



Plant functional types differ between the grassland and savanna biomes along an agro-ecosystem disturbance gradient in South Africa



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ABSTRACT

Intensive, large-scale cultivation of food crops has led to major biodiversity loss worldwide due to fragmentation and degradation of remnant semi-natural habitat within agro-ecosystems. The response of vegetation to these disturbances is often measured in terms of taxonomic diversity loss. However, some plant groups may have more pronounced negative reactions to agricultural disturbance than others, which may not necessarily be expressed in the overall species diversity of the community. It is now widely accepted that the responses of plant taxa to environmental disturbances may be more directly linked to characteristics or traits that enable or hinder their persistence in disturbed environments. This highlights the need to assess the impacts of agricultural disturbance on the abundance patterns and diversity of specific plant traits and functional types. Maize agriculture is a common land-use feature in the grassy biomes of South Africa, but the effect that crop production has on surrounding semi-natural vegetation is still relatively unknown. In this study, we describe the specific functional trait patterns of plant communities associated with maize agro-ecosystems in six localities situated within the Grassland and Savanna biomes of South Africa. Although functional diversity was severely decreased in maize fields, marginal vegetation (30–100 m from crop field edges) displayed no indication of functional diversity loss or major changes in trait composition. Chamaephytic and hemicryptophytic (perennial) life forms, nitrogen-fixing ability and spinescence were trait attributes that were most frequently found in semi-natural vegetation but were lost in the crop field environment. Inside the maize fields, these trait attributes were replaced by annual, low-growing individuals with clonal parts and long-range dispersal mechanisms that can establish in the ephemeral crop field environment. Observed patterns were different for grassland and savanna maize fields, indicating that maize fields situated in the Grassland and Savanna biomes favoured different plant trait assemblages.

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1. Introduction

The large-scale transformation of natural vegetation into agro-ecosystems has detrimental effects on environments worldwide (Sala et al., 2000; Wessels et al., 2003) and affects plant diversity and composition not only within crop fields but also in adjacent semi-natural vegetation (De Snoo and Van der Poll, 1999; Marshall and Moonen, 2002). Since plants represent the basis of most terrestrial food chains, changes in plant diversity or species composition may in turn affect consumer populations (Schellhorn and Sork, 1997; Siemann, 1998; Schaffers et al., 2008; Caballero-López et al., 2010). To regulate the management of diverse and functional ecosystems within an expanding agricultural landscape and to promote sustainable and balanced use of ecosystems

and the services they provide, it has become increasingly important to understand the effect of anthropogenic activities on plant communities.

In sub-Saharan Africa, where rapid population increases and high direct dependence on natural resources coincide, biodiversity loss due to land-use change is of particular concern (Sanderson et al., 2002). Approximately 11 million hectares (9%) of land in South Africa are currently utilised for commercial pivot (irrigated) and non-pivot (dryland) annual crops and a further estimated 2 million hectares (2%) have been transformed for subsistence crop cultivation (DEA, 2016). South Africa's grassy biomes (grassland and savanna) have been classified as one of the most transformed and critically endangered biomes due to the degree of habitat loss, fragmentation and estimated future threats (Reyers et al., 2001). It is estimated that 23% has been transformed for cultivation and only 2% is currently protected (Fairbanks et al., 2000). Most of the savanna vegetation types in South Africa are used as grazing pastures for livestock or game (Cousins, 1999), although crop cultivation causes the greatest loss of savanna habitats in South Africa (Mucina and Rutherford, 2006). An estimated 11% of South Africa's savannas are

Abbreviations: PFT, plant functional type; MZ, maize field; MV, marginal vegetation; RA, rangeland.

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transformed for crop cultivation and only about 5% are formally protected (Fairbanks et al., 2000). With grassland and savanna being two of the most agriculturally productive biomes in South Africa, stock-grazing and dryland crop agriculture are two prominent and growing land-uses in the country (Neke and Du Plessis, 2004; Nazare, 2005; Mucina and Rutherford, 2006). Due to this rapid expansion of agricultural lands, a larger proportion of South Africa's diversity is currently found on farmland than in conservation areas (Wessels et al., 2003).

The response of biota to disturbance is often measured in terms of taxonomic diversity loss (O'Connor, 2005; Siebert, 2011). However, the responses of plant taxa to environmental disturbances may be more directly linked to characteristics or functional traits that enable or hinder their persistence in disturbed environments (Lavorel and Garnier, 2002; Deckers et al., 2004; Lososová et al., 2006). This realisation resulted in the increased popularity of functional trait analyses (Pakeman, 2011b; Zhang et al., 2014). Plants may be defined in terms of functional groups or types, which may be used as an alternative to taxonomic species, and are based on sets of similar traits and, theoretically, similar responses to, or effects on, their environment (Lavorel et al., 1997). When considering the ecosystem functions that species perform, the loss of some species may have a much more pronounced effect on the ecosystem than others, depending on how many functionally similar species are left to perform the function of the lost species (Petchey et al., 2009). Therefore, the loss of any particular species will always decrease taxonomic species numbers, but not necessarily functional traits. Accordingly, the impact of crop and rangeland agriculture on plant communities is often assessed by describing variation and response patterns in the abundance (number of individuals) of major functional groups, e.g. grasses or forbs (Fuhlendorf et al., 2001; Liira et al., 2008; Rutherford et al., 2012). It is also useful to assess responses of functional diversity to agricultural disturbance (i.e. the diversity of plant traits or functions present in a community) to determine impacts to ecosystem functioning since it is widely accepted that functional diversity promotes ecosystem stability and functioning (Petchey and Gaston, 2006; Flynn et al., 2009; Ma and Herzog, 2014). Among the multiple techniques used to measure functional diversity, functional type richness remains one of the most popular (Cadotte et al., 2011; Pakeman, 2011a). This technique involves the analysis of the richness (number) of functional types represented by species in an assemblage.

Considering the rapid transformation and degradation of South Africa's grassy biomes into croplands, there is a need to develop and refine conservation strategies for remaining semi-natural habitats. However, this realisation has not been accompanied by a considerable effort to understand the effects of these agricultural disturbances on species or functional diversity (Neke and Du Plessis, 2004). Information is available on the impact of livestock grazing on plant diversity and trait composition of natural and semi-natural grassland and pasture in South Africa (e.g. Uys, 2006; Geldenhuys, 2011; Rutherford et al., 2012), but similar research in crop agro-ecosystems is scarce, which reflects the overall tendency for plant ecologists to avoid highly disturbed agricultural areas (Robertson, 2000). Some studies have focused on the effect of crop agriculture on species diversity and composition (Wessels et al., 2003; O'Connor, 2005; Walters et al., 2006; Siebert, 2011), but very few studies to date have sought to test the effects of crop agriculture on plant traits and functional diversity (e.g. Kemper et al., 1999).

Addressing the related knowledge gap in African maize-agro-ecosystems, this study contributes towards a basis for in-depth studies into the potential consequences of plant functional diversity loss for changes in ecosystem functions and the provisioning of ecosystem services due to land-use change and habitat transformation, respectively. Specifically, this study describes plant traits and major PFTs commonly associated with disturbance in agricultural landscapes of two biomes in Africa. The following research questions were asked: How are plant functional types and individual plant traits distributed along a disturbance gradient from low-disturbance semi-natural rangelands into high-disturbance maize fields across the two major grassy biomes?

How does the agricultural disturbance intensity influence functional trait diversity? Do these patterns differ between the savanna and grassland biomes?

2. Material and methods

2.1. Experimental layout

Surveys were conducted from November 2009 to March 2012 in the six provinces of South Africa with the highest maize production (Hannon, 2012), namely the Eastern Cape, Free State, KwaZulu-Natal, Limpopo, Mpumalanga and North-West (a map of the study areas and sampling point layout is given in (Botha et al., 2016)). Three representative localities were chosen for each of the two biomes, with one locality per province. The six survey localities had to fulfil pre-selected criteria. Firstly, the maize fields had to border on rangeland that remained unfragmented for approximately 5 km in the direction the transects were laid out. Therefore, the rangelands bordering the fields could not include old fields, strips between two fields, or between fields and tarred roads or buildings. Secondly, fields had to have clearly defined field margins with anthropogenic features such as fences, tracks, farm roads and headlands. Thirdly, fields were only sampled when the maize plants were at the flowering stage of development (specific to each province). The environmental variables and management regimes including biome, vegetation unit, altitude, farming type (commercial/subsistence), presence or absence of irrigation and width between rows of maize for the six sampling sites are given in Appendix, Descriptive data, Table 1. At each of the six localities, four sites (each comprising a maize field bordering on rangeland), were selected approximately 5 km apart. Six sampling points were established per site, resulting in twenty-four points at each locality and therefore 144 in total. Sampling points were placed along a 500 m maize field-field margin gradient, never less than 50 m or more than 100 m apart.

2.2. Land-use intensity classification of sampling points

The six sampling points of each site were classified into three classes based on their distance from the actively cultivated area, namely maize field, marginal vegetation and rangeland with two sampling points in each. This amounted to a total of 48 points per distance class for the entire survey. The maize field points (between 100 m and 30 m from maize field edge) were considered high land-use intensity (and therefore high-disturbance) sites subjected to ploughing and agrochemical (herbicide/pesticide/fertilizer) application, and which have been completely transformed for maize production. Marginal vegetation (30–50 m from maize fields) were medium land-use intensity, medium disturbance uncultivated areas characterised by transformed natural vegetation, but also indirectly influenced by agricultural activities associated with the directly adjacent maize fields. These areas typically included features such as farm tracks, ditches or fences that accompany the field boundary vegetation (Summary of the general habitat information is given in Appendix, Descriptive data, Table 1). Rangeland (100–400 m from maize fields) were low-intensity, low disturbance uncultivated semi-natural vegetation used almost exclusively for livestock grazing. These were classified as low disturbance areas, since there were relatively low stocking rates on all the farms, all of which were predominantly maize production systems.

2.3. Vegetation sampling and trait selection

At each sampling point, a fixed-width (2 m) line transect approach was used (Hill, 2005), including ten parallel transects of 20 m each, spaced approximately 2 m apart. One plant species for every major growth form (grass, herb, shrub and tree) was recorded at 1 m intervals along each transect. In this case, the nearest individual of each major group to the point was recorded. To be recorded a species had to touch

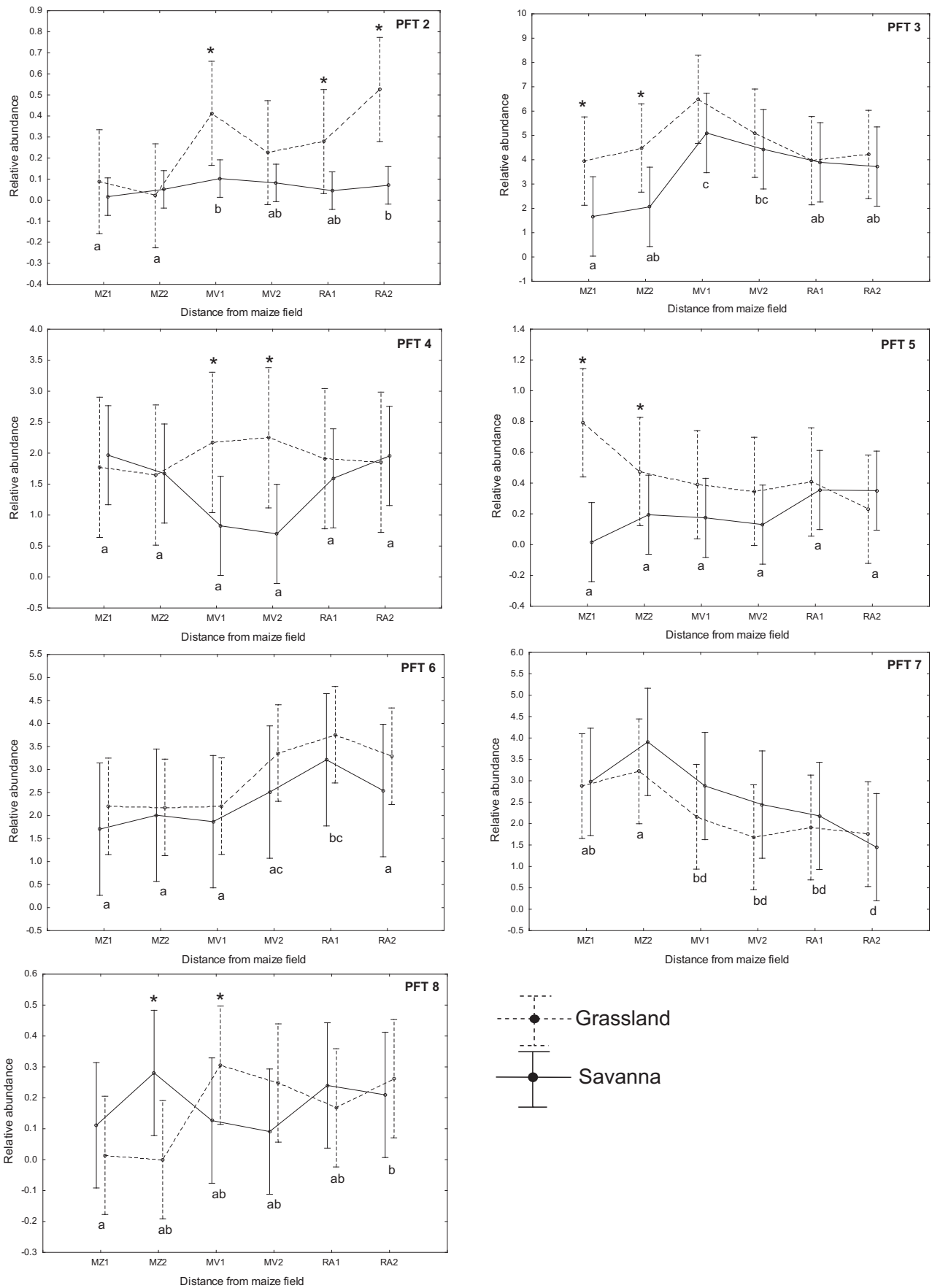


Fig. 1. Relative abundances for plant functional types along maize field-field margin gradient. Vertical bars denote 0.95 confidence intervals. Significant differences ($d \geq 0.5$) between distances along the gradient are indicated by different letters. * indicates significant variation between biomes at similar distances ($d \geq 0.5$). Distances: MZ1 and MZ2, maize field; MV1 and MV2, marginal vegetation (30–100 m); RA1 and RA2, rangeland (100–400 m).

Table 1

Results for Hierarchical linear modelling (HLM) indicating overall differences in relative abundances of plant functional types (PFTs) between distance from maize field, between biomes (grassland and savanna) and interaction effects between biome and distance. F = F value; p = p value. Bold text* indicates significant p values at $p \leq 0.05$. MSE = mean square error, unexplained variance; Variance (transect) = variance explained by transect. Definitions for PFTs are given in Appendix, Descriptive data, Table 4.

		PFT2 ^a	PFT3	PFT4	PFT5	PFT6	PFT7	PFT8
Distance	F	2.574	3.053	0.275	0.337	1.996	2.821	0.832
	p	0.029*	0.012*	0.926	0.890	0.083	0.019*	0.530
Biome	F	13.477	5.961	2.895	7.028	2.067	1.171	0.033
	p	<0.001*	0.016*	0.091	0.009*	0.153	0.281	0.856
Interaction(distance*biome)	F	1.750	0.634	1.234	1.909	0.079	0.257	1.581
	p	0.128	0.674	0.297	0.097	0.995	0.935	0.170
MSE		0.104	8.979	2.892	0.286	4.768	4.264	0.116
Variance(transect)		0.000	0.000	0.000	0.000	0.000	0.436	0.002

^a As there were no phanerophytes present in maize fields, PFT 1 was not included in analyses to compare PFT abundance between maize fields and natural vegetation.

or fall within the 1-m² block around each point. No individual was counted twice, even if it also occupied part of the next 1m². In such cases the next nearest individual was counted. The frequency across the ten transects was used as a measure of species abundances for the sample point. Plants were identified to species with nomenclature following Germishuizen et al. (2006). Plant identifications were confirmed by the South African National Herbarium (PRE) in Pretoria. Ten specimens remained unidentified and were treated as morpho-species.

All recorded plant species were defined according to a number of 'soft' traits that have known responses to factors associated with agricultural disturbance (Cornelissen et al., 2003; Aronson et al., 2007). The traits were identified with emphasis on the ecological adaptations that may play a role in the ability of the species to persist in an agricultural environment. Appendix, Descriptive data, Table 2 presents a list of the traits, trait attribute definitions as well as the proposed ecological adaptations applicable to this study. Species trait information was obtained from a variety of sources in the literature, including Germishuizen et al. (2006), Hyde et al. (2015), South African National Biodiversity Institute (SANBI) (2015), Van Oudtshoorn (2006), as well as personal observations made in the field.

2.4. Data analysis

2.4.1. Identifying plant functional types

For the identification of PFTs only plant species that were present in 10% or more of the sampling points in at least one of the distance classes (maize field, marginal vegetation or rangeland) were considered, following the approach of Díaz and Cabido (1997) and Peco et al. (2005). After rare species were removed, the trait groups had to be represented by at least ten species before being selected for data analysis, as recommended by Landsberg et al. (1999). The final dataset consisted of 155 plant species and eight traits with attributes in categorical (e.g. Phanerophytes = 1, Chamaephytes = 2, Hemicryptophytes = 3) and binary (e.g. 1 = trait present, 0 = trait absent) format (Appendix, Descriptive data, Table 3).

A hierarchical agglomerative clustering analysis with an Unweighted Pair Group Method with Arithmetic Mean (UPGMA)-clustering algorithm and Gower distance measure appropriate for mixed (categorical and binary) data types was used in PRIMER 6 software (Primer-E Ltd, 2007) to detect groupings of plant species based on their trait scores (Franks et al., 2009). The cluster analysis was combined with a Similarity Profile (SIMPROF) test, which is a more objective method for identifying significant groupings than the assignment of arbitrary cut-off levels and provides a way of preventing unwarranted further analysis of sub-structure in cluster analyses (Clarke et al., 2008).

2.4.2. Describing abundance patterns of PFTs and selected trait attributes

The relative frequencies of traits and PFTs obtained for each sampling point were subjected to Hierarchical Linear Model (HLM) analysis using a two-way ANOVA with a random effects model (McMahon and Diez, 2007) in SPSS software to test for significant differences in trait and PFT relative abundance values between biomes and across the

maize field-field margin gradient. The trait and PFT relative abundance values were chosen as response variables to determine if these values differed between distance classes and could therefore be predicted by disturbance intensity. Transects were specified as the primary unit of measure (subject ID) to account for the nestedness of transects within the sampling locality. The covariance structure was specified as unstructured. Each transect along the maize field-field margin gradient was considered an independent variable and sampling points within the same transect were considered dependent variables for statistical analyses. Effect sizes (Cohen's d) were calculated to express practical significance between sampling points where residual variance as well as transect variance were taken into account in the calculation of the effect size (Ellis and Steyn, 2003; Nakagawa and Cuthill, 2007). The effect sizes were interpreted as follows: small effect: $d = 0.2$, (b) medium effect: $d = 0.5$ and (c) large effect: $d = 0.8$ (Ellis and Steyn, 2003).

2.4.3. Quantifying functional diversity

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

3. Results

3.1. Abundance patterns of plant functional types along the disturbance gradient

Cluster analysis identified eight major PFTs for the entire study area based on the functional trait information of 155 species (Appendix, Descriptive data, Table 4; Fig. 1). PFT 2 (herbaceous plants with nitrogen-fixing ability) and PFT 3 (grasses and cyperoid species with below-ground clonal parts) displayed higher relative abundance in uncultivated vegetation compared to maize fields ($d \geq 0.6$, Table 1, Fig. 1). On the other hand, PFT 7 (erect forbs without nitrogen-fixing ability) displayed higher relative abundance in maize fields ($d \geq 0.5$, Table 1). Comparisons between biomes revealed that grassland rangeland hosted higher relative abundances of PFT 2 compared to savanna (Table 1, Fig. 1). The abundance of PFT 3 and PFT 5 (herbaceous creepers with above-ground clonality) was also significantly higher in grassland maize fields than savanna maize fields ($d \geq 0.5$, Table 1). Maize field edges of savanna were characterised by an increased relative abundance of PFT 8 (herbaceous, spinescent plants). Appendix, Means, Table 1a and b display means and pairwise comparisons between distances and biomes.

Table 2
Results for Hierarchical linear modelling (HLM) indicating overall differences in relative abundances of plant trait groups between distance from maize field, between biomes (grassland and savanna) and interaction effects between biome and distance. F = F value; p = p value. Bold text* indicates significant p values at $p \leq 0.05$. MSE = mean square error, unexplained variance; Variance (transect) = variance explained by transect.

Trait group	Distance		Biome		Interaction (distance*biome)		MSE	Variance (transect)
	F	p	F	p	F	p		
Chamaephytes	22.597	<0.001*	56.984	<0.001*	5.617	<0.001*	<0.001	0.000
Hemicryptophytes	30.365	<0.001*	141.262	<0.001*	13.138	<0.001*	<0.001	0.000
Therophytes	49.284	<0.001*	20.013	<0.001*	0.667	0.649	<0.001	<0.001
Geophytes	8.747	<0.001*	12.205	0.001*	3.407	0.006*	<0.001	<0.001
Rosettes	0.662	0.653	3.067	0.082	0.498	0.777	<0.001	<0.001
Erect forbs	6.871	<0.001*	1.355	0.247	1.13	0.348	<0.001	0.000
Creepers	2.33	0.046*	0.008	0.928	2.698	0.023*	<0.001	0.000
Tussocks	0.732	0.601	75.06	<0.001*	0.154	0.978	<0.001	<0.001
N-fixing	11.768	<0.001*	31.958	<0.001*	2.91	0.016*	<0.001	<0.001
Spinescent	11.134	<0.001*	57.516	<0.001*	3.689	0.004*	<0.001	0.000

3.2. Abundance patterns of selected plant traits along the disturbance gradient

Chamaephytes and hemicryptophytes were relatively more abundant in uncultivated vegetation compared to maize fields ($d \geq 0.6$, Table 2, Fig. 2). In contrast, the relative abundance of therophytes, geophytes and erect forbs was higher in maize fields than uncultivated habitats ($d \geq 0.5$, Table 2, Fig. 2). Creepers also displayed significantly higher abundance in maize fields compared to marginal vegetation (30–50 m from maize fields) ($d \geq 0.6$, Table 2, Fig. 2). Comparisons between biomes revealed that hemicryptophytes were more abundant in uncultivated grassland vegetation compared to savanna ($d \geq 1.3$, Table 2, Fig. 2). There were also higher abundances of tussock forming plants across the entire disturbance gradient in grassland ($d \geq 1.2$, Table 2, Fig. 2). On the other hand, chamaephytes were relatively more abundant in uncultivated savanna vegetation ($d \geq 1.3$, Table 2, Fig. 2). Savanna also had higher relative abundances of therophytes ($d \geq 0.7$, Table 2) and also of nitrogen-fixing and spinescent plants ($d \geq 0.6$ and 0.9 , respectively, Table 2, Fig. 2). Refer to Appendix, Means, Table 2a and b for mean values.

3.3. Plant trait diversity patterns along the disturbance gradient

All the diversity indices displayed similar patterns along the disturbance gradient, with significantly higher values in marginal and rangeland vegetation compared to maize fields ($d \geq 0.5$, Table 3, Fig. 3a, b, d, e). On the other hand, Pielou's evenness index values were significantly higher in maize fields than uncultivated (marginal and rangeland) vegetation ($d \geq 0.6$; Table 3, Fig. 3c). Our results also indicated significantly higher diversity and evenness values in savanna compared to grassland ($d \geq 0.7$, Table 3, Fig. 3). Refer to Appendix, Means, Table 3a and b for mean values.

4. Discussion

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

The results indicate that the high degree of agricultural disturbance intensity associated with the maize fields greatly influenced the relative abundance and diversity of PFTs and individual traits. The environmental factors associated with agricultural disturbance act as environmental 'filters' that block species which lack the required traits to persist under a particular set of conditions (e.g. annual soil tillage, crop irrigation, and agro-chemicals) (Keddy, 1992). Our results indicate that the high

agricultural disturbance intensity of the maize fields tended to favour annual, creeping growth forms and cyperoid species. Mechanisms adapted for wind or exozoochorous dispersal (PFT 8) were also found in association with high disturbance levels. These characteristics, in particular the adaptation of a wide dispersal ability and clonality are known characteristics of pioneer species that often occupy disturbed sites (Tainton, 1999). These traits likely represent adaptive strategies that evolved under natural disturbance events but now enable persistence under the intensive management impacts associated with maize agriculture such as soil tillage, agro-chemical application and complete removal of vegetation at the end of the cropping season (Pysek et al., 1995; Boutin and Jobin, 1998; Liira et al., 2008).

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

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

The marginal and rangeland vegetation had relatively higher numbers of spinescent plants as well as chamaephytes and hemicryptophytes compared to maize fields. This was expected as perennial species are removed from maize fields. Also, herbaceous spinescent plants may be more resistant to livestock grazing in rangelands (Laca et al., 2001;

Fig. 2. Relative abundances for selected plant traits along a maize field-field margin gradient. Vertical bars denote 0.95 confidence intervals. Significant differences ($d \geq 0.5$) between distances along the gradient are indicated by different letters. * indicates significant variation between biomes at similar distances ($d \geq 0.5$). Distance classes: MZ1 and MZ2, maize field; MV1 and MV2, marginal vegetation (30–50 m); RA1 and RA2, rangeland (100–400 m).

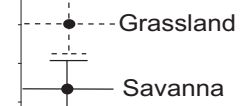
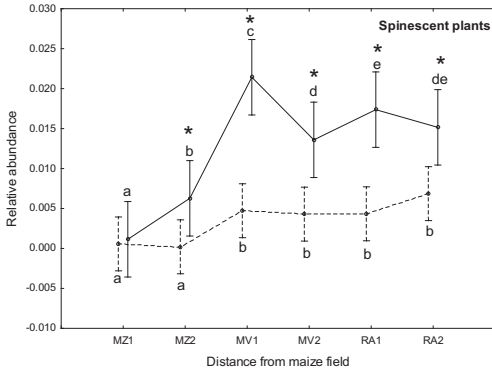
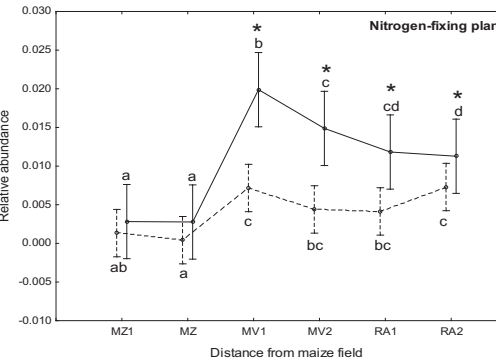
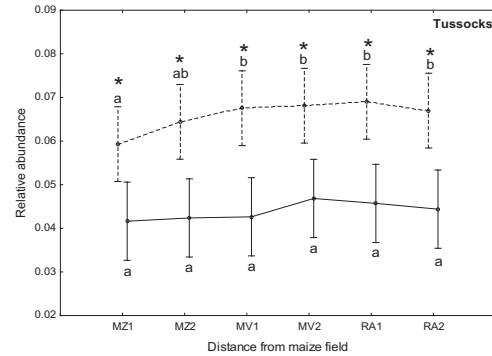
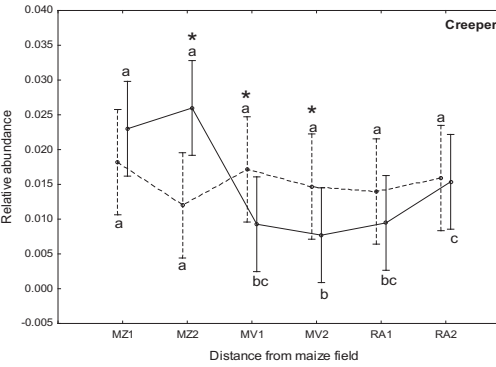
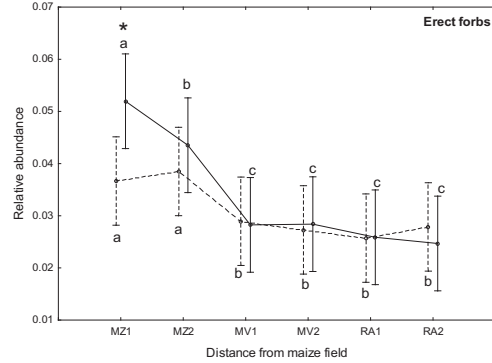
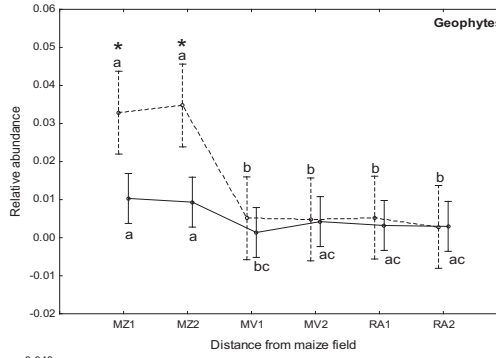
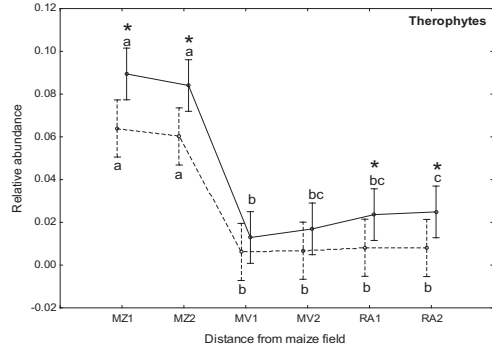
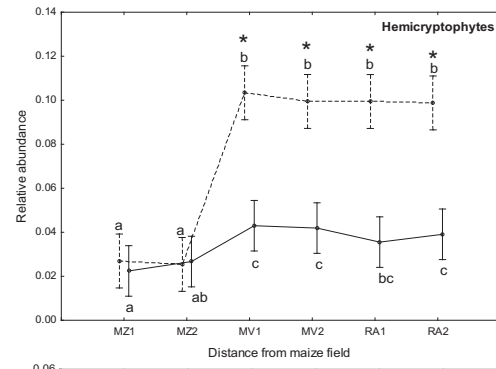
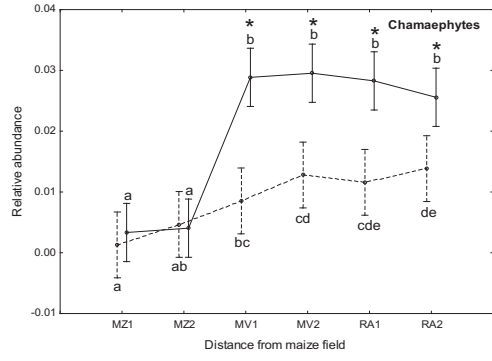


Table 3
Results for Hierarchical linear modelling (HLM) indicating overall differences in trait diversity measures between distance from maize field, between biomes (grassland and savanna) and interaction effects between biome and distance. F = F value; p = p value. Bold text* indicates significant p values at $p \leq 0.05$. MSE = mean square error, unexplained variance; Variance (transect) = variance explained by transect.

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

Hanley et al., 2007). An unexpected result was that the vegetation under medium and low disturbance intensity adjacent to the maize fields had similar trait assemblages. All these sampling sites were invariably high in trait richness and diversity, regardless of their distance from the high disturbance areas. However, it must be acknowledged that this study did not investigate a full range of disturbance levels as the rangeland vegetation was always subjected to low-intensity disturbance such as grazing. Studies by Boutin and Jobin (1998), Fridley et al. (2009) and Gove et al. (2007) demonstrated that agricultural influences on landscape-scale vegetation patterns are very close to agricultural activities and changes in vegetation composition and species richness in field margins occurred within no more than 9 m from crop fields. Therefore, it is likely that possible diversity changes in adjacent vegetation went undetected as it probably occurred at distances less than 30 m from the maize field edges, which were not sampled in this study. Also, similar traits may be able to persist in medium and low disturbance habitats if disturbance is above or at the soil surface (Kleyer, 1999), which was the case at the sampled localities.

A difference between the marginal and rangeland sites was the relative abundances of tussock forming plants (grasses and cyperoid species) with clonal ability (PFT3), which were more prevalent in the marginal vegetation adjacent to maize fields (30–50 m) relative to rangelands. This is consistent with the results of Boutin and Jobin (1998), who found higher abundances of short-lived, grassy-type weeds in habitats adjacent to intensive crop farming activities. Although the exact cause for this increase cannot be verified from this study, we hypothesise that the presence of farm tracks or the removal of vegetation by mowing may have acted as selective pressures that favour grasses and cyperoids that can colonize disturbed sites quickly by means of their clonal ability. Grasses are generally resistant to grazing or mowing, since their meristems are usually situated at the base of the plant close to the ground and removal of the top parts of the plants will generally not have detrimental effects on its subsequent growth (Tainton, 1999).

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

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

This distinction between the non-crop plant species of grassland and savanna maize fields may be due to the dispersal of plants into the fields

from the immediate adjacent vegetation. It is known that frequent dispersal of plants occurs from field margins into crop fields and that marginal vegetation is the main source of crop field weeds (Marshall and Arnold, 1995; Leeson et al., 2005). It may be expected that the non-crop plant species of maize fields in the grassland and savanna biomes are different, since the sources (species pools) from which new species are acquired (the adjacent semi-natural vegetation) have different pioneer species with varying ability to colonize a maize field environment. Studies of secondary succession over several years in Highveld grassland suggest that grasslands in South Africa have relatively few native annual pioneer species (Roux and Roux, 1969). Disturbed sites are often invaded by exotic annuals and are eventually converted to monotypic stands of dominant perennial grass species such as *Hyparrhenia hirta* (Roux and Roux, 1969). In this case, it has been shown that these grasslands often lack a ruderal stage of annual forbs and disturbed sites are often colonized immediately by grasses (e.g. *Cynodon dactylon* and *Eleusine indica*), especially at sites with high levels of available soil nitrogen (Roux and Roux, 1969). This is different for savanna, where the majority of weedy species in semiarid savannas are annual forbs (Shackleton, 2000; Makhabu and Marotsi, 2011).

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

5. Conclusion

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

In relation to our second research question, the high disturbance intensity of the maize fields drastically reduced the abundance and diversity of functional traits. However, we found no evidence for trait abundance or diversity losses, or the transformation of trait assemblage structure in marginal vegetation, at least not at the 30–50 m distance from maize fields considered in this study. Further sampling is required

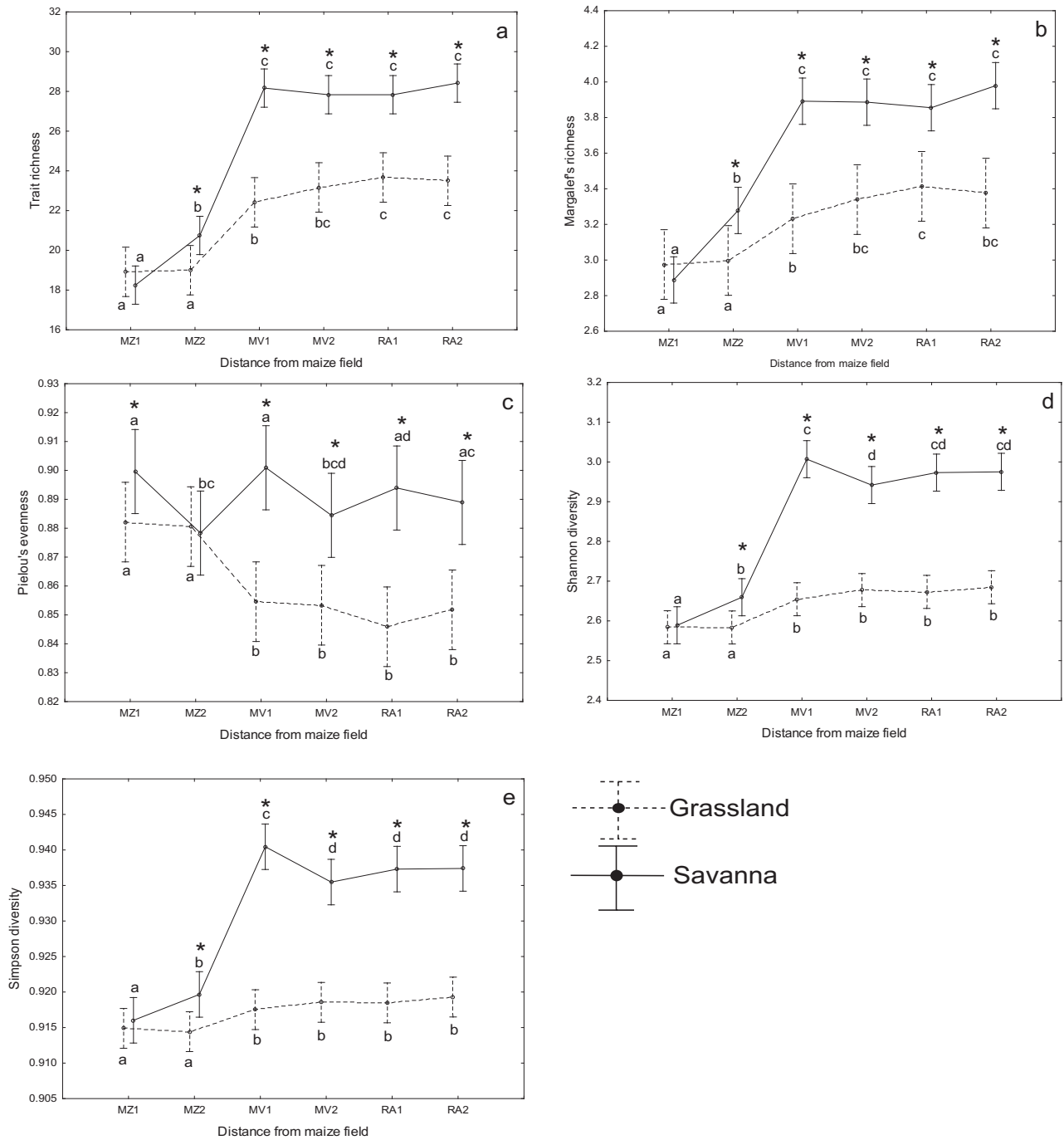


Fig. 3. Diversity measures of plant traits along a maize field-field margin gradient. (a) Trait richness; (b) Margalef's richness index; (c) Pielou's evenness index; (d) Shannon diversity index; (e) Simpson's diversity index. Vertical bars denote 0.95 confidence intervals. Significant differences ($d \geq 0.5$) between distances along the gradient are indicated by different letters * indicates significant variation between biomes at similar distances ($d \geq 0.5$). Distance classes: MZ1 and MZ2, maize field; MV1 and MV2, marginal vegetation (30–50 m) RA1 and RA2, rangeland (100–400 m).

to investigate the trait abundance and composition patterns of vegetation at the maize field-field margin interface (≤ 30 m from maize fields) to make a meaningful contribution. Nevertheless, the indication that plant communities at relatively short distances (30–100 m) from the actively cultivated areas seem relatively unaffected by the associated disturbances highlights the value of these sites as conservation areas for plant trait diversity within the agricultural environment.

Regarding our third research question, maize fields situated in the grassland and savanna biomes hosted different trait assemblages and favoured different functional types (generally grassy weeds in grassland

and forb weeds in savanna). We hypothesise that this is in accord with the different trait compositions associated with the source vegetation (the semi-natural marginal and rangeland vegetation), which has unique characteristics related to the biome in which it is classified. This may have implications for site-specific weed management in South African maize fields, since different strategies may have to be applied for the effective control of dicotyledonous (generally forbs) and monocotyledonous (mostly grassy) weeds. Ultimately, the data presented here may assist in the management and conservation of plant communities in South Africa within a growing agricultural landscape.

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Appendix. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.sajb.2017.09.008>.

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