeding lepidopterans, beetles, dipterans, thrips, grasshoppers and herbivores associated with the vegetation layer and groups such as surface-foraging termites, ants and litter-feeding isopods, millipedes and collembolans. Predaceous groups include carabids and staphylinid beetles, mites, spiders, omnivorous earwigs and parasitic wasps (Curry, 1976).

The sheer numbers of arthropods make them a highly significant component of the environment. In many ecosystems, arthropods represent the most dominant herbivores (Andersen & Lonsdale, 1990; 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). On the other hand, 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 act 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).

Unfortunately crop monocultures remain one of the most difficult environments within which to establish efficient biological control agents as they often lack adequate resources to sustain natural enemies (Altieri & Nicholls, 1999). The diversity of beneficial insects in a cropping system is often linked to undisturbed natural areas (Stary & Pike, 1999). Indeed, it is generally accepted that higher biodiversity results in stronger pest control within agricultural systems (Gurr *et al.*, 2012). Therefore, possible ties between beneficial arthropods and natural plant communities must be identified and preserved to ensure effective biological control of pest species.

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 grasslands and deserts accelerates the rate of nutrient cycling in terrestrial ecosystems while having little impact on standing crops and their production (Curry, 1994). 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).

Perhaps one of the most well-known benefits of arthropods is their role in plant pollination, especially of food crops and forage plants. Insect pollinators are becoming more and more valuable, especially since pollinator-dependent crops make up an increasingly important part of the human diet (Aizen *et al.*, 2008; Klein *et al.*, 2007). It is estimated that one third of our food supply relies directly on pollination by insects (Jolivet, 1998). In agro-ecosystems, honey bees, *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).

1.4.4 The agro-ecosystem

1.4.4.1 Cropping systems

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 domestic livestock (Tivy, 1990). In doing so, a particular type of man-made ecosystem is created, namely the agricultural ecosystem or agro-ecosystem. For the purpose of this study, 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 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. 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).

As with natural ecosystems, 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). 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).

Crop agriculture is based on a variety of spatial designs that involves the nature of the crop structure. Whenever farmers focus on market (commercial) production, high-input monocultures become predominant. As a result, monocultures have increased substantially on a global scale (Altieri, 2011). The term 'monoculture production' refers to the agricultural practice of cultivating a single plant species in a specific area on an annual basis (Mongillo & Zierdt-Warshaw, 2000). Large-scale monoculture production has led to a number of negative consequences both for the environment and for 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). 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 (Frank & McNaughton, 1991; King & Pimm, 1983; Tilman *et al.*, 1997; 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 includes monocultures with border plantings, as well as intercropping systems such as mixed cropping or strip cropping (Altieri, 1983; Ratnadass *et al.*, 2012). 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).

1.4.4.2 General structural features of the crop field

The typical crop field agro-ecosystems consist of a number of basic components. 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 & 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.

The **crop edge** consists of the outer few metres of the crop, sometimes also referred to as the crop 'headland'. It is used as 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).

The **field boundary** 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. The **field boundary strip** includes the area between the crop edge and the physical field boundary and usually contains features such as roads and, less commonly, watercourses like 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 that the spread of beetle species is slower through grassy banks than through barley fields (Frampton *et al.*, 1995). 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).

The **field margin** is usually defined as the whole of the crop edge, any margin strip present and the semi-natural habitat associated with the boundary (Marshall & Moonen, 2002). In developed countries such as Europe, large commercial crop fields are typically separated by relatively narrow margin strips. Margins between 1 and 20 m are already considered of ecological importance under agri-environmental schemes (Hackett & Lawrence, 2014). In contrast, maize fields in South Africa (particularly in rural areas) are often situated further apart with much larger semi-natural vegetation patches between fields. In this study the focus was particularly on maize fields with large semi-natural habitats adjacent to fields (as detailed in the methods, chapter 2) Therefore, the term **marginal vegetation** is introduced to also include any natural vegetation beyond the field boundary up to 100 m from the crop field. The marginal vegetation and any rangeland beyond are typically utilized for livestock grazing in South African farming systems.
These field margins may act as reservoirs for insect pests and weeds (Holland & Fahrig, 2000; Marshall & Arnold, 1995), but also for beneficial arthropods (Landis *et al.*, 2000). 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 the arrival of beneficial insects into crop fields (Grez *et al.*, 2010). 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 (Leeson *et al.*, 2005; Wilson & Aebischer, 1995). 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 as a result of natural environmental gradients or changes in land-use (e.g. crop production to natural rangeland) (Yahner, 1988). This transitional zone may therefore have characteristics of each of its adjacent ecosystems as well as its own unique fauna and flora (Marshall, 1989). Habitat edges are important structures in the landscape as they have the potential to alter ecological processes such as nutrient transport, the outcome of species interactions, species dispersal and community composition (Fagan *et al.*, 1999).

It is known that plant communities respond to transitional zones (e.g. Lin & Cao, 2009). This also seems to be true for arthropod communities. Forest-grass transition zones 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 versus complex agricultural landscapes. As complex crop field systems often involve large numbers of smaller crop patches separated 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 attributed to more alternative resources (such as alternative hosts, pollen sources and moderated microclimates) closer to field interiors.

1.4.4.3 Agro-ecosystem associated diversity

Despite the challenging environment they present to non-crop biota, agro-ecosystems are not invariably low in biodiversity from a global perspective. Many tropical agricultural systems have a high diversity of planted crops and associated non-crop organisms (Perfecto & Vandermeer, 2008). 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, save the crop plants themselves. In fact, these systems is often surprisingly rich in unintentional diversity because of the high dispersal capacities of biota. Crop fields may however differ in terms of how, where and at what rate they acquire new species.

1.4.4.3.1 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 influence arthropod species composition in different ways (Gurr *et al.*, 2012). It is well known that spill-over 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) readily 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, crop field associated invertebrates may spill over into field margins as well (Blitzer *et al.*, 2012), sometimes with detrimental consequences to the natural habitat. It has been shown that spill-over 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. Host shifts of *Ophraella* spp. (Coleoptera: Chrysomelidae) are for instance 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 & Ericson, 2007), plant structure may also play a major role in colonization rate. An insect searching for a host plant may then 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, although only a fraction of them will actually be able to establish. 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 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).

1.4.4.3.2 Determinants of 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 (e.g. prey, hosts, water, pollen and nectar), other specific habitat requirements and intra-and interspecific competition, which are in turn affected by the nature of the cropping system (the spatial and temporal arrangement of crops and the nature 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).

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 then also a greater diversity of predators and parasitoids. Although this concept has proven difficult to prove in the real agro-ecosystem environment, positive evidence has been provided by Cardinale *et al.* (2003), Denys and Tscharntke (2002) and Schellhorn and Sork (1997). Several hypotheses have been proposed to explain higher arthropod diversity in more diverse cropping systems, although different hypotheses may apply to different situations. The resource rarity hypothesis 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. On the other hand, the intraspecific density dependence hypothesis states that 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 (Abrams, 1995).

The type of vegetation in the field margin may influence the arthropod community composition in the agro-ecosystem. As mentioned previously, tall companion plants in crop field borders may act as barriers to the movement of a variety of insect species. 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 options. 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 environment (Altieri, 1999).

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, are considered to be the most challenging 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 complications for relatively immobile arthropod groups. It was shown 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 (Ryszkowski, 1979).

Crop field margins play a vital role in maintaining biodiversity in these ephemeral environments as they provide stable refuge sites and additional resources when crop fields are fallow in the non-growing season. It was shown by Pfiffner and Luka (2000) that five times more arthropod species (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 disperse and increase their diversity annually in adjacent crops.

The position of the crop relative to natural vegetation may greatly influence the composition and diversity of non-intentional diversity (Altieri & Nicholls, 1999). It has been shown that crop plants near field margins tend to harbour more arthropod species. 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.

A major determinant of diversity in agro-ecosystems is the type of management regime in question. 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). 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.

1.4.5 Agricultural intensification and biodiversity loss

Agricultural practices are designed to alter natural systems in such a way that they serve the needs of human populations and as such must continually work against natural processes to ensure the persistence and success of the agricultural system. Therefore, the nature of agro-ecosystems does not favour the continued persistence of biodiversity (Matson *et al.*, 1997; McLaughlin & Mineau, 1995; Reidsma *et al.*, 2006). Management regimes designed to favour crops are often harmful to other organisms and intensively managed habitats tend to be dominated by those few species that are able to tolerate 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 by displacing individuals. Indirect adverse effects may result from the degradation of natural habitats as well as habitat fragmentation.

1.4.5.1 Fertilizers

Organic and inorganic fertilizers are commonly used in agriculture to increase crop yield. However, this often results 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 that the abundance of the common buttercup (*Ranunculus acris*) in field margin habitats decreased significantly in cases where fertilizers were applied (Schmitz *et al.*, 2013). 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 combination of fertilizer application and irrigation had marked effects on plant and arthropod communities. 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. In empirical studies, Kleijn and Snoeijing (1997) 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 the nutrition status of plants as a result of fertilization may also influence the dynamics of the associated arthropod communities. 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 rates.

1.4.5.2 Pesticides

The application of pesticides (insecticides and herbicides) is an intricate part of commercial crop management regimes, often with detrimental consequences for non-crop biota. A growing concern is that these effects may extend to remnant semi-natural habitats through agrochemical drift (Marshall & Moonen, 2002). Several studies indicated that pesticide drift occur 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 to fertilizers. In this case, herbicides 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 of herbicide application on adjacent ditch-bank vegetation was investigated by de Snoo and van der Poll (1999). In unsprayed winter wheat crops 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*. 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.

In addition to the direct effects of herbicides on arthropods, changes in plant species composition may have an indirect effect on the diversity and composition of arthropod communities (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, although this may also have adverse effects on beneficial non-target arthropods (Cessna *et al.*, 2005). It was shown by de Snoo and de Wit (1998) that butterfly species numbers decreased 2-3 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 margin habitats outside crop fields. Bundschuh *et al.* (2012) monitored field margins that bordered 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. Density decreases was attributed to the effects of insecticides on the grasshopper nymphs.

The effect of pesticides on biota in field margins may also depend on other 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 also influence the range at which these toxins affect the biota in field margins. It was found that different spray nozzle designs resulted in large differences in the distance of pesticide deposition inside field margins.(de Snoo & de Wit, 1998).

In some cases, field design has the potential to mitigate the adverse effects of pesticide drift on remnant natural habitats. As such, field margin vegetation may be used as buffers to prevent pesticide drift in which case 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 and unguaranteed success in controlling arthropod pests has placed doubt on the merit of blind application of large amounts of insecticide to crop fields. 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 is 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. There is a need to develop pest control strategies that are more environmentally sound and sustainable. These strategies should include the use of biological control methods in combination with chemical control, cultural control, and host plant resistance in an integrated pest management (IPM) system (Tivy, 1990).

1.4.5.3 Bt-toxins

In addition to insecticides, numerous plant varieties have been genetically modified to be resistant to insect pests. This 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).

There is increasing concern regarding the negative effect these toxins may have on non-target arthropods associated with agro-ecosystems. Non-target arthropods may 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 genetically modified (GM) plant material. Toxic plant material may 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 also enter the environment via root exudates, plant residues left in the field after harvest and pollen drift to adjacent field margins (Viktorov, 2011). Non-target predatory arthropods may be exposed to Bt-toxins in tritrophic interactions by consuming a pest species that fed on Bt plant material (Ferry *et al.*, 2007).

Rosi-Marshall *et al.* (2007) found maize plant by-products and pollen 6 to 40 m from maize fields. Harvest residues containing maize 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.

Although the vast majority of pollen grains land in close proximity to the parent maize field, recent research indicates that a percentage 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). Contamination of milkweed by clothianidin could also function as a stressor to monarch populations (Pecenka & Lundgren, 2015).

Exposure of natural enemy communities to Bt-toxins in tritrophic interactions may be mediated by movement of prey 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. One study 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%. Again, exposure to the amounts offered is unlikely occur under field conditions (Gatehouse *et al.*, 2002).

The unrealistic conditions in laboratory experiments prompted an increasing number of studies that aimed to test the effect of Bt-toxins on arthropod communities under field conditions. The drift of Bt-maize pollen to an adjacent nature reserve was monitored by Hofmann *et al.* (2010). Results 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).

If Bt-crops are present in an agro-ecosystem, the contamination of semi-natural field margin habitats with Bt-plant material is for the most part unavoidable. Fortunately there seems to be little evidence to date for significant negative effects of these Bt-toxins on non-target arthropods in the field (Ferry, 2010). Reviews of Romeis *et al.* (2006) and Wolfenbarger *et al.* (2008) reported little evidence of non-target organisms associated with target pests that were negatively affected by Bt-toxins. To the contrary, the alternative for Bt-maize is often the application of broad-spectrum pesticides, which may have a greater overall adverse impact on ecosystem health in the field margin (Meissle & Lang, 2005). 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).

1.4.5.4 Irrigation

The irrigation of crop fields may have a marked effect on the dynamics of both plant and arthropod communities in agro-ecosystems. 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 caused an increase in weed species. Irrigation practices may act in combination with agrochemical application in modifying the composition of plant communities. Plant productivity (measured in terms of biomass) may be enhanced by irrigation, and this could in turn have an effect on the arthropod communities associated with these plants (Kirchner, 1977). Increased plant density associated with increased irrigation of grain sorghum (*Sorghum bicolor*) 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.

It is well-known that arthropod community assemblages are governed by moisture availability (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. This could be disadvantageous for the crop if the benefitting 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 (*Populus* spp.). 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). Also, the density, number, dry mass and egg deposition of variegated leafhoppers (*Erythroneura variabilis*) (Hemiptera: Cicadellidae) increased on grapevine (*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. It may therefore be possible to manipulate irrigation amounts to control insect pests without compromising crop yield. While irrigation may increase herbivore pest numbers it may also be beneficial for their predators and parasitoids (Daane & Williams, 2003).

1.4.5.5 Soil disturbance

Crop agriculture is inevitably linked to various degrees of soil disturbance depending on the type of management regime applied. The type of tillage practice (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). Tillage 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 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.

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). In a study by Sharley *et al.* (2008), the effect of soil tillage on beneficial invertebrate communities was examined in vineyards. 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 might 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).

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, although the amounts varied greatly with the type of soil and the characteristics of the top soil layer.

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).

1.4.5.6 Livestock grazing

Agricultural land used for crop production in the Grassland and Savanna biomes of South Africa is often interspersed by natural rangelands utilized as grazing pastures for livestock (Mucina & Rutherford, 2006).

As such, the biota of crop field margins may be subjected to the additional disturbances associated with livestock grazing. It is well-known that the abundance and composition of plant species are affected by large herbivore grazing (e.g. McNaughton, 1979; Milchunas *et al.*, 1988; Rutherford & Powrie, 2013). The nature of these responses depends on a number of complex abiotic environmental factors such as differences in soil and climate and also by the type of grazing regime, which involves aspects such as stocking rate and rotation frequency (Tainton, 1999). Therefore, grazing may have different effects on the same plant species in different regions.

Grazing also 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, excessive grazing tends to replace palatable, productive species with less palatable, less productive grasses and forbs (Tainton, 1999) and a reduction in above-ground biomass (Wan *et al.*, 2011). In terms of functional types, 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 also result in lower plant species diversity (Rutherford & Powrie, 2013).

Evidence suggests that livestock grazing has the potential to influence the species composition, diversity and interactions of plant associated arthropod communities, mostly via effects on the vegetation communities. As with plants, livestock grazing probably does not influence all arthropod groups in a similar fashion or to the same degree. Grazing may affect arthropod communities via changes in floral composition and habitat structure which is in turn influenced by grazing intensity (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. It was proposed that this increased insect abundance was due to increased flowers and fruits of *Lotus corniculatus* and *Campanula rotundifolia* in ungrazed grassland. 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 vegetation 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.

East and Pottinger (1983) distinguished between three different types of responses to stocking rate, which were similar to responses commonly recorded for plant species (Tainton, 1999). 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 density 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 attributed 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 smaller 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 semi-natural grasslands. Changes in temperature, food resources, vegetation structure, litter layer and competition have been proposed as explanations for these responses.

1.4.5.7 Habitat fragmentation

The clearing of natural vegetation for crop fields results in habitat loss and has a fragmentation effect on the landscape. As a result, remnant 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 biota between 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 in increased isolation of remnant patches. 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 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) which may have additional adverse impacts on biota in remnant patches.

Increased isolation limits the 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. Supporting the hypothesis that small plant populations are less attractive to pollinators than large populations, Ågren (1996) indicated that a decreased population size of the self-incompatible herb, *Lythrum salicaria* (Lythraceae), had significantly reduced seed production per flower and seed number per plant. This phenomenon was likely the result of inadequate pollination. Furthermore, small and fragmented populations of the tree species *Spondias mombin* (Anacardiaceae) showed significant reductions in germination rate and fruit production compared to large, continuous forest populations (Nason & Hamrick, 1997).

The effect of habitat fragmentation on communities is greatly affected by distance from other patches and organism size (Margules, 1991) as well as the dispersal ability of the biota (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 less sensitive to habitat type and were distributed regardless of obvious landscape boundaries. Flightless arthropod species such as bush crickets (*Metrioptera bicolor*; Orthoptera: Tettigoniidae), are also vulnerable to extinction in small habitat patches (Kindvall, 1992). Habitat fragmentation may ultimately result in the selective extinction of species, depending on their dispersal ability as well as the habitat types and specific regions in question (Samways, 2005).

1.5 Conclusion

It is widely stated in the literature that biodiversity is favourable and has conservation value in agro-ecosystems. One of the most common ways to express the value of biodiversity is its role in providing ecosystem services. Although the complex species dynamics and interactions of ecosystems are difficult to study, the biodiversity-ecosystem stability theory is supported by a multitude of studies in the literature, including grassy rangeland systems. Insuring the long-term stability of agro-ecosystems via increased biodiversity is a somewhat paradoxical situation in that commercial agricultural practices have an inevitable negative effect on non-crop biodiversity. This includes not only taxonomic diversity but also functional diversity, a concept that has only received attention relatively recently.

It is evident from the literature that crop agriculture has major impacts on two of the most prominent and ecologically important groups of biota found in grassland and savanna agro-ecosystems, namely vascular plants and their associated arthropods. Agricultural activities may impact these communities both directly and indirectly in complex ways. The negative impacts of agrochemical usage on non-target organisms are well-known and this effect may extend well beyond the boundaries of the crop field due to agro-chemical drift. Also, the dynamics of plant and arthropod communities may be affected in complex ways through management practices such as soil tillage and irrigation. These impacts are aggravated by large-scale phenomena such as habitat fragmentation.

However, all is not lost in the pursuit of a biologically diverse agro-ecosystem. Evidence from empirical studies suggests that modifications in management regimes can go a long way towards mitigating the negative impacts of agriculture on plant and arthropod diversity. It is evident that uncultivated field margins are key features in this regard. In many cases, agri-environment schemes that promote organic farming, sown grass and wildflower margin strips, uncropped wildlife strips and beetle banks have been successful in enhancing plant and beneficial arthropod diversity in European countries. To implement biodiversity mitigation strategies successfully in South Africa, a thorough knowledge is required regarding the nature and dynamics of the specific biotic communities in question. Several gaps are evident in the literature on this aspect in South Africa’s Grassland and Savanna Biomes, despite the rapidly increasing transformation of natural habitats into crop production systems. Providing insight into the observational patterns of taxonomic and functional diversity, compositional structure and diversity relationships of plants and associated arthropods forms the basic theme of this thesis.

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CHAPTER 2: OVERARCHING METHODOLOGICAL APPROACH

2.1 Overview

A short description is given of the most important environmental features known regarding the study localities at which samples of plants and arthropods were taken. Also, the survey methods are described that were followed to collect the plant and arthropod data for which results are displayed in chapters 3-6 below. The experimental layout for the results displayed in chapter 7 differed from those for chapters 3-6 and is detailed in the methods section of the relevant chapter.

2.2 Description of study localities

Study areas were selected from the six major maize producing provinces of South Africa, namely the Eastern Cape, Free State, KwaZulu-Natal, Limpopo, Mpumalanga and North-West, covering both the Grassland and Savanna Biomes (Figure 2.1). Each locality had its own set of environmental variables and management regimes including biome, vegetation unit, altitude, climate, farming type, presence or absence of irrigation and width between rows of maize (Table 2.1).

2.2.1 Amersfoort

Surveys for Mpumalanga were carried out in February 2010 on 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 (Figure 2.2a).

2.2.1.1 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.

2.2.1.2 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).

2.2.1.3 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).

2.2.1.4 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).

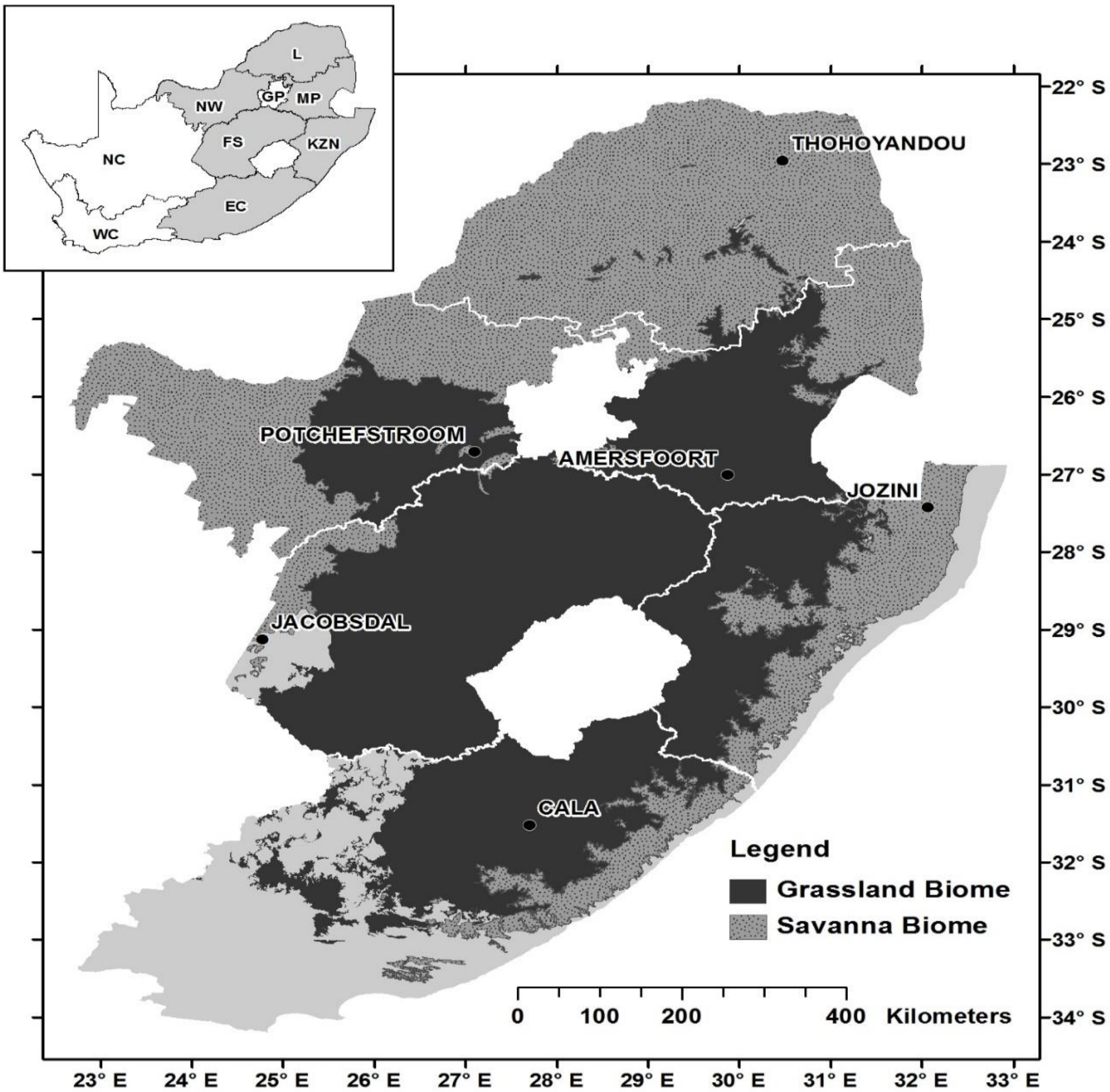

Figure 2.1: Survey localities across the six major maize producing provinces of South Africa in relation to the Grassland and Savanna Biomes and nearest major settlements. L, Limpopo; MP, Mpumalanga; KZN, KwaZulu-Natal; EC, Eastern Cape; FS, Free State; NW, North-West.

Table 2.1: Summary of the general habitat information for all the sampling localities as well as observed features of the maize fields and adjacent uncultivated marginal and rangeland vegetation. Biome and vegetation unit according to Mucina and Rutherford (2006).

(a) Grassland		Amersfoort	Cala	Potchefstroom
Habitat information	Sampling date	12-13 Febr. 2010	20-21 Mar. 2012	25 Febr.-2 Mar. 2010
	Vegetation unit	Amersfoort Highveld Clay Grassland	Tsomo Grassland	Rand Highveld Grassland
	Altitude (m a.s.l.)	1689-1747	836-916	1407-1490
	MAP (mm)	694	609	654
	MAT (°C)	14	15.2	15.8
	MFD (<0°C)	42	28	28
	SMS (%)	74	76	76
Maize fields	Row width (cm)	90-100	100-150	150-200
	Farming type	Commercial	Commercial	Commercial
	Irrigation	No	No	No
	Fertilizer usage	Yes	Yes	Yes
	Herbicide usage	Yes	Yes	Yes
	Insecticide usage	Yes	No	Yes
Uncultivated habitats	Land uses	Grazing (cattle)	Grazing (cattle, horses, sheep) Wood collection	Grazing (cattle)
	Structural features of field boundary	Farm tracks, fences, electricity pylons	Farm tracks, fences	Farm tracks, fences
(b) Savanna		Jacobsdal	Jozini	Thohoyandou
Habitat information	Sampling date	24-25 Febr. 2011	10-11 May 2010	3-5 Nov. 2009
	Vegetation unit	Kimberly Thornveld	Western Maputaland Clay Bushveld	Makuleke Sandy Bushveld
	Altitude (m a.s.l.)	1144-1172	69-112	613-680
	MAP (mm)	407	597	489
	MAT (°C)	17.2	21.8	21.7
	MFD (<0°C)	33	0	1
	SMS (%)	82	78	81
Maize fields	Row width (cm)	75-100	80-100	90-100
	Farming type	Commercial	Subsistence	Subsistence
	Irrigation	Yes	Yes	Yes
	Fertilizer usage	Yes	Yes	Yes
	Herbicide usage	Yes	Yes	No
	Insecticide usage	No	No	No
Uncultivated habitats	Land uses	Grazing (cattle, sheep)	Grazing (cattle, goats) Wood collection	Grazing (cattle, donkeys) Wood collection
	Structural features of field boundary	Farm tracks, fences	Farm tracks, fences	Farm tracks, fences, water drainage canals

MAP = mean annual precipitation; MAT = mean annual temperature; MFD = mean frost days; SMS = Mean annual soil moisture stress

Figure 2.2: Visual representations of the maize fields and field margin vegetation of the six study sites in the vicinity of (a) Amersfoort; (b) Cala; (c) Potchefstroom; (d) Jacobsdal; (e) Jozini and (f) Thohoyandou.

2.2.1.5 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 alien species invading drainage lines (Mucina & Rutherford, 2006).

2.2.2 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'S, 27°44'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 (Figure 2.2b).

2.2.2.1 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. However, the particular maize fields that were surveyed were not cultivated under irrigation. The inter-row spacing was 1.0 – 1.2 m, with bare patches and dwarfed plants in sections of the maize fields. This may have been due to moderate drought stress as well as nitrogen deficiency. 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 (primarily cattle and sheep).

2.2.2.2 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 *Aristida, Cymbopogon, Elionurus, Eragrostis,* and *Themeda* while dwarf shrubs such as species of *Euryops* are common. Typical forbs are those of the family Asteraceae (daisy family) and Fabaceae (legume family) (Mucina & Rutherford, 2006).

2.2.2.3 Geology and soils

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

2.2.2.4 Climate

The area typically receives the bulk of its 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 ranging between 430 and 790 mm. Frost incidence is variable and most common in the northwest (Mucina & Rutherford, 2006).

2.2.2.5 Conservation status

The status of Tsomo Grassland is vulnerable and not protected in any 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 and 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)

2.2.3 Potchefstroom

Surveys in this region were conducted during February and March 2010 on the Enselspoort and Rooipoortjie farms near Potchefstroom (26° 43'S, 27° 15'E; altitude 1407-1490 m a.s.l.), situated in the Rand Highveld Grassland vegetation unit of the Mesic Highveld Grassland Bioregion in the North-West province (Figure 2.2c).

2.2.3.1 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 the lower rainfall.

2.2.3.2 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 belonging to the genera *Eragrostis, Elionurus, Heteropogon and Themeda*. 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 *Celtis africana*, *Protea caffra* subsp. *caffra*, *P. welwitschii* and *Senegalia caffra* and shrubs dominated by the *Searsia* genus (Mucina & Rutherford, 2006).

2.2.3.3 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).

2.2.3.4 Climate

The area is typically warm-temperate, 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).

2.2.3.5 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).

2.2.4 Jacobsdal

Surveys were carried out in February 2011 at two farms (Langhoek and Kempster) situated in the Jacobsdal area near Kimberley (29° 7'S 24°46'E; altitude 1138 m a.s.l.). The farms are located in the Free State province, close to the Northern Cape border (Figure 2.2d). The study area represents the Kimberley Thornveld vegetation unit in the Eastern Kalahari Bushveld bioregion of the Savanna biome (Mucina & Rutherford, 2006).

2.2.4.1 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 might be 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 0.75 m, resulting in a very dense plant stand, which is common under center pivot irrigation systems.

2.2.4.2 Vegetation and landscape features

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

2.2.4.3 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 form and is sandy to loamy in nature (Mucina & Rutherford, 2006).

2.2.4.4 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).

2.2.4.5 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 the 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 *Senegalia mellifera* subsp. *detinens* (Mucina & Rutherford, 2006).

2.2.5 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 Western Maputaland Clay Bushveld vegetation unit of the Lowveld Bioregion, Savanna Biome (Figure 2.2e).

2.2.5.1 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.

2.2.5.2 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 of the Fabaceae such as *Dichrostachys cinerea* (Fabaceae) *and Senegalia/Vachellia* (Acacias). Understory species are typically species of the Poaceae such as *Dactyloctenium australe* and *Panicum maximum* (Hofs *et al.*, 2008).

2.2.5.3 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 latisols (Hutton, Bainsvlei and Shortlands soil forms) as well as calcimorphic soils of the Valsrivier and Avalon soil forms (Mucina & Rutherford, 2006).

2.2.5.4 Climate

The area is characterized by summer rainfall and dry winters with a mean annual precipitation of 500-750mm. The area is typically characterized by very hot sub-tropical summers and no incidence of frost in winter (Mucina & Rutherford, 2006).

2.2.5.5 Conservation status

The unit is considered vulnerable with 11% conserved in protected areas (mostly in Ndumu and Mkuzi game reserves). A large portion has been transformed mainly by cultivation. Severe invasive plant infestations occur sporadically, commonly by *Chromolaena odorata*, *Lantana camara* and *Opuntia* species (Mucina & Rutherford, 2006).

2.2.6 Thohoyandou

Surveys were conducted during November 2009 at Mutshenzheni and Tshiombo communal areas, situated in the Lowveld Bioregion in the Makuleke Sandy Bushveld vegetation unit of the Savanna Biome near Thohoyandou (22°47’S, 30°29’E; altitude 613-680 m a.s.l.) (Figure 2.2f).

2.2.6.1 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 pumpkin, sweet potato and peanut (*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 irrigation 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.

2.2.6.2 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 *Burkea africana, Guibourtia conjugate, Peltophorum africana and Terminalia sericea* 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).

2.2.6.3 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).

2.2.6.4 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).

2.2.6.5 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).

2.3 Survey methods

2.3.1 Experimental layout

Three representative localities were chosen for each of the two biomes, with one locality per province. The six survey localities had to fulfil pre-selected criteria before selection. The maize fields had to border on rangeland that remained unfragmented for up to 5 km. Therefore, the rangelands bordering the fields could not include old fields, strips between two fields, or lie between fields and tarred roads or buildings. Fields had to have clearly defined field margins with anthropogenic features such as fences, tracks, farm roads and headlands. Fields were only sampled when the maize plants were at the flowering stage of development (specific to each province) (Table 2.1).

At each of the six localities, four sites (each comprising a maize field bordering on rangeland), were selected approximately 5 km apart. The four sites were positioned to capture the variability in the topography, namely two sites on hill slopes and two in the valleys. The gradient along hills or valleys was respectively sampled with one site running upslope and the other downslope in relation to the maize field. However, the feasibility of this design depended on access to land and position of other environmental features in the landscape. Six sampling points were established per site, resulting in twenty-four points at each locality and therefore 144 in total. Sampling points were placed along a 500 m long maize field-field margin gradient, never less than 50 m or more than 100 m apart (Figure 2.3a).

2.3.2 Land-use intensity classification of sampling points

The six sampling points of each site were classified into three classes based on their distance from the actively cultivated area, namely maize field, marginal vegetation and rangeland with two sampling points in each. This amounted to a total of 48 points per each distance class for the entire survey. The maize field points (inside maize fields between 100 m and 30 m from the field edge) were considered high land-use intensity (and therefore high-disturbance) sites subjected to ploughing and agrochemical (herbicide/pesticide/fertilizer) application, and which have been completely transformed for maize production. Marginal vegetation points (outside the maize fields between 30-100 m from the field edge) were medium land-use intensity, medium disturbance areas characterized by transformed semi-natural vegetation, but also indirectly influenced by agricultural activities associated with the directly adjacent maize fields. These areas typically contained features such as farm tracks, ditches or fences that accompany the field boundary vegetation beyond (Table 2.1). Rangeland points (100-400 m from maize fields) were characterized by low-intensity, low disturbance semi-natural vegetation used almost exclusively for livestock grazing. These were classified as low disturbance areas, since there were relatively low stocking rates on all the farms, all of which were predominantly maize production systems.

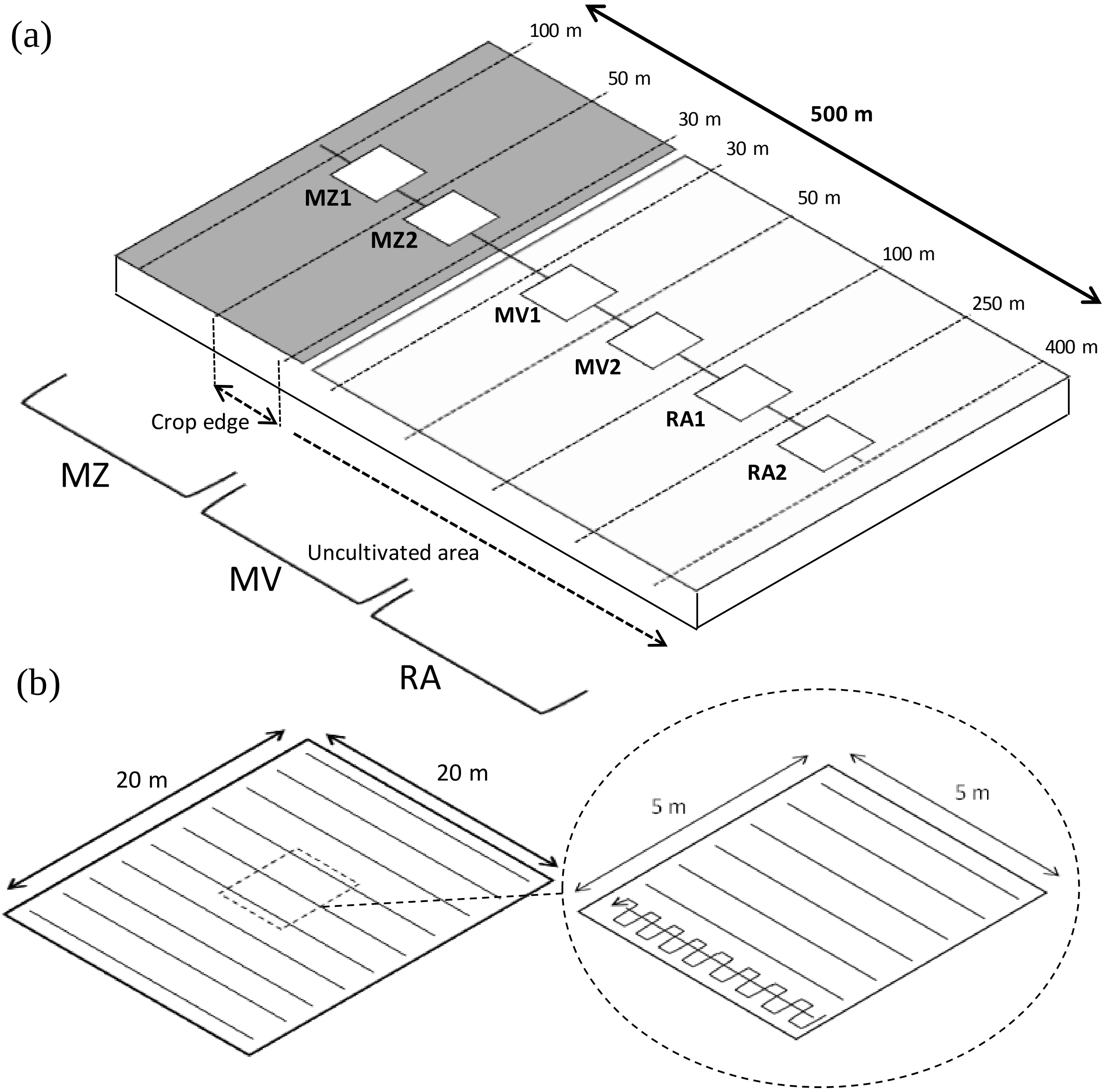

Figure 2.3: (a) Sampling points along a maize field-field margin gradient in a maize agro-ecosystem. Distance classes: MZ, maize field; MV, marginal vegetation; RA, rangeland. (b) Sample points consisted of ten parallel, fixed width (2m) line transects for plant surveys (left). Arthropod surveys (insert right) were conducted in the centre of each plant survey area and D-vac suction sampling was conducted in a zigzag pattern as indicated.

2.3.3 Arthropod sampling

The target group for this survey included plant-dwelling arthropods that occur in the maize agro-ecosystem during the reproductive stages (flowering) of maize. Therefore, surveys were scheduled to coincide with the regional flowering times of maize at each of the study localities. Studies have shown that these plant growth stages capture different trophic levels and that it is an ideal time to sample a comprehensive arthropod community in maize (Eckert *et al.*, 2006).

An adapted D-vac method was used for arthropod collection (Dietrick *et al.*, 1960). This is a relatively fast method for sampling large areas of vegetation, although its effectiveness may be altered by weather conditions and vegetation characteristics. It is really only effective in dry, upright vegetation that is not more than 15 cm high (Southwood & Henderson, 2000). Suction in dense vegetation may selectively extract certain species and under-sample others (Elliott, *et al.* 2006). Therefore, it may be an effective method in grassy habitats, if not in dense woodlands. However, unlike passive methods such as pitfall traps the D-vac method is not as dependent on insect activity and is less prone to sampling error (Thomas & Marshall, 1999) and may represent one of the best techniques for sampling a wide range of arthropod taxa in vegetation.

Because the performance of the D-vac method is dependent on weather conditions, it was attempted to sample arthropods under relatively similar weather conditions across localities and no sampling was conducted in wet conditions or at high wind speeds. Seven swaths per plot were made, following a zigzag pattern with the D-vac nozzle in each swath (Figure 2.3b). No samples were taken of soil arthropods and this study is therefore based on above-ground plant-dwelling arthropods. 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 collected preserved arthropod taxa were assessed following a rapid and cost effective method involving classification to morpho-species level. It has been shown that this method can provide estimates of richness and turnover similar to methods that make use of species classified by taxonomists (Oliver & Beattie, 1996). Care was taken to insure that a morpho-species was regarded as the same 'species' for the entire sample (across all transects and localities) by compiling a photographic guide to which new individuals were compared. Classifications follow Picker *et al.* (2004) and Scholtz and Holm, (1985). The number and abundance of each morpho-species was further determined for each plot.

2.3.4 Vegetation sampling

At each sampling point a fixed width (2m) line transect approach was followed (Hill, 2005) and adapted to include ten parallel transects of 20 m each, along which plant species were recorded (Figure 2.3b). This ensured that the vegetation sampling would overlap with the same area as the arthropod sampling. A continuous single 100 m transect would have extended 47.5 m in two directions away from the arthropod sample point, but the modification reduced this distance to 7.5 m in all directions to provide a more accurate representative sample of the vegetation associated with the arthropods. At 1 m intervals, one plant species was recorded for every major growth form, that is, grass, herb, shrub and tree. Therefore, a maximum of four species were recorded at each 1 m interval if all growth forms were represented. The number of individuals per species across the ten transects was summed to determine the species abundances for the sample point. Plants were identified up to species level and species names follow Germishuizen *et al.* (2006). Only ten specimens remained unidentified and were treated as morpho-species.

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CHAPTER 3: PLANT AND ARTHROPOD DIVERSITY PATTERNS OF MAIZE AGRO-ECOSYSTEMS IN TWO GRASSY BIOMES OF SOUTH AFRICA

3.1 Overview

In this chapter, the total biodiversity patterns of biota associated with maize agriculture at the regional scale in South Africa were investigated. Specifically, the total diversity and species assemblage patterns were compared between maize fields and margins of six localities in South Africa across two biomes for plants and associated arthropods. The results indicated that, although biodiversity loss was apparent in maize fields, plant and arthropod diversity remained the same for marginal vegetation (30 -100 m from maize fields) and rangelands (100-400 m from maize fields), suggesting that distance from maize fields had no effect on biodiversity patterns beyond 30 m. Plant species assemblages were best correlated with agricultural disturbance while arthropod communities were mainly correlated with biome. The results suggest that the marginal vegetation of crop fields (30-100 m from field edge) were not species poor ecosystems, but were surprisingly rich in plant and arthropod diversity. Field margins may therefore be of conservation value in the agricultural landscape with a diversity of species supporting important ecosystem services.

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3.2 Introduction

Commercial cropping systems are unstable ecosystems and simply cannot support levels of non-crop diversity equal to natural ecosystems (Tivy 1990). Hence, the transformation of natural habitat into crop fields inevitably leads to species loss. This effect may extend well beyond the boundary of the crop itself. Several studies have shown that the presence of crop fields often cause significant alterations in plant and invertebrate community structure in adjacent natural habitat (Boutin & Jobin, 1998; Carrière *et al.,* 2009; McKone *et al.,* 2001; Oleszczuk *et al.,* 2010; Piessens *et al.,* 2006) and may result in an overall reduction in diversity and richness in crop field margins. This effect could extend to considerable distances from the fields when aspects such as agrochemical and genetically modified (GM) plant material drift are taken into account. For instance, studies by Beckie and Hall (2008), Devos *et al.* (2009); Hofmann *et al.* (2010); Messeguer *et al.* (2006); Rosi-Marshall *et al.*, 2007 and Viljoen and Chetty, 2011 seem to indicate that the critical zone for maize pollen deposition is in the first 150 m from maize fields; although Sanvido *et al.*, 2008 found 400 m to be the furthest point at which cross fertilisation between GM and non-GM maize occurred.

The effects of the anthropocene on the complexity and interactions of ecosystems are commonly expressed in terms of species diversity losses (Siebert 2011). This is important since higher biodiversity is, for instance, required to escalate suppression of insect pest numbers within agro-ecosystems (Gurr *et al.*, 2012; Ratnadass *et al.*, 2012). It has therefore become increasingly important to understand the effect of our activities on biodiversity to regulate the management and conservation of natural systems for our benefit. However, research concerning fauna and flora of agro-ecosystems often involve only one or two key species (often pests or weeds) and there is a need for studies that include complete diversity (Meissle *et al.*, 2012). Furthermore, there is a need for surveys of arthropod diversity in field margins adjacent to crop fields and to link this data to non-crop plant communities (Meissle *et al.*, 2012).

In South Africa, baseline biodiversity data from agro-ecosystems in either crop fields or surrounding margins are rudimentary at best (e.g. Gaigher *et al.*, 2016; O'Connor, 2005; Siebert, 2011; Walters *et al.*, 2006; Wessels *et al.*, 2003; Witt & Samways, 2004). Maize cropping systems are such a common feature in South Africa (Fairbanks *et al.*, 2000) that it has become necessary to understand what effects these activities may have on the biodiversity of the adjacent landscape. As primary producers, plants form the basis of most terrestrial food chains and it is known that changes in plant diversity or species composition may in turn affect the nature of consumer populations (Caballero-López *et al.*, 2010; Schaffers *et al.*, 2008; Schellhorn & Sork, 1997; Siemann *et al.*, 1998). Furthermore, arthropods increase our knowledge of total biodiversity (or species richness) and in addition serve as useful bio-indicators to disturbance since they are present in almost all environments. They react to environmental changes more rapidly than vertebrates and can provide early detection of ecological changes (Rodríguez *et al.*, 1998; Kremen *et al.*, 1993). They also provide valuable ecosystem services in agro-ecosystems such as biological pest control (Moolman *et al.*, 2013) and pollination (Aizen *et al.*, 2008; Klein *et al.*, 2007; Stary & Pike, 1999) and are an important food source for vertebrate taxa (Ponce *et al.*, 2014). As such, plants and arthropods are useful representatives of total biodiversity within ecosystems. Therefore, the aims of this study were to compare the total diversity and assemblage patterns of plant and arthropod and species of maize agro-ecosystems along a maize field-field margin gradient at the local scale and between two grassy biomes (grassland and savanna) at the regional scale. The following research questions were asked: (1) How do the species richness and diversity of plants and associated arthropods compare along a gradient of agricultural disturbance, and how do these patterns differ between biomes? (2) How are the species compositions of plant and arthropod communities affected by the agricultural disturbance gradient? (3) How do the beta diversity of plants and arthropods compare between maize fields and uncultivated vegetation?

At farm level, crop fields are intensively transformed systems (Tivy 1990) and the disturbances associated with this transformation may affect the diversity and species composition of biota in adjacent rangeland (Bundschuh *et al.*, 2012; de Snoo & de Wit, 1998; de Snoo & van der Poll 1999; Marshall & Moonen 2002). Therefore, it is hypothesized that plant and arthropod diversity of field margins will be negatively affected by maize fields and would result in a reduction of species richness and diversity. To compensate for species loss and to maintain ecosystem functioning in disturbed areas, disturbance-intolerant species would then be replaced by disturbance-tolerant species (Siebert, 2011; Yachi & Loreau, 1999). It was therefore proposed that field margin diversity would be replaced by a unique set of species (assemblages) that are presumably better adapted to tolerate disturbance. At a regional level, climatic differences and management regimes could also have an effect on the diversity and species composition of biota in agro-ecosystems. Also, savanna is multi-layered with more niches than the Grassland Biome (Curry, 1994; Schadek *et al.*, 2009). It is therefore hypothesised that the multi-layered natural vegetation of the Savanna Biome will contain higher plant and arthropod diversity than the Grassland Biome. Anthropogenic activities have a tendency to degrade beta diversity, resulting in biotic homogenization at the regional scale (McKinney & Lockwood, 1999). These activities include agriculture, and therefore it was proposed that maize fields would have lower beta diversity (less species turnover between biomes) compared to natural environments.

It is important to note that the disturbances of agricultural activities should have different effects on different plant and arthropod functional types and traits (Liira *et al.*, 2008; Oliver & Beattie, 1996). The individual responses of separate groups will be investigated in chapters 4 and 5.

3.3 Material and methods

3.3.1 Biodiversity quantification

Sampling methods for this chapter are outlined in chapter 2.2. To describe the multi-facetted nature of biodiversity, diversity indices must be used in conjunction with species richness (Begon *et al.*, 2008). Two types of diversity indices were used on the subsequent dataset, namely those that emphasise species richness and those that condense both species richness and evenness (how equally abundant species are) into a single value, also referred to as heterogeneity indices (Magurran, 1988).

Species richness was quantified by counting the number of species (S) in the sample. Margalef's species richness index (d) was used as an additional species richness measure as it compensates for the sampling effect by dividing richness (S) by the total number of individuals in a sample (N). It may therefore be a more meaningful measure of species richness than simple species counts. It is unfortunately not completely uninfluenced by sampling effort (Magurran, 2004).

The Shannon-Wiener diversity index, Simpson's diversity index and Pielou's evenness were used as heterogeneity measures. The Shannon-Wiener diversity index (H') remains one of the most popular diversity indices used in the literature (Samways, 1984) and is therefore valuable for comparison between studies. As a heterogeneity measure, the index condenses species richness and evenness into a single figure. However, this can make interpretation difficult since an increase in the index value may be attributed to greater species richness, evenness or both. The Shannon-Wiener index however tends to weigh towards species richness and is also dependent on sample size, although not as heavily as species richness (Magurran, 1988).

Simpson's diversity index (Ď) is expressed as 1-D (the complement of Simpson's index). It is considered to be one of the most robust and meaningful diversity indices and it is also known as dominance or evenness measure, as it is weighted towards abundances of the commonest species rather than species richness (Magurran, 2004). Therefore Ď will increase with increasing evenness in a given sample. Despite emphasising evenness over species richness, it is not considered to be an evenness measure *per se* (Magurran, 2004).

As such, Pielou's evenness (J') was used to determine evenness or dominance patterns in the dataset. Also known as the Shannon evenness measure, it is derived from the Shannon-Wiener diversity index and uses the ratio of observed diversity to maximum diversity to measure evenness (Pielou, 1975). Pielou's evenness values range from 0 to 1.0, with 1.0 representing complete evenness (Magurran, 2004).

The abovementioned indices display different aspects of species diversity and were therefore used in combination to provide a more complete picture of species richness and diversity. Index values were calculated using PRIMER 6 software (Clarke & Gorley 2006).

3.3.2 Statistical analyses

Hierarchical Linear Model (HLM) analysis were performed on the dataset using a two-way ANOVA with a random effects model (McMahon & Diez, 2007) in SPSS software to test for overall significant differences in index values between biomes and across maize field-field margin gradients. The index values were chosen as response variables to determine if these values differed between the respective distances from the maize field and therefore if they could be predicted by disturbance intensity. Transects were specified as primary unit of measurement (subject ID) to account for the nestedness of transects within the sampling locality. The covariance structure was specified as unstructured. Each transect along the maize field-field margin gradient was considered an independent variable and sampling points within the same transect were considered dependent variables for statistical analyses. Effect sizes (Cohen's d) were calculated to express practical significance between sampling points where residual variance as well as transect variance were taken into account in the calculation of the effect size (Ellis & Steyn, 2003). The effect sizes were interpreted as follows: small effect: d=0.2, (b) medium effect: d=0.5 and (c) large effect: d=0.8.

Canonical correspondence analysis (CCA) (Ter Braak, 1986) was applied to the data using PAST software (Hammer, 2008) to depict how different points compared in terms of arthropod and plant species composition and to assess the relative importance of the environmental variables and management regimes in determining plant and arthropod species assemblages of the various sampling points. Five factors were considered for a biplot with species data. These included distance from maize field (m), disturbance (negatively related to distance), biome (grassland or savanna), altitude (m a.s.l.) and farming practice (commercial or subsistence).

To test whether overall significant differences exist between points in different distance classes and biomes in terms of species composition, the Adonis programme in package vegan in R (Oksanen, 2011) was used, which is appropriate for taking into account the nestedness of the data within transects. In addition, Analysis of Similarity (ANOSIM), a non-parametric test for significant differences, was performed with PAST software (Hammer, 2008) to illustrate significant differences in a pairwise format.

3.4 Results

3.4.1 Plant diversity patterns

The plant survey recorded 15019 individuals representing 824 native and exotic species (including *Z. mays*) in 95 families, with 148 species recorded from maize fields, 584 from marginal vegetation and 570 from rangeland vegetation. Approximately 10% (86 species) of species were alien weeds. Most were found inside the maize fields (64 species), while the marginal vegetation and rangeland vegetation collectively contained 55 alien species. The largest proportion of alien species relative to the total number of species in each distance class was found in the maize fields (42%) compared to 4% and 5% of alien plant species recorded in the floras of the marginal and rangeland vegetation respectively.

Comparisons of species richness between points along the maize field-field margin gradients of the Grassland and Savanna Biomes revealed that the number of plant species was significantly lower in maize fields compared to the uncultivated vegetation (that is marginal and rangeland vegetation) (Figure 3.1a; Table 3.1, 3.2). However, there were no significant differences in the number of plant species between the marginal and rangeland vegetation. A significant interaction effect was found between biome and distance, indicating that the Grassland and Savanna Biomes reacted differently to distance (Table 3.1). This difference occurred mainly in the uncultivated vegetation, where the points at 30-50 m (MV1) from maize fields in grassland had significantly lower species richness values than points at 50-250 m (MV2 and RA1) (Table 3.3). This was not the case for savanna. Also, plant species richness in the savanna levels off while grassland plant species richness decreases with increasing distance away from maize fields (Figure 3.1).

Table 3.1: Hierarchical Linear Modelling (HLM) results indicating overall differences in plant richness and diversity index values between biomes (grassland and savanna), distance from maize field (m) and interactions (between biome and distance).

		Species richness	Margalef's species richness	Shannon-Wiener diversity	Simpson's diversity	Pielou's evenness
Distance	df	114.66	114.367	114.595	115.414	132
	F	41.016	30.184	55.149	35.525	28.567
	p	**0.000***	**0.000***	**0.000***	**0.000***	**0.000***
Biome	df	18.159	17.904	17.208	16.658	132
	F	11.21	9.088	6.997	2.114	0.352
	p	**0.004***	**0.007***	**0.017***	0.165	0.554
Interaction (Distance* Biome)	df	114.66	114.367	114.595	115.414	132
	F	2.771	2.683	1.232	0.706	1.073
	p	**0.021***	**0.025***	0.299	0.62	0.378
MSE		57.746	4.247	0.132	0.005	0.004
Variance (Transect)		33.523	2.727	0.023	0.000	0.000

F = F value; p = p value. Bold text* indicates significant p values at $p \leq 0.05$
MSE= mean square error, unexplained variance
Variance (transect) = variance explained by transect

The Savanna Biome had higher plant species richness than the Grassland Biome, except inside the main crop (MZ1), approximately 100 m from the field margin (Table 3.4). The effect was most significant for uncultivated vegetation sampling points.

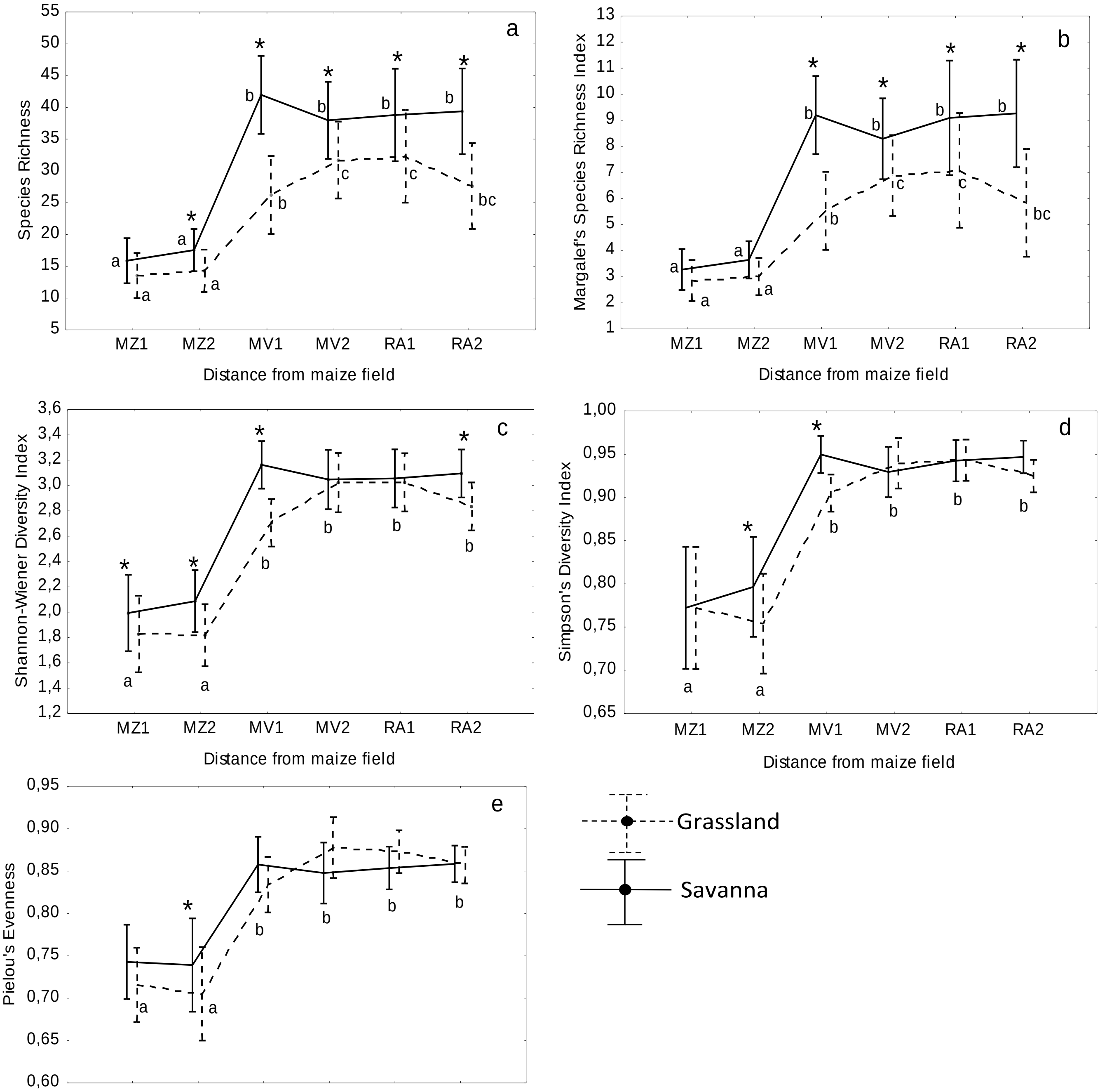

Figure 3.1: Diversity measures for plants along maize field-field margin gradients in two biomes of South Africa. Significant differences (d≥0.5) between distances along the gradient are indicated by different letters (savanna and grassland reacted similarly, except for (a) and (b), where the biomes showed a different effect at RA1). * indicates significant variation between biomes at similar distances (d≥0.5). Vertical bars denote 0.95 confidence intervals. Distances: MZ1 and MZ2, maize field; MV1 and MV2, marginal vegetation (30-100 m) RA1 and RA2, rangeland (100-400 m).

Table 3.2: Mean values for plant diversity indices at various distances from maize fields. MZ1 and MZ2, maize field; MV1 and MV2, marginal vegetation (30-100 m); RA1 and RA2, rangeland (100-400 m). Means with different superscripts differed practically, as indicated by effect sizes (d≥0.5).

	Species Richness	Margalef's species richness	Shannon-Wiener diversity index	Simpson's diversity index	Pielou's evenness
MZ1	15.693^{a}	3.323^{a}	1.925^{a}	0.773^{a}	0.728^{a}
MZ2	16.902^{a}	3.584^{a}	1.967^{a}	0.776^{a}	0.721^{a}
MV1	35.068^{b}	7.620^{b}	2.949^{b}	0.928^{b}	0.845^{b}
MV2	35.818^{b}	7.842^{b}	3.050^{b}	0.935^{b}	0.862^{b}
RA1	36.527^{b}	8.341^{b}	3.055^{b}	0.943^{b}	0.862^{b}
RA2	34.485^{b}	7.804^{b}	2.980^{b}	0.936^{b}	0.857^{b}

Table 3.3: Mean values for plant diversity measures indicating significant interaction effects between biome and distance from maize field in terms of plant species richness and Margalef's species richness index values. MZ1 and MZ2, maize field; MV1 and MV2, marginal vegetation (30-100 m); RA1 and RA2, rangeland (100-400 m). Means with different superscripts differed practically, as indicated by effect sizes (d≥0.5).

		Species richness	Margalef's species richness
Grassland	MZ1	13.417^{a}	2.824^{a}
	MZ2	14.167^{a}	2.975^{a}
	MV1	26.083^{b}	5.495^{b}
	MV2	31.583^{c}	6.847^{c}
	RA1	32.167^{c}	7.046^{c}
	RA2	27.500^{bc}	5.802^{bc}
Savanna	MZ1	17.970^{a}	3.822^{a}
	MZ2	19.637^{a}	4.193^{a}
	MV1	44.053^{b}	9.745^{b}
	MV2	40.053^{b}	8.837^{b}
	RA1	40.887^{b}	9.636^{b}
	RA2	41.470^{b}	9.807^{b}

Table 3.4: Comparisons between grassland and savanna in terms of mean plant richness and diversity index values at similar distances from maize field. MZ1 and MZ2, maize field; MV1 and MV2, marginal vegetation (30-100 m); RA1 and RA2, rangeland (100-400 m). Means with different superscripts differed practically, as indicated by effect sizes ($d \geq 0.5$).

	Species Richness	Margalef's species richness	Shannon-Wiener diversity index	Simpson's diversity index	Pielou's evenness
MZ1 (Grassland)	13.417^{a}	2.824^{a}	**1.821^{a}**	0.771^{a}	0.715^{a}
MZ1 (Savanna)	17.970^{a}	3.822^{a}	**2.030^{b}**	0.774^{a}	0.742^{a}
MZ2 (Grassland)	**14.167^{a}**	2.975^{a}	**1.812^{a}**	**0.753^{a}**	**0.704^{a}**
MZ2 (Savanna)	**19.637^{b}**	4.193^{a}	**2.123^{b}**	**0.798^{b}**	**0.738^{b}**
MV1 (Grassland)	**26.083^{a}**	**5.495^{a}**	**2.699^{a}**	**0.904^{a}**	0.833^{a}
MV1 (Savanna)	**44.053^{b}**	**9.745^{b}**	**3.199^{b}**	**0.952^{b}**	0.857^{a}
MV2 (Grassland)	**31.583^{a}**	**6.847^{a}**	3.016^{a}	0.939^{a}	0.877^{a}
MV2 (Savanna)	**40.053^{b}**	**8.837^{b}**	3.083^{a}	0.931^{a}	0.847^{a}
RA1 (Grassland)	**32.167^{a}**	**7.046^{a}**	3.018^{a}	0.942^{a}	0.872^{a}
RA1 (Savanna)	**40.887^{b}**	**9.636^{b}**	3.092^{a}	0.944^{a}	0.853^{a}
RA2 (Grassland)	**27.500^{a}**	**5.802^{a}**	**2.828^{a}**	0.924^{a}	0.856^{a}
RA2 (Savanna)	**41.470^{b}**	**9.807^{b}**	**3.131^{b}**	0.949^{a}	0.857^{a}

Margalef's species richness index revealed similar trends across the maize field-field margin gradient to that for species richness, with the only significant differences in plant species richness between maize fields and marginal vegetation and also between maize fields and rangeland vegetation (Figure 3.1b; Table 3.1, 3.2). Biomes also reacted differently to distance in the rangeland area in terms of the Margalef index values, as indicated by the significant interaction (Table 3.3). The index also indicated significantly higher Margalef index values for savanna compared to grassland, although this was only true for the uncultivated vegetation (Figure 3.1b; Table 3.4).

All three heterogeneity indices, that is, the Shannon-Wiener diversity index, Simpson's diversity index and Pielou's evenness reacted in a similar way to the species richness measures with the only significant variation in plant diversity between maize fields and uncultivated vegetation (Figure 3.1c, d, e; Table 3.1, 3.2). As the Simpson's diversity index (Figure 3.1d) is weighted towards plant evenness, this indicates that plant species evenness is not statistically different in marginal and rangeland areas. This was also confirmed by the results for Pielou's evenness (Figure 3.1e) and was consistent for both biomes. Significant differences between the Savanna and Grassland Biomes were found for the Shannon index, and to a lesser extent for Simpson's index and Pielou's evenness (Table 3.4). Significant variation was most evident in the first 50 m of the maize field and the first 50 m of the marginal vegetation area, with savanna always displaying the higher values and seemingly peaking at 30-50 m and the grassland diversity peaking at 80-100 m from the maize field. Refer to Appendix A (Tables A.1 – A.3) for effect sizes regarding plant diversity patterns.

3.4.2 Plant species composition patterns

In the biplot of Canonical Correspondence Analysis (CCA) for sample points, the distance from maize field (m) and disturbance level were closely correlated with axis 1, while biome, altitude and farming practice were more strongly correlated with axis 2 (Figure 3.2, Table 3.5). Axis 1 and 2 explained 31.93% and 29.38% of the total variation respectively. The most important factors correlated with plant species assemblages were disturbance (which is positively correlated with distance from fields), separating the maize fields from the rangelands at the local level, and at the regional level, climate, separating the biomes. Altitude and farming practice had weaker correlations with plant species composition.

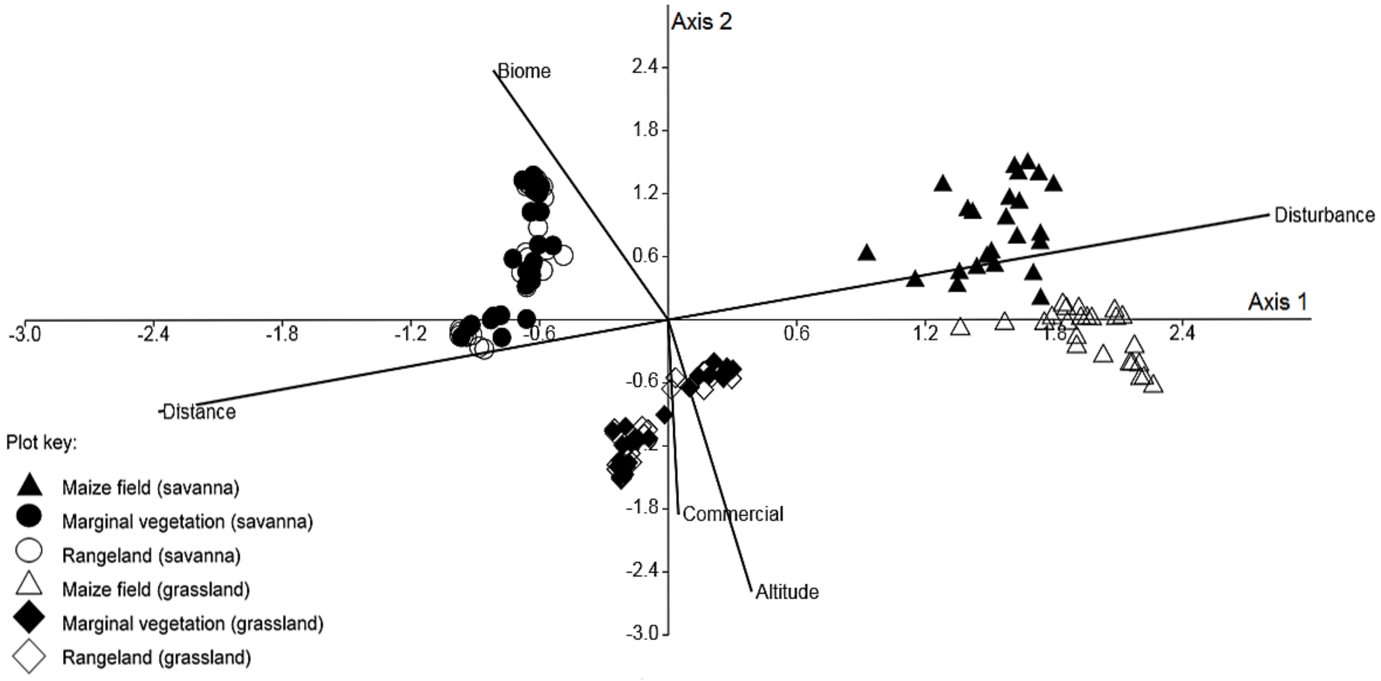

Figure 3.2: Canonical correspondence ordination of all sampled localities, showing correlations for environmental variables of plant sampling points. Environmental variables are represented by lines and sampling points by symbols. Each symbol represents the weighted average of one plot. Environmental factors were: distance (distance from maize field); disturbance (increasing with decreasing distance from maize field); biome (grassland/savanna); altitude (m a.s.l.) and farming practice (commercial/subsistence).

Table 3.5: Correlations of ordination axes with environmental factors as well as eigenvalues and percentage variance explained for canonical correspondence analysis of plants at all localities.

Factor	Axis 1	Axis 2
Distance	-0.793	-0.290
Disturbance	0.936	0.331
Biome	-0.271	0.792
Altitude	0.130	-0.863
Commercial	0.016	-0.620
Eigenvalue	0.830	0.764
% variance explained	31.93	29.38

Overall, the biplot revealed three distinctive groupings of the plant sampling points. The first group represented maize fields that are characterised by high levels of disturbance. The second group represented savanna that are characterised by low levels of disturbance, lower altitudes and subsistence type farming practices. The third group was grassland, characterised by low levels of disturbance, higher altitudes and more commercialised maize production systems. Therefore, maize field points represented distinctive clusters relative to all uncultivated vegetation points, while marginal and rangeland points clustered together according to biome. Therefore, the marginal vegetation and rangeland points of each biome were not different in terms of species assemblages. This was in accordance with the Adonis results (Table 3.6), which displayed highly significant differences between biome and distance class groups at p = 0.001.

Table 3.6: Adonis analysis results, with nestedness of data in a transect taken into account, indicating significance of separation between distance classes (maize field, marginal vegetation and rangeland) within biome for plants based on species composition.

	df	F	R	p
Biome	1	13.526	0.068	**0.001***
Distance class	2	19.810	0.198	**0.001***
Interaction (Biome*Distance class)	2	4.278	0.043	**0.001***
Residuals	138	---	0.691	---

df = degrees of freedom; F = F-value; R = R-value; p = p-value
Bold text* indicates significant p values at $p \leq 0.05$

The pairwise comparisons of ANOSIM analyses (Table 3.7) indicated differences in species composition between maize fields and uncultivated areas, and also between biomes at p<0.005. However, within biomes, the marginal and rangeland vegetation areas did not differ significantly. These results therefore confirmed the groupings found in the CCA analysis. ANOSIM analyses also showed differences in plant species composition between maize fields of grassland and savanna, indicating that maize fields had relatively unique weed communities, specific to biome (note that the analyses were based on a dataset excluding maize plant counts). Furthermore, plant assemblages within rangelands of the Grassland Biome had a much tighter clustering compared to the savanna sampling points. This is confirmed by the lower p-value for the comparison between grassland marginal and rangeland areas (Table 3.7). It must be added that, although all three of the above mentioned analyses displayed similar trends, the results for species composition must be handled with caution due to the abundance of zero values in the datasets and that the ANOSIM analysis could not take into account the nestedness of data within transects.

Table 3.7: ANOSIM analysis p-values indicating significance of separation between plant groups based on species composition. MZ (G) = Maize field, Grassland Biome; MZ (S) = Maize field, Savanna Biome; MV (G) = Marginal vegetation (30-100 m), Grassland Biome; MV (S) = Marginal vegetation, Savanna Biome; RA (G) = Rangeland (100-400 m), Grassland Biome; RA (S) = Rangeland, Savanna Biome.

	MZ (S)	MZ (G)	MV (S)	MV (G)	RA (S)
MZ (G)	**0.0001***	---	---	---	---
MV (S)	**0.0001***	**0.0001***	---	---	---
MV (G)	**0.0001***	**0.0001***	**0.0001***	---	---
RA (S)	**0.0001***	**0.0001***	0.8084	**0.0001***	---
RA (G)	**0.0001***	**0.0001***	**0.0001***	0.6583	**0.0001***

Bold text* indicates significant separations at p<0.05

3.4.3 Arthropod diversity patterns

A total of 117 arthropod families, 1 629 morpho-species and 39 497 individuals were recorded. This amounted to 576 morpho-species for maize fields, 1031 for marginal vegetation points and 1023 for rangeland points. The arthropods collected during the study belonged to 23 orders with the most dominant ones being the Hemiptera (true bugs) followed by the Hymenoptera (bees, wasps and ants), Diptera (flies), Coleoptera (beetles), Araneae (spiders) and Orthoptera (crickets, grasshoppers, and locusts).

The arthropod species richness measures both revealed significant variation in arthropod species numbers between maize fields and uncultivated vegetation, but not between marginal and rangeland areas within the uncultivated habitats (Figure 3.3a, b; Table 3.8, 3.9). This is similar to what was found for plant species richness measures. The non-significant interaction for both species counts and Margalef's species richness index (Table 3.8) indicates that both the Grassland and Savanna Biomes reacted similarly to distance regarding species numbers. However, grassland was found to have significantly higher arthropod species richness than the savanna (Figure 3.3a; Table 3.10), although only in uncultivated vegetation. This is in contrast to the results for plant species richness, where the Savanna Biome had significantly higher richness than the Grassland Biome.

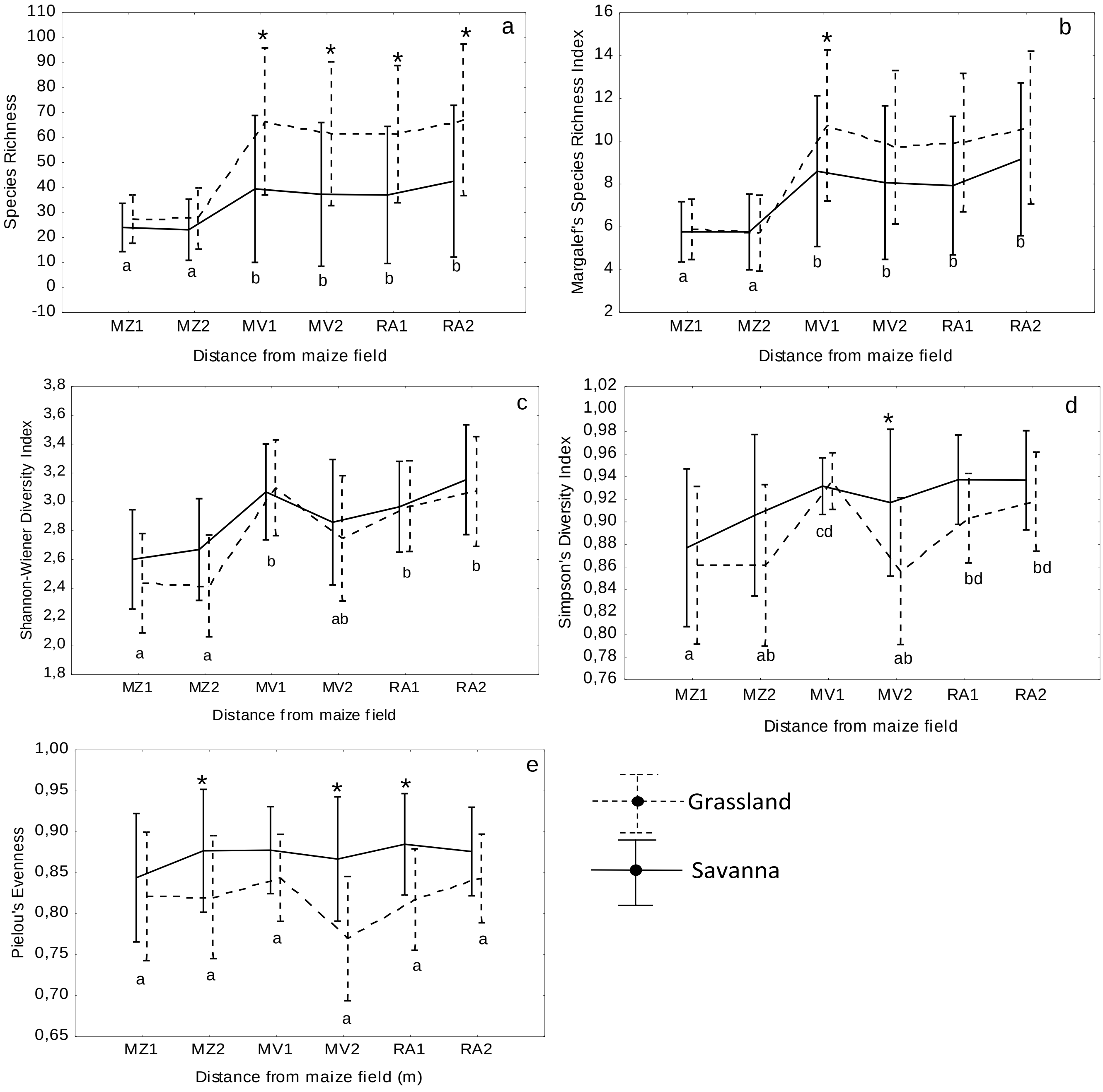

Figure 3.3: Diversity measures for arthropods along maize field-field margin gradients in two biomes of South Africa. Significant differences (d≥0.5) between distances along the gradient are indicated by different numbers (savanna and grassland reacted similarly). * indicates significant variation between biomes at similar distances (d≥0.5) and values in parenthesis indicate size effects. Vertical bars denote 0.95 confidence intervals. Distances: MZ1 and MZ2, maize field; MV1 and MV2, marginal vegetation (30-100 m) RA1 and RA2, rangeland (100-400 m).

Table 3.8: Hierarchical Linear Modelling (HLM) results indicating overall differences in arthropod richness and diversity index values between biomes (grassland and savanna), distance from maize field (m) and interactions (between biome and distance).

		Species richness	Margalef's species richness	Shannon-Wiener diversity	Simpson's diversity	Pielou's evenness
Distance	df	113.818	113.783	113.298	132	112.237
	F	8.964	9.544	6.134	2.038	0.624
	p	**0.000***	**0.000***	**0.000***	0.077	0.681
Biome	df	17.711	17.64	16.656	132	15.311
	F	1.486	0.764	0.039	3.355	3.877
	p	0.239	0.394	0.847	0.069	0.067
Interaction (Distance* Biome)	df	113.818	113.783	113.298	132	112.237
	F	1.45	0.613	0.248	0.374	0.438
	p	0.212	0.69	0.94	0.866	0.821
MSE		497.181	8.919	0.268	0.009	0.011
Variance (Transect)		1417.732	18.947	0.111	0.000	0.002

F = F value; p = p value. Bold text* indicates significant p values at $p \leq 0.05$
MSE= mean square error, unexplained variance
Variance (transect) = variance explained by transect

Table 3.9: Mean values for arthropod diversity indices at various distances from maize fields. MZ1 and MZ2, maize field; MV1 and MV2, marginal vegetation (30-100 m); RA1 and RA2, rangeland (100-400 m). Means with different superscripts differed practically, as indicated by effect sizes ($d \geq 0.5$).

	Species Richness	Margalef's species richness	Shannon-Wiener diversity index	Simpson's diversity index	Pielou's evenness
MZ1	23.685^{a}	5.507^{a}	2.481^{a}	0.869^{a}	0.833^{a}
MZ2	23.352^{a}	5.416^{a}	2.506^{a}	0.883^{ab}	0.849^{a}
MV1	50.935^{b}	9.347^{b}	3.046^{b}	0.933^{cd}	0.861^{a}
MV2	47.394^{b}	8.571^{b}	2.766^{ab}	0.886^{ab}	0.819^{a}
RA1	47.185^{b}	8.610^{b}	2.931^{b}	0.920^{bd}	0.852^{a}
RA2	52.810^{b}	9.577^{b}	3.076^{b}	0.927^{bd}	0.860^{a}

The Shannon-Wiener diversity index revealed similar results to the species richness measures (Figure 3.3c; Table 3.8, 3.9) along the maize field-field margin gradient. Diversity seems to peak in the first 30-50 m from the maize field in the marginal vegetation area. In contrast to richness however, no significant differences were found between the Grassland and Savanna Biomes in terms of the Shannon index. These results were consistent across the two biomes as indicated by the non-significant interaction (Table 3.8).

For Simpson's diversity index (Figure 3.3d), no significant differences were found at any of the distances along the maize field-field margin gradient and were consistent for both biomes, as indicated by the non-significant interaction (Table 3.8, 3.9). This was also found for Pielou's evenness (Figure 3.3e; Table 3.8, 3.9), where arthropod abundances within communities did not differ across the whole gradient.

Table 3.10: Comparisons between grassland and savanna in terms of mean arthropod richness and diversity index values at similar distances from maize field. MZ1 and MZ2, maize field; MV1 and MV2, marginal vegetation (30-100 m); RA1 and RA2, rangeland (100-400 m). Means with different superscripts differed practically, as indicated by effect sizes (d≥0.5).

	Species Richness	Margalef's species richness	Shannon-Wiener diversity index	Simpson's diversity index	Pielou's evenness
MZ1 (Grassland)	27.083^{a}	5.850^{a}	2.429^{a}	0.861^{a}	0.820^{a}
MZ1 (Savanna)	20.287^{a}	5.163^{a}	2.533^{a}	0.876^{a}	0.846^{a}
MZ2 (Grassland)	27.333^{a}	5.674^{a}	2.411^{a}	0.861^{a}	**0.819^{a}**
MZ2 (Savanna)	19.371^{a}	5.158^{a}	2.601^{a}	0.905^{a}	**0.879^{b}**
MV1 (Grassland)	**66.167^{a}**	**10.700^{a}**	3.092^{a}	0.935^{a}	0.843^{a}
MV1 (Savanna)	**35.704^{b}**	**7.994^{b}**	3.001^{a}	0.931^{a}	0.880^{a}
MV2 (Grassland)	**61.250^{a}**	9.682^{a}	2.740^{a}	**0.856^{a}**	**0.769^{a}**
MV2 (Savanna)	**33.537^{b}**	7.460^{a}	2.791^{a}	**0.916^{b}**	**0.869^{b}**
RA1 (Grassland)	**61.083^{a}**	9.898^{a}	2.964^{a}	0.902^{a}	**0.816^{a}**
RA1 (Savanna)	**33.287^{b}**	7.322^{a}	2.898^{a}	0.937^{a}	**0.887^{b}**
RA2 (Grassland)	**66.833^{a}**	10.605^{a}	3.066^{a}	0.917^{a}	0.842^{a}
RA2 (Savanna)	**38.787^{b}**	8.549^{a}	3.086^{a}	0.936^{a}	0.878^{a}

These results indicate that significant increases in arthropod diversity index values in marginal areas were likely due to the increase in species richness and not abundance. Since the values of Pielou's evenness mostly ranged between 0.8 and 0.9 for arthropods (Figure 3.3e), the abundance of arthropod species are evenly distributed with no species dominance in both maize fields and uncultivated vegetation. Refer to Appendix A (Tables A.4 and A.5) for effect sizes regarding arthropod diversity patterns.

3.4.4 Arthropod species composition patterns

A CCA biplot indicated that distance from maize field and disturbance were less correlated with arthropod disturbance than those representing biome, altitude and farming practice (Figure 3.4; Table 3.11). Axis 1 and 2 explained 33.22% and 29.58% of the total variation in species composition respectively. Arthropod species assemblages were more strongly correlated with climatic related factors such as biome and altitude. For arthropod sampling points, the biplot revealed two relatively distinctive groups. The first group represented savanna maize fields and uncultivated vegetation, characterised by lower altitudes and subsistence type farming practices. The second group represented maize fields and uncultivated vegetation located in the Grassland Biome, characterised by higher altitudes and commercialised maize farming systems.

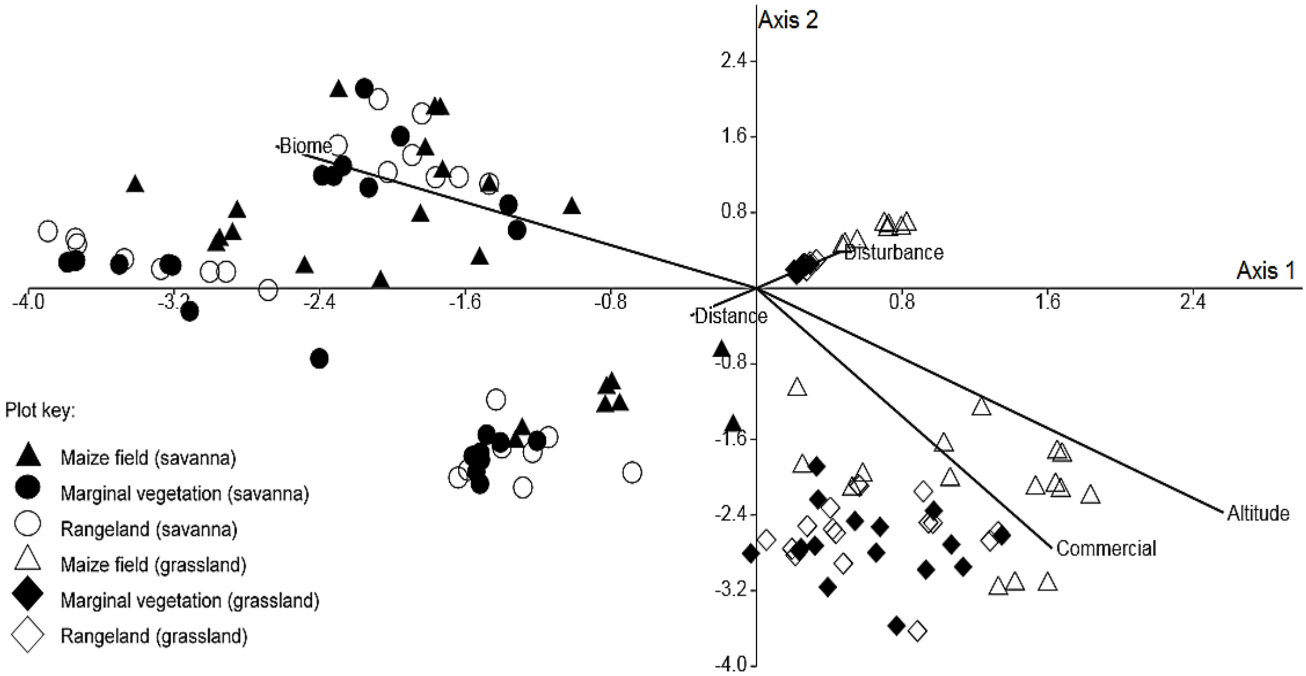

Figure 3.4: Canonical correspondence ordination of all sampled localities, showing correlations for environmental variables of arthropod sampling points. Environmental variables are represented by lines and sampling points by symbols. Each symbol represents the weighted average of one plot. Environmental factors were: distance (distance from maize field); disturbance (increasing with decreasing distance from maize field); biome (grassland/savanna); altitude (m a.s.l.) and farming practice (commercial/subsistence).

Table 3.11: Correlations of ordination axes with environmental factors as well as eigenvalues and percentage variance explained for canonical correspondence analysis arthropod sample points at all localities.

Factor	Axis 1	Axis 2
Distance	-0.121	-0.097
Disturbance	0.152	0.127
Biome	-0.880	0.501
Altitude	0.855	-0.791
Commercial	0.541	-0.917
Eigenvalue	0.645	0.574
% variance explained	33.22	29.58

Adonis analysis (Table 3.12) revealed significant distinctions between biome and distance class groups in terms of species composition at p = 0.001. Although less well defined than for plants, ANOSIM analysis revealed distinctive groupings for arthropod species composition of maize fields and uncultivated vegetation (p=0.001, Table 3.13). However, within the uncultivated vegetation, the marginal and rangeland points did not represent separate clusters in any of the biomes, indicating that arthropod species composition was not different between these two areas. Furthermore, marginal and rangeland points of grassland and savanna were found to be significantly different in terms of species composition and represented separate clusters (Figure 3.4, Table 3.13). From the CCA ordination it also appears as though the overlap in arthropod species between the savanna maize sampling points with its margins was more prominent than within the Grassland Biome, although this was not confirmed by the ANOSIM analysis. Again the results for species composition must be handled with caution due to the abundance of zero values in the datasets and it must also be taken into account that the ANOSIM analysis did not take into account the nestedness of data within transects.

Table 3.12: Adonis analysis results, with nestedness of data in a transect taken into account, indicating significance of separation between distance classes (maize field, marginal vegetation and rangeland) within biome for arthropod groups based on species composition.

	df	F	R	p
Biome	1	6.007	0.039	**0.001***
Distance class	2	2.513	0.033	**0.001***
Interaction (Biome*Distance class)	2	1.777	0.023	**0.001***
Residuals	138	---	0.904	---

df = degrees of freedom; F = F-value; R = R-value; p = p-value

Bold text* indicates significant p values at $p \leq 0.05$

Table 3.13: ANOSIM analysis p-values indicating significance of separation between arthropod groups based on species composition. MZ (G) = Maize field, Grassland Biome; MZ (S) = Maize field, Savanna Biome; MV (G) = Marginal vegetation (30-100 m), Grassland Biome; MV (S) = Marginal vegetation, Savanna Biome; RA (G) = Rangeland (100-400 m), Grassland Biome; RA (S) = Rangeland, Savanna Biome.

	MZ (S)	MZ (G)	MV (S)	MV (G)	RA (S)
MZ (G)	**0.0001***	---	---	---	---
MV (S)	**0.0005***	**0.0001***	---	---	---
MV (G)	**0.0001***	**0.0001***	**0.0001***	---	---
RA (S)	**0.0013***	**0.0001***	0.8324	**0.0001***	---
RA (G)	**0.0001***	**0.0001***	**0.0001***	0.8040	**0.0001***

Bold text* indicates significant separations at $p<0.05$

3.5 Discussion

3.5.1 Plant diversity patterns

Plant diversity is inevitably lost with increased land management or land use intensity (Hamre *et al.*, 2010; Marshall & Arnold, 1995; Niedrist *et al.*, 2009). A crop field environment is unfavourable to many plant species due to application of herbicides and disturbance of the soil (Altieri, 1999) as well as growth and shading effects of crop plants, which may result in weed growth suppression (Khan *et al.*, 2006). This leads to the loss of plant species. Unfortunately, agricultural activities have the potential to influence plant communities at considerable distances outside the area of active cultivation through aspects such as agrochemical drift (De Snoo & Van der Poll, 1999). Disturbances associated with crop fields may ultimately lead to the loss of plant species richness and diversity as well as species evenness in these agro-ecosystems (De Cauwer *et al.*, 2006; Kleijn & Snoeijing, 1997; Marrs, 1993). While marked differences were observed for plant species richness, diversity and evenness between maize fields and uncultivated vegetation, this was not the case for marginal and rangeland areas within the uncultivated vegetation. In both these areas the plant species richness and diversity were found to be similar to pristine grasslands in South Africa (Van Oudtshoorn *et al.*, 2011). In addition, all the plant species were also well represented across the whole uncultivated habitat (high evenness), contrary to maize field plant communities, which is probably dominated by a few hardy plant species able to withstand the high levels of disturbance (Curry, 1994). Plant evenness in crop fields may have been affected by several factors such as fertilization and the application of herbicides. It has been shown that the application of herbicides has a destabilizing effect on plant communities (Kleijn & Snoeijing, 1997). On the other hand, it is commonly stated that the species evenness of a community increases with increasing diversity and stability and decreasing anthropogenic disturbance (Chapin *et al.*,2000; Gurr *et al.*, 2012; Matson *et al.*, 1997) and that plant communities that display higher species evenness are generally healthier (Hillebrand *et al.*, 2008).

These results indicate that the only detectable agricultural disturbance resided within the maize fields and, contrary to the original hypothesis, agricultural practices do not have an overall negative impact on plant diversity of crop field margins, at least not at the distance of 30-100 m. This is further supported by the findings that there was no displacement of indigenous with alien plant species in the marginal area, which would have been an additional indication of active disturbance. It contradicts the notion that crop field margins are disturbed sites with altered plant communities due to their close proximity to agricultural activities (Marshall & Moonen, 2002). Negative effects, if present, may be extremely localized, impacting only the very edge (≤10 m) between the uncultivated habitat and the maize field. It was proposed by Fridley *et al.* (2009) that agricultural influences on landscape-scale vegetation patterns are in close proximity to agricultural activities (≤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). It must also be noted that these results are scale dependent and therefore, studies conducted under different spatial scales may not yield similar results (Ma, 2008).

The mostly consistent trends along the maize field-field margin gradient of both the Grassland and Savanna Biomes indicates that the distinctive plant communities associated with the two different biomes respond similarly to the presence of maize fields. However, it was found that grassland followed slightly different trends than the savanna in the first 30-250 m of the gradient in terms of plant species richness. In this case, grassland species richness increased more gradually along the gradient compared to savanna. This result cannot be explained at this point. It is possible that the two biomes reacted differently to disturbances unrelated to the maize fields. It is known for instance that different vegetation types react differently to livestock grazing (Tainton, 1999), which was a common feature in the marginal habitats. Another probability is that fire wood was extensively harvested at savanna sites, which opens up niches to be colonised and increases diversity.

Overall, plant species richness, diversity and evenness were almost always higher in savanna compared to grassland. However, the significance of these values was not conclusive for plant diversity and evenness. It seems that the only true differences between the Grassland and Savanna Biomes were in terms of plant species richness. The savanna always had significantly higher plant species richness than the Grassland Biome in the uncultivated areas, although not in the maize fields. This is in accord with the hypothesis that savanna should be more specious than the Grassland Biome due to its multi-layered nature (Curry, 1994; Schadek *et al.*, 2009).

3.5.2 Plant species composition patterns

In the CCA ordination results the agricultural intensity factor (along with distance) is represented by the longest vector and is best correlated with axis 1 (the axis explaining most of the variation in species assemblages) than biome, altitude or farming practice (Table 3.11). This indicates that the degree of disturbance in a maize field-rangeland environment was a very strong correlate of plant species assemblages. This was expected given that plants are organisms with high habitat quality requirements and low mobility (Liira *et al.*, 2008). Disturbances associated with agricultural practices such as tillage, irrigation and the application of agrochemicals result in the loss of non-tolerant individuals. This influences species interactions (Begon *et al.*, 2008) and may therefore lead to shifts in plant species assemblages in disturbed compared to natural habitat (Culpepper, 2006; Kirchner, 1977; Kleijn & Snoeijing, 1997). Commercial farming of maize occurs predominantly in the Grassland Biome in South Africa, while savanna is typically characterised by small-scale farming systems in rural communities. Also, grasslands in South Africa are typically found at higher elevations than savanna. This was consistent with the groupings for plant sampling points in the biplot.

From the results it is apparent that marginal vegetation points have a plant species composition that is not different to the rangeland points. Furthermore, the marginal areas housed a minimal number of alien plant species comparable to the rangeland area. This contradicts the notion that field margins of crop fields should gradually change from weedy, annual species to natural vegetation consisting of non-weedy, perennial species with increased distance from crop fields. It has been shown by Boutin & 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.

As the marginal and rangeland areas did not seem to differ significantly in terms of plant species composition, diversity or richness, the findings indicate that the ecotone, ecocline or edge effect hypotheses of crop fields is not applicable at larger scales. Obviously this becomes more pronounced towards the field edge and therefore Piessens *et al.* (2006) found that edge effects of heathland vegetation were confined to the first 8 m outside the crop fields.

Furthermore, clustering of maize field points in the ordination suggest that the weed species composition of maize fields is very unique and few species are shared with uncultivated areas. This is consistent with the results of Marshall (1989) as well as Marshall and Arnold (1995), which 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 25-30%. These patterns were attributed to low seed dispersal into crop fields and fewer opportunities for germination due to cultivation activities. The results show that marginal vegetation areas of the savanna shared only 6.23% of plant species with maize fields. These included species such as *Urochloa panicoides, Cynodon dactylon, Euphorbia inaequilatera, Setaria verticillata, Panicum maximum* and *Phyllanthus parvulus.* Similarly, the marginal areas of the grassland shared 9.09% of species with maize fields with shared species including *Commelina africana, Sporobolus africanus, Eragrostis gummiflua, Kyllinga erecta, Cynodon dactylon* and *Chloris virgata.* The distinct plant species composition of grassland and savanna maize fields may, therefore, be ascribed to the tendency of weeds to spread into crop fields from the surrounding vegetation (Leeson *et al.*, 2005). Grassland and savanna habitats may contain different pioneer species able to spread into maize fields and it can be expected that maize fields situated in different biomes will have different weed communities.

The tendency of grassland localities to have tighter clustering of their uncultivated habitat sampling points seem to indicate that grassland localities have lower beta diversity (diversity between sampling points) than the savanna localities. Therefore, the savanna points had more unique plant species relative to the others when compared to grasslands. This is again possibly the result of the multi-structured nature of savanna, which due to scattered woody plant species with specific climatic preferences, may lead to a greater between-plot variation in species (Schadek *et al.*, 2009).

3.5.3 Arthropod diversity patterns

Arthropod communities in agro-ecosystems may be negatively affected by, among others, agricultural activities directly through the application of insecticides (Bundschuh *et al.*, 2012; De Snoo & De Wit, 1998; Çilgi & Jepson, 1995) or indirectly via changes in the plant community (Feber *et al.*, 1996). The results indicated that arthropod species richness followed relatively similar trends to that for plants, and was considerably higher in uncultivated vegetation compared to maize fields. Arthropod diversity was also higher in uncultivated areas, probably more as a result of the increased species richness than evenness. This suggests that an increase in the number of plant species lead to an increase in arthropod species numbers. These effects may be caused by several factors that are indirectly linked to plant species richness such as structural diversity, specific plant species composition, plant productivity and microclimate availability (Szinicz, 2005). Nevertheless, uncultivated semi-natural habitats are generally more heterogeneous than crop fields and provide opportunities for more arthropod species (Ingham & Samways, 1996) which may lead to increased arthropod species numbers. This is in accord with numerous other studies that demonstrated increased arthropod species richness with increased plant species richness, e.g. Denys & Tscharntke (2002); Hendrickx *et al.* (2007); Schellhorn & Sork (1997) and Siemann *et al.* (1998).

These results reject the hypothesis that, due to possible disturbances associated with the maize fields, the marginal vegetation should have had lower arthropod species richness values compared to the rangelands. As with 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 did not sample arthropods in field margins further than 25 m from crop fields (Hendrickx *et al.*, 2007; Szinicz, 2005; Thomas & Marshall, 1999). Taking the results into account, it is unlikely that any detectable effects on arthropod species richness exist beyond 30 m from maize fields. The high mobility of most arthropods will inevitably complicate the detection of more permanent topological patterns for arthropod communities. Therefore, while crop production activities associated with maize fields may kill off arthropods in marginal vegetation, these individuals may soon be replaced by others. Therefore, further monitoring of arthropod communities over time will be required to confirm these trends.

Inconsistent with the results for plants however is the trends for arthropod species evenness across the gradient. The high evenness index values across the whole maize field-field margin gradient indicate that all arthropod morpho-species were relatively well represented and of equal proportions in both maize fields and uncultivated areas, and therefore no obvious dominance effects occurred. This is contrary to what would be expected for the arthropod species evenness within crop fields. Evidence suggests that evenness or abundance of organisms at higher trophic levels is dependent on plant species richness and diversity (Murdoch *et al.*, 1972; Pimentel, 1961; Root 1973). On the contrary, the results indicate that little species dominance occurred among arthropods inside maize fields despite decreased plant species diversity. However, the type of pest management practices that were used in the maize fields could severely affect dominance of specialist herbivores in the monoculture fields. Also, at least some of the sampled fields were intercropped, which may have influenced the results. Studies indicated 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 practices (Siemann, 1998).

Overall, arthropod communities followed similar trends across the Grassland and Savanna Biomes in terms of species richness, diversity and evenness. Therefore, it may be said that savanna and grassland arthropod communities responded in a similar fashion to the presence of maize fields.

In contrast to the results for plants, arthropod species richness was considerably higher in the uncultivated vegetation of grassland than that of savanna. It is uncertain whether this is a natural occurrence or as a result of sampling error. Since the efficiency of the D-vac method is influenced by vegetation structure (Elliott *et al.*, 2006) woody vegetation in the savanna localities may have caused a decrease in sampling efficiency in the savanna habitats, which resulted in lower species richness values.

3.5.4 Arthropod species composition patterns

The CCA biplot for arthropods revealed that arthropod species assemblages were better explained by biome, altitude and type of farming practice (commercial vs. subsistence) than disturbances associated with the maize fields. This is in contrast to the results for plants. Most arthropods (in adult stages) are highly mobile and readily travel between maize field and natural habitats (Alomar *et al.*, 2002; Garibaldi *et al.*, 2011; Norris & Kogan, 2000). Therefore, the effect of disturbance may be reduced if individuals are constantly able to move to suitable habitats inside a particular maize field-rangeland environment. On a larger scale however, the distinctive climatic conditions (and vegetation) associated with a biome and particularly altitude, may influence the composition of arthropod species that are able to persist in that particular agricultural environment.

Similar to the results for plant species assemblages, the presence of maize fields did not have a detectable effect on species composition of arthropods in marginal vegetation sites as it was found to have a very similar species composition to the rangeland sites. However, clear differences could be observed between maize fields and the uncultivated vegetation in terms of arthropod species composition, supporting the notion that arthropod species may be characterised based on their preference for 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' unique to the crop fields either within certain periods or throughout their lifecycle. As maize fields represent unique environments, this may allow for only a few specialized species to persist. For example, the high fecundity of aphids (Hemiptera: Aphididae) allow them to successfully populate ephemeral habitats such as annual crops where others cannot (Wissinger, 1997). Furthermore, it was found that the grassland and savanna had distinct arthropod communities. This was true not only for the uncultivated areas, but also for maize fields. Schaffers *et al.* (2008) and Symstad *et al.* (2000) also indicated that arthropod species composition is largely determined by plant species composition. As grassland and savanna had very distinct plant communities, this may also have resulted in the distinct arthropod communities. Furthermore, distinctions between grassland and savanna maize field arthropod communities agree with findings that crop fields are colonized by arthropods from the surrounding field margins (Alomar *et al.*, 2002; Norris. & Kogan, 2000). Since it has been shown that grassland and savanna rangelands contained distinctive arthropod communities, it would be expected that maize fields will also have unique species associated with the particular biome in which the maize field is located.

The certain degree of overlap in arthropod species between maize fields and uncultivated vegetation of the Savanna Biome may be an indication that arthropod communities of the Savanna Biome have a greater affinity for maize fields than the arthropod communities of the Grassland Biome. Vegetation structure is considered to be one of the major factors that shape arthropod communities (Strong *et al.*, 1984). Since maize is a grass species it may be said that maize fields are, in effect, man-made grasslands. It would therefore be expected that grassland arthropods should have had a greater affinity for maize fields than savanna arthropods, especially since maize fields rarely contain woody plant species. However, maize fields do not mimic 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 resembles a savanna or woodland habitat more closely than a grassland habitat, and attracts savanna arthropods.

Clustering of arthropods was not as clearly defined as for plants, and maize fields shared many more arthropod species with the uncultivated vegetation than plant species. This is consistent with the results of Procheş and Cowling (2007) that attributed 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 sample points of arthropod species will be less well defined than for plants.

3.6 Conclusion

This chapter described the plant and arthropod species composition and diversity patterns along a maize field-field margin gradient in Grassland and Savanna Biomes of South Africa. Overall, the results indicated that the patterns of plant and arthropod diversity, richness and evenness followed similar trends for maize field-field margin gradients across the two biomes of South Africa. In relation to the first research question, plant and arthropod diversity were constantly found to be lower inside maize fields than in uncultivated vegetation. However, it was shown that the diversity of the uncultivated area were not significantly affected by the presence of maize fields, as marginal areas did not have significantly lower plant and arthropod diversity values than rangeland areas.

In addition to biodiversity patterns, this chapter also compared the species assemblages of plants and arthropods in maize agro-ecosystems of South Africa. The results indicated that the main predictor of plant species assemblages were agricultural disturbances, while biome, altitude and, to a lesser extent, farming practice are better predictors of arthropod species composition. In relation to the second research question, the species assemblage patterns for plants and arthropods were in accord with the results for the diversity patterns, with distinct communities in maize fields and uncultivated vegetation but little difference in species composition between the marginal and rangeland areas within the uncultivated areas. Therefore, the first and second hypothesis are not supported, as the results suggest that the possible disturbance effects of maize fields do not have considerable negative effects on either the diversity or species assemblages of plant and arthropod communities in grassland and savanna habitats at ≥30 m from the area of active cultivation. Further studies will be required to establish the distances at which significant disturbance do occur.

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. Overall, the results indicated that savanna tended to have significantly higher plant species richness (although not diversity or evenness) than the Grassland Biome in uncultivated areas. Results were inconclusive for arthropods. Therefore the third hypothesis is partially supported in terms of plant species richness. The ordination analyses did not contain enough conclusive evidence to support the forth hypothesis stating that maize fields have lower beta diversity compared to uncultivated environments.

These results indicate that crop field margins at distances of 30-100 m 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. The focus of this chapter was mainly on trends of total plant and arthropod diversity. The responses of plant and arthropod taxa at family and functional group level are considered in chapters 4-7. Ultimately, this research will contribute towards a baseline for biodiversity monitoring and could aid in quantifying the conservation value of field margins.

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CHAPTER 4: INSECT DISTRIBUTIONS IN RELATION TO THE GRASSLAND AND SAVANNA BIOMES OF SOUTH AFRICA

4.1 Overview

The long-standing tradition of classifying South Africa's biogeographical area into biomes is commonly linked to vegetation structure and climate. Because arthropod communities are often governed by both these factors, it can be expected that arthropod communities would fit the biomes. To test this hypothesis, it was considered in this chapter how well arthropod species assemblages fit South Africa's grassy biomes. Arthropod assemblages were sampled from six localities across the Grassland and Savanna Biomes by means of suction sampling, to determine whether the two biomes have distinctive arthropod assemblages. Arthropod samples of these biomes clustered separately in multidimensional scaling analyses. Within biomes, arthropod assemblages were more distinctive for savanna localities than grassland. Arthropod samples of the two biomes clustered together when trophic groups were considered separately, suggesting some similarity in functional assemblages. Dissimilarity was greatest between biomes for phytophagous and predacious trophic groups, with most pronounced differentiation between biomes at sub-escarpment localities. The results indicate that different arthropod assemblages do fit the grassy biomes to some extent, but the pattern is not as clear as it is for plant species.

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4.2 Introduction

South Africa's rich biodiversity is largely the result of a wide range of climatic conditions and topographic variation which gave rise to relatively distinctive biomes, each with characteristic plant and animal species (Mucina & Rutherford, 2006; Rutherford & Westfall, 1994). Vegetation categorisation in South Africa is nested within these biome concepts (Mucina & Rutherford, 2006). Insects are particularly relevant in biome comparisons, as a large proportion of insects may be host-specific phytophagous species (Moolman *et al.*, 2013), which is likely to make them vegetation-specific because of intricate relationships. European studies have shown that local plant species composition is the most effective predictor of arthropod assemblage composition, even more so than vegetation structure and environmental conditions (Schaffers *et al.*, 2008). Furthermore, arthropod groups have been shown to be associated with particular plant assemblages in grassland, with certain insect orders responding positively to the increase of specific plant functional groups (Symstad *et al.*, 2000).

Being ectotherms, arthropods are sensitive to their abiotic environments. The vegetation layer provides a biotic environment that buffers arthropods against changes in the abiotic environment. Several studies have shown that factors such as vegetation height, density and percentage cover as well as the associated microclimate, had significant effects on species composition of grasshoppers (Batáry *et al.*, 2007; Gebeyehu *et al.*, 2002; Kuppler *et al.*, 2015) and dung beetles (Pryke *et al.*, 2013).

Despite the proven direct and indirect relationships between plant and insect composition, very little research has been conducted on the specific structures of insect communities in southern African biomes (Procheş & Cowling, 2006; Procheş & Cowling, 2007; Wright & Samways, 1998). A study of four biomes in South Africa revealed that overall, differences between insect assemblages of different biomes are not as convincing as those between plant assemblages (Procheş & Cowling, 2007). This is to be expected, considering the better dispersal ability of most insects because of their high mobility and frequent dispersal events characteristic of winged species. The transition from one biome to another therefore appears smoother for insect assemblages than it is for plant assemblages (Procheş & Cowling, 2007).

In chapter 3, data was collected to compare insect and plant diversity of maize field and marginal uncultivated habitats in two grassy biomes (Botha *et al.*, 2015). In the current chapter, the earlier non-crop dataset of uncultivated areas was used to assess the compositional similarities and differences between the assemblages of arthropods and plants from the Grassland and Savanna Biomes. This contribution provides a first comparison of the arthropod composition of localities in these biomes to establish whether they have distinctive arthropod assemblages.

The following research question was asked: Do arthropod assemblages in the Grassland and Savanna Biomes follow the same biogeographical patterns as plant assemblages and can these biomes therefore be differentiated by arthropod species composition? Savannas are multi-structured and therefore have great structural complexity and niche diversification to house a wider variety of arthropod species (Krüger & McGavin, 1998). As a result, the presence of a tree and shrub layer allows for more arthropod species and higher abundances per unit area compared with habitats that have simpler structures habitats such as grassland (Koricheva *et al.*, 2000; Schadek *et al.*, 2009). Savanna provides a wider variety of conditions and resources to be exploited, allowing a greater degree of species coexistence (Ricklefs & Marquis, 2012; Tews *et al.*, 2004). It is therefore hypothesised that the composition of arthropod assemblages will vary between the Grassland and Savanna Biomes but that these distinctions will not be as clear as for plant assemblages due to the high mobility of many arthropod groups.

4.3 Material and Methods

4.3.1 Experimental design

The sampling design used to collect the data is outlined in chapter 2. For the purposes of this chapter, only data collected in uncultivated habitats were used (all maize field data were removed). Therefore, arthropod data were generated within a total sampled area of 2 400 m^2 (96 plots of 5 m x 5 m), and plant data were generated from a total sampled area of 38 400 m^2 (96 plots of 20 m x 20 m) for this specific study. At each site, two pairs of points 100 m apart at both ends of a 1-km transect was sampled, with one site upslope and the other downslope. This translated to 4 points per site, 16 per locality and 48 points for each of the biomes (Table 4.1). The surveys covered the sub-escarpment (Cala and Jozini), escarpment (Amersfoort and Thohoyandou) and interior plateau (Potchefstroom and Jacobsdal) areas of each biome (refer to Figure 2.1, chapter 2 for study area map). To minimise possible spatial autocorrelation of data, the two localities representing similar elevations were chosen to represent different biomes, (for instance, the sub-escarpment locality Cala represented grassland and the sub-escarpment locality Jozini represented savanna).

Table 4.1: Layout of sampling design indicating the number of sample repeats (n) in brackets for the respective levels.

	Biome	Topographic region	Locality
Levels	Grassland (48)	Sub-escarpment (16)	Cala (16)
		Escarpment (16)	Amersfoort (16)
		Plateau (16)	Potchefstroom (16)
	Savanna (48)	Sub-escarpment (16)	Jozini (16)
		Escarpment (16)	Thohoyandou (16)
		Plateau (16)	Jacobsdal (16)

4.3.2 Statistical analyses

The non-parametric species estimators of observed species counts (Sobs), Chao2 and Jacknife1 (Hortal *et al.*, 2006; Ugland *et al.*, 2003) were calculated using PRIMER 7 (Clarke & Gorley, 2006) to determine how closely the sample resembled the extrapolated species richness. Non-metric multidimensional scaling (NMDS) analyses (samples clustered based on Bray–Curtis dissimilarity) in PRIMER 7 were used to visualise differences between sampling points in ordination space, in terms of plant and arthropod assemblages. For two-dimensional ordinations, the stress value increases with decreasing dimensionality and increasing quantity of data. The general rule is as follows: stress ≤0.05 gives an excellent representation with no prospect of misinterpretation of the data, and stress ≤0.1 represents a good ordination with no real risk of misinterpretation. Stress ≤ 0.2 may still give a potentially useful ordination, but cross-checks with other techniques are recommended (Clarke & Warwick, 2001).

Significance of NMDS clusters were tested by permutational MANOVA (PERMANOVA), analysis of similarities (ANOSIM) and similarity percentage (SIMPER) analysis, using PRIMER 7. PERMANOVA is a multivariate analysis of variance technique suitable for abundance data and where significance is based on permutation of the dissimilarity matrix (Anderson, 2001). First, PERMANOVA was conducted using a Bray-Curtis dissimilarity matrix to determine the main and interactive effects of biome and topographic region on species composition (permutations=999; type III sums of squares). Then, ANOSIM was used as a post hoc test for pairwise comparisons between localities within the Grassland and Savanna Biomes to assess compositional dissimilarity. ANOSIM is a non-parametric test that uses rank dissimilarities based on the Bray–Curtis coefficient of similarity. Significant separation of two distinct clusters in ordinal space is calculated using an R-statistic, which ranges from one (meaning clusters are totally different) and zero (meaning clusters are indistinguishable) (Clarke, 1993). Next, SIMPER was applied to the dataset to assess which taxa were primarily responsible for observed differences in species composition between the biomes. A square root transformation of species data was performed for NMDS, PERMANOVA, ANOSIM and SIMPER analyses to reduce the influence of common species (Anderson, 2001).

As a final measure, canonical correspondence analysis (CCA) with forward selection was applied to the data, using CANOCO 4.5 (Ter Braak & Verdonschot, 1995), as a cross-check to depict how different localities compared in terms of arthropod and plant species composition. The same analysis enabled the assessment of the relative importance of selected environmental variables in determining plant and arthropod assemblages of grouped sampling points. Five biotic and abiotic environmental factors were considered for a biplot with species data. These included latitude and longitude (decimal degrees), altitude (m a.s.l.), tree cover (%) and grass cover (%). Species data for CCA analyses were square-root transformed, and environmental data were normalised.

4.4 Results

4.4.1 Overview of data

The survey recorded 1436 arthropod morpho-species (35 193 individuals) from 23 orders (Table 4.2). The four largest trophic groups of arthropods were distinguished further for comparative analyses, namely herbivores (667 morpho-species), predators (297), parasitoids (204) and pollinators (112) (Table 4.2).

Table 4.2: Number of plant and arthropod species and percentage of individuals per family, order or trophic group for each of the biomes.

		Grassland Biome		Savanna Biome		Total	
		Species (n)	Individuals (%)	Species (n)	Individuals (%)	Species (n)	Individuals (%)
Plant families	Poaceae	62	52.1	73	35.5	109	42.6
	Fabaceae	28	4.7	73	13.2	94	9.6
	Asteraceae	46	17.3	32	6.9	73	11.3
	Acanthaceae	7	1.4	25	7.3	30	4.8
	Rubiaceae	4	3.9	22	1.8	26	2.7
	Apocynaceae	9	0.3	16	1.5	25	1.1
	Euphorbiaceae	4	0.2	23	2.8	25	1.7
	Cyperaceae	17	3.4	7	0.9	24	1.9
	Malvaceae	6	0.6	20	1.9	22	1.4
	Lamiaceae	4	0.2	16	0.9	20	0.6
	Other families (83)	84	15.9	227	27.1	302	22.3
	All plants (93)	272	---	534	---	751	---
Arthropod orders	Hemiptera	198	25.9	194	32.3	340	26.7
	Diptera	126	8.9	128	18.7	233	10.1
	Hymenoptera	128	14.9	120	16.1	225	15.1
	Araneae	97	9.5	87	8.5	165	9.3
	Coleoptera	80	2.7	86	5.5	147	3.1
	Orthoptera	52	1.4	94	7.5	127	2.1
	Lepidoptera	37	0.6	62	3.5	89	0.9
	Acari	25	23.4	15	3.8	32	21.3
	Thysanoptera	15	4.2	15	1.3	22	3.8
	Mantodea	5	0.06	13	0.7	18	0.1
	Other orders (13)	23	8.4	23	2.2	38	7.4
	All arthropods (23)	786	---	837	---	1436	---
Arthropod trophic groups	Herbivores	339	43.1	430	51.4	667	46.4
	Predators	179	22.8	158	18.9	297	20.7
	Parasitoids	115	14.6	104	12.4	204	14.2
	Pollinators	49	6.2	75	9.0	112	7.8
	Other groups (5)	148	18.8	131	15.7	252	17.5

Other groups not included in the analyses were decomposers, parasites, visitors, frugivores and omnivores. For plants, 740 species (10856 individuals) from 93 families were recorded in the field margin habitats (Table 4.2). Some groups of plants and arthropods (mobile, sensitive insects such as butterflies or grasshoppers and cryptic plants such as geophytes) might be under-represented in the samples because of the collection methods and specificity of season.

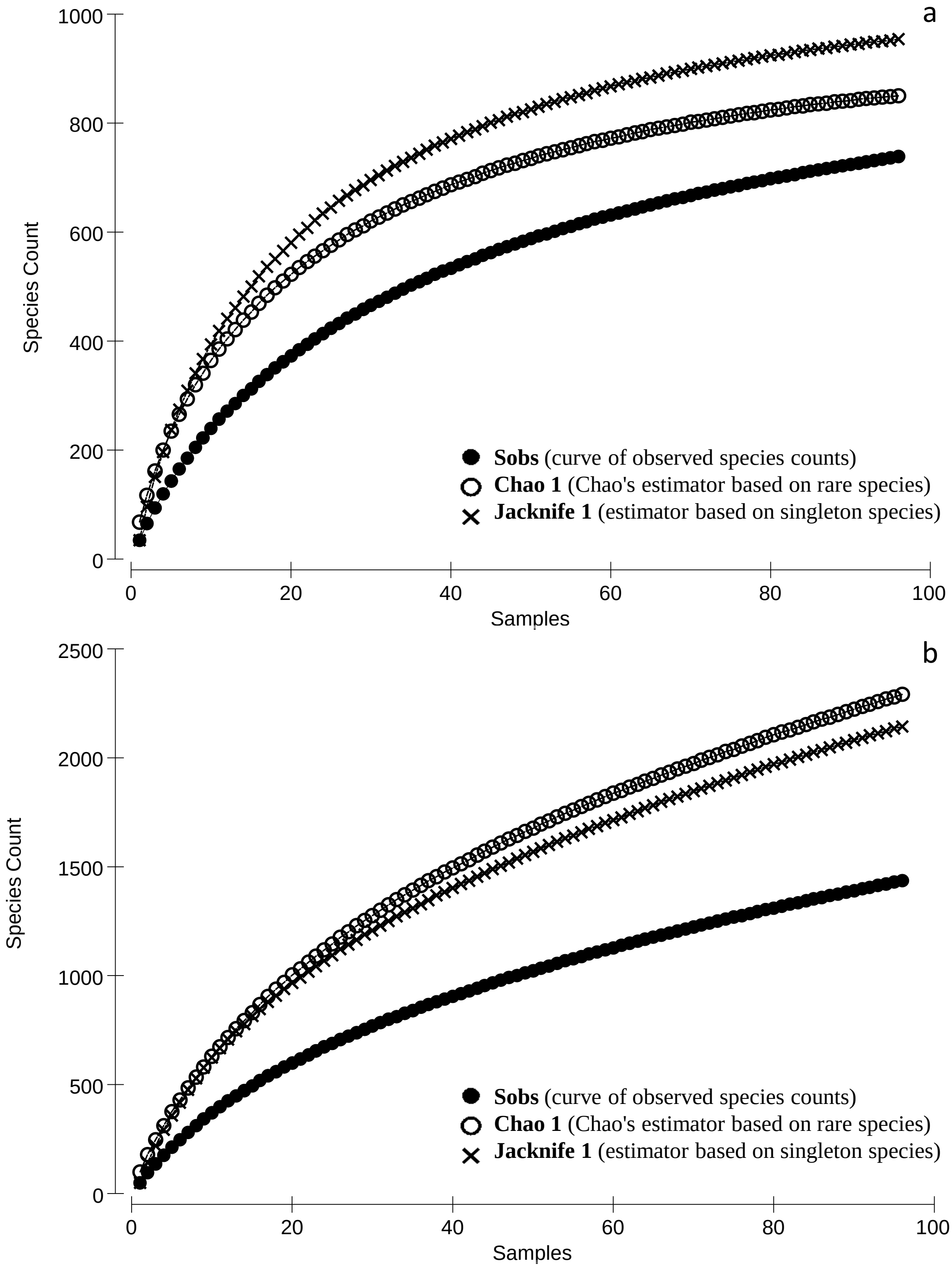

Figure 4.1: Species accumulation curves for (a) plants and (b) arthropods sampled in all grassland and savanna plots.

It must be mentioned that a study targeting soil and flying arthropods could yield very different results. A selection of species accumulation curves (Figure 4.1), suggested that the saturation levels were not satisfactory for arthropods, and should be kept in mind when interpreting the findings (Clarke & Gorley, 2006).

4.4.2 Plant assemblages across biomes

The NMDS analysis for plants revealed the tightest clustering and the lowest stress factor (0.14) compared with the results for arthropods (Figure 4.2). Clear distinctions in plant species composition were found between grassland and savanna sampling points, with a much tighter clustering for grassland samples (Figure 4.2a). Differences in plant species composition between biomes were confirmed by PERMANOVA results (pseudo-*F* =31.28; p=0.001) and Bray–Curtis similarity in ANOSIM (p≤0.001, R=0.68) (Table 4.3a).

A CCA biplot (Figure 4.3) indicated that sampling points were strongly influenced by tree cover and altitude (Table 4.4; Axis 1) Clear distinctions were found between grassland and savanna sampling points in the CCA ordination, with increased tree cover being correlated with savanna plant assemblages. Forward selection results showed that all tested environmental factors contributed significantly (p=0.002) to the variability of the ordination (Table 4.5). However, the effect of tree cover (a differentiating factor between grassland and savanna) was reduced with the inclusion of longitude, latitude and altitude variables (Table 4.5).

4.4.3 Plant assemblages across topographic regions

The NMDS results showed that sampling points for plants from each topographic region clustered together to some extent (Figure 4.2). PERMANOVA confirmed these distinctions between topographic regions (pseudo-*F*=14.39; p=0.001). PERMANOVA also revealed a significant interaction between biome and topographic region (pseudo-*F*=14.83; p=0.001). Samples of savanna localities were more dispersed between sub-escarpment, plateau and escarpment grassland, in terms of plant species composition (Figure 4.2). This was confirmed by ANOSIM analyses, which indicated higher R-values (greater distinctiveness) for comparisons between savanna localities than between grassland localities (Table 4.3a). Grassland sampling points revealed limited distinctiveness of plant species composition between topographic regions (Table 4.3a).

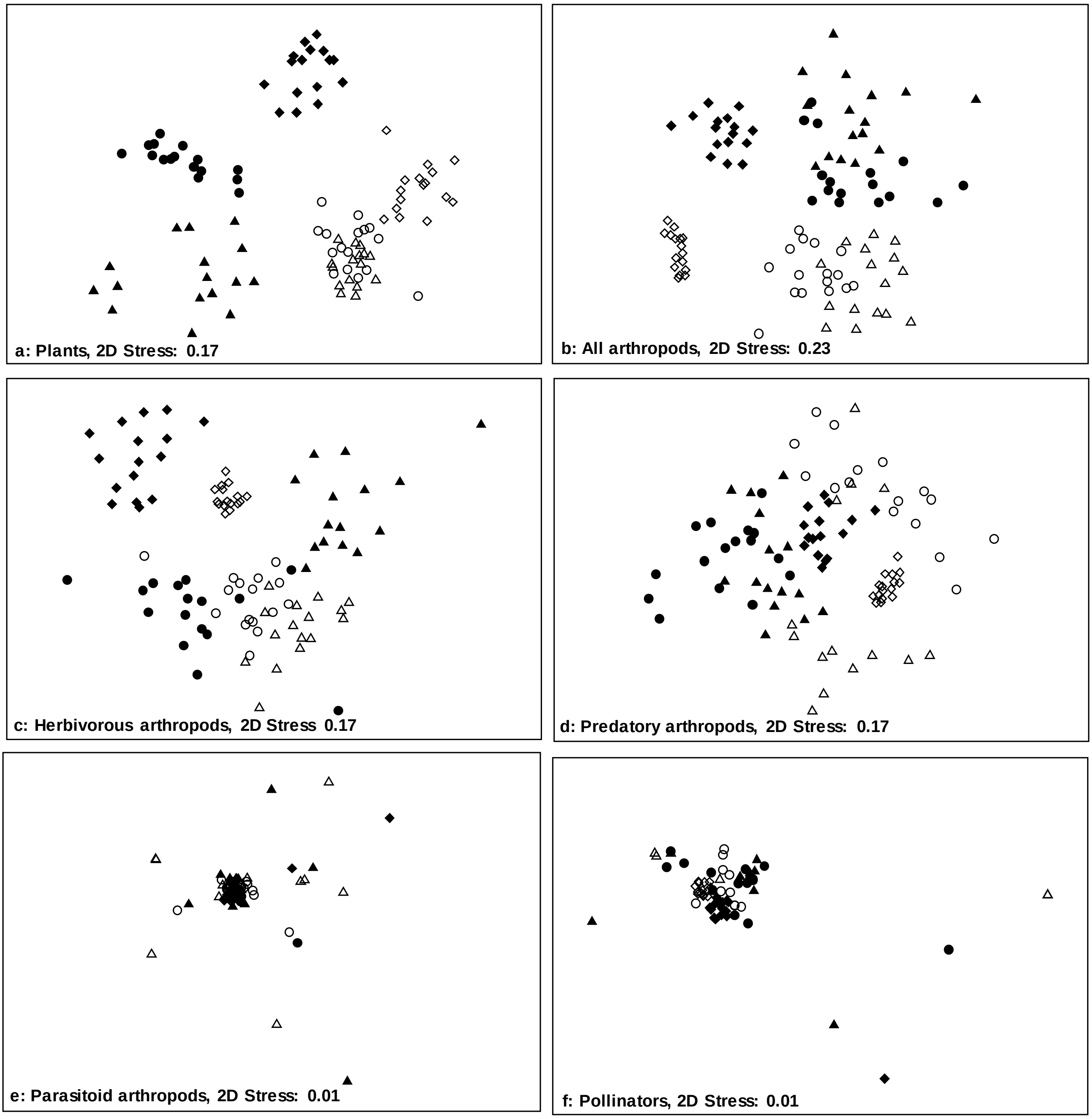

Figure 4.2: Non-metric multidimensional scaling (NMDS) analyses based on abundance data of plant and arthropod species recorded at maize field margin localities.

Table 4.3: Results of ANOSIM and SIMPER analyses for biomes and topographic regions in terms of species composition.

			ANOSIM p-value	ANOSIM R-value	SIMPER overall average dissimilarity
a) All plants	Between-biome comparison	Grassland x Savanna	**0.0001***	0.68†	97.86
	Within-biome comparison (Grassland)	Escarpment x Plateau	**0.0001***	0.52	77.75
		Escarpment x Sub-escarpment	**0.0001***	0.94††	91.37
		Plateau x Sub-escarpment	**0.0001***	0.81††	88.95
	Within-biome comparison (Savanna)	Escarpment x Plateau	**0.0001***	0.99††	99.08
		Escarpment x Sub-escarpment	**0.0001***	0.87††	94.25
		Plateau x Sub-escarpment	**0.0001***	0.99††	97.23
b) All arthropods	Between-biome comparison	Grassland x Savanna	**0.0001***	0.4	98.12
	Within-biome comparison (Grassland)	Escarpment x Plateau	**0.0001***	0.5	92.62
		Escarpment x Sub-escarpment	**0.0001***	0.98††	99.69
		Plateau x Sub-escarpment	**0.0001***	1††	99.41
	Within-biome comparison (Savanna)	Escarpment x Plateau	**0.0001***	0.9††	97.8
		Escarpment x Sub-escarpment	**0.0001***	0.61†	96.07
		Plateau x Sub-escarpment	**0.0001***	0.9††	98.15
c) Herbivores	Between-biome comparison	Grassland x Savanna	**0.0001***	0.24	97.94
	Within-biome comparison (Grassland)	Escarpment x Plateau	**0.0001***	0.39	90.33
		Escarpment x Sub-escarpment	**0.0001***	0.94††	99.35
		Plateau x Sub-escarpment	**0.0001***	0.97††	98.88
	Within-biome comparison (Savanna)	Escarpment x Plateau	**0.0001***	0. 82††	99.56
		Escarpment x Sub-escarpment	**0.0001***	0.57	98.34
		Plateau x Sub-escarpment	**0.0001***	0.83††	99.45
d) Predators	Between-biome comparison	Grassland x Savanna	**0.0001***	0.33	97.55
	Within-biome comparison (Grassland)	Escarpment x Plateau	**0.0001***	0.28	96.13
		Escarpment x Sub-escarpment	**0.0001***	0.49	99.47
		Plateau x Sub-escarpment	**0.0001***	0.70††	98.98
	Within-biome comparison (Savanna)	Escarpment x Plateau	**0.0001***	0.49	93.25
		Escarpment x Sub-escarpment	**0.0001***	0.24	90.1
		Plateau x Sub-escarpment	**0.0001***	0.63†	93.48
e) Parasitoids	Between-biome comparison	Grassland x Savanna	**0.0001***	0.09	98.76
	Within-biome comparison (Grassland)	Escarpment x Plateau	0.0506	0.05	96.02
		Escarpment x Sub-escarpment	**0.0001***	0.56†	99.99
		Plateau x Sub-escarpment	**0.0001***	0.56†	99.98
	Within-biome comparison (Savanna)	Escarpment x Plateau	**0.0001***	0.33	99.22
		Escarpment x Sub-escarpment	**0.0025***	0.12	97.74
		Plateau x Sub-escarpment	**0.0001***	0.35	99.76
f) Pollinators	Between-biome comparison	Grassland x Savanna	**0.0001***	0.07	94.45
	Within-biome comparison (Grassland)	Escarpment x Plateau	**0.0038***	0.11	92.38
		Escarpment x Sub-escarpment	**0.0001***	0.53†	96.48
		Plateau x Sub-escarpment	**0.0001***	0.44	99.09
	Within-biome comparison (Savanna)	Escarpment x Plateau	**0.0001***	0.43	100
		Escarpment x Sub-escarpment	**0.0074***	0.12	93.51
		Plateau x Sub-escarpment	**0.0001***	0.35	99.54

Bold text* indicates significant p values at p≤0.05

††, large effect at R≥0.7; †, medium effect at R≥0.5

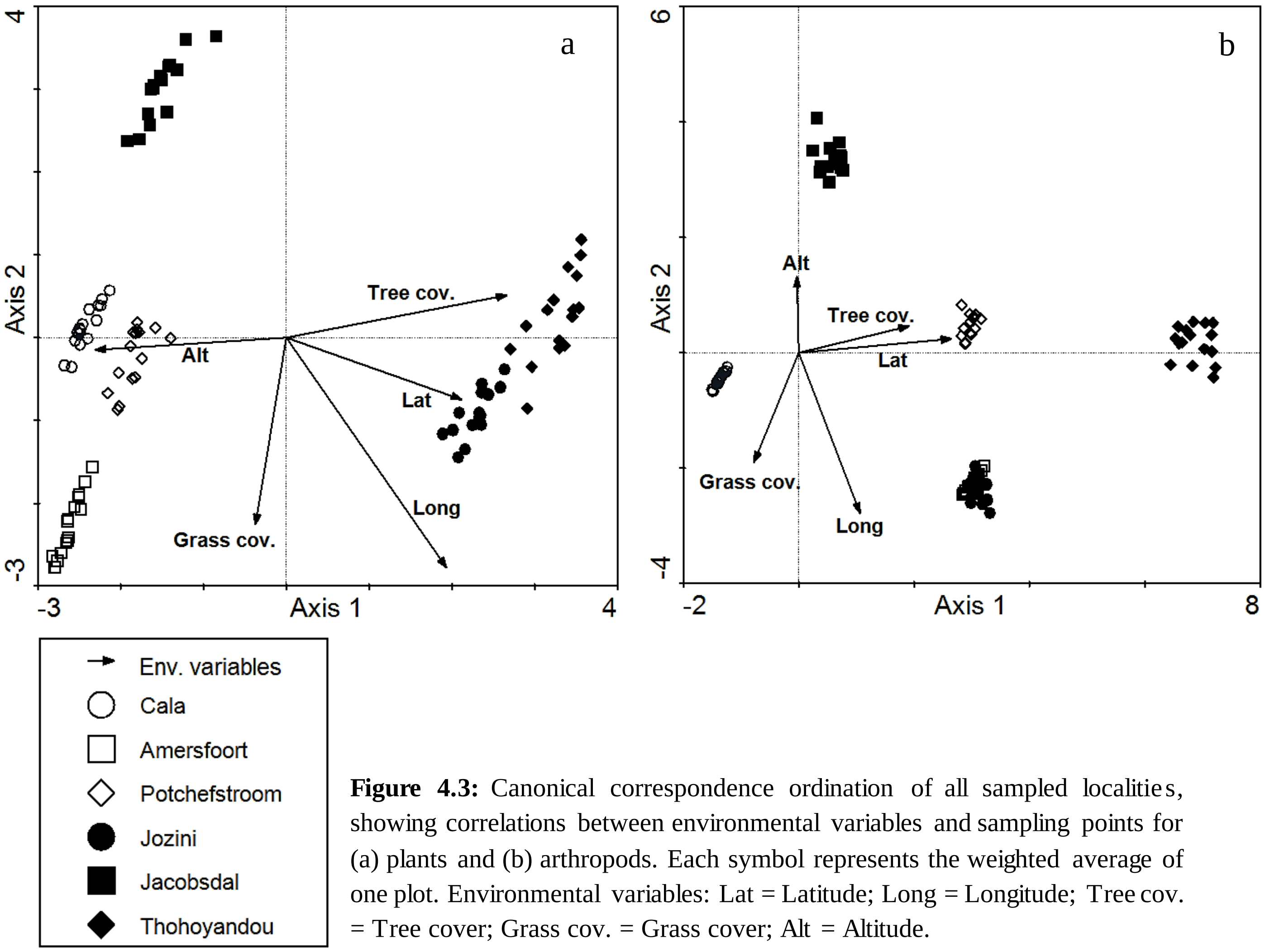

Figure 4.3: Canonical correspondence ordination of all sampled localities, showing correlations between environmental variables and sampling points for (a) plants and (b) arthropods. Each symbol represents the weighted average of one plot. Environmental variables: Lat = Latitude; Long = Longitude; Tree cov. = Tree cover; Grass cov. = Grass cover; Alt = Altitude.

4.4.4 Contributing plant species

A total of 21 plant species each contributed more than 1% to the total variation between the biomes according to SIMPER analysis. Among these, ten species collectively contributed to 21% of the variation (Table 4.6). Six grasses (*Eragrostis curvula, Eragrostis plana, Heteropogon contortus, Hyparrhenia hirta, Sporobolus africanus* and *Themeda triandra*) and one forb (*Helichrysum rugulosum)* characterised the grassland points, whereas one forb (*Pentzia incana*) and two grasses (*Panicum maximum* and *Urochloa mosambicensis*) characterised the savanna points (Table 4.6).

Table 4.4: Correlations of ordination axes with selected environmental factors, eigenvalues and percentage variance explained for canonical correspondence analysis.

Survey	Factor	Axis 1	Axis 2
Plants	Tree cover %	0.8975	0.1274
	Altitude	-0.7770	-0.0368
	Latitude	0.7133	0.1854
	Longitude	0.6511	-0.6904
	Grass cover %	-0.1252	-0.5610
	Eigenvalue	0.860	0.702
	% variance explained	29.8	24.3
Arthropods	Latitude	0.9866	0.0762
	Tree cover %	0.7128	0.1462
	Longitude	0.3969	-0.8754
	Grass cover %	-0.2880	-0.5962
	Altitude	-0.0126	0.4150
	Eigenvalue	0.824	0.717
	% variance explained	28.8	25.1

Table 4.5: Marginal and conditional effects of automatic forward selection conducted for all plants and all arthropods.

	Marginal effects			Conditional effects				
	Variable	Var. N	Lambda1	Variable	Var. N	Lambda A	p	F
Plants	Altitude	1	0.79	Altitude	1	0.79	**0.002***	4.51
	Tree cover	2	0.77	Latitude	3	0.74	**0.002***	4.42
	Latitude	3	0.77	Longitude	4	0.66	**0.002***	4.06
	Longitude	4	0.76	Grass cover	5	0.39	**0.002***	2.42
	Grass cover	5	0.49	Tree cover	2	0.31	**0.002***	1.94
Arthropods	Latitude	1	0.82	Latitude	1	0.82	**0.002***	2.71
	Longitude	2	0.73	Longitude	2	0.71	**0.002***	2.37
	Tree cover	3	0.68	Altitude	4	0.63	**0.002***	2.15
	Altitude	4	0.65	Tree cover	3	0.39	**0.004***	1.32
	Grass cover	5	0.50	Grass cover	5	0.31	0.364	1.03

Bold text* indicates significant p-values at p<0.05 as determined by Monte Carlo permutation tests (permutations = 499)

Table 4.6: Results for SIMPER analyses indicating the top ten plant and arthropod species responsible for groupings of grassland and savanna plots in the NMDS graphs.

	Species	Type	Ave. dis.	% Contr.	Cumul. %	Abund. Grassland	Abund. Savanna
Plants (overall average dissimilarity: 97.86)	*Themeda triandra*	Grass	3.684	3.764	3.764	8.27	1.6
	Panicum maximum	Grass	3.246	3.317	7.082	0	7.6
	Pentzia incana	Forb	2.355	2.406	9.488	0	4.88
	Helichrysum rugulosum	Forb	1.977	2.02	11.51	4.5	0
	Eragrostis curvula	Grass	1.753	1.791	13.3	3.25	1.27
	Eragrostis plana	Grass	1.741	1.779	15.08	3.94	0
	Sporobolus africanus	Grass	1.704	1.741	16.82	3.79	0.292
	Heteropogon contortus	Grass	1.45	1.482	18.3	2.83	0.979
	Hyparrhenia hirta	Grass	1.444	1.475	19.78	3.25	0
	Urochloa mosambicensis	Grass	1.438	1.47	21.25	0	3.21
Arthropods (overall average dissimilarity: 98.12)	Oribatulidae MS1	Detritivore	3.327	3.391	3.391	63	0.125
	Oribatulidae MS2	Detritivore	3.081	3.14	6.531	66.8	0
	Formicidae MS8	Predator	2.675	2.726	9.257	2.63	2.17
	Acrididae MS12	Herbivore	2.384	2.43	11.69	2.25	0.896
	Cicadellidae MS8	Herbivore	2.266	2.309	14	6.6	0.458
	Entomobryidae MS1	Detritivore	2.081	2.121	16.12	35	0.146
	Cicadellidae MS24	Herbivore	1.367	1.393	17.51	0	2.65
	Sciaridae MS10	Detritivore	1.233	1.257	18.77	0	4.79
	Cecidomyiidae MS1	Herbivore	1.227	1.251	20.02	17	1.02
	Formicidae MS9	Predator	1.17	1.192	21.21	14.8	0.313

Key to column headings: Ave. dis, average dissimilarity; % Contr., percentage contribution of each species to the average dissimilarity; Cumul. %, cumulative contribution percentage; Abund., mean abundance per plot

4.4.5 Arthropod assemblages across biomes

In the NMDS analysis for all arthropod species, grassland sampling points were noted to cluster separately from savanna points (Figure 4.2b). The biomes, however, were more similar in arthropod species composition than plant species composition, as was evident from the PERMANOVA results (arthropods: pseudo-F=9.712; p=0.001; plants: pseudo-F=31.278; p=0.001). ANOSIM showed similar results, indicating less similarity among arthropods ($p \leq 0.001$; R=0.4) (Table 4.3b).

The CCA results for arthropods (Figure 4.3) showed that sampling points were more strongly influenced by latitude (i.e. geographic position) than either plant cover or altitude (Table 4.4. Axis 1), Distinctions were not as clear between grassland and savanna sampling points for arthropods as they were for plants. Forward selection results confirmed the CCA ordination results, which suggests that longitude and latitude explained the most variation when all environmental factors were considered (p=0.002) (Table 4.5). This shows a notable division between samples taken from the eastern and western regions of South Africa.

4.4.6 Arthropod assemblages across topographic regions

For the complete arthropod dataset, sampling points from the same topographic region tended to cluster together (Figure 4.2). This pattern was also evident in the PERMANOVA results, which indicated significant differences between the regions (pseudo-*F*=8.009; p=0.001). PERMANOVA indicated a smaller interactive effect between biome and topographic region for arthropods than for plants (arthropods: pseudo-*F* =8.823; p=0.001; Plants: pseudo-*F* = 14.834; p=0.001). Sampling points from sub-escarpment and escarpment localities in the eastern half of South Africa clustered more closely for the savanna than for grassland. However, for plateau and escarpment points in the eastern region of South Africa, grassland clustered together more strongly.

4.4.7 Contributing arthropod morpho-species

In the ordination of the total arthropod dataset, a total of ten arthropod morpho-species each contributed more than 1% to the total variation across the biomes, according to SIMPER analysis (Table 4.6). Collectively these species contributed to 21% of all variation across the biomes. Two mite (Oribatulidae), two ant (Formicidae), one short-horned grasshopper (Acrididae), one leafhopper (Cicadellidae), one springtail (Entomobryoidea) and one gall gnat (Cecidomyiidae) species were more abundant in the grassland sampling points, whereas one leafhopper (Cicadellidae) and one fungus gnat (Sciaridae) species were more abundant in the savanna sampling points, supporting the distinctiveness between the two biomes.

4.4.8 Assemblages of arthropod trophic groups

The NMDS analyses for separate arthropod trophic groups revealed a much more uniform distribution of sampling points than that of plants or the complete arthropod dataset (Figure 4.2c-f). However, PERMANOVA showed that differences in species composition between biomes were still significant for all the arthropod trophic groups (herbivores: pseudo-*F*=9.013; p=0.001; predators: pseudo-*F*=12.317; p=0.001; parasitoids: pseudo-*F*=5.566; p=0.001; pollinators: pseudo-*F*=3.507; p=0.001). These results also indicate that the predators and herbivores displayed the most significant differences in species composition between biomes. The results were confirmed by the R-values of the ANOSIM analyses (Table 4.3c to f).

No clearly distinctive clustering could be observed of topographic regions for any of the arthropod trophic groups in the NMDS analyses. However, PERMANOVA indicated that there were significant differences in species composition between some topographic regions for all the trophic groups (herbivores: pseudo-*F*=8.127; p=0.001; predators: pseudo-*F*=8.207; p=0.001; parasitoids: pseudo-*F*=5.126; p=0.001; pollinators: pseudo-*F*=3.882; p=0.001). These results indicate that the largest distinctions in species composition between topographic regions for the biomes were within the herbivore and predator groups (in both cases mainly between the plateau and sub-escarpment). In the case of parasitoids and pollinators, there was almost complete species homogeneity between regions, as confirmed by ANOSIM ($R \leq 0.09$) (Table 4.3e and f). Across biomes, escarpment localities showed some clustering of points for herbivores (Figure 4.2c). Escarpment and plateau respectively showed clusters for predators across the two biomes (Figure 4.2d). Sub-escarpment localities had the most dissimilar arthropod composition between grassland (Cala) and savanna (Jozini) biomes for the herbivores and predators.

PERMANOVA also indicated significant interaction effects between biome and topographic region for all trophic groups (herbivores: pseudo-*F*=9.463; p=0.001; predators: pseudo-*F*=7.462; p=0.001; parasitoids: pseudo-*F*=5.85; p=0.001; pollinators: pseudo-*F*=4.093; p=0.001). This was again more evident for the herbivores and predators than for the parasitoids and pollinators.

4.5 Discussion

The results confirmed findings that between biomes, plant species assemblages were more distinguishable than arthropod assemblages (Procheş & Cowling, 2007). The ordination of plant species had the tightest clustering and lowest stress value (0.14). The NMDS analysis for all arthropod morpho-species had a high stress value (0.23), which indicates that not too much reliance can be placed on the spacing of plots of the ordination without cross-checking the results through other statistical analyses (Clarke & Warwick, 2001). However, the similar patterns in species composition between this ordination and some of the other NMDS analyses (Figure 4.2a, c), which yielded low stress values, suggests that this plot is a reasonably good representation of the relationships between samples, and can be further interpreted.

Arthropod assemblages, based on all morpho-species, seem to cluster according to the biomes at least to some extent, which is consistent with previous results (Procheş & Cowling, 2007). The effect of tree cover (a differentiating factor between grassland and savanna) remained noteworthy even with the inclusion of longitude, latitude and altitude variables in the CCA forward selection (Table 4.5). Possible causes of this separate clusters of grassland and savanna arthropod assemblages can be ascribed to preferences for specific climatic conditions associated with the biomes (Menéndez *et al.*, 2007). However, the distinction between grassland and savanna arthropod species assemblages was far less marked than it was for plants. This distinction was even smaller for the separate trophic groups.

The phytophagous and predacious arthropod groups showed the most distinctive groupings between the biomes of all the trophic groups. This finding suggests that these groups may be more specialised and adapted to the two biomes than are parasitoids, pollinators or other trophic groups (Krüger & McGavin, 1998; Menéndez *et al.*, 2007; Mitter *et al.*, 1988). High levels of similarity between the biomes with regard to insect species assemblages for parasitoids and pollinators between biomes can be ascribed to the particularly high mobility of this group; many of these species are capable of flight (Procheş & Cowling, 2007). Also, these parasitoids and pollinators may utilize similar nutritional resources. In this study, the homogenisation effect found for arthropods in these groups is probably related more to plant phylogenies of the biomes and host plant specificity (Moolman *et al.*, 2013). These host plant taxa could be typical of either savanna or grassland, which could lead to homogenisation of the insect groups.

Results seem to indicate that arthropod assemblages are better explained by their geographical position, particularly longitude and latitude, than by biome characteristics. This finding could be an effect of altitude (localities generally increase in altitude from north to south) and climate (localities become drier from east to west). In line with this reasoning, relatively distinct plant and arthropod assemblages occurred within each topographic region. The effect of altitude on species composition is well-known (Hodkinson, 2005). Arthropod communities at different elevations often experience markedly different environmental conditions, particularly climatic. Several studies have demonstrated the dependence of species composition on altitude for several arthropod groups (Adams & Bernard, 1981; Eyre *et al.*, 2001; Gutiérrez & Menéndez, 1995).

4.6 Conclusion

When all arthropods are considered, the Grassland and Savanna Biomes have distinct arthropod assemblages. However, the degree of dissimilarity among plant assemblages is higher between Grassland and Savanna Biomes. These results therefore support the hypothesis proposed in 4.1. When trophic levels were compared, the distinction between arthropod assemblages became even more obscured between biomes. Biomes were still distinguishable, albeit weakly, for phytophagous and predacious arthropod assemblages, but not for parasitoids and pollinators. The similarity in arthropod assemblages for different trophic levels can be ascribed to both biomes being characterised by a dominant grass layer, and hence, habitats. Arthropod species assemblages were better explained by their geographical position than by plant features associated with biome, such as tree and grass cover. It must be noted that these results are based on a limited range of environmental factors and species groups and further research is required to confirm these patterns for arthropods under different conditions and spatial scales.

4.7 References

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CHAPTER 5: PLANT-ARTHROPOD DIVERSITY RELATIONSHIPS OF MAIZE AGRO-ECOSYSTEMS IN TWO GRASSY BIOMES OF SOUTH AFRICA

5.1 Overview

A popular strategy for enhancing insect diversity in intensively cultivated habitats involves maintaining plant diversity in field margins by means of sown grass and wildflower strips. Despite extensive cultivation of maize (approximately 3.1 million hectares) in the grassy biomes of South Africa, little effort has been made to understand whether plant groups maintain insect biodiversity within these agro-ecosystems. The diversity relationships between three prominent guilds of arthropods (herbivores, parasitoids and predators) and three large plant families (Asteraceae, Fabaceae and Poaceae) are described at regional scale across the Grassland and Savanna Biomes of South Africa. The results obtained indicate general positive correlations between plant and arthropod diversity of the lower vegetation layers (≤2m). An increased abundance of members of the grass family (Poaceae) led to significantly higher invertebrate numbers in maize fields and adjacent vegetation. This suggests that grasses play a significant role in supporting arthropod diversity within these agro-ecosystems. When considering farm design in maize-agro-ecosystems, these results indicate that maintaining grassy semi-natural vegetation patches adjacent to actively cultivated maize fields may be sufficient to maintain and conserve arthropod diversity within agricultural landscapes.

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5.2 Introduction

There is a long standing tradition of linking arthropod diversity directly to plant diversity. Numerous models have been proposed that predict an increase of consumer diversity in response to an increase in plant diversity (Rosenzweig, 1995; Tilman, 1986; Whittaker, 1970). If more diverse plant communities are characterized by a greater variety of resources, and a high degree of host plant specificity exists for herbivorous insects, then increased plant diversity may well result in increased insect diversity (Schoonhoven *et al.*, 1998). It has been estimated that almost half of all existing insect species feed on living plants, which implies that more than 40 0000 known herbivorous insect species are associated with approximately 30 0000 vascular plant species (Schoonhoven *et al.*, 1998). It is therefore accepted that an increase in host plant richness in an area should result in an increase in herbivore richness, followed by a greater richness of higher trophic groups such as predators and parasitoids via direct or indirect mechanisms (Hunter & Price, 1992; Jervis *et al.*, 1993).

In practice, these relationships have proven difficult to test, particularly as a result of their complexity. Some experimental studies have reported confirmation of direct causal relationships (Haddad *et al.*, 2001; Siemann *et al.*, 1998). More recent research shows that host plant specificity may be lower than previously suggested estimates and also that herbivorous arthropods often feed on several closely related species of plants rather than one particular species (Novotny *et al.*, 2002). Plants also represent more than a food source for arthropods. The vegetation layer acts as a buffer against environmental fluctuations (Gardiner & Hassall, 2009), provides niche spaces in which to live and also provides resources for nest-building (Steckel *et al.*, 2014).

Whether through direct or indirect mechanisms, a diverse vegetation background generally increases beneficial arthropod diversity and decreases pest outbreaks within an agricultural environment (Finch & Collier, 2000; Gurr *et al.*, 2016). The composition of the vegetation in field margins appears to play an important role in enhancing arthropod diversity (Schaffers *et al.*, 2008). Indeed, some plant groups such as legumes support a greater diversity of arthropods than either grasses or non-leguminous forbs (Koricheva *et al.*, 2000).

In South Africa, information on the diversity relationships between plants and insects is available for a relatively limited geographical range. Studies conducted in the Cape Fynbos, Grassland, Subtropical Thicket, Nama-Karoo and Succulent Karroo biomes in South Africa generally report positive relationships between overall plant and insect diversity (Proches & Cowling, 2006; Wright & Samways, 1998) and also show that various feeding guilds of arthropods may differ in their respective relationships with different plant features, although this aspect is often neglected in research (Benadé *et al.*, 2016). In the present chapter, information is provided on the diversity relationships between three prominent trophic guilds of arthropods and the three largest plant families at a regional scale.

The aim was to determine the importance of plant diversity with respect to enhancing arthropod diversity in maize (*Zea mays*) agro-ecosystems along agricultural disturbance gradients situated within the core regions of the Grassland and Savanna Biomes of South Africa. Specifically, the following research questions were asked: (1) Do positive correlations exist between plant and arthropod diversity, richness and abundance and is there a link between their assemblage structures at various distances along an agricultural disturbance gradient? (2) How do these results compare with those for selected insect trophic groups (herbivores, predators and parasitoids) and specific plant family groups (Asteraceae, Fabaceae and Poaceae)? (3) Do plant communities that are more heterogeneous across the landscape result in more heterogeneous arthropod communities?

In accordance with the resource heterogeneity hypothesis, which states that a greater variety of resources should result in a greater variety of consumers (Whittaker, 1970), it is hypothesised that overall positive correlations exist between plant and arthropod richness, diversity and abundance, and that there is a positive link between the species compositions of plants and arthropods (i.e. different plant species assemblages will result in different arthropod species assemblages). The population dynamics of herbivores and predators may be directly or indirectly linked via bottom-up or top-down mechanisms (Hunter & Price, 1992). Therefore, the second hypothesis states that positive correlations will also exist between the richness, diversity and abundance of plants and all of the arthropod trophic groups. Legumes (Fabaceae) as a family contribute significantly towards nutrient provisioning in ecosystems as they increase nitrogen availability as well as pollen and nectar sources, which are often limiting factors to herbivores and natural enemies (Jervis *et al.*, 1993; Mattson, 1980). It has been shown in one study that the abundance of Fabaceae was of particular importance in enhancing arthropod numbers (Koricheva *et al.*, 2000). Resulting from this, the third hypothesis proposes that the species richness, diversity and abundance of Fabaceae have particularly strong correlations with that of arthropods, compared to the Asteraceae and Poaceae. A more heterogeneous landscape provided by increased plant beta diversity may provide niches for a wider variety of arthropod species, and may result in higher arthropod beta diversity (Martínez *et al.*, 2015). From this, the fourth hypothesis states that more heterogeneous plant communities is associated with more heterogeneous arthropod communities, which indicates that there is a link between plant and arthropod beta-diversity.

5.3 Material and methods

5.3.1 Experimental design and data processing

Field data for the results displayed in this chapter were collected in accordance with the methods outlined in chapter 2. All invertebrates were classified into a number of major trophic groups depending on the predominant feeding habit of the species belonging to the families (e.g. carabid beetles were classified as predators even though some species feed on pollen or seeds). Classifying family-level invertebrate data into trophic groups may be less accurate than classifications of species-level data because different species in the same family may exhibit different feeding strategies. However, it was assumed that the error introduced by this approach was cross-cutting and negligible, and did not significantly affect the results. Also, some groups of arthropods (highly mobile insects such as butterflies or grasshoppers) may be under-represented in the samples as a result of the collection methods employed and the specificity of season. It should be noted that a study targeting soil and flying arthropods might well yield very different results.

For plants, tree data (woody species >2m high) were not included for the purpose of the present chapter because the data showed that the D-vac technique was inefficient with respect to sampling insects at heights above 2m. Hence, this chapter only focussed on the ground and shrub vegetation layer (≤2m), which are referred to as the 'lower vegetation layers'.

5.3.2 Statistical analysis

Plant and arthropod species were described in terms of abundance, species richness and diversity. Abundance was calculated as the total number of individuals (n) in any given sample. Species richness represented the total number of species (S) in a sample. Alpha-diversity was expressed using the Shannon–Wiener diversity index, which condenses species richness and evenness into a single value (Samways, 1984). Shannon–Wiener diversity index values were calculated using PRIMER 7 (Clarke & Gorley, 2006). Beta-diversity was quantified by conducting PERMDISP analyses on abundance data in PRIMER 7. This procedure tests for variability in species composition within sampling units by performing an ANOVA on the distances of samples to the centroid of a cluster in multivariate space (Anderson *et al.*, 2006). PERMDISP with 999 permutations was performed on Bray–Curtis similarity matrices of datasets containing all plant and arthropod species after a presence/absence transformation of the abundance data. The separate arthropod trophic groups were not subjected to PERMDISM analyses because they were not represented in all points and the analysis is not suitable for unequally replicated groups (Ratkowsky, 2008).

To determine whether significant differences in plant and arthropod species assemblages exist between sampling points in different distance classes (maize fields, marginal vegetation and rangeland vegetation), permutational multivariate analysis of variance (PERMANOVA) was performed using abundance data.

PERMANOVA is suitable for abundance data where significance is based on permutation of the dissimilarity matrix (Anderson, 2001). All PERMANOVA analyses were conducted with 999 permutations using Bray–Curtis similarity and type III sums of squares after a square-root transformation of species data to reduce the influence of common species (Anderson, 2001). PERMANOVA results of plants and arthropods were then compared to determine whether shifts in plant species composition are mirrored by shifts in arthropod species composition. Spearman's rank order correlation analyses were conducted with STATISTICA, version 13 (Dell Inc., 2015) to test for significant correlations between plant and arthropod abundance, richness and diversity across sampling sites. The Spearman rank method provides a measure of statistical dependence between two variables that assesses how well the relationship between them can be described using a monotonic function. It is a nonparametric version of the Pearson product-moment correlation, although it is computed from ranks and is therefore not influenced by outliers in the data. The Spearman R statistic ranges between +1 and −1, with +1 representing a perfect positive correlation and −1 representing a perfect negative correlation (Gibbons & Chakraborti, 2011).

5.4 Results

5.4.1 Overview of data

A total of 11378 individual plants within the lower vegetation layers were sampled for the present study, representing 569 native and alien non-crop species in 63 families, with 132 species recorded from maize fields, 409 from marginal vegetation and 386 from rangeland (Table 5.1). The plant families Poaceae, Asteraceae and Fabaceae comprised 46.8%, 13.67% and 3.74% of the total number of individuals, respectively, and accounted for 64.2% of all plant abundances (Table 5.1). A total of 117 arthropod families, 1636 morpho-species and 39 396 individuals were considered for the analyses. This amounted to 558 morpho-species for maize fields, 1007 for marginal vegetation and 1003 for rangelands. A list of plant and arthropod morpho-species is provided in the supporting information of Botha *et al.* (2016). The arthropods collected during the study belonged to 23 orders, with the most dominant ones being the Hemiptera (true bugs) followed by the Hymenoptera (bees, wasps and ants), Diptera (flies), Coleoptera (beetles), Araneae (spiders) and Orthoptera (crickets, grasshoppers and locusts). The best represented arthropod trophic groups in the present study were the herbivores, predators and parasitoids, which represented 39.2%, 19.3% and 8.6% of the total number of individuals, respectively, accounting for 67% of all arthropod abundances (Table 5.1). Other trophic groups (32.7%) included detritivores, frugivores, omnivores, parasites and pollinators, although these were not considered for further analysis in the present study as a result of low numbers.

Table 5.1: Number of plant species in the lower vegetation layers (≤2m) and associated arthropod species as well as percentage of individuals per family, order or trophic group for each of the distance classes (maize field, marginal vegetation and rangeland) along an agricultural disturbance gradient.

Plant /Arthropod groups	Total		Maize field		Marginal vegetation		Rangeland vegetation	
	Species	%Individuals	Species	%Individuals	Species	%Individuals	Species	%Individuals
Poaceae	122	46.80	41	28.00	94	52.62	92	51.65
Asteraceae	80	13.67	27	17.18	52	13.79	53	11.57
Cyperaceae	24	6.54	6	20.96	16	1.53	16	3.35
Acanthaceae	28	4.55	0	0	22	5.01	25	6.66
Fabaceae	53	3.74	8	1.43	38	5.36	36	3.46
Rubiaceae	11	2.50	1	2.74	10	2.87	8	1.99
Malvaceae	23	2.16	5	4.22	19	1.60	17	1.56
Amaranthaceae	12	1.63	3	1.47	7	2.21	7	1.16
Commelinaceae	5	1.45	2	3.26	3	0.93	5	0.94
Euphorbiaceae	12	1.43	6	1.99	9	1.34	8	1.21
Other (53)	199	15.52	33	18.74	139	12.74	119	16.44
All plants	569	---	132	---	409	---	386	---
Herbivores	727	39.2	185	60.0	476	32.2	458	43.4
Predators	334	19.3	122	17.9	215	20.8	210	18.4
Parasitoids	242	8.6	98	7.2	136	7.8	143	9.8
Pollinators	13	0.09	1	0.05	6	0.1	12	0.1
Other groups(5)	320	32.7	152	23.9	174	39.1	180	28.3
All arthropods	1636	---	558	---	1007	---	1003	---

5.4.2 Community assemblage patterns

Permutational multivariate analysis of variance (PERMANOVA) results revealed that the separate distance classes (maize field, marginal vegetation or rangeland) differed significantly in terms of all low-growing vegetation groups (Asteraceae, Fabaceae and Poaceae) (p=0.001 (Table 5.2). Assemblage patterns of trees, shrubs and climbers were not significantly affected by distance from the maize fields. Pairwise comparisons between distance classes indicated significant differences in plant species composition between maize field and adjacent uncultivated vegetation. However, marginal vegetation and rangeland vegetation did not have significant differences in plant species assemblages. Similar to the results for plants, species assemblages of all arthropods, herbivores and predators were significantly different between maize fields and adjacent marginal vegetation and rangeland (p=0.001) (Table 5.2). The assemblage patterns of parasitoids were also significantly affected by distance class, although not as strongly as for the herbivores and predators (p=0.01). Within the uncultivated vegetation adjacent to maize fields, arthropod species assemblages were relatively similar (p≥0.4).

5.4.3 Plant–arthropod alpha-diversity relationships

Spearman’s rank order revealed significant positive correlations between plants and arthropods within maize fields (Table 5.3). Here there were significant positive relationships in species richness (S) between

Table 5.2: Permutational multivariate analysis of variance (PERMANOVA) results indicating similarity in species composition of various taxonomic groups between various distance classes along a maize field–field margin gradient: maize fields (MZ), marginal vegetation (MV) and rangelands (RA).

	Distance class	Pairwise comparisons between vegetation communities		
		MZ x MV	MZ x RA	MV x RA
All plants	10.613**	≠ **	≠ **	=
Asteraceae	8.184**	≠ **	≠ **	=
Fabaceae	2.886**	≠ **	≠ **	=
Poaceae	11.483**	≠ **	≠ **	=
All arthropods	2.773**	≠ **	≠ **	=
Herbivores	3.146**	≠ **	≠ **	=
Predators	2.736**	≠ **	≠ **	=
Parasitoids	1.445*	≠ **	≠ **	=

Figures represent pseudo F-values, permutations = 999; Bray-Curtis similarity; $**p\leq0.001$, $*p\leq0.01$;
≠ significantly different species compositions, = statistically equal species compositions

all arthropods and plants. This was specifically true for herbivores, although not for the other arthropod trophic groups. The abundance (n) of predaceous arthropods was significantly correlated with the abundance of grasses (Poaceae) in maize fields. Within marginal vegetation (30–100m from maize fields), there were positive correlations between arthropod abundance and low-growing vegetation. Particularly strong positive relationships ($R\geq0.3$) (Table 5.3) existed between arthropod abundance and grass (Poaceae) abundance. There were also positive relationships in abundance between the Asteraceae plant group and all arthropods and herbivores. Within rangelands (between 100 and 400m from maize fields), species richness and abundance of herbivores was positively correlated with species richness and abundance of grasses. Also, the species richness and abundance of arthropods and the Fabaceae were negatively correlated.

5.4.4 Plant–arthropod beta-diversity relationships

PERMDISP analyses indicated that the heterogeneity of the entire plant dataset was significantly higher in uncultivated vegetation than in maize fields (p=0.001) (Table 5.4). Mean distances to centroids for plants were 58.227, 63.087 and 63.461 for maize fields, marginal vegetation and rangelands respectively, with increasing distance to centroids indicating greater species heterogeneity between sampling points. However, there were no significant differences in plant species heterogeneity between marginal vegetation and rangeland (p=0.730). For arthropods, there were no significant differences in species heterogeneity between any of the distance classes along the maize field–field margin gradient (p>0.1) (Table 5.4). Mean distances to centroids for arthropods were 66.026, 66.074 and 65.412 for maize fields, marginal vegetation and rangeland, respectively. Spearman correlation analyses revealed that there were no overall significant correlations between plant and arthropod species heterogeneity at any of the separate distance classes (p>0.1, data not presented).

Table 5.3: Spearman rank order correlation values (R) between plant and arthropod species richness (S), abundance (N) and Shannon–Wiener diversity (H′), calculated for points situated at similar distances from maize fields: maize fields, field margins and rangeland (n=48).

			All plants	Fabaceae	Asteraceae	Poaceae
Maize field	Species richness (S)	All arthropods	**0.318***	-0.020	0.273	0.164
		Herbivores	**0.303***	0.015	0.083	0.113
		Predators	0.102	-0.068	0.140	0.196
		Parasitoids	0.281	-0.044	0.152	0.156
	Abundance (N)	All arthropods	0.114	-0.117	0.062	0.210
		Herbivores	0.007	-0.186	0.007	0.047
		Predators	0.101	0.104	-0.117	**0.302***
		Parasitoids	0.084	-0.144	0.092	0.255
	Diversity (H')	All arthropods	-0.057	0.054	-0.035	0.049
		Herbivores	0.067	0.072	-0.118	0.163
		Predators	-0.112	-0.054	0.086	0.088
		Parasitoids	0.255	0.091	0.142	0.133
Marginal vegetation	Species richness (S)	All arthropods	-0.082	-0.107	0.039	0.206
		Herbivores	-0.064	-0.061	0.082	**0.288***
		Predators	-0.009	0.012	-0.092	0.182
		Parasitoids	-0.013	0.089	-0.052	0.021
	Abundance (N)	All arthropods	**0.334***	-0.087	**0.309***	**0.550***
		Herbivores	**0.319***	-0.082	**0.364***	**0.648***
		Predators	0.142	0.071	0.186	**0.299***
		Parasitoids	**0.445***	-0.048	0.128	**0.381***
	Diversity (H')	All arthropods	-0.250	-0.196	0.002	-0.073
		Herbivores	-0.088	-0.090	0.100	0.201
		Predators	-0.036	-0.062	-0.021	0.163
		Parasitoids	-0.030	-0.025	-0.028	-0.051
Rangeland vegetation	Species richness (S)	All arthropods	0.026	**-0.322***	-0.047	0.212
		Herbivores	0.016	-0.250	0.0257	**0.294***
		Predators	0.016	**-0.375***	-0.1217	0.182
		Parasitoids	0.160	-0.226	-0.162	0.141
	Abundance (N)	All arthropods	0.271	**-0.409***	0.087	**0.369***
		Herbivores	**0.340***	**-0.382***	0.190	**0.460***
		Predators	0.105	**-0.387***	-0.032	0.253
		Parasitoids	0.281	-0.205	-0.093	0.157
	Diversity (H’)	All arthropods	-0.116	-0.277	-0.105	0.036
		Herbivores	-0.107	-0.135	-0.151	0.149
		Predators	-0.158	**-0.298***	-0.098	-0.030
		Parasitoids	0.011	-0.146	-0.200	0.047

Bold text * indicates significance at $p < 0.05$

Table 5.4: Permutational multivariate analysis of homogeneity in dispersion (PERMDISP) results indicating differences in beta diversity of all plants and all arthropods between various distance classes along a maize field–field margin gradient: maize fields, marginal vegetation and rangelands.

		t	p (perm)
All plants	Maize field X Marginal vegetation	3.805	**0.001****
	Maize field X Rangeland	4.407	**0.001****
	Marginal veg. X Rangeland	0.395	0.730
All arthropods	Maize field X Marginal vegetation	0.099	0.925
	Maize field X Rangeland.	1.379	0.166
	Marginal veg. X Rangeland	1.373	0.149

Permutations = 999; Bray-Curtis similarity; data transformation: presence/absence; Bold text**indicates significant p values at $p \leq 0.001$

5.5 Discussion

5.5.1 Community assemblage patterns

The respective plant communities associated with the maize fields and uncultivated vegetation tended to have relatively distinct arthropod community assemblages, as indicated by the results of the PERMANOVA. Therefore, overall arthropod and trophic group species assemblages appear to be highly influenced by plant community composition because changes in plant communities from maize fields to rangeland were mirrored by the changes in arthropod species assemblages. It is known that local plant species composition is a good determinant of insect assemblages (Schaffers *et al.*, 2008; Symstad *et al.*, 2000). Plant species composition may influence overall arthropod species composition directly through resource availability if a high degree of host-plant specificity exists (Hunter & Price, 1992). However, the relationships between plant and arthropod species composition may also be indirectly linked to factors such as soil chemistry, plant structure variation, genotype diversity and similar responses to environmental factors (Johnson & Agrawal, 2005; Meindl *et al.*, 2013), which are all aspects not tested for in the present study.

5.5.2 Plant–arthropod alpha-diversity relationships

Within maize fields, an increased richness of plant species in general resulted in an increased species richness of all arthropods, and specifically of herbivorous arthropods. The results also indicated that abundance (although not species richness) of weedy grasses significantly increased predator numbers in maize fields. These results are consistent with multiples studies that have shown increases in insect species numbers in response to an increased richness and abundance of weedy vegetation in crop fields (Carvalheiro *et al.*, 2011; Perrin, 1975; Schellhorn & Sork, 1997). Although weeds in large numbers may compete with crops for resources and reduce crop yields (Cousens, 1985), a controlled weed population within crop fields may be beneficial by providing important resources for insects such as additional food sources and microhabitats that are not available in low-diversity monocultures (Landis *et al.*, 2005; Ratnadass *et al.*, 2012). As such, the presence of weedy vegetation in maize fields may provide additional resources (food, shelter or breeding sites) and therefore enable a more diverse arthropod community to persist in the crop field environment. Additionally, weeds may provide alternative prey or host species for predators, when crop pests are not present (Altieri & Letourneau, 1982).

In rangeland vegetation, arthropod species richness and abundance were negatively correlated with that of legumes (Fabaceae). This is consistent with the results of Benadé *et al.* (2016), who also found significant negative relationships between arthropod alpha-diversity and plant species richness. Negative relationships have also been demonstrated by Braschler *et al.* (2012). This contradicts the results of Koricheva *et al.* (2000), who found that the presence of legumes tended to increase arthropod numbers. However, their results were highly dependent on sampling method and the arthropod group in question. Because the Fabaceae is important for pollinators, the particular sampling method used may not sufficiently capture this diversity for analyses. Plant species belonging to the Fabaceae are important food sources for insect pollinators because they generally have a relatively higher pollen protein content compared with other plant families such as the Asteraceae (Hanley *et al.*, 2008).

For the most part, arthropod abundance and diversity did not increase significantly with increased diversity and abundance of Asteraceae. Similar to the Fabaceae, this plant family may play a significant role in enhancing pollinator diversity. Plant species representing the Asteraceae family are a common component of wildflower mixes sown in field margin strips adjacent to crop fields (Briner & Frank, 1998; Hatt *et al.*, 2015; Lemke & Poehling, 2002) and several studies have highlighted the value of Asteraceae in increasing flower-visiting arthropod numbers and diversity (Albrecht *et al.*, 2007; Proches & Cowling, 2006; Souza-Silva *et al.*, 2001). Including sampling techniques more suitable for capturing these pollinator insects in future studies, such as the use of beating trays (Southwood & Henderson, 2000), flight traps, pan traps or sticky traps (Duelli *et al.*, 1999), may yield different results from those observed in this study.

Benadé *et al.* (2016) stated that arthropod abundance (particularly phytophagous arthropods) may increase with an increased relative abundance of specific plant taxa such as grasses. The results confirmed that increases in grass abundance resulted in significant increases in herbivore abundance, as well as in the abundances of all the other arthropod taxa in marginal vegetation. Tussock grasses are often promoted as a means of providing suitable habitats of dense, sheltered vegetation for insects such as carabid and staphylinid beetles and spiders in agro-ecosystems (Marshall & Moonen, 2002; Meek *et al.*, 2002). Caballero-López *et al.* (2010) indicated that the family richness of insect herbivores, as well as that of predators and parasitoids, was closely associated with the cover of grasses. Increased cover by the grass layer may provide a suitable microclimate and enable a greater number of arthropod individuals to persist in these habitats. Factors such as vegetation density, percentage cover and the associated microclimate may have pronounced effects on arthropod communities, even more so than plant species richness *per se* (Kuppler *et al.*, 2015; Pryke *et al.*, 2013; Spalinger *et al.*, 2012; Weiss *et al.*, 2013).

5.5.3 Plant–arthropod beta-diversity relationships

In beta-diversity analyses, high values indicate large differences between sampling points in the identity of species encountered (Clough *et al.*, 2005). Beta-diversity was significantly higher for plant communities of uncultivated vegetation than for those found in maize fields. Therefore, maize fields tended to have a homogenization effect on plant species diversity across the Grassland and Savanna Biomes. Because the physical conditions of maize fields are more or less similar across the landscape, this may result in a similar set of non-crop plant species favoured by these specific conditions (Olden & Poff, 2003). On the other hand, maize fields do not appear to have an effect on the beta-diversity of adjacent uncultivated vegetation, because marginal vegetation and rangeland vegetation had equally high levels of beta-diversity.

Arthropod beta-diversity did not increase with plant beta-diversity. Also, arthropod communities did not display significant differences in beta-diversity between maize fields and uncultivated vegetation. From these results, it appears that maize fields do not have a homogenization effect on arthropods similar to that for plants. Host specialization appears to play a large role in the beta-diversity patterns of herbivorous insects (polyphagous herbivores will display lower beta-diversity than specialists) (Novotny *et al.*, 2002; Moolman *et al.*, 2013). If there is low specialization of the herbivores considered in the present study (and in turn of predators that feed on the herbivores), it could be expected that arthropod beta-diversity will not necessarily be related to plant beta-diversity. This effect may be further obscured by the high mobility of many of the arthropod species (Procheş, & Cowling, 2007). The dispersal ability of species is a major determinant of the magnitude of beta-diversity in a population, with more mobile species typically having lower beta-diversity across the landscape (Novotny *et al.*, 2002).

5.6 Conclusion

Within an agricultural context, the diversity relationships between arthropods and plants may aid in the enhancement of beneficial arthropod numbers in agro-ecosystems (Schoonhoven *et al.*, 1998). However, the implications for improving arthropod diversity in and around maize fields for maize production are not yet known and warrant further study. Relating to the first research question, it was shown that different plant communities tended to have significantly different arthropod communities and that positive correlations do exist between plant species and arthropod morpho-species in maize agro-ecosystems across the Grassland and Savanna biomes of South Africa. These findings support the first hypothesis.

Relating to the second research question, plant-arthropod correlations were highly dependent on the plant family or arthropod trophic group and particular habitat type (maize field or rangeland vegetation) in question. It is apparent that these relationships are complex and are probably not directly linked. The overall tendency was that species richness and abundance (although not diversity) of the separate trophic groups (herbivores, predators and parasitiods) were positively correlated with that of plants, which partially supports the second hypothesis.

From the results of this chapter, it appears that the abundance of grasses (Poaceae) may be of particular importance in enhancing overall arthropod numbers, specifically herbivores and predators, in these agro-ecosystems, even more so than members of Fabaceae and Asteraceae in the lower vegetation layers. The third hypothesis proposing that the species richness, diversity and abundance of Fabaceae should have particularly strong correlations with that of arthropods, are therefore rejected. The Asteraceae and Fabaceae are probably more important for insect pollinator diversity and were not sampled in sufficient numbers for the present study as a result of the collecting technique. Further research is required to confirm these results for insect pollinator groups.

Regarding the third research question, the results indicated no link between plant and arthropod beta-diversity, and the fourth hypothesis is therefore not supported. When considering farm design in maize agro-ecosystems, where pollination services are not of particular importance for crop production, these results indicate that supplying grassy, semi-natural vegetation patches adjacent to actively cultivated maize fields may be sufficient to maintain the overall diversity of arthropods within the agricultural landscape.

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CHAPTER 6: FUNCTIONAL TYPE COMPOSITION AND DIVERSITY OF NON-CROP PLANTS IN MAIZE AGRO-ECOSYSTEMS OF SOUTH AFRICA

6.1 Overview

The response of vegetation to agricultural disturbances is often measured in terms of taxonomic diversity loss. However, it is widely accepted that the responses of plant taxa to environmental disturbances may be more directly linked to characteristics or traits that enable or hinder their persistence in disturbed environments. This highlights the need to assess the impacts of agricultural disturbance on the abundance patterns and diversity of specific plant traits and functional types. In this chapter, the specific functional trait patterns of plant communities associated with maize agro-ecosystems were described in six localities situated within the Grassland and Savanna Biomes of South Africa. Functional diversity was significantly decreased in high disturbance maize fields compared to medium and low disturbance marginal vegetation and rangeland. Chamaephytic and hemicryptophytic (perennial) life forms, nitrogen –fixing ability and spinescence were trait attributes that were most frequently found in marginal and rangeland vegetation but were lost in the maize fields. Inside the maize fields, these traits were replaced by annual, low-growing plants with clonal parts and long-range dispersal mechanisms, which allow survival in the ephemeral maize field environment. However, there was no indication of functional diversity loss or major changes in trait composition in marginal or rangeland vegetation. This indicates that the value of this semi-natural marginal habitat in terms of functional diversity conservation in South African grassy biomes cannot be ignored. Results also indicated that the weedy plant communities of grassland and savanna maize fields had different trait attributes. This could have implications for weed management in that different strategies may have to be applied for effective weed control, depending on the biome in which the maize fields are situated. Ultimately, this data may assist in the management and conservation of plant communities in South Africa within a growing agricultural landscape.

A manuscript has been prepared from the results presented in this chapter and will be submitted for possible publication in **Applied Vegetation Science**.

6.2 Introduction

The large-scale transformation of natural vegetation into agro-ecosystems has detrimental effects on environments worldwide (Sala *et al.*, 2000; Wessels *et al.*, 2003) and affects plant diversity and composition not only within crop fields but also in adjacent uncultivated vegetation (De Snoo & Van der Poll, 1999; Marshall & Moonen, 2002). Livestock-grazing and crop agriculture are two very prominent land-use types in the Grassland and Savanna Biomes of South Africa (Mucina & Rutherford, 2006; Nazare, 2005; Neke & Du Plessis, 2004) and the majority of the country's bird, butterfly, mammal and plant diversity are found on privately-owned farms (Wessels *et al.*, 2003). Since plants represent the basis of most terrestrial food chains, changes in plant diversity or species composition may in turn affect consumer populations (Caballero-López *et al.*, 2010; Schaffers *et al.*, 2008; Schellhorn & Sork, 1997; Siemann, 1998). To regulate the management of diverse and functional ecosystems within an expanding agricultural landscape, it has therefore become increasingly important to understand the effect of anthropogenic activities on plant communities.

The response of biota to disturbance is often measured in terms of taxonomic diversity loss (O'Connor, 2005; Siebert, 2011). However, the responses of plant taxa to environmental disturbances may be more directly linked to characteristics or functional traits that enable or hinder their persistence in disturbed environments (Deckers *et al.*, 2004; Lavorel & Garnier, 2002; Lososová *et al.*, 2006). Plants may then be defined in terms of functional groups or types, which can be used as an alternative to taxonomic species and are based on sets of similar traits and, theoretically, similar responses to or effects on their environment (Lavorel *et al.*, 1997). Accordingly, the impact of crop and rangeland agriculture on plant communities is often assessed by describing variation and response patterns in the abundance (number of individuals) of major functional groups, e.g. grasses or forbs (Fuhlendorf *et al.*, 2001; Liira *et al.*, 2008; Rutherford *et al.*, 2012). It also showed to be useful assessing responses of functional diversity to agricultural disturbance, i.e. the diversity of plant traits or functions present in a community (Flynn *et al.*, 2009; Ma & Herzon, 2014; Petchey & Gaston, 2006).

For most species-based diversity indices, all species are considered equally important. However, when considering ecosystem functions, the loss of some species may have a much more pronounced effect on the ecosystem than others, depending on how many functionally similar species are left to perform the function of the lost species (Petchey *et al.*, 2009). Therefore, the loss of any particular species will always decrease taxonomic diversity, but not necessarily functional diversity. Generally, it is agreed that plant communities with a greater functional diversity are more stable and resilient since there is a wide enough range of functions performed by the species (and a reasonable number of species performing each function) to fill the available niche space, even when disturbance occurs (Díaz & Cabido, 2001). On the contrary, low functional diversity could be an indication of underutilised niche spaces, which could for instance leave the community vulnerable to invasion by exotic species (Díaz & Cabido, 2001; Dukes, 2001). Among the multiple techniques used to measure functional diversity, functional type richness remains one of the most popular (Cadotte *et al.*, 2011; Pakeman, 2011a). This technique involves the analysis of the richness (number) of functional types represented by species in an assemblage.

Whichever analysis method is used to describe functional diversity, choosing an appropriate set of traits is of greatest importance to obtain meaningful results (Petchey *et al.*, 2009). In the context of agricultural disturbance, it is important to consider which traits play the most important roles in the species' ability to cope with the high disturbance levels associated with the agricultural environment. Whole-plant and regenerative traits such as life form, growth form, clonality, stem morphology and dispersal modes are known to be associated with plant responses to agricultural disturbance *(*Cornelissen *et al.*, 2003; Liira et *al.*, 2008; Pakeman, 2011b), and may therefore be important factors in the agricultural landscape. Spinescence is associated with plant defence or protection against herbivores (Hanley & Lamont, 2002), which may play a role in frequently grazed rangelands adjacent to maize fields. Furthermore, the mode of dispersal and pollination vectors utilised by different plant species may be correlated with their range size in fragmented agro-ecosystem habitats (Aronson *et al.*, 2007).

Assessing functional diversity in addition to species diversity has increased in popularity with the realisation that it is not the number of species *per se*, but the identity and diversity of functional traits that drive ecosystem function and its associated services (Pakeman, 2011b; Zhang *et al.*, 2014). Some plant functional types may be more severely impacted by agricultural disturbance than others (Liira *et al.*, 2008). These functional types that are more sensitive to agricultural disturbance may serve as bio-indicators in land-use change monitoring studies (Liira *et al.*, 2008). Considering the rapid transformation and degradation of South Africa's natural grasslands into crop production systems, there is a need to develop strategies to conserve remaining semi-natural habitat. This warrants a considerable understanding of the effects of these agricultural disturbances on species, structural, or functional diversity (Neke & Du Plessis, 2004). A few studies have been conducted on the effect of crop agriculture on species diversity and composition in crop agro-ecosystems (O'Connor, 2005; Siebert, 2011; Walters *et al.*, 2006; Wessels *et al.*, 2003), but very few studies to date sought to test the effects of crop agriculture on plant traits and functional diversity in the country (e.g Kemper *et al.*, 1999).

Addressing the related knowledge gap in South African maize-agro-ecosystems, this study contributes towards a basis for in-depth studies into the potential consequences for changes in ecosystem functions and the provisioning of ecosystem services due to land-use change and habitat transformation, respectively. Specifically, this study describes plant traits and major plant functional types (PFTs) commonly associated with disturbance in agricultural landscapes of two biomes in Africa. The following research questions were asked: (1) How are plant functional types and individual plant traits distributed along a disturbance gradient from low-disturbance semi-natural rangelands into high-disturbance maize fields? (2) How does the agricultural disturbance intensity influence functional trait diversity? (3) Do these patterns differ between the Savanna and Grassland Biomes?

Maize fields and adjacent field margins are intensive management systems that involve the intentional or unintentional removal of non-crop vegetation through soil tillage, herbicide application and infrastructure (farm tracks, footpaths, ditches and fences). Therefore, the first hypothesis states that increased agricultural disturbance (associated with increased land-use intensity) decreases functional diversity of plants and favours pioneer type traits such as clonal ability, long-range dispersal mechanisms and annual lifecycles. The Grassland and Savanna Biomes are subjected to different climatic factors and are defined according to different plant species assemblages and structures (Botha *et al.*, 2016). From this the second hypothesis states that the grassland and savanna habitats will differ in terms of trait and functional type patterns along the disturbance gradient and that different trait attributes will be lost in grassland and savanna with increasing agricultural disturbance.

6.3 Material and methods

6.3.1 Vegetation sampling and trait selection

The experimental layout for the collection of plant data for this chapter is detailed in chapter 2. All recorded plant species were defined according to a number of 'soft' traits that have known responses to factors associated with agricultural disturbance (Aronson *et al.*, 2007; Cornelissen *et al.*, 2003). A complete summary of the procedures followed in the data analysis process are given in Figure 6.1. The traits were identified with emphasis on the ecological adaptations that may play a role in the species' ability to persist in an agricultural environment. Table 6.1 presents a list of the traits, trait attribute definitions as well as the proposed ecological adaptations applicable to this study. Species trait information was obtained from a variety of sources in the literature, including Germishuizen *et al.* (2006), Hyde *et al.* (2015), SANBI (2015), Van Oudtshoorn (2006) as well as personal observations made in the field.

6.3.2 Data processing and analysis

6.3.2.1 Identifying plant functional types

For the identification of PFTs, only plant species that were present in 10% or more of the sampling points in at least one of the distance classes (maize field, marginal vegetation or rangeland) were considered, following the approach of Díaz and Cabido (1997) and Peco *et al.* (2005). After rare species were removed, the trait groups had to be represented by at least ten species before being selected for data analysis, as recommended by Landsberg *et al.* (1999).

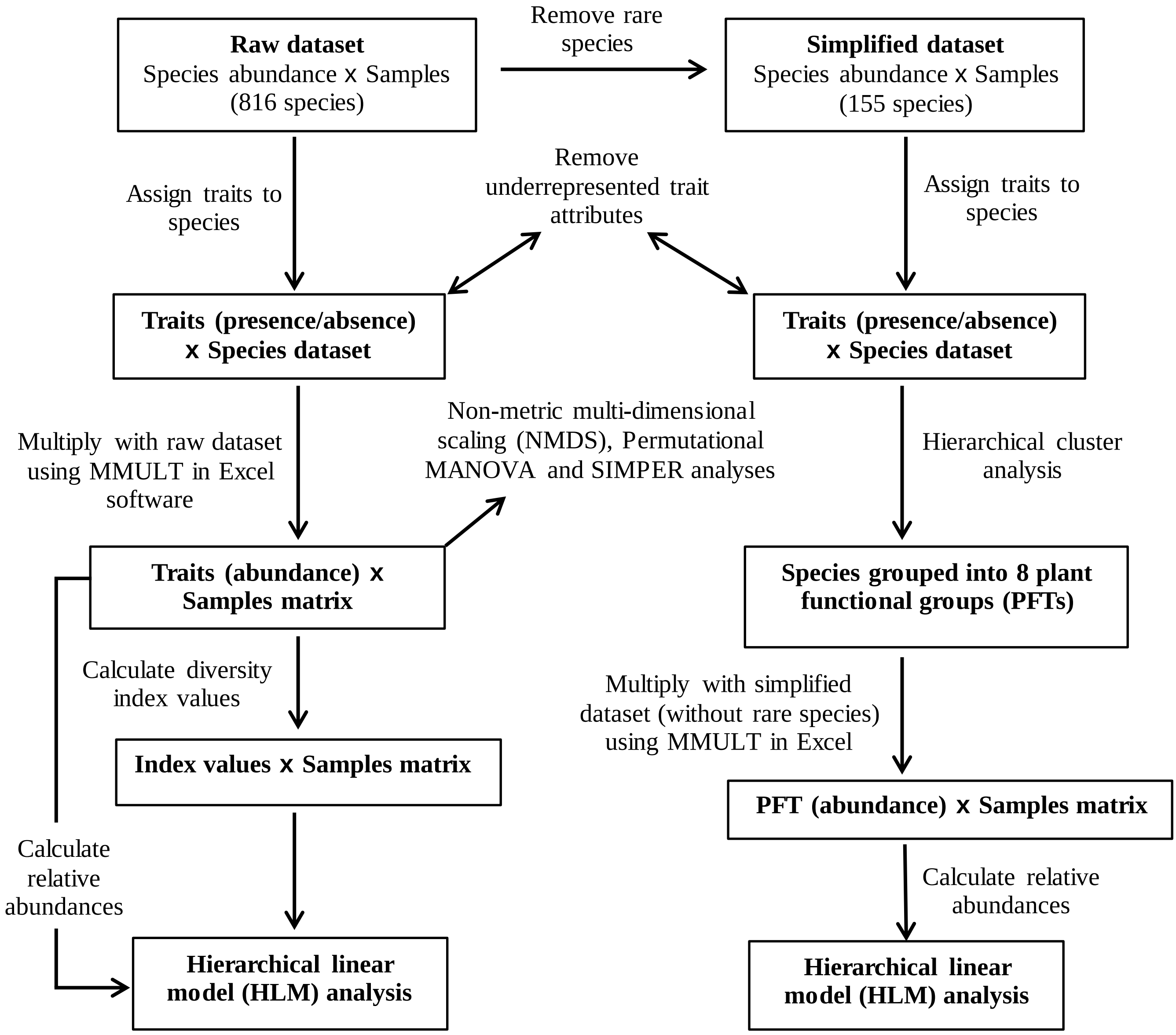

Figure 6.1: Summary of the analytical procedures followed to unravel the functional component of plant communities within maize fields and adjacent uncultivated vegetation. ‘Samples’ refer to the sampling points that were surveyed along an agricultural disturbance gradient.

The final dataset consisted of 155 plant species and eight traits with attributes in categorical (e.g. Phanerophytes = 1, Chamaephytes = 2, Hemicryptophytes = 3) and binary (e.g. 1 = trait present, 0 = trait absent) format. A hierarchical agglomerative clustering analysis with an Unweighted Pair Group Method with Arithmetic Mean (UPGMA)-clustering algorithm and Gower distance measure appropriate for mixed (categorical and binary) data types was used in PRIMER 6 software (Clarke & Gorley, 2006) to detect groupings of plant species based on their trait scores (Franks *et al.*, 2009). The cluster analysis was combined with a Similarity Profile (SIMPROF) test, which is a more objective method for identifying significant groupings than the assignment of arbitrary cut-off levels (Clarke *et al.*, 2008).

Table 6.1: List of plant traits, assigned categories and definitions as well as proposed ecological mechanisms of trait attributes for the species recorded in all localities across the maize field-field margin gradient. Definitions follow Cornelissen *et al.* (2003) and Germishuizen *et al.* (2006).

Plant trait	Trait attribute categories	Ecological adaptation
Life form	**1. Phanerophytes** (plants taller than 0.50 m and whose shoots do not die back periodically to that height) **2. Chamaephytes** (plants smaller than 0.50 m or that die back periodically to that height) **3. Hemicryptophytes** (periodic shoot reduction to a remnant shoot system so that buds in harsh season are close to soil surface, e.g. many grasses and rosette forbs) **4. Therophytes** (root and shoot system dies back after seed production and complete whole life cycle in one year) **5. Geophytes** (perennial plants, usually herbaceous, with renewal buds located on the plant below the soil surface, as on bulbs or rhizomes).	Plant strategy in relation to climate and disturbance
Growth form	**1. Rosette forbs** (herbaceous plants with leaves emanating basally and spreading obliquely or laterally from a central, lateral stem, close to or on the substrate, around a central axis from which a scape often emanates) **2. Erect forbs** (herbaceous vegetation with a typical upright growth habit). **3. Creepers** (typically low-growing plants that creep on the soil surface, often with stolons or rhizomes) **4. Tussocks** (many leaves from basal meristem forming prominent tufts) **5. Multi-stemmed woody** (shoots emanate close to substrate level from one to several main stems, at lateral to oblique angles) **6. Single-stemmed woody** (shoots spread centrally and laterally from a main stem)	Plant strategy in relation to climate and disturbance
Clonality	**0. Non-clonal** **1. Clonal aboveground** (stolons, gemmiparous, other vegetative buds or plant fragments) **2. Clonal belowground** (rhizomes, tubers, bulbs, adventitious root buds on main or lateral roots) **3. Clonal above and belowground**	Resource exploitation
Primary dispersal mode	**1. Self-dispersal** (the seed of fruit has no obvious aid for longer-distance transport and merely falls passively from the plant) **2. Wind dispersal** (includes minute dust-like seeds, seeds with pappus or other long hairs, 'balloons' or comas (trichomes at the end of a seed), flattened fruits or seeds with large 'wings', spores of ferns and related species and 'tumbleweeds' where the whole plant or infrutescence with ripe seeds is rolled over the ground by wind force) **3. Endozoochory** (Internal animal transport via fleshy, often brightly coloured berries, arillate sees, drupes and big fruits that are evidently eaten by vertebrates such as birds or mammals and pass through the gut before the seed enter the soil elsewhere) **4. Exozoochory** (External animal transport via fruits or seeds that become attached it animal hairs, feathers, legs and bills, aided by appendages such as hooks, barbs, awns, burs or sticky substances) **5. Unspecified** (no obvious mode of dispersal, may disperse by means of several of the above mentioned mechanisms)	Plant range size
Primary pollination vector	**1. Abiotic** (wind) **2. Biotic** (animals such as insects, birds or mammals)	Plant range size
Nitrogen-fixing ability	**0. Absent** (no known N-fixing ability) **1. Present** (plants with known or suspected N-fixing ability due to the presence of root nodules, mostly members of the Fabaceace family)	Habitat preference
Leaf periodicity	**0. N/A** (herbaceous plants and grasses which die back completely or withdraw energy into remnant root and or shoot systems in harsh season) **1. Deciduous leaves** **2. Evergreen leaves**	Conservation of nutrients in habitats with environmental stress
Spinescence	**0. Absent** (no spines and/or thorns present) **1. Present** (spines and/or thorns present)	Anti-herbivore defence, land use, disturbance such as periodic grazing, persistence after disturbance

6.3.2.2 Describing abundance patterns of PFTs and selected trait attributes

Using the MMULT function in Microsoft Excel, a species-by-trait matrix with presence/absence data was multiplied with a species-by-point matrix (abundance data) to create a trait-by-point matrix. The same procedure was followed for PFT's to create an abundance-based PFT-by-point matrix. The relative frequencies of traits and PFTs obtained for each point were then subjected to Hierarchical Linear Model (HLM) analysis using a two-way ANOVA with a random effects model (McMahon & Diez, 2007) in SPSS software to test for significant differences in trait and PFT relative abundance values between biomes and across the maize field-field margin gradient. The trait and PFT relative abundance values were chosen as response variables to determine if these values differed between distance classes and could therefore be predicted by disturbance intensity. Transects were specified as primary unit of measurement (subject ID) to account for the nestedness of transects within the sampling locality. The covariance structure was specified as unstructured. Each transect along the maize field-field margin gradient was considered an independent variable and sampling points within the same transect were considered dependent variables for statistical analyses. Effect sizes (Cohen's d) were calculated to express practical significance between sampling points where residual variance as well as transect variance were taken into account in the calculation of the effect size (Ellis & Steyn, 2003). The effect sizes were interpreted as follows: small effect: d=0.2, (b) medium effect: d=0.5 and (c) large effect: d=0.8.

6.3.2.3 Quantifying functional diversity

The dataset containing the abundances of traits in relation to sampling point was used to calculate Shannon-Wiener diversity, Simpson's diversity, Pielou's evenness and Margalef's species richness indices using PRIMER 6 software. The abovementioned indices display different aspects of diversity and were used in combination to provide a more complete picture of trait richness and diversity (Magurran, 1988; Magurran, 2004). The richness and index values obtained for each point were then subjected to Hierarchical Linear Model (HLM) analysis as described above to test for significant differences in trait richness and diversity between biomes and across the maize field-field margin gradient.

6.3.2.4 Assessing trait composition structure

To test for differences in trait composition between sampling points along maize field-field margin gradients across the two biomes, non-metric multidimensional scaling (NMDS) analysis was performed on the trait-by-point matrix. This analysis was performed using Bray-Curtis similarity and square-root transformation of trait abundances. The significance of the NMDS groupings was further tested using Permutational Multivariate Analysis of Variance (PERMANOVA) (permutations = 999; type III sums of squares). PERMANOVA is a suitable technique for abundance data where significance is based on permutation of the dissimilarity matrix (Anderson, 2001). Next, Similarity Percentage (SIMPER) analysis was applied to the dataset to assess which traits were primarily responsible for observed differences in trait composition between the groupings. NMDS, PERMANOVA and SIMPER analyses were conducted in PRIMER 6 software (Clarke & Gorley, 2006).

6.4 Results

6.4.1 Description of plant functional types

Cluster analysis identified eight major PFTs for the entire study area based on the functional trait information of 155 species (Figure 6.2; Table 6.2). PFT 1 represented phanerophytes, i.e. woody species (shrubs and trees) taller than 0.5 m and with shoots that do not die back during the harsh season. PFT 2 comprised herbaceous plants (mostly erect forbs) with nitrogen fixing ability. PFT 3 comprised tussock forming plants (grasses and cyperoid species), mostly with belowground clonal parts. PFT 4 represented rosette forming geophytes, typically with clonal ability. PFT 5 also included herbaceous plants, but mostly creepers with aboveground clonal parts. PFT 6 comprised tussock forming grasses without clonal ability. PFT 7 had similar characteristics to PFT 2, though included mostly erect forbs without nitrogen fixing ability. PFT 8 was representative of herbaceous, spinescent plants.

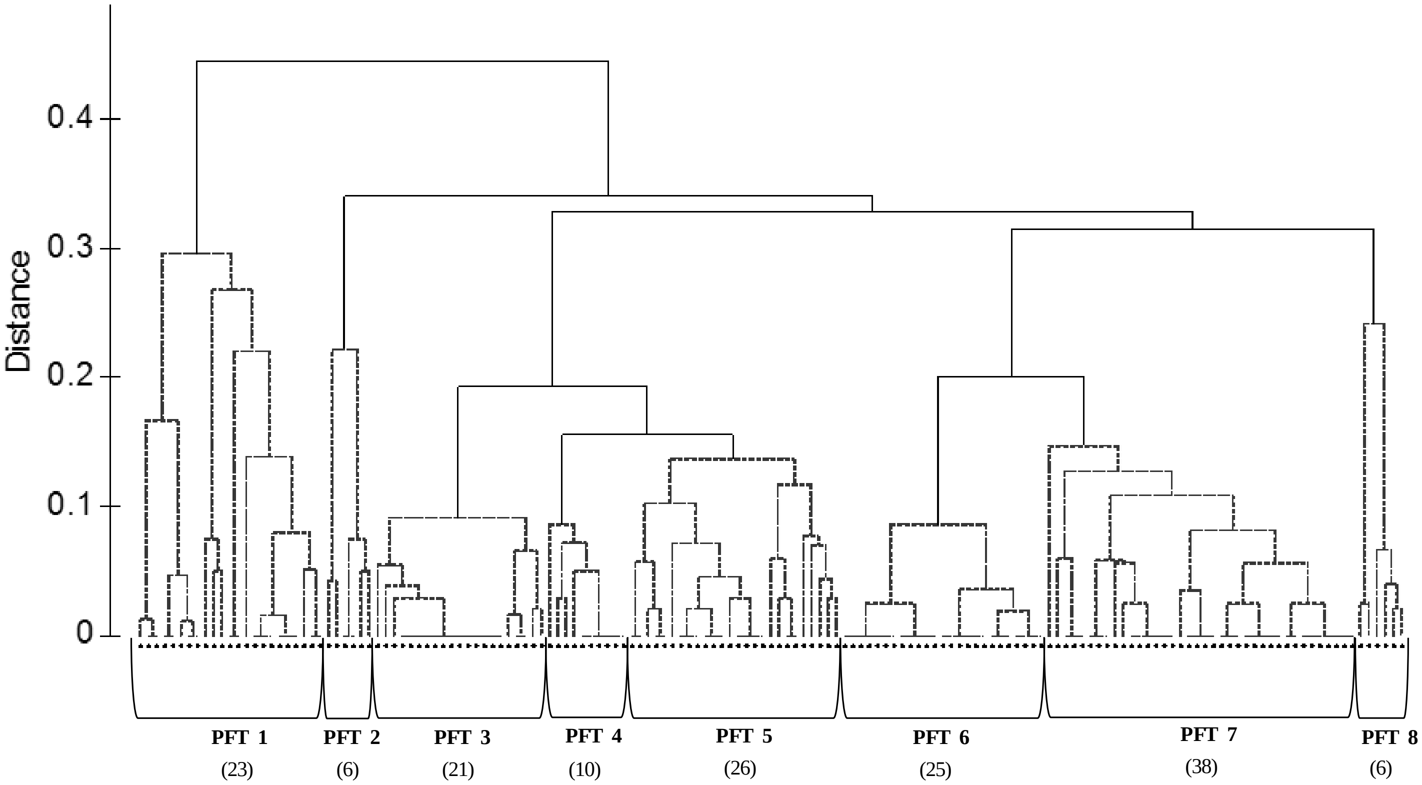

Figure 6.2: Cluster analysis (UPGMA) based on Gower distance measure proposing eight major plant functional types (PFTs) from the functional trait composition of species recorded in maize fields and rangeland. Dashed lines in the dendrogram indicate branching with no remaining significant structure, as determined by SIMPROF analysis. Values in parenthesis indicate the number of species representative of each group.

Table 6.2: Summary of the characteristics associated with the 8 plant functional types (PFTs) identified by means of cluster analysis. Bold text indicates the most prominent trait attributes within each functional type. Values in parenthesis indicate the number of species representing each trait attribute.

PFT	Tot. no. spp.	Life form	Growth form	Clonality	Dispersal mode	Pollination vector	N-fixing ability	Leaf periodicity	Spinescence
1	23	**Phanerophytes (23)**	**Single-stemmed woodies (13)** Multi-stemmed woodies (10)	**Non-clonal (20)** Clonal belowground (2) Clonal aboveground (1)	**Endozoochory (19)** Wind dispersal (3) Self-dispersal (1)	**Biotic (23)**	**Absent (16)** Present (7)	**Deciduous (15)** Evergreen (8)	**Absent (15)** Present (8)
2	6	**Hemicryptophytes (4)** Chamaephytes (1) Therophytes (1)	**Erect forbs (4)** Creepers (2)	**Non-clonal (4)** Clonal aboveground (1) Clonal belowground (1)	**Self-dispersal (4)** Wind dispersal (2)	Biotic (6)	Present (6)	N/A	Absent (6)
3	21	**Hemicryptophytes (20)** Therophytes (1)	Tussocks (21)	**Clonal belowground (17)** Clonal aboveground (3) Clonal above and belowground (1)	**Wind dispersal (16)** Unspecified dispersal (4) Exozoochory (1)	Abiotic (21)	Absent (21)	N/A	Absent (21)
4	10	**Geophytes (9)** Therophytes (1)	**Rosette forbs (8)** Erect forbs (1) Creepers (1)	**Clonal belowground (9)** Clonal aboveground (1)	Self-dispersal (10)	**Biotic (9)** Abiotic (1)	Absent (10)	N/A	Absent (10)
5	26	**Hemicryptophytes (18)** Therophytes (7) Chamaephytes (1)	**Creepers (16)** Erect forbs (9) Rosette forbs (1)	**Clonal aboveground (17)** Clonal belowground (5) Clonal above and belowground (4)	**Self-dispersal (16)** Wind dispersal (7) Exozoochory (2) Endozoochory (1)	**Biotic (24)** Abiotic (2)	Absent (26)	N/A	Absent (26)
6	25	**Hemicryptophytes (13)** Therophytes (12)	Tussocks (25)	Non-clonal (25)	**Wind dispersal (12)** Unspecified dispersal (9) Exozoochory (4)	Abiotic (25)	Absent (25)	N/A	Absent (25)
7	38	**Therophytes (20)** Chamaephytes (9) Hemicryptophytes (8)	**Erect forbs (32)** Rosette forbs (4) Creepers (2)	Non-clonal (38)	**Wind dispersal (16)** Self-dispersal (11) Exozoochory (7) Endozoochory (4)	Biotic (38)	Absent (38)	N/A	Absent (38)
8	6	**Hemicryptophytes (4)** Chamaephytes (1) Therophytes (1)	**Erect forbs (5)** Creepers (1)	**Non-clonal (4)** Clonal belowground (2)	**Wind dispersal (3)** Exozoochory (3)	Biotic (6)	Absent (6)	N/A	Present (6)

6.4.2 Abundance patterns of plant functional types along the disturbance gradient

HLM analysis revealed that PFT 2 and PFT 3 displayed significantly higher relative abundance in adjacent marginal vegetation and rangeland than inside the maize fields (d≥0.6, Figure 6.3; Table 6.3, 6.4). In the case of PFT 3, the abundance of individuals representing this group peaked in marginal vegetation (between 30-100 m from maize fields) (Figure 6.3; Table 6.3, 6.4). PFT 7 displayed significantly higher abundance values in maize fields compared to uncultivated vegetation (d≥0.5, Table 6.3, 6.4), with a noticeable peak in abundance in the maize field edges, 30-100 m from the marginal vegetation (Figure 6.3). Since there were no significant interaction effects between distance from maize field and biome for PFTs, only overall patterns across the disturbance gradient were considered in Table 6.4. In the results for plant traits and trait diversity below, differences between the various distances were considered for grassland and savanna separately to indicate significant interaction effects.

Table 6.3: Results for Hierarchical linear modelling (HLM), indicating overall differences in relative abundances of PFTs between distance from maize field, between biomes (grassland and savanna) and interaction effects between biome and distance. As there were no phanerophytes present in maize fields, PFT 1 was not included in analyses to compare PFT abundance between maize fields and uncultivated vegetation.

	Distance		Biome		Interaction (distance*biome)		MSE	Variance (transect)
	F	p	F	p	F	p		
PFT2	2.574	**0.029***	13.477	**0.000***	1.750	0.128	0.104	0.000
PFT3	3.053	**0.012***	5.961	**0.016***	0.634	0.674	8.979	0.000
PFT4	0.275	0.926	2.895	0.091	1.234	0.297	2.892	0.000
PFT5	0.337	0.890	7.028	**0.009***	1.909	0.097	0.286	0.000
PFT6	1.996	0.083	2.067	0.153	0.079	0.995	4.768	0.000
PFT7	2.821	**0.019***	1.171	0.281	0.257	0.935	4.264	0.436
PFT8	0.832	0.530	0.033	0.856	1.581	0.170	0.116	0.002

F = F value; p = p value. Bold text* indicates significant p values at p≤0.05
MSE= mean square error, unexplained variance
Variance (transect) = variance explained by transect

Table 6.4: Mean relative abundance values for plant functional types (PFTs) at various distances from maize field. MZ1 and MZ2, maize field; MV1 and MV2, marginal vegetation (30-100 m); RA1 and RA2, rangeland (100-400 m). Means with different superscripts differed practically, as indicated by effect sizes (d≥0.5). As there were no phanerophytes present in maize fields, PFT 1 was not included in analyses to compare PFT abundance between maize fields and uncultivated vegetation.

	PFT2	PFT3	PFT4	PFT5	PFT6	PFT7	PFT8
MZ1	0.052^{a}	2.805^{a}	1.869^{a}	0.404^{a}	1.953^{a}	2.926^{ab}	0.063^{a}
MZ2	0.036^{a}	3.272^{ab}	1.658^{a}	0.335^{a}	2.093^{a}	3.565^{a}	0.140^{ab}
MV1	0.250^{b}	5.793^{c}	1.499^{a}	0.282^{a}	2.036^{a}	2.519^{bd}	0.216^{ab}
MV2	0.154^{ab}	4.759^{bc}	1.473^{a}	0.238^{a}	2.935^{ac}	2.064^{bd}	0.169^{ab}
RA1	0.162^{ab}	3.926^{ab}	1.752^{a}	0.381^{a}	3.485^{bc}	2.045^{bd}	0.204^{ab}
RA2	0.298^{b}	3.967^{ab}	1.903^{a}	0.291^{a}	2.917^{a}	1.602^{d}	0.236^{b}

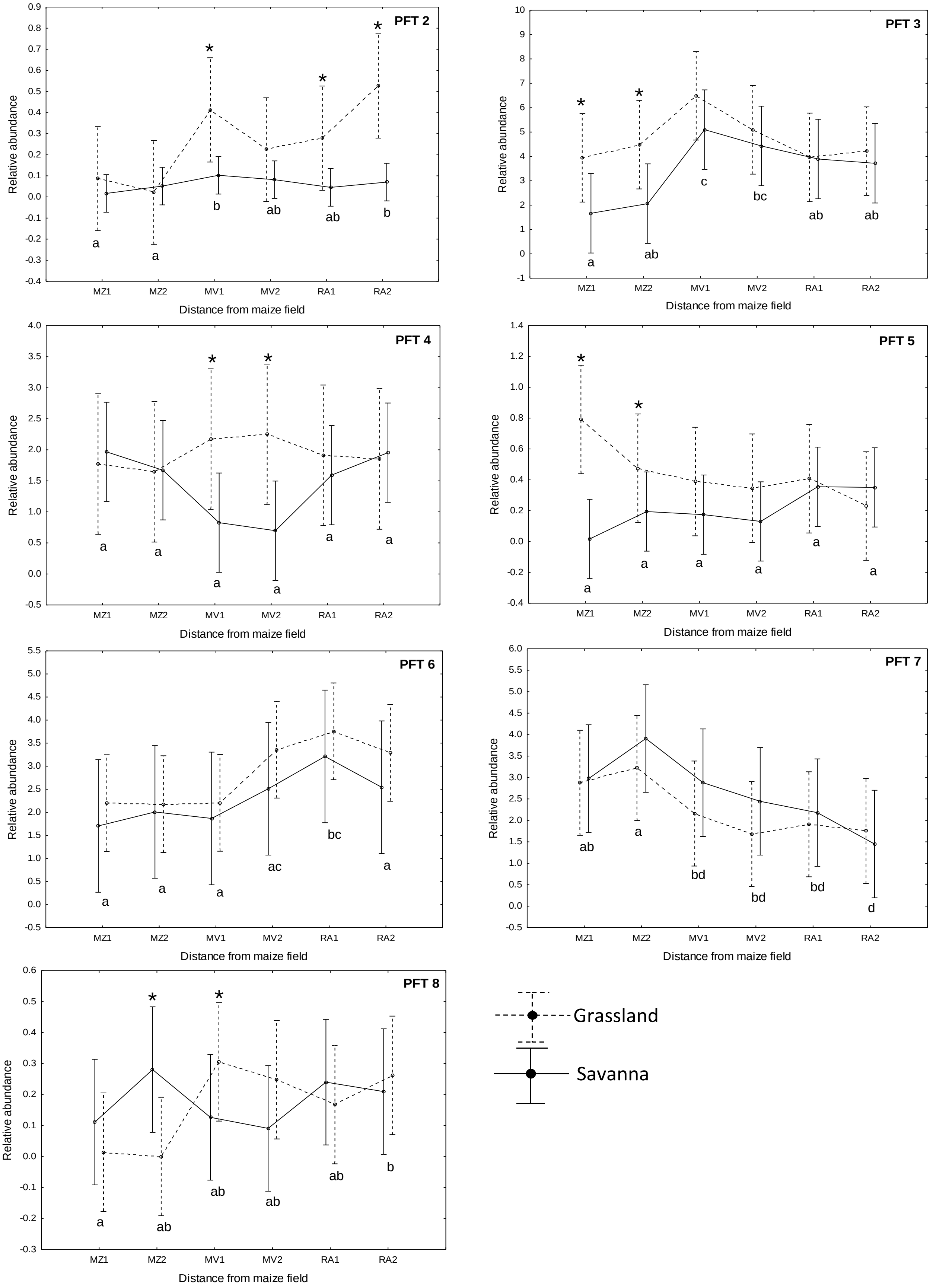

Figure 6.3: Relative abundances for the eight plant functional types along maize field-field margin gradient. Vertical bars denote 0.95 confidence intervals. Significant differences (d≥0.5) between distances along the gradient are indicated by different letters. * indicates significant variation between biomes at similar distances (d≥0.5). Distances: MZ1 and MZ2, maize field; MV1 and MV2, marginal vegetation (30-100 m) RA1 and RA2, rangeland (100-400 m).

For comparisons between biomes, the rangeland vegetation of grassland hosted a higher relative abundance of individuals representing PFT 2 compared to savanna (Figure 6.3; Table 6.3, 6.5). The abundance of PFT 3 was significantly higher in grassland maize fields than savanna maize fields (d≥0.8, Table 6.5). This was also true for PFT 5 at d≥0.5 (Table 6.5). Maize field edges of savanna were characterised by an increased relative abundance of PFT 8. Appendix B Tables B.1 and B.2 display effect sizes for pairwise comparisons between distances and biomes.

Table 6.5: Mean relative abundance values of plant functional types (PFTs) for grassland and savanna at various distances from maize fields MZ1 and MZ2, maize field; MV1 and MV2, marginal vegetation (30-100 m); RA1 and RA2, rangeland (100-400 m). Means with different superscripts differed practically, as indicated by effect sizes (d≥0.5). Comparisons between biomes were made only at similar distances from maize field. As there were no phanerophytes present in maize fields, PFT 1 was not included in analyses to compare PFT abundance between maize fields and uncultivated vegetation.

	PFT2	PFT3	PFT4	PFT5	PFT6	PFT7	PFT8
MZ1 (Grassland)	0.088^{a}	**3.943^{a}**	1.771^{a}	**0.792^{a}**	2.200^{a}	2.876^{a}	0.014^{a}
MZ1 (Savanna)	0.017^{a}	**1.667^{b}**	1.967^{a}	**0.017^{b}**	1.706^{a}	2.975^{a}	0.111^{a}
MZ2 (Grassland)	0.021^{a}	**4.482^{a}**	1.646^{a}	**0.475^{a}**	2.178^{a}	3.221^{a}	**0.000^{a}**
MZ2 (Savanna)	0.051^{a}	**2.061^{b}**	1.671^{a}	**0.194^{b}**	2.008^{a}	3.908^{a}	**0.281^{b}**
MV1 (Grassland)	**0.413^{a}**	6.488^{a}	**2.172^{a}**	0.389^{a}	2.205^{a}	2.160^{a}	**0.306^{a}**
MV1 (Savanna)	**0.103^{b}**	5.098^{a}	**0.826^{b}**	0.174^{a}	1.868^{a}	2.879^{a}	**0.126^{b}**
MV2 (Grassland)	0.226^{a}	5.090^{a}	**2.249^{a}**	0.346^{a}	3.359^{a}	1.683^{a}	0.248^{a}
MV2 (Savanna)	0.082^{a}	4.428^{a}	**0.697^{b}**	0.130^{a}	2.511^{a}	2.445^{a}	0.091^{a}
RA1 (Grassland)	**0.279^{a}**	3.962^{a}	1.911^{a}	0.407^{a}	3.757^{a}	1.909^{a}	0.168^{a}
RA1 (Savanna)	**0.045^{b}**	3.891^{a}	1.592^{a}	0.355^{a}	3.212^{a}	2.180^{a}	0.240^{a}
RA2 (Grassland)	**0.526^{a}**	4.215^{a}	1.853^{a}	0.230^{a}	3.289^{a}	1.754^{a}	0.262^{a}
RA2 (Savanna)	**0.070^{b}**	3.718^{a}	1.954^{a}	0.351^{a}	2.544^{a}	1.450^{a}	0.210^{a}

6.4.3 Abundance patterns of selected plant traits along the disturbance gradient

For comparisons between distances from the maize fields, HLM analysis indicated that chamaephytes and hemicryptophytes were relatively more abundant in adjacent vegetation compared to maize fields (d≥0.6, Figure 6.4; Table 6.6, 6.7). In contrast, the relative abundance of therophytes, geophytes and erect forbs was higher in maize fields than adjacent uncultivated habitats (d≥0.5, Figure 6.4; Table 6.6, 6.7). Creepers also displayed significantly higher abundance in maize fields compared to marginal vegetation (30-100 m from maize fields) (d≥0.6, Figure 6.4; Table 6.6, 6.7).

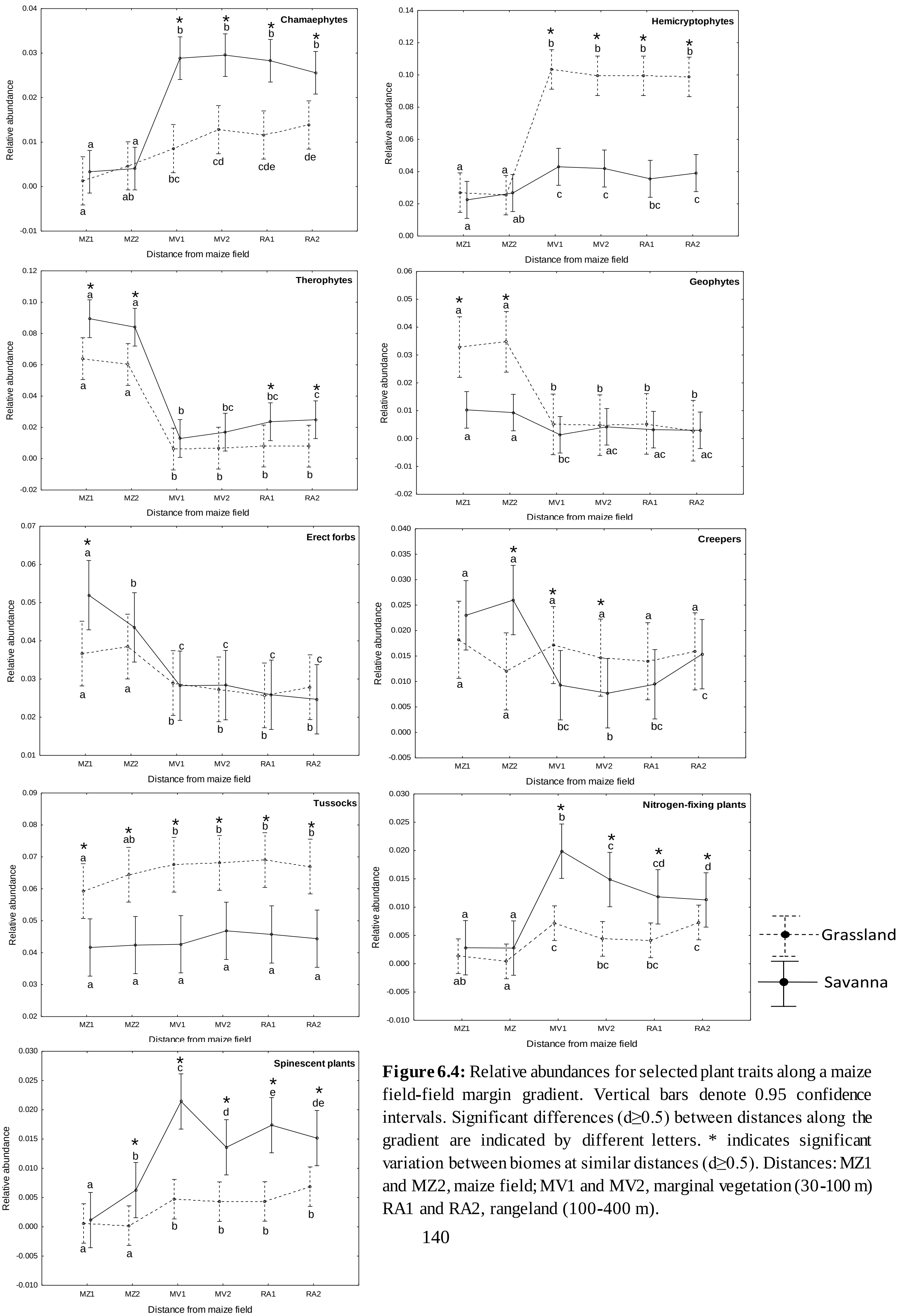

Figure 6.4: Relative abundances for selected plant traits along a maize field-field margin gradient. Vertical bars denote 0.95 confidence intervals. Significant differences (d≥0.5) between distances along the gradient are indicated by different letters. * indicates significant variation between biomes at similar distances (d≥0.5). Distances: MZ1 and MZ2, maize field; MV1 and MV2, marginal vegetation (30-100 m) RA1 and RA2, rangeland (100-400 m).

Table 6.6: Results for Hierarchical linear modelling (HLM) indicating overall differences in relative abundances of trait groups between distance from maize field, between biomes (grassland and savanna) and interaction effects between biome and distance.

	Distance		Biome		Interaction (distance*biome)		MSE	Variance (transect)
	F	p	F	p	F	p		
Chamaephytes	22.597	**0.000***	56.984	**0.000***	5.617	**0.000***	0.000	0.000
Hemicryptophytes	30.365	**0.000***	141.262	**0.000***	13.138	**0.000***	0.000	0.000
Therophytes	49.284	**0.000***	20.013	**0.000***	0.667	0.649	0.000	0.000
Geophytes	8.747	**0.000***	12.205	**0.001***	3.407	**0.006***	0.000	0.000
Rosettes	0.662	0.653	3.067	0.082	0.498	0.777	0.000	0.000
Erect forbs	6.871	**0.000***	1.355	0.247	1.130	0.348	0.000	0.000
Creepers	2.330	**0.046***	0.008	0.928	2.698	**0.023***	0.000	0.000
Tussocks	0.732	0.601	75.060	**0.000***	0.154	0.978	0.000	0.000
N-fixing	11.768	**0.000***	31.958	**0.000***	2.910	**0.016***	0.000	0.000
Spinescent	11.134	**0.000***	57.516	**0.000***	3.689	**0.004***	0.000	0.000

F = F value; p = p value. Bold text* indicates significant p values at p≤0.05
MSE= mean square error, unexplained variance
Variance (transect) = variance explained by transect

Comparisons between biomes revealed that the relative abundance of chamaephytes was significantly higher in marginal and rangeland vegetation of savanna compared to grassland (d≥1.3, Figure 6.4; Table 6.6, 6.8). In contrast, hemicryptophytes were more abundant in marginal and rangeland vegetation of grassland than savanna (d≥2.8, Figure 6.4; Table 6.8). Therophyte abundance differed significantly between savanna and grassland in both maize fields and savanna rangeland (100-400 m from maize fields) (d≥0.7, Table 6.8), with savanna displaying higher relative abundances than grassland (Figure 6.4). Grassland displayed a significantly higher abundance of tussock forming plants across the entire disturbance gradient (d≥1.2, Figure 6.4; Table 6.8). Savanna on the other hand was characterised by a significantly higher abundance of nitrogen-fixing and spinescent plants (d≥0.6 and 0.9, respectively, Figure 6.4; Table 6.8).

There were significant interaction effects between distance from maize field and biome for most of the trait groups (p≤0.02, Table 6.6). The abundance of chamaephytes increased more gradually with increasing distance from the maize fields in grassland compared to savanna (Figure 6.4). The opposite effect was observed for hemicryptophytes, where abundances increased more gradually in savanna rangelands than in grassland rangelands with increasing distance from the maize fields. Geophytes displayed a much more pronounced effect along the disturbance gradient in grassland than in savanna (Figure 6.4). Savanna indicated significant differences in the relative abundance of creeping plants in maize fields compared to adjacent vegetation (d≥0.6, Figure 6.4), while grassland had relatively similar relative abundances of creepers along the disturbance gradient. The effect of distance from maize field was stronger for nitrogen-fixing and spinescent plants in savanna (d≥0.5, Figure 6.4). Refer to Appendix B Tables B.3 and B.4 for effect sizes.

Table 6.7: Mean relative abundance values for plant trait groups at various distances from maize field. MZ1 and MZ2, maize field; MV1 and MV2, marginal vegetation (30-100 m); RA1 and RA2, rangeland (100-400 m). Means with different superscripts differed practically, as indicated by effect sizes (d≥0.5).

		Chamaephytes	Hemicryptophytes	Therophytes	Geophytes	Rosettes	Erect forbs	Creepers	Tussocks	N-fixing	Spinescent
Grassland	MZ1	0.001^{a}	0.027^{a}	0.064^{a}	0.033^{a}	0.011^{ab}	0.037^{a}	0.018^{a}	0.059^{a}	0.001^{ab}	0.001^{a}
	MZ2	0.005^{ab}	0.025^{a}	0.060^{a}	0.035^{a}	0.010^{ab}	0.038^{a}	0.012^{a}	0.064^{ab}	0.000^{a}	0.000^{a}
	MV1	0.009^{bc}	0.103^{b}	0.006^{b}	0.005^{b}	0.009^{a}	0.029^{b}	0.017^{a}	0.068^{b}	0.007^{c}	0.005^{b}
	MV2	0.013^{cd}	0.099^{b}	0.007^{b}	0.005^{b}	0.014^{ab}	0.027^{b}	0.015^{a}	0.068^{b}	0.004^{bc}	0.004^{b}
	RA1	0.012^{cde}	0.099^{b}	0.008^{b}	0.005^{b}	0.016^{b}	0.026^{b}	0.014^{a}	0.069^{b}	0.004^{bc}	0.004^{b}
	RA2	0.014^{de}	0.099^{b}	0.008^{b}	0.003^{b}	0.012^{ab}	0.028^{b}	0.016^{a}	0.067^{b}	0.007^{c}	0.007^{b}
Savanna	MZ1	0.003^{a}	0.022^{a}	0.089^{a}	0.010^{a}	0.009^{ab}	0.052^{a}	0.023^{a}	0.042^{a}	0.003^{a}	0.001^{a}
	MZ2	0.004^{a}	0.027^{ab}	0.084^{a}	0.009^{a}	0.013^{b}	0.044^{b}	0.026^{a}	0.042^{a}	0.003^{a}	0.006^{b}
	MV1	0.029^{b}	0.043^{c}	0.013^{b}	0.001^{bc}	0.004^{a}	0.028^{c}	0.009^{bc}	0.043^{a}	0.020^{b}	0.021^{c}
	MV2	0.03^{b}	0.042^{c}	0.017^{bc}	0.004^{ac}	0.009^{ab}	0.028^{c}	0.008^{b}	0.047^{a}	0.015^{c}	0.014^{d}
	RA1	0.028^{b}	0.036^{bc}	0.024^{bc}	0.003^{ac}	0.009^{ab}	0.026^{c}	0.009^{bc}	0.046^{a}	0.012^{cd}	0.017^{e}
	RA2	0.026^{b}	0.039^{c}	0.025^{c}	0.003^{ac}	0.008^{ab}	0.025^{c}	0.015^{c}	0.044^{a}	0.011^{d}	0.015^{de}

Table 6.8: Mean relative abundance values in plant trait groups for grassland and savanna at various distances from maize fields MZ1 and MZ2, maize field; MV1 and MV2, marginal vegetation (30-100 m); RA1 and RA2, rangeland (100-400 m). Means with different superscripts differed practically, as indicated by effect sizes (d≥0.5). Comparisons between biomes were made only at similar distances from maize field.

	Chamaephytes	Hemicryptophytes	Therophytes	Geophytes	Rosettes	Erect forbs	Creepers	Tussocks	N-fixing	Spinescent
MZ1 (Grassland)	0.001^{a}	0.027^{a}	**0.064^{a}**	**0.033^{a}**	0.011^{a}	**0.037^{a}**	0.018^{a}	**0.059^{a}**	0.001^{a}	0.001^{a}
MZ1 (Savanna)	0.003^{a}	0.022^{a}	**0.089^{b}**	**0.010^{b}**	0.009^{a}	**0.052^{b}**	0.023^{a}	**0.042^{b}**	0.003^{a}	0.001^{a}
MZ2 (Grassland)	0.005^{a}	0.025^{a}	**0.060^{a}**	**0.035^{a}**	0.010^{a}	0.038^{a}	**0.012^{a}**	**0.064^{a}**	0.000^{a}	**0.000^{a}**
MZ2 (Savanna)	0.004^{a}	0.027^{a}	**0.084^{b}**	**0.009^{b}**	0.013^{a}	0.044^{a}	**0.026^{b}**	**0.042^{b}**	0.003^{a}	**0.006^{b}**
MV1 (Grassland)	**0.009^{a}**	**0.103^{a}**	0.006^{a}	0.005^{a}	0.009^{a}	0.029^{a}	**0.017^{a}**	**0.068^{a}**	**0.007^{a}**	**0.005^{a}**
MV1 (Savanna)	**0.029^{b}**	**0.043^{b}**	0.013^{a}	0.001^{a}	0.004^{a}	0.028^{a}	**0.009^{b}**	**0.043^{b}**	**0.020^{b}**	**0.021^{b}**
MV2 (Grassland)	**0.013^{a}**	**0.099^{a}**	0.007^{a}	0.005^{a}	0.014^{a}	0.027^{a}	**0.015^{a}**	**0.068^{a}**	**0.004^{a}**	**0.004^{a}**
MV2 (Savanna)	**0.030^{b}**	**0.042^{b}**	0.017^{a}	0.004^{a}	0.009^{a}	0.028^{a}	**0.008^{b}**	**0.047^{b}**	**0.015^{b}**	**0.014^{b}**
RA1 (Grassland)	**0.012^{a}**	**0.099^{a}**	**0.008^{a}**	0.005^{a}	**0.016^{a}**	0.026^{a}	0.014^{a}	**0.069^{a}**	**0.004^{a}**	**0.004^{a}**
RA1 (Savanna)	**0.028^{b}**	**0.036^{b}**	**0.024^{b}**	0.003^{a}	**0.009^{b}**	0.026^{a}	0.009^{a}	**0.046^{b}**	**0.012^{b}**	**0.017^{b}**
RA2 (Grassland)	**0.014^{a}**	**0.099^{a}**	**0.008^{a}**	0.003^{a}	0.012^{a}	0.028^{a}	0.016^{a}	**0.067^{a}**	**0.007^{a}**	**0.007^{a}**
RA2 (Savanna)	**0.026^{b}**	**0.039^{b}**	**0.025^{b}**	0.003^{a}	0.008^{a}	0.025^{a}	0.015^{a}	**0.044^{b}**	**0.011^{b}**	**0.015^{b}**

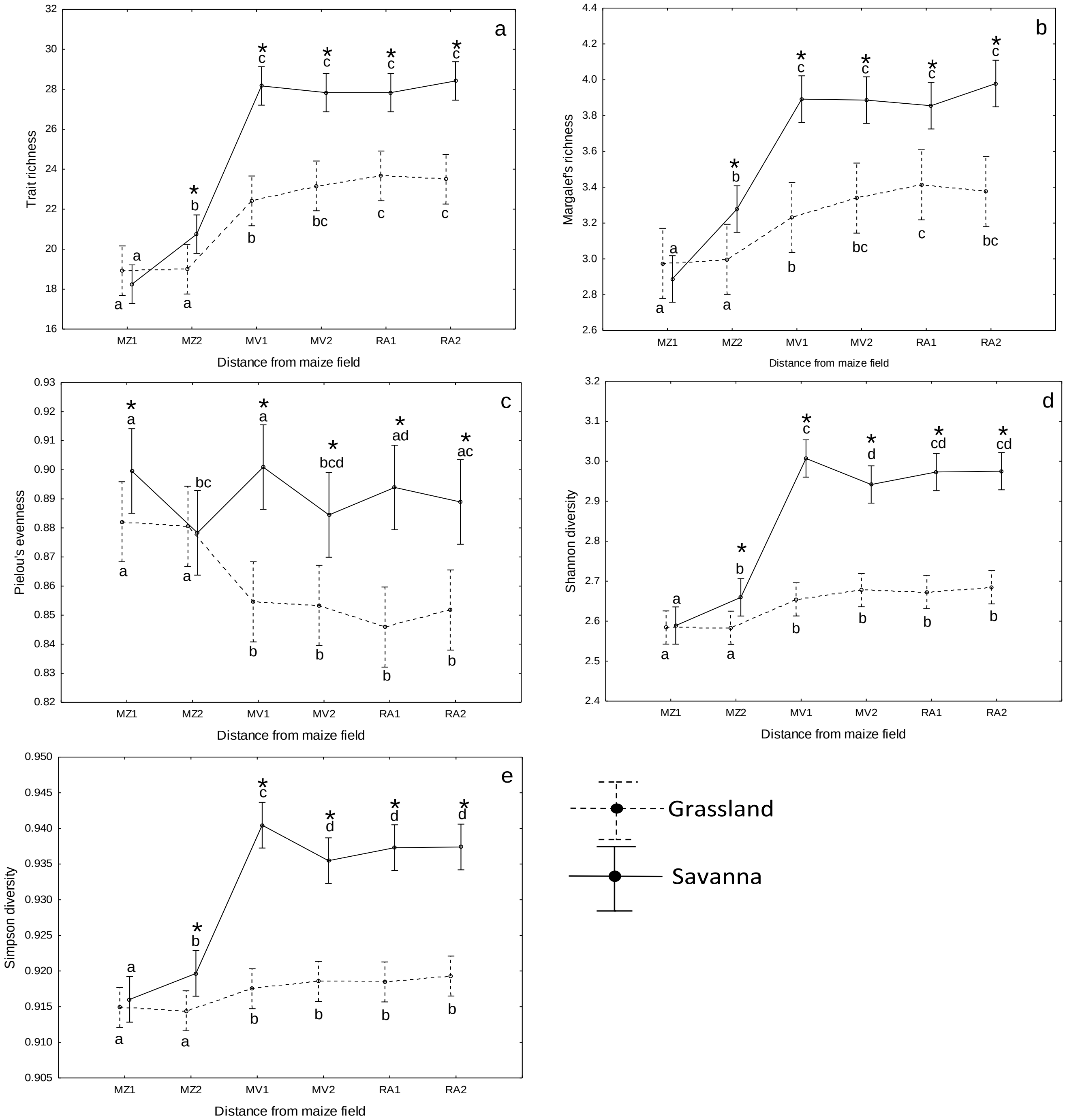

Figure 6.5: Diversity measures of plant traits along a maize field-field margin gradient. (a) Trait richness; (b) Margalef's richness index; (c) Pielou's evenness index; (d) Shannon-Wiener diversity index; (e) Simpson's diversity index. Vertical bars denote 0.95 confidence intervals. Significant differences (d≥0.5) between distances along the gradient are indicated by different letters. * indicates significant variation between biomes at similar distances (d≥0.5). Distances: MZ1 and MZ2, maize field; MV1 and MV2, marginal vegetation (30-100 m) RA1 and RA2, rangeland (100-400 m).

6.4.4 Plant trait diversity patterns along the disturbance gradient

All the diversity indices displayed similar patterns along the disturbance gradient, with significantly higher values in marginal and rangeland vegetation compared to maize fields ($d \geq 0.5$, Figure 6.5a, b, d, e; Table 6.9, 6.10). In contrast, it was evident that Pielou's evenness index values were significantly higher in maize fields than uncultivated vegetation ($d \geq 0.6$; Figure 6.5c; Table 6.10).

Table 6.9: Results for Hierarchical linear modelling (HLM), indicating overall differences in trait diversity measures between distance from maize field, between biomes (grassland and savanna) and interaction effects between biome and distance.

	Distance		Biome		Interaction (distance*biome)		MSE	Variance (transect)
	F	P	F	p	F	p		
Trait richness	73.366	**0.000***	116.407	0.000*	9.650	**0.000***	3.640	0.103
Margalef's richness	28.698	**0.000***	73.405	0.000*	5.635	**0.000***	0.082	0.002
Pielou's evenness	2.874	**0.017***	53.401	0.000*	3.724	**0.004***	0.001	0.000
Shannon diversity	53.081	**0.000***	282.179	0.000*	19.936	**0.000***	0.006	0.000
Simpson's diversity	33.333	**0.000***	253.813	0.000*	16.315	**0.000***	0.000	0.000

F = F value; p = p value. Bold text* indicates significant p values at $p \leq 0.05$
MSE= mean square error, unexplained variance
Variance (transect) = variance explained by transect

Table 6.10: Mean values for plant trait diversity measures at various distances from maize field. MZ1 and MZ2, maize field; MV1 and MV2, marginal vegetation (30-100 m); RA1 and RA2, rangeland (100-400 m). Means with different superscripts differed practically, as indicated by effect sizes ($d \geq 0.5$).

		Trait richness	Margalef's richness	Pielou's evenness	Shannon diversity	Simpson's diversity
Grassland	MZ1	18.917^{a}	2.975^{a}	0.882^{a}	2.584^{a}	0.915^{a}
	MZ2	19.000^{a}	2.998^{a}	0.881^{a}	2.584^{a}	0.914^{a}
	MV1	22.417^{b}	3.232^{b}	0.855^{b}	2.655^{b}	0.918^{b}
	MV2	23.167^{bc}	3.339^{bc}	0.853^{b}	2.677^{b}	0.919^{b}
	RA1	23.667^{c}	3.414^{c}	0.846^{b}	2.673^{b}	0.918^{b}
	RA2	23.500^{c}	3.376^{bc}	0.852^{b}	2.685^{b}	0.919^{b}
Savanna	MZ1	18.250^{a}	2.888^{a}	0.900^{a}	2.589^{a}	0.916^{a}
	MZ2	20.750^{b}	3.278^{b}	0.878^{bc}	2.660^{b}	0.920^{b}
	MV1	28.167^{c}	3.892^{c}	0.901^{a}	3.007^{c}	0.940^{c}
	MV2	27.833^{c}	3.887^{c}	0.884^{bcd}	2.942^{d}	0.935^{d}
	RA1	27.833^{c}	3.855^{c}	0.894^{ad}	2.973^{cd}	0.937^{d}
	RA2	28.417^{c}	3.979^{c}	0.889^{ac}	2.975^{cd}	0.937^{d}

Results indicated significantly higher diversity and evenness values in savanna compared to grassland (d≥0.7, Figure 6.5; Table 6.11). There were also significant interaction effects between distance and biome (p≤0.004). All increases in diversity index values with increasing distance from maize fields were much more pronounced in savanna compared to grassland (Figure 6.5a, b, d, e). Pielou’s evenness index values for trait diversity were significantly higher in maize fields compared to uncultivated vegetation in grassland (d≥1.1, Figure 6.5c; Table 6.10), but this was not the case for savanna. Refer to Appendix B Tables B.5 and B.6 for effect sizes.

Table 6.11: Mean plant trait diversity values for grassland and savanna at various distances from maize fields MZ1 and MZ2, maize field; MV1 and MV2, marginal vegetation (30-100 m); RA1 and RA2, rangeland (100-400 m). Means with different superscripts differed practically, as indicated by effect sizes (d≥0.5). Comparisons

	Trait richness	Margalef’s richness	Pielou's evenness	Shannon diversity	Simpson's diversity
MZ1 (Grassland)	18.917^{a}	2.975^{a}	**0.882^{a}**	2.584^{a}	0.915^{a}
MZ1 (Savanna)	18.250^{a}	2.888^{a}	**0.900^{b}**	2.589^{a}	0.916^{a}
MZ2 (Grassland)	**19.000^{a}**	**2.998^{a}**	0.881^{a}	**2.584^{a}**	**0.914^{a}**
MZ2 (Savanna)	**20.750^{b}**	**3.278^{b}**	0.878^{a}	**2.660^{b}**	**0.920^{b}**
MV1 (Grassland)	**22.417^{a}**	**3.232^{a}**	**0.855^{a}**	**2.655^{a}**	**0.918^{a}**
MV1 (Savanna)	**28.167^{b}**	**3.892^{b}**	**0.901^{b}**	**3.007^{b}**	**0.940^{b}**
MV2 (Grassland)	**23.167^{a}**	**3.339^{a}**	**0.853^{a}**	**2.677^{a}**	**0.919^{a}**
MV2 (Savanna)	**27.833^{b}**	**3.887^{b}**	**0.884^{b}**	**2.942^{b}**	**0.935^{b}**
RA1 (Grassland)	**23.667^{a}**	**3.414^{a}**	**0.846^{a}**	**2.673^{a}**	**0.918^{a}**
RA1 (Savanna)	**27.833^{b}**	**3.855^{b}**	**0.894^{b}**	**2.973^{b}**	**0.937^{b}**
RA2 (Grassland)	**23.500^{a}**	**3.376^{a}**	**0.852^{a}**	**2.685^{a}**	**0.919^{a}**
RA2 (Savanna)	**28.417^{b}**	**3.979^{b}**	**0.889^{b}**	**2.975^{b}**	**0.937^{b}**

6.4.5 Trait assemblage patterns

The non-metric multidimensional scaling (NMDS) ordination indicated distinct groupings between grassland and savanna maize fields and also between grassland and savanna uncultivated vegetation (marginal and rangeland vegetation) in terms of trait composition (Figure 6.6). All the significant groupings were confirmed by the PERMANOVA results (p≤0.02, Table 6.12).

SIMPER analysis revealed that the savanna marginal vegetation were characterized by a greater abundance of endozoochorous plants, chamaephytes and hemicryptophytes and plants without clonal ability compared to the associated maize fields (Appendix B Table B.7a). The savanna rangeland vegetation was also more abundant in endozoochorous taxa, chamaephytic and hemicryptophytic life forms, as well as taxa without nitrogen-fixing ability compared to the savanna maize fields. Within grassland, marginal vegetation was more abundant in hemicryptophytic and therophytic life forms, as well as plants with belowground clonal ability compared to the associated maize fields.

Grassland rangelands were more abundant in hemicryptophytic, therophytic and chamaephytic life forms compared to the associated maize fields. Belowground clonality and geophytes were more abundant in grassland maize fields, while hemicryptophytes were characteristic of savanna maize fields (Appendix B Table B.7b). Savanna marginal vegetation was more abundant in endozoochorous individuals, chamaephytic life forms and spinescent plants compared to grassland marginal vegetation. The most prominent traits in savanna rangelands compared to grassland rangelands were endozoochory, aboveground clonality and hemicryptophytic life forms. Refer to Appendix B Table B.8 for a list of plant species and trait attribute classifications.

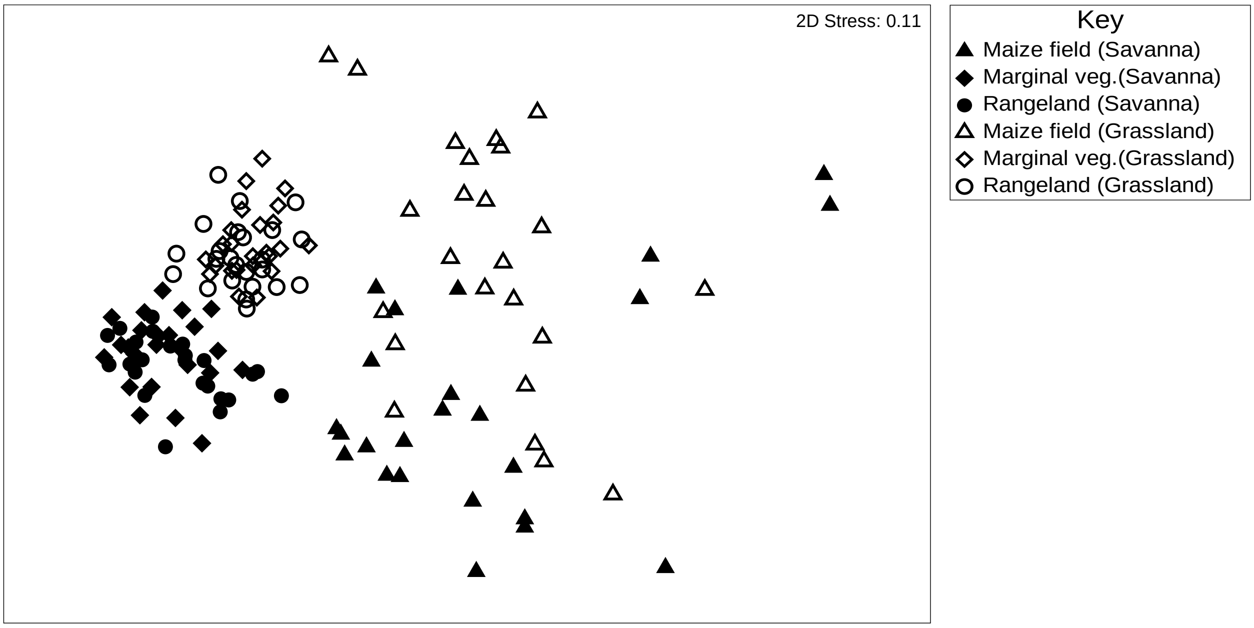

Figure 6.6: Non-metric multidimensional scaling (NMDS) analyses based on trait abundances of plant species recorded inside maize field and adjacent vegetation within the Grassland and Savanna Biomes. Resemblance: Bray Curtis similarity; Data transformation: Square-root.

Table 6.12: Pairwise comparisons of PERMANOVA analysis indicating significance of separation between distance classes (maize fields, marginal vegetation at 30-100 m from field edges and rangeland at 100-400 m from field edges) based on trait composition. (G) = Grassland Biome; (S) = Savanna Biome.

	Maize (S)	Maize (G)	Marginal veg. (S)	Marginal veg. (G)	Rangeland (S)
Maize (G)	**0.002***	---	---	---	---
Marginal veg. (S)	**0.001***	**0.001***	---	---	---
Marginal veg. (G)	**0.001***	**0.001***	**0.001***	---	---
Rangeland (S)	**0.001***	**0.001***	0.246	**0.001***	---
Rangeland (G)	**0.001***	**0.001***	**0.001***	0.411	**0.001***

Bold text* indicates significant separations at $p<0.05$ as determined by Monte Carlo tests
Data transformation: Square-root

6.5 Discussion

6.5.1 Plant functional types, traits and trait diversity in relation to disturbance intensity

The results indicate that the high degree of agricultural disturbance intensity associated with the maize fields greatly influenced the relative abundance, diversity and composition of PFTs and individual traits. The environmental factors associated with agricultural disturbance act as environmental 'filters' that block species which lack the required traits to persist under a particular set of conditions (Keddy, 1992). The high agricultural disturbance intensity of the maize fields tended to favour annual, creeping growth forms and cyperoid species. Mechanisms adapted for wind or external animal dispersal (PFT 8) were also found in association with high disturbance levels. These characteristics, in particular the adaptation of a wide dispersal ability and clonality are known characteristics of pioneer species that often occupy disturbed sites (Tainton, 1999). These traits likely represent adaptive strategies that evolved under natural disturbance events but now enable persistence under the intensive management impacts associated with maize agriculture such as soil tillage, agro-chemical application and complete removal of vegetation at the end of the cropping season (Boutin & Jobin, 1998; Liira *et al.*, 2008; Pysek *et al.*, 1995).

Since the maize field soil is disturbed by tillage on an annual basis, this favours plants that timeously reach the field (by effective dispersal mechanisms) and complete their entire lifecycle within the growth period of a single maize crop. These respective species can therefore be considered r-strategists (Gadgil & Solbrig, 1972). Alternatively, some perennial plants may be able to persist in the field by means of clonal parts. Species such as *Cyperus esculentus* and *C. rotundus* (which were two of the most abundant non-crop plants recorded in the fields) have long been economically important weed species of maize fields in South Africa (Bendixen & Nandihalli, 1987). They are tolerant of herbicides and have effective clonal reproductive parts in the form of tubers, which can break off (probably aided by soil tillage) and disperse like seeds throughout the field where they may lie dormant for extended periods (Stoller & Sweet, 1987). These strategies allow for their persistence in the annual maize field environment.

The maize fields were also characterised by a greater relative abundance of herbaceous growth forms without nitrogen fixing ability (PFT 7). The differentiation in the relative abundance of nitrogen-fixing ability may be the result of fertilizer application in maize fields which overrides the competitive advantage enjoyed by nitrogen fixers in the natural vegetation. The symbiotic relationships between vascular plants and nitrogen-fixing bacteria are considered costly except when nitrogen availability is low (Monks *et al.*, 2012). In the case of low nitrogen levels, nitrogen-fixing plants may be able to compete with non-fixing species and occur relatively more frequently.

The marginal and rangeland vegetation had relatively higher numbers of spinescent chamaephytes and hemicryptophytes than maize fields, which was expected, as perennial and/or woody species are removed from maize fields. Also, herbaceous spinescent plants may be more resistant to livestock grazing in rangelands (Hanley *et al.*, 2007; Laca *et al.*, 2001). An unexpected result was that the medium and low disturbance intensity of vegetation adjacent to the maize fields had relatively similar trait assemblages. All these sampling sites were invariably high in trait richness and diversity, regardless of their distance from the high disturbance areas. This result contradicts the intermediate disturbance hypothesis that states that diversity should be highest at intermediate disturbance levels (Huston, 1979). Studies by Boutin and Jobin (1998), Fridley *et al.* (2009) and Gove *et al.* (2007) demonstrated that agricultural influences on landscape-scale vegetation patterns are very close to agricultural activities and changes in vegetation composition and species richness in field margins occurred within no more than 9 m from crop fields. Therefore, it is likely that possible diversity changes in adjacent vegetation went undetected as they probably occurred at distances less than 30 m from the maize field edges, which were not sampled in this study. Also, similar traits may be able to persist in medium and low disturbance habitats if disturbance is above or at the soil surface (Kleyer, 1999), which was the case at the sampled localities.

A difference between the marginal and rangeland sites was the relative abundances of tussock forming plants (grasses and cyperoid species) with clonal ability (PFT3), which were more prevalent in the marginal vegetation adjacent to maize fields (between 30-100 m) relative to rangelands. This is consistent with the results of Boutin and Jobin (1998), who found higher abundances of short-lived, grassy-type weeds in habitats adjacent to intensive crop farming activities. Although the exact cause for this increase cannot be verified from this study, it was hypothesised that the presence of farm tracks or the removal of vegetation by mowing may have acted as selective pressures that favoured grasses and cyperoids that can colonize disturbed sites quickly by means of their clonal ability. Grasses are generally resistant to grazing or mowing, since their meristems are usually situated at the base of the plant close to the ground and removal of the top parts of the plants will generally not have detrimental effects on its subsequent growth (Tainton, 1999).

6.5.2 Plant functional types, traits and trait diversity in relation to biome

This study provides new evidence that the abundance patterns of plant traits within maize fields differed between the Grassland and Savanna Biomes. Vegetation inside maize fields of the Savanna Biome typically hosted a higher abundance of creeping and erect annual forbs with aboveground clonality, while maize fields of the Grassland Biome were characterised by abundant grass- and cyperoid species with belowground clonality. These results suggest that the two biomes tended to have different trait patterns in maize fields, where disturbed sites are covered predominantly by forbs in savanna and mainly by grasses in grassland. It seems that this pattern was only true for the highly disturbed sites, as grassland and savanna vegetation adjacent to maize fields hosted relatively similar numbers of grasses and forbs.

This distinction between the non-crop plant species of grassland and savanna maize fields may be due to the dispersal of plants into the fields from the immediate adjacent vegetation. It is known that frequent dispersal of plants occur from field margins into crop fields and that marginal vegetation is the main source of crop field weeds (Leeson *et al.*, 2005; Marshall & Arnold, 1995). It may be expected that the non-crop plant species of maize fields in the Grassland and Savanna Biomes are different, since the sources (species pools) from which new species are acquired (the adjacent uncultivated vegetation) have different pioneer species with varying ability to colonize a maize field environment. Studies of secondary succession over several years in Highveld Grassland suggest that grasslands in South Africa have relatively few native annual pioneer species. Disturbed sites are often invaded by exotic annuals and are eventually converted to monotypic stands of dominant perennial grass species such as *Hyparrhenia hirta* (Roux & Roux, 1969). In this case, it has been shown that these grasslands often lack a ruderal stage of annual forbs and disturbed sites are often colonized immediately by grasses (e.g. *Cynodon dactylon* and *Eleusine indica*), especially at sites with high levels of available soil nitrogen (Roux & Roux, 1969). This is different for savanna, where the majority of weedy species in semiarid savannas are annual forbs (Makhabu & Marotsi, 2012; Shackleton, 2000).

The reasons why grasslands seem to have a shortage of forb pioneers compared to savanna in South Africa is not known, although this could potentially explain the different weedy traits associated with grassland and savanna maize fields. Therefore, the species sources of grassland maize fields may be poor in specialized forb pioneer species (Roux & Roux, 1969), resulting in grass-type pioneer species dominating in grassland maize fields. In contrast, the species sources of savanna maize fields may have more forb pioneers available (Shackleton, 2000), resulting in more forb-type pioneers in savanna maize fields. However, there is a considerable lack of research on these phenomena in South Africa, and warrants further investigation.

In terms of trait diversity, the marginal and rangeland vegetation of savanna hosted much higher trait richness than grassland. This is probably due to the multi-structured nature of savanna, with added traits associated with the woody layer (trees, shrubs and climbers) (Curry, 1994; Schadek *et al.*, 2009). There also seems to be a general pattern of higher trait diversity inside maize fields at the headland (the outer few metres of the crop closest to the crop field edges), particularly in savanna. It is known that the crop headland often contains more weeds due to the spread of non-crop plants from the field margins and that crop yields are often lower at the edges due to competition with weed species (Cousens, 1985; Sparkes *et al.*, 1998). An increased abundance of weeds may potentially also increase the chances of encountering new traits, and therefore increase the trait richness and diversity of these sites.

Interestingly, these results indicated that, although the richness and diversity of traits increased rapidly in adjacent marginal and rangeland vegetation, maize fields in the Grassland Biome generally displayed a higher evenness of traits than the adjacent marginal and rangeland vegetation (i.e. the traits are better represented in maize fields). Evenness in marginal and rangeland grassland may be low due to ineffective competition of annual forbs with tussock grasses, thereby lowering the number of individuals representing the forb-related traits and causing the dominance of grass-related traits. Dickson and Busby (2009) found that high seeding densities of dominant grasses in restoration management decreased forb cover, biomass, and richness. Their results suggest that dominant grasses compete strongly with native forb species and that many forb species thrive when they are spatially separated from dominant grasses. On the other hand, this competition may be alleviated in the Savanna Biome by the woody layer that allows for more niche spaces (Botha *et al.*, 2016) for both forbs and grasses and, therefore, better representation of different trait attributes.

6.6 Conclusion

This chapter described the specific patterns of plant functional types and specific trait attributes associated with maize and rangeland agro-ecosystems in two grassy biomes of South Africa. Relating to the first research question, chamaephytic and hemicryptophytic life forms, nitrogen –fixing ability and spinescence are the traits that are most frequently lost or 'filtered out' when rangeland is transformed into maize fields. In response to high agricultural disturbance intensity, plant strategies change from perennial to annual life cycles, erect to low-growing forms, non-clonal to clonal abilities and short to long-range dispersal mechanisms (wind or exozoochorous). These traits may promote the colonization of and the persistence in the ephemeral crop field environment more effectively. This also supports the first hypothesis.

In relation to the second research question, the high disturbance intensity of the maize fields drastically reduced the abundance and diversity of functional traits. However, there were no evidence for trait abundance or diversity losses, or the transformation of trait assemblage structure in marginal vegetation, at least not at the 30-100 m distance from maize fields considered in this study. Further sampling is required to investigate the trait abundance and composition patterns of vegetation at the maize field-field margin interface (≤ 30 m from maize fields) to make a meaningful contribution. Nevertheless, the indication that plant communities at relatively short distances (30-100 m) from the actively cultivated areas seem relatively unaffected by the associated disturbances highlights the value of these sites as conservation areas for plant trait diversity within the agricultural environment.

Regarding the third research question, maize fields situated in the Grassland and Savanna Biomes hosted different trait assemblages and favoured different functional types (generally grassy weeds in grassland and forb weeds in savanna). This is probably in accord with the different trait compositions associated with the source vegetation (the uncultivated marginal and rangeland vegetation), which has unique characteristics related to biome. The second hypothesis is therefore also supported. This may have implications for site-specific weed management in South African maize fields, since different strategies may have to be applied for the effective control of dicotyledonous (generally forbs) and monocotyledonous (mostly grassy) weeds. Ultimately, the data presented here may assist in the management and conservation of plant communities in South Africa within a growing agricultural landscape.

6.7 References

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CHAPTER 7: SPECIES DIVERSITY PATTERNS OF SELECTED PREDACEOUS INSECT GROUPS OF MAIZE AGRO-ECOSYSTEMS IN SOUTH AFRICA

7.1 Overview

Within the twentieth century, there has been a growing popularity of biological pest control as a pest management strategy in agriculture, following the increased awareness of the adverse effects of agrochemicals in natural environments and increased resistance of insect pests to insecticides. However, classical biological control tends to have low success rates in terms of pest suppression. Conservation biological control on the other hand focuses on enhancing the habitats of arthropod enemies by increasing the natural resources required for their survival and reproduction. This strategy requires knowledge on the specific requirements of the arthropod enemies in question, which can only be acquired from species-level data. However, there is an almost complete lack of species-level data of predatory non-pest arthropod species in South African crops and adjacent uncultivated habitat. This chapter served to describe the abundance and diversity patterns of four selected arthropod predator groups, Araneae (Spiders), Coccinellidae (Ladybugs), Mantodea (Praying mantids) and Neuroptera (Lacewings), classified to species level for maize fields and associated uncultivated vegetation. Predators were sampled by means of a sweep-net at regional and local scales throughout the Dry Highveld Grassland Bioregion of the Grassland biome. A list is provided of arthropod predators that occurred naturally inside the maize agro-ecosystem, which may be good candidates for biological control. However, it was found that predator diversity was severely decreased in maize fields and predator diversity was probably dependent on adjacent uncultivated vegetation. This needs to be taken into consideration when adapting pest management regimes in maize to promote biocontrol and conservation of predatory arthropod diversity.

A manuscript has been prepared from the results presented in this chapter and will be submitted for possible publication in **Biodiversity and Conservation**.

7.2 Introduction

The detrimental environmental effects of agrochemical usage and increased resistance of insect pests to insecticides have led to the growing popularity of biological pest control as pest management strategy in agriculture. Several approaches exist by which crop managers can implement this strategy. The most classical form of biological control involves the intentional importation of a non-native agent into the crop field environment for permanent establishment and control of a selected pest species (Radcliffe *et al.*, 2009). However, the evidence to date shows that classical biological control has a relatively low success rate (around 10%) in terms of reducing pest populations to economically acceptable levels (Goldson *et al.*, 2014). Despite numerous attempts at the release of exotic control agents in African maize fields to target a variety of prominent pest species, the only real success achieved thus far in terms of reducing pest numbers (at least short-term) is the use of the hymenopteran parasitoid *Cotesia flavipes* against the maize stemborer *Chilo partellus* in Kenya (Neuenschwander *et al.*, 2003; Soul-kifouly *et al.*, 2016).

Long-term failures in classical biological control worldwide may be caused by inappropriate management regimes (e.g. the application of agrochemicals), a lack of suitable spatial or temporal refugia and alternative food resources and also, although rarely, the development of biological control resistance of the target pest (Goldson *et al.*, 2014). In addition to these factors, the failures of classical biological control in African maize fields have been attributed to mutual interference caused by unduly high natural enemy densities at release (Kfir, 1981). Overall, little information is available to explain classical biological control failures in African crops (Neuenschwander *et al.*, 2003).

Two other strategies, augmentation and conservation biological control, involve elevating the numbers of native arthropods, i.e. arthropod enemies that already occur naturally in the environment. Augmentation focuses on the natural enemy populations themselves and involves mass-rearing and releasing pre-selected species into the crop field to increase their numbers temporarily, and in so-doing increases their predation efficiency (Radcliffe *et al.*, 2009). Conservation biological control focuses on enhancing the habitats of arthropod enemies by limiting harmful agricultural management regimes and increasing the natural resources required for their survival and reproduction (Bostanian *et al.*, 2012). Increased non-prey food sources, shelter, microclimate and alternative prey or hosts are mostly effective strategies for the enhancement of beneficial arthropods in crop field environments (Landis *et al.*, 2000; Lundgren, 2009).

There has been a fair amount of research on the types of economically important arthropod pest species that occur in South African maize fields (Annecke & Moran, 1982; Prinsloo & Uys, 2015). However, in an effort to simplify analyses, all other arthropod species recorded in maize with a negligible pest status are often ignored (Moran, 1983) and there is an almost complete lack of family or species-level data of non-pest arthropod species in South African crops and adjacent uncultivated semi-natural habitat (but see Botha *et al.*, (2015) and Truter *et al.*, (2014)). The best studied arthropod group in this regard is the Araneae (spiders), with a fair amount of data on the occurrence of spider species in maize fields and rangelands (Dippenaar-Schoeman *et al.*, 2013; Midega *et al.*, 2008). However, species data on other beneficial groups is lacking despite their potential value as economically important bio-control agents and or pollinators in the agri-environment.

The general evidence is that naturally occurring arthropod predators have the potential to reduce herbivorous insect pest numbers in crops and suppress pest outbreaks (Symondson *et al.*, 2002). Many economically important pest species of South African maize fields are targeted by a variety of naturally occurring arthropod predators. Maize aphids (*Rhopalosiphum maidis*) are readily attacked by the coccinellids, *Cheilomenes* and *Hippodamia*, as well as a variety of Neuroptera (lacewing) species (Prinsloo & Uys, 2015). Eggs and small larvae of African armyworm (*Spodoptera exempta*), African bollworm (*Helicoverpa armigera*) and cereal borers (*Chilo partellus)* are predated by spiders, coccinellids and lacewings and a variety of naturally occurring hymenopteran parasitoids. Ground weevils (*Protostrophus* spp.) are also targeted by generalist predators such as spiders (Bonhof *et al.*, 1997; Prinsloo & Uys, 2015).

The implementation and management of conservation biological control inevitably require knowledge on the specific requirements and population dynamics of the arthropod enemies in question (Radcliffe *et al.*, 2009). In this case, the value of using species-level rather than the customary family-level classifications must be recognised, as two species in the same family may be very different in terms of specific resource requirements and also their responses to or effects on their environment. The Coccinellidae may overall be considered a predatory group, even though they have in fact adopted a broad feeding range (including specialized herbivory, pollenophagy and fungivory) and may therefore be beneficial, negligible or even disadvantageous in crops, depending on the species in question (Booth *et al.*, 1990; Picker *et al.*, 2004). Species-level data may provide more detailed and accurate information regarding predatory arthropod functional guilds, which is particularly important in biological assessments (Lenat & Resh, 2001). However, lack of expertise, time and funding and the general tedious nature of taxonomic classification of diverse arthropod groups often lead to a shortage of species-level data (Kim, 1993).

This chapter described the abundances and diversity patterns of four selected arthropod predator groups classified to species level in South African maize fields and associated remnant patches of uncultivated semi-natural vegetation associated with the Grassland Biome. The following research questions were asked: (1) How do the predatory arthropod species abundance, richness and diversity patterns compare between maize fields and adjacent uncultivated vegetation at various distances from the site of active cultivation at local and regional scales? (2) How do the abundance patterns of selected functional guilds of spiders compare between maize fields and adjacent uncultivated vegetation at local and regional scales? (3) Are there specific habitat preferences (based on occurrence patterns) among predator species for maize field, marginal or rangeland vegetation?

Commercial crop monocultures are intensively disturbed habitats that typically do not have adequate resources to sustain natural enemies (Altieri & Nicholls, 1999). Therefore, the first hypothesis states that predator species abundance, richness and diversity will decrease with decreasing distance to the maize fields and that this is true at regional and local scales. Functional feeding guilds of spiders utilise different prey sources and use different techniques to acquire them. Also, habitat structure may play a significant role in hunting efficiency of many natural enemies (Langellotto & Denno, 2004; Uetz, 1991). Since the disturbances associated with maize agriculture may significantly affect the composition and distribution of prey (Duelli & Obrist, 2003) and tend to simplify habitat structure (Tivy, 1990), the second hypothesis states that the abundances of the various functional spider guilds is affected in different ways by agricultural disturbance, with some groups showing a decrease with increasing agricultural disturbance, while others increase. There is evidence that arthropod species may be characterised based on their preference of cultivated or natural habitat, with some species characterised as being crop field species, while others may be typical of an ecotone or undisturbed natural habitat (Duelli & Obrist, 2003). From this, the third hypothesis states that groups of arthropods can be distinguished based habitat type (maize field, marginal vegetation and rangeland).

Information on the occurrence frequencies of arthropod predator species in maize fields and adjacent uncultivated vegetation is a good starting point towards establishing which species have adapted unaided by human intervention to these highly transformed maize agro-ecosystems and may therefore be good candidates for conservation biological control in South African maize agro-ecosystems. From a biodiversity conservation perspective, it is important to identify those species that are sensitive to agricultural disturbance and which require patches of semi-natural vegetation adjacent to crop fields for their continued persistence within the agricultural environment.

7.3 Material and methods

7.3.1 Experimental layout

The target predator groups for this survey were Araneae (Spiders), Coccinellidae (Ladybugs), Mantodea (Praying mantids) and Neuroptera (Lacewings), which represent four major groups of predaceous arthropods inside maize fields and associated uncultivated grassland vegetation in South Africa (Botha *et al.*, 2015; Truter *et al.*, 2014). Surveys of these selected arthropod groups were conducted throughout the Dry Highveld Grassland Bioregion of the Grassland Biome (Mucina & Rutherford, 2006) and consisted of a two-part approach. Firstly, a regional survey of 25 sites was conducted in the vicinity of Ventersdorp, Potchefstroom and Viljoenskroon to illustrate broad-scale patterns of predator communities associated with the maize agro-ecosystems (Figure 7.1). Secondly, one farm in the vicinity of Ventersdorp was selected for intensive surveys to determine patterns of selected predator groups associated with maize agro-ecosystems at a local scale.

Figure 7.1: Study area indicating the three nearest towns to the survey sites situated in the North-West province of South Africa. FS, Free State; GP; Gauteng province; NW, North-West.

7.3.1.1 Regional scale arthropod surveys

Surveys were conducted in late summer of 2013, during the reproductive (flowering) stages of maize. A total of 25 sites were sampled, each comprising a maize field bordering on semi-natural rangeland in commercial maize production farmland. Within each site, sampling points were laid out in three transects along an agricultural disturbance gradient (Figure 7.2). Sampling points were laid out so that three points were located in each of three distance classes along the disturbance gradient: in maize fields (between 50 and 20 m from crop edge), in adjacent marginal vegetation (30-50 m from the last maize plant row) and in rangeland (80-100 m from the last maize plant row). This amounted to three samples being taken for each of the three distance classes per site. Sample points were placed parallel along the disturbance gradient, never less than 50 m or more than 100 m apart. The three replicates at each site were pooled to present a compounded sample of the three distance classes. Each point were measured at 100 m^2 (10 x 10 m) and sampled by means of a sweep net method slightly adapted to the standard method developed by Whittaker (1952). Inside maize fields sweeping was conducted with an up and down motion along the length of the maize plants, covering the leaves of plant from the lowest to highest. In uncultivated vegetation, sweeping was done using the standard side to side motion. For regional surveys, each point was sampled only once and each sample consisted of 30 sweeps.

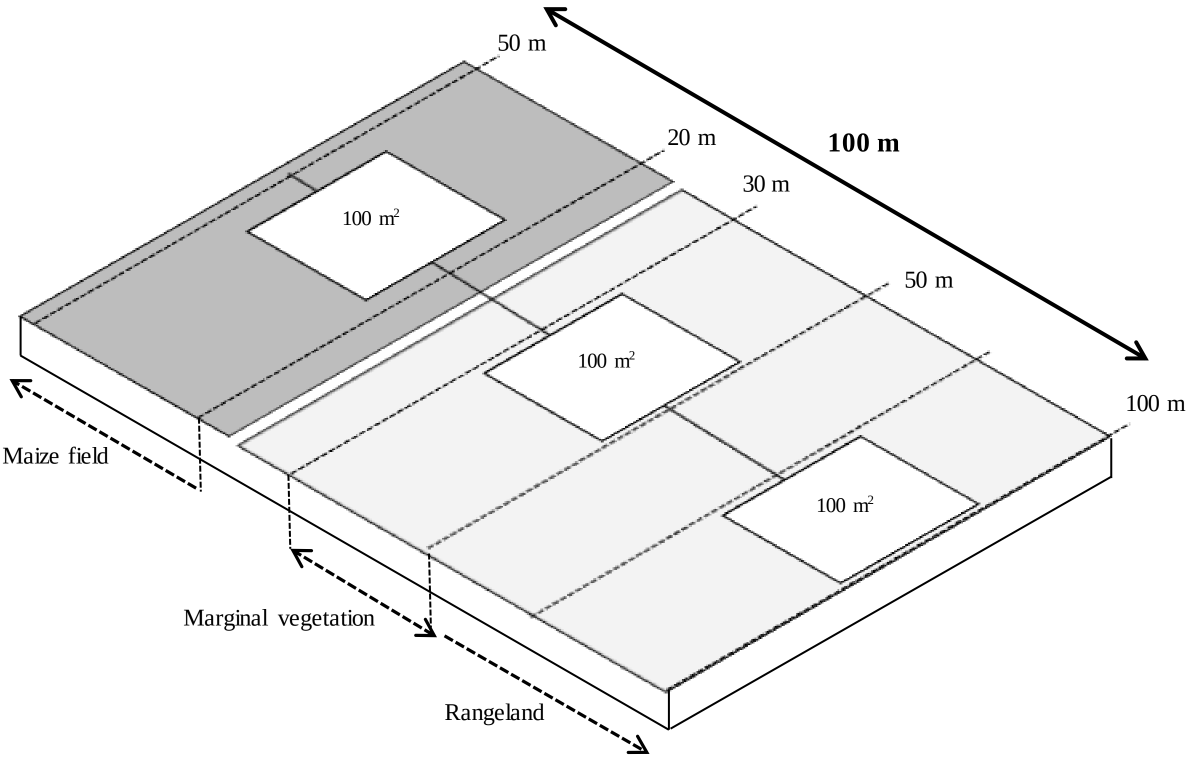

Figure 7.2: Sampling points situated within three distance classes along a maize field disturbance gradient. Distance classes: maize field (20-50 m from field edges), marginal vegetation (30-50 m from last maize row) and rangeland (80-100 m from last maize row).

7.3.1.2 Intensive local scale arthropod surveys

Intensive local scale surveys of selected predatory arthropod groups were conducted in March, 2014 and 2015 during the regional flowering periods of maize. Three sites, characterized by a maize field bordering on uncultivated rangeland were selected on one maize farm in the vicinity of the Ventersdorp district (Figure 7.1). The layout of the sampling points were identical to the regional surveys described above, with three transects in each site and points representing each of three distance classes along the disturbance gradient (maize fields, marginal vegetation and rangeland). Sampling was also done by sweep net method in 100 m^2 (10 x 10 m) points, never less than 50 m or more than 100 m apart.

For local scale surveys, each point was sampled four times during the day (07:00, 12:00, 15:00 and 17:00). These local scale surveys were conducted three times (on three separate days) during the course of two years (2014-2015). To minimize the possible influence of soil type and climate, the same sites (maize fields) were used for all three replicates. The purpose of this study was not to specify the effects of specific sampling times *per se* on arthropod abundance and diversity patterns and the data for the different sampling times were pooled to provide a comprehensive sample of each of the sampling points. This amounted to 12 repeats for each distance class (maize field, marginal vegetation and rangeland) in the three localities.

7.3.2 Site description

To describe the habitat features associated with the sampling areas, one of the three transects at each site was selected and a 1 m^2 collecting frame was thrown randomly into each of the 100 m^2 sampling points in the transect. Percentage cover was estimated for forbs, grasses, dead plant material and bare soil in each of the eight blocks of the 1m^2 frames. Vegetation structure was determined by measuring the height (cm) of the tallest forb and grass in each distance class. For each of the 100 m^2 sampling sites, a disturbance index was compiled by scoring different disturbance features according to their presence (1) or absence (0). Features were chosen to represent any animal or anthropogenic activity that breaks the soil and therefore has the potential to disrupt the plant growth in the vicinity. These included cultivation associated disturbances (tilled soil and turn rows), animal activity (livestock grazing, anthills, molehills and aardvark or porcupine dens), weedy growth (indicators of previous soil disturbances) and infrastructure (fences, tracks, footpaths and electricity pylons).

The standing biomass of each sampling point was measured by using a 250x250 mm biomass frame to collect plant material. The frame was thrown into the larger 1m^2 collecting frame at random. All the rooted plant material in the biomass frame was removed with a pruner and stored in marked paper bags. The plant material was then left to dry for four weeks. The dry plant material of each point was weighed in grams (g) and converted to kilograms per hectare (kg/ha) to determine the standing biomass at each of the sampling points.

7.3.3 Identification of arthropod species

Arthropod samples were placed into marked bags and preserved in a freezer. The selected arthropod predatory groups were then systematically identified to species level as far as possible with the assistance of the Biosystematic division of the Agricultural Research Council (ARC) in Pretoria, Gauteng. Mantid species were identified by using the reference collection at the ARC as well as a more recently updated collection at the Ditsong Museum in Pretoria. Individuals that could only be identified to genus level were treated as morpho-species. In this case, care was taken to insure that a morpho-species was regarded as the same 'species' for the entire sample (across all transects and sampling sites) by comparing new individuals with preserved specimens collected previously. The number of individuals representing each species was counted to generate abundance data for each point.

7.3.4 Data processing and analysis

7.3.4.1 Species diversity

For regional and local surveys, the arthropod species were described in terms of abundance, species richness and diversity. Abundance was calculated by counting the total number of individuals (N) in any given sample. Species richness represented the total number of species (S) in a sample. Taxonomic species diversity was expressed using a combination of indices to provide a more complete picture of richness and diversity (Magurran, 2004), namely Margalef's species richness index (d), Shannon-Wiener diversity index (H'), Pielou's evenness (J') and Simpson's diversity index (Ď). Diversity index values were calculated using PRIMER 6 software (Clarke & Gorley, 2006).

7.3.4.2 Spider guilds

All recorded spider species for regional and local surveys were divided into a number of alpha guilds, which represent groups of species that potentially exploit and compete for similar resources (Wilson, 1999). The guild categories were associated with the species' lifestyle (free-living or web-dwelling), hunting technique (free-living active hunter, free-living ambush hunter, orb-web builder, gumfoot-web builder or sheet-web builder) and primary hunting activity (diurnal or nocturnal). Information on the species characteristics was obtained from a variety of sources in the literature, including Dippenaar-Schoeman (2014); Picker *et al.* (2004) as well as personal observations in the field. A species-by-guild matrix with presence/absence data was multiplied with a species-by-sampling point matrix (abundance data) to create a guild-by-sampling point matrix using the MMULT function in Microsoft Excel.

7.3.4.3 Habitat preference

To classify predatory arthropod species into groups according to the habitat types (maize fields, marginal vegetation or rangeland) in which they were most frequently observed, abundance data of all arthropods recorded in this study (for regional and local surveys) were combined into one dataset and converted to percentage values (i.e. percentage of individuals recorded in the maize fields, marginal vegetation and rangeland for each species). This dataset was then subjected to a hierarchical agglomerative clustering analysis with Unweighted Pair Group Method with Arithmetic mean (UPGMA) clustering algorithm, Gower distance measure (Anderson *et al.*, 2006) and Similarity Profile (SIMPROF) test (Clarke *et al.*, 2008) in PRIMER 6 software. The cluster analysis was considered more objective to detect differences between species in terms of habitat occurrence than pure manual selection of groupings. The resulting groupings of the cluster analysis were then assessed and in some cases adapted by pooling similar groups.

7.3.4.4 Statistical analyses

Hierarchical Linear Modelling (HLM) analyses using a two-way ANOVA with random effects type model (McMahon & Diez, 2007) were performed on the datasets in SPSS software package to test for overall significant differences in species diversity index values and guild abundance between the three distance classes (maize fields, marginal vegetation and rangelands) for regional and local surveys. Transects were specified as the primary unit of measurement (subject ID) to account for the nestedness of transects within sampling site. The covariance structure was specified as unstructured. Each transect along the maize field-field margin gradient was considered an independent variable for statistical analyses. Effect sizes (Cohen's d) were used to express practical significance between sampling points where residual variance as well as transect variance were taken into account in the calculation of the effect size (Ellis & Steyn, 2003). The effect sizes were interpreted as follows: small effect: d=0.2, (b) medium effect: d=0.5 and (c) large effect: d=0.8.

To assess species composition differences between sites for regional and local surveys, Non-metric Multidimensional Scaling (NMDS) analysis was applied to a Bray-Curtis similarity matrix. The NMDS ordination groupings were statistically verified with Permutational Multivariate Analysis of Variance (PERMANOVA) (999 permutations, Bray-Curtis similarity, type III sums of squares), which is suitable for abundance data where significance is based on permutation of the dissimilarity matrix (Anderson, 2001). NMDS and PERMANOVA analyses were conducted using PRIMER 6 software and all abundance data were square-root transformed prior to analysis to reduce the influence of common species (Anderson, 2001).

7.4 Results

7.4.1 Descriptive results

7.4.1.1 Habitat description

Overall, the marginal vegetation adjacent to crop fields had the highest cover of grasses (43.3%) while rangelands hosted the highest cover (11.89%) of forbs (Table 7.1). The maize fields were most frequently characterized by bare soil (36.01%), while the marginal and rangeland habitats were characterized by the highest percentage cover of dead plant material (21.24% and 20.26% respectively). The maize plants themselves represented the tallest grass species at 225.95 cm inside the maize fields. Rangelands housed the tallest non-crop grass species (131.55 cm), and also the tallest forb species (46.59 cm). Rangelands also had the highest occurrence of animal activity (livestock grazing, anthills, molehills and aardvark or porcupine dens) while the marginal vegetation had slightly higher numbers of weeds and also a higher occurrence of structural features such as fences, tracks, footpaths and electricity pylons. The highest average standing biomass was measured in the rangelands (2402.91 kg/ha), followed by maize fields (including the maize plants) at 2034.18 kg/ha.

Table 7.1: Plant cover, height, averages of presence/absence scores for disturbances and mean biomass for habitat features in a regional survey of 25 sampling sites situated within three distance classes along maize field-rangeland gradients within the Highveld Grassland. Distance classes: maize field (20-50 m from field edges), marginal vegetation (30-50 m from last maize row) and rangeland (80-100 m from last maize row).

		Maize field	Marginal veg.	Rangeland
Cover (%)	Grasses	36.21	43.30	38.30
	Forbs	10.49	8.80	11.89
	Bare patches	36.01	25.74	28.17
	Dead plant material	10.27	21.24	20.26
Height (cm)	Tallest grass	225.95	96.86	131.55
	Tallest forb	28.82	37.68	46.59
Disturbance index	Cultivation	1.23	0.00	0.00
	Animal activity	0.05	0.95	1.14
	Weed presence	0.05	0.45	0.41
	Structural	0.45	1.77	1.41
Biomass (kg/ha)		2034.18	1807.27	2402.91

7.4.1.2 Predatory arthropod species

A total of 54 species and 1450 individuals were captured representing the four predatory arthropod groups targeted in this study (Table 7.2). Of these, 12 specimens could only be identified to genus level and were treated as morpho-species. Overall, 27 species and 291 individuals were captured in maize fields while 47 species and 556 individuals were recorded in marginal vegetation. A total of 41 species and 603 individuals were captured in rangelands. The Coccinellidae represented the highest abundance of the four predatory groups, with 587 individuals recorded in total across all sites and contributing to 40.5% of the total number of predatory arthropods captured. The Araneae represented the most species rich group, with a total of 37 recorded species across all sampling sites.

Table 7.2: Number of predatory arthropod species per family and percentage contribution of each family to the total number of individuals for the entire dataset of 25 sampling sites situated within three distance classes along maize field-rangeland gradients within Highveld Grassland. Distance classes: maize field (20-50 m from field edges), marginal vegetation (30-50 m from last maize row) and rangeland (80-100 m from last maize row).

Order	Family	Total		Maize field		Marginal veg.		Rangeland	
		Species	% indivi.	Species	% indivi.	Species	% indivi.	Species	% indivi.
Coleoptera	Coccinelidae	7	40.48	6	74.91	7	22.84	7	40.13
Araneae	Thomisidae	9	19.31	5	9.62	8	27.16	6	16.75
Mantodea	Mantidae	5	10.55	2	0.69	5	17.27	5	9.12
Neuroptera	Chrysopidae	2	9.79	2	8.93	2	8.63	2	11.28
Araneae	Araneidae	11	5.24	4	2.06	9	5.04	8	6.97
Mantodea	Tarachodidae	1	4.97	1	0.34	1	5.22	1	6.97
Araneae	Philodromidae	2	3.66	1	0.69	2	4.86	2	3.98
Araneae	Salticidae	7	3.38	1	0.69	5	5.04	6	3.15
Araneae	Theridiidae	4	1.66	2	1.03	4	2.52	2	1.16
Araneae	Linyphiidae	1	0.55	1	0.34	1	0.90	1	0.33
Araneae	Lycosidae	1	0.14	1	0.34	0	0.00	1	0.17
Araneae	Oxyopidae	2	0.14	1	0.34	1	0.18	0	0.00
Mantodea	Empusidae	1	0.07	0	0.00	1	0.18	0	0.00
Mantodea	Hymenopodidae	1	0.07	0	0.00	1	0.18	0	0.00

7.4.1.3 Spider guilds

Definitions for the guild groups considered in this study are provided in Table 7.3. Appendix C, Table C.1 also provides a list of all the spider species and their guild classifications. For the entire dataset, the free-living spiders represented the most species rich and abundant group, contributing to 79.15% of the total number of captured individuals (Table 7.4). The free-living spider guild was also the most prominent group in each of the separate distance classes (maize fields, marginal vegetation and rangeland). The most common hunting technique was the free-living ambush-hunting type, followed by orb-web building and free-living active hunting types, which together contributed to 93.52% of the total number of individuals captured during this study. In terms of primary hunting activity, most species and individuals were representative of the diurnal hunting group, which made up 80.77% of the total number of recorded spider individuals.

Table 7.3: List of guild groups and associated definitions for the spider species recorded in all localities across the maize field-field margin gradient. Definitions follow Dippenaar-Schoeman (2014).

Category	Guild	Description
Lifestyle	Free-living	No permanent association with silk structures. May occasionally construct retreat webs for shelter, although not for capturing prey.
	Web-dwelling	Permanent association with silk structures used to capture prey.
Hunting technique	Free-living active hunting	Actively search for and run down prey.
	Free-living ambush hunting	Sit motionless in one position, capturing prey that comes within striking distance.
	Orb-web building	Circular spiral structure with bride lines and radii all made with adhesive threads that adhere to flying insects colliding with the structure. Usually oriented vertically.
	Gumfoot-web building	Two-part structure, with the upper part comprising mooring, signal and catch threads while the lower part consists of catch threads tied to the ground under high tension with sticky droplets. Ground-running insects dislodge ground threads and adhere to sticky droplets.
	Sheet-web building	Complex three-dimensional structures with the sheets orientated horizontally and flat, concave or convex. Convex webs catch more insects from below and concave webs catch more insects from above.
Primary hunting activity	Diurnal	Primary hunting activity takes place during the day.
	Nocturnal	Primary hunting activity takes place at night.

Table 7.4: Number of spider species per guild and percentage contribution of each guild to the total number of individuals for the entire dataset of all 25 sampling sites situated within three distance classes along maize field-rangeland gradients throughout the Highveld Grassland Biome. Distance classes: maize field (20-50 m from field edges), marginal vegetation (30-50 m from last maize row) and rangeland (80-100 m from last maize row).

		Total		Maize field		Marginal veg.		Rangeland	
Category	Guild	Species	% indiv.	Species	% indiv.	Species	% indiv.	Species	% indiv.
Lifestyle	Free-living	22	79.15	10	81.82	17	81.89	16	75.00
	Web-dwelling	15	20.85	6	18.18	13	18.11	10	25.00
Hunting technique	Ambush hunting	12	66.60	8	75.00	10	68.50	9	62.24
	Orb-webs	10	14.37	3	9.09	8	10.63	7	20.41
	Active hunting	10	12.55	2	6.82	7	13.39	7	12.76
	Gumfoot-webs	4	4.86	2	6.82	4	5.51	2	3.57
	Sheet-webs	1	1.62	1	2.27	1	1.97	1	1.02
Primary activity	Diurnal	23	80.77	11	84.09	18	83.86	17	76.02
	Nocturnal	14	19.23	5	15.91	12	16.14	9	23.98

7.4.2 Species diversity patterns

For the regional survey, HLM results indicated an overall significant effect of distance from maize field on predatory arthropod species richness and also on values of Margalef's species richness index (p=0.04 Table 7.5). Significant differences between the means for species diversity in Table 7.6 (as for spider guilds following below) were indicated with different superscript symbols. Therefore a value assigned the superscript (a) symbol differed practically from a value with a (b) symbol, as determined by effect sizes displayed in Appendix C, Table C.2.

Significantly higher species richness and Margalef index values occurred in marginal vegetation and rangeland compared to maize fields, as indicated by significant effect sizes (d≥0.5; Table 7.6). Shannon-Wiener diversity index values were also significantly higher in rangelands compared to maize fields (d≥0.5; Table 7.6). Analyses for the local survey indicated a highly significant effect of distance from maize field on all of the diversity indices (p≤0.01; Table 7.5), with significantly higher index values in marginal vegetation and rangeland than in maize fields (d ≥1.05; Table 7.6).

Table 7.5: Hierarchical Linear Modelling (HLM) results for a regional survey of 25 sampling sites and a local survey of a Ventersdorp sampling site indicating overall differences in insect predator diversity measures between distance classes.

		F	p	MSE	Variance (transect)
Regional survey	Species richness (S)	3.51	**0.04***	6.86	1.81
	Abundance (N)	0.80	0.45	61.24	13.36
	Margalef (d)	3.34	**0.04***	0.69	0.20
	Shannon-Wiener (H')	2.73	0.08	0.35	0.11
	Simpson (Ď)	0.82	0.45	0.09	0.02
Local survey	Species richness (S)	25.43	**0.00***	7.72	1.66
	Abundance (N)	6.45	**0.00***	354.24	12.45
	Margalef (d)	28.89	**0.00***	0.39	0.10
	Shannon-Wiener (H')	31.90	**0.00***	0.16	0.05
	Simpson (Ď)	5.96	**0.00***	0.05	0.01

F = F value; p = p value. Bold text* indicates significant p values at p≤0.05
MSE= mean square error, unexplained variance
Variance (transect) = variance explained by transect

Table 7.6: Mean values for predatory arthropod diversity measures at three distance classes: maize field (20-50 m from field edges), marginal vegetation (30-50 m from last maize row) and rangeland (80-100 m from last maize row). Means with different superscript symbols differed practically according to effect sizes (d $\geq$0.5).

		Maize field	Marginal vegetation	Rangeland
Regional survey	Species richness (S)	3.44^{a}	5.12^{b}	5.16^{b}
	Abundance (N)	9.04^{a}	11.00^{a}	11.76^{a}
	Margalef (d)	1.17^{a}	1.69^{b}	1.70^{b}
	Shannon-Wiener (H')	0.91^{a}	1.20^{ab}	1.28^{b}
	Simpson (Ď)	0.60^{a}	0.65^{a}	0.71^{a}
Local survey	Species richness (S)	2.83^{a}	10.25^{b}	9.33^{b}
	Abundance (N)	7.50^{a}	29.50^{b}	32.92^{b}
	Margalef (d)	0.99^{a}	2.76^{b}	2.55^{b}
	Shannon-Wiener (H')	0.79^{a}	1.90^{b}	1.92^{b}
	Simpson (Ď)	0.59^{a}	0.83^{b}	0.86^{b}

7.4.3 Species composition

The NMDS ordination for the regional survey revealed relatively non-distinctive groupings for the respective distance classes (maize fields, marginal vegetation and rangeland) (stress: 0.01; Figure 7.3a). However, PERMANOVA analyses on the same dataset revealed overall significant differences in species composition between maize field and marginal vegetation and also between maize field and rangeland vegetation (p=0.001; Table 7.7). The NMDS ordination for the local survey revealed somewhat more

Table 7.7: Permutational multivariate analysis of variance (PERMANOVA) results indicating similarity in species composition of predatory arthropods between three distance classes in a regional survey (25 sampling sites) and a local survey (Ventersdorp farm). Distance classes: maize field (20-50 m from field edges), marginal vegetation (30-50 m from last maize row) and rangeland (80-100 m from last maize row).

			Regional survey	Local survey
Overall effect		Pseudo-F	3.611	8.622
		p	**0.001***	**0.001***
Pairwise comparisons	Maize field x Marginal vegetation	t	2.350	3.721
		p	**0.001***	**0.001***
	Maize field x Rangeland	t	2.102	3.416
		p	**0.001***	**0.001***
	Marginal vegetation x Rangeland	t	1.078	1.222
		p	0.302	0.176

Figures represent pseudo F-values, t-values and p-values
Permutations = 999; Bray-Curtis similarity
Bold text* indicates significant p-values at $p \leq 0.001$

distinctive groupings between maize fields and adjacent uncultivated vegetation (marginal and rangeland) (stress: 0.01; Figure 7.3b).

These groupings were confirmed by PERMANOVA results, which indicated significant differences in predatory arthropod composition between maize field and marginal vegetation, and also between maize field and rangeland vegetation (p=0.001; Table 7.7). There were no distinctive differences in predatory arthropod species composition between the marginal vegetation and rangeland vegetation.

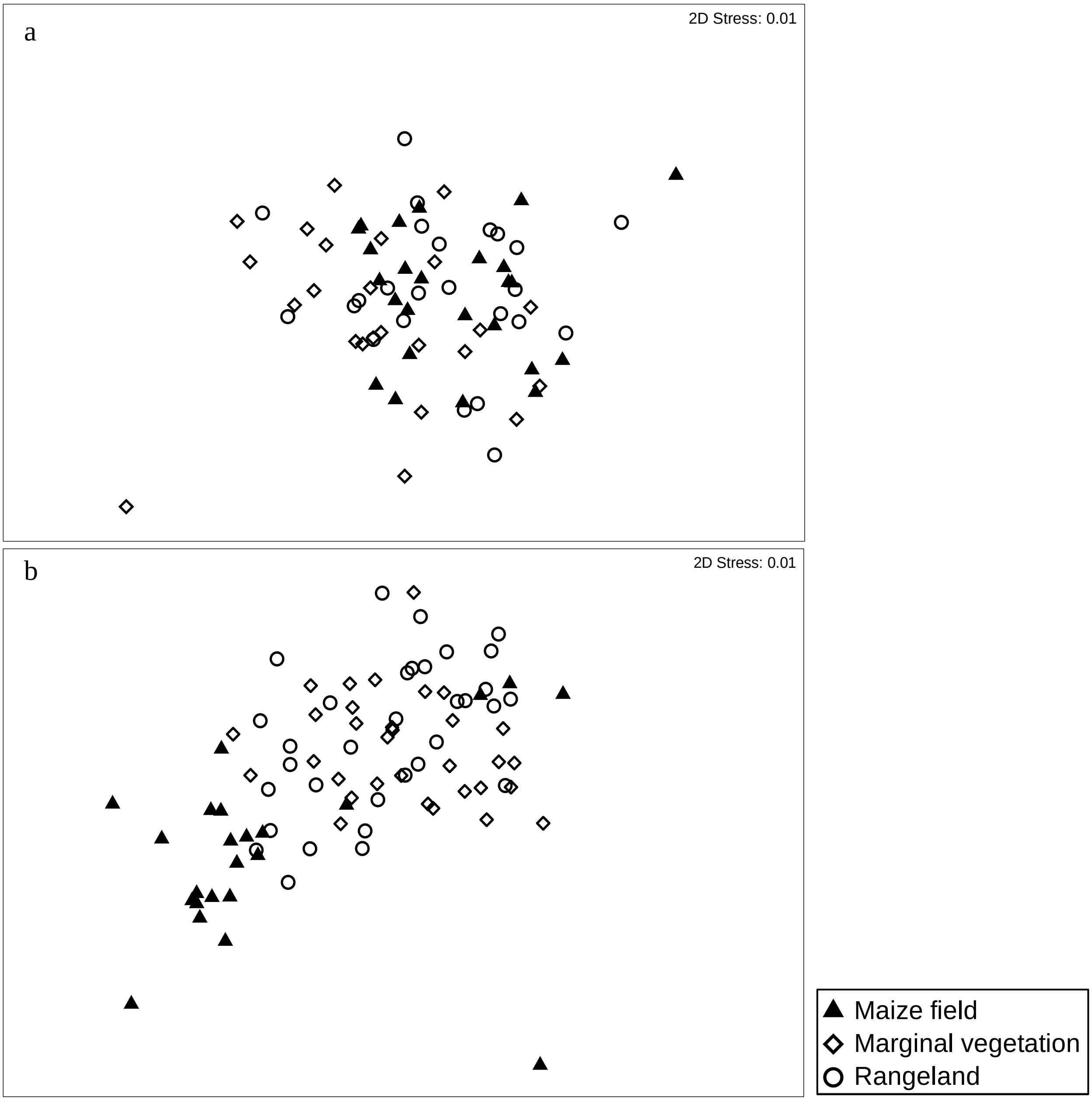

Figure 7.3: Non-metric multidimensional scaling (NMDS) analyses based on abundance data of predatory arthropod species recorded for (a) a regional survey (25 sampling sites) and for (b) a local survey (one Ventersdorp sampling site) to indicate differences in species composition between three distance classes: maize field (20-50 m from field edges), marginal vegetation (30-50 m from last maize row) and rangeland (80-100 m from last maize row). Resemblance: S17 Bray Curtis similarity; Data transformation: Square root.

7.4.4 Spider guild abundance patterns

Most of the functional guilds defined by the spider species' specific hunting technique were not represented by adequate numbers to be considered for HLM analysis. As such only the results for the guilds associated with lifestyle and primary hunting activity will be presented. HLM results for the regional survey indicated a significant effect of distance from maize field on the abundance of free-living, web-dwelling, diurnal and nocturnal individuals ($p \leq 0.04$; Table 7.8). There were significant differences in the abundance of free-living spiders between maize fields and marginal vegetation (d=0.85; Table 7.9), Refer to Appendix C, Table C.2 for effect sizes. The abundances of web-dwelling and diurnal spiders were significantly different between maize fields and marginal vegetation and also between maize fields and rangelands ($d \geq 0.5$; Table 7.9). Maize fields and rangelands also differed significantly in terms of nocturnal spider abundance (d=0.70; Table 7.9).

Table 7.8: Hierarchical Linear Modelling (HLM) results for a regional survey of 25 sampling sites and a local survey of a Ventersdorp sampling site indicating overall differences in spider guild abundance between distance classes.

		F	p	MSE	Variance (transect)
Regional survey	Free-living (N)	5.69	**0.01***	12.44	3.03
	Web-dwelling (N)	3.52	**0.04***	1.94	0.38
	Diurnal (N)	6.20	**0.00***	12.52	3.22
	Nocturnal (N)	3.80	**0.03***	1.55	0.35
Local survey	Free-living (N)	17.96	**0.00***	19.22	2.41
	Web-dwelling (N)	13.07	**0.00***	1.51	0.07
	Diurnal (N)	17.96	**0.00***	19.22	2.41
	Nocturnal (N)	13.07	**0.00***	1.51	0.07

F = F value; p = p value. Bold text* indicates significant p values at $p \leq 0.05$
MSE= mean square error, unexplained variance
Variance (transect) = variance explained by transect

Table 7.9: Mean values for spider guild abundance at three distance classes: maize field (20-50 m from field edges), marginal vegetation (30-50 m from last maize row) and rangeland (80-100 m from last maize row). Means with different superscript symbols differed practically according to effect sizes ($d \geq 0.5$).

		Maize field	Marginal vegetation	Rangeland
Regional survey	Free-living (N)	1.16^{a}	4.52^{b}	3.00^{ab}
	Web-dwelling (N)	0.32^{a}	1.08^{b}	1.32^{b}
	Diurnal (N)	1.20^{a}	4.72^{b}	3.08^{b}
	Nocturnal (N)	0.28^{a}	0.88^{ab}	1.24^{b}
Local survey	Free-living (N)	0.75^{a}	11.08^{b}	8.42^{c}
	Web-dwelling (N)	0.08^{a}	1.83^{b}	2.58^{c}
	Diurnal (N)	0.75^{a}	11.08^{b}	8.42^{c}
	Nocturnal (N)	0.08^{a}	1.83^{b}	2.58^{c}

Results for HLM analyses also indicated significant effects of distance from maize field on the abundances of all guilds considered for analyses in the local survey ($p<0.001$; Table 7.8). There were highly significant differences in the spider guild abundance between maize fields and marginal vegetation and also between maize fields and rangelands ($d\geq1.39$; Table 7.9), with the guild abundance being lower inside maize fields. In this case, there were also significant differences in spider guild abundance between marginal vegetation and rangeland ($d\geq0.57$; Table 7.9).

7.4.5 Habitat preference

The abundance data of all recorded arthropod predators revealed that 39% of species were present in all three distance classes and 26% of species were unique to only one of the distance classes (Figure 7.4). Hierarchical cluster analysis in combination with SIMPROF analysis revealed 14 groups of predatory arthropods based on their occurrence frequency in maize fields, marginal vegetation and rangeland habitats (Figure 7.5). Further adaptation of these initial clusters led to six final groups of species based on habitat preference (Figure 7.6, also refer to Appendix C, Table C.3 for a complete list of species, full species names and final habitat preference groupings).

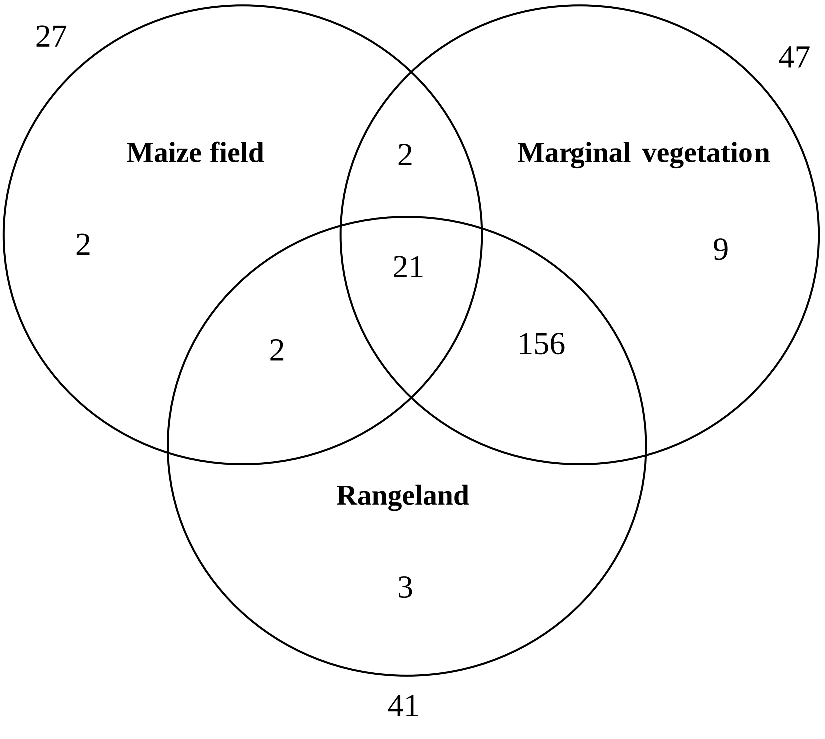

Figure 7.4: Venn diagram indicating numbers of unique and shared species in three distance classes: maize field (20-50 m from field edges), marginal vegetation (30-50 m from last maize row) and rangeland (80-100 m from last maize row). The numbers outside the circles indicate the total number of species in each distance class.

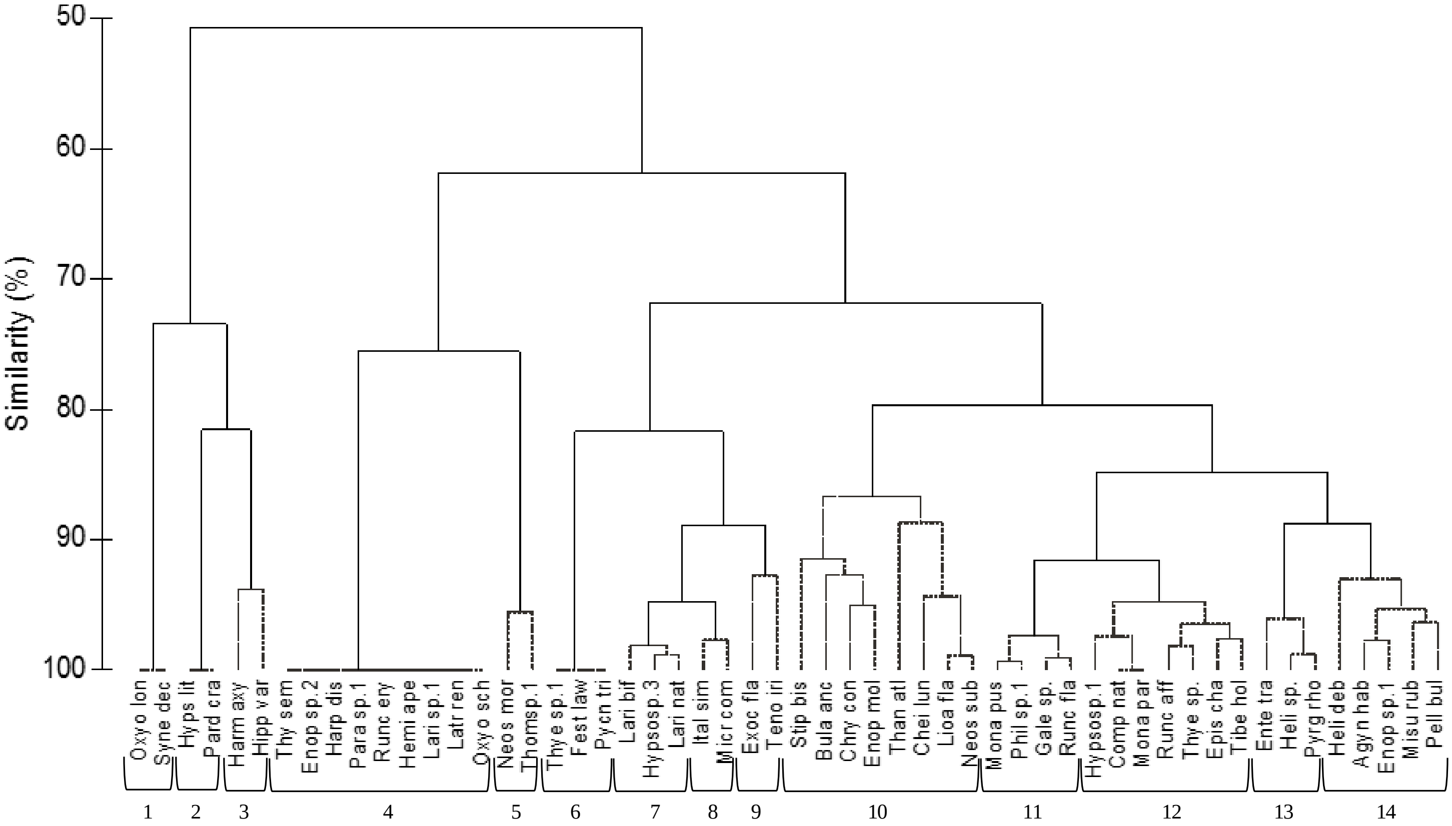

Figure 7.5: Cluster analysis with Unweighted Pair Group Method with Arithmetic Mean (UPGMA) based on Gower distance measure indicating 14 groupings of predatory arthropod species based on their percentage occurrence in three distance classes (maize fields, marginal vegetation and rangeland). Dashed lines in the dendrogram indicate branching with no remaining significant structure, as determined by Similarity Profile (SIMPROF) analysis. Refer to Appendix C, Table C3 for full species names.

Group (a) represented potential maize field specialists, species of which at least 70% of the individuals were found in maize fields. Group (b) represented potential marginal vegetation specialists and represented species whose individuals were found almost exclusively (or at least in 60% of cases) in marginal vegetation. Group (c) was characteristic of marginal and rangeland vegetation but tended to be more abundant in marginal vegetation. Group (d) were considered potential rangeland specialists as all species in this group were found exclusively in rangeland vegetation. Group (e) was similar to group (c) and represented species that were mostly associated with marginal and rangeland vegetation, but in this group tended to be more abundant in rangeland vegetation. Species classified in group (f) were distributed relatively evenly across the maize field, marginal and rangeland habitats and were considered potential agro-ecosystem generalists.

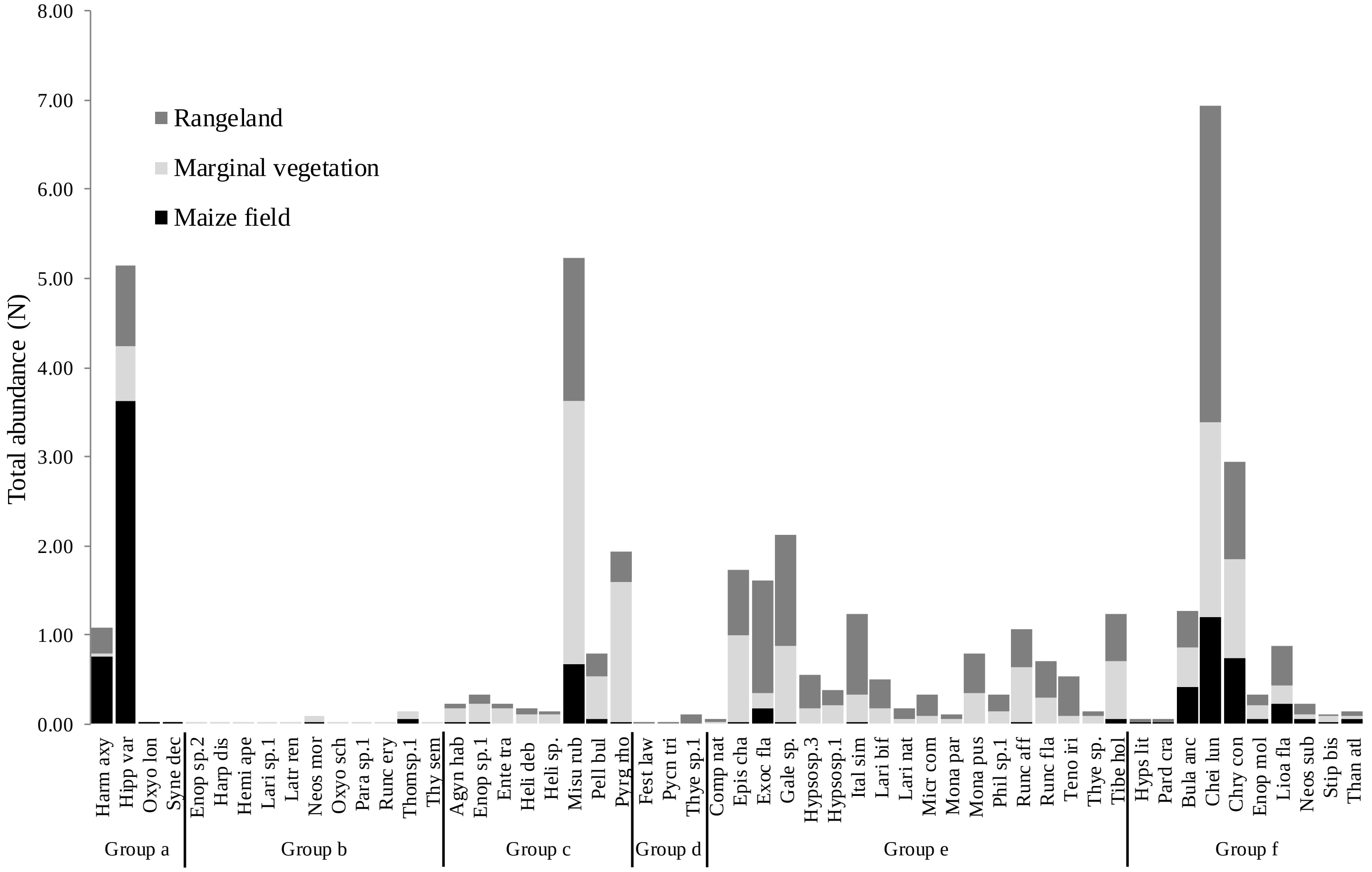

Figure 7.6: Total abundances of all recorded predatory arthropod species in each of three distance classes and assigned groups according to habitat preference. Distance classes: maize field (20-50 m from field edges), marginal vegetation (30-50 m from last maize row) and rangeland (80-100 m from last maize row). Refer to Appendix C, Table C3 for full species names.

7.5 Discussion

7.5.1 Predatory arthropod diversity patterns

As expected, the results indicated a strong negative effect of maize field environments on predatory arthropod species richness and diversity. This was remarkably clear in the intensive local survey, which indicated significantly lower species richness and diversity between maize fields and the adjacent habitat. It was found that the maize fields contained around 30% of the species compared to the uncultivated habitats, which is consistent with the results of Schmid *et al.* (2015). It is well known that the commercial crop field environment generally does not favor predatory arthropod species since it lacks many of the food and shelter resources required by grassland adapted arthropod communities (Grez *et al.*, 2010).

From the results, no decreased arthropod species richness and diversity in adjacent marginal vegetation could be detected compared to the rangeland. This suggests that the structural features (fences, tracks, footpaths and electricity pylons) associated with the marginal vegetation habitats and the close approximation thereof to maize fields probably did not have significant adverse effects on the predator communities considered in this study. This is consistent with the results of the previous results chapters, where arthropod morpho-species were used as substitute for taxonomic species (Botha *et al.*, 2015).

The uncultivated grassland habitats adjacent to the maize fields (marginal and rangeland vegetation) were also characterized by more (dead and living) plant cover compared to the maize fields, which may provide a buffer against changes in the abiotic environment. Several studies have pointed to the potential benefits of high vegetation cover and the associated favorable microclimate, alternative prey and alternative food resources in enhancing arthropod diversity (Dennis *et al.*, 1994; Halaj *et al.*, 2000; Silva *et al.*, 2010). Also, the highest proportion of anthills, molehills and aardvark dens were found in the rangeland habitats, which points to a lack of recent anthropogenic soil disturbances in these areas. In general, a reduction in soil disturbance by means of tillage is beneficial for most invertebrate macrofauna due to increased soil moisture and smaller fluctuations in soil temperature (Kladivko, 2001).

7.5.2 Spider guild abundance patterns

The abundances of free-living, web-dwelling, diurnal and nocturnal spiders were reduced inside the maize fields compared to the adjacent uncultivated vegetation, which is consistent with the results for total predator diversity and abundance. This illustrates the need for semi-natural vegetation in maize agro-ecosystems to conserve spider abundance. It has been shown by numerous studies that semi-natural vegetation margins in cropping systems often benefit spider abundance and diversity (Clough *et al.*, 2005; Hendrickx *et al.*, 2007; Pfiffner & Luka, 2000).

The intensive local surveys also indicated significant differences in spider abundance between marginal and rangeland vegetation. In this case, the free-living spiders tended to be characteristic of the marginal vegetation. On the other hand, web-dwelling spiders seemed to prefer rangeland vegetation over marginal vegetation. This is consistent with the results of Young and Edwards (1990), who found that wandering spiders tended to be associated with agricultural disturbance, while web-builders preferred more undisturbed semi-natural sites. This may be the result of the increased habitat complexity associated with rangeland habitats, which had a higher percentage forb cover and also the tallest non-crop plant growth. Woody growth may enhance web-building spider diversity by allowing for more positions to attach their webs to (Rypstra, 1983). Inclusion of remnant patches of semi-natural vegetation adjacent to actively cultivated areas may therefore be of particular importance for the conservation of web-building spiders in maize agro-ecosystems.

Conserving diverse hunting strategies in agro-ecosystems may be beneficial for controlling a wide variety of crop pests. Active hunting and web-building spiders utilize different prey sources and may therefore be important for the control of different invertebrate pest species. Web-building spiders are usually more effective in capturing flying insects (Dippenaar-Schoeman *et al.*, 2013) such as lepidopteran pest adults (Dippenaar-Schoeman *et al.*, 1999) as well as aphids and leafhoppers (Nyffeler *et al.*, 1988). Active wandering spiders tend to utilize a wider range of prey items compared to web-builders (Nyffeler, 1999), and may be an important generalist control agent of pest species in crops. This suggests that wandering spiders may be more likely to find suitable food than web-spinners in a field crop, which would further explain the results that there were relatively few web-building spiders compared to active wandering spiders in maize fields and that rangelands hosted the largest numbers of web-building spiders.

The results also indicated that diurnal species were most abundant in marginal vegetation while nocturnal species were characteristic of the rangelands. This is probably an indirect effect as free-living individuals tended to be diurnal and the web-builders were often nocturnal. Also, sampling was conducted during the day (between 07:00 and 17:00). As a result, nocturnal individuals may have been under-sampled in this study and results for these two guilds needs to be verified.

7.5.3 Habitat preference of predator species

Two coccinellids (*Harmonia axyridis* and *Hippodamia variegata*) were narrowly associated with the maize field environment. This is consistent with other studies that pointed to coccinellids and spiders as frequent visitors to flowering maize fields (Lundgren *et al.*, 2015; Lundgren, 2009). High levels of aphid infestation on the maize plants were observed during the time of sampling, which most likely attracted the coccinellid species to the maize fields. *H. axyridis* is an exotic species in South Africa (originally from Asia) that has shown a marked range expansion since the specie's first record in 2002 in the Western Cape (Stals & Prinsloo, 2007). In conjunction with the results presented in this chapter, *H. axyridis* have been observed in association with the naturalized *H. variegata* ladybird (an exotic species from Europe) in cereal crops (Stals & Prinsloo, 2007). In the present surveys, *H. axyridis* was also found to be associated with adjacent grassland rangelands. *H. axyridis* is an effective predator of crop aphids, but its value in terms of biological pest control is debatable due to its tendency to be a generalist predator, preying on a multitude of non-target invertebrates (Koch, 2003). As yet, the implications of this species for insect biodiversity conservation in South Africa's grasslands are unknown.

A lynx spider (*Oxyopes longispinosus*) and a crab spider (*Synema decens*) were also very abundant within the maize fields. These two species are free-living spiders that are commonly found on plants (including grass, shrubs, flowers and trees) and have also been recorded frequently on crops in other studies where they act as generalist predators (Dippenaar-Schoeman, 2014).

Ten species were classified as potential agro-ecosystem generalists, i.e. they were recorded in relatively equal frequencies in maize fields, marginal vegetation and rangelands. These included six spiders in the Araneidae family (*Hypsosinga lithyphantoides*, *Neoscona subfusca* and *Thanatus atlanticus*), Lycosidae family (*Pardosa crassipalpis*), Theridiidae family (*Enoplognatha molesta*) and Thomisidae family (*Stiphropus bisigillatus)*. Three coccinellids (*Bulaea anceps*, *Cheilomenes lunata* and *Lioadalia flavomaculata*) and one Chrysopidae lacewing species (*Chrysoperla congrua*) also belonged to this assemblage (Appendix C, Table C.3). Being habitat generalists these species may be best adapted to the highly dynamic agro-ecosystem environment and switch between crop field and uncultivated vegetation according to prey availability (Denys & Tscharntke, 2002; Rand *et al.*, 2006). These species may be the best candidates for conservation biological pest control in South African maize fields since they can persist in the agro-ecosystem, even when crop fields are fallow, by moving into the marginal vegetation.

The majority of arthropod predators recorded in this study (93% of the species) were also found on semi-natural vegetation away from the actively cultivated area. This points to the importance of remnant semi-natural vegetation in maintaining predatory arthropod diversity in the agro-ecosystem mosaic (Gaigher *et al.*, 2016; Henri *et al.*, 2015; Landis *et al.*, 2000). Conserving semi-natural vegetation patches in the maize farming system may be one of the most cost-effective and least time-consuming approaches to pest control by natural enemies. While classical biological control is typically aimed at only one or a few specific crop pests, natural enemies that occur in the agro-ecosystem naturally may suppress outbreaks of a wide range of potential crop pests.

To support sufficient numbers of predatory arthropod species, it must be considered that these uncultivated vegetation patches will probably have to contain a variety of non-prey food sources (Lundgren, 2009). Many spiders include floral and extrafloral nectar and honeydew in their diet and in some cases sugar promotes their longevity (Pollard *et al.*, 1995). Species in the Thomisidae (crab-spiders) have been observed actively brushing pollen grains into their mouths (Vogelei & Greissl, 1989). Floral and extrafloral nectar and pollen is also a significant food source for many coccinellid species (Lundgren, 2009). Adult stages of *Chrysoperla* lacewings also consume nectar and pollen on a regular basis, which promotes their reproduction and serve as valuable alternative sustaining food sources when aphids are absent (Patt *et al.*, 2003; Villenave *et al.*, 2005). Some mantid species also seem to benefit from pollen, as individuals that were given pollen as a supplement to their diets tended to have greater body mass under laboratory conditions (Beckman & Hurd, 2003).

In the agro-ecosystems that were sampled during this study, these non-prey food sources were probably already present, either in the maize fields themselves or in the adjacent uncultivated vegetation (Botha *et al.* 2015; Botha *et al.* 2016) because the predators were present in large numbers without any anthropogenic interference. However, this aspect needs to be taken into consideration when farmers intend to establish semi-natural vegetation patches in previously cultivated areas where the entire original plant community has been removed. Plant types should be chosen carefully by selecting for those that may provide sufficient resources for arthropod predators.

7.6 Conclusions

Addressing the first research question stated at the outset of this chapter, the overall tendency was that predator abundance, species richness and diversity were severely decreased in maize fields and most species were found almost exclusively in uncultivated marginal and rangeland vegetation. This supports the first hypothesis. It is assumed that these predators are dependent on semi-natural vegetation to persist in the agricultural environment which needs to be taken into consideration when adapting management regimes in maize field agriculture to promote bio-control and conservation of predatory arthropod diversity.

Relating to the second research question, the abundances of all the spider guild groups were negatively affected by the maize fields. However, the results suggested that the hunting strategies of certain spider guilds were favored by the agricultural activities. Therefore, while the abundances of all the spider guild groups were reduced inside maize fields, the abundance of active hunters were higher relative to the web-builders in the cultivated area. In intensive local surveys, the free-living spiders also tended to be characteristic of the marginal vegetation while web-dwelling spiders seemed to prefer rangeland vegetation. These results support the second hypothesis.

In relation to the third research question, different habitat preference groups could be distinguished based on occurrence frequency and the third hypothesis is therefore also supported. The results pointed to a number of arthropod predators (coccinelid and spider species) that occurred exclusively or most frequently inside the highly disturbed maize field environment, which suggests adaptability to agricultural disturbance. Also, ten species were classified as potential agro-ecosystem generalists, which may be the best candidates for conservation biological pest control since they can persist in the agro-ecosystem, even when crop fields are fallow. The possibility that these species could act as predators of economically important maize pests and therefore serve as additional bio-control agents in South African maize fields needs to be further investigated. Given the numerous failed attempts at controlling maize pests by means of classical biological control, augmentation and conservation biological control may be more cost effective options for reducing pest numbers in maize by means of arthropod enemies.

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CHAPTER 8: CONCLUSIONS

8.1 Summary of research

This study observed and analysed the patterns of taxonomic and functional diversity, compositional structure and diversity relationships of two major groups of biota (vascular plants and plant-associated arthropods) in relation to a gradient of agricultural disturbance at local and regional scales in the Grassland and Savanna Biomes of South Africa. The most important findings of this study were as follows:

8.1.1 Chapter 3

- Maize fields had severely reduced diversity of non-crop plant and arthropod species and had significantly different plant and arthropod species compositions compared to uncultivated vegetation.
- Marginal areas were higher in species diversity than maize fields and were comparable to the diversity of low land-use intensity rangelands. Marginal and rangeland habitats also had similar plant and arthropod species compositions.
- The main predictor of plant species assemblages were agricultural disturbances, while biome, altitude and, to a lesser extent, farming practice were better predictors of arthropod species composition.
- The Savanna Biome tended to have significantly higher plant species richness than the Grassland Biome in uncultivated areas.

8.1.2 Chapter 4

- Uncultivated semi-natural vegetation of the Grassland and Savanna Biomes had distinct arthropod assemblages although these distinctions were not as clear as for plant species.
- Biomes were distinguishable, albeit weakly, for phytophagous and predacious arthropod assemblages, but not for parasitoid and pollinator arthropod groups.
- Arthropod species assemblages were better explained by their geographical position than by plant features associated with biome, such as tree and grass cover.

8.1.3 Chapter 5

- Overall positive correlations were found between plant species and arthropod morpho-species in maize agro-ecosystems across the Grassland and Savanna biomes of South Africa.
- Different plant communities tended to be associated with different arthropod communities.
- The strength of correlations differed depending on plant family (Asteraceae, Fabaceae and Poaceae), arthropod trophic group (herbivores, predators and pollinators) and distance class (maize field, marginal vegetation and rangeland).
- An increase in the abundance of grasses (Poaceae) was most frequently correlated with an increase in overall arthropod abundance, herbivore abundance and predator abundance.

8.1.4 Chapter 6

- High agricultural disturbance intensity areas (maize fields) housed more annual, low-growing, clonal plants with long-range dispersal mechanisms (wind or exozoochorous) while medium and low disturbance intensity uncultivated areas (marginal and rangeland vegetation) typically hosted more perennial, erect and non-clonal plants associated with no specific adaptive dispersal mechanisms.
- Chamaephytic and hemicryptophytic life forms, nitrogen –fixing ability and spinescence were the traits that were most frequently lost in high disturbance intensity maize field areas.
- The high disturbance intensity of the maize fields had drastically reduced abundance and diversity of functional traits.
- There was no evidence for trait abundance or diversity losses or the transformation of trait assemblage structure in marginal vegetation at the 30-100 m distance from maize fields.
- Maize fields situated in the Grassland and Savanna Biomes hosted different trait assemblages and favoured different functional types (generally grassy weeds were found in grassland and forb weeds in savanna).

8.1.5 Chapter 7

- At local and regional scales, species richness and diversity of selected arthropod predator groups (Araneae, Coccinellidae, Mantodea and Neuroptera) were severely decreased in maize fields and most species were found almost exclusively in uncultivated marginal and rangeland vegetation.
- There were no decreased arthropod predator species richness and diversity in adjacent marginal vegetation compared to rangelands.
- Although the abundance of most spider guild groups was reduced inside the maize fields, the abundance of the active hunters showed an increase in the actively cultivated areas.
- Ten arthropod predator species were found in relatively equal frequencies inside the three disturbance intensity classes (maize fields, marginal vegetation and rangeland) and as such were classified as potential agro-ecosystem generalists.

8.2 Hypotheses and future research

Without exception, the results indicated that habitat loss associated with the transformation of semi-natural grassland and savanna to high agricultural disturbance intensity maize fields resulted in severely decreased species diversity, functional diversity and abundance of plants and associated arthropods. However, there was no evidence to suggest that marginal areas (30-100 m from the maize field edges) had reduced levels of species diversity, functional diversity or trait abundance of plants and associated arthropods. The pattern was consistent across the Grassland and Savanna Biomes. This suggests that the possible disturbance effects of maize fields do not have considerable negative effects on either the diversity or species assemblages of plant and arthropod communities in grassland and savanna habitats at ≥30 m from the area of active cultivation. Resulting from this, the **first hypothesis** stating that taxonomic and functional diversity of plants and associated arthropods in uncultivated vegetation will decrease with decreasing distance to maize fields across the Grassland and Savanna Biomes is rejected. Any diversity losses associated with agricultural disturbances is concentrated <30 m from the area of active cultivation, but the exact size and effect still needs to be determined.

It was evident that the composition of plant and arthropod communities was very different between high agricultural disturbance level maize fields and the uncultivated vegetation. Typically, plant strategies changed from perennial to annual life cycles, erect to low-growing forms, non-clonal to clonal abilities and short to long-range dispersal mechanisms (wind or exozoochorous). These traits may promote the colonization of and the persistence in the ephemeral crop field environment more effectively. Regarding spider guild groups, maize fields seemed to favour active hunting types, while web-building types were more numerous in the uncultivated habitats. Patterns for plant traits were different for the two biomes. Maize fields situated in the grassland typically contained a greater relative abundance of grassy weeds while maize fields in savanna had relatively more forb weeds.

From the above, **the second hypothesis**, stating that maize field and marginal vegetation in close proximity to the actively cultivated area will be replaced by a unique set of species and or functional types, is partially supported. However, there was little evidence to suggest that the marginal vegetation were associated with different plant species or traits compared to the rangeland vegetation. In fact, the only distinctions in community composition in uncultivated habitats were found between the Grassland and Savanna biomes. Therefore the second part of the hypothesis, proposing that the marginal vegetation will also have a unique set of species and functional traits compared to rangelands, is rejected.

The results provided evidence for positive relationships between low-growing (>2m) plant species and arthropod richness, diversity and abundance, both in maize fields and in uncultivated vegetation. The results also suggested that arthropod species composition is (either directly or indirectly) related to plant species composition, since different plant communities tended to be associated with different arthropod communities. However, it was evident that these relationships are complex and may not be directly linked. Also, not all the plant families that were considered for analysis (Asteraceae, Fabaceae and Poaceae) had similar effects. In this case, the results suggested that grasses (Poaceae) were especially important in supporting high levels of arthropods in maize agro-ecosystems. **The third hypothesis**, stating that a general positive relationship exists between overall plant and arthropod diversity and that the strength of these relationships will be dependent on specific plant families and arthropod guilds, is therefore supported.

One of the purposes of real-world observational datasets such as this is the generation of hypotheses which may then be tested in manipulative (experimental) studies on a local scale. Naturally, there are many more aspects regarding the plant and arthropod community dynamics of these agro-ecosystems that need to be investigated in future research. Some key questions that may be addressed include the following:

- What is the average distance from the maize fields at which plant and arthropod communities are negatively affected by maize-agriculture? Disturbance effects probably occur <30 m from the perimeter of the site of active cultivation and this will therefore require samples of field margin vegetation at the crop field-margin interface (0-30 m from the fields). This may be important to determine the optimal sizes of field margins, so that they can be of value for biodiversity conservation and planning for conservation agriculture.
- How do the patterns of plant and arthropod communities along the maize field-field margin gradient fluctuate over time? This work provides information on the plant and arthropod community patterns in one specific timeframe. However, these patterns may differ depending on the specific year, season or even time of day in question. To acquire a comprehensive knowledge on the community dynamics of non-crop biodiversity and to monitor priority species such as arthropod biocontrol agents, temporal studies are necessary.
- To what extent are plant and arthropod communities affected by specific characteristics such as management practices, field size, and field specific environmental factors? Since these factors 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 dryland crops. It may also be necessary to take into account other gradients (besides the agricultural disturbance intensity gradient) that may be present, such as slope, moisture and soil characteristics. This will require the collection of environmental data in the field and conducting manipulative studies in experimental setups.
- How do the results for field-measured plant functional traits compare to those derived from the literature? The phenotypic plasticity of plants allows for a single species to have several growth or life form strategies, depending on the environmental factors they are subjected to. Therefore, specific, real-world fluctuations in trait attribute abundances may therefore be obscured by trait data acquired from the literature (as could be the case for some species in this study).
- How are insect pollinator communities affected by agricultural disturbance intensity? While the arthropod samples in this study were taken using a relatively broad-range sampling technique, it may be useful to use a technique specifically designed to capture highly mobile pollinator insects, such as sticky traps or coloured bait traps. This could provide more accurate information on the abundance and diversity fluctuations of pollinating insects along the agricultural disturbance gradient.
- Which plant species are of particular importance (i.t.o. enhancing abundance and diversity) for arthropod predators in a grassland or savanna agro-ecosystem? This may be achieved by testing for correlations between pre-selected plant species (with particularly high pollen and or nectar production) and predator abundance. In this case, field-measured environmental factors must be included in the

analyses to separate the possible effects of plant species abundance and environmental fluctuations. Plant lists generated from this data could serve as a tool to compose seed mixtures that may then be sown in field margins where natural vegetation are no longer present.

In conclusion, the uncultivated, marginal vegetation associated with maize agro-ecosystems in South Africa were surprisingly rich in plant and associated arthropod diversity. This is contrary to the greatly held idea that agricultural systems are invariably poor in biodiversity. The patterns recorded at both regional and local scales across two different biomes indicate that crop field margins ≥ 30 m from the site of active cultivation cannot be overlooked as conservation sites for the continued persistence of species and functional diversity of non-crop plants and associated arthropods. These uncultivated habitats were also shown to house a high diversity of arthropod predators, many of which have the potential to suppress a variety of economically important pest species in maize fields. The fact that these high levels of biodiversity exist in a semi-natural setting without any attempts at artificial enhancement of the environment (e.g. sown wildflower mixes) is a very promising prospect for low-cost conservation of beneficial biodiversity in agricultural landscapes of South Africa.

APPENDIX A: Supplementary tables relating to chapter 3

Table A.1: Effect sizes of Hierarchical Linear Modelling (HLM) analysis for comparisons between distances from maize field in terms of mean plant richness and diversity index values. MZ1 and MZ2, maize field; MV1 and MV2, marginal vegetation (30-100 m); RA1 and RA2, rangeland (100-400 m). Significance codes: **, large effect at d ≥ 0.8; *, medium effect at d ≥ 0.5.

Distance comparison		Species richness	Margalef's species richness	Shannon-Wiener diversity	Simpson's diversity	Pielou's evenness
MZ1 with:	MZ2	0.126	0.099	0.107	0.040	0.114
	MV1	**2.028****	**1.63****	**2.605****	**2.210****	**1.861****
	MV2	**2.107****	**1.711****	**2.862****	**2.310****	**2.131****
	RA1	**2.181****	**1.900****	**2.876****	**2.430****	**2.139****
	RA2	**1.967****	**1.697****	**2.684****	**2.330****	**2.052****
MZ2 with:	MV1	**1.902****	**1.528****	**2.498****	**2.170****	**1.975****
	MV2	**1.980****	**1.613****	**2.755****	**2.270****	**2.245****
	RA1	**2.054****	**1.801****	**2.769****	**2.390****	**2.253****
	RA2	**1.841****	**1.598****	**2.577****	**2.290****	**2.166****
MV1 with:	MV2	0.079	0.084	0.257	0.100	0.270
	RA1	0.153	0.273	0.270	0.220	0.278
	RA2	0.061	0.070	0.078	0.120	0.191
MV2 with:	RA1	0.074	0.189	0.014	0.120	0.008
	RA2	0.140	0.014	0.179	0.020	0.079
RA1 with:	RA2	0.214	0.203	0.192	0.100	0.087

Table A.2: Effect sizes of Hierarchical Linear Modelling (HLM) analysis for plant diversity measures indicating significant interaction effects between biome and distance from maize field in terms of plant species richness and Margalef's species richness index values. MZ1 and MZ2, maize field; MV1 and MV2, marginal vegetation (30-100 m); RA1 and RA2, rangeland (100-400 m). Highlighted text indicates key differences between biomes. Significance codes: **, large effect at d ≥ 0.8; *, medium effect at d ≥ 0.5.

	Distance comparison		Species richness	Margalef's species richness
Grassland	MZ1 with:	MZ2	0.079	0.057
		MV1	**1.326****	**1.011****
		MV2	**1.902****	**1.523****
		RA1	**1.963****	**1.599****
		RA2	**1.474****	**1.128****
	MZ2 with:	MV1	**1.247****	**0.954****
		MV2	**1.823****	**1.466****
		RA1	**1.884****	**1.542****
		RA2	**1.396****	**1.071****
	MV1 with:	MV2	**0.576***	**0.512***
		RA1	**0.637***	**0.587***
		RA2	0.148	0.116
	MV2 with:	RA1	0.061	0.075
		RA2	0.427	0.396
	RA1 with:	RA2	0.488	0.471
Savanna	MZ1 with:	MZ2	0.174	0.141
		MV1	**2.730****	**2.243****
		MV2	**2.312****	**1.899****
		RA1	**2.399****	**2.202****
		RA2	**2.460****	**2.266****
	MZ2 with:	MV1	**2.556****	**2.102****
		MV2	**2.137****	**1.759****
		RA1	**2.224****	**2.061****
		RA2	**2.285****	**2.126****
	MV1 with:	MV2	0.419	0.344
		RA1	0.331	0.041
		RA2	0.270	0.023
	MV2 with:	RA1	0.087	0.302
		RA2	0.148	0.367
	RA1 with:	RA2	0.061	0.065

Table A.3: Effect sizes of Hierarchical Linear Modelling (HLM) analysis for plant richness and diversity indicating differences between grassland and savanna in terms of mean index values at similar distances from maize field. MZ1 and MZ2, maize field; MV1 and MV2, marginal vegetation (30-100 m); RA1 and RA2, rangeland (100-400 m). Significance codes: **, large effect at d ≥ 0.8; *, medium effect at d ≥ 0.5.

	Species richness	Margalef's species richness	Shannon-Wiener diversity	Simpson's diversity	Pielou's evenness
MZ1	0.477	0.378	**0.531***	0.042	0.435
MZ2	**0.573***	0.461	**0.793***	**0.647***	**0.543***
MV1	**1.881****	**1.609****	**1.273****	**0.678***	0.380
MV2	**0.887****	**0.754***	0.171	0.103	0.480
RA1	**0.913****	**0.981****	0.187	0.032	0.307
RA2	**1.462****	**1.517****	**0.772***	0.357	0.022

Table A.4: Effect sizes of Hierarchical Linear Modelling (HLM) analysis for comparisons between distances from maize field in terms of mean arthropod diversity index values. MZ1 and MZ2, maize field; MV1 and MV2, marginal vegetation (30-100 m); RA1 and RA2, rangeland (100-400 m). Significance codes: **, large effect at d ≥ 0.8; *, medium effect at d ≥ 0.5.

Distance comparison		Species richness	Margalef's species richness	Shannon-Wiener diversity	Simpson's diversity	Pielou's evenness
MZ1 with:	MZ2	0.008	0.017	0.041	0.155	0.140
	MV1	**0.623***	**0.727***	**0.918****	**0.699***	0.248
	MV2	**0.542***	**0.580***	0.462	0.189	0.126
	RA1	**0.537***	**0.588***	**0.731***	**0.552***	0.163
	RA2	**0.666***	**0.771***	**0.966****	**0.629***	0.237
MZ2 with:	MV1	**0.630***	**0.745***	**0.877****	**0.544***	0.107
	MV2	**0.549***	**0.598***	0.421	0.033	0.267
	RA1	**0.545***	**0.605***	**0.690***	0.397	0.022
	RA2	**0.673***	**0.788***	**0.925****	0.474	0.097
MV1 with:	MV2	0.081	0.147	0.456	**0.511***	0.374
	RA1	0.086	0.140	0.188	0.147	0.085
	RA2	0.043	0.044	0.048	0.070	0.010
MV2 with:	RA1	0.005	0.007	0.268	0.364	0.289
	RA2	0.124	0.191	0.504	0.441	0.364
RA1 with:	RA2	0.129	0.183	0.235	0.077	0.075

Table A.5: Effect sizes of Hierarchical Linear Modelling (HLM) analysis for arthropod richness and diversity indicating differences between grassland and savanna in terms of mean index values at similar distances from maize field. MZ1 and MZ2, maize field; MV1 and MV2, marginal vegetation (30-100 m); RA1 and RA2, rangeland (100-400 m). Significance codes: **, large effect at d ≥ 0.8; *, medium effect at d ≥ 0.5.

	Species richness	Margalef's species richness	Shannon-Wiener diversity	Simpson's diversity	Pielou's evenness
MZ1	0.155	0.130	0.169	0.168	0.229
MZ2	0.182	0.098	0.309	0.480	**0.529***
MV1	**0.696***	**0.513***	0.148	0.048	0.327
MV2	**0.633***	0.421	0.082	**0.656***	**0.886****
RA1	**0.635***	0.488	0.108	0.371	**0.624***
RA2	**0.641***	0.389	0.032	0.205	0.320

APPENDIX B: Supplementary tables relating to chapter 6

Table B.1: Effect sizes of Hierarchical Linear Modelling (HLM) analysis for comparisons between distances from maize field in terms of the relative abundances of plant functional types (PFTs). MZ1 and MZ2, maize field; MV1 and MV2, marginal vegetation (30-100 m); RA1 and RA2, rangeland (100-400 m). Significance codes: **, large effect at d ≥ 0.8; *, medium effect at d ≥ 0.5.

Distance comparison		PFT 2	PFT 3	PFT 4	PFT 5	PFT 6	PFT 7	PFT 8
MZ1 with:	MZ2	0.050	0.156	0.124	0.130	0.064	0.309	0.229
	FM1	**0.638***	**0.997****	0.217	0.229	0.038	0.197	0.452
	FM2	0.316	**0.652***	0.233	0.311	0.450	0.417	0.314
	RA1	0.341	0.374	0.069	0.043	**0.702***	0.427	0.416
	RA2	**0.764***	0.388	0.020	0.213	0.441	**0.641***	**0.510***
MZ2 with:	FM1	**0.687***	**0.841****	0.093	0.099	0.026	**0.506***	0.223
	FM2	0.365	0.496	0.109	0.181	0.385	**0.727***	0.086
	RA1	0.390	0.219	0.055	0.087	**0.637***	**0.736***	0.187
	RA2	**0.813****	0.232	0.144	0.083	0.377	**0.950****	0.281
FM1 with:	FM2	0.322	0.345	0.016	0.081	0.411	0.221	0.137
	RA1	0.297	**0.623***	0.148	0.186	**0.663***	0.230	0.036
	RA2	0.126	**0.609***	0.237	0.017	0.403	0.444	0.058
FM2 with:	RA1	0.025	0.278	0.164	0.268	0.252	0.009	0.101
	RA2	0.448	0.264	0.253	0.098	0.008	0.224	0.195
RA1 with:	RA2	0.423	0.013	0.089	0.169	0.260	0.214	0.094

Table B.2: Effect sizes of Hierarchical Linear Modelling (HLM) analysis for comparisons between grassland and savanna in terms of relative abundances of plant functional types (PFTs) at similar distances from maize field. MZ1 and MZ2, maize field; MV1 and MV2, marginal vegetation (30-100 m); RA1 and RA2, rangeland (100-400 m). Significance codes: **, large effect at d ≥ 0.8; *, medium effect at d ≥ 0.5.

Distance	PFT 2	PFT 3	PFT 4	PFT 5	PFT 6	PFT 7	PFT 8
MZ1	0.220	**0.760***	0.115	**1.450****	0.226	0.045	0.284
MZ2	0.095	**0.808****	0.015	**0.525***	0.078	0.317	**0.820****
MV1	**0.962****	0.464	**0.791***	0.401	0.155	0.332	**0.523***
MV2	0.447	0.221	**0.912****	0.404	0.388	0.352	0.459
RA1	**0.724***	0.023	0.187	0.097	0.250	0.125	0.212
RA2	**1.414****	0.166	0.059	0.226	0.341	0.140	0.153

Table B.3: Effect sizes of Hierarchical Linear Modelling (HLM) analysis for comparisons between distances from maize fields indicating interaction effects between biome and distance from maize field in terms of plant relative trait abundance. MZ1 and MZ2, maize field; MV1 and MV2, marginal vegetation (30-100 m); RA1 and RA2, rangeland (100-400 m). Highlighted text indicates key differences between biomes. Significance codes: **, large effect at d ≥ 0.8; *, medium effect at d ≥ 0.5.

	Distance comparison		Chamaephytes	Hemicryptophytes	Therophytes	Geophytes	Rosettes	Erect forbs	Creepers	Tussocks	N-fixing	Spinescent
Grassland	MZ1 with:	MZ2	0.380	0.075	0.168	0.121	0.061	0.120	0.497	0.336	0.130	0.051
		MV1	**0.817****	**3.712****	**2.612****	**1.779****	0.120	**0.506***	0.083	**0.542***	**0.829****	**0.583***
		MV2	**1.297****	**3.520****	**2.587****	**1.797****	0.240	**0.615***	0.281	**0.579***	0.435	**0.524***
		RA1	**1.162****	**3.519****	**2.524****	**1.768****	0.400	**0.719***	0.337	**0.638***	0.399	**0.529***
		RA2	**1.416****	**3.488****	**2.529****	**1.924****	0.077	**0.578***	0.183	**0.506***	**0.847****	**0.884****
	MZ2 with:	MV1	0.436	**3.787****	**2.445****	**1.900****	0.059	**0.626***	0.414	0.206	**0.959****	**0.635***
		MV2	**0.917****	**3.596****	**2.420****	**1.918****	0.300	**0.735***	0.217	0.243	**0.565***	**0.575***
		RA1	**0.781***	**3.594****	**2.356****	**1.888****	0.461	**0.838****	0.160	0.302	**0.528***	**0.580***
		RA2	**1.036****	**3.563****	**2.362****	**2.045****	0.138	**0.698***	0.315	0.170	**0.977****	**0.935****
	MV1 with:	MV2	0.481	0.191	0.025	0.018	0.359	0.109	0.197	0.037	0.394	0.060
		RA1	0.345	0.193	0.088	0.011	**0.520***	0.212	0.254	0.096	0.430	0.054
		RA2	**0.600***	0.224	0.083	0.145	0.197	0.072	0.099	0.036	0.018	0.301
	MV2 with:	RA1	0.135	0.001	0.063	0.030	0.160	0.103	0.057	0.059	0.036	0.006
		RA2	0.119	0.033	0.058	0.127	0.162	0.037	0.098	0.073	0.412	0.360
	RA1 with:	RA2	0.255	0.032	0.006	0.157	0.323	0.141	0.155	0.132	0.449	0.355
Savanna	MZ1 with:	MZ2	0.080	0.207	0.245	0.062	0.313	**0.554***	0.240	0.049	0.008	**0.721***
		MV1	**2.879****	**0.998****	**3.462****	**0.573***	0.397	**1.556****	**1.099****	0.066	**2.424****	**2.849****
		MV2	**2.955****	**0.945****	**3.279****	0.390	0.030	**1.547****	**1.225****	0.342	**1.712****	**1.749****
		RA1	**2.813****	**0.636***	**2.977****	0.455	0.031	**1.712****	**1.084****	0.268	**1.278****	**2.279****
		RA2	**2.509****	**0.808****	**2.920****	0.471	0.119	**1.790****	**0.610***	0.181	**1.200****	**1.968****
	MZ2 with:	MV1	**2.799****	**0.791***	**3.217****	**0.511***	**0.711***	**1.002****	**1.338****	0.017	**2.432****	**2.129****
		MV2	**2.875****	**0.739***	**3.034****	0.328	0.283	**0.993****	**1.464****	0.293	**1.719****	**1.028****
		RA1	**2.733****	0.429	**2.732****	0.393	0.344	**1.158****	**1.323****	0.219	**1.286****	**1.559****
		RA2	**2.429****	**0.601***	**2.675****	0.408	0.432	**1.236****	**0.850****	0.132	**1.208****	**1.248****
	MV1 with:	MV2	0.076	0.052	0.183	0.183	0.427	0.009	0.126	0.276	**0.712***	**1.101****
		RA1	0.066	0.362	0.485	0.118	0.366	0.156	0.015	0.202	**1.146****	**0.570***
		RA2	0.370	0.190	**0.542***	0.103	0.279	0.234	0.488	0.115	**1.224****	**0.881****
	MV2 with:	RA1	0.142	0.310	0.302	0.065	0.061	0.165	0.141	0.074	0.433	**0.531***
		RA2	0.446	0.137	0.359	0.081	0.149	0.243	**0.614***	0.161	**0.511***	0.220
	RA1 with:	RA2	0.304	0.172	0.057	0.016	0.088	0.078	0.473	0.087	0.078	0.311

Table B.4: Effect sizes of Hierarchical Linear Modelling (HLM) analysis for comparisons between grassland and savanna in terms of relative abundances of selected plant traits at similar distances from maize field. MZ1 and MZ2, maize field; MV1 and MV2, marginal vegetation (30-100 m); RA1 and RA2, rangeland (100-400 m). Significance codes: **, large effect at d ≥ 0.8; *, medium effect at d ≥ 0.5.

Distance	Chamaephytes	Hemicryptophytes	Therophytes	Geophytes	Rosette forbs	Erect forbs	Creepers	Tussocks	N-fixing ability	Spinescence
MZ1	0.231	0.219	**1.155****	**1.445****	0.161	**1.004****	0.384	**1.161****	0.212	0.081
MZ2	0.069	0.063	**1.077****	**1.628****	0.213	0.330	**1.121****	**1.448****	0.334	**0.853****
MV1	**2.293****	**2.933****	0.305	0.239	0.438	0.046	**0.631***	**1.637****	**1.807****	**2.347****
MV2	**1.889****	**2.794****	0.463	0.037	0.370	0.073	**0.560***	**1.398****	**1.489****	**1.306****
RA1	**1.882****	**3.102****	**0.701***	0.132	**0.592***	0.011	0.362	**1.531****	**1.092****	**1.831****
RA2	**1.323****	**2.899****	**0.764***	0.009	0.357	0.208	0.043	**1.486****	**0.565***	**1.165****

Table B.5: Effect sizes of Hierarchical Linear Modelling (HLM) analysis for comparisons between distances from maize fields indicating interaction effects between biome and distance from maize field in terms of plant functional diversity. MZ1 and MZ2, maize field; MV1 and MV2, marginal vegetation (30-100 m); RA1 and RA2, rangeland (100-400 m). Highlighted text indicates key differences between biomes. Significance codes: **, large effect at d ≥ 0.8; *, medium effect at d ≥ 0.5.

	Distance comparison		Trait richness	Margalef's richness	Pielou's evenness	Shannon diversity	Simpson's diversity
Grassland	MZ1 with:	MZ2	0.043	0.079	0.063	0.007	0.088
		MV1	**1.809****	**0.891****	**1.118****	**0.919****	**0.505***
		MV2	**2.197****	**1.263****	**1.168****	**1.218****	**0.702***
		RA1	**2.455****	**1.520****	**1.471****	**1.160****	**0.688***
		RA2	**2.369****	**1.389****	**1.232****	**1.313****	**0.844****
	MZ2 with:	MV1	**1.766****	**0.812****	**1.055****	**0.926****	**0.593***
		MV2	**2.154****	**1.183****	**1.105****	**1.225****	**0.790***
		RA1	**2.412****	**1.441****	**1.407****	**1.167****	**0.776***
		RA2	**2.326****	**1.310****	**1.169****	**1.320****	**0.932****
	MV1 with:	MV2	0.388	0.372	0.050	0.299	0.197
		RA1	**0.646***	**0.629***	0.352	0.242	0.183
		RA2	**0.560***	0.498	0.114	0.394	0.339
	MV2 with:	RA1	0.258	0.257	0.302	0.058	0.014
		RA2	0.172	0.126	0.064	0.095	0.142
	RA1 with:	RA2	0.086	0.131	0.238	0.152	0.157
Savanna	MZ1 with:	MZ2	**1.292****	**1.352****	**0.864****	**0.921****	**0.697***
		MV1	**5.126****	**3.477****	0.054	**5.451****	**4.679****
		MV2	**4.954****	**3.458****	**0.615***	**4.601****	**3.726****
		RA1	**4.954****	**3.350****	0.231	**5.009****	**4.076****
		RA2	**5.255****	**3.779****	0.433	**5.036****	**4.094****
	MZ2 with:	MV1	**3.834****	**2.125****	**0.918****	**4.530****	**3.982****
		MV2	**3.661****	**2.107****	0.249	**3.681****	**3.029****
		RA1	**3.661****	**1.998****	**0.633***	**4.089****	**3.379****
		RA2	**3.963****	**2.427****	0.431	**4.115****	**3.397****
	MV1 with:	MV2	0.172	0.018	**0.668***	**0.850****	**0.954****
		RA1	0.172	0.127	0.284	0.441	**0.603***
		RA2	0.129	0.302	0.487	0.415	**0.586***
	MV2 with:	RA1	0.000	0.109	0.384	0.408	0.350
		RA2	0.302	0.320	0.181	0.434	0.368
	RA1 with:	RA2	0.302	0.429	0.203	0.026	0.018

Table B.6: Effect sizes of Hierarchical Linear Modelling (HLM) analysis for comparisons between grassland and savanna in terms of plant functional diversity at similar distances from maize field. MZ1 and MZ2, maize field; MV1 and MV2, marginal vegetation (30-100 m); RA1 and RA2, rangeland (100-400 m). Significance codes: **, large effect at d ≥ 0.8; *, medium effect at d ≥ 0.5.

Distance	Trait richness	Margalef's richness	Pielou's evenness	Shannon diversity	Simpson's diversity
MZ1	0.345	0.300	**0.710***	0.064	0.218
MZ2	**0.905****	**0.973****	0.091	**0.992****	**1.004****
MV1	**2.972****	**2.286****	**1.882****	**4.596****	**4.393****
MV2	**2.412****	**1.896****	**1.264****	**3.447****	**3.242****
RA1	**2.154****	**1.530****	**1.950****	**3.913****	**3.607****
RA2	**2.541****	**2.090****	**1.509****	**3.787****	**3.468****

Table B.7a: Results for SIMPER analyses indicating comparisons between distance classes within biomes in terms of average abundance per plot, average dissimilarity, % contribution of each species to the average dissimilarity and cumulative % contribution for the ten most important plant traits responsible for NMDS groupings. M(G) = Maize field Grassland; M(S) = Maize field Savanna; MV(G) = marginal vegetation Grassland; MV(S) = marginal vegetation Savanna; R(G) = Rangeland Grassland; R(S) = Rangeland Savanna.

Groups M(S) & MV(S)	Abund. M(G)	Abund. MV(S)	Av. Diss.	Contrib.%	Cum.%
Internal animal transport	1.14	5.72	2.38	7.24	7.24
Chamaeophyte	0.89	5.40	2.35	7.13	14.37
Hemicryptophyte	2.78	6.43	2.07	6.28	20.65
Non-clonal	5.36	9.03	1.93	5.87	26.52
Biotic pollination vector	5.43	9.07	1.90	5.77	32.29
Spinescence absent	7.06	10.57	1.86	5.64	37.93
N-fixing ability absent	7.07	10.56	1.85	5.61	43.54
Spinescence present	0.58	4.11	1.81	5.51	49.05
N-fixing ability present	0.71	4.06	1.75	5.31	54.36
Clonal belowground	1.88	4.89	1.60	4.87	59.22
Average dissimilarity = 32.94					

Groups M(S) & R(S)	Abund. M(S)	Abund. R(S)	Av. Diss.	Contrib.%	Cum.%
Internal animal transport	1.14	5.47	2.25	7.08	7.08
Chamaeophyte	0.89	5.19	2.23	7.02	14.09
N-fixing ability absent	7.07	10.77	1.95	6.13	20.22
Hemicryptophyte	2.78	6.00	1.87	5.87	26.09
Spinescence absent	7.06	10.56	1.84	5.80	31.89
Biotic pollination vector	5.43	8.87	1.79	5.63	37.52
Spinescence present	0.58	4.00	1.76	5.53	43.05
Non-clonal	5.36	8.60	1.71	5.38	48.43
Tussock	4.01	6.72	1.46	4.59	53.02
Abiotic pollination vector	4.33	6.99	1.43	4.49	57.51
Average dissimilarity = 31.78					

Groups MV(S) & R(S)	Abund. MV(S)	Abund. R(S)	Av. Diss.	Contrib.%	Cum.%
Therophyte	3.56	4.34	0.88	6.77	6.77
Clonal aboveground	4.17	5.3	0.88	6.75	13.52
Unspecified dispersal mode	3.66	3.55	0.83	6.35	19.87
Internal animal transport	5.72	5.47	0.81	6.26	26.12
Hemicryptophyte	6.43	6.00	0.77	5.92	32.04
N-fixing ability present	4.06	3.27	0.69	5.34	37.38
External animal transport	3.09	3.46	0.67	5.16	42.54
Wind dispersal	6.31	6.17	0.67	5.14	47.68
Self-dispersal	4.75	5.07	0.61	4.69	52.37
Clonal above & belowground	1.11	1.12	0.60	4.62	56.99
Average dissimilarity = 13.00					

Table B.7a cont.

Groups M(G) & MV(G)	Abund. M(G)	Abund. MV(G)	Av. Diss.	Contrib.%	Cum.%
Hemicryptophyte	2.48	8.78	3.62	13.09	13.09
Therophyte	4.79	1.86	1.77	6.40	19.49
Clonal belowground	4.24	6.67	1.48	5.34	24.82
Spinescence absent	7.24	9.58	1.37	4.95	29.78
Chamaeophyte	0.40	2.57	1.36	4.92	34.7
N-fixing ability absent	7.22	9.53	1.35	4.87	39.56
Tussock	5.04	7.17	1.25	4.53	44.09
Wind dispersal	5.53	7.57	1.25	4.51	48.6
Geophyte	3.38	1.76	1.24	4.50	53.09
Abiotic pollination vector	5.31	7.32	1.24	4.48	57.57
Average dissimilarity = 27.65					
Groups M(G) & R(G)	Abund. M(G)	Abund. R(G)	Av. Diss.	Contrib.%	Cum.%
Hemicryptophyte	2.48	8.76	3.57	12.52	12.52
Therophyte	4.79	2.15	1.61	5.64	18.16
Chamaeophyte	0.40	2.94	1.53	5.36	23.52
N-fixing ability absent	7.22	9.62	1.38	4.85	28.37
Spinescence absent	7.24	9.62	1.38	4.83	33.20
Unspecified dispersal mode	1.33	3.40	1.37	4.80	38.00
Clonal belowground	4.24	6.13	1.35	4.74	42.74
Geophyte	3.38	1.48	1.33	4.66	47.40
Non-clonal	4.72	6.90	1.31	4.60	52.00
Tussock	5.04	7.24	1.28	4.48	56.48
Average dissimilarity = 28.48					
Groups MV(G) & R(G)	Abund. MV(G)	Abund. R(G)	Av. Diss.	Contrib.%	Cum.%
Therophyte	1.86	2.15	0.70	6.04	6.04
External animal transport	2.27	2.64	0.70	6.00	12.04
Spinescence present	1.38	1.67	0.68	5.84	17.88
Chamaeophyte	2.57	2.94	0.66	5.64	23.52
Creeper	3.33	3.24	0.65	5.61	29.12
Unspecified dispersal mode	3.12	3.40	0.65	5.59	34.71
Clonal above & belowground	1.41	1.39	0.65	5.58	40.29
N-fixing ability present	1.66	1.91	0.64	5.46	45.75
Clonal aboveground	1.82	2.11	0.62	5.34	51.09
Clonal belowground	6.67	6.13	0.60	5.12	56.21
Average dissimilarity = 11.65					

Table B.7b: Results for SIMPER analyses indicating comparisons between biomes within distance classes in terms of average dissimilarity, contribution of each species to the average dissimilarity, cumulative percent contribution and average abundance per plot for the ten most important plant traits responsible for NMDS groupings. M(G) = Maize field Grassland; M(S) = Maize field Savanna; MV(G) = marginal vegetation Grassland; MV(S) = marginal vegetation Savanna; R(G) = Rangeland Grassland; R(S) = Rangeland Savanna.

Groups M(S) & M(G)	Abund. M(S)	Abund. M(G)	Av. Diss.	Contrib.%	Cum.%
Clonal belowground	1.88	4.24	2.03	7.65	7.65
Geophyte	0.95	3.38	1.91	7.19	14.84
Hemicryptophyte	2.78	2.48	1.68	6.33	21.17
Clonal aboveground	3.40	1.73	1.49	5.59	26.76
Creeper	3.03	1.98	1.42	5.34	32.1
Self-dispersal	3.89	2.76	1.38	5.21	37.31
Therophyte	5.90	4.79	1.33	5.01	42.32
Abiotic pollination vector	4.33	5.31	1.32	4.95	47.27
Tussock	4.01	5.04	1.28	4.82	52.1
Wind dispersal	4.34	5.53	1.27	4.77	56.86
Average dissimilarity = 26.59					
Groups MV(S) & MV(G)	Abund. MV(S)	Abund. MV(G)	Av. Diss.	Contrib.%	Cum.%
Internal animal transport	5.72	0.43	2.34	12.12	12.12
Chamaeophyte	5.40	2.57	1.28	6.63	18.74
Spinescence present	4.11	1.38	1.25	6.48	25.23
Biotic pollination vector	9.07	6.43	1.17	6.08	31.31
N-fixing ability present	4.06	1.66	1.17	6.06	37.37
Non-clonal	9.03	6.48	1.14	5.93	43.29
Clonal aboveground	4.17	1.82	1.14	5.88	49.18
Hemicryptophyte	6.43	8.78	1.06	5.48	54.66
Therophyte	3.56	1.86	0.94	4.88	59.54
Unspecified dispersal mode	3.66	3.12	0.83	4.28	63.82
Average dissimilarity = 19.31					
Groups R(S) & R(G)	Abund. R(S)	Abund. R(G)	Av. Diss.	Contrib.%	Cum.%
Internal animal transport	5.47	0.59	2.16	11.41	11.41
Clonal aboveground	5.30	2.11	1.45	7.63	19.04
Hemicryptophyte	6.00	8.76	1.25	6.58	25.62
Therophyte	4.34	2.15	1.15	6.07	31.69
Spinescence present	4.00	1.67	1.11	5.83	37.52
Biotic pollination vector	8.87	6.43	1.09	5.74	43.26
Chamaeophyte	5.19	2.94	1.02	5.36	48.62
Clonal belowground	4.36	6.13	0.93	4.89	53.51
External animal transport	3.46	2.64	0.82	4.34	57.85
Non-clonal	8.60	6.90	0.78	4.13	61.98
Average dissimilarity = 18.96					

Table B.8: List of the plant species present in 10% or more of the plots in at least one of the distance classes (maize field, marginal vegetation or rangeland), with corresponding plant functional type (PFT) as determined by cluster analysis as well as their functional traits.

PFT	Species	Life form	Growth form	Clonality	Dispersal mode	Pollination vector	N-fixing ability	Leaf periodicity	Spinescence
1	*Acalypha glabrata*	Phanerophyte	Single-stemmed woody	Non-clonal	Self-dispersal	Biotic	Absent	Evergreen	Absent
1	*Afzelia quanzensis*	Phanerophyte	Single-stemmed woody	Non-clonal	Internal animal transport	Biotic	Absent	Deciduous	Absent
1	*Artabotrys brachypetalus*	Phanerophyte	Multi-stemmed woody	Non-clonal	Internal animal transport	Biotic	Absent	Deciduous	Absent
1	*Asparagus cooperi*	Phanerophyte	Multi-stemmed woody	Non-clonal	Internal animal transport	Biotic	Absent	Deciduous	Present
1	*Bauhinia galpinii*	Phanerophyte	Multi-stemmed woody	Clonal belowground	Internal animal transport	Biotic	Absent	Evergreen	Absent
1	*Cissus rotundifolia*	Phanerophyte	Multi-stemmed woody	Clonal aboveground	Internal animal transport	Biotic	Absent	Evergreen	Absent
1	*Coddia rudis*	Phanerophyte	Multi-stemmed woody	Non-clonal	Internal animal transport	Biotic	Absent	Deciduous	Absent
1	*Dichrostachys cinerea*	Phanerophyte	Multi-stemmed woody	Non-clonal	Internal animal transport	Biotic	Present	Deciduous	Present
1	*Diospyros lycioides*	Phanerophyte	Multi-stemmed woody	Clonal belowground	Internal animal transport	Biotic	Absent	Deciduous	Absent
1	*Ehretia amoena*	Phanerophyte	Single-stemmed woody	Non-clonal	Internal animal transport	Biotic	Absent	Evergreen	Absent
1	*Lycium cinereum*	Phanerophyte	Multi-stemmed woody	Non-clonal	Internal animal transport	Biotic	Absent	Deciduous	Present
1	*Ochna inermis*	Phanerophyte	Single-stemmed woody	Non-clonal	Internal animal transport	Biotic	Absent	Deciduous	Absent
1	*Parinari curatellifolia*	Phanerophyte	Single-stemmed woody	Non-clonal	Internal animal transport	Biotic	Absent	Evergreen	Absent
1	*Peltophorum africanum*	Phanerophyte	Single-stemmed woody	Non-clonal	Wind dispersal	Biotic	Present	Deciduous	Absent
1	*Phyllanthus reticulatus*	Phanerophyte	Multi-stemmed woody	Non-clonal	Internal animal transport	Biotic	Absent	Deciduous	Absent
1	*Sarcostemma viminale*	Phanerophyte	Multi-stemmed woody	Non-clonal	Wind dispersal	Biotic	Absent	Evergreen	Absent
1	*Senna petersiana*	Phanerophyte	Single-stemmed woody	Non-clonal	Wind dispersal	Biotic	Present	Deciduous	Absent
1	*Tabernaemontana elegans*	Phanerophyte	Single-stemmed woody	Non-clonal	Internal animal transport	Biotic	Absent	Deciduous	Absent
1	*Vachellia gerrardii*	Phanerophyte	Single-stemmed woody	Non-clonal	Internal animal transport	Biotic	Present	Deciduous	Present
1	*Vachellia karroo*	Phanerophyte	Single-stemmed woody	Non-clonal	Internal animal transport	Biotic	Present	Deciduous	Present
1	*Vachellia nilotica*	Phanerophyte	Single-stemmed woody	Non-clonal	Internal animal transport	Biotic	Present	Evergreen	Present
1	*Vachellia tortilis*	Phanerophyte	Single-stemmed woody	Non-clonal	Internal animal transport	Biotic	Present	Evergreen	Present
1	*Ziziphus mucronata*	Phanerophyte	Single-stemmed woody	Non-clonal	Internal animal transport	Biotic	Absent	Deciduous	Present
2	*Argyrolobium pauciflorum*	Hemicryptophyte	Erect forb	Non-clonal	Wind dispersal	Biotic	Present	N/A	Absent
2	*Crotalaria sphaerocarpa*	Therophyte	Erect forb	Non-clonal	Self-dispersal	Biotic	Present	N/A	Absent
2	*Indigofera schimperi*	Chamaeophyte	Erect forb	Non-clonal	Self-dispersal	Biotic	Present	N/A	Absent
2	*Lotononis eriantha*	Hemicryptophyte	Creeper	Clonal aboveground	Self-dispersal	Biotic	Present	N/A	Absent

Table B.8 cont.

PFT	Species	Life form	Growth form	Clonality	Dispersal mode	Pollination vector	N-fixing ability	Leaf periodicity	Spinescence
2	*Rhynchosia totta*	Hemicryptophyte	Creeper	Clonal belowground	Self-dispersal	Biotic	Present	N/A	Absent
2	*Tephrosia capensis*	Hemicryptophyte	Erect forb	Non-clonal	Wind dispersal	Biotic	Present	N/A	Absent
3	*Abildgaardia ovata*	Hemicryptophyte	Tussock	Clonal belowground	Wind dispersal	Abiotic	Absent	N/A	Absent
3	*Brachiaria serrata*	Hemicryptophyte	Tussock	Clonal belowground	Wind dispersal	Abiotic	Absent	N/A	Absent
3	*Cyperus albostriatus*	Hemicryptophyte	Tussock	Clonal belowground	Wind dispersal	Abiotic	Absent	N/A	Absent
3	*Cyperus esculentus*	Geophyte	Tussock	Clonal belowground	Wind dispersal	Abiotic	Absent	N/A	Absent
3	*Cyperus rotundus*	Hemicryptophyte	Tussock	Clonal belowground	Wind dispersal	Abiotic	Absent	N/A	Absent
3	*Digitaria eriantha*	Hemicryptophyte	Tussock	Clonal above & belowground	Wind dispersal	Abiotic	Absent	N/A	Absent
3	*Eragrostis lehmanniana*	Hemicryptophyte	Tussock	Clonal belowground	Unspecified	Abiotic	Absent	N/A	Absent
3	*Heteropogon contortus*	Hemicryptophyte	Tussock	Clonal belowground	External animal transport	Abiotic	Absent	N/A	Absent
3	*Hyparrhenia filipendula*	Hemicryptophyte	Tussock	Clonal belowground	Wind dispersal	Abiotic	Absent	N/A	Absent
3	*Hyparrhenia hirta*	Hemicryptophyte	Tussock	Clonal belowground	Wind dispersal	Abiotic	Absent	N/A	Absent
3	*Kyllinga erecta*	Hemicryptophyte	Tussock	Clonal belowground	Wind dispersal	Abiotic	Absent	N/A	Absent
3	*Panicum coloratum*	Hemicryptophyte	Tussock	Clonal belowground	Unspecified	Abiotic	Absent	N/A	Absent
3	*Panicum maximum*	Hemicryptophyte	Tussock	Clonal aboveground	Unspecified	Abiotic	Absent	N/A	Absent
3	*Panicum schinzii*	Therophyte	Tussock	Clonal aboveground	Unspecified	Abiotic	Absent	N/A	Absent
3	*Setaria nigrirostris*	Hemicryptophyte	Tussock	Clonal belowground	Wind dispersal	Abiotic	Absent	N/A	Absent
3	*Setaria sphacelata*	Hemicryptophyte	Tussock	Clonal belowground	Wind dispersal	Abiotic	Absent	N/A	Absent
3	*Sporobolus africanus*	Hemicryptophyte	Tussock	Clonal belowground	Wind dispersal	Abiotic	Absent	N/A	Absent
3	*Sporobolus fimbriatus*	Hemicryptophyte	Tussock	Clonal belowground	Wind dispersal	Abiotic	Absent	N/A	Absent
3	*Themeda triandra*	Hemicryptophyte	Tussock	Clonal belowground	Wind dispersal	Abiotic	Absent	N/A	Absent
3	*Trachypogon spicatus*	Hemicryptophyte	Tussock	Clonal belowground	Wind dispersal	Abiotic	Absent	N/A	Absent
3	*Urochloa mosambicensis*	Hemicryptophyte	Tussock	Clonal aboveground	Wind dispersal	Abiotic	Absent	N/A	Absent
4	*Acanthospermum hispidum*	Therophyte	Creeper	Clonal aboveground	External animal transport	Biotic	Absent	N/A	Absent
4	*Barleria elegans*	Chamaeophyte	Erect forb	Clonal aboveground	Self-dispersal	Biotic	Absent	N/A	Absent
4	*Centella asiatica*	Hemicryptophyte	Creeper	Clonal above & belowground	Wind dispersal	Biotic	Absent	N/A	Absent
4	*Centella glabrata*	Hemicryptophyte	Creeper	Clonal aboveground	Self-dispersal	Biotic	Absent	N/A	Absent

Table B.8 cont.

PFT	Species	Life form	Growth form	Clonality	Dispersal mode	Pollination vector	N-fixing ability	Leaf periodicity	Spinescence
4	*Chenopodium carinatum*	Therophyte	Creeper	Clonal aboveground	Self-dispersal	Biotic	Absent	N/A	Absent
4	*Commelina africana*	Hemicryptophyte	Erect forb	Clonal aboveground	Self-dispersal	Biotic	Absent	N/A	Absent
4	*Commelina benghalensis*	Therophyte	Creeper	Clonal aboveground	Self-dispersal	Biotic	Absent	N/A	Absent
4	*Conyza podocephala*	Hemicryptophyte	Creeper	Clonal aboveground	Wind dispersal	Biotic	Absent	N/A	Absent
4	*Corchorus trilocularis*	Hemicryptophyte	Erect forb	Clonal aboveground	Self-dispersal	Biotic	Absent	N/A	Absent
4	*Cynodon dactylon*	Hemicryptophyte	Creeper	Clonal above & belowground	Self-dispersal	Abiotic	Absent	N/A	Absent
4	*Cynodon hirsutus*	Hemicryptophyte	Creeper	Clonal aboveground	Self-dispersal	Abiotic	Absent	N/A	Absent
4	*Euphorbia inaequilatera*	Hemicryptophyte	Creeper	Clonal aboveground	Self-dispersal	Biotic	Absent	N/A	Absent
4	*Galenia pubescens*	Hemicryptophyte	Creeper	Clonal aboveground	Self-dispersal	Biotic	Absent	N/A	Absent
4	*Geranium multisectum*	Hemicryptophyte	Erect forb	Clonal aboveground	Self-dispersal	Biotic	Absent	N/A	Absent
4	*Helichrysum rugulosum*	Hemicryptophyte	Erect forb	Clonal belowground	Wind dispersal	Biotic	Absent	N/A	Absent
4	*Hermannia depressa*	Hemicryptophyte	Creeper	Clonal above & belowground	Self-dispersal	Biotic	Absent	N/A	Absent
4	*Hermannia transvaalensis*	Hemicryptophyte	Creeper	Clonal belowground	Self-dispersal	Biotic	Absent	N/A	Absent
4	*Ipomoea purpurea*	Therophyte	Creeper	Clonal aboveground	Wind dispersal	Biotic	Absent	N/A	Absent
4	*Ipomoea sinensis*	Therophyte	Creeper	Clonal aboveground	Wind dispersal	Biotic	Absent	N/A	Absent
4	*Monopsis decipiens*	Hemicryptophyte	Erect forb	Clonal aboveground	Self-dispersal	Biotic	Absent	N/A	Absent
4	*Phyllanthus incurvus*	Hemicryptophyte	Erect forb	Clonal belowground	Internal animal transport	Biotic	Absent	N/A	Absent
4	*Portulaca oleracea*	Therophyte	Creeper	Clonal aboveground	Self-dispersal	Biotic	Absent	N/A	Absent
4	*Ruellia cordata*	Hemicryptophyte	Erect forb	Clonal above & belowground	Self-dispersal	Biotic	Absent	N/A	Absent
4	*Senecio ruwenzoriensis*	Hemicryptophyte	Rosette forb	Clonal belowground	Wind dispersal	Biotic	Absent	N/A	Absent
4	*Tribulus terrestris*	Therophyte	Creeper	Clonal aboveground	External animal transport	Biotic	Absent	N/A	Absent
4	*Vernonia natalensis*	Hemicryptophyte	Erect forb	Clonal belowground	Wind dispersal	Biotic	Absent	N/A	Absent
5	*Cheilanthes involuta*	Geophyte	Rosette forb	Clonal belowground	Self-dispersal	Abiotic	Absent	N/A	Absent
5	*Hypoxis rigidula*	Geophyte	Rosette forb	Clonal belowground	Self-dispersal	Biotic	Absent	N/A	Absent
5	*Ipomoea crassipes*	Geophyte	Creeper	Clonal belowground	Self-dispersal	Biotic	Absent	N/A	Absent
5	*Ledebouria ovatifolia*	Geophyte	Rosette forb	Clonal belowground	Self-dispersal	Biotic	Absent	N/A	Absent
5	*Ledebouria revoluta*	Geophyte	Rosette forb	Clonal belowground	Self-dispersal	Biotic	Absent	N/A	Absent

Table B.8 cont.

PFT	Species	Life form	Growth form	Clonality	Dispersal mode	Pollination vector	N-fixing ability	Leaf periodicity	Spinescence
5	*Oxalis corniculata*	Therophyte	Rosette forb	Clonal aboveground	Self-dispersal	Biotic	Absent	N/A	Absent
5	*Oxalis depressa*	Geophyte	Rosette forb	Clonal belowground	Self-dispersal	Biotic	Absent	N/A	Absent
5	*Oxalis latifolia*	Geophyte	Rosette forb	Clonal belowground	Self-dispersal	Biotic	Absent	N/A	Absent
5	*Oxalis obliquifolia*	Geophyte	Rosette forb	Clonal belowground	Self-dispersal	Biotic	Absent	N/A	Absent
5	*Sansevieria hyacinthoides*	Geophyte	Erect forb	Clonal belowground	Self-dispersal	Biotic	Absent	N/A	Absent
6	*Aristida adscensionis*	Therophyte	Tussock	Non-clonal	External animal transport	Abiotic	Absent	N/A	Absent
6	*Aristida congesta*	Therophyte	Tussock	Non-clonal	External animal transport	Abiotic	Absent	N/A	Absent
6	*Cenchrus ciliaris*	Hemicryptophyte	Tussock	Non-clonal	Wind dispersal	Abiotic	Absent	N/A	Absent
6	*Chloris virgata*	Therophyte	Tussock	Non-clonal	Wind dispersal	Abiotic	Absent	N/A	Absent
6	*Cymbopogon caesius*	Hemicryptophyte	Tussock	Non-clonal	Wind dispersal	Abiotic	Absent	N/A	Absent
6	*Dichanthium annulatum*	Hemicryptophyte	Tussock	Non-clonal	Wind dispersal	Abiotic	Absent	N/A	Absent
6	*Digitaria sanguinalis*	Therophyte	Tussock	Non-clonal	Wind dispersal	Abiotic	Absent	N/A	Absent
6	*Digitaria ternata*	Therophyte	Tussock	Non-clonal	Wind dispersal	Abiotic	Absent	N/A	Absent
6	*Eleusine coracana*	Therophyte	Tussock	Non-clonal	Unspecified	Abiotic	Absent	N/A	Absent
6	*Elionurus muticus*	Hemicryptophyte	Tussock	Non-clonal	Wind dispersal	Abiotic	Absent	N/A	Absent
6	*Enneapogon desvauxii*	Therophyte	Tussock	Non-clonal	Wind dispersal	Abiotic	Absent	N/A	Absent
6	*Eragrostis chloromelas*	Hemicryptophyte	Tussock	Non-clonal	Unspecified	Abiotic	Absent	N/A	Absent
6	*Eragrostis curvula*	Hemicryptophyte	Tussock	Non-clonal	Unspecified	Abiotic	Absent	N/A	Absent
6	*Eragrostis obtusa*	Hemicryptophyte	Tussock	Non-clonal	Unspecified	Abiotic	Absent	N/A	Absent
6	*Eragrostis plana*	Hemicryptophyte	Tussock	Non-clonal	Unspecified	Abiotic	Absent	N/A	Absent
6	*Eragrostis pseud-obtusa*	Hemicryptophyte	Tussock	Non-clonal	Unspecified	Abiotic	Absent	N/A	Absent
6	*Eragrostis racemosa*	Hemicryptophyte	Tussock	Non-clonal	Unspecified	Abiotic	Absent	N/A	Absent
6	*Eragrostis superba*	Hemicryptophyte	Tussock	Non-clonal	Wind dispersal	Abiotic	Absent	N/A	Absent
6	*Melinis repens*	Therophyte	Tussock	Non-clonal	Wind dispersal	Abiotic	Absent	N/A	Absent
6	*Microchloa kunthii*	Hemicryptophyte	Tussock	Non-clonal	Wind dispersal	Abiotic	Absent	N/A	Absent
6	*Setaria verticillata*	Therophyte	Tussock	Non-clonal	External animal transport	Abiotic	Absent	N/A	Absent
6	*Sorghum bicolor*	Therophyte	Tussock	Non-clonal	Unspecified	Abiotic	Absent	N/A	Absent

Table B.8 cont.

PFT	Species	Life form	Growth form	Clonality	Dispersal mode	Pollination vector	N-fixing ability	Leaf periodicity	Spinescence
6	*Tragus berteronianus*	Therophyte	Tussock	Non-clonal	External animal transport	Abiotic	Absent	N/A	Absent
6	*Tristachya leucothrix*	Hemicryptophyte	Tussock	Non-clonal	Wind dispersal	Abiotic	Absent	N/A	Absent
6	*Urochloa panicoides*	Therophyte	Tussock	Non-clonal	Unspecified	Abiotic	Absent	N/A	Absent
7	*Abutilon mauritianum*	Chamaeophyte	Erect forb	Non-clonal	Wind dispersal	Biotic	Absent	N/A	Absent
7	*Achyranthes aspera*	Chamaeophyte	Creeper	Non-clonal	External animal transport	Biotic	Absent	N/A	Absent
7	*Ageratum conyzoides*	Therophyte	Erect forb	Non-clonal	External animal transport	Biotic	Absent	N/A	Absent
7	*Amaranthus hybridus*	Therophyte	Erect forb	Non-clonal	Internal animal transport	Biotic	Absent	N/A	Absent
7	*Amaranthus viridis*	Therophyte	Erect forb	Non-clonal	Internal animal transport	Biotic	Absent	N/A	Absent
7	*Anthospermum rigidum*	Chamaeophyte	Erect forb	Non-clonal	Self-dispersal	Biotic	Absent	N/A	Absent
7	*Aster squamatus*	Hemicryptophyte	Erect forb	Non-clonal	Wind dispersal	Biotic	Absent	N/A	Absent
7	*Bidens pilosa*	Therophyte	Erect forb	Non-clonal	External animal transport	Biotic	Absent	N/A	Absent
7	*Cleome monophylla*	Therophyte	Erect forb	Non-clonal	Wind dispersal	Biotic	Absent	N/A	Absent
7	*Conyza bonariensis*	Therophyte	Erect forb	Non-clonal	Wind dispersal	Biotic	Absent	N/A	Absent
7	*Crabbea acaulis*	Hemicryptophyte	Rosette forb	Non-clonal	External animal transport	Biotic	Absent	N/A	Absent
7	*Datura stramonium*	Therophyte	Erect forb	Non-clonal	External animal transport	Biotic	Absent	N/A	Absent
7	*Euphorbia heterophylla*	Therophyte	Erect forb	Non-clonal	Self-dispersal	Biotic	Absent	N/A	Absent
7	*Felicia muricata*	Chamaeophyte	Erect forb	Non-clonal	Wind dispersal	Biotic	Absent	N/A	Absent
7	*Gerbera piloselloides*	Hemicryptophyte	Rosette forb	Non-clonal	Wind dispersal	Biotic	Absent	N/A	Absent
7	*Helichrysum nudifolium*	Hemicryptophyte	Erect forb	Non-clonal	Wind dispersal	Biotic	Absent	N/A	Absent
7	*Hermannia parviflora*	Hemicryptophyte	Erect forb	Non-clonal	Self-dispersal	Biotic	Absent	N/A	Absent
7	*Hibiscus trionum*	Therophyte	Erect forb	Non-clonal	Wind dispersal	Biotic	Absent	N/A	Absent
7	*Justicia flava*	Chamaeophyte	Erect forb	Non-clonal	Self-dispersal	Biotic	Absent	N/A	Absent
7	*Kyphocarpa angustifolia*	Therophyte	Erect forb	Non-clonal	Wind dispersal	Biotic	Absent	N/A	Absent
7	*Lactuca inermis*	Hemicryptophyte	Rosette forb	Non-clonal	Wind dispersal	Biotic	Absent	N/A	Absent
7	*Lantana rugosa*	Chamaeophyte	Erect forb	Non-clonal	Internal animal transport	Biotic	Absent	N/A	Absent
7	*Lobelia flaccida*	Therophyte	Erect forb	Non-clonal	Self-dispersal	Biotic	Absent	N/A	Absent
7	*Melhania forbesii*	Chamaeophyte	Erect forb	Non-clonal	Wind dispersal	Biotic	Absent	N/A	Absent

Table B.8 cont.

PFT	Species	Life form	Growth form	Clonality	Dispersal mode	Pollination vector	N-fixing ability	Leaf periodicity	Spinescence
7	*Parthenium hysterophorus*	Therophyte	Erect forb	Non-clonal	Self-dispersal	Biotic	Absent	N/A	Absent
7	*Pentzia incana*	Chamaeophyte	Erect forb	Non-clonal	Wind dispersal	Biotic	Absent	N/A	Absent
7	*Pupalia lappacea*	Therophyte	Erect forb	Non-clonal	External animal transport	Biotic	Absent	N/A	Absent
7	*Richardia brasiliensis*	Hemicryptophyte	Creeper	Non-clonal	Self-dispersal	Biotic	Absent	N/A	Absent
7	*Schkuhria pinnata*	Therophyte	Erect forb	Non-clonal	Wind dispersal	Biotic	Absent	N/A	Absent
7	*Selago densiflora*	Chamaeophyte	Erect forb	Non-clonal	Self-dispersal	Biotic	Absent	N/A	Absent
7	*Sida alba*	Therophyte	Erect forb	Non-clonal	Self-dispersal	Biotic	Absent	N/A	Absent
7	*Sida rhombifolia*	Therophyte	Erect forb	Non-clonal	Self-dispersal	Biotic	Absent	N/A	Absent
7	*Solanum nigrum*	Therophyte	Erect forb	Non-clonal	Internal animal transport	Biotic	Absent	N/A	Absent
7	*Sonchus nanus*	Hemicryptophyte	Rosette forb	Non-clonal	Wind dispersal	Biotic	Absent	N/A	Absent
7	*Sonchus oleraceus*	Therophyte	Erect forb	Non-clonal	Wind dispersal	Biotic	Absent	N/A	Absent
7	*Tagetes minuta*	Therophyte	Erect forb	Non-clonal	Wind dispersal	Biotic	Absent	N/A	Absent
7	*Wahlenbergia stellarioides*	Therophyte	Erect forb	Non-clonal	Self-dispersal	Biotic	Absent	N/A	Absent
7	*Xanthium strumarium*	Therophyte	Erect forb	Non-clonal	External animal transport	Biotic	Absent	N/A	Absent
8	*Argemone ochroleuca*	Therophyte	Erect forb	Non-clonal	External animal transport	Biotic	Absent	N/A	Present
8	*Berkheya pinnatifida*	Hemicryptophyte	Erect forb	Non-clonal	External animal transport	Biotic	Absent	N/A	Present
8	*Berkheya setifera*	Hemicryptophyte	Erect forb	Non-clonal	Wind dispersal	Biotic	Absent	N/A	Present
8	*Blepharis integrifolia*	Hemicryptophyte	Creeper	Non-clonal	External animal transport	Biotic	Absent	N/A	Present
8	*Mestoklema arboriforme*	Chamaeophyte	Erect forb	Clonal belowground	Wind dispersal	Biotic	Absent	N/A	Present
8	*Solanum panduriforme*	Hemicryptophyte	Erect forb	Clonal belowground	Wind dispersal	Biotic	Absent	N/A	Present

APPENDIX C: Supplementary tables relating to chapter 7

Table C.1: List of the spider species recorded at all sampling sites with corresponding functional traits associated with their hunting behaviour, hunting technique and primary hunting activity period.

Family	Species	Lifestyle	Hunting technique	Activity
Araneidae	*Hypsosinga lithyphantoides* Caporiacco, 1947	Web-dwelling	Orb-web builder	Nocturnal
Araneidae	*Hypsosinga* sp. 3	Web-dwelling	Orb-web builder	Nocturnal
Araneidae	*Hypsosinga* sp.1	Web-dwelling	Orb-web builder	Nocturnal
Araneidae	*Larinia bifida* Tullgren, 1911	Web-dwelling	Orb-web builder	Nocturnal
Araneidae	*Larinia natalensis* (Grasshoff, 1971)	Web-dwelling	Orb-web builder	Nocturnal
Araneidae	*Larinia* sp.1	Web-dwelling	Orb-web builder	Nocturnal
Araneidae	*Neoscona moreli* (Vinson, 1863)	Web-dwelling	Orb-web builder	Nocturnal
Araneidae	*Neoscona subfusca* (C.L.Koch, 1837)	Web-dwelling	Orb-web builder	Nocturnal
Araneidae	*Pararaneus* sp.1	Web-dwelling	Orb-web builder	Nocturnal
Araneidae	*Pycnacantha tribulus* (Fabricius, 1781)	Web-dwelling	Orb-web builder	Nocturnal
Linyphiidae	*Agyneta habra* (Locket, 1968)	Web-dwelling	Sheet-web builder	Diurnal
Lycosidae	*Pardosa crassipalpis* Purcell, 1904	Free-living	Ambush hunter	Diurnal
Oxyopidae	*Oxyopes longispinosus* Lawrence, 1939	Free-living	Active hunter	Diurnal
Oxyopidae	*Oxyopes schenkeli* Lessert, 1928	Free-living	Active hunter	Diurnal
Philodromidae	*Philodromus* sp.1	Free-living	Active hunter	Diurnal
Philodromidae	*Thanatus atlanticus* Berland, 1936.	Free-living	Ambush hunter	Diurnal
Philodromidae	*Tibellus hollidayi* Lawrence, 1953	Free-living	Ambush hunter	Diurnal
Salticidae	*Festucula lawrencei* Lessert, 1934	Free-living	Active hunter	Diurnal
Salticidae	*Heliophanus debilis* Simon, 1901	Free-living	Active hunter	Diurnal
Salticidae	*Heliophanus* sp.	Free-living	Active hunter	Diurnal
Salticidae	*Pellenes bulawayoensis* Wesołowska, 2000	Free-living	Active hunter	Diurnal
Salticidae	*Thyene semiargentea* (Simon, 1884)	Free-living	Active hunter	Diurnal
Salticidae	*Thyenula* sp. 1	Free-living	Active hunter	Diurnal
Salticidae	*Thyenula* sp. 2	Free-living	Active hunter	Diurnal
Theridiidae	*Enoplognatha molesta* O.P. Cambridge, 1904	Web-dwelling	Gumfoot-web builder	Nocturnal
Theridiidae	*Enoplognatha* sp. 1	Web-dwelling	Gumfoot-web builder	Nocturnal
Theridiidae	*Enoplognatha* sp. 2	Web-dwelling	Gumfoot-web builder	Nocturnal
Theridiidae	*Latrodectus renivulvatus* Dahl, 1903	Web-dwelling	Gumfoot-web builder	Nocturnal
Thomisidae	*Misumenops rubrodecoratus* Millot, 1942	Free-living	Ambush hunter	Diurnal
Thomisidae	*Monaeses paradoxus* Lucas, 1867	Free-living	Ambush hunter	Diurnal
Thomisidae	*Monaeses pustulosus* Pavesi, 1896	Free-living	Ambush hunter	Diurnal
Thomisidae	*Runcinia affinis* Simon, 1897	Free-living	Ambush hunter	Diurnal
Thomisidae	*Runcinia erythrina* Jézéquel, 1964	Free-living	Ambush hunter	Diurnal
Thomisidae	*Runcinia flavida* (Simon, 1881)	Free-living	Ambush hunter	Diurnal
Thomisidae	*Stiphropus bisigillatus* Lawrence, 1955	Free-living	Ambush hunter	Diurnal
Thomisidae	*Synema decens* (Karsch, 1878)	Free-living	Ambush hunter	Diurnal
Thomisidae	*Thomisus* sp.1	Free-living	Ambush hunter	Diurnal

Table C.2: Effect sizes for Hierarchical Linear Modelling (HLM) for a regional survey of all 25 sampling sites and a local survey of the Ventersdorp sampling site. Pairwise differences in predatory arthropod diversity measures are given between three distance classes: MZ, maize field (20-50 m from field edges), MV, marginal vegetation (30-50 m from last maize row) and RA, rangeland (80-100 m from last maize row). * indicates medium effect size at d ≥ 0.5; **, large effect size at d ≥ 0.8.

		MZ x MV	MZ x RA	MV x RA
Diversity measures (Regional survey)	Species Richness (S)	**0.57***	**0.58***	0.01
	Abundance (N)	0.23	0.31	0.09
	Margalef's species richness (d)	**0.55***	**0.57***	0.01
	Shannon-Wiener diversity (H')	0.43	**0.55***	0.12
	Simpson's diversity (Ď)	0.14	0.32	0.33
Diversity measures (Local survey)	Species Richness (S)	**2.42****	**2.12****	0.30
	Abundance (N)	**1.15****	**1.33****	0.18
	Margalef's species richness (d)	**2.52****	**2.23****	0.30
	Shannon-Wiener diversity (H')	**2.41****	**2.45****	0.04
	Simpson's diversity (Ď)	**1.05****	**1.15****	0.10
Guild abundance (Regional survey)	Free-living (N)	**0.85****	0.47	0.39
	Web-dwelling (N)	**0.50***	**0.66***	0.16
	Diurnal (N)	**0.89****	**0.47***	0.41
	Nocturnal (N)	0.44	**0.70***	0.26
Guild abundance (Local survey)	Free-living (N)	**2.22****	**1.65****	**0.57***
	Web-dwelling (N)	**1.39****	**1.99****	**0.60***
	Diurnal (N)	**2.22****	**1.65****	**0.57***
	Nocturnal (N)	**1.39****	**1.99****	**0.60***

Table C.3: List of all the predatory arthropod species recorded at all sampling sites with corresponding percentage occurrence in maize field (20-50 m from field edges), marginal vegetation (30-50 m from last maize row) and rangeland (80-100 m from last maize row) as well as associated habitat preference group.

Order	**Family**	**Species name**	**Abbreviation**	**% Maize**	**% Margin**	**% Rangeland**	**Cluster group***	**Habitat preference group**
Araneae	Oxyopidae	*Oxyopes longispinosus* Lawrence, 1939	Oxyo lon	100.00	0.00	0.00	1	(a) Maize field specialists
Araneae	Thomisidae	*Synema decens* (Karsch, 1878)	Syne dec	100.00	0.00	0.00	1	
Coleoptera	Coccinelidae	*Harmonia axyridis* (Pallas, 1773)	Harm axy	70.27	2.70	27.03	3	
Coleoptera	Coccinelidae	*Hippodamia variegata* (Goeze, 1777)	Hipp var	70.29	12.00	17.71	3	
Araneae	Theridiidae	*Enoplognatha* sp. 2	Enop sp.2	0.00	100.00	0.00	4	(b) Marginal vegetation specialists
Mantodea	Hymenopodidae	*Harpagomantis discolour* Stal, 1877	Harp dis	0.00	100.00	0.00	4	
Mantodea	Empusidae	*Hemiepusa capensis* Burmeister, 1838	Hemi ape	0.00	100.00	0.00	4	
Araneae	Araneidae	*Larinia* sp.1	Lari sp.1	0.00	100.00	0.00	4	
Araneae	Theridiidae	*Latrodectus renivulvatus* Dahl, 1903	Latr ren	0.00	100.00	0.00	4	
Araneae	Oxyopidae	*Oxyopes schenkeli* Lessert, 1928	Oxyo sch	0.00	100.00	0.00	4	
Araneae	Araneidae	*Pararaneus* sp.1	Para sp.1	0.00	100.00	0.00	4	
Araneae	Thomisidae	*Runcinia erythrina* Jézéquel, 1964	Runc ery	0.00	100.00	0.00	4	
Araneae	Salticidae	*Thyene semiargentea* (Simon, 1884)	Thy sem	0.00	100.00	0.00	4	
Araneae	Araneidae	*Neoscona moreli* (Vinson, 1863)	Neos mor	33.33	66.67	0.00	5	
Araneae	Thomisidae	*Thomisus* sp.1	Thomsp.1	40.00	60.00	0.00	5	
Mantodea	Mantidae	*Entella transvaalica* Beier, 1955	Ente tra	0.00	75.00	25.00	13	(c) Uncultivated vegetation, tending towards marginal vegetation
Araneae	Salticidae	*Heliophanus* sp.	Heli sp.	0.00	80.00	20.00	13	
Mantodea	Mantidae	*Pyrgomantis rhodesica* Giglio-Tos, 1917	Pyrg rho	1.52	80.30	18.18	13	
Araneae	Linyphiidae	*Agyneta habra* (Locket, 1968)	Agyn hab	12.50	62.50	25.00	14	
Araneae	Theridiidae	*Enoplognatha* sp. 1	Enop sp.1	9.09	63.64	27.27	14	
Araneae	Salticidae	*Heliophanus debilis* Simon, 1901	Heli deb	0.00	66.67	33.33	14	
Araneae	Thomisidae	*Misumenops rubrodecoratus* Millot, 1942	Misu rub	12.92	56.18	30.90	14	
Araneae	Salticidae	*Pellenes bulawayoensis* Wesołowska, 2000	Pell bul	7.41	59.26	33.33	14	
Araneae	Salticidae	*Festucula lawrencei* Lessert, 1934	Fest law	0.00	0.00	100.00	6	(d) Rangeland specialists
Araneae	Araneidae	*Pycnacantha tribulus* (Fabricius, 1781)	Pycn tri	0.00	0.00	100.00	6	
Araneae	Salticidae	*Thyenula* sp. 1	Thye sp.1	0.00	0.00	100.00	6	

Table C.3: cont.

Order	**Family**	**Species name**	**Abbreviation**	**% Maize**	**% Margin**	**% Rangeland**	**Cluster group***	**Habitat preference group**
Araneae	Araneidae	*Hypsosinga* sp. 3	Hypsosp.3	0.00	31.58	68.42	7	(e) Uncultivated vegetation, tending towards rangeland
Araneae	Araneidae	*Larinia bifida* Tullgren, 1911	Lari bif	0.00	35.29	64.71	7	
Araneae	Araneidae	*Larinia natalensis* (Grasshoff, 1971)	Lari nat	0.00	33.33	66.67	7	
Neuroptera	Chrysopidae	*Italochrysa similis* Tjeder, 1966	Ital sim	2.38	23.81	73.81	8	
Coleoptera	Coccinelidae	*Micraspis comma* Thunberg, 1781	Micr com	0.00	27.27	72.73	8	
Coleoptera	Coccinelidae	*Exochomus flavipes* (Thunberg, 1781)	Exoc fla	10.91	10.91	78.18	9	
Mantodea	Mantidae	*Tenodera iringana* Giglio-Tos, 1912	Teno iri	0.00	16.67	83.33	9	
Mantodea	Tarachodidae	*Galepsus* sp.	Gale sp.	1.39	40.28	58.33	11	
Araneae	Thomisidae	*Monaeses pustulosus* Pavesi, 1896	Mona pus	0.00	44.44	55.56	11	
Araneae	Philodromidae	*Philodromus* sp.1	Phil sp.1	0.00	45.45	54.55	11	
Araneae	Thomisidae	*Runcinia flavida* (Simon, 1881)	Runc fla	0.00	41.67	58.33	11	
Mantodea	Mantidae	*Compsothespis natalica* Westwood, 1889	Comp nat	0.00	50.00	50.00	12	
Mantodea	Mantidae	*Episcopomantis chalybea* Burmeister, 1838	Epis cha	1.69	55.93	42.37	12	
Araneae	Araneidae	*Hypsosinga* sp.1	Hypsosp.1	0.00	53.85	46.15	12	
Araneae	Thomisidae	*Monaeses paradoxus* Lucas, 1867	Mona par	0.00	50.00	50.00	12	
Araneae	Thomisidae	*Runcinia affinis* Simon, 1897	Runc aff	2.78	58.33	38.89	12	
Araneae	Salticidae	*Thyenula* sp. 2	Thye sp.	0.00	60.00	40.00	12	
Araneae	Philodromidae	*Tibellus hollidayi* Lawrence, 1953	Tibe hol	4.76	52.38	42.86	12	
Araneae	Araneidae	*Hypsosinga lithyphantoides* Caporiacco, 1947	Hyps lit	50.00	0.00	50.00	2	(f) Generalists
Araneae	Lycosidae	*Pardosa crassipalpis* Purcell, 1904	Pard cra	50.00	0.00	50.00	2	
Coleoptera	Coccinelidae	*Bulaea anceps* (Mulsant 1850)	Bula anc	32.56	34.88	32.56	10	
Coleoptera	Coccinelidae	*Cheilomenes lunata* (Fabricius, 1775)	Chei lun	17.37	31.36	51.27	10	
Neuroptera	Chrysopidae	*Chrysoperla congrua* (Walker, 1853)	Chry con	25.00	38.00	37.00	10	
Araneae	Theridiidae	*Enoplognatha molesta* O.P. Cambridge, 1904	Enop mol	18.18	45.45	36.36	10	
Coleoptera	Coccinelidae	*Lioadalia flavomaculata* (De Geer, 1778)	Lioa fla	26.67	23.33	50.00	10	
Araneae	Araneidae	*Neoscona subfusca* (C.L.Koch, 1837)	Neos sub	25.00	25.00	50.00	10	
Araneae	Thomisidae	*Stiphropus bisigillatus* Lawrence, 1955	Stip bis	25.00	50.00	25.00	10	
Araneae	Araneidae	*Thanatus atlanticus* Berland, 1936.	Than atl	40.00	20.00	40.00	10	

* Relating to UPGMA cluster analysis