

Diversity of non-crop plants and arthropods in soybean agro-ecosystems in South Africa

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Abstract

Soybean is widely cultivated in the Grassland Biome of South Africa (>700 000 ha per annum). Yet the possible effects large-scale cultivation of soybean has on biodiversity in adjacent habitat is not fully understood. It is important to expand current data in order to assess and adapt methods of agriculture – where possible – to ensure the future functionality of soybean agro-ecosystems. This study aimed to describe plant and arthropod species assemblages, diversity patterns and relationships between plant and arthropod diversity within soybean agro-ecosystems in South Africa. Surveys were conducted in three treatment zones, i.e., the soybean crop, field boundary (transition zone between soybean fields and adjacent habitat) and adjacent untransformed grassland. A total of 4910 individuals and 320 plant species and 9216 individuals and 373 arthropod morpho-species were recorded from 60 plots (5 localities x 2 sites x 2 transects x 3 treatments). The soybean crop had significantly lower plant and arthropod diversity than adjacent habitats. Plant diversity remained the same between the field boundary and grassland. A higher diversity of arthropods was collected in the boundary than the grassland. These results suggest soybean fields had no adverse effects on biodiversity patterns in the adjacent habitat. However, the boundary, dominated by alien plant species, did contain a significantly different plant species composition from the untransformed grassland that was mirrored by unique assemblages of arthropods. This suggests that disturbance, resulting from the soybean crop, led to species losses and gains that changed the plant and arthropod species composition of the field boundary but had no effect on grassland beyond the boundary (>50 m). Correlations between plant and arthropod species richness and diversity index values were generally weak and non-significant suggesting other factors, for instance, plant functional and structural diversity, may be important to explain arthropod diversity. Unique species assemblages and high diversity of plants and arthropods in the boundary and untransformed grassland suggest that these zones may have important conservation value in soybean agro-ecosystems by supporting unique species and ecosystem services.

Keywords: Agro-ecosystem; Biodiversity; Species Richness; Soybean; Arthropods; Plants; Grassland; Field Boundary; Ecosystem Services

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Chapter 1: Introduction

1.1 Introduction

Diverse terrestrial biomes, ranging from desert to forest, contribute to South Africa being recognized as one of the 17 megadiverse countries of the world (Crane, 2006; Skowno *et al.*, 2019). This is attributed to the high plant and arthropod diversity within the country. South Africa has the highest species richness of temperate plants in the world, with 20 700 indigenous plant taxa. These comprise of 252 families, of which 8 families and 67% of taxa are endemic to South Africa (Von Staden *et al.*, 2013). South Africa has a rich arthropod fauna with more than 50 000 species described while the actual number is estimated to be as high as 250 000 species (Picker *et al.*, 2019; Skowno *et al.*, 2019).

Plants and arthropods are key components to ecosystem function and stability (Harrison *et al.*, 2014). As primary producers, plant material may be browsed by herbivores, pollen and nectar sustain pollinators, and plant structures provide reproduction sites and shelter to various organisms (Marshall, 2001). Plants not only provide habitat for beneficial arthropods but in agricultural habitats plants may also reduce soil erosion, buffer the movement of agrochemicals to natural habitats and function as windbreaks for crops (De Snoo and De Wit, 1998; Clarke *et al.*, 2005; Marshall, 2005). Arthropods are present in most terrestrial habitats and serve as useful bioindicators of disturbance since they react more rapidly to environmental change than vertebrates (Rodríguez *et al.*, 1998). As consumers, arthropods comprise many important functional groups including herbivores, pollinators, detritivores, predators, and parasitoids. The multiple benefits of these organisms to humans are referred to as arthropod-mediated ecosystem services (AMES) and include nutrient cycling, detoxification of harmful chemicals, regulation of pests and pollination of crops (Altieri, 1999; Power, 2010; Harrison *et al.*, 2014).

South Africa's rich biodiversity is not only important for ecosystem functioning and the provision of ecosystem services (Hooper *et al.*, 2005; Chan *et al.*, 2006; Turner *et al.*, 2007; Egoh *et al.*, 2009), but also contributes significantly to the economy (Wynberg, 2002). The country's biodiversity is, however, facing increasing pressure from anthropogenic activities, including habitat conversion for urban developments, mining, agricultural land, and invasive alien species (Wynberg, 2002). South Africa covers a land area of 127 million hectares, of which more than 80% is zoned for and livestock grazing and cultivation of crops (DAFF, 2018).

Globally, soybean has become an important crop due to its high nutritional value, the ability for nitrogen fixation, usage in livestock feed, production of biofuels and a wide range of pharmaceutical applications (Ali, 2010). In the 2018/2019 growing season, a total of 125

million hectares of soybean were cultivated worldwide, with the United States, Brazil, and Argentina leading production (USDA, 2019). Since the introduction of genetically modified soybean in the late 1990s, it has become an increasingly important crop in South Africa as well. The continued growth in soybean cultivation in South Africa is facilitated by agricultural policies that enable the use of transgenic herbicide-tolerant crops and the benefits of crop rotation systems with soybean and maize (Dlamini *et al.*, 2014). In the 2018/2019 growing season, approximately 787 000 hectares of soybean, of which 95% were genetically modified to be herbicide-tolerant, was planted in South Africa (DAFF, 2019; ISAAA, 2018).

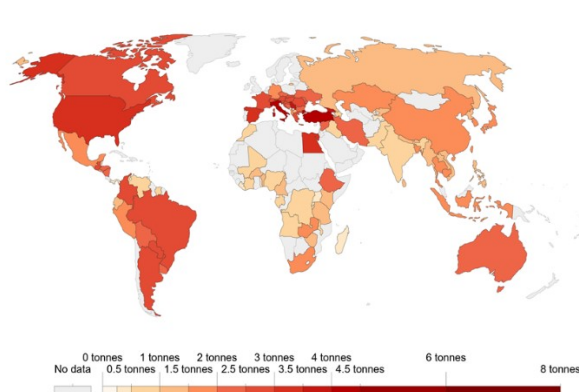


Figure 1.1: Global soybean production for 2014 (FAO, 2017; OWID, 2020).

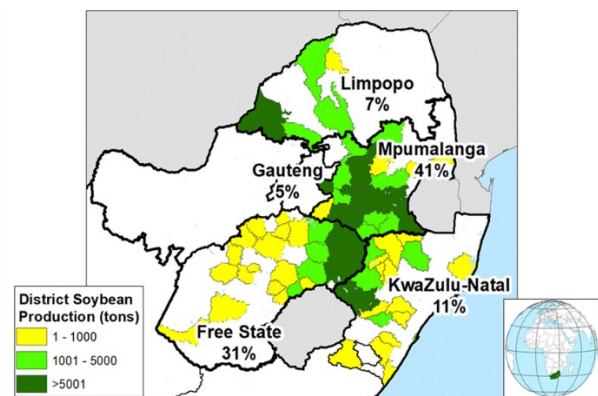


Figure 1.2: Average soybean production in South Africa from 2011 to 2016 (USDA 2020).

Large-scale and intensive agriculture brings about the destruction and fragmentation of natural ecosystems and may result in loss of the environments' biodiversity by substituting it with domesticated animals and crops (Altieri, 1999; Altieri and Nicholls, 2004; Duru *et al.*, 2015). This gives rise to a man-made ecosystem that is not capable to perform basic ecosystem services (Altieri, 1999). These systems are highly reliant on human intervention and in some instances the use of agro-chemicals (pesticides and fertilizers) that may result in further degradation of remaining natural habitat through agro-chemical drift (Felsot *et al.*, 2010).

1.2 Aims, objectives and hypotheses

Soybean is widely cultivated throughout South Africa, and it is important to understand what potential impact the associated cultivation practices have on natural biodiversity. Apart from knowledge on certain key pest species of soybean (DAFF, 2010; Van Wyk and Smit, 2010; Du Plessis, 2015), there is limited data available on plant and arthropod biodiversity associated with soybean cropping systems in South Africa. It is important to expand the currently available data in order to assess any potential consequences for biodiversity in order to evaluate and adapt, where possible, current agricultural practices to ensure the conservation and future persistence of natural biodiversity in South Africa. Therefore, the aim

of the study was to provide insight into the plant and arthropod diversity patterns and species assemblages that are associated with soybean agro-ecosystems in South Africa.

Specific objectives were to:

- compare the diversity and composition patterns of plants and plant-dwelling arthropods between soybean fields, boundary zones (transition zone between cropland and natural habitat) and adjacent untransformed grassland across five different localities (Bapsfontein, Tarlton, Winterton, Belfast, and Reitz), situated within the main soybean production regions of South Africa;
- test for a general relationship between plant and arthropod diversity in soybean fields and adjacent habitats.

Experimental hypotheses were:

- monocultures, invasive species, application of agro-chemicals and tillage practices contribute to a high level of disturbance in crop fields (Feber *et al.*, 1996; Stamps and Linit, 1998; Witmer *et al.*, 2003). Therefore, the first hypothesis proposes that soybean fields will have a lower diversity of plants and arthropods than natural habitats;
- the disturbance associated with crop fields may also affect the plant and arthropod diversity and species composition of adjacent habitats (Boutin and Jobin, 1998; Piessens *et al.*, 2006). Therefore, the second hypothesis proposes that plant and arthropod species richness and diversity of the field boundary (zone directly adjacent to the crop) will be negatively affected by the presence of crop fields but untransformed grassland beyond the field boundary will not be affected;
- agricultural disturbance can be seen as a selection force allowing species able to tolerate the disturbance to grow and outcompete less tolerant species (Yachi and Loreau, 1999). The third hypothesis proposes that the plant and arthropod species compositions of the field boundary will be replaced by unique assemblages that are able to tolerate the disturbance in the boundary;
- it is generally argued that high diversity of plants facilitates high arthropod diversity (Siemann, 1998; Knops *et al.*, 1999; Haddad *et al.*, 2009; Botha *et al.*, 2015). Therefore, the fourth and final hypothesis for the study proposes that arthropod diversity will increase in response to increasing plant diversity.

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Chapter 2: Literature review

2.1 Biodiversity and biodiversity measurement

2.1.1 General principles of biodiversity

Biodiversity forms a fundamental part of all ecosystems. It supports various ecological functions, recycling of nutrients, regulation of pests and disease, degradation of toxic chemicals, water purification and regulation of the microclimate (Altieri, 1999; Power, 2010; Harrison *et al.*, 2014; Garcia *et al.*, 2018). All ecosystems are impacted by some form of anthropological disturbance, whether by habitat modification or pollution. Biodiversity can be used as an indicator to evaluate the effects of, for example, pollution, climate change and habitat disturbances on ecosystem health (Schulze *et al.*, 2004; Griffiths *et al.*, 2016; Peters *et al.*, 2016). Therefore, it is important to understand what biodiversity entails more especially since there is increasing concern about the possible consequences that anthropological activities may have on the environment.

Species richness is the most frequently considered facet of biodiversity and it refers to the number of species in a specific area, habitat or community (Purvis and Hector, 2000). Within the component of biodiversity, there is an element of genetic diversity. This refers to genetic variation between and within species. Genetic diversity provides species with the ability to survive and adapt to a changing environment (Ammann, 2009). At a broader spectrum, ecosystem diversity is also recognized. Ecosystem diversity is concerned with the variety of ecosystems or habitats across landscapes (Ammann, 2009). Biodiversity is also expressed by evenness, which is the relative abundance of each species in a habitat or community (Purvis and Hector, 2000; Hooper *et al.*, 2005).

Probably one of the most important facets of biodiversity, relating to its importance, is functional diversity, which refers to functions that species perform within communities and ecosystems (Díaz and Cabido, 2001; Petchey and Gaston, 2006). The functional traits of species are important to assess or predict how changing biodiversity can influence the ecosystem (Hooper *et al.*, 2005). Species that have similar traits and similar effects on an ecosystem can be grouped into functional groups (Hooper *et al.*, 2005). For example, nitrogen-fixing plants versus non-nitrogen-fixing plants. In other instances, it can be more descriptive like the grouping of arthropods into predators, parasitoids, herbivores, pollinators, and detritivores. When functional diversity is assessed, a vast array of information on different traits for plant and arthropod species is used (Petchey and Gaston, 2006). The chosen traits used will depend on the objectives of the study.

2.1.2 Biodiversity measurement

Biodiversity measurements can be categorized into three components. Alpha-diversity is measured within a single or specific community or habitat (Whittaker, 1972; Zhuravlev and Naimark, 2005). The difference in diversity between different habitats or communities is known as beta-diversity (Hamilton, 2005; Zhuravlev and Naimark, 2005). Gamma-diversity is the total diversity within a large region or landscape and is usually the combined alpha diversities of all the communities and habitats in that landscape (Whittaker, 1972; Zhuravlev and Naimark, 2005).

The different components of biodiversity make it a multidimensional concept, which is difficult to characterize (Purvis and Hector, 2000). For example, a habitat with a high species richness might not appear diverse if most individuals belong to the same species, compared to habitat where individuals are distributed more evenly between species. The biodiversity status of a community or habitat is best characterized by means of biodiversity indices.

Biodiversity indices are equations that describe the diversity characteristics of an ecosystem or community. Different indices may emphasize certain components of biodiversity more than others. For example, some indices are used as an indication of species richness, while others provide a good indication of evenness. The number of species in an ecosystem or community, or species richness (S), is the simplest and most frequently used measurement of diversity (Whittaker, 1972). Margalef's species richness index (d) is also a good indication of species richness index, and it brings sampling effect into consideration to some degree (Magurran, 2004). Pielou's evenness (J') sets the focus on how evenly a particular species is distributed in terms of its relative abundance.

The Shannon-Wiener diversity index (H') and Simpson's diversity index ($\tilde{D}$) are widely used as heterogeneity indices (Magurran, 2004; Bandeira *et al.*, 2013). Heterogeneity indices provide an indication of both species richness and evenness. Heterogeneity indices will increase as either species richness or evenness increase. However, Simpson's diversity index is more sensitive to evenness and less sensitive to species richness than the Shannon-Wiener diversity index (Colwell, 2009). Most biodiversity studies use a combination of indices to get an accurate assessment of a system's biodiversity. Diversity indices can be used to assess the impact of a disturbance on the ecosystem as a comparison of biodiversity between different ecosystems or communities (Morris *et al.*, 2014).

2.2 Agro-ecosystems

2.2.1 General description of agro-ecosystems

South Africa covers a total land surface area of 127 million hectares, of which more than 80% is zoned for the cultivation of crops and livestock grazing (DAFF, 2018). The result is a large-scale transformation of natural habitat. Thereby, an artificial ecosystem (which will be referred to as an agro-ecosystem) is formed and consists of an assortment of pastures, crop fields, infrastructure such as roads and fences, and natural and semi-natural habitat (Marshall, 2005).

Agro-ecosystems may be based on different cropping systems (monocultures and polycultures). With commercial farming, monocultures have become a predominant feature and entail the cultivation of a single plant species over a large area. Although monocultures can be productive, the large-scale replacement of natural biodiversity with domesticated crops and livestock often results in a general reduction of environmental complexity and biodiversity (Tivy, 1990; Altieri, 1999; Altieri and Nicholls, 2004; Liere *et al.*, 2017). The environmental costs of this reduced complexity can be high since biodiversity is considered to facilitate function and stability in ecosystems (Elton, 1958; McNaughton, 1977; Harrison *et al.*, 2014). On the other hand, polycultures, traditional farming systems, conservation agriculture, intercropping systems, agroforestry, cover crops, and crop rotations have higher levels of biodiversity (Altieri, 1999; Kassam *et al.*, 2009; Clough *et al.*, 2011; Duru *et al.*, 2015).

The basic structure of agro-ecosystems remains the same regardless of the type of cropping system. The **crop edge** refers to the outermost region of the main crop and often has higher biodiversity of weeds and arthropods than the crop centre since biota enters from the adjacent field margin (Free and Williams, 1979; Romero *et al.*, 2008; Molina *et al.*, 2014). The **field margin** consists of the field boundary and natural to semi-natural habitat surrounding the crop (Fig. 1.1). The **field boundary** can be seen as a barrier between cropland and adjacent natural habitat (Marshall and Moonen, 2002). It may consist of a physical barrier, such as fences and dirt roads, it may contain naturally regenerated vegetation or it may be cultivated with wild species of grass and flowers (Marshall, 2005). In many cases, this area is sprayed with herbicides to generate a sterile strip (Marshall and Moonen, 2002).

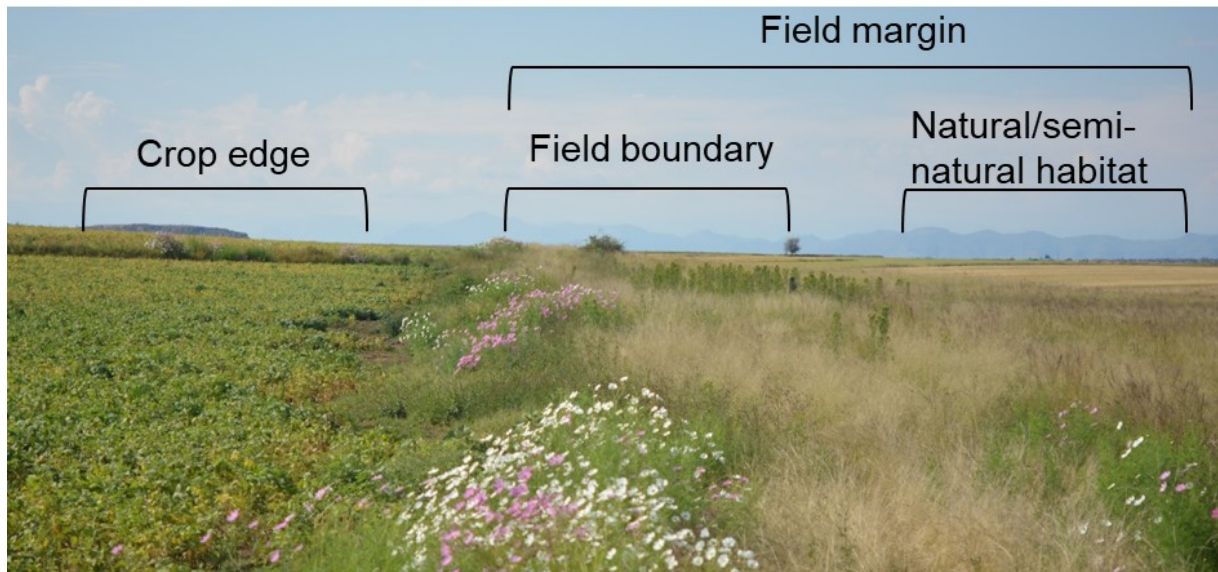


Figure 2.1: Typical structure of a soybean agro-ecosystem, comprising of a crop edge and field margin, which may consist of a field boundary and natural to semi-natural habitat (simplified from Greaves and Marshall, 1987).

2.2.2 Biodiversity of agro-ecosystems

Agro-ecosystems consist of planned and associated biodiversity. The planned biodiversity refers to the diversity chosen by the farmer, including the crops, livestock, windbreaks and trap crops (Duru *et al.*, 2015). The associated biodiversity is all the flora and fauna able to colonize the agro-ecosystem from adjacent environments and can be classified as destructive or beneficial organisms (Altieri, 1999; Marshall, 2005). Destructive organisms (arthropod pests, weeds, and pathogens) have adverse effects on the productivity of the system while organisms that are beneficial to the productivity of the system include pollinators, detritivores, predators and parasitoids (Marshall, 2005; Duru *et al.*, 2015).

As part of planned biodiversity, the field boundary may be cultivated with selected plant species in favour of the crop. For instance, Napier grass (*Pennisetum purpureum* Schumach.) is an attractive host plant for stem borers, *Busseola fusca* (Fuller) (Lepidoptera: Noctuidae), and is planted in field boundaries as a trap crop (Khan *et al.*, 2000; Midega *et al.*, 2008). This forms part of the push-pull strategy and is an effective management strategy against stem borer pests of maize and sorghum (Khan *et al.*, 2000; Midega *et al.*, 2008). The field boundary can be cultivated with wild grass and flower species, with the purpose of increasing abundance of pollinators and natural enemies of pests, as well as decreasing growth of weed species known to spread into crop fields (Marshall and Moonen, 2002; Haaland *et al.*, 2011; Pollier *et al.*, 2019).

Biodiversity associated with agro-ecosystems will vary in response to a range of conditions, including habitat age, level of isolation from the natural environment, diversity and structure of

non-crop plants, and the intensity of management practices (Altieri, 1999; Denys and Tscharntke, 2002; Haddad *et al.*, 2009; Carvalheiro *et al.*, 2012):

Habitat age and degree of isolation from natural habitat

Habitat age may have a significant effect on plant and arthropod diversity. For instance, higher plant and arthropod diversity are generally reported with increasing age of forest plantations (Schowalter, 1995; Sax, 2002; Magura *et al.*, 2003; Jeffries *et al.*, 2006). Perennial and semi-perennial crops are grown for longer periods while annual monocultures are only present for a part of the year. The longevity of perennial crops can support greater arthropod diversity, depending on the crop type, since the life-cycles of the biota associated with annual crops is interrupted after cultivation and harvest (Stamps and Linit, 1998). This may be a problem for natural enemies since their prey, refugia and alternative food resources are only available for a certain part of the year (Stamps and Linit, 1998). Habitat age of the field boundary can also be significant for the establishment of arthropod communities. For instance, increasing arthropod biodiversity were reported with successional age of boundary zones planted with wild grass and flower mixtures (Denys and Tscharntke, 2002; Thomas *et al.*, 2002; Frank and Reichhart, 2004).

The position or extent of isolation of the crop from natural vegetation is also an important determinant of its biodiversity. Garibaldi *et al.* (2011) found a significant decrease in species richness of pollinators in crops that were far away from adjacent natural vegetation. Similarly, increased abundance and diversity of flower-visiting arthropod were observed in mango orchards of South Africa after small patches of native flowering plants were planted in adjacent mango orchards (Carvalheiro *et al.*, 2012). The crop edge often contains greater diversity and abundance of arthropods than the crop interior due to its proximity to the field margin (Free and Williams, 1979). Therefore, it comes to reason that the crop centres of smaller crop fields, or crops interspaced with natural vegetation, may have a greater diversity of arthropods because of its proximity to field margins.

Diversity and structure of non-crop plants

It is argued that higher diversity of plants will sustain higher diversity of phytophagous arthropods (Root, 1973; Siemann, 1998; Siemann *et al.*, 1998; Knops *et al.*, 1999; Haddad *et al.*, 2009; Dassou and Tixier, 2016; Welts *et al.*, 2017; Schuldt *et al.*, 2019). It comes to reason that if phytophagous arthropods exhibit host specificity (Andow and Imura, 1994; Norris and Kogan, 2000), greater plant diversity may facilitate greater arthropod diversity (Schoonhoven *et al.*, 1998). Subsequently, greater phytophagous arthropod diversity and abundance could

increase the diversity of predators and parasitoids (Siemann, 1998; Siemann *et al.*, 1998). Also, arthropods are dependent on plants for shelter, overwintering sites, oviposition sites, food, and other resources. Diverse plant communities may have a greater variety of these resources and therefore may increase the diversity of predators and parasitoids (Price *et al.*, 1980; Jervis *et al.*, 1993; Ratnadass *et al.*, 2012; Kaiser *et al.*, 2017).

Few studies of this nature have been conducted in South Africa. General positive correlations between insect species richness and plant species richness were reported in the Cape Floristic Region (Wright and Samways, 1998; Proches and Cowling, 2006; Kemp and Ellis, 2017). Botha *et al.* (2017) surveyed plant and arthropod diversity along a maize and field margin gradient in Grassland and Savanna biomes of South Africa and reported that greater species richness of Poaceae resulted in a general increase in arthropod species richness. Furthermore, the species composition of the plant community influenced the arthropod community assemblages. The maize field and field margins were characterized by distinct plant communities, which were mirrored by distinct arthropod communities.

Plant species composition will determine the plant structure, functional groups, and microclimate which may be an important facet in determining arthropod diversity. Siemann *et al.* (1998) found a strong correlation between arthropod diversity and both plant species richness and the number of plant functional groups. The numbers of arthropod herbivore, predator and parasitoid species increased in response to grassland plots with higher functional diversity (Siemann *et al.*, 1998). However, Symstad *et al.* (2000) found no relationship between functional groups (forbs, C₄- and C₃ graminoids) of different grassland habitats and total arthropod diversity. Nevertheless, the functional group composition did affect individual arthropod orders. Hemiptera diversity was lower in grasslands with abundant C₄ graminoids while Coleoptera diversity was higher in grassland with abundant forbs (Symstad *et al.*, 2000). These effects were ascribed to the low nutritional quality of C₄ graminoids having a negative impact on Hemiptera diversity, while the majority of Coleoptera, that were identified, were phytophagous and had forb species listed as host plants.

Studies indicate that the diversity and structure of field boundary vegetation may have varying effects on the arthropod communities inside crop fields (Marshall and Moonen, 2002). Beetle species exhibit faster movement through field boundaries planted with barley crop compared to a boundary with a less permeable grassy bank (Frampton *et al.*, 1995). Sheet-web spiders (Araneae: Linyphiidae) exhibit a faster dispersal rate through cereal fields than grass fields (Thomas and Jepson, 1999). This is attributed to differences in microclimate resulting from the different vegetation groups (Thomas and Jepson, 1999).

Management practices

Agro-ecosystems are dependent on human intervention, often in the form of soil management practices and pesticide and fertilizer application (Marshall, 2005). Jobin *et al.* (1997) observed lower vegetation diversity in field margins adjacent to grain crops that were regularly treated with atrazine, dicamba, metolachlor, and glyphosate. Studies have demonstrated higher plant cover and diversity of adjacent ditch bank vegetation along unsprayed wheat crop edges compared to edges sprayed with herbicide (De Snoo and Van der Poll, 1999). Changes in the abundance and species composition of the plant community may affect arthropod diversity and species assemblages. Feber *et al.* (1996) observed that over an extended period, herbicide application significantly altered the plant community. After each year of herbicide application, flowering forbs became less abundant. As a result, the species richness and abundance of butterflies decreased. Similarly, simulated drift of dicamba and 2,4-D in field boundaries adjacent alfalfa fields resulted in significantly altered forb cover which was mirrored by increased abundance of *Sitona hispidulus* (F.) (Coleoptera: Curulionidae) and reduced abundance of other pest species, i.e. *Acyrtosiphon pisum* (Harris), *Therioaphis maculate* (Buckton) (Hemiptera: Aphididae) and *Empoasca fabae* (Harris) (Hemiptera: Cicadellidae) (Egan *et al.*, 2014).

Fertilizer application may result in the deposition of additional nutrients such as phosphorus and nitrogen into non-target areas (Marshall and Moonen, 2002). It was shown by Schmitz *et al.* (2014) that although it may lead to an increase in the overall productivity of a system, fertilizer application has marked effects on field margins by increasing species dominance of plant species with high nutrient uptake, while decreasing overall plant diversity. Higher primary production may lead to greater arthropod diversity and abundance. Kirchner (1977) observed higher diversity and biomass of arthropods in a grass prairie subject to nitrogen fertilization and irrigation. It was shown by Botha *et al.* (2017) that increasing grass abundance increased arthropod diversity. However, fertilizer may also increase plant vigour and tolerance to phytophagous arthropods as seen by Sudoi *et al.* (2001) who observed reduced outbreaks of *Brevipalpus phoenicis* (Geijskes) (Trombidiformes: Tenuipalpidae) in tea plantations.

Tillage practices can also influence the biodiversity and abundance of non-crop plants. Conservation tillage refers to practices that minimize soil disruption and may reduce the frequent use of fertilizers, irrigation and other inputs (Holland, 2004). Higher diversity and abundance of non-crop plants are generally reported in conservation tillage fields compared to conventionally tilled fields (Buhler, 1992; Menalled *et al.*, 2001; Santín-Montanyá *et al.*, 2013). Left-over crop residues from conservation tillage may provide essential resources and habitat as well as a stable microclimate, which can attract and maintain arthropod populations.

Most studies report higher abundance and diversity of epigeal arthropods in no-tillage systems (House and Stinner, 1983; Anderson, 1999; Witmer *et al.*, 2003; Rodríguez *et al.*, 2006; Mashavakure *et al.*, 2019; Patterson *et al.*, 2019). Tillage can also affect plant-associated arthropods through alterations in habitat and food availability. Sharley *et al.* (2008) observed a decreased in abundance of parasitoid wasps such as Trichogrammatidae after tillage, whereas the abundance of beetles in various families (Anthicidae, Staphylinidae, Byrrhidae, and Nitidulidae) increased after tillage.

The biodiversity of agro-ecosystems may further be influenced by the grazing of livestock. Not all plant species react the same to grazing. More palatable species tend to decrease in abundance, due to excessive grazing (Van Oudtshoorn, 2012). In severely grazed habitats, less palatable species, which are often less productive as well, will replace the palatable species (Van Oudtshoorn, 2012). As a result, excessive grazing may reduce the overall plant biomass, alter the plant species composition and reduce species richness (Rutherford and Powrie, 2013). Grazing may affect plant-associated arthropods through changes in the species composition and vegetation structure of the plant community, and the effects of defoliation on the microclimate (Van Klink *et al.*, 2015). Seymour and Dean (1999) found a greater number of arthropod species in moderately grazed habitats compared to excessively grazed habitats in the Succulent Karoo of South Africa. In grassland in South Africa, grazing by large indigenous mammals increased the diversity of insects when compared to livestock grazing (Pryke *et al.*, 2016).

2.2.3 Spillover of species between the crop and non-crop habitat

The dissemination of seeds and movement of arthropods between the crop and non-crop environment readily occur (Tscharntke *et al.*, 2005; Dong *et al.*, 2015; Madeira *et al.*, 2016). It is a common perception that field boundaries may contain flora with the ability to disperse seeds into the crop area to become weeds (Marshall, 2005). Although this is true for some weeds, studies indicate that only a few of the plant species that occur in the field boundary, disperse into crop fields to become serious weeds (Marshall, 2004). In barley and wheat farms of Europe, it was reported that only 30% of the plant species recorded in the field boundary also occurred inside crop fields, most of which were only found in the crop within 2.5 m of the field boundary (Marshall, 1989).

It is common for native insect species to adapt and utilize a new host plant (the introduced crop). Since its introduction in Africa, maize has become one of the most widely cultivated crops. Consequently, several arthropod species switched hosts from wild plants to become pests of maize (Sezonlin *et al.*, 2006). *Busseola fusca* started to utilize maize as a host plant (Sezonlin *et al.*, 2006). It is also considered that native grass species in the field margin can

still function as a reservoir for stem borer (Moolman *et al.*, 2013). Certain arthropods can transmit plant disease. The virus that causes maize streak disease, and its vector, *Cicadulina* sp. (Hemiptera: Cicadellidae), can survive on native grass species during the offseason and infect maize soon after it is planted (Martin and Shepherd, 2009).

The field boundary may also contain beneficial organisms able to provide valuable ecosystem services (Marshall, 2005). Biological pest control is an important arthropod-mediated ecosystem services that is dependent on natural enemies of pests colonizing crop fields. Non-crop habitats provide permanent refuge areas, alternative food sources, and a favourable microclimate for natural enemies, and, as a result, field margins function as reservoirs of natural enemies of pests from where the crop is invaded (Landis *et al.*, 2000). For example, larvae of hoverflies (Diptera: Syrphidae) is an important group of generalist predators inside crop fields, while the adults feed on nectar and pollen provided by plant species inside field margins (MacLeod, 1999; Kaiser *et al.*, 2017). Sheet-web spiders (Araneae: Linyphiidae) are major predators of aphids, and they can disperse over large areas into crop fields to aid in pest regulation (Thomas and Jepson, 1997). Similarly, species spillover was observed for parasitoid flies (Tachinidae) between apple orchards and natural forest in Italy (Inclán *et al.*, 2015), lady beetles (Coccinellidae) between wheat fields and shelterbelts in China (Dong *et al.*, 2015) and lacewings (Chrysopidae) between mandarin orchards and shelterbelts in Spain (Sorribas *et al.*, 2016).

Although it is not often studied, the spillover of pest species from the crop can occur into adjacent field margins and natural habitat, often with adverse effects on the natural ecosystem (Tscharrntke *et al.*, 2005; Rand *et al.*, 2006). McKone *et al.* (2001) found large numbers of *Diabrotica* spp. (Coleoptera: Chrysomelidae) invading natural prairies from adjacent maize fields in the United States. At the end of the growing season, after maize began to desiccate, the beetles moved into adjacent prairie habitats with damaging effects on native sunflower (*Helianthus annuus* L.) that inhabit these prairie habitats (McKone *et al.*, 2001). In Germany, species spillover from wheat fields to adjacent grassland resulted in higher species richness and abundance of spiders, carabid beetles and staphylinid beetles in grassland adjacent wheat fields compared to grassland adjacent meadows (Madeira *et al.*, 2016). Similarly, Gladbach *et al.* (2011) observed spillover of *Tersilochus heterocerus* Thomson (Hymenoptera: Ichneumonidae), a parasitoid of *Meligethes aeneus* F. (Coleoptera: Nitidulidae), from oilseed rape (*Brassica napus* L.) into the adjacent habitat. Rand *et al.* (2006) suggested that the spillover of agriculturally supported insect natural enemies may affect prey populations in natural habitats. This is supported by Oksanen (1990) who found that predator spillover from high productive habitats can impact prey populations of low productive habitat. Crops are often

more productive than natural habitat. The high productivity of crops may support higher numbers of insect herbivores (Rand *et al.*, 2006). Generalist predators may colonize crops from adjacent natural habitat. A large amount of prey in crop fields may increase predator population densities (Rand *et al.*, 2006). After the crop is harvested, crop subsidized predators migrate back to adjacent natural habitat, resulting in possible higher predation pressure in the natural habitat (Rand *et al.*, 2006).

In general, arthropods have high mobility, and as such crops are frequently visited by a wide range of species. However, most arthropods are not able to establish on the crop. Many arthropods found on a crop at any given moment may be there by chance. Duelli and Obrist (2003) classified five different distribution patterns for arthropods in agro-ecosystems. Cultural species are specialists inside the crop habitat (Duelli *et al.*, 1990), while others prefer the non-crop habitat (Martin and Major, 2001), and both will rarely be found in the adjacent habitat. Ecotone species are found in both the crop and non-crop habitat, but they tend to be more abundant in the crop and field edges (Duelli and Obrist, 2003). While some species are abundant in the non-crop habitat from which they disperse into and colonize the crop habitat, and other species occur ubiquitously in both habitats without a preference for a specific habitat (Duelli and Obrist, 2003).

The field boundary can be viewed as a transition zone where the vegetation of the crop habitat meets the adjacent natural habitat. Traditionally, a transition zone is referred to as an ecotone, which may be defined as the area where two adjacent habitats, ecosystems or communities meet, and it may exhibit characteristics of both ecosystems (Van der Maarel, 1990). According to this definition, the field boundary of most agro-ecosystems can be considered as an ecotone. However, field boundary vegetation is highly vulnerable to the physical disturbance caused by farm operations and agro-chemical drift. As a result, field boundary vegetation is often dominated by weeds and other vegetation that grows well in these stressed areas, whereas natural vegetation is found further away from crop edges (Clark *et al.*, 2005).

Previous studies on transition zones between cereal fields and natural grassland showed distinct plant species assemblages along the cereal field-grassland gradient but did not observe a difference in species richness between the transition zone and adjacent habitats (Dutoit *et al.*, 2007). However, in some cases, it may have higher species richness than the adjacent habitats as it may contain a mixture of species from adjacent habitats, as well as a group of unique species (Baker *et al.*, 2002). This increase in species richness is ascribed, by some, to an edge effect (Murcia, 1995; Dutoit *et al.*, 2007).

2.2.4 Importance of biodiversity in agro-ecosystems

The primary importance of biodiversity to humans is the provision of resources such as food, timber, fibre, and fuel. Natural biodiversity provided the genetic resources for all agriculturally important domesticated crops and animals (Hainzelin, 2013). Although an estimated 7000 plant species have in the past been used in agriculture, only 30 species provide close to 90% of the world's calorie requirements (Wood *et al.*, 2005). Wild relatives of crop plants still function as a genetic resource to introduce specific traits into crop plants. Biodiversity also provides a range of wild food sources, ranging from fruits, fungi, fish and even arthropods (Wood *et al.*, 2005; Kelemu *et al.*, 2015; Söukand and Kalle, 2016).

Biodiversity is important for the provision of essential ecosystem services. Many ecosystem services, including provisioning services (medicines, building material, fibre, food, fuel, and genetic resources) and cultural services (tourism, recreation, spiritual, religious, education, inspiration, and aesthetic values) are directly dependent on biodiversity components such as a variety of species of plants, arthropods and animals (Hooper *et al.*, 2005; Egoh *et al.*, 2009; Cilliers *et al.*, 2013; Sandifer *et al.*, 2015). Regulatory and supportive ecosystem services (nutrient cycling, hydrological processes, pest control, pollination, detoxification of toxic compounds and control of the microclimate) are influenced by a combination of biotic and abiotic factors and their dependence on biodiversity may not be as direct, however, biodiversity still forms an important function in the provision of most of these services (Altieri, 1999; Egoh *et al.*, 2009; Le Maitre *et al.*, 2013; Mori *et al.*, 2017).

In the Grassland and Savanna biomes of South Africa, positive correlations were observed between areas with high vegetation diversity and areas that provide high levels of ecosystem services such as carbon storage, soil retention, water flow regulation and surface water supply (Egoh *et al.*, 2009). Similarly, other studies reported correlations between biodiversity and areas that provide high level of ecosystem services such as carbon storage, biological pest control, pollination, flood control, outdoor recreation and water purification (Chan *et al.*, 2006; Barral *et al.*, 2015; Felipe-Lucia and Comín, 2015; Manhães *et al.*, 2016). These studies indicate that biodiversity conservation may also contribute to the conservation of ecosystem services (Chan *et al.*, 2006; Turner *et al.*, 2007; Egoh *et al.*, 2009; Felipe-Lucia *et al.*, 2015).

In addition to ecosystem services, it is also hypothesized that biodiversity facilitates function and stability in ecosystems and that more diverse systems are less vulnerable to environmental changes whereas simplified ecosystems may result in destructive fluctuations in population densities (Elton, 1958; McCann, 2000; Isbell *et al.*, 2015; Wang and Loreau, 2016). This is explained by the insurance hypothesis which states it is more likely that diverse ecosystems will contain the necessary traits to allow some species to thrive during a

disturbance to compensate for other species affected by that disturbance (McNaughton, 1977; Isbell *et al.*, 2015; García-Palacios *et al.*, 2018). For example, diverse plant communities have a higher likelihood of containing drought-resistant species that could thrive during drought periods and compensate for the reduced growth of other species (Tilman and Downing, 1994). Up to 50% reduction in productivity was observed in low-diversity communities (with one or two plant species) after certain climatic changes, whereas high diversity communities (between 16 to 32 species) experiences only a 25% change in productivity (Isbell *et al.*, 2015). Similarly, other studies have shown that ecosystem stability and recovery after disturbance from equilibrium is generally higher with increasing biodiversity (Frank and McNaughton, 1991; Tilman, 1996; Tilman *et al.*, 2006; Haddad *et al.*, 2011).

Agriculture delivers provisioning services (food, bioenergy, and pharmaceuticals), but is dependent on regulatory and supportive services (biological pest control, pollination, nutrient cycling, and hydrological services) (Power, 2010). However, large-scale agriculture has led to simplified artificial ecosystems dominated by a few domesticated species of plants and animals (Altieri, 1999; Duru *et al.*, 2015). This may result in the loss of many important ecosystem services (Altieri, 1999). The economic cost of biodiversity loss can be significant because agro-ecosystems that are unable to perform pest and nutrient regulatory processes require high external input costs. Fertilizers are used to maintain soil fertility in the absence of natural decomposition, pesticides are used to regulate weeds, pathogens and arthropod pests, and genetic manipulation and breeding programs replace natural processes of selection and evolution (Altieri, 1999). In contrast, the higher biodiversity in traditional farming systems, polycultures, conservation agriculture, and agroforestry are often comparable to the biodiversity of natural ecosystems (Altieri, 1999).

There are multiple cases in the literature documenting reduced arthropod pest outbreaks in diversified cropping systems (Dempster, 1969; Garcia and Altieri, 1992; Bianchi *et al.*, 2006; Cai *et al.*, 2007; Rusch *et al.*, 2016; Leandro *et al.*, 2018). The resource concentration hypothesis state it is easier for arthropods to locate and establish a colony on host plants growing in low diversity stands (Root, 1973). The crop habitat provides almost unlimited resources for the development of specific crop associated herbivores (Rand *et al.*, 2014), but natural enemies benefit from diverse landscapes. According to the enemies hypothesis, diverse plant stands will support greater diversity and number of natural enemies, such as predators and parasitoids (Root, 1973). The plant community determines the quality, diversity, and abundance of herbivores (Bottrell *et al.*, 1998), which indirectly affects natural enemy abundance (Siemann, 1998). Natural enemies also require a range of plant species, not just to harbour their prey or hosts, but also to mate, develop and even feed on (Kaiser *et al.*, 2017).

Plants also provide natural enemies with overwintering sites and shelter against harsh weather conditions and other predators (Kaiser *et al.*, 2017). In addition, increased diversity in agricultural fields may also aid in pollination, windbreaks for crops and prevent soil erosion and movement of harmful pesticides to adjacent habitats (Altieri *et al.*, 1983; Marshall and Moonen, 2002; Brandle *et al.*, 2004).

The importance of biodiversity becomes apparent in the ecology of spiders. Spiders use different methods to catch prey, they occupy different microhabitats and they are active at different times of the year, and as a result, they can be classified in several functional groups (Uetz, 1991; Marc and Canard, 1997; Borges and Brown, 2001; Podgaiski *et al.*, 2013). For instance, wolf spiders (Lycosidae) are associated with ground debris, whereas sheet-web spiders (Linyphiidae) are frequently found in webs in high grasses (Dippenaar-Schoeman, 2014). Increasing plant diversity, vegetation types and landscape diversity will increase species richness of spiders and result in increased overall predation rates throughout the entire ecosystem (Marc and Canard, 1997; Sunderland and Samu, 2000).

The chemical and physical traits of plant communities can have direct effects on natural enemy behaviour and physiology. Plants release a range of volatile compounds which may attract natural enemies (Hilker and Fatouros, 2015; Dicke, 2016). *Melinis minutiflora* P.Beauv. (molasses grass), for example, releases volatile chemicals that attract the parasitoid *Xanthopimpla stemmator* (Thunberg) (Hymenoptera: Ichneumonidae) (Kals, 2004). *Xanthopimpla stemmator* is a pupal parasitoid of *Eldana saccharina* Walker (Lepidoptera: Pyralidae), a major pest of sugarcane. *Melinis minutiflora* is also repellent towards adult *E. saccharina* moths (Harraca *et al.*, 2011). Barker *et al.* (2006) observed reduced infestation levels of *E. saccharina* and reduced yield loss in sugarcane intercropped with rows of *M. minutiflora*.

Entomophagous arthropods are recognized for eating other arthropods, but they also consume a range of non-prey resources, including plant tissue, pollen, nectar and seeds (Lundgren, 2009). Hoverflies (Diptera: Syrphidae) and many parasitoid wasps only feed on host insects as larvae, while the adults are mandatory feeders on pollen and nectar (Kaiser *et al.*, 2017). Optional consumers of plant-derived resources include spider, ants, predatory bugs and predatory mites (Kaiser *et al.*, 2017). Non-prey resources function as an important supplement to the diet of natural enemies, especially when prey is not abundant, but also affects many aspects of their behaviour and physiology (Lundgren, 2009). Pollen and nectar are rich in lipids and carbohydrates which may be important for flight and migrations of natural enemies (Lundgren, 2009). Wanner *et al.* (2006) observed longer flight periods of parasitoid wasps, *Cotesia glomerata* (L.) (Hymenoptera: Braconidae), that fed on the nectar of *Anethum*

graveolens L. Hausmann *et al.* (2005) showed the importance of sugars in the recovery of *C. glomerata* after flight exhaustion.

Floral resources can increase the fitness of natural enemies. Araj and Wratten (2015) observed significantly higher longevity, fecundity and egg load in the aphid parasitoid, *Diaeretiella rapae* (M'Intosh) (Hymenoptera: Braconidae), that feed on nectar. Similarly, Robinson *et al.* (2008) showed how floral resources can increase the longevity and oviposition rate of lacewings, *Micromus tasmaniae* (Walker) (Neuroptera: Hemerobiidae) in the absence of prey. Some plants produce extrafloral nectar specifically to attract natural enemies including ants, spiders, lacewings, wasps, mites and predatory beetles (Heil, 2015). When prey is scarce, floral and extrafloral food resources is important to increase the longevity of natural enemies until a suitable host or prey is found. Olson and Nechols (1995) observed that female parasitoids, *Gryon pennsylvanicum* (Ashmead) (Hymenoptera: Scelionidae), can live up to 17 days when feeding on extrafloral nectar, but only 3 days in the total absence of food.

Pollination is another essential arthropod-mediated ecosystem service, without which many crops cannot function. Although bees are considered the primary agents for pollination, wasps, flies, beetles, moths, and butterflies also serve as important pollinators (Cassman *et al.*, 2005). The conservation of pollinators is also important in crops that can self-pollinate because pollinators are required for the persistence of farmland biodiversity and crops that require pollinators may be planted in subsequent seasons. Ricketts (2004) found higher species richness and abundance of wild bee species in coffee crops adjacent to forest patches compared to crops that were far away from forest margins. Subsequently, an 20% increase in coffee yields were reported (Ricketts, 2004). Insect pollination is also reported to increase crop quality and commercial value (Klatt *et al.*, 2014; Garatt *et al.*, 2014).

2.3 Soybean agro-ecosystems

2.3.1 Weed and arthropod diversity of soybean agro-ecosystems

There is limited data available on biodiversity associated with soybean agro-ecosystems as most studies focus on key pest species and economic benefits for farmers (Dlamini *et al.*, 2014). Studies were conducted in the early 1900s to identify potential arthropods pests for soybean. One of the earliest studies identified 209 species of insects on soybean and adjacent vegetation in the United States (Baldur, 1923). The majority belonged to the families Cicadellidae, Coccinellidae, Fulgoridae, Miridae, Chrysomelidae, Acrididae, Tettigoniidae, and Noctuidae. Evans (1985) surveyed soybean arthropods in southeast Queensland and collected a total of 304 species representing 104 families and 17 orders. Of all the species collected, 42% were phytophagous, 28% were predators, 24% were parasitoids and 6% were

classified as non-pests. In Cambodia, a total of 87 Hemiptera and 207 Hymenoptera morpho-species were collected (Chanthy *et al.*, 2013). Yu *et al.* (2014) sampled more than 63 000 arthropods on soybean in China during a two-year study, representing 51 families of spiders and insects. In Carolina, more than 37 000 individuals were collected in pitfall traps in a single growing season of which Collembola, Acari, Coleoptera, and Hymenoptera comprised the most abundant arthropod orders (Adams *et al.*, 2017). In Argentina, 12 arthropod orders, comprising of 65 families and 246 species were collected on soybean of which Hemiptera, Coleoptera, Hymenoptera, and Araneae were the most species-rich arthropod orders and Acari and Thysanoptera had the highest number of individuals (González *et al.*, 2017).

De la Feunte *et al.* (2006) surveyed 66 weed species that were associated with soybean in Argentina. The most abundant species were *Chenopodium album* L., *Cyperus rotundus* L., *Digitaria sanguinalis* (L.) Scop., *Dysphania ambrosioides* (L.) Mosayakin & Clemants, *Euphorbia lasiocarpa* Klotzsch, *Portulaca oleracea* L. and *Sida rhombifolia* (L.) Also, in Argentina, a total of 48 weed species were associated with soybean of which *Anoda cristata* (L.) Schlecht., *C. album*, *Stellaria media* (L.) Vill., *D. sanguinalis* were the most abundant (Scursoni and Satorre, 2010). In the United States, Rankins Jr *et al.* (2005) reported 68 weed species on 192 randomly selected soybean fields. The most abundant species were *Brachiaria platyphylla* (Griseb.) Nash., *Cyperus esculentus* L., *D. sanguinalis*, *Echinochloa crus-galli* (L.) P. Beauv., *Ipomoea hederacea* Jacq., *I. wrightii* Gray and *Sida spinosa* L. Chunyan *et al.* (2000) found 41 weed species that were associated with soybean fields in China of which *E. crus-galli* and *Commelina communis* L. were the most abundant species.

The diversity and abundance of weeds appear to be an important determinant of arthropod diversity. Shelton and Edwards (1983) surveyed insects in weed-free and weedy soybean fields. A total of 305 species were recorded with the highest diversity recorded in soybean fields with a mixture of grass and broadleaf weeds, whereas the weed-free soybean field had the lowest diversity. The most abundant predators included *Coleomegilla maculate* (DeGeer) (Coleoptera: Coccinellidae), *Orius insidiosus* (Say) (Hemiptera: Anthocoridae), and *Nabis* sp. (Hemiptera: Nabidae). All three predators showed reduced abundance in the weed-free soybean fields, whereas *Epilachna varivestis* Mulsant (Coleoptera: Coccinellidae), a pest of soybean, were more abundant in the weed-free soybean fields, possibly due to reduced predation rates.

Several biodiversity surveys have been done on economically important arthropod groups that occur on soybean in the United States:

- Wiedenmann *et al.* (1992) collected 42 species of ground beetles (Coleoptera: Carabidae) during a two-year study of which *Pterostichus chalcites* Say, *Harpalus pensylvanicus* De Geer and *Scarites subterraneus* F. were the most abundant predatory species in soybean.
- Pearce *et al.* (2004) collected 102 spider morpho-sepecies specimens from 27 families during a two-year study.
- Temple *et al.* (2013) surveyed stink bugs (Hemiptera: Pentatomidae) and collected more than 13 000 individuals during a three-year study. These belonged to 12 species of which *Piezodorus guildinii* (Westwood), *Nezara viridula* (L.), *Euschistus servus* (Say) and *Acrosternum hilare* (Say) were the most abundant species.
- During a two-year survey of soybean in, Gill and O'Neal (2015) sampled 50 species of pollinators of which the most abundant groups were Hymenoptera (Halictidae and Apidae) and Diptera (Syrphidae). Of the collected species that were covered in pollen, 38% were covered in soybean pollen.

The arthropod diversity associated with soybean cultivation systems has always considered to be low. However, from the above studies, it seems that soybean cropping systems may harbour higher diversity than originally thought. Arthropods are often looked at negatively as pests of crops. Yet, considering the high arthropod diversity found in agro-ecosystems, there are relatively few species that are regarded as pests of soybean (Tables 2.1 and 2.2). Soybean agro-ecosystems harbour arthropod functional groups that are beneficial to the productivity of the system (LeSar and Unzicker, 1978; Evans, 1985; Wiedenmann *et al.*, 1992; Gill and O'Neal, 2015). This includes a rich diversity of predators and parasitoids which function as natural enemies to suppress pest populations, as well as pollinators which may, despite the self-pollinating nature of soybean flowers, increase the seed set to further increase yield. Therefore, the preservation of arthropod diversity in soybean production systems is important because it provides essential ecosystem services.

Table 2.1: Arthropod pests of soybean in South Africa.

Common name	Scientific name	Source
African bollworm	<i>Helicoverpa armigera</i> Hübner (Lepidoptera: Noctuidae)	DAFF (2010)
Cabbage semi-looper	<i>Thysanoplusia orichalcea</i> L. (Lepidoptera: Noctuidae)	DAFF (2010)
Common cutworm	<i>Agrotis segetum</i> Schiff. (Lepidoptera: Noctuidae)	Van Wyk and Smit (2010)
Peanut leaf miner	<i>Aproaerema modicella</i> (Deventer) (Lepidoptera: Gelechiidae)	DAFF (2010)
Groundnut leaf miner	<i>Bilobata subsecivella</i> (Zeller) (Lepidoptera: Gelechiidae)	Du Plessis (2015)
Painted lady	<i>Venessa cardui</i> (L.) (Lepidoptera: Nymphalidae)	Van Wyk and Smit (2010)
False wireworm	<i>Somaticus</i> spp. (Coleoptera: Tenebrionidae)	Van Wyk and Smit (2010)
Chafer beetles	<i>Adoretus tessulatus</i> Burmeister (Coleoptera: Scarabaeidae)	Du Plessis (2015)
Black maize beetle	<i>Heteronychus arator</i> (F.) (Coleoptera: Scarabaeidae)	Du Plessis (2015)
Green vegetable bug	<i>Nezara viridula</i> (L.) (Hemiptera: Pentatomidae)	Van Wyk and Smit (2010)
Tip wilter	<i>Anoplocnemis curvipes</i> (F.) (Hemiptera: Coreidae)	Du Plessis (2015)
Peanut aphid	<i>Aphis craccivora</i> Koch (Hemiptera: Aphididae)	Du Plessis (2015)
Red spider mite	<i>Tetranychus cinnabarinus</i> (Boisduval) (Trombidiformes: Tetranychidae)	Van Wyk and Smit (2010)

Table 2.2: Arthropod pests of soybean in other parts of the world.

Order and Family	Name	USA	South America	Asia	Africa	Source
Lepidoptera: Noctuidae	<i>Hypena Scabra</i> (F.)	X				Baldur (1923)
	<i>Pseudoplusia includens</i> (Walker)	X	X			Panizzi and Corrêa-Ferreira (1997); O'Neal and Johnson (2010)
	<i>Trichoplusia ni</i> (Hübner)	X				Boldt <i>et al.</i> (1975)
	<i>Anticarsia gemmatilis</i> Hübner	X	X			Funderburk <i>et al.</i> (1999); Panizzi and Corrêa-Ferreira (1997)
	<i>Helicoverpa</i> spp.	X		X		Funderburk <i>et al.</i> (1999); Biswas (2013)
	<i>Chrysodeixis includens</i> (Walker)	X				Funderburk <i>et al.</i> (1999)
	<i>Spodoptera</i> spp.	X	X	X		Panizzi and Corrêa-Ferreira (1997); O'Neal and Johnson (2010); Biswas (2013)
	<i>Agrotis</i> spp.	X	X	X		Panizzi and Corrêa-Ferreira (1997); O'Neal and Johnson (2010)
	<i>Heliothis</i> spp.	X		X		O'Neal and Johnson (2010)
Lepidoptera: Pyralidae	<i>Elasmopalpus lignosellus</i> (Zeller)	X	X			Funderburk <i>et al.</i> (1999); Panizzi and Corrêa-Ferreira (1997)
	<i>Etiella zinckenaella</i> (Treitschke)		X	X		Panizzi and Corrêa-Ferreira (1997); Talekar and Chen (1983)
Lepidoptera: Eribidae	<i>Spilosoma obliqua</i> Walker			X		Biswas (2013)
Lepidoptera: Tortricidae	<i>Epinotia aporema</i> (Walsingham)		X			Panizzi and Corrêa-Ferreira (1997)
Coleoptera: Coccinellidae	<i>Epilachna varivestis</i> Mulsant	X				Shelton and Edwards (1983)
Coleoptera: Chrysomelidae	<i>Cerotoma</i> spp.	X	X			Funderburk <i>et al.</i> (1999); Panizzi and Corrêa-Ferreira (1997)
	<i>Megascelis</i> spp.		X			Panizzi and Corrêa-Ferreira (1997)
	<i>Diabrotica speciose</i> (Ger.)		X			Panizzi and Corrêa-Ferreira (1997)
Coleoptera: Scarabaeidae	<i>Anomala</i> spp.		X	X		Panizzi and Corrêa-Ferreira (1997); O'Neal and Johnson (2010)
	<i>Sternechus subsignatus</i> Boheman		X			Panizzi and Corrêa-Ferreira (1997)
Hemiptera: Pentatomidae	<i>Nezara viridula</i> (L.)	X	X	X	X	Clarke (1992); Panizzi and Corrêa-Ferreira (1997)
	<i>Piezodorus</i> spp.	X	X	X	X	Wada <i>et al.</i> (2006); Panizzi and Corrêa-Ferreira (1997); Funderburk <i>et al.</i> (1999); Abate and Ampofo (1996)
	<i>Acrosternum</i> spp.	X	X			Funderburk <i>et al.</i> (1999); Panizzi and Corrêa-Ferreira (1997)
	<i>Euschistus</i> spp.	X	X			Funderburk <i>et al.</i> (1999); Panizzi and Corrêa-Ferreira (1997)
	<i>Dichelops furcatus</i> (F.)		X			Panizzi and Corrêa-Ferreira (1997)
	<i>Dolycoris baccarum</i> (L.)			X		O'Neal and Johnson (2010)
Hemiptera: Membracidae	<i>Spissistilus festinus</i> (Say)	X				Funderburk <i>et al.</i> (1999)
Hemiptera: Alydidae	<i>Riptortus clavatus</i> Thunberg			X		Wada <i>et al.</i> (2006)
Hemiptera: Cicadellidae	<i>Empoasca fabae</i> (Harris)	X				Lam and Pedigo (1998)
Hemiptera: Aleyrodidae	<i>Bemisia</i> spp.		X	X		Panizzi and Corrêa-Ferreira (1997); Biswas (2013)
Hemiptera: Aphididae	<i>Aphis glycines</i> Matsumura	X		X		O'Neal and Johnson (2010)
	<i>Aulacorthum solani</i> (Kalt.)			X		O'Neal and Johnson (2010)
Hemiptera: Coreidae	<i>Clavigralla</i> spp.				X	Abate and Ampofo (1996)
	<i>Anoplocnemis curvipes</i> F.				X	Abate and Ampofo (1996)
Orthoptera: Acrididae	<i>Melanoplus</i> spp.	X				Lam and Pedigo (1998)
Diptera: Agromyidae	<i>Ophiomyia</i> spp.			X		Talekar and Chen (1983)
	<i>Melanagromyza</i> spp.			X		Talekar and Chen (1983)
Diptera: Anthomyiidae	<i>Delia platura</i> Meigen	X		X		O'Neal and Johnson (2010)
Diptera: Cecidomyiidae	<i>Asphondylia</i> spp.			X		O'Neal and Johnson (2010)
Trombidiformes: Tetranychidae	<i>Tetranychus urticae</i> Koch	X				O'Neal and Johnson (2010)

2.4 Glyphosate-tolerant soybean

2.4.1 Background

Glyphosate is a non-selective and systemic herbicide that is used globally to control a broad spectrum of non-crop plants under varied conditions (Perez-Jones and Mallory-Smith, 2010). Soybean is among the most extensively cultivated glyphosate-tolerant crops in the world (ISAAA, 2018). In South Africa, policies that enable the use of transgenic crops also resulted in the rapid adoption of glyphosate-tolerant soybean (Dlamini *et al.*, 2014). In the 2018/2019 growing season, approximately 787 000 hectares of soybean, of which 95% were genetically modified to be herbicide-tolerant, was planted in South Africa (DAFF, 2018; ISAAA, 2018).

2.4.2 Impact on plants

Literature reports general decreasing species richness and abundance of non-crop plants in Glyphosate-tolerant crops (Buckelew *et al.*, 2000; Gulden *et al.*, 2009). However, glyphosate drift may also affect non-target areas in adjacent crop fields. Agro-chemical drift into adjacent field margins is facilitated through air and water transport, which include droplet drift during application and vapour drift after application (Cessna *et al.*, 2005). With the proper application method and procedures, drift levels are low but incorrect procedures and strong winds may cause high levels of drift. Carlsen *et al.* (2006) measured the drift of commonly used herbicides and reported drift ranging between 0.1 and 9% of the applied field dose and reaching up to 150 m in severe cases. Alves *et al.* (2017) reported drift of glyphosate from nearly 70% at 2 m and only 0.1% at a distance of 12 m from the application area.

The impact of agro-chemical drift can be highly variable, but a wide range of non-target plant species is at potential risk from herbicide drift. Gove *et al.* (2007) simulated the effects of glyphosate spray drift and found that the biomass and proportion of flowering of the most sensitive plant species were affected at levels as low as 1% of the field-applied dose. The adverse effects on non-target plants may range from plant death to minor effects on vegetation cover, structure, and biomass as well as effects on flowering and seed production and germination (Marshall, 2001). Kleijn and Snoeiijing (1997) found that low levels of fluroxypyr (5 and 10%) significantly reduced species richness while decreasing biomass of forbs and increasing the biomass of grasses. Boutin *et al.* (2014) observed a delay in flowering time as well as a significant reduction in the number of plants that flowered as well as a shortening of the flowering period of margin flora adjacent crop fields managed with herbicide.

2.4.3 Herbicide-resistant weeds in glyphosate-tolerant crops

Globally, there are 42 weed species listed to be resistant against glyphosate (Heap, 2018). The first case of glyphosate resistance was observed in 1996 in rigid ryegrass (*Lolium rigidum* Gaudin), over 20 years after glyphosate herbicides were first introduced (Heap, 2018). In the Western Cape of South Africa, biotypes of three weed species (*Conyza bonariensis* (L.) Cronquist., *Plantago lanceolata* L. and *Lolium rigidum*) evolved resistance against glyphosate (Heap, 2018). Before the advent of glyphosate-resistant crops, weed control involved a range of methods including the application of herbicides with different modes of action and tillage practices. Adoption of glyphosate-resistant crops made reduced- or no-tillage possible, which removed diversity in weed control practices, which increases the likelihood of resistance development (Powles, 2008).

2.4.4 Weeds shifts due to glyphosate use and changes in cultivation practices

Herbicide-resistant crops resulted in significant changes in weed management practices. The application of postemergence herbicides such as glyphosate increased, the use of soil-applied herbicide declined and the adoption of conservation tillage increased (Carpenter and Gianessi, 1999; Young, 2006). Shifts occur among weeds that exhibit natural tolerance to the herbicide, while weeds more susceptible to the herbicide is killed, and consequently repeated glyphosate application may cause a shift towards weed species that is difficult to control (Reddy and Norsworthy, 2010). Weed surveys in the United States revealed increased importance of some species of weeds (*Ambrosia trifida* L., *Commelina benghalensis* L., *Mollugo verticillata* L., *Oenothera laciniata* Hill, *Physalis* spp. And *Taraxacum officinale* Weber) in soybean cultivation systems from 1995 to 2009, while other species (*Abutilon theophrasti* Medic., *Cynodon dactylon* (L.) Pers., *Desmodium tortuosum* (Sw.) DC and *Sorghum halepense* (L.) Pers.) decreased in importance (Webster and Nichols, 2012). From 1995 to 2009 the biggest agronomic change was the arrival and rapid adoption of glyphosate-tolerant soybean. Although some species with high tolerance to glyphosate may increase in abundance, sensitive species that emerge after glyphosate application may also increase in abundance. Hilgenfeld *et al.* (2004) showed that in glyphosate-tolerant soybean in the United States, 50% morning glory (*Ipomoea hederacea*) survived the standard field dose of glyphosate and is thus naturally tolerant, while *Sorghum bicolor* (L.) Moench emerges late in the season after glyphosate application.

2.4.5 Impact on arthropods

Herbicides may have direct or indirect effects on arthropods. Changes in the diversity and species assemblages of the plant community resulting from herbicide application may subsequently impact the arthropod community (Cerdeira and Duke, 2006). This is referred to

as indirect effects. Direct effects include any adverse effect on the biology, survival or behaviour of the non-target organism. For example, no direct harmful effect of glyphosate on the survival and behavior of the spider *Lepthyphantes tenuis* (Blackwall) (Araneae, Linyphiidae) were found in laboratory studies (Haughton *et al.*, 2001a), whereas field surveys revealed a lower abundance of *L. tenuis* in plots treated with glyphosate because of decreased plant height and increased amounts of dead vegetation (Haughton *et al.*, 2001b).

Indirect effects

Lower species richness and abundance of butterflies were observed in field margins treated with glyphosate (Feber *et al.*, 1996). Herbicide application reduced flower abundance and subsequently butterfly abundance. The decline of the monarch butterfly, *Danaus plexippus* L. (Lepidoptera: Nymphalidae) in North America is partly attributed to the large-scale adoption of glyphosate-tolerant soybean and maize in the United States (Brower *et al.*, 2012). Large-scale adoption of glyphosate-tolerant soybean and maize significantly reduced the abundance of milkweed (*Asclepias syriaca* L.) in agricultural fields (Brower *et al.*, 2012). Hartzler (2010) observed a 90% reduction of *A. syriaca* in agricultural fields of Iowa between 1999 to 2009, which led to the subsequent reduction in the abundance of *D. plexippus*.

Jackson and Pitre (2004a) found reduced population densities of a predatory bug, *Geocoris punctipes* (Say) (Hemiptera: Geocoridae), in soybean fields which received glyphosate applications that resulted in decreased weed abundance and diversity. Studies also generally indicate lower diversity and abundance of arthropods in weed-free soybean fields compared with soybean fields with high weed diversity and abundance (Shelton and Edwards, 1983; Balfour and Rypstra, 1998; Buckelew *et al.*, 2000). Therefore, maintaining at least some weed species may facilitate higher arthropod diversity. Dewar *et al.* (2003) used band spraying of glyphosate in sugarbeet to increase diversity and biomass of weeds without compromising yield. Consequently, Dewar *et al.* (2003) found higher diversity and abundance of beetles (Carabidae and Staphylinidae) and spiders in pitfall traps in fields in which glyphosate was band-sprayed onto sugarbeet compared to fields that received the overall application.

Direct effects

Increased outbreaks of spider mite, *Tetranychus urticae* Koch (Trombidiformes: Tetranychidae), were observed after glyphosate application (Pedigo *et al.*, 2002). This effect was largely ascribed to fungicidal effects of glyphosate formulations on entomopathogenic fungi which usually suppresses spider mite populations (Pedigo *et al.*, 2002). Significantly more lacewings, *Chrysopa* spp. (Neuroptera: Chrysopidae), were sampled using yellow sticky

traps in conventional soybean production system compared to glyphosate-tolerant soybean systems (Jasinski *et al.*, 2003). This was ascribed to the reduction of prey (soybean aphid, *Aphis glycines* Matsumura) in glyphosate-tolerant soybean varieties. The reason for the reduced abundance of soybean aphid in glyphosate-tolerant varieties is unclear. Soybean aphid may either have a higher preference for conventional varieties or is negatively influenced by the application of glyphosate. Glyphosate was found to perturb the gut microbiota of honey bees, *Apis mellifera* L. (Hymenoptera: Apidae), with potential effects on the health of bees, for instance, bees exposed to glyphosate exhibited increased susceptibility to *Serratia marcescens* Bizio, a pathogen of bees (Motta *et al.*, 2018).

Some studies indicate that some aspects of arthropod biology might be affected. For example, reduced fertility, fecundity, adult longevity, prey consumption, and locomotive activity were observed in some agriculturally important pest enemies after exposure to glyphosate (Schneider *et al.*, 2009; Benamú *et al.*, 2010; Evans *et al.*, 2010). However, the majority of studies report no direct adverse effects of herbicide-tolerant soybean and its associated weed management systems on arthropod biology and diversity (Buckelew *et al.*, 2000; Bitzer *et al.*, 2002; Pedigo *et al.*, 2002; Jasinski *et al.*, 2003; McPherson *et al.*, 2003; Jackson and Pitre, 2004b; Imura *et al.*, 2010). It appears that commercially available glyphosate-based herbicides have minimal direct effect on arthropods, although certain aspects of arthropod biology and behaviour may be affected. This is still important to consider since reduced arthropod performance may adversely affect arthropod diversity in the long-run.

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Chapter 3: Materials and Methods

3.1 Study sites

Five localities (Table 3.1) were selected in the major soybean-producing provinces of South Africa namely the Free State, Gauteng, KwaZulu-Natal and Mpumalanga (Dlamini *et al.*, 2014). These provinces are represented by the Grassland Biome. Together these provinces produced a total of 1 175 200 tons of soybean during the 2018/2019 production season (DAFF, 2019).

Table 3.1 Vegetation units, altitude and climatic conditions of the five localities (Mucina and Rutherford, 2006).

Localities	Altitude (m a.s.l.)	MAP (mm)	MAT (°C)	MFD	Vegetation unit
Bapsfontein	1300-1635	654	15.8	28	Rand Highveld Grassland
Tarlton	1420-1760	662	14.8	41	Soweto Highveld Grassland
Winterton	1040-1440	836	16.2	20	Northern KwaZulu-Natal Moist Grassland
Belfast	1520-1780	726	14.7	32	Eastern Highveld Grassland
Reitz	1380-1740	634	14.4	50	Eastern Free State Clay Grassland

MAP – Mean annual precipitation; MAT – Mean annual temperature; MFD – Mean number of frost days.

Soybean is used in crop rotation systems with maize at all the sampling sites. Farm fences and small dirt roads formed anthropogenic boundaries between soybean fields and field margins. Livestock grazing (cattle and sheep) was common in field margins surrounding crop fields. Sample sites were selected to include a range of management regimes and environmental variables to acquire baseline data for biodiversity associated with soybean agroecosystems in general (Table 3.1 and 3.2). At each locality, two sites with soybean fields were selected for surveys (Figure 3.1; Table 3.3).

Table 3.2 Summary of general information regarding sampling sites.

Localities and sites	Production system	Insecticide application	Row width (cm)	Irrigation	Soil disturbances
Bapsfontein A	C	×	70-80	Dry	CT
Bapsfontein B	GT	×	70-80	Dry	CT
Tarlton A	C	✓	90-100	Irrigation	CT
Tarlton B	GT	✓	90-100	Irrigation	CT
Winterton A	C	✓	70-80	Dry	CT
Winterton B	GT	✓	70-80	Dry	CT
Belfast A	GT	✓	70-80	Dry	RT
Belfast B	GT	✓	70-80	Dry	RT
Reitz A	GT	✓	90-100	Dry	RT
Reitz B	GT	✓	90-100	Dry	RT

C – Conventional (Non-glyphosate tolerant); GT – Glyphosate tolerant; CT – Conventional tillage; RT – Reduced tillage.



Figure 3.1: Visual representation of the soybean fields and field margin vegetation at the ten study sites.

Table 3.3: Sample site locations and altitude.

Sampling sites	Province	Altitude (m a.s.l.)	Coordinates
Bapsfontein A	Gauteng	1634	26°04'27.2"S, 28°23'03.5"E
Bapsfontein B	Gauteng	1636	26°04'20.9"S, 28°25'00.5"E
Tarlton A	Gauteng	1565	26°03'10.3"S, 27°36'00.7"E
Tarlton B	Gauteng	1564	26°12'29.4"S, 27°22'06.4"E
Winterton A	KwaZulu-Natal	1210	29°00'36.2"S, 29°28'47.1"E
Winterton B	KwaZulu-Natal	1147	28°56'42.7"S, 29°30'48.5"E
Belfast A	Mpumalanga	1844	25°47'16.6"S, 29°56'43.8"E
Belfast B	Mpumalanga	1766	25°48'36.8"S, 30°03'58.7"E
Reitz A	Free State	1724	28°03'02.0"S, 28°36'41.2"E
Reitz B	Free State	1644	27°53'05.8"S, 28°24'01.9"E

3.2 General method

At each of the five localities, two sites were selected at random (Fig.3.2). At each site, a soybean field surrounded by natural grassland were selected, and two transects (along the soybean field – natural grassland gradient) were placed 250 m apart (Fig. 3.3).

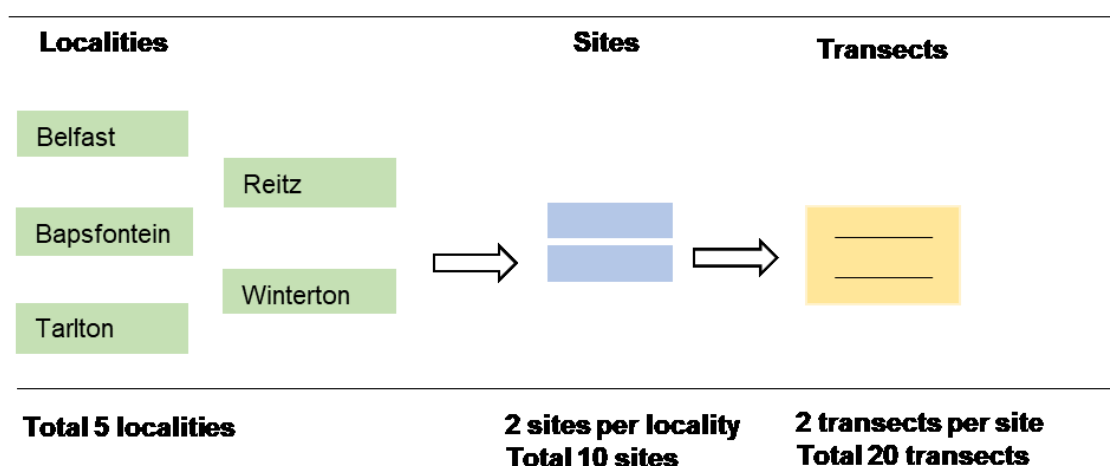


Figure 3.2: Five localities were selected. At each locality two sites were surveyed, each with two transects to cover the soybean field – field margin gradient.

In each transect, there were 3 treatment zones (sampling plots): the soybean crop, field boundary and natural grassland (Fig. 3.3). Plots were 50 m apart, with the first plot situated 50 m within the soybean crop, the second within the field boundary (30m wide zone adjacent to the crop margin with a high level of anthropological disturbance) and the third plot 50 m into the adjacent natural grassland. The 50 m distance from the soybean field for the natural grassland sample was chosen in accord with a study from Botha *et al.* (2015) who observed plant and arthropod diversity patterns remained the same beyond 30 m from maize fields.

Sampling plots were 5 × 5 m (25 m²) in size for arthropod sampling and 10 × 10 m (100 m²) for the plant diversity surveys as per previous studies (Botha *et al.*, 2015).

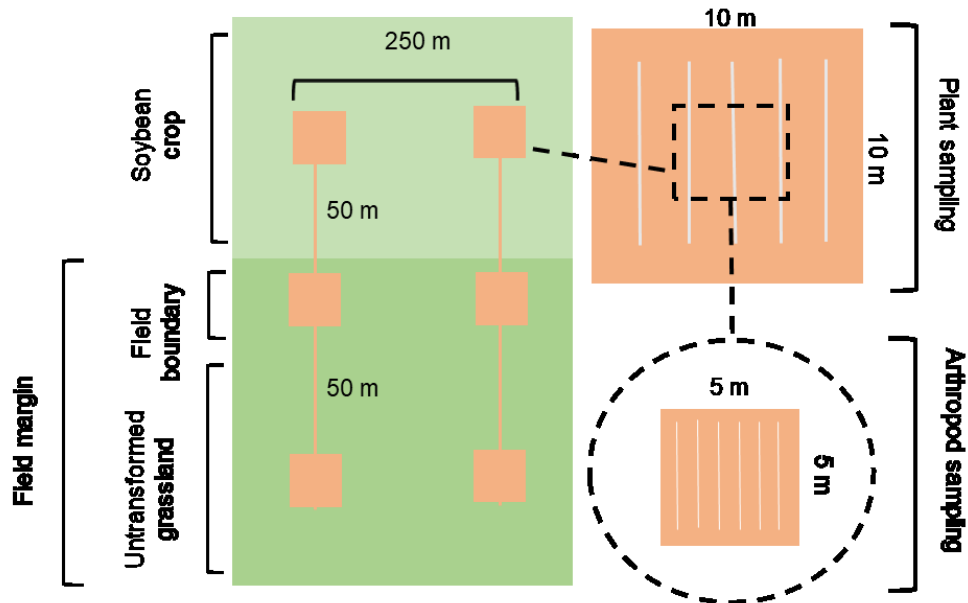


Figure 3.3: Transect and sampling plot layout at each of the ten sites. Dashed lines indicated arthropod sampling.

3.3 Arthropod sampling

Surveys in Bapsfontein and Tarlton were conducted in March 2018, and surveys at Winterton, Belfast and Reitz were conducted in February 2019. The target arthropod group for this study was plant-dwelling arthropod species since one of the main objectives of the study was to investigate plant-arthropod diversity relationships. Surveys were conducted during the reproductive stages (flowering stages) of the crop. Studies have shown this period is ideal to sample a comprehensive arthropod community (Chanthy *et al.*, 2013; González *et al.*, 2017). This also ensured that all the soybean plants were at a similar growth stage during the survey. Surveys were conducted between 07:00 and 17:00, which has been shown to not affect the diversity and richness of predacious arthropods (Greyvenstein 2019).

Suction sampling by means of an adapted D-vac method was used for arthropod collection (Dietrick *et al.* 1960). The D-vac suction machine was moved slowly over plant material in each plot. Seven swaths per plot were made by moving the D-vac nozzle in a zigzag-pattern over plant material in each swath. Within soybean plots, the D-vac was moved in an up and down motion to collect arthropods that occurred on lower and upper foliage of plants, and to collect arthropods on other plants such as weeds that often occurred inside the crop fields. This study focussing on above-ground and plant dwelling arthropods, therefore, soil arthropods were not sampled in this study. Soil dwelling arthropods that were present at the

lower parts of plants during sampling were easily sampled, but the aim was to avoid collecting from the soil surface with the D-vac.

The samples collected in each plot were placed in separate plastic bags and frozen to preserve the contents. The contents of each bag were then sorted in the laboratory to separate the arthropods from the plant material and other debris. The arthropods were preserved in bottles containing 70% alcohol. Arthropods were classified up to morpho-species level with the aid of literature such as Picker *et al.* (2019), Scholtz and Holm (2012) and Dippenaar-Schoeman (2014). This method was shown to provide estimations of arthropod species richness and diversity similar to methods that classify arthropods in species by taxonomists (Oliver and Beattie, 1996). Care was taken to ensure morpho-species were regarded as the same species across all localities and treatment zones. The number of morpho-species, as well as the abundance of each morpho-species, was determined for each plot.

3.4 Vegetation sampling

Inside each 10 x 10 m treatment zone, five line-transects of 10 m each were placed, with the first transect 1 m inside the sampling plot and the others spaced 2 m apart and parallel to each other. The closest shrub, forb and grass species were identified and recorded at intervals of 1 m along the 10 m transect. If no plant occurred within 0.5 m before or after the point, bare ground was recorded. Plants were identified to species level and species names follow Germishuizen *et al.* (2006).

3.5 Data analysis

3.5.1 Plant and arthropod species composition

To illustrate how the different treatment zones (soybean crop, boundary and grassland) compared in terms of arthropod and plant species composition, Non-metric Multidimensional Scaling (NMDS), based on the Bray-Curtis Dissimilarity Index, was performed with PRIMER 6 software (Clarke and Gorley, 2006). Permutational Multivariate Analysis of Variance (PERMANOVA) was performed in PRIMER 6 using abundance data to test whether significant differences in plant and arthropod communities existed between the different zones. All PERMANOVA analyses were performed with 999 permutations using Bray-Curtis similarity and type III sums of squares. Indicator species analysis (IndVal) was applied in R software to determine indicator species for each zone (Dufrêne and Legendre, 1997).

3.5.2 Plant and arthropod diversity patterns

Species richness and species diversity indices were applied to express the diversity of plants and arthropods in each of the plots and across treatments, sites, and localities (Table 3.4). Index values were calculated with PRIMER 6 software (Clarke and Gorley, 2006). Hierarchical

linear modelling (HLM) was performed in SPSS software to test for significant differences in index values along the soybean field-field margin gradient (Hancock and Mueller, 2010). Transects were specified as subject (ID) to account for the nestedness of transects within localities. The covariance structure was specified as unstructured. Effect sizes (Cohen's *d*) were used to express practical significance between sampling points where residual as well transect variance were taken into account in the calculation of the effect sizes (Ellis and Steyn, 2003).

Table 3.4: Parameters that were used to calculate plant and arthropod diversity.

Indices	Equation	Description
Species richness (S)	---	Includes the number of species. It does not take abundance into account.
Abundance (N)	---	The number of individuals per species.
Margalef's species richness (d)	$(d) = \frac{(S-1)}{\ln N}$	S is the number of species and N is the number of individuals in the sample.
Simpson's diversity index (D')	$(D') = \frac{\sum n_i(n_i-1)}{N(N-1)} - 1$	N is the total number of individuals for the species n_i is the number of individuals for the <i>i</i> 'th species.
Shannon-Wiener diversity index (H')	$(H') = - \sum p_i \ln p_i$	p_i is the relative abundance of the <i>i</i> 'th species.
Pielou's evenness index (J')	$(J') = H'/H'_{\max} = \frac{H'}{\ln S}$	H' is the Shannon-Wiener diversity index. S is the species richness.

3.5.3 Effect of land-use intensity and environmental variables on plant and arthropod species assemblages

Canonical Correspondence Analysis (CCA) was applied in PAST software to depict how different points compared in terms of plant and arthropod species composition and to assess the importance of certain environmental variables (altitude, mean annual temperature, mean annual precipitation, latitude and longitude), farming type (cultivation of conventional soybean or glyphosate-tolerant soybean) and land-use intensity in determining plant and arthropod species assemblages (Hammer *et al.*, 2001).

The land-use intensity was used as an indication of anthropological disturbance. The land-use in approximately 1 km radius surrounding each sample plot was observed with satellite images and measurement tools using Google My Maps. Three land-use types were recorded. These were cropland, buildings and settlements and roads and farm fences. For each sample plot, a land-use intensity rating was calculated. Refer to Table 3.5 for a description of the scoring system. A score out of a possible 8 was given for each land-use type. The scores for each of

the three land-use types were then added together to acquire a land-use intensity rating for each sample plot.

Table 3.5: Scoring system to describe the frequency of each of the three land-use types within a 1 km radius around each sample plot.

Score	Description
8	Frequent presence of land-use in area. Sample plot completely surrounded by land-use.
6	Frequent presence of land-use in area. Sample plot surrounded by land-use and natural habitat.
4	Occasional and scattered presence of land-use in area. Close proximity to sample plot.
2	Occasional and scattered presence of land-use in area. Distant from sample plot.
0	Land-use not present

3.5.4 Correlations between plant-arthropod diversity and predator-prey diversity

Permutational Multivariate Analysis of Variance (PERMANOVA) was performed in PRIMER 6 using abundance data to test whether significant differences in plant and arthropod communities existed between the three treatment zones. Analyses were performed on the overall plant and arthropod sample as well as separately on dominant plant families (Poaceae, Asteraceae and Fabaceae) and dominant arthropod functional groups (herbivores, spiders, other predators and parasitoids). All PERMANOVA analyses were performed with 999 permutations using Bray-Curtis similarity and type III sums of squares. Multivariate Homogeneity of group dispersions (PERMDISP) was performed to test for significant differences in beta-diversity between the three treatment zones. PERMDISP with 999 permutations was performed on Bray-Curtis similarity matrices of datasets containing all plant and arthropods after a presence/absence transformation of the abundance data.

Spearman's rank-order correlation analyses were conducted in SPSS software to test for significant correlations between plant and arthropod species richness, abundance and diversity index values. Correlations were determined between major plant groups (all plants, Fabaceae, Asteraceae and Poaceae) and major arthropod groups (all arthropods, spiders, other predators, parasitoids and herbivores). Correlations were also determined between species richness, abundance and diversity index values for herbivores and entomophagous arthropods (spiders, other predators and parasitoids).

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Chapter 4: Plant species composition and diversity patterns of soybean agro-ecosystems

Abstract

Large-scale cultivation of crops and the associated degradation and fragmentation of natural habitat has led to a general decrease in global biodiversity. South Africa has an established grain industry. Soybean is one such crop that is widely cultivated in the Grassland Biome of South Africa, but the effects that its cultivation practices have on biodiversity in adjacent habitat are not fully known. It is important to expand current knowledge about effects on biodiversity to assess and adapt current agricultural practices to ensure that important ecosystem services are not lost from these agro-ecosystems. To assess the effect of soybean fields on plant diversity, ten sites were surveyed in major soybean production regions of South Africa. Sample plots were placed in three zones at each site, i.e. the soybean crop, field boundary (transition zone between cropland and natural habitat) and adjacent untransformed grassland. A total of 4910 plant individuals were recorded from 60 plots (5 localities x 2 sites x 2 transects x 3 treatments), which amounted to 320 species. As shown previously for maize agro-ecosystems, plant richness and diversity loss were apparent in soybean fields, while there was no significant difference between plant species richness and diversity of the field boundary and adjacent untransformed grassland. However, the boundary, dominated by alien plant species, did contain a significantly different species composition from the untransformed grassland. This suggests that disturbance, resulting from the adjacent crop field, led to species losses and gains that changed the plant species assemblages of the field boundary but had no effect on natural grassland beyond the boundary (> 50 m). Furthermore, unique assemblages of plant species and high species richness and diversity in the boundary and untransformed grassland suggest that these zones may have important conservation value by supporting unique plant species and ecosystem services.

Keywords Agriculture, Species Richness, Biodiversity, Grassland, Ecosystem Services, Soybean, Grassland, Field Boundary.

4.1 Introduction

As primary producers, plants perform an important function in terrestrial ecosystems. Plant diversity also performs important ecosystem services in agricultural landscapes, such as reducing soil erosion, providing habitat for beneficial arthropods, and functioning as windbreaks for crops (Clark *et al.*, 2005; Marshall, 2005). Therefore, the value of wild and cultivated plants for agricultural systems is manifold, especially in strong agricultural economies such as is the case for South Africa. However, large-scale transformation and fragmentation of natural habitat through agriculture result in loss of plant diversity by substituting it with domesticated crops (Altieri, 1999) and alien weed species (Botha *et al.*, 2015). In this context, remnants of natural habitat become important reservoirs and conservation areas for biodiversity and ecosystem services. However, remnants of natural habitat are facing increasing pressure from indirect threats, most often through deposition and drift of agrochemicals into non-target areas (Wynberg, 2002; Felsot *et al.*, 2010).

It has become important to continually assess the potential impact that agricultural activities have on natural biodiversity in South Africa. In order to understand the nature and complexity of agro-ecosystems, it is important to gather baseline biodiversity data. Soybean is a widely cultivated crop in the Grassland Biome of South Africa and it is therefore important to describe baseline plant diversity patterns and species assemblages for this agro-ecosystem. This baseline is important for the selection of priority species for future monitoring and management (Bakker, 2008).

Croplands are generally considered to be disturbed habitats through agro-chemical application, tillage practices and cultivation of monocultures (Feber *et al.*, 1996; Stamps and Linit, 1998; Witmer *et al.*, 2003). Therefore, the first hypothesis proposes that soybean fields will have lower diversity and evenness of plants than untransformed grassland. The disturbance associated with crop fields may also affect the plant diversity and species composition of adjacent habitats although the most significant effects are reported in the zone directly adjacent crop fields (Boutin and Jobin, 1998; Piessens *et al.*, 2006; Pryke and Samways, 2012; Botha *et al.*, 2015). Therefore, the second hypothesis proposes that plant species richness and diversity of the field boundary (zone directly adjacent to the crop) will be negatively affected in terms of diversity and evenness by crop fields. The third hypothesis proposes that the field boundary vegetation will be replaced by a unique assemblage of plant species that are adapted to tolerate the disturbance in the boundary and differs from the adjacent untransformed grassland.

4.2 Materials and Method

Ten sites were surveyed in the major soybean production regions of South Africa. Refer to section 3.1 and 3.2 of Chapter 3 for a description of the study sites and the general experimental layout. Plant diversity was recorded in the soybean crop, field boundary (transition zone between crop fields and adjacent natural habitat) and untransformed grassland adjacent crop fields. Plant species were recorded following an adapted fixed width (2 m) line transect method (Chapter 3, section 3.4). Plant species composition was expressed using Non-metric Multidimensional Scaling (NMDS), Permutational Multivariate Analysis of Variance (PERMANOVA) and Indicator Species Analysis (IndVal) (Chapter 3, section 3.5.1). Plant diversity patterns were expressed through diversity indices and analysed with Hierarchical Linear Modelling (HLM) (Chapter 3, section 3.5.2). The influence of environmental variables on plant assemblages was assessed with Canonical Correspondence Analyses (CCA) (Chapter 3, section 3.5.3).

4.3 Descriptive results

Rarefaction curves indicated sufficient sampling effort for the plant diversity survey (Appendix A, Figure 8.1). A total of 320 plant species were recorded and 4910 plants were tallied (refer to Appendix A, Tabel 8.5 for a full list of plant species recorded in soybean agro-ecosystems during this study). The lowest number of species was recorded in the soybean crop with 39 species, while 127 and 246 species were recorded in the field boundary and grassland respectively (Refer to Appendix A, Figure 8.2 for the percentage shared and unique species between the three zones). Overall, 52 plant families were represented by the study. Table 4.1 lists the ten best-represented families according to the number of species from each family and the percentage contribution of each family to the total number of plants counted. According to the number of species collected from each family, the Poaceae, Asteraceae and Fabaceae were the best-represented families across all the zones and collectively amounted to 54% of the total number of species (Table 4.1). The Poaceae and Asteraceae were dominant in the boundary and grassland and respectively made up 78% and 71% of plants counted from each of theses zones (Table 4.1). Cyperaceae, Oxalidaceae, and Commelinaceae were the most abundant plant families in the soybean crop, representing a combined 65% of the plants counted within soybean fields.

Table 4.1: Best-represented plant families (according to the number of species from each family and percentage contribution of each family to the total number of plants counted, excluding *Glycine max*) for the overall sample, soybean crop, field boundary, and grassland.

Family	Overall		Soybean		Boundary		Grassland	
	No. of Species	% of individuals	No. of Species	% of individuals	No. of Species	% of individuals	No. of Species	% of individuals
Poaceae	74	41.61	10	8.21	41	56.02	52	50.29
Asteraceae	72	17.52	7	5.98	34	21.85	58	21.09
Cyperaceae	9	4.58	1	19.83	1	4.51	8	1.43
Oxalidaceae	5	3.85	3	26.32	4	0.46	2	1.29
Commelinaceae	3	3.12	1	18.80	1	1.71	2	0.62
Rubiaceae	7	2.44	0	0	2	1.08	7	4.82
Fabaceae	27	2.42	1	0.17	7	0.97	22	4.82
Amaranthaceae	3	2.40	1	4.10	2	5.31	1	0.05
Solanaceae	10	1.28	3	3.74	7	1.43	3	0.76
Malvaceae	5	1.06	2	4.44	3	1.03	3	0.38
Other	105	22.84	10	8.41	25	5.63	88	14.45
All plants	320	---	39	---	127	---	246	---

Collectively, 59 alien plant species were recorded, which represents 18% of all the recorded plant species. A higher number of alien than indigenous plant species were recorded within the soybean crop (Fig. 4.1), with *Oxalis latifolia* Kunth and *Commelina benghalensis* L. being the most abundant species (Table 4.2). The field boundary was also represented by a high number of problematic weeds with the most prominent species being *Amaranthus hybridus* L., *Bidens pilosa* L. and *Tagetes minuta* L. (Table 4.2). Only 15 species from the 246 species recorded from the grassland were alien species with the most abundant species being *Richardia brasiliensis* Gomes (Table 4.2).

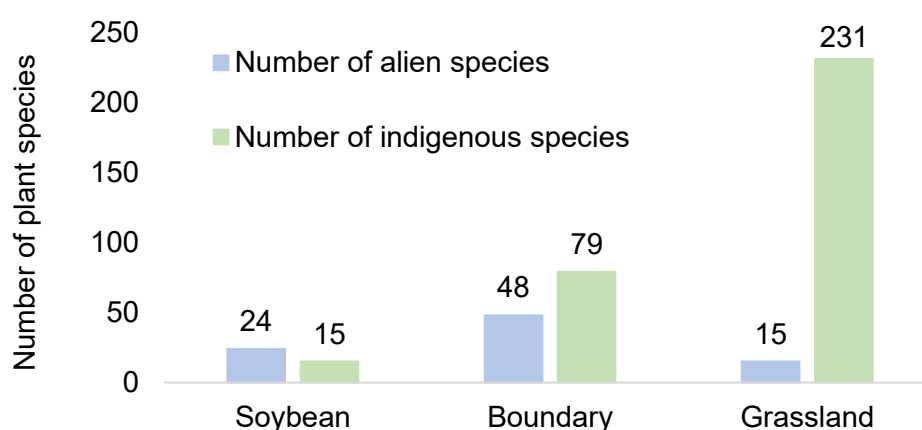


Figure 4.1: Comparison of the number of indigenous and alien plant species within the soybean crop, boundary, and grassland. Plot numbers were equal per treatment (n=20).

Table 4.2: The ten best represented alien plant species (excluding *Glycine max*) in the soybean crop and adjacent field margins.

Alien plant species	Total number of individuals	Soybean Crop	Field Boundary	Grassland
<i>Commelina benghalensis</i> L.	140	110	30	0
<i>Oxalis latifolia</i> Kunth	117	116	1	0
<i>Amaranthus hybridus</i> L.	111	24	87	0
<i>Tagetes minuta</i> L.	86	4	82	0
<i>Bidens pilosa</i> L.	78	0	78	0
<i>Richardia brasiliensis</i> Gomes	70	0	18	52
<i>Pennisetum clandestinum</i> Hochst. ex Chiov.	59	1	58	0
<i>Conyza bonariensis</i> (L.) Cronquist	43	10	28	5
<i>Paspalum dilatatum</i> Poir.	39	0	38	1
<i>Digitaria sanguinalis</i> (L.) Scop.	31	2	29	0

4.4 Plant species composition along the soybean field-field margin gradient

4.4.1 Results

Non-metric Multidimensional Scaling (NMDS) analysis showed separate groupings for each treatment zone (soybean crop, field boundary and grassland) (Fig. 4.2). Distinct groupings indicate that each treatment zone had a unique plant community. Stress values of ≤ 0.14 for the NMDS analysis were adequately low to provide a reliant two-dimensional picture (Clarke and Gorley, 2006). Permutational multivariate analysis of variance (PERMANOVA) confirmed that the species composition differed significantly between the soybean field, boundary and grassland (Table 4.3).

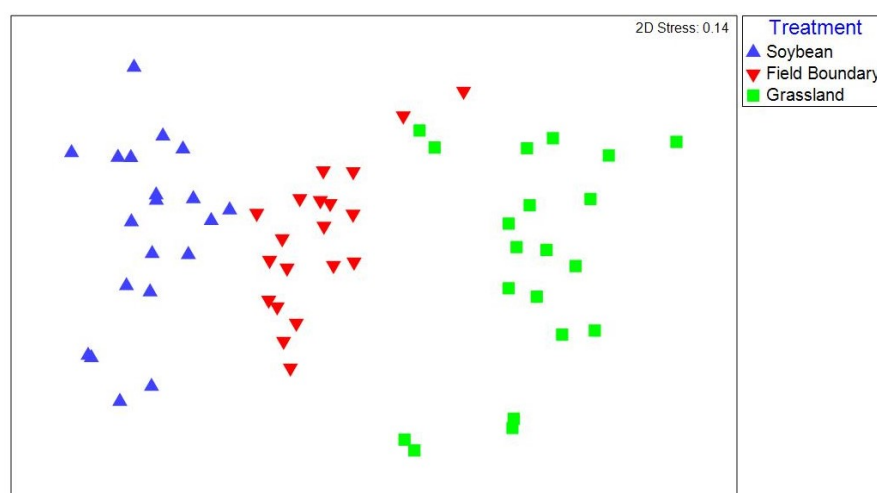


Figure 4.2: Non-metric multidimensional scaling analyses based on all plant species (excluding *Glycine max*) at all sites for the soybean crop, field boundary, and grassland.

Table 4.3: Results for PERMANOVA pair-wise tests indicating significant separations between treatment zones based on plant species composition.

Treatment	t-value	P-value
Soybean, Field boundary	2.762	0.001
Soybean, Grassland	3.498	0.001
Field Boundary, Grassland	2.852	0.001

Values in red indicate significant separations at $p < 0.05$ (permutation $N = 999$)

Indicator species analysis revealed five indicator plant species for the soybean crop, 19 indicator species for the field boundary and 36 indicator species for the grassland (Table 4.4). The indicator value (IndVal) ranges from 0 to 1 and shows how reliant a species is to describe or identify a particular zone. Indicator values of most indicator species were low (< 0.5). *Commelina benghalensis*, *Cyperus esculentus* L. and *Oxalis latifolia* had the highest indicator values for the soybean crop, *Bidens pilosa*, *Cynodon dactylon* (L.) Pers. and *Eleusine coracana* (L.) Gaertn. for the boundary and *Eragrostis curvula* (Schrud.) Nees, *E. chloromelas* Steud. and *Themeda triandra* Forssk. for the grassland (Table 4.4).

Table 4.4: Indicator species analysis representing the five indicator species with the highest indicator values for the soybean crop, field boundary, and grassland.

Soybean Crop				Field Boundary				Grassland			
Species	IndVal	Freq	P-value	Species	IndVal	Freq	P-value	Species	IndVal	Freq	P-value
<i>Cyperus esculentus</i> L.	0.446	31	0.007	<i>Eleusine coracana</i> (L.) Gaertn.	0.656	30	0.001	<i>Eragrostis curvula</i> (Schrud.) Nees	0.536	25	0.001
<i>Commelina benghalensis</i> L.	0.393	21	0.009	<i>Bidens pilosa</i> L.	0.600	12	0.001	<i>Themeda triandra</i> Forssk.	0.526	12	0.001
<i>Oxalis latifolia</i> Kunth	0.297	7	0.005	<i>Cynodon dactylon</i> (L.) Pers.	0.597	25	0.001	<i>Eragrostis chloromelas</i> Steud.	0.463	17	0.002
<i>Zea mays</i> L.	0.200	4	0.026	<i>Amaranthus hybridus</i> L.	0.549	22	0.001	<i>Eragrostis racemosa</i> (Thunb.) Steud.	0.450	9	0.001
<i>Datura ferox</i> L.	0.185	5	0.041	<i>Paspalum dilatatum</i> Poir.	0.536	12	0.001	<i>Setaria sphacelata</i> (Schumach.) Stapf & C.E.Hubb. ex M.B.Moss	0.450	9	0.001
---	---	---	---	<i>Tagetes minuta</i> L.	0.477	13	0.001	<i>Eragrostis plana</i> Nees	0.438	20	0.002
---	---	---	---	<i>Setaria pallida fusca</i> (Schumach.) Stapf & C.E.Hubb.	0.400	8	0.002	<i>Senecio coronatus</i> (Thunb.) Harv.	0.400	8	0.001
---	---	---	---	<i>Cyniza bonariensis</i> (L.) Cronquist	0.391	20	0.003	<i>Brachiaria serrata</i> (Thunb.) Stapf	0.400	8	0.001
---	---	---	---	<i>Bidens formosa</i> (Bonato) Sch.Bip.	0.350	7	0.001	<i>Selago densiflora</i> Rolfe	0.381	9	0.003
---	---	---	---	<i>Panicum schinzii</i> Hack.	0.342	8	0.005	<i>Oxalis obliquifolia</i> Steud. ex A.Rich.	0.345	10	0.003
---	---	---	---	<i>Digitaria sanguinalis</i> (L.) Scop.	0.327	9	0.001	<i>Anthospermum rigidum</i> Eckl. & Zeyh.	0.325	8	0.003
---	---	---	---	<i>Verbena bonariensis</i> L.	0.318	8	0.004	<i>Helichrysum rugulosum</i> Less.	0.323	13	0.007
---	---	---	---	<i>Chenopodium carinatum</i> R.Br.	0.300	6	0.003	<i>Justicia anagalloides</i> (Nees) T.Anderson	0.300	6	0.005
---	---	---	---	<i>Schkuhria pinnata</i> (Lam.) Kuntze ex Thell.	0.250	5	0.013	<i>Haplocarpha scaposa</i> Harv.	0.300	6	0.004
---	---	---	---	<i>Bidens bipinnata</i> L.	0.200	4	0.028	<i>Helichrysum nudifolium</i> (L.) Less. var. nudifolium	0.300	6	0.005
---	---	---	---	<i>Cynodon incompletus</i> Nees	0.200	4	0.024	<i>Sonchus nanus</i> Sond. ex Harv.	0.300	6	0.003
---	---	---	---	<i>Urochloa mosambicensis</i> (Hack.) Dandy	0.200	4	0.031	<i>Tephrosia capensis</i> (Jacq.) Pers.	0.300	6	0.005
---	---	---	---	<i>Verbena brasiliensis</i> Vell.	0.200	4	0.026	<i>Cymbopogon pospischilii</i> (K.Schum.) C.E.Hubb.	0.291	7	0.005
---	---	---	---	<i>Pennisetum clandestinum</i> Hochst. ex Chiov.	0.197	5	0.049	<i>Heteropogon contortus</i> (L.) Roem. & Schult.	0.279	7	0.009
---	---	---	---	---	---	---	---	<i>Cyniza podocephala</i> DC.	0.264	11	0.025
---	---	---	---	---	---	---	---	<i>Commelina africana</i> L.	0.250	5	0.01
---	---	---	---	---	---	---	---	<i>Bulbostylis burchellii</i> (Ficalho & Hiern) C.B.Clarke	0.250	5	0.012
---	---	---	---	---	---	---	---	<i>Scabiosa columbaria</i> L.	0.250	5	0.014
---	---	---	---	---	---	---	---	<i>Acalypha angustata</i> Sond.	0.250	5	0.013
---	---	---	---	---	---	---	---	<i>Eragrostis gummiflua</i> Nees	0.250	5	0.013
---	---	---	---	---	---	---	---	<i>Andropogon schirensis</i> Hochst. ex A.Rich.	0.240	6	0.027
---	---	---	---	---	---	---	---	<i>Berkheya radula</i> (Harv.) De Wild.	0.232	6	0.022
---	---	---	---	---	---	---	---	<i>Chamaecrista mimosoides</i> (L.) Greene	0.232	6	0.027
---	---	---	---	---	---	---	---	<i>Gerbera ambigua</i> (Cass.) Sch.Bip.	0.200	4	0.036
---	---	---	---	---	---	---	---	<i>Schistostephium heptalobum</i> (DC.) Hutch.	0.200	4	0.029
---	---	---	---	---	---	---	---	<i>Wahlenbergia undulata</i> (L.f.) A.DC.	0.200	4	0.02
---	---	---	---	---	---	---	---	<i>Coleochloa setifera</i> (Ridl.) Gilly	0.200	4	0.033
---	---	---	---	---	---	---	---	<i>Kohautia amatymbica</i> Eckl. & Zeyh.	0.200	4	0.02
---	---	---	---	---	---	---	---	<i>Pentstemon prunellifolius</i> (Klotzsch ex Eckl. & Zeyh.) Walp.	0.200	4	0.038
---	---	---	---	---	---	---	---	<i>Hermannia depressa</i> N.E.Br.	0.200	4	0.028
---	---	---	---	---	---	---	---	<i>Felicia muricata</i> (Thunb.) Nees	0.196	7	0.046

IndVal: Indicator value. Frequency refers to the number of survey plots the species were recorded from. P-values in red indicate significant indicator species at $P < 0.05$

4.4.2 Discussion

Both the soybean crop and field boundary were characterized by an abundance of weeds. It is generally regarded that spillover of weeds between the crop and non-crop habitat frequently occurs (Holland and Fahrig, 2000; Tschardtke *et al.*, 2005). However, NMDS and PERMANOVA analyses of the present study, indicate a unique plant species assemblage in the soybean crop and that few species are shared with the field boundary. It can be argued that some weeds may originate from the field boundary, for example, *C. esculentus* and *E. coracana* were abundant in both the soybean crop and field boundary. However, it appears that only a few plant species of the field boundary disperse into the soybean crop to become serious weeds. In winter wheat and barley agro-ecosystems in Europe, it was revealed that only 30% of the plant species located in the field boundary also occurred in the crop, most of which were recorded within 2.5 m of the field boundary (Marshall, 1989). Similarly, in this study, it was found that only 20% of the plant species located in the field boundary is shared with the soybean crop.

The field boundary zone also had a different plant species composition compared to adjacent grassland. A low number of alien plant species were found in the untransformed grassland in contrast to the field boundary. Close proximity to cropland means the boundary is exposed to disturbances including fertilizer drift, pesticide drift, soil disturbance from turning farm machinery, and the presence of fences and dirt roads (Marshall, 2005; Piessens *et al.*, 2006; Felsot *et al.*, 2010). In Belgium, a significant shift in plant species assemblages was observed in field margin vegetation in a zone eight meters from the crop edge (Piessens *et al.*, 2006). In habitat adjacent to intensely managed cropland, Boutin and Jobin (1998) observed a significant shift in the plant community towards short-lived weedy species. This effect was most profound in the first nine meters of the boundary. In maize agro-ecosystems in South Africa, no significant shift in the plant species assemblages was observed in natural habitat beyond 30 m from maize fields (Botha *et al.*, 2015). Similarly, in timber plantations of South Africa, no effect on biodiversity was observed in grassland beyond 32 m from adjacent plantations (Pryke and Samways, 2012). Therefore, the disturbance effects of crop cultivation on plant diversity and composition seem to be confined to the field boundary and hence, the observed difference in species assemblage compared to untransformed grassland.

Indicator species analysis did reveal indicator species to describe or identify a particular zone. However, the majority of these species were not good indicator species. The indicator value (IndVal) is a product of relative abundance of each species and relative frequency (frequency refers to the number of sample plots the species were recorded from) (Dufrêne and Legendre, 1997). A good indicator species should have a high frequency in a specific zone as well as

high abundance. Low frequency and abundance and the occasional presence of indicator species in other treatment zones resulted in most species having low indicator values (< 0.5).

All indicator species for the grassland were indigenous. Of the 36 grassland indicator species, 12 were grass species and 24 were forb species. However, grass species such as *E. chloromelas*, *E. curvula*, and *T. triandra* were the strongest indicators. The identity of these species indicates a level of disturbance in the grassland. *Eragrostis curvula* and *E. chloromelas* are known to perform well in disturbed areas of agricultural landscapes (Van Oudtshoorn, 2012), and although they were found in almost all grassland sample plots and were abundant as well, they were also frequently recorded in the disturbed boundary. *Themeda triandra* is known to perform poorly in disturbed areas (Snyman *et al.*, 2013) and were almost exclusively found in the grassland, but were not common. Forb indicator species were mostly recorded from the grassland. The most significant of these was *Senecio coronatus* (Thunb.) Harv., *Selago densiflora* Rolfe, and *Oxalis obliquifolia* Steud. ex Rich. However, they were not frequently found in survey plots, resulting in poor indicator values for these species.

The boundary contained six indigenous indicator species and 13 alien species suggesting the presence of disturbance in the boundary since weedy alien species tend to be abundant in disturbed areas. The most significant alien indicator species were *B. pilosa*, *A. hybridus*, *Paspalum dilatatum* Poir., and *T. minuta*. Although *B. pilosa* was exclusively found in the boundary, it was not always present. The other indicator species for the boundary were not frequently sampled resulting in low indicator values. The most significant indicator species were, however, indigenous. These were *C. dactylon* and *E. coracana*. It is a common perception among farmers that the field boundary act as a reservoir for weeds from where weeds disseminate into crop fields soon after crops are planted (Marshall, 2005), and as a result, field boundaries are often sprayed with herbicides or tilled to remove unwanted weeds. Consequently, pioneer species such as *E. coracana* and *C. dactylon* will often be the first species to colonize the boundary (Van Oudtshoorn, 2012).

Cyperus esculentus and *C. benghalensis* had a high abundance within the crop and were present in most samples, but were also sampled in the boundary, resulting in a low indicator value. *Oxalis latifolia*, *Zea mays* L. and *Datura ferox* L., had a high specificity for the crop but were only occasionally sampled, also resulting in low indicator values. The indicator species for the soybean crop are well-known weeds in agricultural landscapes across South Africa (Bromilow, 2010). *Commelina benghalensis* and *C. esculentus* were the most important indicator species in the soybean crop. *Commelina benghalensis* is an alien weed which is common in crop fields. Through asexual, vegetative reproduction this species can quickly

increase its population density in areas with a disturbed soil surface (Bromilow, 2010). *Cyperus esculentus* is a native grassland species with strong competitive traits allowing it to invade crop fields (Bromilow, 2010). The ability of *O. latifolia* to reproduce through bulbs and rapid seed production, and the aggressive and rapid growth of *D. ferox*, enable these weeds to grow well in soil disturbed areas (Bromilow, 2010). *Zea mays* were also listed as an indicator species for the soybean crop but were likely present as volunteer maize from the previous cultivation season since it is cultivated in crop rotation with soybean.

Specific trends in species distribution patterns were observed, similar to the plant species distribution patterns described by Marshall (1989) for agro-ecosystems in Europe. There were species confined to each treatment zone, for instance, *Malva parviflora* L. and *O. latifolia* were confined to the soybean crop, *B. pilosa*, *T. minuta* and *Urochloa mossambicensis* (Hack.) Dandy to the field boundary and *Andropogon schirensis* Hochst. ex Rich. and *Brachiaria serrata* (Thunb.) Stapf to the grassland. Several species occurred in both the soybean crop and field boundary, for example, *A. hybridus*, *E. coracana*, *C. esculentus*, and *C. benghalensis*. There were species that occurred in both the boundary and grassland, for instance, *E. curvula*, *Conyza podocephala* DC. and *C. dactylon*. This agrees with the idea that species can be classified according to their preference of habitat (in this case cultivated, semi-natural and natural habitat).

4.5 Plant species diversity patterns along the soybean field-field margin gradient

4.5.1 Results

The five localities followed a similar pattern for the diversity index values across the three zones, except for Reitz (Fig. 4.3). The deviation of the plant diversity patterns observed at Reitz was further confirmed by significant interaction effects between locality and zone for Shannon-Wiener diversity, Margalef's species richness, Pielou's evenness, and Simpson's diversity, indicating that all the localities did not react similarly to zone (Table 4.5). At Reitz, lower Shannon-Wiener diversity was observed in the grassland compared to the boundary, whereas the grassland for other localities tended to be marginally more diverse than the boundary.

Simpson's diversity and Pielou's evenness values for the grassland at Reitz were low, whereas the soybean crop had an unexpected high evenness compared to the other localities. Simpson's diversity and Pielou's evenness are primarily indicators of species evenness which refers to the relative proportional abundance of species in a community. The crop fields of other localities often had dominating weed species, most often *C. benghalensis*, *C. esculentus* or *O. latifolia*, while the weed abundance was more evenly distributed at the Reitz sites. While the grassland at the Reitz localities was exposed to a high level of disturbance in the form of

alien weeds and grazing, it was also surrounded by intensely managed cropland on all sides, contributing to a lower evenness in the grassland. The grassland at other localities was also exposed to similar disturbances although not as severe (refer to chapter 3 for a full description of sites).

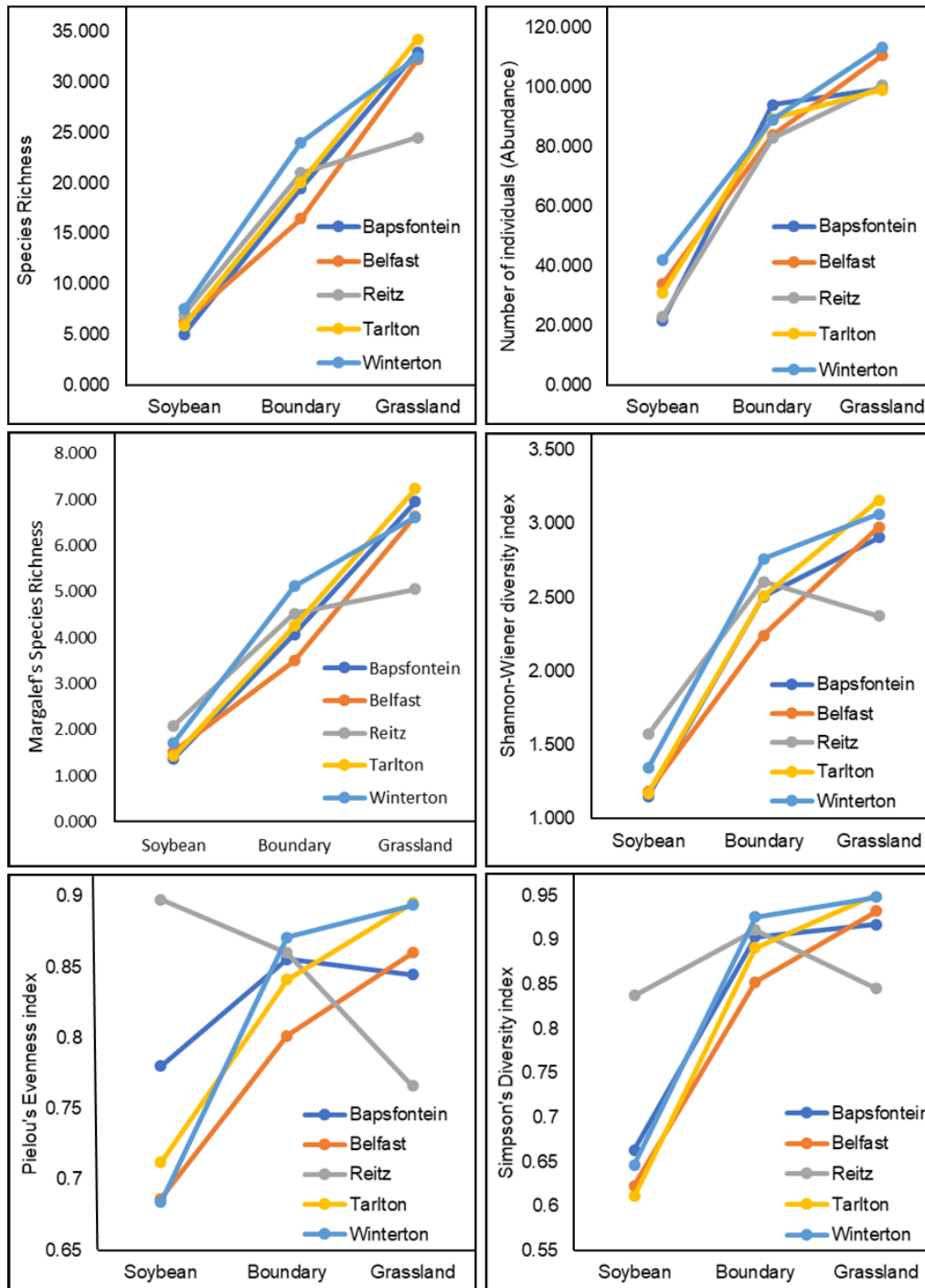


Figure 4.3: Diversity index values for plants along a soybean crop-field margin gradient at five localities in soybean agro-ecosystems of South Africa.

Table 4.5: Hierarchical linear modelling (HLM) results for the total plant sample indicating significant interaction effects between locality and treatment zone.

Diversity indices	Locality*Zone interaction effect	
	F-value	P-value
Species Richness	1.872	0.095
Abundance	1.782	0.113
Margalef Species Richness	2.572	0.025
Shannon-Wiener Diversity	4.158	0.001
Pielou's Evenness	4.66	0.001
Simpson Diversity Index	7.619	<0.001

Hierarchical Linear Modelling (HLM) confirmed that the soybean crop had significantly lower plant species richness and plant abundance than both the boundary and grassland (Table 4.6; Effect sizes listed in Table 8.4, Appendix A). The crop fields also had significantly lower diversity and evenness index values (Shannon-Wiener diversity, Margalef's species richness, Pielou's evenness, and Simpson's diversity) than the boundary and grassland. Although the grassland tended to be more diverse than the boundary, there was no significant difference between the plant diversity and evenness of the boundary and grassland which contradicts the hypothesis that possible disturbances from adjacent cropland will result in lower diversity within the boundary.

Table 4.6: Hierarchical linear modelling (HLM) results for the total plant sample. Mean value measures are given for the soybean crop, field boundary, and grassland.

Diversity indices	Soybean		Boundary		Grassland		Residual variance	Transect variance	F-value	P-value
	Mean	Standard error	Mean	Standard error	Mean	Standard error				
Species Richness	6.26 ^a	0.95	20.58 ^b	0.95	32.03 ^b	0.90	14.926	0	184.26	<0.001
Abundance	30.83 ^a	2.34	89.15 ^b	2.34	104.56 ^b	2.24	91.648	0	276.99	<0.001
Margalef's Species Richness	1.58 ^a	0.20	4.37 ^b	0.20	6.66 ^b	0.19	0.649	0	160.81	<0.001
Shannon-Wiener Diversity Index	1.26 ^a	0.06	2.55 ^b	0.06	2.95 ^b	0.06	0.066	0	178.30	<0.001
Pielou's Evenness	0.76 ^a	0.09	0.85 ^b	0.09	0.87 ^b	0.09	0.006	0	8.40	0.001
Simpson Diversity Index	0.67 ^a	0.08	0.90 ^b	0.08	0.93 ^b	0.07	0.007	<0.001	107.37	<0.001

Means with different subscript symbols differed practically according to effect sizes ($d \geq 0.5$). Values in red indicate statistical significance at $P < 0.05$.

4.5.2 Discussion

The underlying goal of most crop production systems is to decrease weed densities in order to increase crop yield. As expected, the soybean crop had a significantly lower plant diversity and abundance than the field boundary and grassland. Crop fields are unfavourable environments for most plant species due to a high level of agricultural disturbance, which may lead to a reduction in overall plant diversity and abundance (Altieri, 1999; Hamre *et al.*, 2010).

All sites had a degree of soil disturbance through tillage as well as the implementation of weed control measures, either through herbicide usage or cultural weed control (hand weeding and conventional tillage). These factors have been shown to reduce the abundance and diversity of weeds (Puricelli and Tuesca, 2005; Santin-Montanyá *et al.*, 2013). Furthermore, the shading effects of soybean plants may further reduce weed densities (Murphy and Gossett, 1981).

The soybean crop also had significantly lower evenness than the boundary and grassland. Evenness is important to consider since it is generally stated that ecosystem stability and function increases with increasing diversity and evenness (Frank and McNaughton, 1991; Tilman, 1996; Maestre *et al.*, 2012). Agricultural disturbances (predominantly herbicide usage, soil disturbance, and invasion by alien species) tend to have a destabilizing effect on evenness, for example, significantly lower evenness of non-crop plants was observed in herbicide treated vineyards (Sanguankee and León, 2011). Higher evenness was observed in conservation tillage systems compared to conventionally tilled systems (Dorado and López-Fando, 2006). Hejda *et al.* (2009) observed a general reduction in species richness and evenness in vegetation plots invaded by alien plant species. Disturbance gives the opportunity for species, that are able to tolerate the disturbance, to dominate. In this study, species dominating within the crop field were often *C. esculentus*, *C. benghalensis*, and *O. latifolia*.

Agricultural disturbance may also affect plant diversity in adjacent crop fields (Felsot *et al.*, 2010). For instance, Jobin *et al.* (1997) observed lower plant diversity in field margins adjacent to grain crop fields regularly treated with herbicide, and Schmitz *et al.* (2014) observed a reduction in overall plant diversity in field margins due to fertilizer drift. However, in this study, no significant differences were observed between diversity index values of the field boundary and grassland. There was also no significant difference between the species evenness of the boundary and grassland. The boundary had surprisingly high species evenness despite the abundance of alien plant species in this zone. Thus, contradictory to the notion that disturbance prone boundaries will have reduced diversity and evenness (Marshall and Moonen, 2002), the diversity did not differ between the boundaries and natural areas. However, the boundary had an altered plant species assemblage as shown earlier. Therefore, although agricultural activities in adjacent cropland did not result in a decrease in the overall plant diversity of the boundary, in this case at least, it did significantly change the species composition of the plant community in the boundary.

From this and similar studies, it can be concluded that properly vegetated boundary zones may provide protection for natural habitats against agricultural activities (Boutin and Jobin, 1998; Marshall and Moonen, 2002). Boundary zones may reduce soil erosion and buffer the movement of agro-chemicals toward natural habitats (Cooper *et al.*, 1995; De Snoo and De

Wit, 1998). The notion of using buffer strips between cropland and natural habitats have been experimentally tested before. For instance, in 18 m wide grass buffer strips, Patty *et al.* (1997) observed up to a 100% reduction in pesticide runoff, 89% reduction in phosphorus runoff and a 100% reduction in nitrate runoff. Similarly, Borin *et al.* (2010) observed up to 90% reduction in herbicide runoff. Glyphosate drift has been reported from nearly 70% at 2 m and 0.1% at 12 m from cropland (Alves *et al.*, 2017).

Furthermore, several studies report on the importance of plant diversity for the provision of ecosystem services, as well as the effect the identity of the species (species composition) may have on ecosystem services (Symstad *et al.*, 1998; Schwartz *et al.*, 2000; Díaz and Cabido, 2001; Downing and Leibold, 2002). Therefore, the high plant diversity of the field boundary and grassland (compared to cropland), and the unique species composition from each zone, is of further conservation value through its support of species that perform important ecosystem services beneficial to the entire agro-ecosystem. Furthermore, alteration of the plant species composition is important to consider since it may have varying effects on the consumer populations. Different structures and microclimate resulting from different vegetation types will affect movement and colonization of arthropods within the field boundary (Marshall and Moonen, 2002; Thomas and Jepson, 1999).

4.6 Effect of land-use intensity and environmental variables on plant species assemblages

4.6.1 Results

In the Canonical Correspondence Analysis (CCA) for plant sample plots, the land-use intensity was strongly correlated with axis 1, while mean annual precipitation (MAP) and altitude were strongly correlated with axis 2 (Fig. 4.4; Table 4.7). Mean annual temperature (MAT), latitude and longitude also had a relatively high correlation with axis 2. Farming type (cultivation of conventional soybean or glyphosate-tolerant soybean) had a weak correlation with both axis 1 and 2. Axis 1 accounted for 24.13% of the variance, while axis 2 accounted for 20.72% of the variance.

Land-use intensity was the most important factor in determining plant species assemblages and resulted in three distinctive groupings for plant sample plots in the biplot (Fig. 4.4). The first group was soybean fields that were characterized by high land-use intensity. The second was the field boundary, characterized by lower, but still high, land-use intensity while the third was grassland plots, characterized by low land-use intensity.

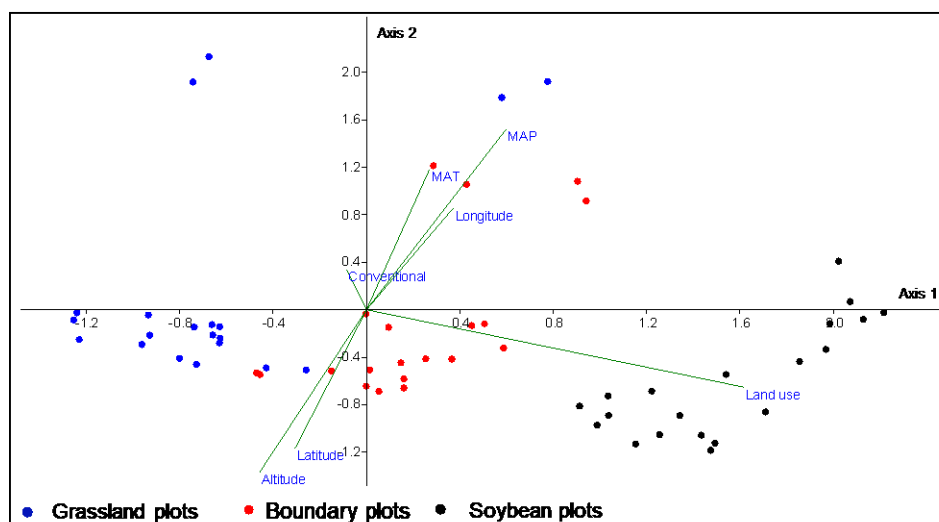


Figure 4.4: Canonical correspondence analysis (CCA) of all the localities showing correlation of environmental variables with plant sample plots. Each symbol represents the weighted average of one plot in relation to environmental variables. The environmental variables were altitude, latitude, longitude, mean annual precipitation (MAP), mean annual temperature (MAT), farming type (Conventional soybean or glyphosate-tolerant soybean) and land-use intensity.

Table 4.7: Correlations of ordination axes with environmental variables and eigenvalues and percentage variance explained for canonical correspondence analysis of plant species assemblages at all localities.

Variable	Axis 1	Axis 2
Land use intensity	0.808	-0.326
Conventional soybean	-0.043	0.171
Altitude	-0.230	-0.688
Latitude	-0.152	-0.583
Longitude	0.186	0.428
Mean annual precipitation	0.299	0.761
Mean annual temperature	0.135	0.591
Eigenvalue	0.661	0.567
% variance explained	24.13	20.72

The three different land-use types (crops, buildings and settlements, and roads and fences) were also analyzed separately, which showed that crops made the largest contribution to the variance in plant species composition, followed by buildings and settlements, while roads and fences made the smallest contribution (Figure 4.5 and Table 4.8).

At a regional scale MAP and altitude, and to a lesser extent MAT, latitude and longitude, separated Winterton from other localities. Plant species composition of Winterton showed correlations with high annual precipitation and temperature. Species composition at the other

localities showed strong positive correlations with altitude. Plant species assemblages of all sample plots had a weak correlation with farming type.

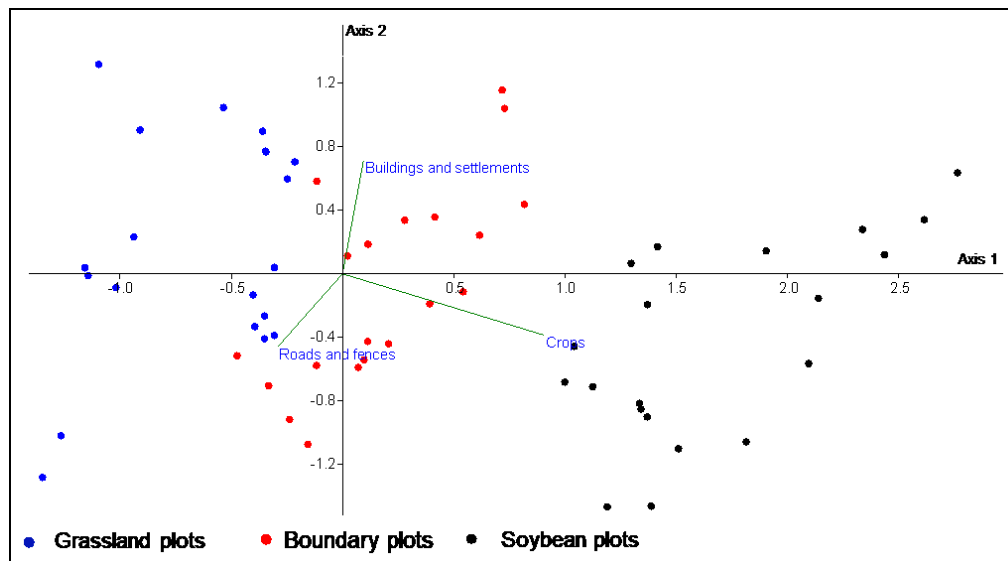


Figure 4.5: Canonical correspondence analysis (CCA) of all the localities showing correlation of land-use types with plant sample plots. Each symbol represents the weighted average of one plot in relation to a land-use type. The land-use types were crop fields, buildings and settlement, and roads and fences.

Table 4.8: Correlations of ordination axes with land-use types and eigenvalues and percentage variance explained for canonical correspondence analysis of plant species assemblages at all localities.

Variable	Axis 1	Axis 2
Crops	0.908	-0.387
Buildings and settlements	0.094	0.716
Roads and fences	-0.291	0.460
Eigenvalue	0.660	0.375
% variance explained	63.71	36.18

4.6.2 Discussion

In the CCA ordination, land-use intensity (consisting of crops, building and small settlements, and roads and fences) had a strong correlation with axis 1, which accounted for most of the variation in plant species assemblages. This indicates that land-use intensity in the soybean agro-ecosystem was a strong determinant of the variation of plant species assemblages. Within the land-use intensity variable, the presence of crop fields (and its associated activities) made the largest contribution to variation in plant species composition. This was expected as crop fields are associated with high levels of disturbances. Frequent disturbances associated with crop fields are for example pesticide and fertilizer application and tillage practices (Feber *et al.*, 1996; Kleyer, 1999; Witmer *et al.*, 2003). Disturbance is regarded as a selection force

that allows species that are able to tolerate disturbances to grow and outcompete less tolerant species (Yachi and Loreau, 1999). For instance, it was observed that fertilizer application can increase the abundance of species with high nutrient uptake requirements while decreasing the overall diversity (Schmitz *et al.*, 2014). These results follow on that of section 4.3 where significantly different plant species assemblages were observed between the soybean crop, boundary, and grassland.

The presence of buildings and settlements also accounted for variance in the species assemblages. Other studies showed a general decrease in biodiversity with increasing urbanization (Blair, 1999; McKinney, 2002; Hansen *et al.*, 2005). In addition, intensive land-use also contributes to fragmentation, which can be defined as habitat loss and division of habitat into smaller patches (Fahrig, 2003). Studies show that species richness tends to decrease with decreasing natural habitat (Debinski and Holt, 2000). Furthermore, remnants of natural habitat are separated from each other by land-use, especially by crop species which form very different assemblages from vegetation types in natural habitat. This will impact the dispersal of species between remnants of natural habitat and ultimately the species diversity and composition of a particular community (Fahrig, 2003).

At a regional scale, the variance in plant species assemblages that were observed between Winterton and other localities were accounted for by environmental variables. PERMANOVA analyses also revealed that soybean, boundary and grassland species assemblages of Winterton were significantly different from the respective zones of the other localities (Appendix A, Fig. 8.4 and Table 8.1-8.3). In the CCA ordination, the vegetation of Winterton reacted strongly with high rainfall and high temperatures while the vegetation of other localities reacted strongly with high altitude. Winterton forms part of the Northern KwaZulu-Natal Moist Grassland vegetation unit. This unit is characterized by high annual temperatures and precipitation as well as being at lower altitudes than the other localities (Mucina and Rutherford, 2006).

The possible impact that cultivation of glyphosate-tolerant crops may have on farmland biodiversity, either through direct effects (e.g. weed shifts or glyphosate drift into adjacent habitats) or indirect effects through changes in cultivation practices (glyphosate-tolerant crop allows for the adoption of conservation tillage) have been reported in literature (Heard *et al.*, 2003; Young, 2006; Reddy and Norsworthy, 2010; Motta *et al.*, 2018). However, the CCA biplot revealed that farming type had no contribution to the variation observed in plant species assemblages between localities. The study sites were characterized by a range of management practices that were not constant between sites. Although the latter factors did not allow for direct comparison between farming types, this study included all types of soybean

production systems. The results are therefore representative baseline data for soybean agro-ecosystems in general.

Conclusion

Plant diversity was lower in the soybean crop fields than the boundary and grassland, supporting the first hypothesis of the study. No significant difference was found between the plant diversity of the boundary and grassland. Therefore, the results indicate, contrary to the second hypothesis of the study, that the presence of soybean fields do not significantly affect the plant diversity and evenness in the field boundary.

Each zone had a unique plant species composition. At a local scale, land-use intensity (predominantly disturbance resulting from crop fields) was the best predictor for plant species assemblages. This supports the third hypothesis of the study since agricultural disturbance significantly changed the plant species composition in the boundary zone, causing a shift towards alien plant species. This effect was not observed in the grassland (> 50 m from the soybean crop). Boundary zones, therefore, have an important conservation function in soybean agro-ecosystems by buffering the effects of agricultural disturbance resulting from the soybean crop into the adjacent habitat.

Furthermore, the results indicated that field margins are not a species-poor habitat but that these margins are rich in plant diversity. Therefore, these zones may have further conservation value in soybean agro-ecosystems by supporting high diversity of unique species capable of performing important ecosystem services.

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Chapter 5: Arthropod species composition and diversity patterns of soybean agro-ecosystems

Abstract

Agriculture is dependent on arthropods for the provision of ecosystem services such as pollination, biological pest regulation, and nutrient cycling. However, large-scale cultivation of crops, resulting in transformation and degradation of natural habitat, pose a serious threat to biodiversity. Soybean is widely cultivated in South Africa, but arthropod diversity associated with soybean agro-ecosystems are unknown. In an attempt to address this knowledge gap, arthropod diversity and species assemblages were assessed at ten localities in major soybean production areas of South Africa. Arthropods were collected in soybean fields as well as the boundary (transition zone between the soybean crop and adjacent grassland) and adjacent natural grassland, using suction sampling. A total of 9216 individuals were collected amounting to 373 species. Distinct arthropod species assemblages were observed for the different sampling zones. The soybean crop was species-poor compared to the untransformed grassland. The field boundary had significantly higher arthropod species richness and diversity than both the crop and untransformed grassland. This can be attributed to an edge effect. At a local scale, the land-use intensity was the most important determinant for arthropod species assemblages. At a regional scale, species assemblages were influenced by mean annual precipitation and geographical position (latitude and longitude). Furthermore, the species-rich boundary and untransformed grassland supported diverse communities of entomophagous arthropods. This emphasized the conservation value of natural and semi-natural habitat since crop fields (as a sink) are largely dependent on the colonization of natural enemies of pests from these sources.

Keywords Agriculture, Soybean, Biodiversity, Species Richness, Arthropods, Field margin, Ecosystem Services.

5.1 Introduction

As consumer populations, arthropods consist of many functional groups such as herbivores, pollinators, detritivores, predators, and parasitoids. The multiple benefits provided by these organisms are referred to as arthropod-mediated ecosystem services (AMES) such as pollination, biological pest regulation, and nutrient cycling (Altieri, 1999). Agricultural activities such as soil management practices and the application of agro-chemicals pose a serious threat to arthropod diversity and services. Lower diversity of epigeal arthropods have been reported in conventionally tilled crop fields compared to reduced and no-tillage fields (Witmer *et al.*, 2003; Pretorius *et al.*, 2018) and reductions in butterfly diversity were observed in arable field edges after repeated applications of herbicide (Feber *et al.*, 1996). In this context, small patches of natural and semi-natural habitat may provide important source populations to enhance beneficial arthropod diversity in depleted crop fields (Duelli and Obrist, 2003; Midega *et al.*, 2008), as well as reduce the colonization of pests in crop fields. For instance, reduced stem borer colonization was observed in diversified push-pull maize systems compared to monocrop systems (Midega *et al.*, 2014)

Soybean cropping systems are a prominent feature across the South African landscape with nearly 800 000 hectares planted annually in South Africa (ISAAA, 2017). The rapid growth of soybean cultivation in South Africa is mediated by policies that enable the use of genetically modified herbicide-tolerant soybean, as well as the benefits of crop rotation between soybean and maize (Dlamini *et al.*, 2014). Due to the increases in cultivation area, it is important to assess the potential effects these activities may have on natural habitat surrounding crop fields. This will enable the formulation of good practices towards ensuring the better management and conservation of biodiversity and associated ecosystem services within soybean agro-ecosystems in South Africa. In addition to plant diversity, it is important to survey arthropod diversity across the entire agro-ecosystem to increase baseline data on total biodiversity. Furthermore, arthropods serve as useful bioindicators of disturbance because they react more rapidly to environmental change than vertebrates (Rodríguez *et al.*, 1998). Therefore, the aim of this chapter was to provide insight into arthropod species assemblages and diversity patterns along a soybean field-field margin (field boundary and untransformed grassland) gradient in South Africa.

Disturbance prone crop fields are expected to have a negative effect on arthropod diversity (Stamps and Linit, 1998; Witmer *et al.*, 2003). Negative effects may arise through direct impact on the arthropod community through pesticide application, or indirect impact through changes in the plant community, which primarily dictates the arthropod species composition. Therefore, the first hypothesis for testing in this chapter states that the soybean crop will have low

abundance and diversity of arthropods compared to the adjacent zones (field margin). Literature has shown disturbance arising from crop fields (for instance agrochemical drift and invasion of alien plant species) may affect the diversity of arthropods in adjacent habitat (Boutin and Jobin, 1998; Piessens *et al.*, 2006; Pryke and Samways, 2012). The second hypothesis proposes that the boundary will contain lower diversity and abundance of arthropods than the untransformed grassland. This will also serve as a filter for disturbance tolerant species. The third hypothesis proposes that the boundary will have different arthropod species composition than the grassland.

5.2 Materials and Methods

Ten sites were surveyed in the major soybean production areas of South Africa (Chapter 3: 3.1). Arthropod diversity was recorded in the soybean crop, field boundary (transition zone between crop fields and adjacent natural habitat) and natural grassland adjacent to crop fields (Chapter 3: 3.2). Arthropods were collected using an adapted D-vac method (Chapter 3: 3.3). Arthropod species composition was expressed using Non-metric Multidimensional Scaling (NMDS), Permutational Multivariate Analysis of Variance (PERMANOVA) and Indicator Species Analysis (IndVal) (Chapter 3: 3.5.1). Arthropod diversity patterns were expressed through diversity indices and analysed with Hierarchical Linear Modelling (Chapter 3: 3.5.2). The influence of environmental variables on arthropod assemblages was assessed with Canonical Correspondence Analyses (CCA) (Chapter 3: 3.5.3).

5.3 Descriptive data

Rarefaction curves indicated a sufficient sampling effort for the arthropod diversity survey (Appendix B, Figure 9.1). The data presented here form part of the first assessment of arthropod assemblages in soybean cropping systems in South Africa. A total of 373 morphospecies were collected. The soybean crop contained the lowest number of morphospecies (170), compared to the field boundary (280) and grassland (256) (Refer to Appendix B, Figure 9.2 for the percentage of shared and unique species between the three zones). A total of 9216 arthropod individuals were collected. Most of the individuals (4105) were collected from the field boundary, whereas 3053 individuals were collected from the grassland and 2058 from the soybean crop. Fifteen arthropod orders were represented with the most significant contributions from Hemiptera, Coleoptera, Diptera, Araneae, Hymenoptera and Thysanoptera (Fig. 5.1).

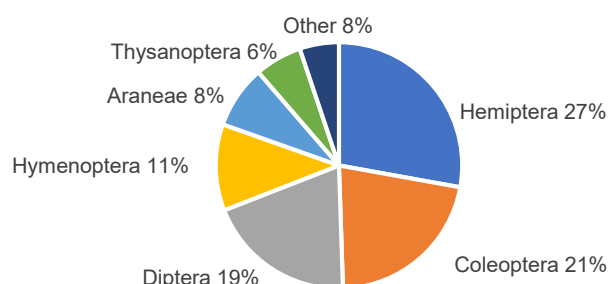


Figure 5.1: Percentage contribution (according to the number of individuals) of arthropod orders to the total individuals collected in soybean agro-ecosystems in South Africa (Other arthropod orders were Lepidoptera, Orthoptera, Blattodea, Acari, Dermaptera, Collembola, Psocoptera, Neuroptera and Mantodea).

A total of 97 arthropod families were recorded. In terms of the number of species, parasitoid wasps (Hymenoptera: Chalcidoidea) made the largest contribution and represented 23 morphospecies (Table 5.1). Leafhoppers (Hemiptera: Cicadellidae) and leaf beetles (Coleoptera: Chrysomelidae) also made large contributions and were each represented by 19 morphospecies. In all the zones, leafhoppers (Hemiptera: Cicadellidae) made large contributions with a total of 1043 individuals (11% of the total sample).

Table 5.1: The best-represented families/superfamilies according to the number of morpho-species and the percentage contribution (% of individuals) of each arthropod family to the total number of individuals collected for the overall sample, the soybean crop, boundary and grassland.

Family	Overall		Soybean		Boundary		Grassland	
	No. of species	% individuals	No. of species	% of individuals	No. of species	% of individuals	No. of species	% of individuals
Cicadellidae	19	11.31	8	9.91	15	10.66	18	13.25
Melyridae	2	8.94	1	2.82	2	18.64	1	0.03
Mycetophilidae	2	6.87	2	8.07	1	3.87	1	10.15
Thysanoptera	17	5.43	13	8.41	11	4.39	13	6.06
Lygaeidae	12	5.27	6	2.24	11	8.40	6	3.13
Formicidae	6	4.82	3	0.92	6	3.97	5	8.44
Chalcidoidea	23	4.18	10	2.19	19	4.14	20	5.60
Chrysomelidae	19	3.86	7	4.62	14	2.97	12	4.58
Anthicidae	9	3.50	6	3.45	9	2.51	7	5.01
Thomisidae	11	3.07	4	0.38	7	2.43	9	4.88
Miridae	13	2.03	6	4.71	11	1.75	6	0.63
Braconidae	13	1.70	6	1.55	7	1.34	8	2.31
Coccinellidae	9	1.70	4	1.02	9	2.51	5	1.09
Curculionidae	10	1.24	3	0.34	8	0.34	8	3.07
Salticidae	12	0.84	3	0.53	8	1.00	8	0.82
Other	143	35.24	86	48.84	142	31.08	129	30.95
All Arthropods	320	---	168	---	280	---	256	---

5.4 Arthropod species composition along the soybean field-field margin gradient

5.4.1 Results

Non-metric Multidimensional Scaling (NMDS) analysis of overall arthropod species composition (Fig. 5.2) had a relatively high-stress value (0.23) indicating that it is not a meaningful two-dimensional representation (Clarke and Gorley, 2006). However, NMDS analyses of species composition performed separately for the different localities (Appendix B, Fig. 9.3) had similar groupings with much lower stress values. Overall, the NMDS analyses indicated distinct groupings for the different zones (soybean crop, field boundary and grassland). Permutational Multivariate Analysis of Variance (PERMANOVA) confirmed that the three treatment zones had significantly different species compositions (Table 5.2).

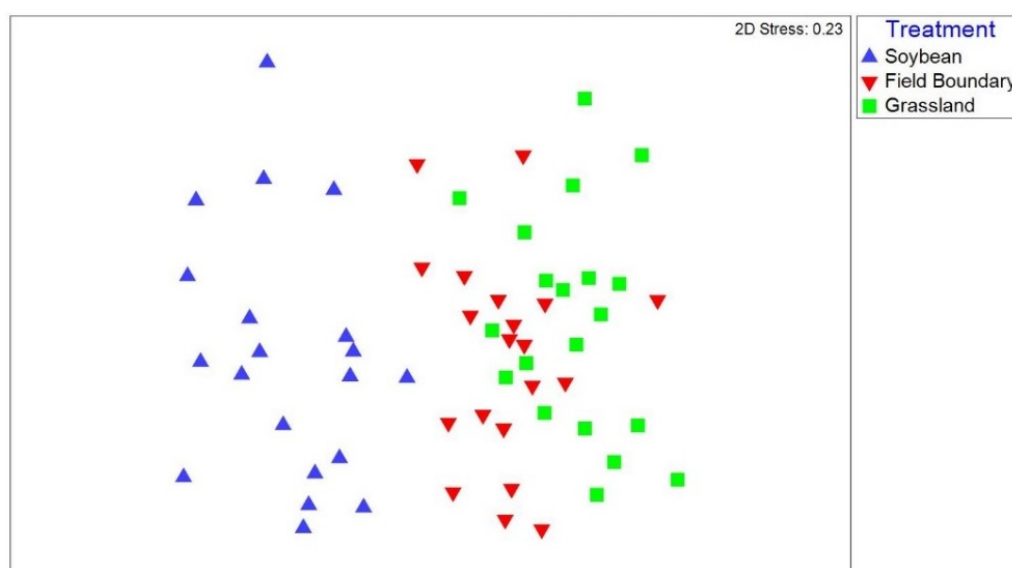


Figure 5.2: Non-metric multidimensional scaling analyses of all arthropod species recorded at all sites for the soybean crop, field boundary and grassland.

Table 5.2: Results for PERMANOVA pair-wise tests indicating significant separations between treatment zones based on arthropod species composition.

Treatment	t-values	P-value
Soybean, Field boundary	2.506	0.001
Soybean, Grassland	2.699	0.001
Field Boundary, Grassland	1.435	0.002

Values in red indicate significant separations at $p < 0.05$ (permutation $N = 999$)

There were 13 arthropod indicator morpho-species for the soybean crop, 21 morpho-species for the field boundary and 13 morpho-species for the grassland. Indicator species for the soybean crop were mostly phytophagous, with only one parasitoid species (Tachinidae MS 4). Tachinidae MS 4, as well as a thrip species (Thysanoptera MS 6), were the strongest indicators for the soybean crop (Table 5.3). The boundary and grassland had high numbers of parasitoid and predator indicator species, especially lynx spiders (Araneae: Oxyopidae), Sheet web spiders (Araneae: Linyphiidae), lady beetles (Coleoptera: Coccinellidae), and chalcid wasps (Hymenoptera: Chalcidoidea). Two species, Melyridae MS 1 (soft-wing flower beetle) and Lygaeidae MS 1 (seed bug) had a relatively high indicator value for the boundary (Table 5.3). The strongest indicator species for the grassland were an ant species (Formicidae MS 1) (Table 5.3).

Table 5.3: Indicator species analysis representing the five indicator morpho-species with the highest indicator values for the soybean crop, field boundary and grassland.

Soybean Crop				Boundary				Grassland			
Morpho-Species	IndVal	Freq	P-value	Morpho-Species	IndVal	Freq	P-value	Morpho-Species	IndVal	Freq	P-value
Thysanoptera MS 6	0.700	14	0.001	Melyridae MS 1	0.696	27	0.001	Formicidae MS 1	0.532	31	0.001
Tachinidae MS 4	0.685	22	0.001	Lygaeidae MS 1	0.590	29	0.001	Chrysomelidae MS 4	0.488	11	0.001
Pentatomidae MS 2	0.580	13	0.001	Chloropidae MS 1	0.467	37	0.001	Chalcidoidea MS 16	0.465	21	0.001
Chrysomelidae MS 2	0.503	24	0.003	Cicadellidae MS 1	0.408	37	0.024	Mycetophilidae MS 2	0.442	45	0.013
Cicadellidae MS 13	0.472	25	0.012	Acrididae MS 1	0.403	31	0.027	Cicadellidae MS 3	0.406	21	0.011
Noctuidae MS 3	0.450	9	0.001	Chalcidoidea MS 14	0.392	32	0.016	Cicadellidae MS 12	0.330	16	0.007
Nymphalidae MS 1	0.450	9	0.001	Lygaeidae MS 5	0.385	24	0.01	Anthomyiidae MS 1	0.320	9	0.002
Miridae MS 4	0.389	9	0.001	Coccinellidae larf MS 1	0.349	15	0.008	Anthicidae MS 5	0.280	16	0.032
Thysanoptera MS 12	0.350	7	0.001	Cicadellidae MS 10	0.317	15	0.008	Thomisidae MS 2	0.255	11	0.038
Miridae MS 1	0.324	16	0.006	Cicadellidae MS 8	0.316	19	0.03	Fulgoridae MS 1	0.250	5	0.012
Noctuidae MS 1	0.277	12	0.028	Sepsidae MS 1	0.307	10	0.008	Thysanoptera MS 16	0.2105	6	0.035
Anthicidae MS 3	0.266	15	0.037	Delphacidae MS 4	0.269	11	0.02	Cercopidae MS 1	0.200	4	0.035
Noctuidae MS 2	0.208	6	0.034	Lygaeidae MS 2	0.259	11	0.03	Curculionidae MS 5	0.196	5	0.049
---	---	---	---	Chalcidoidea MS 15	0.250	11	0.028	---	---	---	---
---	---	---	---	Oxyopidae MS 1	0.233	8	0.031	---	---	---	---
---	---	---	---	Linyphiidae MS 2	0.229	6	0.014	---	---	---	---
---	---	---	---	Coccinellidae MS 4	0.222	7	0.027	---	---	---	---
---	---	---	---	Miridae MS 5	0.220	8	0.027	---	---	---	---
---	---	---	---	Pentatomidae MS 5	0.219	6	0.03	---	---	---	---
---	---	---	---	Coccinellidae MS 7	0.200	4	0.036	---	---	---	---
---	---	---	---	Chalcidoidea MS 21	0.200	4	0.033	---	---	---	---

IndVal: Indicator value. Frequency refers to the number of sample plots the species was recorded from. P-values in red indicate significant indicator species at $P < 0.05$

5.4.2 Discussion

Distinct arthropod species assemblages were observed for each zone. This follows on the findings of chapter 4, where unique assemblages of plant species were observed in each zone. Plant diversity and composition are widely considered an important determinant for arthropod diversity and composition (Siemann, 1998; Siemann *et al.*, 1998; Schaffers *et al.*, 2008; Haddad *et al.*, 2009; Moolman *et al.*, 2014; Botha *et al.*, 2017). Therefore, different assemblages of arthropods in each zone likely resulted from different plant species

assemblages in each zone. It is generally agreed that some herbivores exhibit a degree of host specificity (Andow and Imura, 1994; Norris and Kogan, 2000), which comes to reason that plant species assemblages will directly affect herbivores dependent on these species (Schoonhoven *et al.*, 1998). Plant species assemblages also determine the vegetation structure, plant chemical complexity and microclimate which may further affect phytophagous arthropods and higher trophic groups such as parasitoids and predators (Schaffers *et al.*, 2008). For example, grassland with low forb cover contained higher numbers of the egg clusters of the leaf beetle, *Galeruca tanacetii* L. (Coleoptera: Chrysomelidae), and parasitism by *Oomyzus galerucivorus* (Hedqvist) (Hymenoptera: Eulophidae) was reported to be strongly influenced by a sunny microclimate (Meiners and Obermaier, 2004). Vegetation structure and microclimate affects the mobility of arthropods, their mating and foraging success, and ultimately influence the arthropod community composition (Randlkofer *et al.*, 2010).

Conservation biological pest control is an important ecosystem service in agro-ecosystems and is largely dependent on predators and parasitoids that colonize the crop from adjacent habitats. For instance, it was found that less disturbed habitat (meadows) increased ant species richness in adjacent, disturbed crop fields (Dauber and Wolters, 2004), and aphid parasitoids (Hymenoptera: Braconidae) were observed moving from natural habitat into canola fields (Macfadyen and Muller, 2013). Crop fields are unfavourable environments to pest enemies due to cultivation practices and agro-chemical application (Thomas and Jepson, 1997; Thorbek and Bilde, 2004; Geiger *et al.*, 2010). High diversity and abundance of predators and parasitoids were collected from the boundary and grassland in this study. Prominent families were chalcid wasps (Hymenoptera: Chalcidoidea), braconid wasps (Hymenoptera: Braconidae), predatory lady beetles (Coleoptera: Coccinellidae), crab spiders (Araneae: Thomisidae) and jumping spiders (Araneae: Salticidae). The field margin provides permanent refuge and alternative food resources and can be considered a reservoir from where biological control agents invade crop fields (Landis *et al.*, 2000). For example, hoverflies (Diptera: Syrphidae) have predatory larvae that are important biological control agents (White *et al.*, 1995; Hickman and Wratten, 1996), however, hoverfly adults are mandatory feeders of pollen and nectar, resources often provided by field margin vegetation (Kaiser *et al.*, 2017). In this study, 70% of lady beetle larvae were collected from the field boundary, 30% from the grassland and 0% from the soybean crop. Pollen and nectar resources from the boundary and grassland supplement the diet of predatory lady beetle larvae (Lundgren, 2009), and these resources were low to absent in the soybean crop which may have contributed to the absence of lady beetle larvae in this zone.

Arthropod distribution patterns observed in this study were similar to the distribution patterns of arthropods in agro-ecosystems described by Duelli and Obrist (2003). Cultural species occur only in the crop while ubiquitous species occur in both the crop and non-crop habitat. In this study, 9% of species were confined to the soybean crop while 38% were shared between the crop and non-crop habitat. Ecotone species tend to be more abundant in the transition zone between the crop and non-crop habitat, and in this study, 13% of the species occurred only in the boundary. Stenotopic species have a high affinity for natural areas and in this study, 40% of the species occurred only in the boundary and grassland. Arthropod species are considered dependent on natural and semi-natural because they require resources from these habitats for development, feeding, maturation, oviposition or hibernation (Duelli and Obrist, 2003). Ecotone species and ubiquitous species with their highest population densities in the natural and semi-natural habitat can also be assumed to have a basic dependence on these habitats since crop fields are only temporarily present (Kennedy and Storer, 2000; Duelli and Obrist, 2003).

Indicator species analysis revealed several indicator species for each zone. However, most indicator species in this study were frequently absent from the zone that they are indicative of. Good indicator species should have a high abundance and specificity for a specific zone. They are, therefore, considered poor indicator species. It is important to note, that the boundary and grassland had multiple entomophagous indicator species while most indicator species for the soybean crop were phytophagous. This further emphasizes the conservation value of these zones since these entomophagous species will likely not be present in the absence of boundary zones and natural habitats in soybean agro-ecosystems

Prominent families sampled in the soybean crop were Noctuidae, Pentatomidae, Cicadellidae, Chrysomelidae, Thomisidae, Lygaeidae, Miridae, and Chalcidoidea. These are similar to prominent families collected in soybean surveys in the United States (Balduf, 1923), Australia (Evans, 1985), Cambodia (Chanthy *et al.*, 2013) and China (Yu *et al.*, 2014). Interestingly, the strongest indicator for the soybean crop was a species of thrips. This is likely a thrips species with a high affinity for leguminous plants. This may warrant further investigation into this species since there are several thrip species regarded as pests of soybean in the United States (Reisig *et al.*, 2012; Regan *et al.*, 2017). Indicator species analysis also revealed several Noctuidae species and a Nymphalidae and Pentatomidae species as indicator species for the soybean crop. In South Africa, these families represent pest species of soybean. The most economically important of these species are *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae), *Thysanoplusia orichalcea* (F.) (Lepidoptera: Noctuidae), *Vanessa*

cardui (L.) (Lepidoptera: Nymphalidae), and *Nezara viridula* (L.) (Hemiptera: Pentatomidae) (DAFF, 2010; Van Wyk and Smit, 2010; Du Plessis, 2015).

5.5 Arthropod species diversity along the soybean field-field margin gradient

5.5.1 Results

The five localities showed a similar pattern for species richness, abundance and diversity of arthropods across the three zones with a few exceptions (Fig. 5.3). A low abundance of arthropods was recorded from the boundary zone at the Winterton (sub-escarpment) locality compared to other localities. At Bapsfontein (Highveld plateau), there was a high species evenness for the soybean crop while other sites had lower evenness in the crop compared to the boundary and grassland zones. The deviation of arthropod evenness patterns observed at Bapsfontein was further confirmed by significant interaction effects between locality and zone for Pielou's Evenness (Table 5.4). However, for most species diversity parameters there were no significant interaction effects between locality and zone. This indicated that arthropod diversity at all localities reacted similarly to sample gradient.

Table 5.4: Hierarchical linear modeling (HLM) results for the total arthropod sample indicating significant interaction effects between locality and treatment zone.

Diversity indices	Locality*Zone interaction effect	
	F-value	P-value
Species Richness	1.64	0.167
Abundance	1.45	0.225
Margalef's Species Richness	1.605	0.179
Shannon-Wiener Diversity	1.862	0.12
Pielou's Evenness	4.041	0.004
Simpson Diversity Index	2.33	0.054

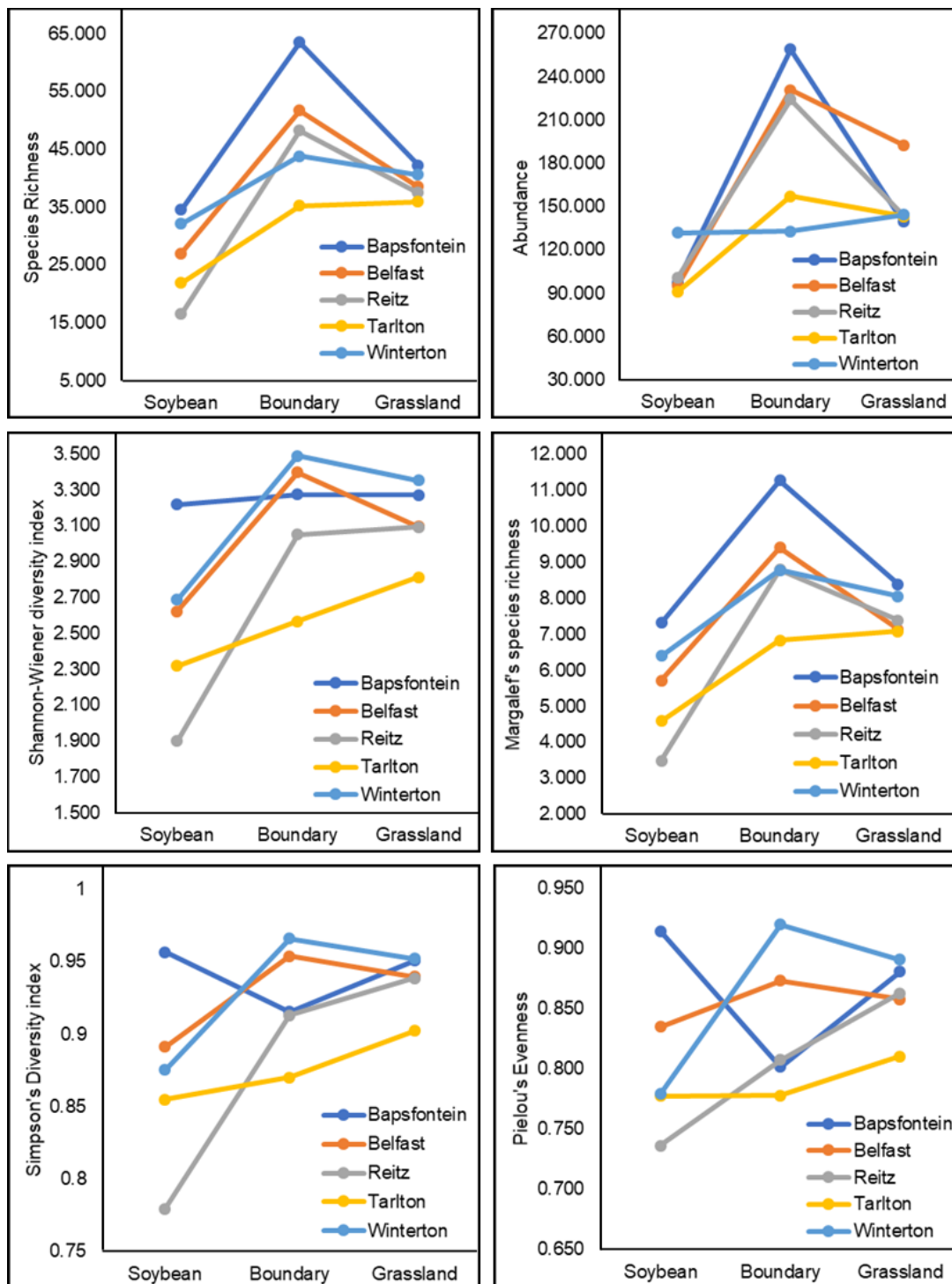


Figure 5.3: Diversity index values for arthropods along a soybean crop-field margin gradient for five localities in soybean agro-ecosystems of South Africa.

Hierarchical Linear Modelling (HLM) analyses revealed significantly lower arthropod species richness, abundance and diversity index values for the soybean crop than both the boundary and grassland (Table 5.5). However, there were no significant differences between Pielou's evenness of the soybean crop and the boundary zone. Pielou's evenness was however significantly lower in the soybean crop than the grassland. Arthropod species richness, abundance and Margalef's species richness of the boundary was significantly higher than the grassland. However, no significant differences were found between the Shannon-Wiener diversity index, Pielou's Evenness and Simpson Diversity index values of the boundary and grassland.

Table 5.5: Hierarchical linear modelling (HLM) results for the total arthropod sample. Mean value measures are given for the soybean crop, field boundary and grassland.

Diversity indices	Soybean		Boundary		Grassland		Residual variance	Transect variance	F-value	P-value
	Mean	Standard error	Mean	Standard error	Mean	Standard error				
Species Richness	27.54 ^a	2.30	48.15 ^b	2.30	39.20 ^c	2.20	68.639	20.840	25.63	<0.001
Abundance	104.59 ^a	16.6	194.19 ^b	16.6	148.90 ^c	15.87	3636.918	982.840	10.60	<0.001
Margalef's										
Species Richness	5.73 ^a	0.37	9.00 ^b	0.37	7.70 ^c	0.35	1.618	0.670	26.94	<0.001
Shannon-Wiener										
Diversity Index	2.62 ^a	0.10	3.14 ^b	0.10	3.13 ^b	0.10	0.103	0.061	12.94	<0.001
Pielou's										
Evenness	0.83 ^a	0.10	0.85 ^{ab}	0.10	0.86 ^b	0.09	0.004	0.002	1.47	0.250
Simpson										
Diversity Index	0.90 ^a	0.13	0.93 ^b	0.13	0.94 ^b	1.13	0.004	0.002	4.94	0.016

Means with different subscript symbols differed practically according to the effect sizes ($d \geq 0.5$).

5.5.2 Discussion

Significantly lower diversity of arthropods was collected from the soybean crop than both the field boundary and grassland. This supports findings by Botha *et al.*, (2015), who also found significantly lower arthropod species richness and diversity in maize fields compared to their field margins. Similarly, Pfiffner and Luka (1999) found significantly higher abundance and diversity of arthropods in field margin zones compared to wheat fields of Switzerland. In crop fields, management and cultivation practices (agro-chemical application and tillage) can directly affect the diversity and abundance of arthropods (Kirchner, 1977, Jasinski *et al.*, 2003; Schneider *et al.*, 2009). For instance, reduced diversity and abundance of sheet web spiders (Araneae: Linyphiidae), wolf spiders (Araneae: Lycosidae) and ground beetles (Coleoptera: Carabidae) were observed after tillage in different cropping systems in the United States (Witmer *et al.*, 2003). Cultivation and management practices of soybean fields can also indirectly affect arthropods through changes in plant diversity (Kleijn and Snoeijsing, 1997; Haughton *et al.*, 2001). In Chapter 4 of this study, the soybean crop was found to have low abundance and diversity of non-crop plants – a contributing factor to this trend observed on arthropod diversity. Numerous studies demonstrated that decreasing plant species richness

and diversity leads to decreased arthropod diversity and species richness (Siemann *et al.*, 1998; Denys and Tschardtke, 2002; Haddad *et al.*, 2009; Botha *et al.*, 2017).

Crowder *et al.* (2010) observed low evenness of natural enemies in intensely managed agricultural fields, with one species accounting for almost 80% of all the individuals collected. This study revealed no significant differences between Pielou's Evenness for arthropod species in the soybean crop and the boundary. Arthropod evenness was unexpectedly high in the crop. This contradicts the notion that intensely managed crop fields are often dominated by a few species that are well adapted to the crop and able to tolerate the high level of disturbance that results from management practices (Hillebrand *et al.*, 2008; Crowder *et al.*, 2010). Reduction of arthropod evenness was reported following increased arthropod abundance and species richness in diversified cropping systems (Lichtenberg *et al.*, 2017). The decreased evenness reported in the latter study was reflected by a higher number of rare species in diversified cropping systems. However, the presence of weeds may influence these dynamics and render the crop fields not to be a true or outright monoculture. Although plant diversity recorded within the soybean crop (see Chapter 4) was significantly lower than in the field margin, all the crop fields were still characterized by the presence of weeds. Shelton and Edwards (1983) collected significantly higher arthropod diversity for weedy soybean fields compared to weed-free fields. Therefore, weeds support a variety of arthropod species that would otherwise not be supported by the soybean crop, which may reduce the dominance of some species.

No significant differences for Pielou's Evenness and Simpson's Diversity were found for arthropods between the boundary and grassland. Similar to Pielou's evenness, Simpson's diversity emphasizes the relative abundance of species and, thus, is a good indication of homogeneity. Significantly higher species richness, abundance and Margalef's species richness for arthropods were observed in the boundary than the grassland. This shows that the boundary had more species and higher abundance than the grassland but the evenness of species was similar between the two zones. The Shannon-Wiener diversity index brings both species richness and evenness into account and it is probably due to the evenness component that no significant differences were found for this index between the boundary and grassland in this study.

These results reject the hypothesis that the field boundary has lower arthropod diversity than the grassland due to disturbances associated with this zone. This is also different from what was observed for the plant diversity survey where no significant differences were found between the boundary and grassland. The field boundary can be viewed as the transition zone between crop fields and adjacent natural habitats. Transitions zones are often referred to as

an ecotone, an area where two adjacent habitats meet (Van der Maarel, 1990). However, Van der Maarel (1990) proposed that ecotones should be distinguished from ecoclines. An ecocline is a stable transition between two habitats resulting in higher diversity than the adjacent habitats, whereas an ecotone is a stressed transition between two habitats typically resulting in lower diversity than adjacent habitats (Van der Maarel, 1990).

The soybean crop has a different vegetation composition, plant structure and microclimate than the adjacent grassland (Chapter 4). This means there is high contrast between the two habitats which is likely to result in a stressed transition between the two. In this study, plant diversity was higher in boundary than the soybean crop and although not statistically significant, tended to be lower than in the grassland. Thus, plant diversity in the field boundary correlated with the ecotone definition proposed by Van der Maarel (1990). Similarly, Dutoit *et al.* (2007) observed distinct plant communities along a cereal field-field margin gradient with similar species richness between the transition zone and adjacent grassland. Arthropod diversity was significantly higher in the boundary zone than in both the soybean crop and grassland, correlating with the ecocline definition of Van der Maarel (1990). The increased arthropod diversity in the field boundary may be attributed to a possible edge effect.

The term edge effect was originally coined to describe an increased species richness between two adjacent habitats because it is believed that edges contain characteristics of both habitats as well as unique characteristics (Murcia, 1995; Dutoit *et al.*, 2007). Arthropods are more mobile than plants, and in agro-ecosystems, a spillover of arthropod species between the crop and non-crop habitat frequently occurs (Tscharntke *et al.*, 2005). Also, the Intermediate Disturbance Hypothesis states that biodiversity is highest when a disturbance of intermediate intensity or frequency is present (Connell, 1978). At any given moment, the boundary may contain species from the soybean crop and the grassland, as well as a unique set of species adapted to the environment within the boundary. In Germany, the establishment of boundaries between crop fields and meadows did not increase ant (Hymenoptera: Formicidae) species richness (Dauber and Wolters, 2004). However, the abundance of certain species (such as *Lasius niger* (L.)) increased while that of other species (such as *Myrmica scabrinodis* Nyl.) decreased.

The boundary was characterized by an abundance of alien plant species while the grassland had few alien species. Alien plants are known to have significant effects on native arthropod populations. For instance, it was found that more than 40% of native butterfly fauna in California breed exclusively on alien plants and would likely disappear if these alien plants should be removed (Shapiro, 2002). Higher abundance and diversity of arthropods were also

observed in weed-dominated naturally regenerated field margin vegetation compared to field margins sowed with wild grass and leguminous species (Lagerlof and Wallin, 1993).

However, the majority of studies do not report increasing arthropod diversity in response to the invasion of alien plant species (Litt *et al.*, 2014). For example, up to 39% reduction in arthropod abundance and a 19% reduction of arthropod species richness were observed in habitats invaded by stilt grass (*Microstegium vimineum* (Trin.) A. Camus), an invasive weed in the United States (Carolina *et al.*, 2010). The reduction in arthropod diversity was largely attributed to a reduction in species richness of native flora after invasion by stilt grass. However, it remains unclear how invasive plants affect dietary and habitat requirements of arthropods (Litt *et al.*, 2014). It was reported that invasion of alien plants can significantly alter the vegetation structure and microclimate of the plant community (Toft *et al.*, 2001; Standish, 2004; Spyreas *et al.*, 2010). In the present study, the presence of weeds meant the boundary had more diverse plant structures (which likely increased the range of microclimates as well) and floral resources than both the grassland and soybean. Numerous studies report a general increase of arthropod diversity and abundance with increasing vegetation types, plant structures and floral resources (Hegland and Boeke, 2006; Morris, 2000; Randlkofer *et al.*, 2010; Bennet and Gratton, 2013).

5.6 Effect of land-use intensity and environmental variables on arthropod species assemblages

5.6.1 Results

In the Canonical Correspondence Analysis (CCA) for arthropod sample plots, land-use intensity had strong correlations with both axis 1 and 2 (Fig. 5.4; Table 5.6). The longitude and mean annual precipitation (MAP) had relatively strong correlations with axis 2. Farming type (cultivation of conventional or glyphosate-tolerant soybean) and latitude had weak correlations with axis 2. Axis 1 accounted for 23.06% of the variance in arthropod species assemblages, while axis 2 accounted for 20.98% of the variance.

At a local scale, land-use intensity resulted in three distinctive groupings (Fig. 5.4). The first was arthropod sample plots in the soybean crop that were characterized by high land-use intensity. The second was arthropod sample plots of the boundary that were characterized by moderately high land-use intensity, and finally, arthropod sample plots of the grassland were characterized by low land-use intensity.

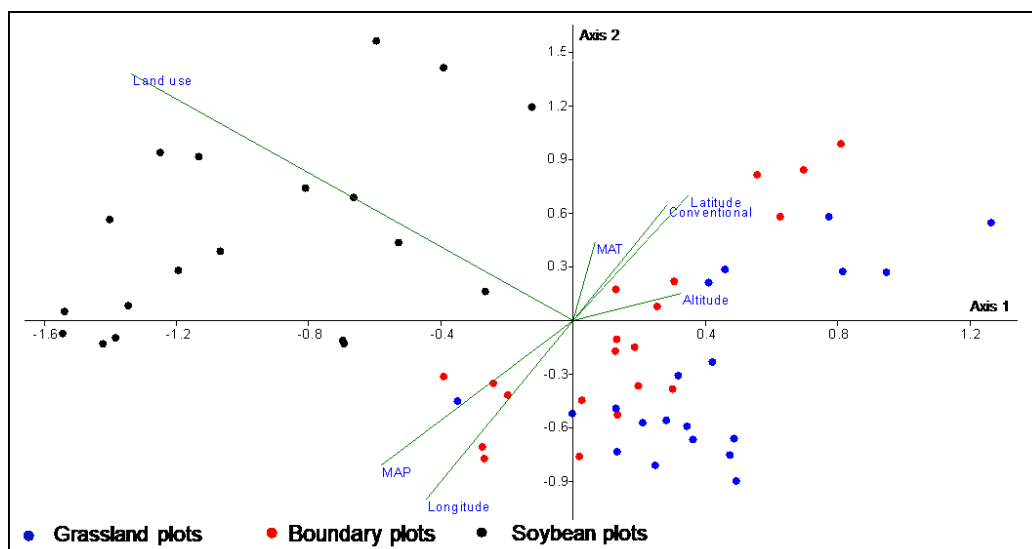


Figure 5.4: Canonical correspondence analysis (CCA) of all the localities showing correlations of environmental variables with arthropod sample plots. Each symbol represents the weighted average of one plot in relation to environmental variables. The environmental variables were altitude, latitude, longitude, mean annual precipitation (MAP), mean annual temperature (MAT), farming type (Conventional soybean or glyphosate-tolerant soybean) and land-use intensity.

Table 5.6: Correlations of ordination axes with environmental variables and eigenvalues and percentage variance explained for canonical correspondence analysis of arthropod species assemblages at all localities.

Variable	Axis 1	Axis 2
Land use intensity	-0.668	0.689
Conventional soybean	0.143	0.324
Altitude	0.163	0.075
Latitude	0.175	0.351
Longitude	-0.223	-0.501
Mean annual precipitation	-0.291	0.406
Mean annual temperature	0.033	0.220
Eigenvalue	0.351	0.319
% variance explained	23.06	20.98

There were three land-use types that accounted for the land-use intensity variable (crops, buildings and settlements, roads and fences). The separate analyses of each land-use type (Figure: 5.5; Table 5.7), showed that crops made the largest contribution to the variance in arthropod species assemblages, followed by buildings and settlements, while the presence of roads and fences made a small contribution to the variance in arthropod species assemblages.

At a regional scale, localities were separated into three groupings by environmental variables. The most important of these variables were MAP and longitude, while latitude and farming type made a small contribution to the variation in arthropod species assemblages. The arthropod species assemblages at the Winterton and Belfast localities were correlated with high MAP and longitude, while Bapsfontein was correlated with low MAP, longitude, and the presence of conventional soybean.

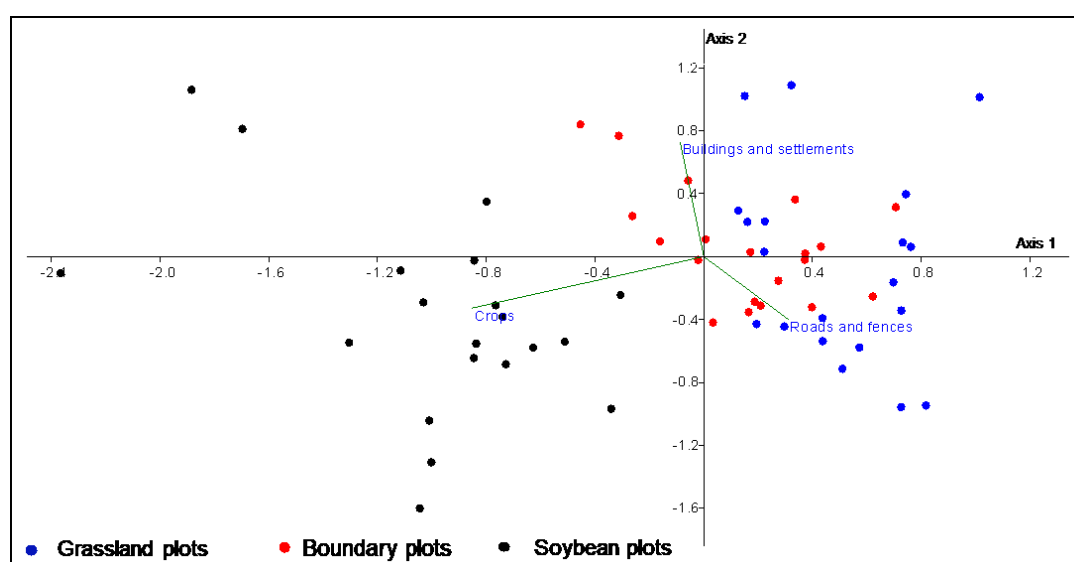


Figure 5.5: Canonical correspondence analysis (CCA) of all the localities showing correlations of land-use types with arthropod sample plots. Each symbol represents the weighted average of one plot in relation to a land-use type. The land-use types were crop fields, buildings and settlement and roads and fences.

Table 5.7: Correlations of ordination axes with land-use types and eigenvalues and percentage variance explained for canonical correspondence analysis of arthropod morph-species assemblages at all localities.

Variable	Axis 1	Axis 2
Crops	-0.852	-0.327
Buildings and settlements	-0.087	0.729
Roads and fences	0.312	-0.400
Eigenvalue	0.364	0.235
% variance explained	60.6	39.18

5.6.2 Discussion

Farming type (cultivation of conventional or glyphosate-tolerant soybean) made a small contribution to the variation in species assemblages. Arthropod species assemblages at Bapsfontein were characterized by conventional soybean while the other localities reacted stronger to glyphosate-tolerant soybean. The cultivation practices associated with glyphosate-

tolerant soybean can indirectly affect arthropods through changes in the plant community (Kleijn and Snoeiijing, 1997; Jackson and Pitre, 2004; Brower *et al.*, 2012; Egan *et al.*, 2014). However, in the present study, farming type did not contribute to the variation in plant species assemblages (Chapter 4, section 4.6), and could, therefore, not contribute to variation in arthropod species assemblages. Most studies report minimal direct effect of glyphosate-soybean cultivation on arthropods (Buckelew *et al.*, 2000; Bitzer *et al.*, 2002; Pedigo *et al.*, 2002; Jasinski *et al.*, 2003; McPherson *et al.*, 2003; Jackson and Pitre, 2004), with a few studies reporting possible effects on the behaviour and biology of arthropods (Schneider *et al.*, 2009; Benamú *et al.*, 2010; Evans *et al.*, 2010; Motta *et al.*, 2018). Adoption of glyphosate-tolerant crops may also change cultivation practices, primarily through increasing adoption of conservation tillage (Young, 2006), which may further influence the arthropod community (Anderson, 1999; Rodríguez *et al.*, 2006; Sharley *et al.*, 2008). Regardless, the study show that the farming type only made a small contribution to the variation in species assemblages and that land-use intensity was the most important determinant for arthropod species assemblages.

The land-use intensity variable was dominated by typical activities and infrastructure found in agricultural landscapes, namely crop fields, buildings, roads and fences. Crop fields made the most important contribution to variation in arthropod species assemblages, followed by the presence of buildings. This is expected as agricultural activities that entail large-scale transformation and fragmentation of natural habitat with the potential to further degrade remaining habitat via agro-chemical drift have documented adverse effects on arthropod abundance and species richness (Feber *et al.*, 1996; Stamps and Linit, 1998; Seymore and Dean, 1999; Santín-Montanyá *et al.*, 2013). Furthermore, these activities may ultimately have effects on arthropod species composition. For instance, increasing the intensity of agricultural land-use was found to decrease species richness and abundance of social bees, while the abundance and richness of solitary bees and trap-nesting species increased (Klein *et al.*, 2002a). In cocoa agro-ecosystems, species richness of phytophagous arthropods increased and entomophagous arthropods decreased with increasing agricultural land-use (Klein *et al.*, 2002b). Furthermore, arthropod species assemblages were indirectly affected by changes in plant assemblages resulting from increased land-use intensity (Chapter 4, section 4.6), since its widely reported that plant species composition can have a significant effect on arthropod species assemblages (Haddad *et al.*, 2001; Harvey *et al.*, 2008; Schaffers *et al.*, 2008).

At a regional scale, mean annual precipitation (MAP) and the geographical position (latitude and longitude) created groupings between localities. Belfast and Winterton lie on similar longitudinal lines and were grouped together. Bapsfontein, Tarlton and Reitz also had a similar

longitude and grouped together, except Bapsfontein that was separated from Reitz and Tarlton by farming type. Similarly, longitude and latitude explained most of the variation in arthropod species assemblages in the Grassland and Savanna biomes of South Africa (Botha *et al.*, 2016). These effects were ascribed to possible differences in climatic conditions between geographical positions. For example, South Africa tends to become drier from east to west. Belfast and Winterton lie on similar longitudinal lines in the eastern parts of the country, and the CCA biplot did show that these two localities were characterized by high MAP. Belfast is located in the Eastern Highveld Grassland vegetation unit and Winterton is located in the Northern KwaZulu-Natal Moist Grassland vegetation unit which lies on similar longitudinal lines. Both these vegetation units are characterized by high annual precipitation in comparison with the other localities (Mucina and Rutherford, 2006). This is similar to the CCA ordination for plant sample plots (Chapter 4, section 4.6). Plant sample plots at Winterton were separated from other localities by high MAP. Although plant species assemblages were also affected by MAT and altitude resulting from different geographical positions, the same did not apply to arthropod species assemblages.

Conclusion

The soybean crop had low species richness, abundance and diversity of arthropods. This supports the first hypothesis that soybean fields will harbour lower diversity than the adjacent boundary and grassland zones. This may result from crop-associated disturbance that may directly affect arthropods or indirectly through alterations of the plant community.

The boundary had a significantly higher species richness and abundance of arthropods than the grassland, although no significant differences of evenness occurred between the two zones. This rejects the second hypothesis stating that the boundary will have lower diversity due to the disturbance effects of adjacent crop fields. The boundary had species from both the crop and grassland (resulting from the high mobility of arthropods), as well as a set of its own unique species. This supports the third hypothesis that the boundary will have unique species assemblages that are able to tolerate possible disturbances in this zone. A possible edge effect and high diversity of native grass species and invasive weeds in the boundary (as observed in Chapter 4) resulted in high structural diversity of boundary vegetation which is able to support increased arthropod diversity.

Land-use intensity (especially the presence of crop fields) explained most of the variation in arthropod species assemblages. Soybean sample plots grouped according to high land-use intensity, boundary plots grouped according to moderate land-use intensity and grassland plots grouped according to low land-use intensity. At a regional scale, geographical position

(longitude and latitude), MAP, and to a lesser degree, farming type, accounted for variation in species assemblages between localities.

The results also disregard the perceptions that field boundary zones harbour crop pests. There were no soybean arthropod pest species recorded from the boundary. There were, however, the high diversity of entomophagous arthropods (that were absent in the soybean crop) collected from the boundary and grassland. This emphasizes the conservation value of these zones because soybean fields are largely dependent on entomophagous arthropods colonizing the crop from these zones.

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Chapter 6: Plant and arthropod diversity relationships

Abstract

Soybean is extensively cultivated in the Grassland Biome of South Africa. Yet little information is available whether plant diversity maintains arthropod diversity in these landscapes. Understanding the relationships between plant and arthropod diversity is important since this knowledge could facilitate the development of strategies to enhance the diversity of beneficial arthropods such as pollinators and natural enemies of crop pests in agricultural landscapes. To address this knowledge gap, this study aimed to describe the diversity correlations between prominent arthropod groups (herbivores, parasitoids, spiders and other predators) and prominent plant families (Poaceae, Fabaceae and Asteraceae). Plant and arthropod diversity were surveyed at ten sites in major soybean production regions of South Africa. Sample plots were placed in three zones at each site, i.e., the soybean crop, adjacent natural grassland and field boundary (transition zone between cropland and natural habitat). Each zone had a distinct plant species assemblage which was mirrored by distinct arthropod species assemblages. The abundance of Poaceae had a general negative correlation with spider diversity in the soybean crop, and with herbivore and predator diversity in the boundary and grassland. A low diversity of parasitoids was associated with a high diversity of Asteraceae. Species Richness and Pielou's Evenness of Fabaceae (as well as species richness and evenness of all plants) had general positive correlations with evenness of predators and parasitoids that may result in more effective pest regulation within the crop environment. The findings indicate that plant species composition may be an important determinant for arthropod species composition. Furthermore, increased diversity of Poaceae and Asteraceae species may reduce diversity of the natural enemies of pests in soybean agro-ecosystems.

Keywords

Abundance, biodiversity, Poaceae, Soybean, alpha-diversity, beta-diversity, natural enemy.

6.1 Introduction

It is widely considered that plant diversity is a determinant of arthropod diversity. Some arthropod herbivores may exhibit a degree of host specificity (Andow and Imura, 1994; Norris and Kogan, 2000). For example, some may prefer grasses (Tscharntke and Greiller, 1995) and other forbs (Jonas and Joern, 2008). As a result, increasing plant species richness may diversify vegetation structure and increase herbivore richness. In addition, increasing herbivore richness could potentially increase predator and parasitoid diversity (Hunter and Price, 1992; Siemann, 1998; Siemann *et al.*, 1998). Therefore, increasing plant diversity could potentially increase natural enemy diversity indirectly through higher herbivore diversity. Plant diversity can affect natural enemies directly through the provision of alternative food resources, oviposition sites, and shelter (Tilman, 1986; Hunter and Price, 1992; Rosenzweig, 1995; Ratnadass *et al.*, 2012; Kaiser *et al.*, 2017).

Large-scale agriculture has in most instances led to simplified agro-ecosystems and ultimately resulted in biodiversity loss (Altirre, 1999; Liere *et al.*, 2017). Subsequently, this has resulted in the loss of important ecosystem services such as biological pest regulation (Altieri, 1999). For instance, weakened biological control of pests was observed in crop fields with reduced species richness (Snyder *et al.*, 2006; Straub and Snyder, 2008; Letourneau *et al.*, 2009) and species evenness (Hillebrand *et al.*, 2008; Crowder *et al.*, 2010) of biological control agents. In contrast, diversified cropping systems such as traditional farming systems, polycultures, conservation agriculture and agroforestry are generally associated with higher diversity and abundance of natural enemies and reduced pest outbreaks (Altieri *et al.*, 1978; Hooks and Johnson, 2003; Bianchi *et al.*, 2006; Cai *et al.*, 2007). Understanding the relationship between plants and arthropods may aid efforts to enhance beneficial arthropod diversity and abundance in agricultural landscapes.

Literature has reported positive correlations between plant and arthropod diversity (Siemann *et al.*, 1998; Knops *et al.*, 1999; Sperber *et al.*, 2004; Haddad *et al.*, 2009). Few studies of this nature have been conducted in South Africa. The majority of these focused on the Cape Floristic Region and reported general positive correlations between insect species richness and plant species richness (Wright and Samways, 1998; Proches and Cowling, 2006; Kemp and Ellis, 2017). In South Africa, general positive correlations were also recorded between Poaceae abundance and arthropod diversity in maize agro-ecosystems (Botha *et al.*, 2017).

However, it remains unclear how arthropod diversity will react to changing plant diversity in soybean cropping systems of South Africa. Therefore, the aim here was to determine whether relationships exist between components of plant and arthropod diversity in soybean agro-ecosystems. It is hypothesized that arthropod diversity will increase in response to increasing

plant diversity. Specific objectives were to determine whether relationships exist between arthropod functional groups (spiders, other predators, parasitoids and herbivores) and dominant plant families (Poaceae, Fabaceae and Asteraceae), and to determine whether relationships exist between herbivores and natural enemies.

6.2 Materials and Methods

Ten sites were surveyed in major soybean production areas of South Africa (Chapter 3: 3.1). Plant and arthropod diversity was recorded in the soybean crop, field boundary (transition zone between crop fields and adjacent natural habitat) and natural grassland adjacent crop fields (Chapter 3: 3.2). Plant species were recorded following an adapted fixed-width (2 m) line transect method (Chapter 3: 3.4). Arthropods were collected following an adapted D-vac suction method (Chapter 3: 3.3). Permutational Multivariate Analyses of Variance and Multivariate Homogeneity of group dispersions (PERMDISP) were performed to test for significant differences in plant and arthropod species assemblages and beta-diversity between the three zones (Chapter 3: 3.5.4). Spearman's rank-order correlation analyses were conducted to test for significant correlations between plant and arthropod species richness, abundance and diversity index values (Chapter 3: 3.5.4). Correlations were determined between major plant (all plants, Fabaceae, Asteraceae and Poaceae) and major arthropod groups (all arthropods, spiders, other predators, parasitoids and herbivores). Correlations were also determined between herbivores and entomophagous arthropods (spiders, other predators and parasitoids).

6.3 Descriptive data

A total of 9216 arthropod individuals, 373 morpho-species and 97 families were collected. This amounted to 170 morpho-species in the soybean crop, 280 in the boundary and 256 in the grassland. The best-represented arthropod functional groups were herbivores, predators and parasitoids, collectively accounting for 67% of all arthropod abundances (Table 6.1). Other trophic groups were pollinators, detritivores, omnivores, and frugivores. These were not collected in high enough numbers to be considered for further analysis.

Table 6.1: Number of species of each trophic group as well percentage contribution (% individuals) of each trophic group to the total number of individuals collected for the overall sample.

Trophic group	Overall		Soybean		Boundary		Grassland	
	No. of Species	% of individuals	No. of Species	% of individuals	No. of Species	% of individuals	No. of Species	% of individuals
Herbivores	155	39.49	69	43.29	119	36.81	105	40.77
Other Predators	45	10.12	25	14.14	38	10.01	27	11.36
Parasitoids	49	8.92	21	9.62	37	7.36	38	10.61
Spiders	45	8.16	22	7.92	36	7.06	34	9.85
Other	79	33.31	31	25.03	50	38.76	52	27.41
All arthropods	373	---	168	---	280	---	256	---

A total of 4910 plants were counted, amounting to 320 species and 52 families. This amounted to 39 species from the soybean crop, 127 from the boundary and 246 from the grassland. The best-represented plant families were Poaceae, Asteraceae and Fabaceae which collectively represented 71% of all plant abundances (Table 6.2).

Table 6.2: Number of species of dominant plant families and contribution (% individuals) of each family to the total number of individuals collected for the overall sample (including *Glycine max*).

Trophic group	Overall		Soybean		Boundary		Grassland	
	No. of Species	% of individuals	No. of Species	% of individuals	No. of Species	% of individuals	No. of Species	% of individuals
Poaceae	74	41.61	10	8.21	41	56.02	52	50.29
Asteraceae	72	17.52	7	5.98	34	21.85	58	21.09
Fabaceae	27	12.11	2	44.96	7	0.97	22	4.82
Other	147	28.76	20	40.85	45	21.16	114	23.80
All plants	320	---	39	---	127	---	246	---

6.4 Plant and arthropod beta-diversity

6.4.1 Results

PERMANOVA analysis for the overall plant species composition as well as analyses performed separately on the species assemblages of Asteraceae and Poaceae revealed significant differences between the soybean crop, field boundary and untransformed grassland (Table 6.3). Analysis of the species composition of Fabaceae did reveal significant differences between the soybean crop and field margin but there were no differences between the boundary and grassland. Similarly, PERMANOVA analysis of species composition of all arthropods and separate analyses of predators and herbivores species composition revealed significant differences between the soybean crop, boundary and grassland. Analyses of species assemblages of spiders and parasitoids did reveal significant differences between the

soybean crop and field margin but there were no differences between the boundary and grassland.

Table 6.3: Pairwise Permutational Multivariate Analysis of Variance (PERMANOVA) indicating significant separations between treatment zones based on plant and arthropod species composition.

Taxonomic group	Soybean*Boundary		Soybean*Grassland		Boundary*Grassland	
	t-value	P-value	t-value	P-value	t-value	P-value
All plants	2.628	0.001	7.482	0.001	4.312	0.001
Poaceae	3.540	0.001	4.173	0.001	2.841	0.001
Asteraceae	1.931	0.001	2.238	0.001	2.556	0.001
Fabaceae	4.878	0.001	5.478	0.001	1.139	0.218
All arthropods	1.380	0.001	0.380	0.001	1.112	0.002
Spiders	1.554	0.008	1.705	0.003	0.892	0.622
Other predators	1.379	0.038	1.746	0.001	1.470	0.022
Parasitoids	3.055	0.001	3.158	0.001	0.950	0.526
Herbivores	2.793	0.001	2.952	0.001	1.018	0.018

Values in red indicate significant separations at $P < 0.05$ (permutation N = 999)

Multivariate homogeneity of dispersions (PERMDISP) can be used as a measurement for beta-diversity. For all plants, PERMDISP analyses revealed significantly less heterogeneity in plant species assemblages in the soybean crop compared to the boundary and grassland (Table 6.4). Mean distances from centroids were 42.2, 48.3 and 57.7 for the soybean crop, boundary and grassland respectively. Increasing distance to centroids indicates greater species heterogeneity in species assemblages between sampling points. However, for all arthropods, PERMDISP analyses revealed no significant differences in the heterogeneity of arthropod species assemblages between the soybean crop, boundary and grassland (Table 6.4). Distances to centroids were 50.933, 48.379 and 50.228 for the soybean crop, boundary and grassland respectively.

Table 6.4: Permutational multivariate analysis of homogeneity in dispersion (PERMDISP) results indicate differences in beta-diversity of all plants and all arthropods between the soybean crop, boundary and grassland.

Taxonomic group	Zone	t	P (Perm)
All plants	Soybean*Boundary	2.628	0.018
	Soybean*Grassland	7.482	0.001
	Boundary*Grassland	4.312	0.001
All arthropods	Soybean*Boundary	1.380	0.174
	Soybean*Grassland	0.380	0.708
	Boundary*Grassland	1.112	0.263

Permutations: 999; Bray-Curtis similarity; data transformed: presence/absence; Values in red indicate significant separations at $P < 0.05$.

6.4.2 Discussion

In general, the soybean crop, boundary and grassland had unique assemblages of plant species. This was mirrored by unique assemblages of arthropod species. It appears that plant species composition influences the arthropod species composition because changes in plant species assemblages (from the soybean crop to the boundary and grassland) were followed by changes in arthropod species assemblages. Plant species composition is generally considered a good determinant for arthropod species assemblages (Haddad *et al.*, 2001; Schaffers *et al.*, 2008; Harvey *et al.*, 2008).

However, it is important to consider beta-diversity, which is a measurement of variation in plant and arthropod species assemblages between plots (Clough *et al.*, 2007). Zones with high beta-diversity have large differences in species assemblages between plots. For the plant community, beta-diversity was significantly lower in the soybean crop than the boundary and grassland. Therefore, soybean crops tend to have homogenous assemblages of plants across the entire landscape. Similar results were recorded in maize agro-ecosystems of South Africa (Botha *et al.*, 2017). Natural areas had more heterogenous assemblages of plants than maize fields. This was expected and supported by literature with general reductions of beta-diversity being reported with intensive agriculture (Clough *et al.*, 2007; Flohre *et al.*, 2011; Karp *et al.*, 2012). Crop fields are exposed to similar conditions and disturbances across the landscape. This will result in similar assemblages of non-crop plants able to colonize crop fields in these specific set of conditions. Furthermore, the grassland also had significantly higher beta-diversity than the boundary. Therefore, it appears that disturbances arising from crop fields also have a homogenization effect on plant assemblages in the boundary, although not as great as the soybean crop.

For the arthropod community, beta-diversity did not differ between the soybean crop and field margin (boundary and grassland). Arthropod beta-diversity also did not increase with increasing plant beta-diversity. Therefore, the soybean crop did not have a homogenization effect on the arthropod species assemblages like it had for plant assemblages. The study by Botha *et al.* (2017) also found no difference in arthropod beta-diversity between maize fields and natural areas. The boundary and grassland had high beta-diversity of plants, which meant that there was heterogeneity between sample plots. The low beta-diversity for arthropods meant homogeneity between plots. This can partly be explained by the high mobility and dispersal ability of arthropods compared to plants. Species with limited dispersal ability are unlikely to be shared among distant sample plots, which results in high beta-diversity. Literature does report increasing beta-diversity of organisms with limited dispersal ability (Condit *et al.*, 2002; Soininen *et al.*, 2007; Qian, 2009).

6.5 Diversity correlations within the arthropod community

6.5.1 Results

Table 10.1 (Appendix C) lists the Spearman rank correlation values between species richness, abundance and diversity index values of herbivores and entomophagous arthropods in the soybean crop, boundary and grassland. In the soybean crop, there were significant positive correlations between herbivore species richness, spider species richness and abundance.

Analyses within the boundary zone showed 31 significant correlations between herbivores and higher trophic groups. Species richness, abundance, Margalef's species richness and Shannon-Wiener diversity of herbivores had general positive correlations with the corresponding indices of spiders, other predators and parasitoids.

In the grassland, herbivore abundance had significant positive correlations with Shannon-Wiener diversity and Simpson's diversity of spiders. Species richness, Margalef's species richness and Shannon-Wiener diversity of herbivores showed significant positive correlations with the corresponding indices of other predators. There were no significant correlations between herbivore and parasitoid diversity in the grassland.

6.5.2 Discussion

Distinct plant species assemblages were observed between the soybean crop, boundary and grassland which may potentially alter the interactions between herbivores and their natural enemies (Siemann, 1998). For instance, the structural complexity of the environment may affect the ease at which natural enemies can locate and catch herbivores (Andow and Prokrym, 1990; Gingras *et al.*, 2002; Harvey and Fortuna, 2002; Legrand and Barbosa, 2003). This may result in different associations between herbivores and natural enemies among the three zones. Regardless, similar to other studies (Hunter and Price, 1992; Siemann, 1998; Siemann *et al.*, 1998), increasing herbivore species richness and abundance generally resulted in higher richness and abundance of natural enemies of pests. There were strong associations between herbivore species richness and abundance with i) spider diversity in the soybean crop, ii) spider, predator and parasitoid diversity in the boundary and, iii) predator diversity in the grassland.

Other studies indicate an increase in pest suppression with increasing natural enemy diversity (Snyder *et al.*, 2006; Straub and Snyder, 2008; Letourneau *et al.*, 2009). Crop fields are generally disturbed habitats and more species-rich communities of natural enemies will perform more effective biological pest control because some species are likely to be tolerant to disturbance even though others are adversely affected (Naeem and Li, 1997; Yachi and

Loreau, 1999; Crowder and Jabbour, 2014; Liere *et al.*, 2017). The results also suggest that predator and parasitoid diversity may be important to maintain herbivore diversity, and in turn, be maintained by herbivore diversity (Cramer and May, 1972; Holt *et al.*, 1994; Leibold, 1996; Power *et al.*, 1996). As a result, increasing herbivore diversity may support a higher diversity of natural enemies (Hunter and Price, 1992; Siemann, 1998; Siemann *et al.*, 1998). In return, herbivore abundance can be limited by natural enemy diversity, preventing some species from becoming dominant, thus maintaining evenness so more species can co-exist (Siemann, 1998). Using chain modelling, Siemann *et al.* (1998) found that although increasing plant diversity resulted in higher herbivore and natural enemy diversity, predator-prey and parasitoid-host interactions were a more important determinant for arthropod diversity. Natural enemy diversity increased herbivore diversity, more so than plant diversity. Appropriate tradeoffs between the competitive ability of herbivores and their susceptibility to natural enemies may allow for more herbivore species to co-exist with increasing natural enemy diversity (Tilman, 1986; Holt *et al.*, 1994; Leibold, 1996).

6.6 Plant-arthropod diversity relationships

6.6.1 Results

Table 10.2 (Appendix C) lists the Spearman rank correlation values between species richness, abundance and diversity index values of aspects of plant and arthropod diversity. Insufficient number of Fabaceae species were collected in the soybean crop and boundary to provide accurate values for J'. However, Fabaceae still formed the dominant plant group, in terms of the abundance of *Glycine max* plants) in the soybean crop and, therefore, was necessary to include in the assessment. In the grassland, species richness and abundance of all plants had positive correlations with Pielou's Evenness for predators. Species Richness and Pielou's Evenness of Fabaceae had a positive correlation with Pielou's Evenness of spiders and predators. However, Pielou's Evenness of all plants had negative correlations with Pielou's Evenness of predators. This was followed by negative correlations between Pielou's Evenness of Asteraceae and other predators. However, Pielou's evenness of all plants had positive correlations with Pielou's evenness of parasitoids.

In the boundary and grassland, there were significant negative correlations between the abundance of all plants and the species richness, abundance and Shannon-Wiener diversity of parasitoids. Further analysis revealed that this effect was largely due to the presence of Asteraceae. There were no correlations between parasitoid diversity and the diversity of Poaceae and Fabaceae, while the species richness and abundance of Asteraceae negatively correlated with species richness and abundance of parasitoids.

In the soybean crop, the abundance of all plants had significant negative correlations with the species richness, abundance and Shannon-Wiener diversity of spiders. This was largely due to the presence of Poaceae. The species richness, abundance and Shannon-Wiener diversity of Poaceae had negative correlations with corresponding indices of spiders. No significant correlation was found between spider diversity and the diversity of Fabaceae and Asteraceae. The abundance of Poaceae also had negative correlations with the species richness and Margalef's species richness of herbivores in the boundary and with the species richness and Shannon-Wiener diversity of both herbivores and other predators in the grassland.

6.6.2 Discussion

Arthropod evenness is important to consider since it affects ecosystem function and stability (Wittebolle *et al.*, 2009), and natural enemy evenness may have a significant effect on pest regulation (Hillebrand *et al.*, 2008; Crowder *et al.*, 2010; Crowder and Jabbour, 2014). For example, in the potato crop, increased pest suppression was observed with increasing natural enemy evenness (Hillebrand *et al.*, 2008; Crowder *et al.*, 2010). The authors suggested that natural enemy communities with high species evenness had reduced intraspecific competition, leading to greater natural enemy survival and increased pest regulation. In the grassland, evenness of all plants was associated with a high evenness of parasitoids. At the same time, it is important to note that literature on the relationships between plant evenness and arthropod evenness is generally limited.

Higher evenness of phytophagous Hemiptera was observed in response to increasing plant evenness (Murdoch *et al.*, 1972; Sanderson, 1992). This was expected as phytophagous arthropods are generally considered to be associated with certain plant species (Andow and Imura, 1994; Norris and Kogan, 2000). Therefore, the dominance of some plant species (i.e. low evenness) will result in dominance of its associated arthropod species. Similarly, parasitoids may also have associations with certain plant species through the dependence of some adult parasitoids on floral resources (Lewis *et al.*, 1997; Gillespie *et al.*, 2016), as well as their use of plant-released volatile compounds to locate insect hosts on these plants (De Moraes *et al.*, 1998). However, in this study the opposite was true for. Low evenness of all plants was associated with high predator evenness. A possible explanation would be that the dominance of some plant species (resulting in low plant evenness) favoured rare and uncommon predator species. This may have allowed uncommon species to gain individuals and balance the community. For instance, it was found that controlled burning in conservation sites favoured rare plant species more than others, which allowed them to increase their abundance and subsequently increase community evenness (Crowder *et al.*, 2012). Furthermore, it was found that increasing species richness and abundance of all plants

resulted in higher evenness of predators. Predators require plant resources for shelter, oviposition and alternative food sources (Kaiser *et al.*, 2017). Increasing plant species richness possibly provided a more diverse range of resources that benefits a wider range of predator species, which will reduce the tendency of single species to become dominant.

In the boundary and grassland, high species richness and abundance of Asteraceae were associated with low species richness and abundance of parasitoids. This may be due to trophic interactions between herbivores and parasitoids. Siemann *et al.* (1998) found a positive correlation between plant diversity and parasitoid diversity. Their study reported parasitoid species richness not to be directly affected by changes in plant diversity, but rather indirectly through changes in herbivore species richness. In the boundary and grassland, there were general negative correlations between Asteraceae diversity and herbivore diversity, although the only significant correlation was between the abundance of herbivores and Margalef's species richness and Shannon-Wiener diversity of Asteraceae of the grassland. Symstad *et al.* (2000) recorded strong positive correlations between ichneumonid parasitoid diversity and the diversity of Lepidoptera hosts, and that plant diversity affected ichneumonid parasitoid diversity indirectly through alterations in the herbivore community. Therefore Asteraceae diversity was possibly negatively correlated with parasitoid diversity, as a result of fewer parasitoid hosts that were associated with Asteraceae.

In the soybean crop, high abundance, species richness and Shannon-Wiener diversity of Poaceae resulted in low abundance, species richness, and Shannon-Wiener diversity of spiders. The soybean crop had a distinct spider species composition compared to the boundary and grassland. The vegetation structure of the boundary and grassland was predominantly grass dominated and attracted different spider guilds than the soybean crop. Spiders are associated with specific plant structures and microclimate, which they use for shelter and to hunt prey (Uetz, 1991; Borges and Brown, 2001; Podgaiski *et al.*, 2013). Groups of species that utilize and prey on arthropods in similar ways are classified into similar guilds (Uetz *et al.*, 1999). Significantly different spider species assemblages and guilds were recorded on soybean and maize (a grass) with soybean being dominated by ground runners and web wanderers while maize was dominated by stalkers and orb weavers (Uetz *et al.*, 1999). The difference in spider guild between the two habitats in the latter study was ascribed to differences in plant structure and microclimate. Therefore, a soybean dominated habitat will attract specific types of spiders that are adapted to utilize the structure and microclimate resulting from soybean plants to capture prey. The addition of grass species in the soybean crop will result in alterations of the overall plant structure and microclimate and may adversely affect spider abundance and species richness.

In the boundary and grassland, high abundance of grasses was generally associated with low species richness and abundance of predators and herbivores. On the contrary, in a study by Botha *et al.*, (2017) there was a positive correlation between Poaceae abundance and arthropod diversity in boundary and grassland zones adjacent maize agro-ecosystems in South Africa. At the same time, different crops are known to harbour different arthropod species assemblages. For example, significantly different species assemblages of ground beetles (Coleoptera: Carabidae) were observed between wheat, potato and bean crops (Bourassa *et al.*, 2008). Higher epigeal arthropod species richness and abundance were observed in the soybean crop and field edges compared to maize systems (Molina *et al.*, 2014). Different assemblages of spiders were observed between soybean and maize crops (Uetz *et al.*, 1999). Also, species such as Orthoptera (grasshoppers), Phasmida (stick insects), Symphyta (sawflies), Curculionidae (weevils), Sternorrhyncha (aphids and scale insects), Noctuidae (owl moths) and Pyralidae (snout moths), which are generally abundant arthropod groups on grasses (Tscharncke and Greiler, 1995), were not abundantly documented in this study. Spillover of species between the crop and non-crop habitat frequently occurs (Tscharncke *et al.*, 2005; Rand *et al.*, 2006; Blitzer *et al.*, 2012; Schneider *et al.*, 2013; Adler *et al.*, 2014), suggesting that crop fields may have a significant effect on the arthropod assemblages in the boundary and grassland. However, the studies of Molina *et al.* (2014) and Uetz *et al.* (1999) did not compare arthropod diversity and assemblages of maize and soybean cropping systems beyond the field boundary. It is therefore unclear whether crop type will affect plant-arthropod interactions beyond the field boundary. Moreover, contradictory results between this study and that of Botha *et al.* (2017) emphasizes the importance of case by case studies, as different crop environments may yield different results.

Overall, there were few positive correlations between the species richness and diversity of arthropod and plants. This is contradictory to multiple studies reporting on positive correlations between plant and arthropod species richness (Siemann *et al.*, 1998; Knops *et al.*, 1999; Sperber *et al.*, 2004; Haddad *et al.*, 2009; Dassou and Tixier, 2016; Welti *et al.*, 2017). However, the relationship between plant and arthropod diversity is more complex than relationships between plant and arthropod species richness. Factors such as plant functional and structural diversity (Symstad *et al.*, 2000; Brose, 2003), plant genetic diversity (Wimp *et al.*, 2005; Crawford and Rudgers, 2013; Koricheva and Hayes, 2018), plant productivity (Siemann, 1998; Perner *et al.*, 2005), plant chemical complexity (Randlkofer *et al.*, 2010; Salazar *et al.*, 2016), habitat complexity (Lassau and Hochuli, 2004; Lassau *et al.*, 2005) and habitat age (Frank and Reichhart, 2004; Frank *et al.*, 2012) may play a significant role in structuring arthropod assemblages. These factors were not analyzed in this study and may yield different results if considered in future studies. This lack of relationships may further have

resulted from the sampling method that was used. For instance, it was shown that vacuum sampling (used in this study) recorded different arthropod taxa than sweep netting (Buffington and Redak, 1998; Doxon *et al.*, 2011). Doxon *et al.* (2011) reported that vacuum sampling was very effective for small arthropods, but not as effective for fast-flying insects (Buffington and Redak, 1998). This means that a portion of the arthropod diversity that was present in the study areas was not recorded. A combination of sampling methods may yield a more accurate representation of the arthropod community and plant-arthropod associations. However, it is important to note that vacuum sampling method was appropriate for this study given the aim and objectives. Therefore, the findings are not insufficient or insignificant in any manner.

Conclusion

This study showed that distinct arthropod communities followed on distinct plant communities in soybean agro-ecosystems of South Africa. However, low beta-diversity of plants in soybean fields compared to significantly higher beta-diversity in the field margins were not mirrored by differences in arthropod beta diversity between soybean fields and field margins. Low mobility of plants results in heterogenous plant assemblages in the non-crop habitat, whereas management practices used in soybean fields resulted in homogenous weed assemblages.

There were generally positive relationships between herbivore and natural enemy diversity. This suggests that the diversity of herbivores and natural enemies may be important to sustain each other. Furthermore, understanding plant-arthropod diversity relationships may aid to enhance natural enemy diversity for natural pest suppression. Increased species richness of all plants resulted in high evenness of predators, which may increase the efficiency of pest regulation (Crowder *et al.*, 2010). Correlations between arthropod and plant diversity were rarely significant and generally weak. This rejects the hypothesis that high arthropod diversity will be maintained by high plant diversity.

Asteraceae diversity was negatively correlated with parasitoid diversity, probably as a result of fewer parasitoid hosts that were associated with Asteraceae. A general negative correlation was recorded between Poaceae abundance and arthropod diversity. Previous studies have shown positive correlations between Poaceae and arthropod diversity in maize agro-ecosystems (Botha *et al.*, 2017), which shows how different crop environments can yield different results. However, further research is required to further expand these findings in the context of more robust biodiversity and environmental parameters as well as additional sampling methods that would accommodate other arthropod groups.

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Chapter 7: Conclusion and recommendations

7.1 Chapter 4 and 5: Plant and arthropod diversity patterns and species assemblages of soybean agro-ecosystems in South Africa

7.1.1 Conclusions and hypotheses

This is the first study describing the diversity patterns and species assemblages of non-crop plants and arthropods of soybean fields, boundary zones (transition zone between soybean fields and adjacent habitat) and adjacent natural grassland in South Africa. Similar to that of maize agro-ecosystems in South Africa (Botha *et al.*, 2015), arthropod and non-crop plant diversity were severely decreased in the soybean crop. The first hypothesis stating that plant and arthropod diversity of disturbance-prone soybean fields should be lower than the adjacent natural and semi-natural habitats is accepted. Plant diversity remained the same for the boundary and adjacent untransformed grassland. Higher diversity of arthropods was recorded in the boundary than the grassland. The second hypothesis stating that the boundary will have a lower diversity of plants and arthropods due to possible disturbances arising from adjacent crop fields is rejected.

Disturbance from crop fields significantly changed the plant and arthropod species assemblages in the boundary. This effect was not visible in the untransformed grassland (> 50 m from the crop). This supports the third hypothesis that plant and arthropod species composition of the field boundary will be replaced by unique assemblages of plant and arthropod species that are able to tolerate endo- and exogenous disturbances. Plant and arthropod assemblages in the soybean crop were correlated with high land-use intensity, grassland assemblages with low land-use intensity, while boundary assemblages fell in between. Therefore, this confirms the importance of boundary zones to buffer the effects of crop activities on adjacent natural habitat. Furthermore, contrary to the perception that the boundary is a source for pests and weeds, the boundary zones in this study did not record any soybean arthropod pests or weeds but rather beneficial species (such as predators and parasitoids, and fast-growing pioneer grasses and wildflowers). Therefore, maintaining field boundaries is not only important to buffer the effect of crop activities, but functions as a reservoir for beneficial biota in soybean agro-ecosystems.

7.1.2 Limitations and future research

In this study, the field margin only included two survey zones, 0-10 m directly adjacent to the soybean fields (field boundary zone) and 50-60 m from the soybean crop (grassland zone). Further studies, that include survey plots between these zones, are required to determine the exact distances at which significant changes occur in soybean agro-ecosystems. This may be

important to determine the optimal width of field boundary zones to establish buffer zones for the conservation of biodiversity and ecosystem services.

This study provides information on plant and arthropod diversity patterns for one specific time-frame. It is unknown how biodiversity patterns that were observed will vary over time since these patterns may be different depending on year or season. Therefore, temporal studies to acquire data on the community dynamics of non-crop plant and arthropod diversity is necessary. For instance, surveys of this study were conducted during the reproductive stages of the crop. For maize, it is known that plants in the flowering stage harbor different and higher diversity and abundance of arthropods than during other growth stages (Dively 2005; Eckert *et al.*, 2006). Therefore, it may be useful to survey different growth stages of soybean to determine whether arthropod diversity and abundance change during the growing season.

This study describes the plant and arthropod diversity of soybean fields in general and did not rely on specific characteristics associated with individual fields. Therefore, it is unclear to what extent plant and arthropod communities are affected by management practices such as field sizes, row width, crop rotation, irrigation, tillage practices, and agro-chemical usage, or specific environmental variables such as moisture and soil characteristics. Since these factors may influence plant and arthropod communities, future research in this regard is sensible and may aid biodiversity conservation, although this will require experimental studies with manipulative setups.

7.2 Chapter 6: Plant and arthropod diversity relationships of soybean agro-ecosystems in South Africa

7.2.1 Conclusions and hypotheses

This study also set out to test for a general relationship between plant and arthropod diversity in soybean fields and adjacent habitats. The results suggest that arthropod species assemblages (either directly or indirectly) are correlated with plant species assemblages since different plant communities were mirrored by different arthropod communities.

Correlations between plant and arthropod diversity were generally weak and non-significant. There were, however, positive correlations between plant diversity and the evenness of entomophagous arthropods. This is significant when considering natural pest suppression in biodiversity-based agriculture. Negative correlations existed between Poaceae abundance and spider diversity in the soybean crop and Asteraceae abundance and parasitoid diversity in the boundary and grassland. This rejects the fourth hypothesis that arthropod diversity will increase in response to increasing plant diversity.

It is apparent that plant and arthropod relationships are complex. For instance, negative correlations between Poaceae abundance and spiders in this study is different from positive correlations between these groups in maize agro-ecosystems in South Africa (Botha *et al.*, 2017). Further research that encompasses all the different crops, boundary zones, untransformed habitat and pastures are required to better understand the relationships between plant and arthropod diversity throughout the entire agro-ecosystem. When considering farm design, this may aid farmers to enhance natural enemies of pests in biodiversity-based agriculture.

7.2.2 Limitations and future research

Only aspects of arthropod functional diversity were analyzed in this study and it might be useful to study how plant functional diversity and aspects such as plant structure, height and density changes along the soybean crop-field margin gradient. This will aid to better define the differences in the different zones and help understand the population dynamics of arthropods in soybean agro-ecosystems.

Vacuum sampling was used in this study to collect arthropods. However, different sampling techniques are known to collect different arthropod taxa with varying efficiencies (Buffington and Redak, 1998; Doxon *et al.*, 2011). Therefore, vacuum sampling in combination with other methods, such as pitfall traps for epigeal arthropods and sticky traps for highly mobile flying arthropods. This will provide a more comprehensive estimate of overall biodiversity and aid in understanding how other arthropod groups, such as insect pollinators, are affected by the plant community.

7.3 Recommendations

7.3.1 Monitoring of soybean agro-ecosystems

The results indicate that the field margins are of conservation value, especially since increasing land is being transformed into cropland in South Africa. Therefore, it is important to monitor current agricultural practices to detect any potential consequences for biodiversity in soybean agro-ecosystems. However, the classification method used for arthropods can hamper this process. Classification of arthropods in morpho-species is a subjective process and time-consuming. Therefore, other methods for assessing biodiversity, for instance using priority species, may be a more useful monitoring technique. The priority species concept requires only a handful of species that can be identified up to species level and monitored. This study provides baseline data for selecting priority species by means of indicator species analyses. The analyses revealed several plant and arthropod indicator species for each zone. However, the value of using these indicator species as priority species for monitoring is

questionable since they were often absent from the zone that they are indicative of. It is sensible to investigate other methods for selecting priority species as well. For instance, using an ecological model whereby species are classified functionally and priority species are identified using ecological criteria (the nature of which will depend on the reason for monitoring) (Andow and Hilbeck, 2004).

7.3.2 Management of soybean agro-ecosystems

The objective of this study was to describe plant and arthropod diversity in general. Therefore, no recommendations regarding specific management practices are made. However, the fact that the boundary and grassland zones harbour high diversity without artificial enhancement (such as sown grass and wildflower mixes) is a promising outlook for agriculture and the possibility of implementing biodiversity-based management in soybean agro-ecosystems. Therefore, these zones should be recognized as important sites for the maintenance of biodiversity and the ecosystem services they deliver in soybean agro-ecosystems in South Africa.

For instance, the highest arthropod diversity (particularly that of natural enemies of pests) were found in the field boundary. There were also no arthropod pest species of soybean recorded in the boundary. Therefore, it is recommended that soybean farmers maintain and manage this area in order to increase natural pest suppression on soybean farms. From the existing results, it is also important to maintain high plant diversity in soybean agro-ecosystems since results showed that high plant diversity may increase natural enemy evenness and subsequently pest suppression.

Continued research in this regard is necessary since biodiversity-based agriculture is knowledge dependent. Understanding and integrating knowledge contributions from agricultural, ecological and management sciences will aid farm managers to enhance essential services provided by biodiversity. This may ultimately reduce external input requirements, increase overall productivity and improve the sustainability of soybean agro-ecosystems in South Africa.

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Appendix A: Plant species composition and diversity patterns of soybean agro-ecosystems

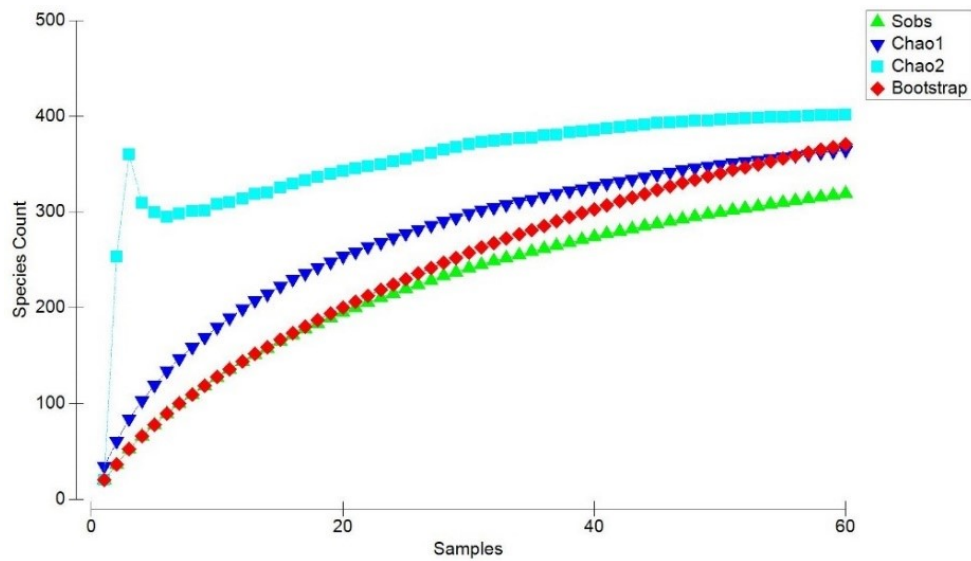


Figure 8.1: Rarefaction curve for the total plant sample, with species richness estimates based on all species observed (Sobs), number of rare species (Chao 1), presence/absence data (Chao 2) and proportion of quadrants containing each species (Bootstrap).

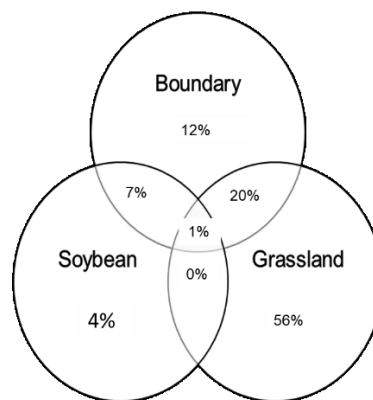


Figure 8.2: Venn diagram indicating the percentage of unique and shared plant species between the soybean crop, field boundary, and grassland.

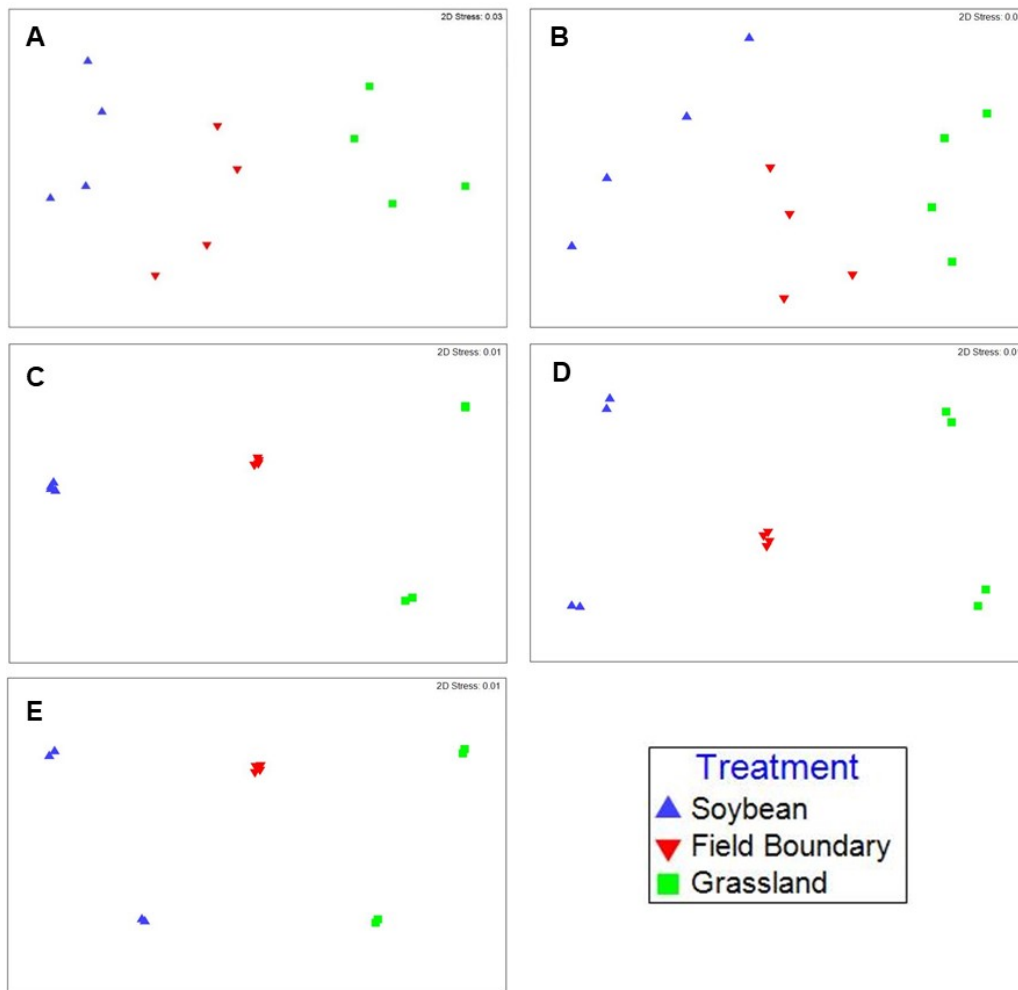


Figure 8.3: Non-metric multidimensional scaling analyses based on all plant species (excluding *Glycine max*) recorded at different localities for the soybean crop, field boundary and grassland (Bapsfontein – A; Tarlton - B; Winterton - C; Belfast - D; Reitz - E).

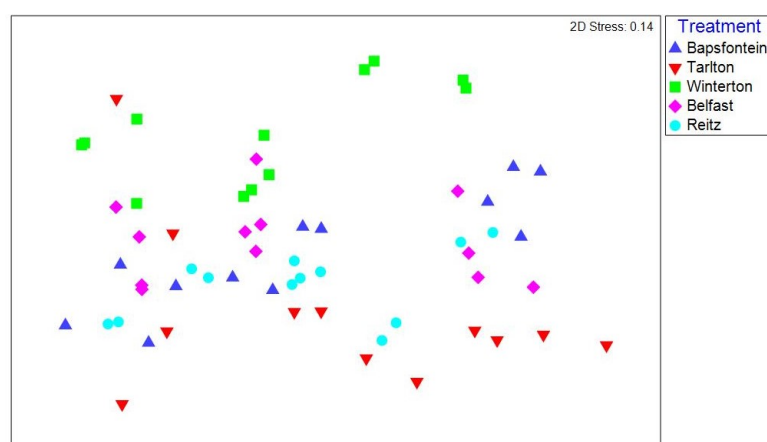


Figure 8.4: Non-metric multidimensional scaling analyses based on all plant species (excluding *Glycine max*) for the five localities (Bapsfontein, Tarlton, Winterton, Belfast, and Reitz).

Table 8.1: Pairwise PERMANOVA results comparing soybean plots between five localities.

Localities	Bapsfontein	Tarlton	Winterton	Belfast	Reitz
Bapsfontein	-	0.363	0.044	0.141	0.249
Tarlton	0.363	-	0.030	0.101	0.085
Winterton	0.044	0.030	-	0.048	0.028
Belfast	0.141	0.363	0.048	-	0.265
Reitz	0.249	0.085	0.028	0.265	-

Values in red indicate significant separations at $p < 0.05$ (permutation $N = 999$)

Table 8.2: Pairwise PERMANOVA results comparing boundary plots between five localities.

Localities	Bapsfontein	Tarlton	Winterton	Belfast	Reitz
Bapsfontein	-	0.033	0.039	0.028	0.033
Tarlton	0.033	-	0.024	0.032	0.028
Winterton	0.039	0.024	-	0.037	0.034
Belfast	0.028	0.032	0.037	-	0.043
Reitz	0.033	0.028	0.034	0.043	-

Values in red indicate significant separations at $p < 0.05$ (permutation $N = 999$)

Table 8.3: Pairwise PERMANOVA results comparing grassland plots between five localities.

Localities	Bapsfontein	Tarlton	Winterton	Belfast	Reitz
Bapsfontein	-	0.031	0.030	0.039	0.032
Tarlton	0.031	-	0.024	0.027	0.031
Winterton	0.030	0.024	-	0.026	0.031
Belfast	0.039	0.027	0.026	-	0.035
Reitz	0.032	0.031	0.031	0.035	-

Values in red indicate significant separations at $p < 0.05$ (permutation $N = 999$)

Table 8.4: Effect sizes of Hierarchical Linear Modelling (HLM) for comparisons of the mean plant diversity index values between the soybean crop, boundary, and grassland.

	Soybean*Boundary	Soybean*Grassland	Boundary*Grassland
Species Richness	3.71**	6.67**	-2.96
Abundance	6.09**	7.7**	-1.61
Shannon-Wiener diversity index	5.02**	6.58**	-1.56
Margalef's species richness	3.45**	6.31**	-2.85
Pielou's Evenness	1.67**	1.81**	-0.14
Simpson's diversity index	3.12**	3.42**	-0.3

** large effect at $d \geq 0.8$; * medium effect at $d \geq 0.3$

Table 8.5: List of plant species recorded during this study in soybean agro-ecosystems of South Africa.

Family	Fullname	Growth	Alien/	Soybean	Boundary	Grassland
Acanthaceae	<i>Barleria macrostegia</i> Nees	Forb	Indigenous	Absent	Absent	Present
Acanthaceae	<i>Blepharis innocua</i> C.B. Clarke	Forb	Indigenous	Absent	Absent	Present
Acanthaceae	<i>Chaetacanthus costatus</i> Nees	Forb	Indigenous	Absent	Absent	Present
Acanthaceae	<i>Chaetacanthus setiger</i> (Pers.) Lindl.	Forb	Indigenous	Absent	Absent	Present
Acanthaceae	<i>Crabbea angustifolia</i> Nees	Forb	Indigenous	Absent	Absent	Present
Acanthaceae	<i>Justicia anagalloides</i> (Nees) T. Anderson	Forb	Indigenous	Present	Absent	Present
Amaranthaceae	<i>Amaranthus hybridus</i> L.	Forb	Alien	Absent	Present	Absent
Amaranthaceae	<i>Brunsvigia radulosa</i> Herb.	Forb	Indigenous	Absent	Absent	Present
Amaranthaceae	<i>Guilleminea densa</i> (Willd. ex Roem. &	Forb	Alien	Absent	Present	Absent
Amaryllidaceae	<i>Boophone disticha</i> (L.f.) Herb.	Forb	Indigenous	Absent	Absent	Present
Anthericaceae	<i>Chlorophytum cooperi</i> (Baker) Nordal	Forb	Indigenous	Absent	Absent	Present
Anthericaceae	<i>Chlorophytum fasciculatum</i> (Baker) Kativu	Forb	Indigenous	Absent	Absent	Present
Apiaceae	<i>Alepidea amatymbica</i> Eckl. & Zeyh.	Forb	Indigenous	Absent	Absent	Present
Apiaceae	<i>Centella glabrata</i> L.	Forb	Indigenous	Absent	Absent	Present
Apiaceae	<i>Ciclospermum leptophyllum</i> (Pers.)	Forb	Alien	Absent	Present	Absent
Apocynaceae	<i>Asclepias eminens</i> (Harv.) Schltr.	Forb	Indigenous	Absent	Absent	Present
Apocynaceae	<i>Asclepias multicaulis</i> (E. Mey.) Schltr.	Forb	Indigenous	Absent	Absent	Present
Apocynaceae	<i>Gomphocarpus fruticosus</i> (L.) Aiton f.	Forb	Indigenous	Absent	Present	Present
Apocynaceae	<i>Xysmalobium undulatum</i> (L.) Aiton f.	Forb	Indigenous	Absent	Absent	Present
Asteraceae	<i>Acanthospermum australe</i> (Loefl.) Kuntze	Forb	Alien	Present	Present	Present
Asteraceae	<i>Arctotis arctotoides</i> (L.f.) O. Hoffm.	Forb	Indigenous	Absent	Absent	Absent
Asteraceae	<i>Berkheya onopordifolia</i> (DC.) O. Hoffm. ex	Forb	Indigenous	Absent	Absent	Present
Asteraceae	<i>Berkheya pinnatifida</i> (Thunb.) Thell.	Forb	Indigenous	Absent	Present	Absent
Asteraceae	<i>Berkheya radula</i> (Harv.) De Wild.	Forb	Indigenous	Absent	Present	Present
Asteraceae	<i>Berkheya rhapontica</i> (DC.) Hutch. & Burtt	Forb	Indigenous	Absent	Absent	Present
Asteraceae	<i>Berkheya setifera</i> DC.	Forb	Indigenous	Absent	Absent	Present
Asteraceae	<i>Bidens bipinnata</i> L.	Forb	Alien	Absent	Present	Absent
Asteraceae	<i>Bidens formosa</i> (Bonato) Sch. Bip.	Forb	Alien	Absent	Present	Absent
Asteraceae	<i>Bidens pilosa</i> L.	Forb	Alien	Absent	Present	Absent
Asteraceae	<i>Campuloclinium macrocephalum</i> (Less.)	Forb	Alien	Present	Present	Absent
Asteraceae	<i>Cirsium vulgare</i> (Savi) Ten.	Forb	Alien	Present	Absent	Absent
Asteraceae	<i>Conyza bonariensis</i> (L.) Cronquist	Forb	Alien	Absent	Present	Present
Asteraceae	<i>Conyza chilensis</i> Spreng.	Forb	Alien	Absent	Present	Absent
Asteraceae	<i>Conyza podocephala</i> DC.	Forb	Indigenous	Absent	Present	Present
Asteraceae	<i>Conyza sumatrensis</i> (Retz.) E. Walker	Forb	Alien	Absent	Present	Absent
Asteraceae	<i>Crepis hypochaeridea</i> (DC.) Thell.	Forb	Alien	Absent	Present	Present
Asteraceae	<i>Denekia capensis</i> Thunb.	Forb	Indigenous	Absent	Absent	Present
Asteraceae	<i>Dicoma anomala</i> Sond.	Forb	Indigenous	Absent	Absent	Present
Asteraceae	<i>Euryops gilfillanii</i> Bolus	Forb	Indigenous	Absent	Absent	Present
Asteraceae	<i>Euryops transvaalensis</i> Klatt	Forb	Indigenous	Absent	Absent	Present
Asteraceae	<i>Felicia filifolia</i> (Vent.) Burtt Davy	Forb	Indigenous	Absent	Present	Present
Asteraceae	<i>Felicia muricata</i> (Thunb.) Nees	Forb	Indigenous	Absent	Absent	Present
Asteraceae	<i>Garuleum sonchifolium</i> (DC.) Norl.	Forb	Alien	Absent	Present	Present
Asteraceae	<i>Gazania krebsiana</i> Less.	Forb	Indigenous	Absent	Absent	Present
Asteraceae	<i>Geigeria aspera</i> Harv.	Forb	Indigenous	Absent	Absent	Present

Asteraceae	<i>Geigeria burkei</i> Harv.	Forb	Indigenous	Absent	Absent	Present
Asteraceae	<i>Gerbera ambigua</i> (Cass.) Sch.Bip.	Forb	Indigenous	Absent	Absent	Present
Asteraceae	<i>Gerbera piloselloides</i> (L.) Cass.	Forb	Indigenous	Absent	Absent	Present
Asteraceae	<i>Gerbera viridifolia</i> (DC.) Sch.Bip.	Forb	Indigenous	Present	Absent	Present
Asteraceae	<i>Gnaphalium pensylvanicum</i> Willd.	Forb	Indigenous	Absent	Absent	Absent
Asteraceae	<i>Haplocarpha scaposa</i> Harv.	Forb	Indigenous	Absent	Absent	Present
Asteraceae	<i>Helichrysum aureonitens</i> Sch.Bip.	Forb	Indigenous	Absent	Present	Present
Asteraceae	<i>Helichrysum aureum</i> (Houtt.) Merr.	Forb	Indigenous	Absent	Absent	Present
Asteraceae	<i>Helichrysum caespititium</i> (DC.) Harv.	Forb	Indigenous	Absent	Absent	Present
Asteraceae	<i>Helichrysum callicomum</i> Harv.	Forb	Indigenous	Absent	Absent	Present
Asteraceae	<i>Helichrysum coriaceum</i> Harv. [2]	Forb	Indigenous	Absent	Present	Present
Asteraceae	<i>Helichrysum harveyanum</i> Wild	Forb	Indigenous	Absent	Present	Present
Asteraceae	<i>Helichrysum miconiifolium</i> DC.	Forb	Indigenous	Absent	Absent	Present
Asteraceae	<i>Helichrysum mixtum</i> (Kuntze) Moeser	Forb	Indigenous	Absent	Absent	Present
Asteraceae	<i>Helichrysum nudifolium</i> (L.f.) Less.	Forb	Indigenous	Absent	Absent	Present
Asteraceae	<i>Helichrysum oreophilum</i> Klatt	Forb	Indigenous	Absent	Absent	Present
Asteraceae	<i>Helichrysum pilosellum</i> (L.f.) Less.	Forb	Indigenous	Absent	Absent	Present
Asteraceae	<i>Helichrysum rugulosum</i> Less.	Forb	Indigenous	Absent	Present	Present
Asteraceae	<i>Helichrysum tenax</i> M.D.Hend.	Forb	Indigenous	Absent	Absent	Present
Asteraceae	<i>Hypochaeris radicata</i> L.	Forb	Alien	Absent	Present	Present
Asteraceae	<i>Lactuca inermis</i> Forssk.	Forb	Indigenous	Absent	Present	Present
Asteraceae	<i>Lactuca tysonii</i> (E.Phillips) C.Jeffrey	Forb	Indigenous	Absent	Present	Present
Asteraceae	<i>Nidorella anomala</i> Steetz	Forb	Indigenous	Absent	Absent	Present
Asteraceae	<i>Nidorella hottentotica</i> DC.	Forb	Indigenous	Absent	Present	Present
Asteraceae	<i>Pseudognaphalium luteo-album</i> (L.)	Forb	Alien	Absent	Present	Present
Asteraceae	<i>Schistostephium crataegifolium</i> (DC.)	Forb	Indigenous	Absent	Present	Present
Asteraceae	<i>Schistostephium heptalobum</i> (DC.) Hutch.	Forb	Indigenous	Absent	Absent	Present
Asteraceae	<i>Schkuhria pinnata</i> (Lam.) Kuntze ex Thell.	Forb	Alien	Absent	Absent	Present
Asteraceae	<i>Senecio bupleuroides</i> DC.	Forb	Indigenous	Absent	Present	Absent
Asteraceae	<i>Senecio consanguineus</i> DC.	Forb	Indigenous	Present	Absent	Present
Asteraceae	<i>Senecio coronatus</i> (Thunb.) Harv.	Forb	Indigenous	Absent	Present	Present
Asteraceae	<i>Senecio inaequidens</i> DC.	Forb	Alien	Absent	Absent	Present
Asteraceae	<i>Senecio inornatus</i> DC.	Forb	Indigenous	Absent	Present	Present
Asteraceae	<i>Senecio pentactinus</i> Klatt	Forb	Indigenous	Absent	Present	Present
Asteraceae	<i>Senecio venosus</i> Harv.	Forb	Indigenous	Absent	Absent	Present
Asteraceae	<i>Seriphium plumosum</i> L.	Forb	Indigenous	Absent	Absent	Present
Asteraceae	<i>Sonchus maritimus</i> L.	Forb		Absent	Present	Present
Asteraceae	<i>Sonchus nanus</i> Sond. ex Harv.	Forb	Indigenous	Present	Absent	Present
Asteraceae	<i>Tagetes minuta</i> L.	Forb	Alien	Absent	Present	Absent
Asteraceae	<i>Tripteris aghillana</i> DC.	Forb	Indigenous	Absent	Absent	Present
Asteraceae	<i>Ursinia nana</i> DC.	Forb	Indigenous	Absent	Present	Present
Asteraceae	<i>Vernonia hirsuta</i> (DC.) Sch.Bip. ex Walp.	Forb	Indigenous	Absent	Present	Absent
Asteraceae	<i>Vernonia natalensis</i> Sch.Bip. ex Walp.	Forb	Indigenous	Absent	Present	Present
Asteraceae	<i>Vernonia oligocephala</i> (DC.) Sch.Bip. ex	Forb	Indigenous	Absent	Present	Present
Asteraceae	<i>Vernonia sutherlandii</i> Harv.	Forb	Indigenous	Present	Absent	Present
Asteraceae	<i>Xanthium strumarium</i> L.	Forb	Alien	Absent	Present	Absent
Boraginaceae	<i>Cynoglossum hispidum</i> Thunb.	Forb	Indigenous	Absent	Absent	Present
Brassicaceae	<i>Heliophila rigidiuscula</i> Sond.	Forb	Indigenous	Absent	Absent	Present

Brassicaceae	<i>Lepidium africanum</i> (Burm.f.) DC. [1]	Forb	Indigenous	Absent	Present	Present
Campanulaceae	<i>Wahlenbergia grandiflora</i> Brehmer	Forb	Indigenous	Absent	Absent	Present
Campanulaceae	<i>Wahlenbergia undulata</i> (L.f.) A.DC.	Forb	Indigenous	Present	Absent	Present
Capparaceae	<i>Cleome monophylla</i> L.	Forb	Indigenous	Absent	Present	Absent
Capparaceae	<i>Cleome rubella</i> Burch.	Forb	Indigenous	Absent	Absent	Present
Caryophyllaceae	<i>Pollichia campestris</i> Aiton	Forb	Indigenous	Absent	Present	Present
Caryophyllaceae	<i>Silene burchellii</i> Otth	Forb	Indigenous	Present	Absent	Present
Caryophyllaceae	<i>Stellaria media</i> (L.) Vill.	Forb	Indigenous	Present	Absent	Absent
Chenopodiaceae	<i>Chenopodium ambrosioides</i> L.	Forb	Alien	Absent	Present	Absent
Chenopodiaceae	<i>Chenopodium carinatum</i> R.Br.	Forb	Alien	Absent	Present	Absent
Clusiaceae	<i>Hypericum lalandii</i> Choisy	Forb	Indigenous	Absent	Absent	Present
Commelinaceae	<i>Commelina africana</i> L.	Forb	Indigenous	Present	Absent	Present
Commelinaceae	<i>Commelina benghalensis</i> L.	Forb	Alien	Absent	3Absent	Absent
Commelinaceae	<i>Cyanotis pachyrrhiza</i> Oberm.	Forb	Indigenous	Absent	Absent	Present
Convolvulaceae	<i>Convolvulus sagittatus</i> Thunb.	Forb	Indigenous	Absent	Absent	Present
Convolvulaceae	<i>Ipomoea crassipes</i> Hook.	Forb	Indigenous	Absent	Absent	Present
Convolvulaceae	<i>Ipomoea ommanneyi</i> Rendle	Forb	Indigenous	Present	Absent	Present
Convolvulaceae	<i>Ipomoea purpurea</i> (L.) Roth.	Forb	Alien	Present	Absent	Absent
Cucurbitaceae	<i>Citrullus lanatus</i> (Thunb.) Matsum. &	Forb	Indigenous	Absent	Absent	Absent
Cucurbitaceae	<i>Cucumis hirsutus</i> Sond.	Forb	Indigenous	Absent	Present	Present
Cyperaceae	<i>Abildgaardia ovata</i> (Burm.f.) Kral	Forb	Indigenous	Absent	Absent	Present
Cyperaceae	<i>Bulbostylis burchellii</i> (Ficalho & Hiern)	Forb	Indigenous	Absent	Absent	Present
Cyperaceae	<i>Coleochloa setifera</i> (Ridl.) Gilly	Forb	Indigenous	Present	Absent	Present
Cyperaceae	<i>Cyperus esculentus</i> L.	Forb	Indigenous	Absent	Present	Absent
Cyperaceae	<i>Cyperus rupestris</i> Kunth	Forb	Indigenous	Absent	Absent	Present
Cyperaceae	<i>Fimbristylis dichotoma</i> (L.) Vahl [9]	Forb	Indigenous	Absent	Absent	Present
Cyperaceae	<i>Kyllinga alba</i> Nees	Forb	Indigenous	Absent	Absent	Present
Cyperaceae	<i>Kyllinga erecta</i> Schumach.	Forb	Indigenous	Absent	Absent	Present
Cyperaceae	<i>Mariscus congestus</i> (Vahl.)	Forb	Indigenous	Absent	Absent	Present
Dennstaedtiaceae	<i>Pteridium aquilinum</i> (L.) Kuhn	Forb	Indigenous	Absent	Absent	Present
Dipsacaceae	<i>Scabiosa columbaria</i> L.	Forb	Indigenous	Absent	Absent	Present
Eriospermaceae	<i>Eriospermum cooperi</i> Baker	Forb	Indigenous	Absent	Absent	Present
Euphorbiaceae	<i>Acalypha angustata</i> Sond.	Forb	Indigenous	Absent	Absent	Present
Euphorbiaceae	<i>Acalypha peduncularis</i> E.Mey. ex Meisn.	Forb	Indigenous	Absent	Absent	Present
Euphorbiaceae	<i>Euphorbia hirta</i> L.	Forb	Alien	Absent	Present	Absent
Euphorbiaceae	<i>Euphorbia inaequilatera</i> Sond.	Forb	Indigenous	Absent	Absent	Present
Euphorbiaceae	<i>Euphorbia striata</i> Thunb.	Forb	Indigenous	Absent	Present	Present
Fabaceae	<i>Alysicarpus rugosus</i> (Willd.) DC.	Forb	Indigenous	Absent	Absent	Present
Fabaceae	<i>Argyrolobium speciosum</i> Eckl. & Zeyh.	Forb	Indigenous	Absent	Absent	Present
Fabaceae	<i>Chamaecrista biensis</i> (Steyaert) Lock	Forb	Indigenous	Absent	Absent	Present
Fabaceae	<i>Chamaecrista comosa</i> E.Mey.	Forb	Indigenous	Absent	Present	Present
Fabaceae	<i>Chamaecrista mimosoides</i> (L.) Greene	Forb	Indigenous	Absent	Present	Present
Fabaceae	<i>Crotalaria virgulata</i> Klotzsch	Forb	Indigenous	Absent	Present	Absent
Fabaceae	<i>Eriosema cordatum</i> E.Mey.	Forb	Indigenous	Present	Absent	Present
Fabaceae	<i>Glycine max</i> L. Merrill.	Forb	Alien	Absent	Absent	Absent
Fabaceae	<i>Hoffmannseggia sandersonii</i> (Harv.) Engl.	Forb	Indigenous	Absent	Absent	Present
Fabaceae	<i>Indigofera hedyantha</i> Eckl. & Zeyh.	Forb	Indigenous	Absent	Absent	Present
Fabaceae	<i>Lessertia stricta</i> L.Bolus	Forb	Indigenous	Absent	Absent	Present

Fabaceae	<i>Lotononis calycina</i> (E.Mey.) Benth.	Forb	Indigenous	Absent	Absent	Present
Fabaceae	<i>Lotononis eriantha</i> Benth.	Forb	Indigenous	Absent	Absent	Present
Fabaceae	<i>Lotononis lotononoides</i> (Scott-Elliot) B.-	Forb	Indigenous	Absent	Absent	Present
Fabaceae	<i>Lotononis tenella</i> (E.Mey.) Eckl. & Zeyh.	Forb	Indigenous	Absent	Present	Absent
Fabaceae	<i>Melolobium candicans</i> (E.Mey.) Eckl. &	Forb	Indigenous	Absent	Absent	Present
Fabaceae	<i>Ophrestia oblongifolia</i> (E.Mey.)	Forb	Indigenous	Absent	Absent	Present
Fabaceae	<i>Otholobium polystictum</i> (Benth. ex Harv.)	Forb	Indigenous	Absent	Absent	Present
Fabaceae	<i>Pearsonia sessilifolia</i> (Harv.) Dummer	Forb	Indigenous	Absent	Absent	Present
Fabaceae	<i>Rhynchosia adenodes</i> Eckl. & Zeyh.	Forb	Indigenous	Absent	Absent	Present
Fabaceae	<i>Rhynchosia nervosa</i> Benth. ex Harv.	Forb	Indigenous	Absent	Absent	Present
Fabaceae	<i>Rhynchosia totta</i> (Thunb.) DC.	Forb	Indigenous	Absent	Absent	Present
Fabaceae	<i>Tephrosia capensis</i> (Jacq.) Pers.	Forb	Indigenous	Absent	Absent	Present
Fabaceae	<i>Tephrosia elongata</i> E.Mey.	Forb	Indigenous	Absent	Absent	Present
Fabaceae	<i>Trifolium repens</i> L.	Forb	Alien	Present	Present	Absent
Fabaceae	<i>Vigna vexillata</i> (L.) A.Rich.	Forb	Indigenous	Absent	Present	Absent
Fabaceae	<i>Zornia capensis</i> Pers.	Forb	Indigenous	Absent	Present	Present
Gentianaceae	<i>Chironia purpurascens</i> (E.Mey.) Benth. &	Forb	Indigenous	Absent	Absent	Present
Gentianaceae	<i>Sebaea sedoides</i> Gilg	Forb	Indigenous	Absent	Absent	Present
Geraniaceae	<i>Geranium multiseptum</i> N.E.Br.	Forb	Indigenous	Absent	Absent	Present
Geraniaceae	<i>Geranium wakkerstroomianum</i> R.Knuth	Forb	Indigenous	Absent	Absent	Present
Geraniaceae	<i>Monsonia angustifolia</i> E.Mey. ex A.Rich.	Forb	Indigenous	Absent	Present	Absent
Geraniaceae	<i>Monsonia attenuata</i> Harv.	Forb	Indigenous	Absent	Absent	Present
Geraniaceae	<i>Pelargonium luridum</i> (Andrews) Sweet	Forb	Indigenous	Absent	Absent	Present
Hyacinthaceae	<i>Albuca setosa</i> Jacq.	Forb	Indigenous	Absent	Absent	Present
Hyacinthaceae	<i>Ledebouria cooperi</i> (Hook.f.) Jessop	Forb	Indigenous	Absent	Absent	Present
Hyacinthaceae	<i>Ledebouria ovalifolia</i> (Schrud.) Jessop	Forb	Indigenous	Absent	Absent	Present
Hyacinthaceae	<i>Ledebouria revoluta</i> (L.f.) Jessop	Forb	Indigenous	Absent	Absent	Present
Hyacinthaceae	<i>Trachyandra saltii</i> (Baker) Oberm.	Forb	Indigenous	Absent	Absent	Present
Hypoxidaceae	<i>Hypoxis filiformis</i> Baker	Forb	Indigenous	Absent	Absent	Present
Hypoxidaceae	<i>Hypoxis iridifolia</i> Baker	Forb	Indigenous	Absent	Absent	Present
Hypoxidaceae	<i>Hypoxis multiceps</i> Buchinger ex Baker	Forb	Indigenous	Absent	Absent	Present
Hypoxidaceae	<i>Hypoxis rigidula</i> Baker	Forb	Indigenous	Absent	Absent	Present
Iridaceae	<i>Aristea cognata</i> N.E.Br. ex Weim.	Forb	Indigenous	Absent	Absent	Present
Iridaceae	<i>Gladiolus crassifolius</i> Baker	Forb	Indigenous	Absent	Absent	Present
Iridaceae	<i>Gladiolus dalenii</i> Van Geel	Forb	Indigenous	Absent	Absent	Present
Iridaceae	<i>Hesperantha coccinea</i> (Backh. & Harv.)	Forb	Indigenous	Absent	Absent	Present
Iridaceae	<i>Moraea inclinata</i> Goldblatt	Forb	Indigenous	Absent	Absent	Present
Lamiaceae	<i>Acrotome hispida</i> Benth.	Forb	Indigenous	Absent	Present	Present
Lamiaceae	<i>Ajuga ophrydis</i> Burch. ex Benth.	Forb	Indigenous	Absent	Absent	Present
Lamiaceae	<i>Becium obovatum</i> (E. Mey. ex Benth.)	Forb	Indigenous	Present	Absent	Present
Lamiaceae	<i>Salvia reflexa</i> Hornem.	Forb	Alien	Absent	Absent	Absent
Lobeliaceae	<i>Lobelia flaccida</i> (C.Presl) A.DC.	Forb	Indigenous	Absent	Absent	Present
Lobeliaceae	<i>Monopsis decipiens</i> (Sond.) Thulin	Forb	Indigenous	Absent	Absent	Present
Malvaceae	<i>Hibiscus aethiopicus</i> L.	Forb	Indigenous	Absent	Absent	Present
Malvaceae	<i>Hibiscus microcarpus</i> Garcke	Forb	Indigenous	Present	Absent	Present
Malvaceae	<i>Hibiscus trionum</i> L.	Forb	Alien	Present	Present	Absent
Malvaceae	<i>Malva parviflora</i> L.	Forb	Alien	Absent	Present	Absent
Malvaceae	<i>Sida rhombifolia</i> L.	Forb	Indigenous	Absent	Present	Present

Mesembryanthemaceae	<i>Delosperma sutherlandii</i> (Hook.f.) N.E.Br.	Forb	Indigenous	Absent	Absent	Present
Onagraceae	<i>Oenothera rosea</i> L'Her. ex Aiton	Forb	Alien	Absent	Absent	Present
Onagraceae	<i>Oenothera tetraptera</i> Cav.	Forb	Alien	Absent	Present	Present
Ophioglossaceae	<i>Ophioglossum vulgatum</i> L.	Forb	Indigenous	Absent	Absent	Present
Orchidaceae	<i>Habenaria mossii</i> (G.Will.) J.C.Manning	Forb	Indigenous	Absent	Absent	Present
Orobanchaceae	<i>Alectra sessiliflora</i> (Vahl) Kuntze	Forb	Indigenous	Absent	Absent	Present
Orobanchaceae	<i>Striga asiatica</i> (L.) Kuntze	Forb	Indigenous	Present	Present	Present
Orobanchaceae	<i>Striga bilabiata</i> (Thunb.) Kuntze	Forb	Indigenous	Absent	Absent	Present
Oxalidaceae	<i>Oxalis corniculata</i> L.	Forb	Alien	Present	Present	Absent
Oxalidaceae	<i>Oxalis depressa</i> Eckl. & Zeyh.	Forb	Alien	Absent	Absent	Present
Oxalidaceae	<i>Oxalis latifolia</i> Kunth	Forb	Alien	Present	Present	Absent
Oxalidaceae	<i>Oxalis obliquifolia</i> Steud. ex A.Rich.	Forb	Indigenous	Absent	Present	Present
Oxalidaceae	<i>Oxalis semiloba</i> Sond.	Forb	Indigenous	Present	Present	Absent
Papaveraceae	<i>Argemone ochroleuca</i> Sweet	Forb	Alien	Absent	Present	Absent
Plantaginaceae	<i>Plantago lanceolata</i> L.	Forb	Alien	Absent	Present	Absent
Plantaginaceae	<i>Plantago virginica</i> L.	Forb	Alien	Absent	Absent	Present
Poaceae	<i>Alloterospis semialata</i> (R.Br.) Hitchc.	Grass	Indigenous	Absent	Absent	Present
Poaceae	<i>Andropogon chinensis</i> (Nees) Merr.	Grass	Indigenous	Absent	Absent	Present
Poaceae	<i>Andropogon eucomus</i> Nees	Grass	Indigenous	Absent	Present	Present
Poaceae	<i>Andropogon schirensis</i> Hochst. ex A.Rich.	Grass	Indigenous	Absent	Present	Present
Poaceae	<i>Aristida congesta</i> Roem. & Schult.	Grass	Indigenous	Absent	Present	Present
Poaceae	<i>Aristida junciformis</i> Trin. & Rupr.	Grass	Indigenous	Absent	Absent	Present
Poaceae	<i>Bewisia biflora</i> (Hack.) Gooss.	Grass	Indigenous	Absent	Absent	Present
Poaceae	<i>Brachiaria eruciformis</i> (Sm.) Griseb.	Grass	Indigenous	Absent	Present	Absent
Poaceae	<i>Brachiaria serrata</i> (Thunb.) Stapf	Grass	Indigenous	Absent	Absent	Present
Poaceae	<i>Bromus catharticus</i> Vahl	Grass	Alien	Absent	Present	Absent
Poaceae	<i>Chloris gayana</i> Kunth	Grass	Indigenous	Absent	Present	Absent
Poaceae	<i>Chloris virgata</i> Sw.	Grass	Indigenous	Absent	Present	Absent
Poaceae	<i>Cymbopogon nardus</i> (L.) Rendle	Grass	Indigenous	Absent	3Absent	Present
Poaceae	<i>Cymbopogon pospischilii</i> (K.Schum.)	Grass	Indigenous	Absent	Present	Present
Poaceae	<i>Cynodon dactylon</i> (L.) Pers.	Grass	Indigenous	Present	Present	Present
Poaceae	<i>Cynodon hirsutus</i> Stent	Grass	Indigenous	Absent	Present	Present
Poaceae	<i>Cynodon incompletus</i> Nees	Grass	Indigenous	Absent	Present	Absent
Poaceae	<i>Digitaria argyrograptia</i> (Nees) Stapf	Grass	Indigenous	Absent	Absent	Present
Poaceae	<i>Digitaria eriantha</i> Steud.	Grass	Indigenous	Absent	Present	Present
Poaceae	<i>Digitaria longiflora</i> (Retz.) Pers.	Grass	Indigenous	Absent	Absent	Present
Poaceae	<i>Digitaria nuda</i> Schumach.	Grass	Alien	Present	Absent	Absent
Poaceae	<i>Digitaria sanguinalis</i> (L.) Scop.	Grass	Alien	Present	Present	Absent
Poaceae	<i>Digitaria tricholaenoides</i> Stapf	Grass	Indigenous	Absent	Absent	Present
Poaceae	<i>Diheteropogon amplexans</i> (Nees)	Grass	Indigenous	Absent	Absent	Present
Poaceae	<i>Diplachne fusca</i> (L.) P.Beauv. ex Roem. &	Grass	Indigenous	Absent	Absent	Present
Poaceae	<i>Echinochloa crus-galli</i> (L.) P.Beauv.	Grass	Indigenous	Absent	Present	Absent
Poaceae	<i>Eleusine coracana</i> (L.) Gaertn.	Grass	Indigenous	Present	Present	Absent
Poaceae	<i>Elionurus muticus</i> (Spreng.) Kunth	Grass	Indigenous	Absent	Absent	Present
Poaceae	<i>Eragrostis capensis</i> (Thunb.) Trin.	Grass	Indigenous	Absent	Absent	Present
Poaceae	<i>Eragrostis chloromelas</i> Steud.	Grass	Indigenous	Absent	Present	Present
Poaceae	<i>Eragrostis cilianensis</i> (All.) Vignolo ex	Grass	Indigenous	Absent	Absent	Present
Poaceae	<i>Eragrostis curvula</i> (Schrad.) Nees	Grass	Indigenous	Absent	Present	Present

Poaceae	<i>Eragrostis gummiflua</i> Nees	Grass	Indigenous	Absent	Absent	Present
Poaceae	<i>Eragrostis micrantha</i> Hack.	Grass	Indigenous	Absent	Absent	Present
Poaceae	<i>Eragrostis plana</i> Nees	Grass	Indigenous	Absent	Present	Present
Poaceae	<i>Eragrostis planiculmis</i> Nees	Grass	Indigenous	Absent	Present	Present
Poaceae	<i>Eragrostis racemosa</i> (Thunb.) Steud.	Grass	Indigenous	Absent	Absent	Present
Poaceae	<i>Helictotrichon turgidulum</i> (Stapf)	Grass	Indigenous	Absent	Absent	Present
Poaceae	<i>Heteropogon contortus</i> (L.) Roem. &	Grass	Indigenous	Absent	Present	Present
Poaceae	<i>Hyparrhenia filipendula</i> (Hochst.) Stapf	Grass	Indigenous	Absent	Absent	Present
Poaceae	<i>Hyparrhenia hirta</i> (L.) Stapf	Grass	Indigenous	Absent	Present	Present
Poaceae	<i>Hyparrhenia tamba</i> (Steud.) Stapf	Grass	Indigenous	Absent	Absent	Present
Poaceae	<i>Imperata cylindrica</i> (L.) Raeusch.	Grass	Indigenous	Absent	Present	Present
Poaceae	<i>Tristachya biseriata</i> Stapf	Grass	Indigenous	Absent	Absent	Present
Poaceae	<i>Loudetia simplex</i> (Nees) C.E.Hubb.	Grass	Indigenous	Absent	Absent	Present
Poaceae	<i>Melinis repens</i> (Willd.) Zizka	Grass	Indigenous	Absent	Present	Absent
Poaceae	<i>Microchloa caffra</i> Nees	Grass	Indigenous	Absent	Absent	Present
Poaceae	<i>Monocymbium ceresiiforme</i> (Nees) Stapf	Grass	Indigenous	Absent	Absent	Present
Poaceae	<i>Panicum coloratum</i> L.	Grass	Indigenous	Absent	Present	Present
Poaceae	<i>Panicum natalense</i> Hochst.	Grass	Indigenous	Absent	Present	Present
Poaceae	<i>Panicum schinzii</i> Hack.	Grass	Indigenous	Present	Present	Absent
Poaceae	<i>Panicum volutans</i> J.G.Anderson	Grass	Indigenous	Absent	Present	Absent
Poaceae	<i>Paspalum dilatatum</i> Poir.	Grass	Alien	Absent	Present	Present
Poaceae	<i>Paspalum notatum</i> Flugge	Grass	Alien	Absent	Present	Absent
Poaceae	<i>Paspalum scrobiculatum</i> L.	Grass	Indigenous	Absent	Present	Present
Poaceae	<i>Pennisetum clandestinum</i> Hochst. ex	Grass	Alien	Present	Present	Absent
Poaceae	<i>Pogonarthria squarrosa</i> (Roem. & Schult.)	Grass	Indigenous	Absent	Present	Present
Poaceae	<i>Schizachyrium sanguineum</i> (Retz.) Alston	Grass	Indigenous	Absent	Absent	Present
Poaceae	<i>Setaria nigrirostris</i> (Nees) T.Durand &	Grass	Indigenous	Absent	Absent	Present
Poaceae	<i>Setaria pallide-fusca</i> (Schumach.) Stapf &	Grass	Indigenous	Absent	Present	Absent
Poaceae	<i>Setaria sphacelata</i> (Schumach.) Stapf &	Grass	Indigenous	Absent	Absent	5Absent
Poaceae	<i>Setaria verticillata</i> (L.) P.Beauv.	Grass	Indigenous	Present	Present	Absent
Poaceae	<i>Sorghum halepense</i> (L.) Pers.	Grass	Alien	Present	Absent	Absent
Poaceae	<i>Sporobolus africanus</i> (Poir.) Robyns &	Grass	Indigenous	Absent	Present	Present
Poaceae	<i>Sporobolus fimbriatus</i> (Trin.) Nees	Grass	Indigenous	Absent	Present	Absent
Poaceae	<i>Sporobolus pyramidalis</i> P.Beauv.	Grass	Indigenous	Absent	Present	Present
Poaceae	<i>Themeda triandra</i> Forssk.	Grass	Indigenous	Absent	Present	Present
Poaceae	<i>Trachypogon spicatus</i> (L.f.) Kuntze	Grass	Indigenous	Absent	Absent	Present
Poaceae	<i>Trichoneura grandiglumis</i> (Nees) Ekman	Grass	Indigenous	Absent	Absent	Present
Poaceae	<i>Triraphis andropogonoides</i> (Steud.)	Grass	Indigenous	Absent	Absent	Present
Poaceae	<i>Tristachya leucothrix</i> Trin. ex Nees	Grass	Indigenous	Absent	Absent	Present
Poaceae	<i>Urochloa mosambicensis</i> (Hack.) Dandy	Grass	Indigenous	Absent	Present	Absent
Poaceae	<i>Urochloa panicoides</i> P.Beauv.	Grass	Indigenous	Present	Present	Absent
Poaceae	<i>Zea mays</i> L.	Grass	Alien	Present	Absent	Absent
Polygalaceae	<i>Polygala africana</i> Chodat	Forb	Indigenous	Absent	Absent	Present
Polygalaceae	<i>Polygala hottentotta</i> C.Presl	Forb	Indigenous	Absent	Absent	Present
Polygonaceae	<i>Rumex acetosella</i> L.	Forb	Indigenous	Absent	Absent	Present
Portulacaceae	<i>Portulaca oleracea</i> L.	Forb	Alien	Present	Present	Absent
Rubiaceae	<i>Anthospermum rigidum</i> Eckl. & Zeyh.	Forb	Indigenous	Absent	Present	Present
Rubiaceae	<i>Kohautia amatymbica</i> Eckl. & Zeyh.	Forb	Indigenous	Absent	Absent	Present

Rubiaceae	<i>Oldenlandia tenella</i> (Hochst.) Kuntze	Forb	Indigenous	Absent	Absent	Present
Rubiaceae	<i>Pentanisia angustifolia</i> (Hochst.) Hochst.	Forb	Indigenous	Absent	Absent	Present
Rubiaceae	<i>Pentanisia prunelloides</i> (Klotzsch ex Eckl.	Forb	Indigenous	Absent	Absent	Present
Rubiaceae	<i>Richardia brasiliensis</i> Gomes	Forb	Alien	Absent	Present	Present
Rubiaceae	<i>Spermacoce natalensis</i> Hochst.	Forb	Indigenous	Absent	Absent	Present
Santalaceae	<i>Thesium costatum</i> A.W.Hill	Forb	Indigenous	Absent	Absent	Present
Santalaceae	<i>Thesium magalismontanum</i> Sond.	Forb	Indigenous	Absent	Absent	Present
Scrophulariaceae	<i>Diclis rotundifolia</i> (Hiern) Hilliard &	Forb	Indigenous	Absent	Absent	Present
Scrophulariaceae	<i>Nemesia fruticans</i> (Thunb.) Benth.	Forb	Indigenous	Absent	Absent	Present
Scrophulariaceae	<i>Selago densiflora</i> Rolfe	Forb	Indigenous	Absent	Present	Present
Scrophulariaceae	<i>Selago tenuifolia</i> (Rolfe) Hilliard	Forb	Indigenous	Absent	Present	Absent
Solanaceae	<i>Datura ferox</i> L.	Forb	Alien	Present	Present	Absent
Solanaceae	<i>Datura stramonium</i> L.	Forb	Alien	Present	Present	Absent
Solanaceae	<i>Physalis viscosa</i> L.	Forb	Alien	Absent	Present	Absent
Solanaceae	<i>Solanum retroflexum</i> Dunal	Forb	Alien	Present	Present	Absent
Solanaceae	<i>Solanum catombelense</i> Peyr.	Forb	Indigenous	Absent	Absent	Present
Solanaceae	<i>Solanum chenopodioides</i> Lam.	Forb	Indigenous	Absent	Present	Absent
Solanaceae	<i>Solanum elaeagnifolium</i> Cav.	Forb	Alien	Absent	Present	Absent
Solanaceae	<i>Solanum lichtensteinii</i> Willd.	Forb	Indigenous	Absent	Absent	Present
Solanaceae	<i>Solanum panduriforme</i> Drege ex Dunal	Forb	Indigenous	Absent	Absent	Present
Solanaceae	<i>Solanum sisymbriifolium</i> Lam.	Forb	Alien	Absent	Present	Absent
Sterculiaceae	<i>Hermannia cordata</i> (E.Mey. ex E.Phillips)	Forb	Indigenous	Absent	Absent	Present
Sterculiaceae	<i>Hermannia depressa</i> N.E.Br.	Forb	Indigenous	Absent	Absent	Present
Sterculiaceae	<i>Hermannia oblongifolia</i> (Harv.) Hochr.	Forb	Indigenous	Absent	Absent	Present
Thymelaeaceae	<i>Gnidia capitata</i> L.f.	Forb	Indigenous	Absent	Absent	Present
Thymelaeaceae	<i>Gnidia sericocephala</i> (Meisn.) Gilg ex	Forb	Indigenous	Absent	Absent	Present
Tiliaceae	<i>Corchorus asplenifolius</i> Burch.	Forb	Indigenous	Absent	Absent	Present
Urticaceae	<i>Urtica urens</i> L.	Forb	Alien	Present	Absent	Absent
Verbenaceae	<i>Chascanum adenostachyum</i> (Schauer)	Forb	Indigenous	Absent	Absent	Present
Verbenaceae	<i>Verbena bonariensis</i> L.	Forb	Alien	Absent	Present	Present
Verbenaceae	<i>Verbena brasiliensis</i> Vell.	Forb	Alien	Absent	Present	Absent
Verbenaceae	<i>Verbena officinalis</i> L.	Forb	Alien	Absent	Present	Present
Verbenaceae	<i>Verbena rigida</i> Spreng.	Forb	Alien	Absent	Present	Absent
Zygophyllaceae	<i>Tribulus terrestris</i> L.	Forb	Indigenous	Absent	Present	Absent

Appendix B: Arthropod species composition and diversity patterns of soybean agro-ecosystems

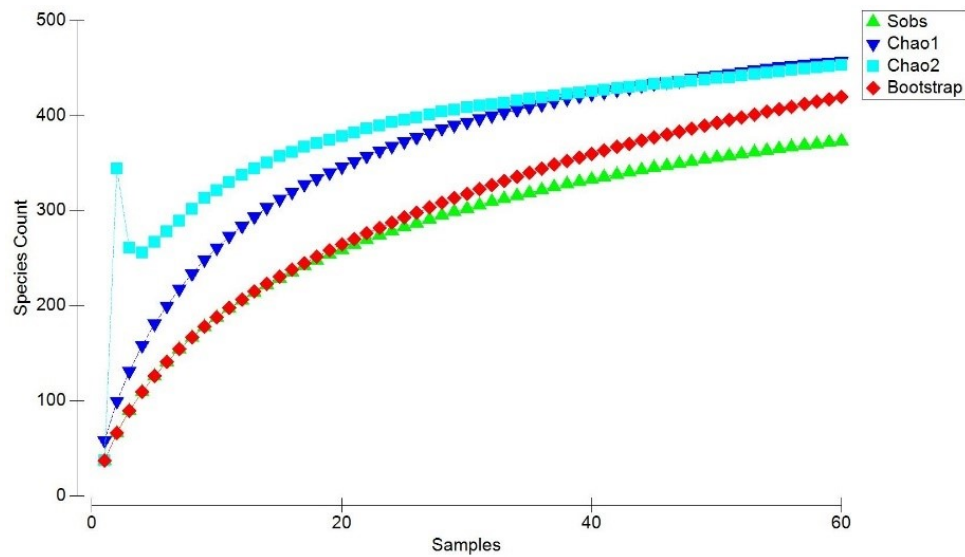


Figure 9.1: Rarefaction curve for the total arthropod sample, with species richness estimates based on all species discovered (Sobs), number of rare species (Chao 1), presence/absence data (Chao 2) and proportion of quadrants containing each species (Bootstrap).

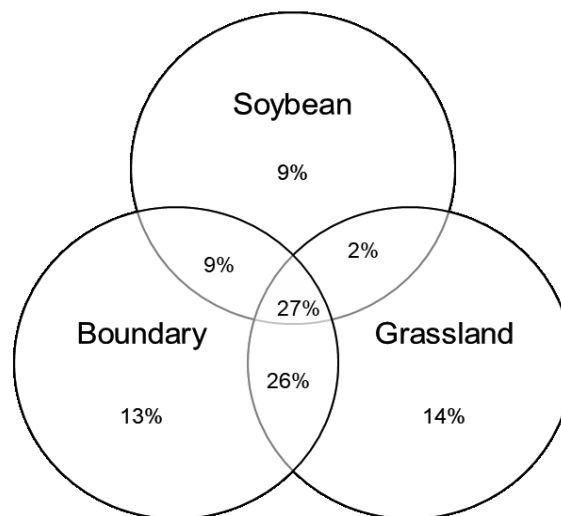


Figure 9.2: Venn diagram indicating the percentage of unique and shared species between the soybean crop, field boundary and grassland.

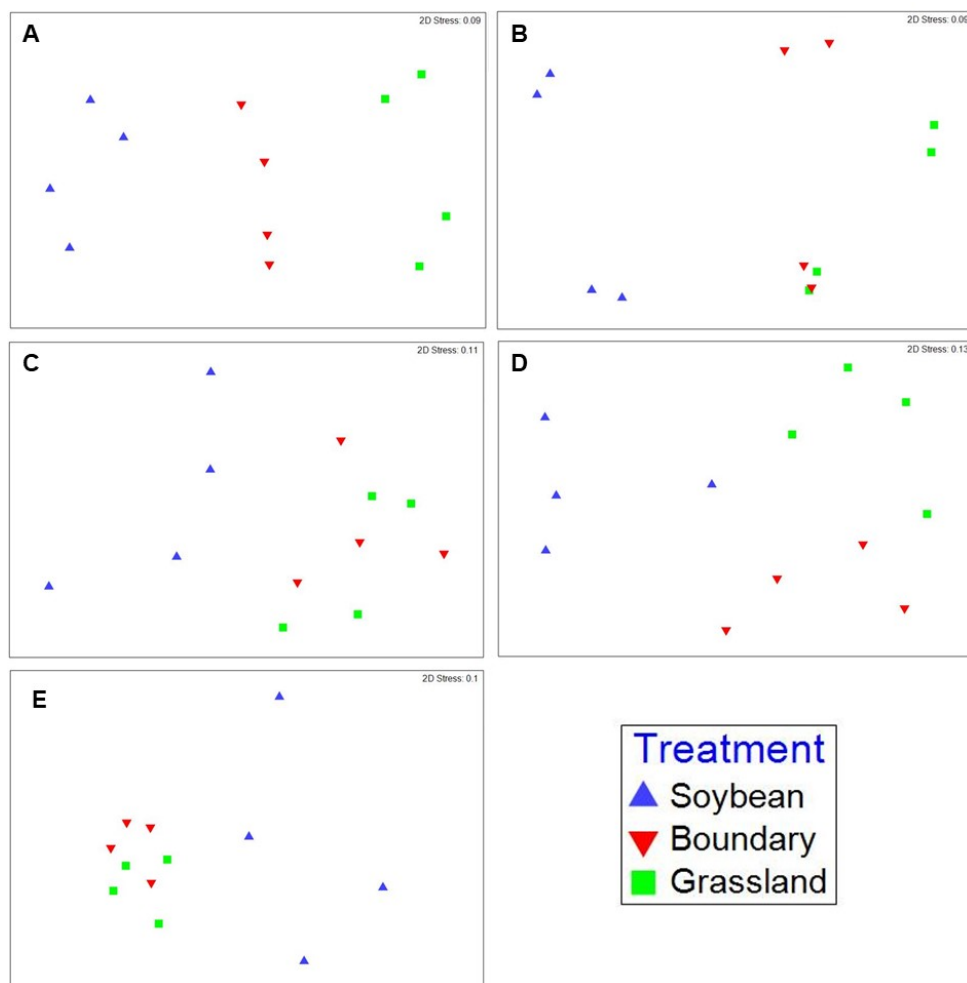


Figure 9.3: Non-metric multidimensional scaling analyses of the total arthropod species recorded at different localities for the soybean crop, field boundary and grassland (Bapsfontein - A; Tarlton – B; Winterton - C; Belfast - D; Reitz - E).

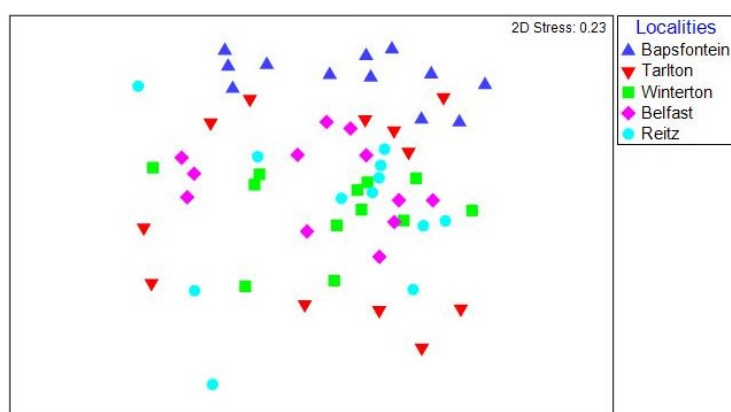


Figure 9.4: Non-metric multidimensional scaling analyses based on all arthropod morpho-species for the five localities (Bapsfontein, Tarlton, Winterton, Belfast, and Reitz).

Table 9.1: Pairwise PERMANOVA results comparing soybean plots for the arthropod survey between five localities

	Bapsfontein	Tarlton	Winterton	Belfast	Reitz
Bapsfontein	-	0.027	0.033	0.025	0.022
Tarlton	0.027	-	0.060	0.028	0.038
Winterton	0.033	0.060	-	0.030	0.085
Belfast	0.025	0.028	0.030	-	0.031
Reitz	0.022	0.038	0.085	0.031	-

Values in red indicate significant separations at $p < 0.05$ (permutation $N = 999$)

Table 9.2: Pairwise PERMANOVA results comparing boundary plots for the arthropod survey between five localities

	Bapsfontein	Tarlton	Winterton	Belfast	Reitz
Bapsfontein	-	0.021	0.033	0.030	0.031
Tarlton	0.021	-	0.027	0.028	0.038
Winterton	0.033	0.028	-	0.061	0.265
Belfast	0.030	0.028	0.061	-	0.030
Reitz	0.031	0.038	0.265	0.030	-

Values in red indicate significant separations at $p < 0.05$ (permutation $N = 999$)

Table 9.3: Pairwise PERMANOVA results comparing grassland plots for the arthropod survey between five localities

	Bapsfontein	Tarlton	Winterton	Belfast	Reitz
Bapsfontein	-	0.028	0.030	0.026	0.043
Tarlton	0.028	-	0.031	0.026	0.025
Winterton	0.030	0.031	-	0.022	0.038
Belfast	0.026	0.025	0.038	-	0.036
Reitz	0.043	0.025	0.038	0.036	-

Values in red indicate significant separations at $p < 0.05$ (permutation $N = 999$)

Table 9.4: Effect sizes of Hierarchical Linear Modelling (HLM) for comparisons of the mean arthropod diversity index values between the soybean crop, boundary, and grassland.

Diversity index	Soybean*Boundary	Soybean*Grassland	Boundary*Grassland
Species Richness	4.51**	2.55**	1.96**
Abundance	1.32**	0.65*	0.67*
Shannon-Wiener diversity index	1.28**	1.26**	0.01
Margalef's species richness	4.00**	2.41**	1.59**
Pielou's Evenness	0.23	0.66*	-0.43
Simpson's diversity index	0.52*	0.92**	-0.4

** High practical significance at $d \geq 0.8$; * Medium practical significance at $d \geq 0.5$

Appendix C: Plant and arthropod diversity relationships

Table 10.1: Spearman's rank-order correlation values between herbivore and entomophagous arthropod diversity for the soybean crop, field boundary and grassland.

Zone	Herbivore diversity	Spiders						Other predators						Parasitoids					
		S	N	d	J'	H'	Ď	S	N	d	J'	H'	Ď	S	N	d	J'	H'	Ď
Soybean	S	.449*	.501*	0.185	-0.467	0.285	-0.285	0.432	0.254	0.199	0.019	0.432	0.087	0.202	0.115	0.270	0.122	0.222	0.215
	N	0.052	0.263	-.468*	-.667**	-0.095	-.697**	0.316	0.125	0.235	0.237	0.355	0.122	0.115	0.041	0.069	0.282	0.180	0.114
	d	0.367	0.360	0.265	-0.427	0.219	-0.167	0.332	0.186	0.191	-0.066	0.298	0.068	0.086	0.020	0.224	0.068	0.097	0.157
	J'	-0.131	-0.222	0.182	0.022	-0.184	0.074	-0.084	-0.126	0.005	-0.115	-0.124	-0.079	-0.223	-0.104	-0.085	-0.230	-0.241	-0.090
	H'	0.386	0.407	0.202	-0.394	0.247	-0.194	0.353	0.197	0.190	-0.055	0.347	0.093	0.096	0.081	0.150	0.083	0.121	0.150
	Ď	0.164	0.134	0.161	-0.294	0.046	-0.136	0.135	0.064	0.027	-0.137	0.097	-0.054	-0.067	-0.044	0.054	0.029	-0.035	0.106
Boundary	S	.623**	0.366	.751**	0.235	.735**	.736**	.525*	0.435	0.429	0.091	.503*	0.354	0.403	.528*	0.211	-0.083	0.415	-0.163
	N	.503*	0.266	.631**	0.307	.591**	.702**	.686**	.613**	.546*	0.028	.626**	0.445	.574**	.598**	0.429	-0.078	.562**	-0.051
	d	.623**	0.374	.732**	0.188	.735**	.695**	0.439	0.335	0.331	0.147	0.435	0.282	0.359	.507*	0.158	-0.112	0.371	-0.202
	J'	-0.348	-0.309	-0.301	-0.158	-.451*	-0.290	-0.381	-.470*	-0.023	-0.190	-0.384	-0.116	-0.216	-0.205	-0.102	0.347	-0.223	0.335
	H'	.557**	0.312	.684**	0.200	.645**	.704**	0.391	0.297	0.352	0.028	0.356	0.249	0.386	.550*	0.187	-0.082	0.386	-0.171
	Ď	0.269	0.090	0.408	0.137	0.323	.486*	0.106	0.017	0.208	-0.021	0.084	0.120	0.263	0.438	0.099	0.029	0.254	-0.044
Grassland	S	0.165	-0.031	0.248	0.319	0.230	0.419	.572**	.588**	0.205	-0.429	.589**	0.085	-0.004	0.150	-0.089	0.175	0.040	0.054
	N	0.444	0.307	0.418	0.068	.491*	.464*	0.257	0.258	0.132	-0.200	0.375	0.064	0.254	0.384	0.047	0.160	0.269	0.138
	d	-0.008	-0.156	0.155	0.351	0.026	0.341	.616**	.604**	0.274	-0.267	.556*	0.141	-0.094	-0.036	-0.119	0.123	-0.077	-0.011
	J'	-0.106	-0.017	-0.057	-0.161	-0.197	-0.138	0.002	-0.120	0.155	0.117	-0.089	0.187	-0.294	-0.293	-0.033	0.093	-0.198	0.003
	H'	0.145	-0.002	0.290	0.289	0.140	.466*	.521*	.482*	0.256	-0.067	.509*	0.169	-0.203	-0.120	-0.135	0.215	-0.125	0.053
	Ď	0.006	0.014	0.160	0.037	-0.077	0.176	0.302	0.181	0.205	-0.033	0.242	0.210	-0.336	-0.305	-0.107	0.129	-0.245	-0.010

S- Species Richness, N- Abundance, d- Margalef's Species Richness, J'- Pielou's Evenness, H'- Shannon-Wiener Diversity, Ď- Simpson's Diversity. Values in red indicate significant correlations. ** Correlation is significant at the P < 0.01 level. * Correlation is significant at the P < 0.05 level.

Table 10.2: Spearman's rank-order correlation values between plant and arthropod diversity for the soybean crop, field boundary and grassland.

Zone	Arthropods Diversity	All plants					Fabaceae					Asteraceae					Poaceae								
		S	N	d	J'	H'	S	N	d	J'	H'	S	N	d	J'	H'	S	N	d	J'	H'	S			
Soybean crop	All arthropods	S	-0.097	-0.392	-0.065	0.158	0.127	0.130	-0.259	-0.068	-0.259	-0.259	-0.259	-0.319	-0.350	-0.358	0.100	-0.264	-0.331	-0.246	-0.187	-0.201	0.156	-0.244	-0.033
		N	0.346	0.107	0.337	0.220	.464*	.470*	0.020	-0.311	0.020	0.020	0.020	0.147	0.053	0.270	0.600	0.212	0.171	-0.070	-0.004	-0.159	-0.045	-0.152	0.000
		d	-0.117	-0.426	-0.070	0.108	0.078	0.089	-0.298	-0.091	-0.298	-0.298	-0.298	-0.285	-0.306	-0.405	0.000	-0.233	-0.293	-0.235	-0.185	-0.208	0.097	-0.237	-0.076
		J'	-0.137	-0.375	-0.057	0.000	-0.032	-0.128	-0.099	0.267	-0.099	-0.099	-0.099	-0.287	-0.258	-0.503	-0.600	-0.257	-0.512	-0.080	-0.107	-0.035	0.356	-0.010	0.000
		H'	-0.046	-0.379	0.008	0.162	0.138	0.101	-0.219	-0.034	-0.219	-0.219	-0.219	-0.274	-0.282	-0.331	-0.200	-0.158	-0.268	-0.167	-0.140	-0.119	0.200	-0.151	-0.038
	Spiders	d	0.021	-0.372	0.091	0.174	0.198	0.108	-0.099	0.084	-0.099	-0.099	-0.099	-0.273	-0.224	-0.466	-0.700	-0.148	-0.537	-0.127	-0.121	-0.144	0.058	-0.100	-0.143
		S	-0.279	-.579*	-0.216	0.261	0.039	0.102	-0.141	-0.168	-0.141	-0.141	-0.141	-0.415	-0.376	-0.394	-0.154	-0.218	-0.224	-.526*	-.496*	-0.245	-0.007	-.573*	-0.255
		N	-0.188	-.460*	-0.119	0.301	0.100	0.192	-0.060	-0.208	-0.060	-0.060	-0.060	-0.298	-0.309	-0.255	-0.103	-0.144	-0.111	-.494*	-0.412	-0.216	0.079	-.563*	-0.169
		d	-0.387	-.567*	-0.358	-0.038	-0.196	-0.186	-0.258	0.201	-0.258	-0.258	-0.258	-0.461	-0.317	-0.475	-0.667	-0.284	-0.380	-0.245	-0.391	0.328	0.325	-0.175	0.172
		J'	-0.096	0.161	-0.198	0.122	0.007	0.036	-0.372	-0.228	-0.372	-0.372	-0.372	0.086	0.178	0.277	-0.500	0.167	0.277	0.229	0.205	0.339	-0.263	0.327	-0.088
	Other predators	H'	-0.341	-.591**	-0.291	0.218	-0.030	0.036	-0.180	-0.196	-0.180	-0.180	-0.180	-.467*	-0.425	-0.167	-0.154	-0.223	0.037	-.512*	-.522*	-0.062	0.186	-.537*	-0.140
		d	-0.363	-0.263	-0.388	-0.022	-0.316	-0.318	-0.211	0.031	-0.211	-0.211	-0.211	-0.359	-0.178	-0.429	-0.359	-0.248	-0.259	-0.088	-0.216	0.325	0.277	-0.030	0.139
		S	0.123	-0.240	0.156	-0.044	0.135	0.056	-0.081	-0.238	-0.081	-0.081	-0.081	-0.257	-0.289	-0.025	0.112	-0.135	0.088	-0.150	-0.179	0.108	0.369	-0.182	0.121
		N	0.244	0.082	0.250	-0.215	0.172	0.081	-0.140	-0.421	-0.140	-0.140	-0.140	-0.016	-0.163	0.111	0.400	0.049	0.282	0.014	-0.008	-0.037	0.026	-0.092	0.043
		d	-0.160	-.553*	-0.098	0.331	-0.034	0.111	-0.062	0.031	-0.062	-0.062	-0.062	-0.178	-0.023	-0.265	-1.000**	-0.145	-0.290	-0.307	-0.321	0.281	0.692	-0.155	0.258
	Herbivores	J'	0.136	-0.230	0.223	0.308	0.143	0.236	0.231	0.122	0.231	0.231	0.231	0.024	0.203	-0.872	-1.000**	-0.107	-.900*	0.100	0.112	0.304	0.224	0.180	0.030
		H'	0.062	-0.361	0.123	0.037	0.126	0.095	-0.020	-0.189	-0.020	-0.020	-0.020	-0.218	-0.206	-0.050	-0.600	-0.085	-0.025	-0.220	-0.247	0.140	0.448	-0.229	0.130
		d	-0.051	-0.512	0.039	0.202	-0.043	0.097	0.062	0.007	0.062	0.062	0.062	-0.070	0.105	-0.177	-1.000**	-0.034	-0.203	-0.240	-0.278	0.421	0.617	-0.105	0.307
		S	-0.142	-.497*	-0.087	0.066	-0.006	-0.023	-0.180	0.164	-0.180	-0.180	-0.180	-0.233	-0.223	-0.356	0.000	-0.199	-0.415	-0.232	-0.178	-0.123	0.301	-0.197	0.072
		N	0.333	0.091	0.339	0.304	0.421	0.389	0.259	0.053	0.259	0.259	0.259	0.067	0.026	0.270	0.300	0.144	0.073	-0.002	0.131	-0.296	-0.091	-0.058	-0.148
	Parasitoids	d	-0.254	-.532*	-0.213	-0.074	-0.188	-0.218	-0.179	0.244	-0.179	-0.179	-0.179	-0.329	-0.309	-0.503	0.100	-0.298	-0.488	-0.251	-0.221	-0.074	0.252	-0.199	0.114
		J'	-0.306	-0.232	-0.307	-0.226	-0.335	-0.421	-0.338	0.360	-0.338	-0.338	-0.338	-0.183	-0.154	-0.663	-0.600	-0.393	-0.659	0.084	0.084	0.005	0.200	0.155	0.086
		H'	-0.210	-.485*	-0.168	0.038	-0.095	-0.128	-0.219	0.228	-0.219	-0.219	-0.219	-0.297	-0.278	-0.466	0.000	-0.267	-0.512	-0.223	-0.144	-0.223	0.200	-0.193	-0.038
		d	-0.268	-0.378	-0.262	-0.053	-0.186	-0.244	-0.259	0.304	-0.259	-0.259	-0.259	-0.307	-0.287	-0.466	0.000	-0.350	-0.512	-0.076	-0.023	-0.099	0.187	-0.033	0.048
S		0.109	-0.109	0.112	0.393	0.339	0.378	-0.284	-0.381	-0.284	-0.284	-0.284	0.045	0.138	-0.658	-0.205	-0.067	-0.604	-0.083	-0.095	0.071	-0.059	0.014	0.049	
Field boundary	All arthropods	N	0.091	-0.036	0.095	0.320	0.214	0.228	-0.239	-0.242	-0.239	-0.239	-0.239	0.018	0.149	-0.503	-0.300	-0.059	-0.464	-0.006	-0.012	0.035	-0.123	0.108	-0.086
		d	-0.010	-0.147	-0.010	0.240	0.231	0.362	-0.408	-0.183	-0.408	-0.408	-0.408	0.161	0.135	-0.094	0.600	0.036	-0.111	-0.036	-0.011	-0.017	-0.146	0.035	0.153
		J'	-0.151	-0.007	-0.208	0.475	0.147	0.327	-0.074					-0.199	-0.259	0.225	0.600	-0.107	0.148	-0.111	0.090	-0.542	-0.220	-0.259	-0.451
		H'	0.103	-0.044	0.078	.509*	0.431	.499*	-0.320	-0.424	-0.320	-0.320	-0.320	-0.042	-0.004	-0.479	0.000	-0.150	-0.415	-0.030	0.042	-0.159	-0.162	-0.009	-0.120
		d	-0.061	-0.087	-0.097	0.475	0.307	.490*	-0.409	-0.260	-0.409	-0.409	-0.409	0.066	0.032	0.094	0.600	-0.003	0.037	-0.006	0.129	-0.279	-0.220	-0.028	-0.102
	Spiders	S	-0.304	-0.342	-0.244	-0.057	-0.256	-0.161	-0.129	-0.133	-1.000	-0.219	-1.000	-0.147	-0.147	-0.107	0.048	-0.097	0.031	-0.214	-.480*	-0.180	0.129	-0.092	0.035
		N	-0.161	-0.232	-0.132	0.055	-0.055	-0.009	0.170	0.161	1.000	0.259	1.000	-0.199	-0.368	-0.101	-0.116	-0.213	-0.089	-0.126	-0.346	-0.095	0.222	0.060	0.185
		d	-0.329	-0.406	-0.253	-0.089	-0.278	-0.176	-0.149	-0.147	-1.000	-0.298	-1.000	-0.149	-0.109	-0.135	0.007	-0.101	-0.002	-0.210	-0.433	-0.182	0.089	-0.107	-0.002
		J'	-0.137	-0.336	-0.045	-0.141	-0.131	-0.101	-0.267	-0.266	-1.000	-0.378	-1.000	-0.371	-0.147	-0.361	0.044	-0.254	-0.205	0.207	0.084	0.204	-0.086	0.110	0.030
		H'	-0.373	-0.412	-0.280	-0.203	-0.343	-0.236	-0.321	-0.316	-1.000	-0.378	-1.000	-0.243	-0.099	-0.262	-0.030	-0.188	-0.120	-0.142	-0.271	-0.133	-0.056	-0.119	-0.068
	Other predators	d	-0.214	-.471*	-0.099	-0.197	-0.203	-0.164	-0.285	-0.292	-1.000	-0.378	-1.000	-0.322	-0.232	-0.295	0.019	-0.215	-0.155	-0.068	-0.042	0.063	-0.089	0.021	-0.003
		S	-0.386	-0.170	-0.373	-0.001	-0.308	-0.150	-0.093	-0.065	-1.000	0.040	-1.000	-0.254	-0.242	-0.221	-0.087	-0.277	-0.154	0.014	-0.241	0.058	0.285	0.203	0.259
		N	-0.275	-0.156	-0.268	0.048	-0.171	-0.026	-0.025	0.016	-1.000	0.140	-1.000	-0.265	-0.327	-0.234	-0.171	-0.328	-0.245	0.017	-0.073	0.198	0.347	0.371	0.395
		d	-0.408	-0.232	-0.387	-0.105	-0.378	-0.247	-0.098	-0.077	-1.000	-0.060	-1.000	-0.240	-0.250	-0.205	0.015	-0.214	-0.079	-0.011	-0.249	0.025	0.183	0.102	0.156
		J'	-0.173	-0.292	-0.129	-0.167	-0.275	-0.236	-0.156	-0.174	-1.000	-0.219	-1.000	-0.021	0.070	-0.041	-0.040	0.006	-0.009	-0.234	-0.094	-0.245	-0.123	-0.218	-0.209
	Herbivores	H'	-0.290	-0.219	-0.265	0.092	-0.211	-0.057	-0.033	-0.009	-1.000	0.020	-1.000	-0.137	-0.182	-0.101	-0.063	-0.149	-0.033	-0.060	-0.300	-0.017	0.334	0.177	0.275
		d	-0.280	-0.293	-0.232	0.075	-0.302	-0.203	-0.121	-0.133	1.000	-0.099	1.000	-0.178	-0.171	-0.137	-0.011	-0.128	-0.017	-0.096	-0.284	-0.063	0.092	-0.009	0.039
		S	-0.340	-0.236	-0.331	-0.304	-0.394	-0.359	-0.326	-0.325	-1.000	-0.280	-1.000	-0.206	0.003	-0.272	-0.156	-0.233	-0.233	-0.254	-0.248	-0.274	-0.122	-0.294	-0.245
		N	-0.186	-0.149	-0.193	-0.301	-0.265	-0.272	-0.195	-0.191	-1.000	-0.179	-1.000	-0.342	-0.091	-0.434	-0.248	-0.358	-0.368	-0.125	-0.175	-0.152	-0.146	-0.227	-0.177
		d	-0.270	-0.074	-0.266	-0.280	-0.311	-0.383	-0.467	-.488*	-1.000	-0.408	-1.000	0.098	0.291	-0.004	-0.062	0.087	0.011	-0.446	-0.196	-0.452	-0.289	-.542*	-.531*
	Parasitoids	J'	0.143	-0.025	0.122	0.371	0.219	0.230	-0.141	-0.158				.517*	0.124	.587*	0.222	0.464	0.425	-0.235	-0				