

CHAPTER FIVE: PLANT SPECIES DIVERSITY AND FUNCTIONAL DIVERSITY

5.1 Introduction

“There are clear winners and losers among species as a result of human activity.” (Chapin *et al.*, 1998).

Humans as part of urban ecosystems, alter ecosystem dynamics through influencing atmospheric, climatic and hydraulic processes, as well as land surfaces (Elmqvist *et al.*, 2003; Folke *et al.*, 2004). Urbanisation has a wide spectrum of effects on species and influence different aspects of biodiversity such as species richness and evenness. Urban environments are often characterised by high plant species diversity (Deutschewitz *et al.*, 2003; Klotz, 1990; Pyšek & Pyšek, 1990; Stadler, *et al.*, 2000; Thuiller *et al.*, 2006), which may be contributed to the habitat heterogeneity of cities (Rebele, 1994; Savard *et al.*, 2000; Pickett *et al.*, 2011; Wania *et al.*, 2006). Certain pressures (i.e. habitat transformation, fragmentation, urban environmental circumstances, and human influence) of urban areas filter urban flora to result in an assemblage of plant species (Williams *et al.*, 2009) that are often characterised by species adapted to human-induced perturbation, and high non-native (exotic) species diversity (Pyšek, 1998; Niemelä, 1999a; Pickett *et al.*, 2011).

5.1.1 Plant species diversity

“Plant communities are affected by land-use and landscape heterogeneity and can be used as indicators of environmental change.” (Fédoroff *et al.*, 2005).

Biotic communities are diverse due to local factors (e.g. abiotic condition, disturbance and competition) interacting with landscape structure (Hillebrand & Blenckner, 2002; Niemelä, 1999a). Plants are a key component of the biosphere acting as the basis for maintenance of life on earth and providing an array of goods (i.e. food and shelter) and services (i.e. oxygen production through photosynthesis and climate regulation) from which humans benefit (Henry, 2005). Declines in species diversity may lead to ecological instability as biodiversity acts as „insurance“ against ecological perturbation, keeping communities stable in the face of disturbance and environmental change (Chapin *et al.*, 1995; McNaughton, 1977; Pimm, 1984; Schulze & Mooney, 1993; Tilman *et al.*, 1998).

The grasslands occurring on the high central plateau of South Africa are characterised by herbaceous vegetation consisting of mainly grass species (Mucina & Rutherford, 2006). Due to human influences the Rand Highveld Grassland vegetation unit has been extensively transformed and fragmented (Mucina & Rutherford, 2006) which hold dire consequences for native biodiversity, as a high diversity of exotic species are likely to invade these disturbed areas (Chapin *et al.*, 2002; Gibson,

2009; Hooper *et al.*, 2005; Lindenmayer & Fischer, 2006; NWDACE, 2008; Saunders *et al.*, 1991; Vitousek *et al.*, 1997; With, 2004). Exotic species contribute to the deterioration of the environment and indigenous ecosystems in several ways (Vankat & Roy, 2000) these include: competing with native species for resources; preventing the natural regeneration of native species; alteration of disturbance regimes (e.g. fire); changes in biomass; and intensifying soil erosion by eradicating ground cover and erosion-limiting species (Williams & West, 2000).

5.1.2 Plant functional diversity

“...functional diversity has the potential to link morphological, physiological, and phenological variation at the individual level to ecosystem processes and patterns.” (Petchey *et al.*, 2009)

Functional diversity reflects the variety of functions performed by species within a community (Diaz & Cabido, 2001; Petchey & Gaston, 2006). There has been a growing body of literature focusing on species functional diversity instead of the traditional taxonomic diversity, and how functional diversity effects ecosystem functioning. The loss of a species within a group of functionally similar species that access the same resource reserve would result in an insignificant loss of species functional diversity and another similar species would compensate for its role in resource pool utilisation. But if a species that is functionally unique (i.e. functionally very dissimilar from other species) is lost, both resource pool utilisation and species functional diversity will decrease (Chapin *et al.*, 1995; Petchey, 2003; Petchey *et al.*, 2009). One of the main concerns for biodiversity conservation is the invasion of exotic species. Many studies have shown that ecosystems that do not have high functional diversity are vulnerable to biotic invasions, as there is a part of the trait niche that is underutilised, or not utilised at all, providing a resource stratum that may be exploited by an exotic species possessing the functional characteristics to do so (Diaz & Cabido, 2001; Dukes, 2001; Elton, 1958; Pimm, 1984; Pokorny *et al.*, 2005). It is thus also possible for exotic species to fulfil the functional roles of native species in an ecosystem. For instance an exotic nitrogen-fixing tree in Hawaii enriches soils with nitrogen much more successfully than other native nitrogen-fixing species (Vitousek *et al.*, 1987). Schwartz *et al.* (2000) stated, however, that ecosystem function should depend on native species. The reason for this is that if ecosystem processes are maintained by conserving exotic species, native species would not hold conservation priority over exotic species, leading to uncontrolled exotic invasions.

5.1.2.1 Functional diversity indices

Although the concept of functional diversity may seem uncomplicated, the measurement thereof may be quite complex. The development of functional diversity indices aimed at providing an easier way to determine functional diversity instead of using plant functional type diversity, which has been widely criticised (Petchey *et al.*, 2009). Functional diversity indices describe the extent and manner in which species fill a hypothetical functional niche space (Schleuter *et al.*, 2010), and have been used in various functional diversity studies across many taxa (Lepš *et al.*, 2006; Lambdon *et al.*, 2008;

Villéger *et al.*, 2010; Barragán *et al.*, 2011; Laliberté, 2011; Mouillot, *et al.*, 2011; Pakeman, 2011; Baraloto *et al.*, 2012). Table 5.1 provides a list of some of the most common available functional diversity metrics.

Table 5.1: Table presenting some of the most common functional diversity indices (after Casanoves *et al.*, 2010).

Functional diversity metric		Reference
Convex hull volume	CHV	Cornwell <i>et al.</i> , 2006
Functional divergence	FDvar	Mason <i>et al.</i> , 2003
Rao's quadratic entropy	Q	Botta-Dukát, 2005
Functional diversity	FD	Petchey & Gaston, 2002
Weighted functional diversity	wFD	Pla <i>et al.</i> , 2008
Functional richness	Fric	Villéger <i>et al.</i> , 2008
Functional attribute diversity	FAD	Walker <i>et al.</i> , 1999

Three major components of functional diversity were identified by Mason *et al.* (2005) namely: (1) functional richness, (2) functional evenness, and (3) functional divergence. The successful calculation of these three functional diversity elements uncomplicated the measurement of functional diversity, and aided in studying and describing diversity-ecosystem function relationships (Mason *et al.*, 2005). The limitation of the indices for calculating three components of functional diversity, as proposed by Mason *et al.* (2005), is that these measures are only applicable to single-trait (univariate niche space) and not multi-trait approaches (Villéger *et al.*, 2008). The concept of studying several aspects of functional diversity (e.g. functional richness, functional evenness, functional divergence) separately, led to the development of indices by Villéger *et al.* (2008) that encompassed not only the various elements of functional diversity, but also enabled these elements to be calculated for multiple traits.

5.1.3 Objectives and hypotheses

The aim of this chapter was to determine the total plant species composition in the selected Rand Highveld Grassland fragments within the Tlokwe Municipal area. The data obtained from the vegetation sampling enabled us to determine plant species richness and calculate various aspects of plant functional diversity. Possible patterns of plant species diversity and plant functional diversity across an urbanisation gradient were also explored to determine whether the intensity of urbanisation has an effect on these aspects within the grassland fragments selected in the study area. The selected grassland fragments were classified as either “rural/peri-urban” or “urban” based on the urbanisation measure values for the 500 m radius matrix area surrounding them (refer to *Chapter 4*).

The hypotheses for this chapter are that selected grassland fragments situated in urban matrix areas exposed to increased human impacts will:

- Have higher plant species diversity.

- Contain more exotic species.
- Support different proportions of specific plant traits.
- Have higher plant functional diversity, than rural/peri-urban areas.

5.2 Methods

5.2.1 Vegetation survey

The vegetation surveys were conducted from January to March, 2012. The vegetation survey consisted of recording the presence, and estimating the percentage cover of plant species in a 20x20 m sample plot. The size of the sample plots was determined using a species-area curve (Kent, 2012). All species as well as their percentage cover were visually estimated in the sample plots. Because of the absence of a substantial tree layer in the grassland habitat, absolute cover was estimated. The number of plots per selected grassland remnant was determined by the size of the grassland fragment under observation (Table 5.2). Plots within the selected grassland fragments were randomly set out, and were representative of the entire grassland remnant. A total of 79 plots were sampled in 30 selected grassland fragments. Although subjective due to the chance of observer bias (Dethier *et al.*, 1993), the visual estimation of plant cover within sample plots is quicker and more effective than the point or line intercept methods, and therefore allowing rare species with low cover to also be recorded (Hanley, 1978). Species which covered less than 1 m² (1%) of the sample plots were given a percentage cover value of 0.5%. Additional species adjacent to, but not included in, the sample plots were also recorded and given a low percentage cover value (0.1%) to ensure that less common species, species of conservation concern and invasive species are included. Unknown plant species were collected and identified with the use of herbarium specimens, various field guides of the regional vegetation (Van Oudtshoorn, 2006; Van Wyk & Malan, 1988), as well as personal communication with the personnel at the National Herbarium of the South African National Biodiversity Institute (SANBI). Plant species names are according to Germishuizen *et al.* (2006).

5.2.2 Plant functional traits

“Empirical studies on plant functional types and traits have flourished recently and are rapidly progressing towards an understanding of plant traits relevant to local vegetation and ecosystem dynamics.” (Cornelissen *et al.*, 2003)

Certain plant functional traits were identified at the species level (taxon-explicit (Lavorel *et al.*, 2008)) in order to group species together based on functional attributes. Functional properties to be considered are listed in Table 5.3. The list has been compiled from a combination of soft traits found

by Cornelissen *et al.* (2003) and Aronson *et al.* (2007) that are easy to determine. Similar life history traits have also been used in other urban studies (Duncan *et al.*, 2011; Knapp *et al.*, 2008; 2009; Mayfield *et al.*, 2005; Thompson & McCarthy, 2008; Williams *et al.*, 2005). Species trait information was obtained from a variety of sources including Flora Zambesica (2012), PROTA (2012), SANBI (2012), Van Oudtshoorn (2006), Van Wyk & Malan (1988) and WCSP (2012), as well as own observations in the field and herbarium specimens.

Table 5.2: Attributes of the 30 selected rural/peri-urban and urban grassland fragments within the study area, arranged in the direction of increasing percentage impervious surfaces.

Site	Fragment size (ha)	No. of sample plots	Anthropogenic influence	Urbanisation
21	11.54	3	Grazing	Rural / peri-urban
30	38.69	3	N/A	Rural / peri-urban
28	19.85	3	Grazing	Rural / peri-urban
27	10.77	3	Grazing	Rural / peri-urban
23	116.3	5	Grazing	Rural / peri-urban
26	172.83	5	Grazing	Rural / peri-urban
25	179.41	5	N/A	Rural / peri-urban
29	169.26	5	Grazing	Rural / peri-urban
22	9.49	3	Grazing	Rural / peri-urban
4	26.17	3	N/A	Rural / peri-urban
24	3.76	2	N/A	Rural / peri-urban
1	5.52	2	N/A	Urban
20	2.99	2	N/A	Urban
7	2.36	2	Mowing	Urban
19	0.59	2	Mowing	Urban
16	3.42	2	N/A	Urban
13	0.82	2	Mowing	Urban
9	7.27	2	N/A	Urban
5	4.43	2	N/A	Urban
8	3.03	2	Mowing	Urban
3	18.13	3	N/A	Urban
11	2.29	2	N/A	Urban
10	1.63	2	N/A	Urban
6	6.26	2	Mowing	Urban
12	2.13	2	N/A	Urban
17	1.03	2	N/A	Urban
15	1.74	2	N/A	Urban
14	0.74	2	Mowing	Urban
18	0.65	2	N/A	Urban
2	3.84	2	N/A	Urban

Increasing urbanisation / human impact

Functional traits are defined as the attributes of species which have an effect on ecosystem properties (effect traits) or the species' response to their environmental conditions (response traits) (Hooper *et al.*, 2005; Violle *et al.*, 2007). The vegetation characteristics (plant functional traits) selected for this study reflect certain ecological mechanisms (Table 5.4). These plant traits may reflect the environmental conditions in grassland fragments situated in areas of differing matrix quality (e.g. no urbanisation to highly urbanised).

Table 5.3: List of traits and their categorical units determined for the species encountered in selected grassland fragments (adapted from Cornelissen *et al.* (2003) and Aronson *et al.* (2007)).

Plant trait	Categorical unit
1. Status	1. Exotic 2. Native
2. Growth Form	1. Forb (herb) 2. Ferns 3. Graminoids (grasses, sedges, rushes) 4. Shrub 5. Tree 6. Succulents 7. Epiphyte 8. Vine (climber) 9. Parasite 10. Aquatic
3. Life Form (Raunkaier, 1973)	1. Phanerophytes 2. Chamaephytes 3. Hemicryptophytes 4. Geophytes 5. Therophytes 6. Helophytes 7. Hydrophytes
4. Life Span	1. Annual 2. Biennial 3. Perennial
5. Clonality	1. Non-clonal 2. Clonal aboveground (stolons, gemmiparous, other vegetative buds or plant fragments) 3. Clonal belowground (rhizomes, tubers, bulbs, adventitious root buds on main or lateral roots) 4. Clonal above- and belowground
6. Spinescence	1. No spines and/or thorns 2. Spines and/or thorns are present
7. Leaf periodicity	1. Evergreen leaves 2. Deciduous leaves 3. Semi-evergreen leaves
8. Primary dispersal mode	1. Unassisted dispersal (seed or fruit has no obvious aids for longer-distance transport and merely falls passively from the plant) 2. Wind dispersal (includes: minute dust-like seeds, seeds with pappus or long hairs, balloons or comas, flattened fruits or seeds with large “wings”, spores of ferns and related vascular cryptogams, tumbleweeds) 3. Internal animal dispersal 4. External animal dispersal 5. Dispersal by hoarding (brown or green seeds or nuts that are hoarded and buried by mammals or birds) 6. Water (dispersules are adapted to prolonged floating on the water surface, aided for instance by corky tissues and low specific gravity) 7. Unassisted and/or internal animal dispersal
9. Primary pollination vector	1. Abiotic 2. Biotic

Table 5.4: Plant traits and the ecological mechanisms they represent that will be observed during this study (after Cornelissen *et al.*, 2003 and Aronson *et al.*, 2007).

Plant trait	Corresponding mechanism
Clonality	Resource exploitation
Dispersal mode	Plant range size
Growth form	Plant strategy
Leaf periodicity	Conservation of nutrients in habitats with environmental stress
Life form	Climate
Life span	Persistence under disturbance
Pollination vector	Plant range size
Spinescence	Anti-herbivore defence; climate; land use; disturbance such as periodic grazing; persistence after disturbance; heat or drought stress tolerance; growth-rate – protection trade-off

5.2.3 The selection of functional diversity indices

“...functional diversity studies have to describe a multi-dimensional cloud of points in trait space (i.e., each coordinate corresponds to a measured trait), each point representing an individual or a species.” (Schleuter *et al.*, 2010)

Plant functional diversity indices were determined using FDiversity software (Casanoves *et al.*, 2010). This software includes a wide variety of indices and metrics available for the assessment of functional diversity (Casanoves *et al.*, 2010). Figure 5.1 depicts a schematic representation of the functional diversity indices which may be calculated using the FDiversity software, providing a method for selection of the best indices for the study.

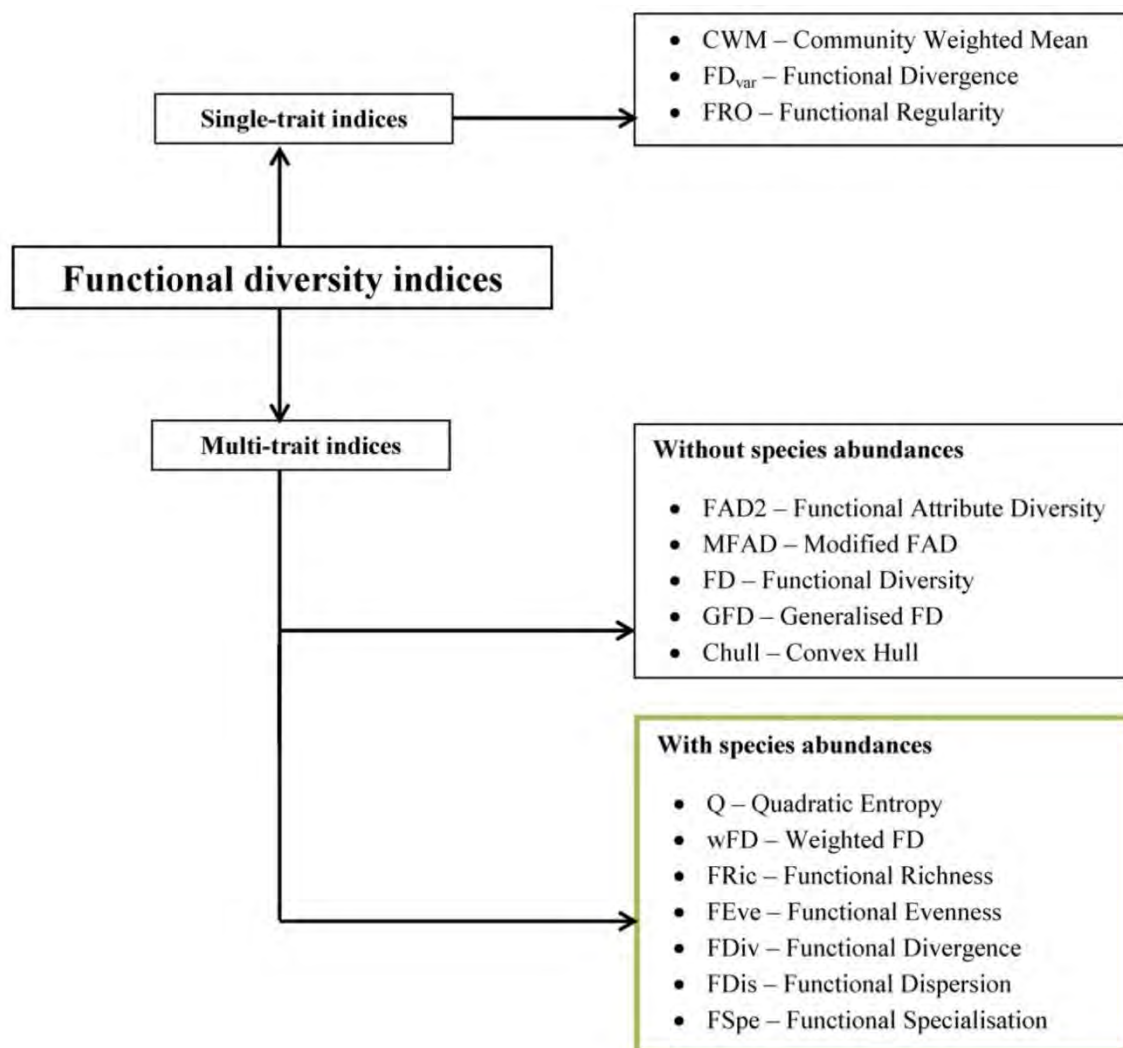


Figure 5.1: Guide to choosing the correct functional diversity indices (adapted from Pla *et al.*, 2012). Indices from the green box (multi-trait indices with species abundances) were selected for the purpose of this study.

As the data collected in this study includes the categorical values of 9 vegetation traits, as well as the percentage cover of the species within the study sites, functional diversity indices from the *multi-trait, with species abundances* list was selected.

Functional richness (FRic), functional evenness (FEve), functional divergence (FDiv), functional dispersion (FDis), and functional specialisation (FSpe) diversity indices were selected to describe the plant functional diversity of selected grassland fragments in the Tlokwe Municipal area. Mason *et al.* (2005) suggested that richness, evenness and divergence as components of functional diversity should be examined dependently of each other to better explain biodiversity-ecosystem functioning relationships. Villéger *et al.* (2008) agreed but proposed that trait values and abundance must be taken into account, and thereby created multidimensional functional diversity indices. Functional dispersion (Laliberté & Legendre, 2010) and functional specialisation (Villéger *et al.*, 2010) were also selected to describe the aspects of functional diversity within the study area (Table 5.5). These indices were calculated for the current study using the FDiversity software (Casanoves *et al.*, 2010). Table E.2 in Appendix E lists the definitions of the specific notation used in the functional diversity indices equations.

1. Functional richness (FRic)

FRic (Villéger *et al.*, 2008) reflects the volume of trait space comprising of species within a community, and is not constrained between 0 and 1 (Mason *et al.*, 2005). This index is based on the convex hull hyper-volume (minimum convex hull which includes all the species) (Cornwell *et al.*, 2006) (Figure 5.2a). One biotic community may have lower functional richness than another, implying that resources available to said biotic community within a system are potentially unused (Mason *et al.*, 2005). FRic shares a positive correlation with species richness, thus the more species the higher the functional richness. But when two communities have identical species richness, the community containing a more diverse suite of traits, will have higher functional richness (Schleuter *et al.*, 2010).

2. Functional evenness (FEve)

FEve represents the regularity with which species are distributed within the functional trait niche (Mason *et al.*, 2005), and is weighted by species abundance (Villéger *et al.*, 2008). FEve will decrease when species abundances are distributed unevenly between species within a community or when functional distances between species are irregular (Villéger *et al.*, 2008). The distances between species are calculated using the Minimum Spanning Tree which links the points based on the minimum sum of branch lengths (Villéger *et al.*, 2008) (Figure 5.2b). If the assumption that resources are distributed evenly throughout the niche space is upheld, lower FEve will indicate that parts of the niche are under-utilised even though species are present there (Mason *et al.*, 2005). FEve functional

diversity index ranges from 0 (entirely uneven) to 1 (entirely even) and is independent of the convex hull (Villéger *et al.*, 2008).

3. Functional divergence (FDiv)

FDiv describes the manner in which trait values are positioned along the range of the trait niche, and ranges from 0 to 1 (Villéger *et al.*, 2008). The FDiv index nears zero when abundant species are closer to the centre of gravity relative to rare species (Villéger *et al.*, 2008) (Figure 5.2c). Higher functional divergence is an indicator of high niche differentiation and consequently lower competition for resources (Mason *et al.*, 2005).

4. Functional dispersion (FDis)

FDis represents the mean distance of species in the trait niche from the centroid (weighted towards more abundant species) of all species within the multivariate trait niche (Laliberté & Legendre, 2010) (Figure 5.2d). This index has no upper limit (Laliberté & Legendre, 2010).

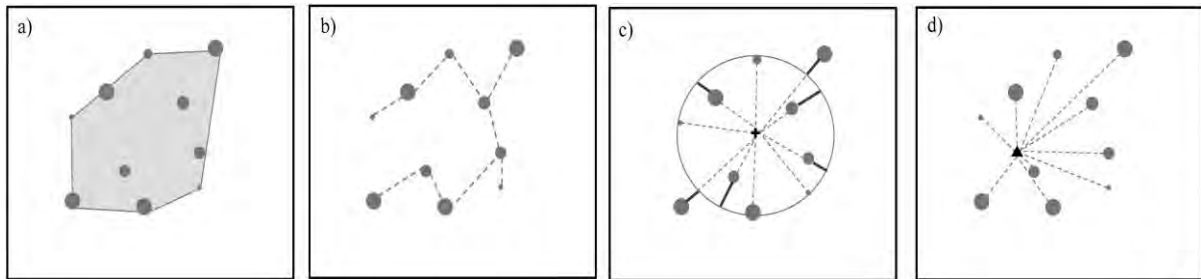


Figure 5.2: Visual representation of estimation of functional diversity indices. The points represent species according to their trait values and the size of the points represents species abundance. The species are distributed in a hypothetical trait niche. a) functional richness (Fric) (Villéger *et al.*, 2008) based on the convex hull volume (shaded in grey) (Cornwell *et al.*, 2006); b) functional evenness (FEve) (Villéger *et al.*, 2008) where the species are linked by the Minimum Spanning Tree (dotted lines); c) functional divergence (FDiv) (Villéger *et al.*, 2008) where the black cross represents the centre of gravity ($\overline{dG}$), the circle is the mean distance of species to the centre of gravity ($\overline{dG}$) and the dark lines linking each species to the $\overline{dG}$ represent the deviation of each species from the $\overline{dG}$. If the distance of more abundant species from the $\overline{dG}$ is greater than the $\overline{dG}$ the FDiv will be higher; d) functional dispersion (FDis) (Laliberté & Legendre, 2010) where the black triangle represents the abundance weighted centroid of the species. The dotted lines constitute the distance of each species from the weighted centroid. (after Villéger *et al.*, 2008 and Laliberté & Legendre, 2010).

5. Functional specialisation (FSpe)

The FSpe diversity index was developed by Villéger *et al.* (2010) to compliment the main elements of functional diversity (functional richness, functional evenness and functional divergence) originally proposed by Mason *et al.* (2005). It is based on the relative distance of species from the centroid of a Principle Component Analysis (PCA), only using the axes that explained more than 85% of the variation among species (Bellwood *et al.*, 2006).

Table 5.5: Concise description of the five functional diversity indices (Villéger *et al.*, 2008; 2010; Laliberté & Legendre, 2010) used to characterise the functional diversity of the selected grassland fragments. Functional diversity indices were calculated by the FDiversity software (Casanoves *et al.*, 2008).

Measure	Description	Formula
Functional richness	FRic Trait niche filled by the community (Villéger <i>et al.</i> , 2008).	-
Functional evenness	FEve Regularity in distance between species in the trait space (Villéger <i>et al.</i> , 2008).	$FEve = \frac{\sum_{i=1}^{S-1} \min \left(PEW_i, \frac{1}{S-1} \right) - \frac{1}{S-1}}{1 - \frac{1}{S-1}}$
Functional divergence	FDiv The manner in which trait values are positioned along the range of the trait niche (Villéger <i>et al.</i> , 2008).	$FDiv = \frac{\Delta d + \overline{dG}}{\Delta d + \overline{dG}}$
Functional dispersion	FDis Mean distance of one species in the community from the centroid of all species in the community. (Laliberté & Legendre, 2010).	$FDis = \sum_{i=1}^S w_i z_i$
Functional specialisation	FSpe The distance of species from the centre of gravity within the multidimensional trait niche of the regional species pool (Villéger <i>et al.</i> , 2010).	$FSpe = \sum_{i \in plot}^S (dG_i \times w_i)$

5.2.4 Data analysis

5.2.4.1 Plant species diversity

The number of species (species richness) in each plot per grassland fragment was used as input to calculate the mean species richness for each grassland fragment. The percentage cover data of the species recorded in the study plots of each selected grassland fragment was used to calculate the average percentage cover for each species per site, and the FDiversity software (Casanoves *et al.*, 2010) was used to determine two species diversity indices namely Shannon's Diversity Index (H') (Shannon & Weaver, 1949) and Pielou's Evenness Index (E) (Pielou, 1975) (Table 5.6) (see Appendix E, Table E.1 for annotations used in the species diversity indices). The FDiversity software (Casanoves *et al.*, 2010) provides a quick and easy way to calculate diversity indices as a built-in function of the software. Shannon's diversity index was used as it places emphasis on rare species compared to Simpson's diversity index that weights common species (Odum, 1983; Peet, 1974). This study also focuses on the functional role of plant species, therefore the potentially important part rare species have to play in influencing invasion dynamics and ecosystem function maintenance cannot be ignored (Chapin *et al.*, 2000; Lyons & Schwartz, 2001; Walker *et al.*, 1999).

Table 5.6: Species diversity indices calculated for the selected grassland fragments in the study area.

Measure	Description	Formula
Shannon's Diversity (Shannon & Weaver, 1949)	Considers both species richness and their abundances (Begon <i>et al.</i> , 2006; Pla <i>et al.</i> , 2012) and gives greater weight to rare species (Odum, 1983).	$H' = - \sum_{i=1}^S w_i \ln(w_i)$
Pielou's Evenness (Pielou, 1975)	Based on the maximum of the Shannon Index, an evenness index may be derived using the maximum value as reference for the actual value (Pielou, 1975).	$E = H' / H'_{max}$

A correlation matrix was created in STATISTICA (version 10) (StatSoft, Inc., 2011) to indicate possible relationships (expressed as the Pearson r correlation coefficient) between the degree of urbanisation in the 500 m radius matrix surrounding the grassland fragments and the plant diversity, functional trait composition, and functional diversity. Pearson's r value ranges between -1.00 and 1.00, with -1.00/1.00 indicating a perfect linear relationship (Quinn & Keough, 2002). If the correlation matrix indicates that a relationship exists between two variables, it does not necessarily signify a cause-and-effect relationship (Brase and Brase, 1999). Multiple regression analysis (Pearson, 1908) was therefore also performed to determine possible links between the degree of urbanisation / human impact (as described by the four urbanisation measures selected in *Chapter 4*) and plant species- and functional diversity. An r^2 (coefficient of determination) value of <0.1 is considered small and unimportant; $0.1 < r^2 < 0.25$ indicates a medium correlation and possible relation; whilst $r^2 > 0.25$ is considered as a practically important correlation (Ellis, 2013; Steyn, 2009; Steyn, 2012). Species richness and species diversity index values of each selected grassland fragment for rural/peri-urban and urban grassland fragments was used to execute an Analysis Of Variance (ANOVA) test in STATISTICA (version 10) (StatSoft, Inc., 2011) in order to determine statistically significant differences between grassland fragments exposed to similar urbanisation pressures.

5.2.4.2 Plant functional diversity

A Cluster Analysis was executed (PRIMER-E, 2012) using the functional trait composition data of each species. An arbitrary cut-off point of 90% Bray-Curtis similarity was selected (Kent, 2012). The purpose of the cluster analysis was not to determine functional groups, but rather to identify species that are functionally distinct from all other species, which for the purpose of this study will be termed “keystone species”. Keystone species are species that are ecologically unique species (Chapin *et al.*, 2002), and that have a much larger effect on an ecosystem than was originally expected or predicted with regards to their biomass or abundance (Bond, 1993; Power *et al.*, 1996). A NMDS ordination (PRIMER-E, 2012) based on Bray-Curtis similarity was also created using the functional trait composition data of each species to indicate the distribution of species, based on their combination of functional traits, within the ordination space.

The percentage of the species in each selected grassland characterised by certain plant traits (e.g. 25% of the species in a grassland fragment consisted of hemicryptophytes) was used as input for the NMDS ordination (PRIMER-E, 2012) to compare the plots within grassland fragments based on the composition of species functional traits. The percentage of total species richness consisting of each plant trait type for rural/peri-urban and urban selected grassland fragments was used to execute an Analysis Of Variance (ANOVA) test in STATISTICA (version 10) (StatSoft, Inc., 2011) to determine statistically significant differences between grassland fragments situated in matrix areas of differing urbanisation intensities. Correlation matrices and multiple regressions were also executed in STATISTICA (version 10) (StatSoft, Inc., 2011) to determine possible links between the degree of urbanisation / human impact and the plant functional composition of the study area.

Functional diversity indices

The traits used for this study are categorical (refer to Table 5.3), and therefore the categorical variables were transformed into dummy variables in the F Diversity software (Casanoves *et al.*, 2010) prior to further analysis. Dummy variables allow identifying categories of categorical variables by means of 1 and 0 values (Casanoves, 2012a; StatSoft, 2012). That is, each trait has been given character status and the presence (1) or absence (0) of that specific trait in each species is noted. Many functional diversity indices cannot (except for distance matrix indices) be effectively calculated for categorical values, and therefore the data was transformed from categorical to continuous variables via distance ordination methods (Casanoves, 2012b; Schleuter *et al.*, 2010). In order for certain functional diversity indices to be calculated, the dataset containing the dummy variables had to be transformed into continuous indices called principle coordinates (multidimensional scaling) (Pla *et al.*, 2012; Casanoves, 2012b). This analysis was done using InfoStat (version 2012) (Di Rienzo *et al.*, 2012). The dataset consisted of 2268 rows (plant species in the various grassland fragments) and 34

columns (trait variables). Therefore the first 18 principle coordinates, which are known to be effective in summarising complex data (Basilevsky 1994; Everitt & Dunn 1992), were subsequently used as input for calculating the selected functional diversity indices using the FDiversity software (Casanoves *et al.*, 2010).

The five selected functional diversity indices (FRic, FEve, FDiv, FDis and FSpe) were calculated for each site using the species richness, percentage cover, and categorical functional trait data of each species within each selected grassland fragment. The functional diversity indices for each rural/peri-urban and urban selected grassland fragment was used to execute an Analysis Of Variance (ANOVA) test in STATISTICA (version 10) (StatSoft, Inc., 2011) in order to determine statistically significant differences between grassland fragments situated in matrix areas of differing urbanisation intensities. Correlation matrices and multiple regressions were also executed in in STATISTICA (version 10) (StatSoft, Inc., 2011) to determine possible links between the degree of urbanisation / human impact and the plant functional indices, reflecting the plant functional diversity of the selected grassland fragments.

All the variables (plant species diversity, plant functional traits, and plant functional diversity) were compared between rural/peri-urban and urban grassland fragments, and it was also determined whether they correlated with the urbanisation measures (PURBLC, ED, DENSPEOP, and PGRALC) calculated for the 500 m matrix area surrounding the selected grassland fragments.

5.3 Results and discussion

5.3.1 Plant diversity

A total of 350 plant species were recorded in 81 sample plots situated in the 30 selected grassland fragments during this study (see Appendix F for complete species list). The 350 species consisted of 266 indigenous species and 84 exotic species.

Moderate negative correlations were found between the density of people (DENSPEOP) in the matrix surrounding selected grassland fragments, and the mean plant species richness and Shannon's diversity index within the grassland remnants (Table 5.7). This indicates that selected grassland fragments situated in more densely inhabited areas have less species. Edge density (ED), which indicated the degree of fragmentation in the 500 m radius matrix area, showed a moderate negative linear relationship with the Shannon diversity index (Table 5.7). Positive moderate correlations between the PGRALC and Shannon's and Pielou's diversity indices (Table 5.7) indicate that plant species are more diverse and evenly distributed in grassland fragments surrounded by more Rand Highveld Grassland habitat in the matrix. It is possible that grassland habitat in the matrix surrounding grassland fragments act as corridors for the dispersal of plant species between

surrounding “natural” habitat and grassland fragments with distinct edges. Refer to Table G.1, Appendix G for full multiple regression analysis results.

Table 5.7: Correlation matrix and multiple regression analysis results for species richness and –diversity indices with the selected four urbanisation measures (representing pattern/process associated with urbanisation). Only significant correlations ($p < 0.05$) are indicated. Correlation directions are indicated in grey and moderate linear relationships ($0.1 < r^2 < 0.25$) in orange.

		PURBLC		ED		PGRALC		DENSPEOP
		% Impervious surfaces		Fragmentation		Habitat loss		Urbanisation
Mean species richness	-	0.035264	-	0.087942	+	0.124803	-	0.183420
Shannon's Diversity Index (H')	-	0.086400	-	0.141234	+	0.229278	-	0.187762
Pielou's Evenness Index (E)	-	0.043700	-	0.062198	+	0.162456	-	0.108064

Figure 5.3 describes the distribution of the sample plots within the ordination space based on their species composition. The sample plots have been classified as rural/peri-urban and urban (see *Chapter 4*). Although distinct boundaries between rural/peri-urban and urban cannot be observed, a delineation (indicated by grey dotted line) may be seen between grassland fragments situated in rural/peri-urban areas, situated to the lower left of the ordination plot, and grassland fragments situated in urban areas, situated to the upper right (Figure 5.3). There appears to be a gradient of increasing human impact from the bottom left to the top right of the ordination axis (Figure 5.3), indicating that the plant species composition of some of the sample plots within the selected grassland fragments situated in more urbanised landscape context (matrix area) may differ greatly from those in more rural areas.

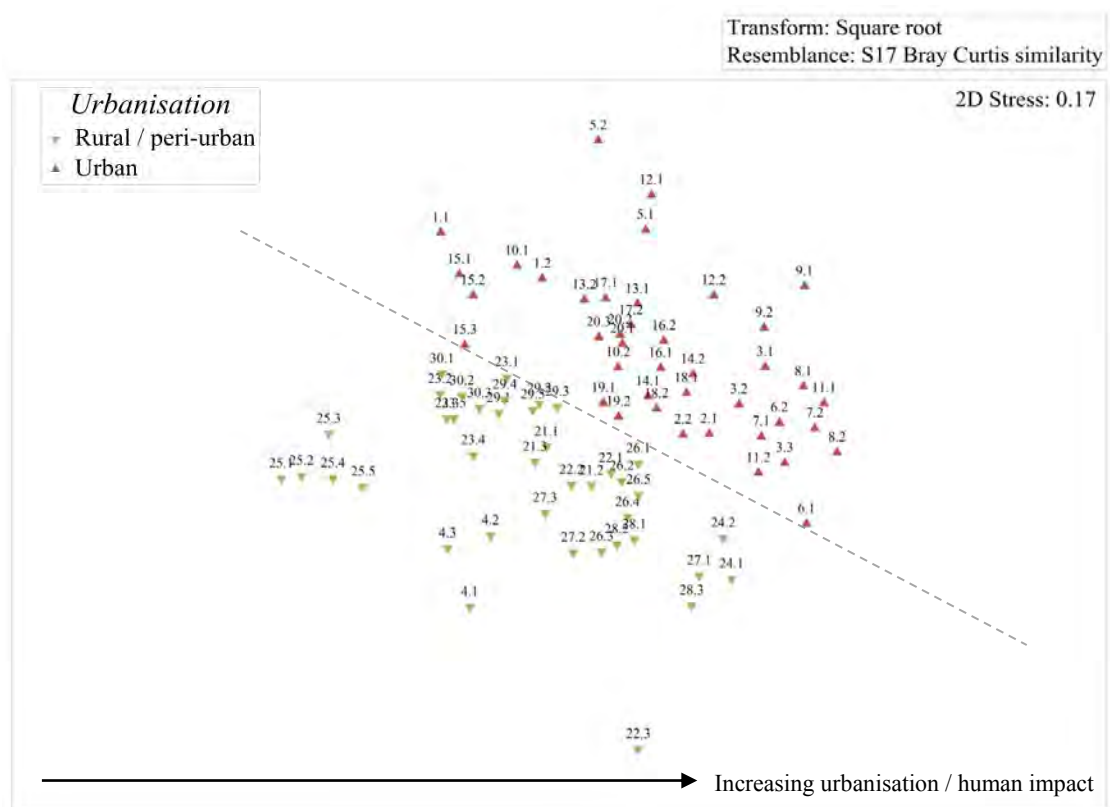


Figure 5.4 presents the mean species richness for each selected rural/peri-urban and urban grassland fragment arranged along increasing percentage impervious surfaces. Site 23 (rural/peri-urban) had the highest mean number of species per 400 m² (74 species of which 84% were native), whilst site 3 (urban) had the least number of species (30 species of which 71.4% were native). Site 23 was visually estimated to undergo grazing, whilst no specific management practice was observed in site 3 (Figure 5.4).

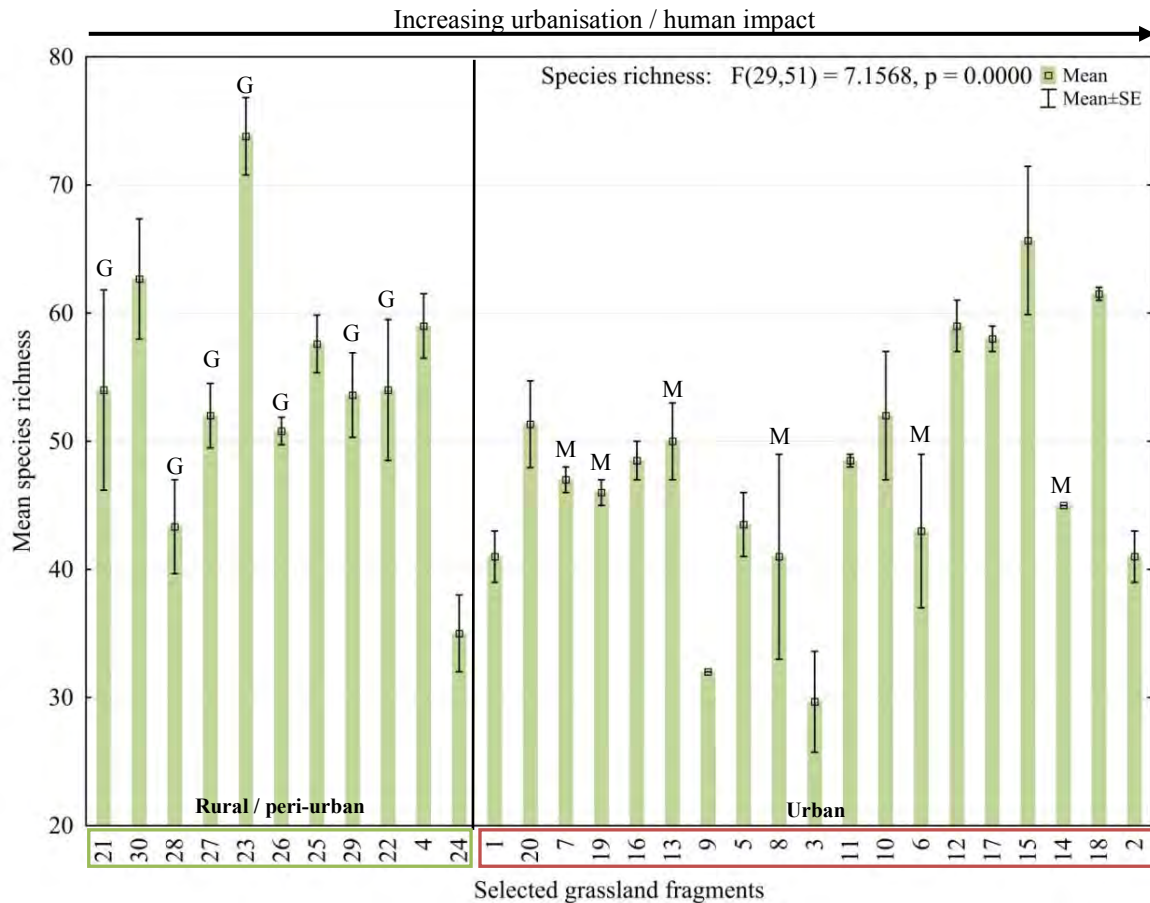


Figure 5.4: Mean species richness for rural/peri-urban and urban selected grassland fragment. The selected grassland fragments are arranged in the direction of increasing percentage impervious surfaces. The presence anthropogenic influences and management practices of mowing (M) and grazing (G) are also indicated.

Figure 5.5 illustrates the mean species richness for all rural/peri-urban and all urban selected grassland fragments. The mean species richness in grassland fragments situated in an urban landscape matrix was the lower than the mean species richness for rural/peri-urban areas. However, the mean species richness of rural/peri-urban and urban did not differ significantly from each other (see Table H.1, Appendix H for specific Tukey's HSD (ANOVA) results).

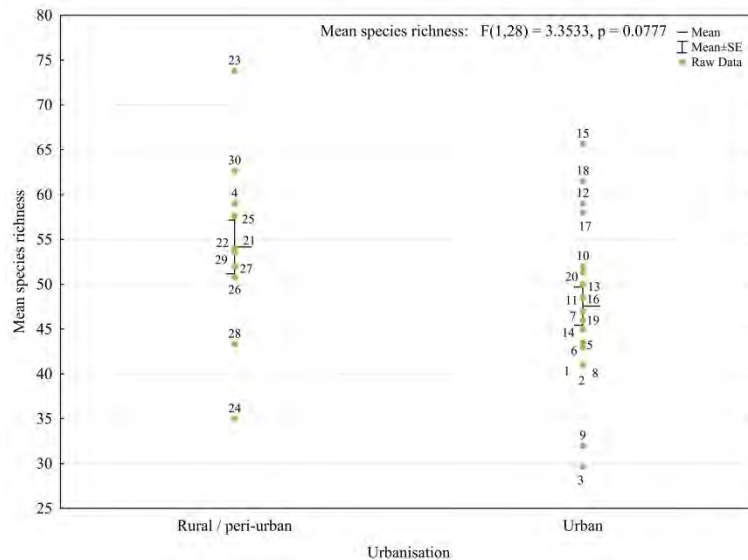


Figure 5.5: Mean species richness for rural/peri-urban and urban grassland fragments. The green dots represent the mean species richness (raw data) for each selected grassland fragment.

Figure 5.6 illustrates the mean Shannon diversity (Figure 5.6a) and Pielou evenness (Figure 5.6b) index values for the selected grassland fragments. The Shannon diversity index (H') of the selected grassland fragments were quite variable. Site 23 (rural/peri-urban) had the highest Shannon diversity index ($H' = 4.05$) (Figure 5.6a) and the individuals within this selected grassland fragment were most evenly distributed between species within the community ($E = 0.83$) (Figure 5.6b). Site 3 (urban) had the lowest Shannon diversity ($H' = 1.83$) (Figure 5.6a) and Pielou's evenness index ($E = 0.47$) (Figure 5.6b), possibly because this grassland fragment was dominated by the indigenous and characteristic grass species of the Rand Highveld Grassland vegetation unit, *Themeda triandra* (mean percentage cover 75%) which resulted in the Pielou evenness index for this site to be very low.

The mean Shannon species diversity (H') value for urban selected grassland fragments was significantly lower ($p < 0.05$) than that of rural/peri-urban grassland fragments, as indicated by similar symbols in Figure 5.6a. This contradicts several other studies (Deutschewitz *et al.*, 2003; Klotz, 1990; Pyšek & Pyšek, 1990; Stadler, *et al.*, 2000; Thuiller *et al.*, 2006) which indicated that urban areas may have higher plant species diversity than rural areas. In the studied grasslands it was clear that urbanisation decreases plant species diversity. This is confirmed by the fact three of the four urbanisation measures correlated with the Shannon diversity index (Table 5.7). The mean Pielou species evenness index did not differ significantly (see Table H.1, Appendix H for full ANOVA results).

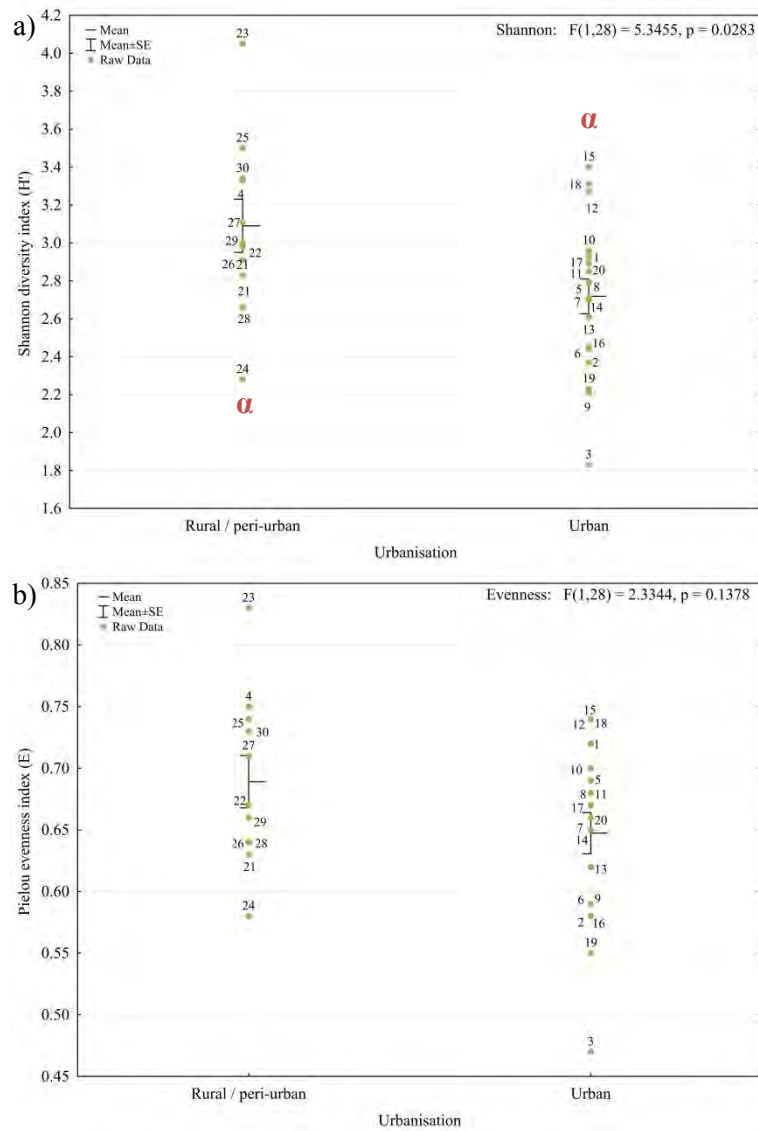


Figure 5.6: a) Mean Shannon diversity index (H') and b) mean Pielou evenness index (E) for rural/peri-urban and urban grassland fragments. The green dots represent the index values (raw data) for each selected grassland fragment. Symbols (α) indicate statistically significant differences between the mean species diversity indices for rural/peri-urban and urban grassland fragments ($p < 0.05$).

5.3.2 Plant functional diversity

The number and proportion of plant species and associated plant functional traits recorded during this study are provided in Table 5.8. The proportion of each exotic and native species possessing certain plant functional traits is also indicated. The success of establishment and persistence of exotic species in a landscape may be ascribed to certain plant functional attributes they possess (Aronson, 2007; Kowarik, 1995; Pyšek *et al.*, 1995). Tree growth forms and therophyte and phanerophyte life forms were characterised by the highest percentage exotic species. Many exotics were also annual species and species with aboveground clonal organs (e.g. stolons). Aronson *et al.* (2007) found that wind pollinated and deciduous species were mostly associated with native species and that exotic trees have successfully distributed in the New York Metropolitan, which is also consistent with the results

presented in Table 5.8. Exotic species characterised by certain plant functional traits such as tree growth form, therophyte life form (annuals), and species with aboveground clonality has established well within the Tlokwe Municipal area, and newly introduced species containing these functional attributes should be controlled and managed.

Table 5.8: Properties of the plant functional composition for the selected grassland fragments in the Tlokwe Municipal area.

Category	Trait	Number	% of total species richness	Native		Exotic	
				Number	%	Number	%
1 Status	Native	266	76%	-	-	-	-
	Exotic	84	24%	-	-	-	-
2 Growth form	Forb	223	63.71%	160	71.75%	63	28.25%
	Graminoid	75	21.43%	68	90.67%	7	9.33%
	Shrub	19	5.43%	18	94.74%	1	5.26%
	Trees	15	4.29%	6	40%	9	60%
	Succulent	5	1.43%	4	80%	1	20%
	Vine (climber)	9	2.57%	8	88.89%	1	11.11%
	Parasite	4	1.14%	2	50%	2	50%
3 Life form	Phanerophyte	27	7.71%	17	62.96%	10	37.04%
	Chamaephyte	102	29.14%	83	81.37%	19	18.63%
	Hemicryptophyte	125	35.71%	107	85.6%	18	14.4%
	Geophyte	33	9.43%	32	96.97%	1	3.03%
	Therophyte	63	18.00%	27	42.86%	36	57.14%
4 Life span	Annual	66	18.86%	28	42.42%	38	57.58%
	Perennial	284	81.14%	239	84.15%	45	15.85%
5 Clonality	Non-clonal	252	72%	184	73.02%	68	26.98%
	Clonal aboveground	13	3.71%	4	30.77%	9	69.23%
	Clonal belowground	84	24%	77	91.67%	7	8.33%
	Clonal above- and belowground	1	0.29%	0	0%	1	100%
6 Spinescence	Spines	22	6.29%	18	81.82%	4	18.18%
	No spines	328	93.71%	248	75.61%	80	24.39%
7 Leaf periodicity	Deciduous leaves	296	84.57%	226	76.35%	70	23.65%
	Evergreen leaves	38	10.86%	29	76.32%	9	23.68%
	Semi-evergreen leaves	16	4.57%	11	68.75%	5	31.25%
8 Dispersal mode	Unassisted dispersal	146	41.71%	100	68.49%	46	31.51%
	Wind dispersal	153	43.71%	128	83.66%	25	16.34%
	Internal animal transport	26	7.43%	20	76.92%	6	23.08%
	External animal transport	19	5.43%	12	63.16%	7	36.84%
	Unassisted dispersal / internal animal	6	1.71%	6	100%	0	0%
9 Pollination vector	Biotic pollination	258	73.71%	183	70.93%	75	29.07%
	Abiotic pollination	92	26.29%	83	90.22%	9	9.78%

5.3.2.1 Plant functional traits

Each plant species contained a specific combination of the nine functional traits selected for this study. In Figure 5.7 the species were clustered at a Bray Curtis similarity of 90% (grey dashed line). The species that did not cluster with other species, and are thus functionally distinct from other species based on their specific suite of functional traits are called “keystone species” for the purpose of this study, and consist of exotic and native species (Figure 5.7). Information on the species clusters (groups A – BD) and functionally distinct (“keystone”) species are presented in Table 5.9.

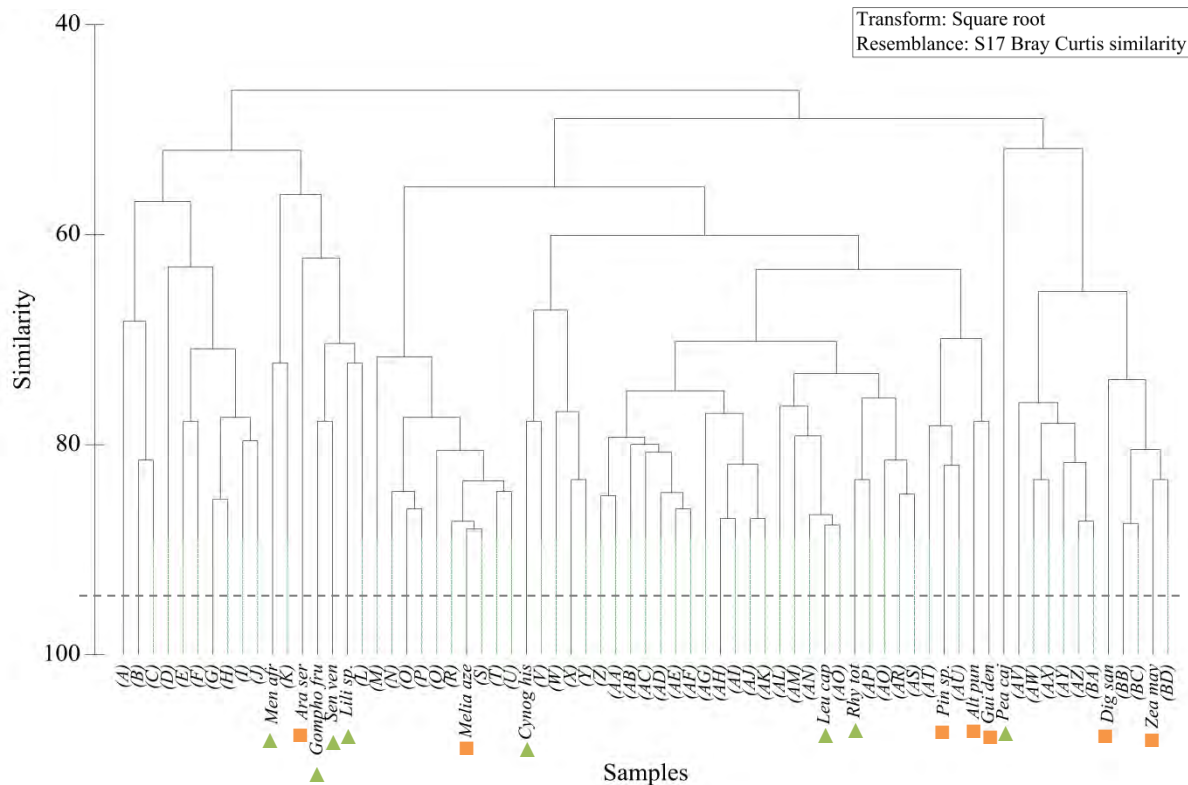


Figure 5.7: Cluster analysis (group average) based on the Bray-Curtis similarity index of the functional trait composition of each species recorded during this study. The grey dashed line indicates the 90% arbitrary cut-off point. Orange squares indicate exotic keystone species (*Ara ser* = *Araujia sericifera*; *Melia aze* = *Melia azedarach*; *Pin sp.* = *Pinus* species; *Alt pun* = *Alternanthera pungens*; *Gui den* = *Guilleminea densa*; *Dig san* = *Digitaria anguinalis*; *Zea may* = *Zea mays*), and green triangles indicate native keystone species (*Men afr* = *Menodora africana*; *Gompho fru* = *Gomphocarpus fruticosus*; *Sen ven* = *Senecio venosus*; *Lili sp.* = *Liliaceae* species; *Cynog his* = *Cynoglossum hispidum*; *Leu cap* = *Leucas capensis*; *Rhy tot* = *Rhynchosia totta*; *Pea caj* = *Pearsonia cajanifolia*).

Seven exotic (*Alternanthera pungens*, *Araujia sericifera*, *Guilleminea densa*, *Digitaria sanguinalis*, *Melia azedarach*, *Pinus* species, and *Zea mays*), and eight native (*Cynoglossum hispidum*, *Gomphocarpus fruticosus*, *Leucas capensis*, *Liliaceae* species, *Menodora africana*, *Pearsonia cajanifolia*, *Rhynchosia totta*, and *Senecio venosus*) keystone species were found in the selected grassland fragments (Table 5.10). Keystone species in the selected grassland fragments did not have high mean percentage cover; often only one individual (0.5%) was recorded in the sample plots, or observed outside the sample plots (0.1%). *A. sericifera* (category 1 weed), *M. azedarach* (category 3 invader), and *Pinus* species (category 2 invader) are presently declared weeds and invaders in South Africa (Conservation of Agricultural Resources Act (43 of 1984); Henderson, 2001), confirming that these species possess functional attributes that enables them to successfully exploit unused resource strata. Only two of the seven exotic keystone species (*A. pungens* and *G. densa*) were found in rural/peri-urban grassland fragments, whilst all the exotic species were prevalent in urban grassland fragments, indicating that these species have the functional traits to exploit unutilised resources and successfully establish and persist in urban areas. *Rhynchosia totta* was the most abundant native keystone species throughout the study area, whilst *Cynoglossum hispidum* and *Leucas capensis* were

unique to two respective rural/peri-urban grassland fragments, and *Liliaceae* species and *Senecio venosus* to two urban grassland fragments (Table 5.10).

Table 5.9: Plant functional groups (based on 90% Bray Curtis similarity cut-off point). “Keystone” species are functionally distinct from all other species that were recorded during this study. Refer to Appendix F for species codes and associated full species names.

A	B	C	D	E	F	G	H	I	J	K	L	M	N	O
Asp lan	Acac caf	Ery zey	Phys vis	Ces lue	Sea col	Dia lye	Cel afr	Gile tri	Cel aus	Ani ang	Dal her	Cr val	Dice eri	Siri asi
Asp sel	Acac eri	Gym bux	Poly hot	Euc cam	Schb pin	Gre fla	Comb ery	Ziz mic	Med sat	Oni tet	Sed suf	Cos bip	Hib tri	Siri ele
Asp sta	Acac heb	Ziz zey		Euc sid	Sea pyc	Her rig	Sea lan		Mon ang			Oon ros	Pse lut-ab	
	Acac ka										Sed den		Yern pas	

P	Q	R	S	T	U	V	W	X	Y	Z	AA	AB	AC	AD
Alc ses ses	Amo lyb	Cus cam	Che alb	Ar sem	Ann maj gla	Cuc zey	Cony pad	Ber car mag	Alu gre	Cya spe	Dia mao	Lac ser	Bar mac	Helio ump
Chum mam	Amo lha	Pop del	Che car	Bid bip	Arg och och	Dev bur	Sol run	Ber ono ono	Ber rud	Ela ele	Gni cap	Pun max	Med lac	
Cro sph		Sta spa	Che muc	Bid pil	Cum han		Sen gre				Koh cae	Pog sap	Mic caf	
Eri aus			Ciel lep	Sri ges	Coi mic						Med lin rep		Rue cor	
Eup lha			Comm ben	Lac ine	Oen ind						Phys sp		Set sph tor	
Ipo pur			Eup hel	Por qua	Schiz san						Rub hor		Sol pan	
Mal coro			Ipo oan oan	Led rev	San nan						Sid spi		Tur off	
Ser pla			Lep bon	Man par lin	Zin per						Sol lhc		Verb ari	
			Nol rar	Phyl mad							Vig vex		Verb bon	

AE	AF	AG	AH	AI	AJ	AK	AL	AM	AN	AO	AP	AQ	AR
Ar lei	Indigo fil	Lep did	Rap vel	Acid ang	Anth rig	Comm af	Cich int	Orn flt	Alb set	Cr bul	Cle bra	Cor asp	Gaz kre ser
Pol cam	Indigo hed	Lot cul	Rhy min	Ipo obl	Fial obl	Cra ang	Hyp hir	Verb off	Alb sp	Gla cra	Conv sag	Fel mir	Hib pus
Poly ama	Indigo hat			Ipo sp		Her dep			Bon dis	Gla per		Hap lye	Pyc mac
Trig min	Indigo nev			Jun aur					Budbi cap	Hue mon		Hap sca	Sen ino
	Indigo sp.1			Oxa coro		Indigo zey			Budbi nar	Hypox rud		Kyl alb	
	Chae cos			Sor had		Ipo cra			Chloro coo	Hypox hem		Mor nig	
	Chum hie					Ipo hol			Chloro tra	Hypox tri		Nid ano	
	Chas hed					Ipo sin			Dip vir	Ran mul		Oro cap	
	Comm pen					Sea rig			Eriose xal	Rap hir		Pena ins	
	Cro lot					Spa nit			Lan rig			Sen con	
	Eriosp coo coo					Trif rep			Led coo			Sen eru	
	Har coc					Woh und			Led ova			Sen har	
	Har gla								Merr tri			Sol rig	
	Hypox rig								Pse un			Sen dra	
	Indiga bur											Sen ole	
	Indigo cry											Tragu her	
	Indigo dal											Yern sta	
												Yys und	

AS	AT	AU	AV	AW	AX	AY	AZ	BA	BB	BC	BD
Dico ano	Lot lis	Dich mic	Cyp den	Afr mag	Helic acv	Par cap	Cymod dac	Era obl	Ari con con	Trago dub	Bra eru
Dico mac	Tal caf	Gomphr cel	Cyp exc	Koh vir	Helic cur mon	Pas dil	Cymod hir	Era pat	Ari ads	Uro mos	Bro cau
Gai bur	Trac spl	Ipo obs	Cyp obt obt		Helic cue	Son wil	Dig eri	Era pla	Ari con bar	Uro mios	
Hib aet		Mr jul	Cyp rap		Helic cul		Uro bra	Era rac	Chlori var	Chlori pyc	
Hib mic		Ost mur	Cyp sp		Helic mud		Set sph ser	Era rig	Era hif	Era hif	
Nid hot		Phys ang			Helic rig		Set sph sph	Era sup	Set pun	Melin ner	
Penn cla		Pyg zey			Pre spe		Cyp bel	Era tri	Spo fim	Set nig	
Thes ati		Trichon gra					Dig arg	Eua pas	Tea tri	Trir and	
							Era obl	Hel con	Tal cap		
							Ses tra	Mell alb	Trichod ang ang		
								Era cur	Trip ugh		
								Merv plu	Yern oli		
								Era mic			
								Era tin			

Native keystone species	Exotic keystone species
<i>Cynodactylon hispidum</i>	<i>Alternanthera pungens</i>
<i>Gomphocarpus fruticosus</i>	<i>Araulitia sericeifera</i>
<i>Leucas capensis</i>	<i>Digitaria sanguinalis</i>
<i>Liliaceae</i> sp.	<i>Guilleminea densa</i>
<i>Menodora africana</i>	<i>Melia azedarach</i>
<i>Pearsonia calanifolia</i>	<i>Pinus</i> sp.
<i>Rhynchosia totia</i>	<i>Zea mays</i>
<i>Senecio venosus</i>	

Table 5.10: The occurrence and mean percentage cover of native and exotic “keystone” species in the selected rural/peri-urban and urban grassland fragments. (*Ara ser* = *Araujia sericifera*; *Alt pun* = *Alternanthera pungens*; *Cynog his* = *Cynoglossum hispidum*; *Dig san* = *Digitaria anginalis*; *Leu cap* = *Leucas capensis*; *Gompho fru* = *Gomphocarpus fruticosus*; *Gui den* = *Guilleminea densa*; *Lili sp.* = *Liliaceae* species; *Melia aze* = *Melia azedarach*; *Men afr* = *Menodora africana*; *Pea caj* = *Pearsonia cajanifolia*; *Pin sp.* = *Pinus* species; *Sen ven* = *Senecio venosus*; *Rhy tot* = *Rhynchosia totia*; *Zea may* = *Zea mays*). Declared weeds and invaders are indicated in red boxes (Conservation of Agricultural Resources Act (43 of 1984); Henderson, 2001)

Selected grassland fragment	Urbanisation	Native										Exotic				
		<i>Cynog his</i>	<i>Gompho fru</i>	<i>Leu cap</i>	<i>Lili sp.</i>	<i>Men afr</i>	<i>Pea caj</i>	<i>Rhy tot</i>	<i>Sen ven</i>	<i>Alt pun</i>	<i>Ara ser</i>	<i>Dig san</i>	<i>Gui den</i>	<i>Melia aze</i>	<i>Pin sp.</i>	<i>Zea may</i>
21	Rural / peri-urban		0.1			0.5	0.5	0.5								
30	Rural / peri-urban		0.5			0.5	0.5	0.5								
28	Rural / peri-urban															
27	Rural / peri-urban							0.5								
23	Rural / peri-urban		0.5			0.5		0.6		0.5			0.5			
26	Rural / peri-urban							0.5								
25	Rural / peri-urban		0.1					0.5								
29	Rural / peri-urban							0.8								
22	Rural / peri-urban	0.5		0.5		0.5		0.5								
4	Rural / peri-urban					0.5			0.5							
24	Rural / peri-urban															
1	Urban							0.5						0.1		
20	Urban									0.5			0.5			
7	Urban										0.5					
19	Urban							0.5								
16	Urban							2						0.1		
13	Urban							1								
9	Urban															
5	Urban							0.5								
8	Urban															
3	Urban															
11	Urban														0.1	
10	Urban		0.1					1.25						0.5		
6	Urban				0.5			0.5								
12	Urban															
17	Urban									0.1						
15	Urban							0.5					0.5			
14	Urban							0.5			0.1					
18	Urban							0.75			0.1		0.1			
2	Urban							0.75								0.5

The presence of exotic keystone species, (e.g. *Araujia sericifera*, *Guilleminea densa* and *Melia azedarach*– Table 5.9 and 5.10) may be a cause for concern as these species are able to utilise a

different part of the resource stratum or functional niche than indigenous species, and are thus able to easily establish and persist as invaders in a system. The loss of native keystone species will also expose a functional niche that may be susceptible to the establishment of exotic invaders, and therefore these functionally distinct native species (e.g. *Gomphocarpus fruticosus*, *Cynoglossum hispidum* and *Rhynchosia totta*) need to be conserved.

In the NMDS ordination presenting species based on their functional trait composition (Figure 5.8) the grey dashed line circle indicates a group of only exotic species (e.g. *Melia azedarach*, *Schinus molle*, *Melilotus albus*, *Atriplex semibaccta*, *Commelina benghalensis*). Although the border between this group of species and the rest of the species is not discrete, it still indicates that these exotic species (especially species closer to the outer edge of the “species cloud”, such as *Alternanthera pungens* and *Gleditsia triacanthos*) own a unique set of traits not found in other species. This may be a cause for concern as it once more indicates that these exotic species are able to utilise resources or encompass a functional trait volume that is unused by other species, and are therefore most likely to establish and persist within an ecosystem, and may possibly become invasive (e.g. *Alternanthera pungens* and *Gleditsia triacanthos*) as indicated earlier as well. It may also be observed from Figure 5.8 that there are many exotic species that are functionally very similar to native species, which indicates that native and exotic species are in competition for the same resource strata / functional niche. Only species names of the plant species mentioned above are included in Figure 5.8.

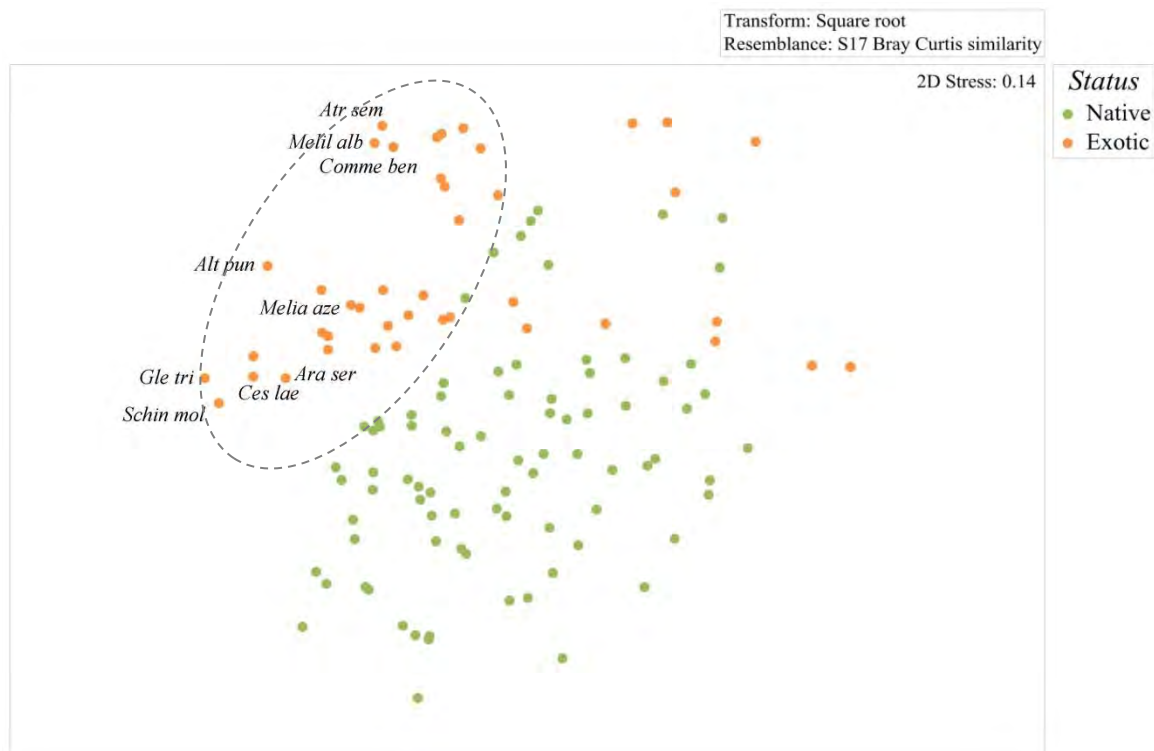


Figure 5.8: NMDS ordination of each plant species based on functional trait composition within the study area. The grey dashed line circle indicates a group of only exotic species. Only species codes of the plant species mentioned in the discussion above are included. See Appendix F for species codes and associated full species names.

Figure 5.9 represents the NMDS ordination plot with the species functional trait composition of each sample plot within each selected grassland fragment. This ordination did not show distinct clusters, and plots within the same grassland fragment did not necessarily group together (Figure 5.9), because each site contained combinations of species that have similar suites of traits.

Outliers from the main cluster of sample plot may be seen as plots 3.1, 9.2 and 9.3 (urban), 22.3 and 28.3 (rural/peri-urban) (indicated by grey circles in Figure 5.9). Possible reasons for these deviations were explored and are mainly ascribed to the most or least presence (extremes) of a specific plant trait. For instance sample plot 3.1 had the least exotic species, forbs, therophytes / annuals, semi-green species, and species that are transported externally by animals, but had the most hemicryptophytes, perennials, species with spines, and deciduous and evergreen species; whilst sample plot 9.1 had no shrubs, parasites, species with spines, and no species that are transported externally by animals, but the most graminoids.

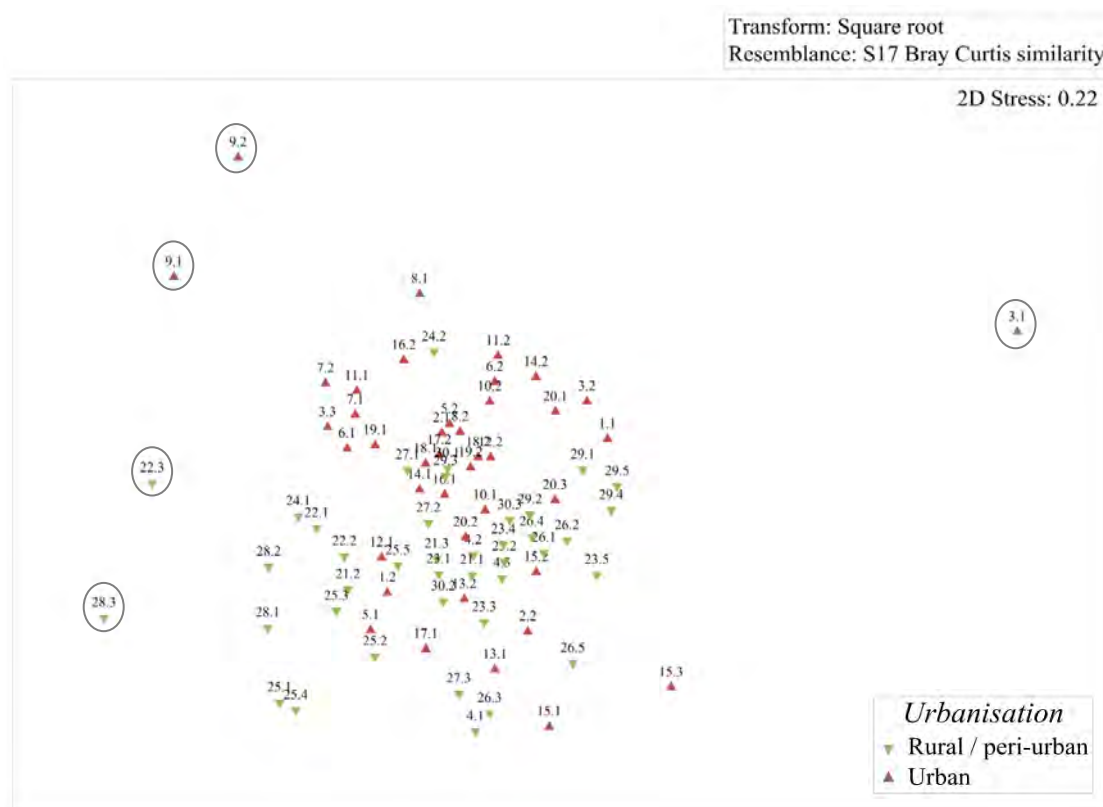


Figure 5.9: NMDS ordination of species functional trait composition for the sample plots within selected rural/peri-urban (green) and urban (red) grassland fragments. The sample plots that are indicated in grey circles are outliers.

The proportion of the species richness consisting of each selected functional trait for each selected grassland fragment will now be discussed. The presence of plant species characterised by certain

functional attributes may be associated with environmental conditions and reflective of biotic, climatic, and disturbance pressures (Díaz *et al.*, 1998).

Significant correlations ($p < 0.05$) were found between the four urbanisation measures calculated for the matrix area directly surrounding the selected grassland fragments and selected species functional attributes (Table 5.11). This indicated that increased urbanisation and its associated pattern and process characteristics (e.g. fragmentation; habitat loss; landscape heterogeneity) may possibly, to some degree, influence the species composition and the prevalence of certain plant functional attributes in the selected grassland fragments.

The mean percentage of the total species richness consisting of native/exotic species showed strong linear relationships ($r^2 \geq 0.25$) with all four urbanisation measures. The percentage native species of the total species richness decreased with the presence of more impervious surfaces, habitat fragmentation (ED), and human habitation (DENSPEOP) in the matrix surrounding the selected grassland fragments, and also increased in grassland fragments surrounded by more remaining Rand Highveld Grassland habitat (PGRALC) (Table 5.11).

Mean percentage Graminoid and mean percentage shrubs correlate moderately with only the density of people (DENSPEOP) for the 500 m matrix area around each grassland fragment (Table 5.11). Graminoid cover increased with increased human inhabitation, whilst the mean percentage shrubs decreased (moderate linear relationships; $0.1 < r^2 < 0.25$). This may be due to mowing in the urban grassland fragments preventing vegetation with aerial meristems (such as shrubs) to establish and persist, resulting in dense grass cover.

Mean percentage Phanerophytes (consisting of woody tree and shrub species belonging to *Celtis*, *Eucalyptus*, and *Acacia* genera) and mean percentage trees showed moderate positive linear relationship with PURBLC and ED (Table 5.11), which may be attributed to possible planting of trees and woody species in more urbanised areas for aesthetic reasons.

The mean percentage of the total species richness consisting of annual / perennial and therophyte species showed moderate linear relationships with DENSPEOP (Table 5.11). The amount of annual species (therophytes) increased in grassland fragments surrounded by higher human inhabitation and are often associated with more urbanised areas (Čepelová & Münzbergová, 2012; Kleyer, 1999; Pellissier *et al.*, 2008).

The mean percentage of the total species richness that consisted of geophytes also showed strong linear relationships ($r^2 \geq 0.25$) with PURBLC and ED, and moderate linear relationships ($0.1 < r^2 < 0.25$) with PGRALC, and DENSPEOP (Table 5.11). The mean percentage geophytes thus decreased with increasing urbanisation / human impact, and increased with Rand Highveld Grassland habitat availability in the 500 m matrix area surrounding the grassland fragments (Table 5.11). In other

studies geophytes have been found to be sensitive to disturbances (McIntyre *et al.*, 1995) and are vulnerable to extinction in urbanised areas (Čepelová & Münzbergová, 2012; Williams *et al.*, 2005).

Non-clonal plants were more abundant in grassland fragments surrounded by more urbanised and fragmented matrices (Table 5.11), probably due to the smaller grassland remnant size in Potchefstroom city than surrounding rural areas where clonal species have less potential to persist (Robinson *et al.*, 1992). Degree of fragmentation (ED) strongly influenced percentage clonal belowground (Table 5.11), where less species with belowground clonal organs (e.g. tubers; woody rootstock; rhizomes) occurred in grassland remnants in fragmented matrices. Refer to Table G.2, Appendix G for full multiple regression analysis results.

Table 5.11: Correlation matrix and multiple regression analysis results for the plant functional traits with the selected four urbanisation measures (representing pattern/process associated with urbanisation). Only significant correlations ($p < 0.05$) are indicated. Correlation directions are indicated in grey, moderate linear relationships ($0.1 \leq r^2 < 0.25$) in orange, and strong linear relationships ($r^2 \geq 0.25$) in red.

		PURBLC		ED		PGRALC		DENSPEOP
		% Impervious surfaces		Fragmentation		Habitat loss		Urbanisation
%Native	-	0.254115	-	0.267102	+	0.260911	-	0.341062
%Exotic	+	0.254115	+	0.267102	-	0.260911	+	0.341062
%Graminoid	+	0.025426	+	0.046713	-	0.066169	+	0.156714
%Shrub	-	0.045975	-	0.047378	+	0.100997	-	0.165452
%Tree	+	0.194278	+	0.216686	-	0.102093	+	0.040684
%Phanerophyte	+	0.170289	+	0.150092	-	0.061569	+	0.018736
%Therophyte	+	0.010921	+	0.013025	-	0.063906	+	0.183103
%Geophyte	-	0.300783	-	0.367219	+	0.242932	-	0.136371
%Perennial	+	0.017477	-	0.023992	+	0.085575	-	0.198490
%Annual	-	0.017477	+	0.023992	-	0.085575	+	0.198490
%Non-clonal	+	0.164238	+	0.185972	-	0.202637	+	0.248406
%Clonal belowground	-	0.226838	-	0.297796	+	0.236119	-	0.268433
%Clonal aboveground	+	0.083367	+	0.165608	-	0.038434	+	0.021580
%Clonal above+below	+	0.034979	+	0.033372	-	0.083261	+	0.170320
%Semi-evergreen	+	0.223092	+	0.189430	-	0.127826	+	0.092555
%Unassisted/internal animal	+	0.173787	+	0.209836	-	0.207971	+	0.447979

Differences in specific plant traits between rural/peri-urban and urban areas will now be discussed.

1. Status

Site 15 (urban) had the highest total percentage native species (94%), whilst sites 8 and 9 (urban) had the most exotic species (46%) (Figure 5.10).

Urban grassland fragments had the highest percentage exotic species (site 8) and the lowest percentage exotic species (site 15) (Figure 5.10). This indicates the variability of species composition within the more urbanised study sites. Overall the grassland fragments situated in a more urbanised landscape context had significantly higher ($p < 0.05$) mean percentage exotic plant species than grasslands situated in rural/peri-urban landscape contexts (as indicated by similar symbols in Figure

5.10). Urban areas are often characterised by higher exotic plant species richness (Gilbert, 1989; Grobler *et al.*, 2006; Niemelä, 1999b; Pickett *et al.*, 2011; Pyšek, 1998). See Table H.2, Appendix H for complete ANOVA results.

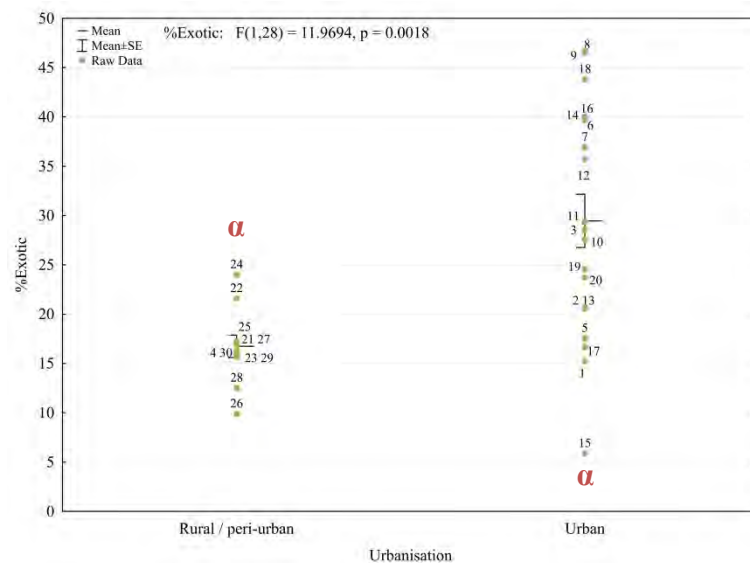


Figure 5.10: Status – mean percentage exotic plant species for rural/peri-urban and urban grassland fragments. The green dots represent the percentage exotic species of the total species richness (raw data) for each selected grassland fragment. Symbols (α) indicate statistically significant differences between the mean percentage exotic plant species for rural/peri-urban and urban grassland fragments ($p < 0.05$).

2. Growth form

Figure 5.11 describes the functional species composition (based on growth form) of the selected grassland fragments in the Tlokwe Municipal area. Forbs and graminoids were the most common growth form in the selected grassland fragments (Table 5.8 and Figure 5.11). Parasitic plants were recorded in only sites 9, 15, 16, 18, and 20 (urban), as well as sites 23 and 30 (rural/peri-urban).

Grasslands situated in urban areas had the highest mean percentage graminoid species, the lowest mean percentage forb species (significantly, as indicated by similar symbols), and the lowest mean percentage shrub species (Figure 5.11a, b and c). This may be attributed to mowing as a recognised management practice in urban grassland fragments (Cilliers *et al.*, 2008). Fynn *et al.* (2004) found that forb species richness was reduced by summer mowing, whilst the species richness of grasses were unaffected. Plant species with aerial meristems (e.g. forbs and shrubs) may be compromised and removed through mowing practices (Fynn *et al.*, 2004). Lower mean percentage graminoids and higher mean percentage forbs and percentage shrubs in more rural/peri-urban grassland fragments (Figure 5.11a, b and c) are the result of absence of mowing disturbance as forbs have the opportunity to establish, persist and compete with other plant species, such as grass species, for space and resources.

The mean percentage tree species richness was significantly higher in the grassland fragments situated in the most urbanised matrix areas, and lowest in the rural/peri-urban grassland remnants (indicated by similar symbols in Figure 5.11d). This may possibly be attributed to fire preventing the establishment of a woody layer in rural areas (Bond *et al.*, 2003), and planting of trees in more urban areas for aesthetic reasons. See Table H.2, Appendix H for complete ANOVA results.

The mean percentage succulent species richness for the selected grassland fragments did not vary much (range 0% – 3.85%; Figure 5.11e). The highest mean percentage vine species richness was found in urban grassland fragments (Figure 5.11f). This may be due to the higher presence of trees (see Figure 5.11d) that provide vertical structure, in a vegetation type that is characterised predominantly by herbaceous vegetation (Mucina & Rutherford, 2006), on which vines and climbers were able to establish. Very little parasitic plants were found throughout the study area (Figure 5.11g).

Although some difference between the different types of growth forms for plant species in rural/peri-urban and urban landscape surroundings became evident, it is also clear that urbanisation / human impact does not necessarily determine the species composition based on plant species growth form only.

3. Life form

Raunkaier (1937) life form classification is a well-known physiognomic technique based on the height of perennating buds (plant parts where growth in the next favourable growing season originates). The morphological position of the perennating buds is closely related to environmental, especially climatic, filters (Kent, 2012).

Phanerophytes bear perennating buds >2 m above the ground (Raunkaier, 1937). In the selected grassland fragments plant species that classified as phanerophytes were predominantly woody shrubs (for example *Erythrina zeyheri*, *Gomphocarpus fruticosus*), and trees (for example *Eucalyptus* species, *Grewia flava* and *Melia azedarach*) (see Appendix F for full species list and corresponding plant traits). The mean percentage phanerophytes species richness was highest in the grassland fragments situated in more urbanised matrix areas, and lowest in rural/peri-urban grassland remnants (Figure 5.12a). This may possibly be attributed to planting of trees in more urbanised areas for aesthetic reasons and the presence of fire preventing the establishment of a woody layer in rural areas (Bond *et al.*, 2003), as was indicated for the growth forms as well.

The most abundant plant species in the selected grassland fragments were hemicryptophytes (Table 5.8 and Figure 5.12b) and chamaephytes (Table 5.8 and Figure 5.12c). Most of the grass species and some rosette forb species (e.g. *Amaranthus* species, and *Senecio* species) in the selected grassland fragments were hemicryptophytes which are characterised by perennating buds borne at ground level

that die back in unfavourable conditions (Raunkaier, 1937). Rural/peri-urban grassland fragments marginally had the highest mean percentage hemicryptophytes; whilst the abundance of hemicryptophytes was very variable in urban grassland fragments having the highest and lowest percentage hemicryptophytes (Figure 5.12b). Williams *et al.* (2005) found that hemicryptophytes were vulnerable to extinction in urban landscapes.

Chamaephytes are woody or herbaceous species that have perennating buds close to the ground (<2 m) (Raunkaier, 1937). The species recorded in the selected grassland fragments that were classified as chamaephytes belong to genera such as *Asclepias*, *Asparagus* and *Verbena*. Chamaephytes were slightly less abundant in urban grassland fragments, which contained grassland fragments with the highest (site 13) and lowest (site 8) percentage chamaephytes. (Figure 5.12c)

More urbanised grassland fragments had the highest mean percentage therophytes and also showed the most variability for this growth form (Figure 5.12d). Sites 8 and 9 (urban) had the most total percentage therophytes (annuals) consisting of a respective 31% and 28% of the total species richness (Figure 5.12d). Therophytes survive harsh environmental conditions as seeds and complete their entire life cycle in one year (annuals) (Raunkaier, 1937). Therophytes have been found to be associated with more urbanised areas in several other studies (Kleyer, 1999; Sudnik-Wójcikowska & Galera, 2005; Pellissier *et al.*, 2008; Čepelová & Münzbergová, 2012).

The mean percentage geophytes (plants with underground perennating buds such as bulbs or tubers (Raunkaier, 1937)) were significantly lower in grassland fragments in urban surroundings (as indicated by similar symbols in Figure 5.12e; see Table H.2, Appendix H for complete ANOVA results). Geophytes have been found to be sensitive to disturbances (McIntyre *et al.*, 1995) and are vulnerable to extinction in urbanised areas (Williams *et al.*, 2005; Čepelová & Münzbergová, 2012).

The variability of plant life forms in the more urbanised areas are evident (Figure 5.12a-e) mainly due to the variability of habitat and disturbances found in areas exposed to greater human impacts. Differences in the percentage species richness of various Raunkaier life forms for rural/peri-urban and urban grassland fragments cannot be very clearly observed. The ANOVA results revealed that rural/peri-urban and urban grassland remnants did not differ significantly (except for percentage geophytes; see Table F.2, Appendix H for complete ANOVA results). Therefore it cannot be said that the degree of urbanisation / human impact affected species composition based on the life form of plant species within the selected grassland remnants in the Tlokwe Municipal area.

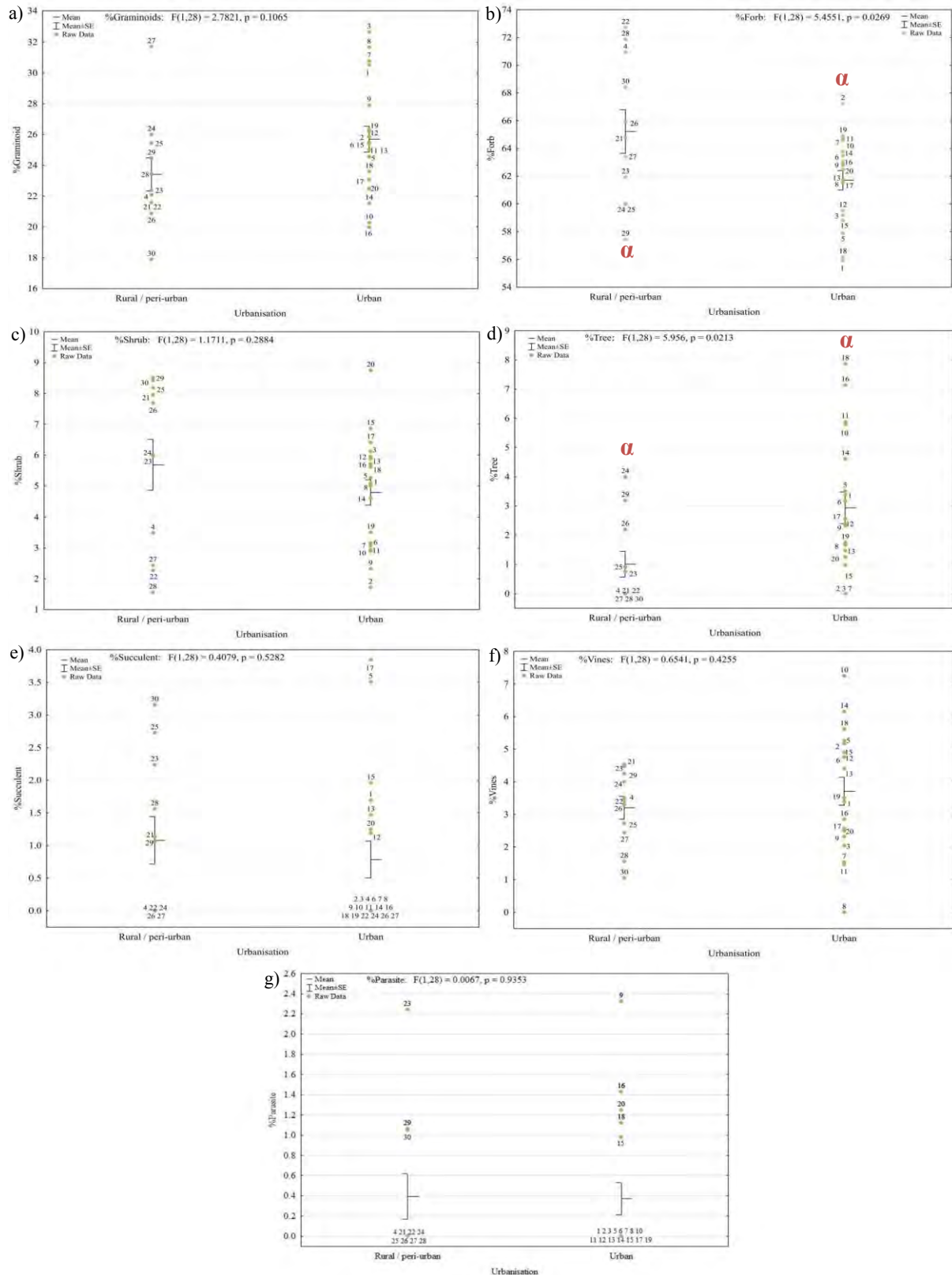


Figure 5.11: Growth form – mean percentage a) graminoids, b) forbs, c) shrubs, d) trees, e) succulents, f) vines, and g) parasitic plants for rural/peri-urban and urban grassland fragments. The green dots represent the percentage of each growth form of the total species richness (raw data) for each selected grassland fragment. Symbols (α) indicate statistically significant differences between the mean percentage specific growth forms for rural/peri-urban and urban grassland fragments ($p < 0.05$).

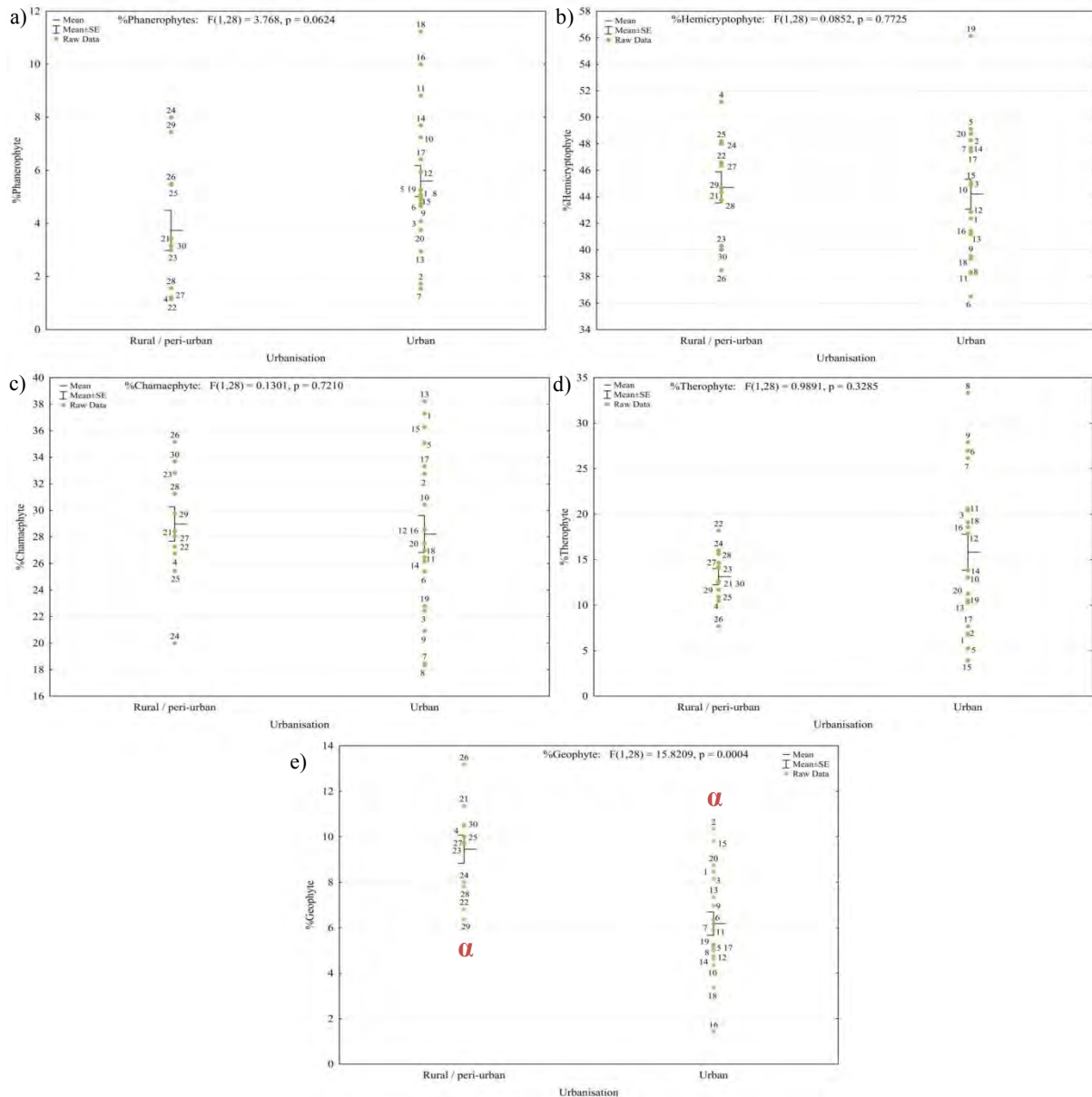


Figure 5.12: Life form – mean percentage a) phanerophytes, b) hemicryptophytes, c) chamaephytes d) therophytes, and e) geophytes for rural/peri-urban and urban grassland fragments. The green dots represent the percentage of each life form from of the total species richness (raw data) for each selected grassland fragment. Symbols (α) indicate statistically significant differences between the mean percentage specific life forms for rural/peri-urban and urban grassland fragments ($p < 0.05$).

4. Life span

Site 15 (urban) was characterised by the most long-lived perennial vegetation (Figure 5.13). The percentage annual species recorded in the selected grassland fragments reflects the mean percentage therophytes graph (Figure 5.12d in the previous section), and include, among others, species such as the *Amaranthus* species, *Medicago laciniata*, certain *Aristida* grass species, and *Zinnia peruviana*. More urbanised grassland fragments had the lowest mean percentage perennial vegetation (Figure 5.13). Annuals are able to persist in harsh environmental conditions as seeds and complete their life cycle in a single year (Raunkaier, 1937). Annuals have been found to be associated with more

urbanised areas (Čepelová & Münzbergová, 2012; Kleyer, 1999; Pellissier *et al.*, 2008). The mean percentage perennial plant species for rural/peri-urban and urban grassland fragments did not differ significantly (see Table F.2, Appendix H for complete ANOVA results).

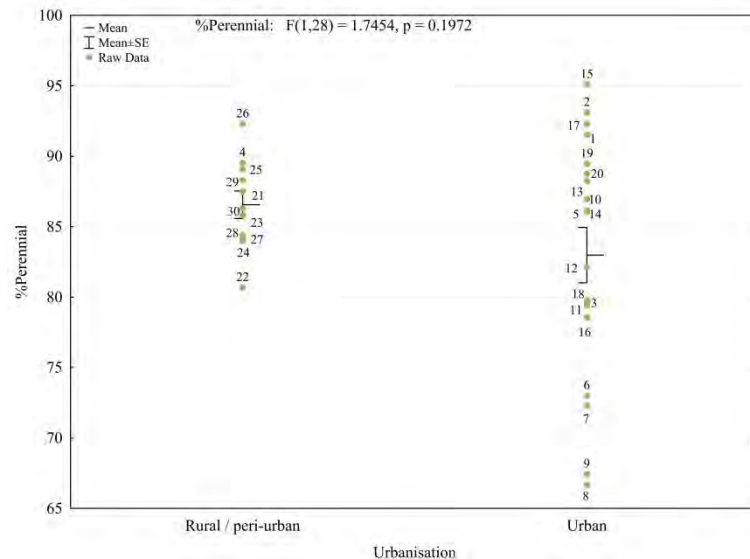


Figure 5.13: Life span – mean percentage perennial species richness for rural/peri-urban and urban grassland fragments. The green dots represent the percentage perennial plant species of the total species richness (raw data) for each selected grassland fragment.

5. Clonality

Clonal growth may provide plants with the opportunity to exploit resources and persist after environmental disruption (Cornelissen *et al.*, 2003), that occurs typically in urban areas.

Non-clonal plants were most abundant within the study area (Table 5.8 and Figure 5.14a), followed by plants that are characterised by clonal underground organs (such as rhizomes (e.g. *Rhynchosia totta*) and bulbs (e.g. *Bulbine* species), as well as above-ground clonal organs such as stolons found in *Guilleminea densa*. All sites (except sites 1 and 18 (urban)) contained *Cynodon dactylon* which is both clonal above- and below ground (both stolons and rhizomes are present) (Figure 5.14d).

Urban grassland fragments contained significantly higher mean percentage non-clonal species (Figure 5.14a), and significantly lower mean percentage clonal belowground species (Figure 5.14b), possibly due to their size (see Table F.2, Appendix H for complete ANOVA results). The grassland fragments in the more urbanised matrix areas (size (ha) ranging from 0.59 to 18.13) are smaller than the grassland fragments situated in rural/peri-urban matrix areas (size (ha) ranging from 10.77 to 179.41) (refer to Table 4.7 in *Chapter 4: Quantifying an urbanisation gradient*). Clonal species are less likely to persist in smaller habitat fragments (Robinson *et al.*, 1992). Species recorded in the selected grassland fragments that are characterised with belowground propagating plant organs include species belonging to the *Bulbine* and *Ledebouria* genera (see Appendix F for full species list and

corresponding plant traits). The mean percentage species that have aboveground clonal plant organs such as stolons (e.g. *Dichondra repens*, *Guilleminea densa*, and *Urochloa mosambicensis*) showed high variation in urban grassland fragments, which also had the highest mean percentage clonal aboveground species (Figure 5.14c). This may possibly be due to mowing which may encourage aboveground clonal growth (e.g. stolons) in plant species as an adaptation to the mowing management practices. Variability in mean percentage clonal above- and belowground species for rural/peri-urban and urban was small (Figure 5.14d). The only species in the study areas that possessed both stolons and rhizomes were *Cynodon dactylon* grass species. *Cynodon dactylon* was thus more abundant in grassland fragments situated in more urbanised matrix areas. This universal invasive grass has the ability to exploit resources in urban areas which may have been exposed to disturbance (Cilliers & Bredenkamp, 2000; Van Oudtshoorn, 2006).

Although some differences in plant clonality between rural/peri-urban and urban grassland fragments became evident, it cannot be said that urbanisation influences all aspects of plant species clonality in the Tlokwe Municipal area. Thompson & McCarthy (2008) found that plant species persistence in urban environments was not linked to the clonality of the species.

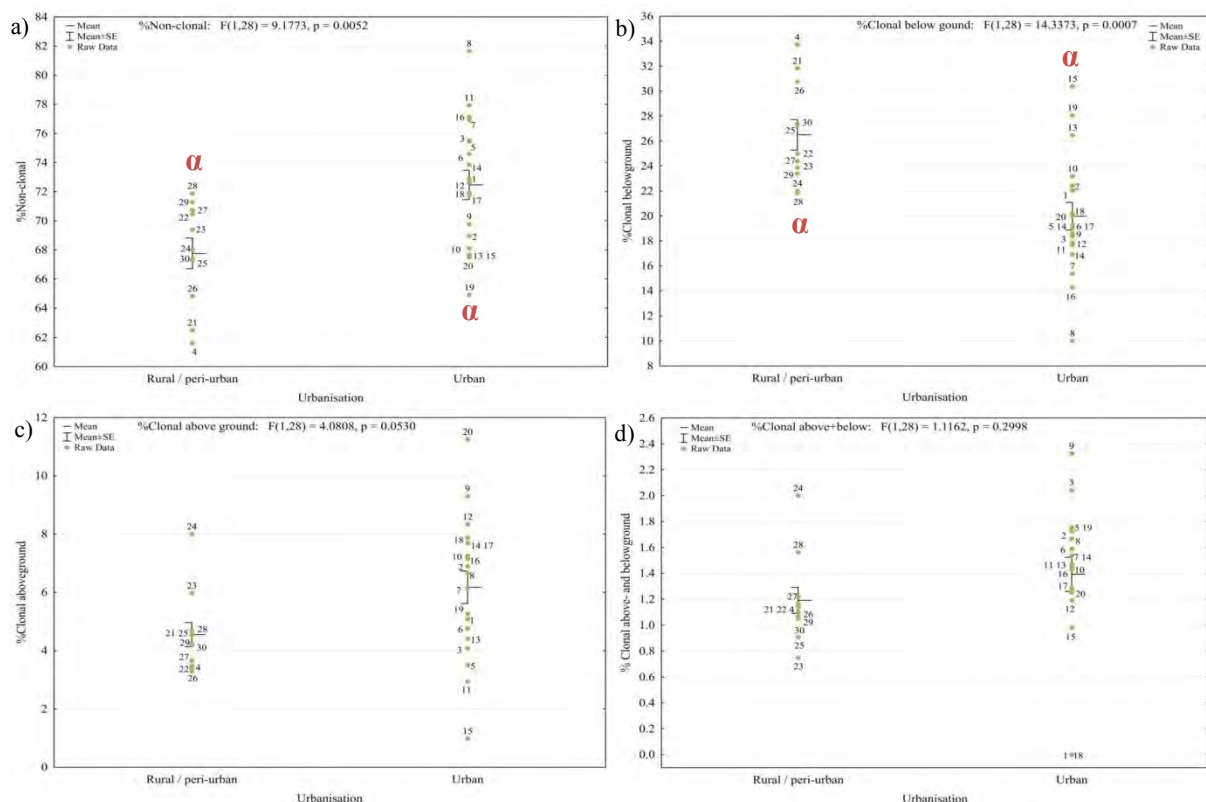


Figure 5.14: Clonality – mean percentage a) non-clonal, b) clonal belowground, c) clonal aboveground, and d) clonal above- and belowground for rural/peri-urban and urban grassland fragments. The green dots represent the percentage of each clonality type of the total species richness (raw data) for each selected grassland fragment. Symbols (α) indicate statistically significant differences between the mean percentage clonality type for rural/peri-urban and urban grassland fragments ($p < 0.05$).

6. Spinescence

The function of spines on plant species are mainly for protection against herbivores, and may even provide a mechanism to reduce the effects of drought and heat (Cornelissen *et al.*, 2003). Less than 7% of all the species in the study area had a physical defence (i.e. spines or thorns) (Table 5.8 and Figure 5.15). The species that were characterised by spines within the study area belonged to the genera *Acacia*, *Asparagus*, *Berkheya*, and *Ziziphus* amongst others. Rural/peri-urban grassland fragments had the highest mean percentage species possessing spines (Figure 5.15), mainly due to the presence of many spiny forb species such as *Aloe greatheidii*, *Berkheya radula*, and *Barleria macrostegia*. The proportion species possessing spines in grassland fragments in the urban landscape matrix showed the most variation. Species in urban areas may possess spines as an adaptation to heat stress due to the urban heat island effect (Oke, 1982). The mean percentage spines of the rural/peri-urban and urban grassland remnants did not show any statistically significant differences (see Table H.2, Appendix H for complete ANOVA results).

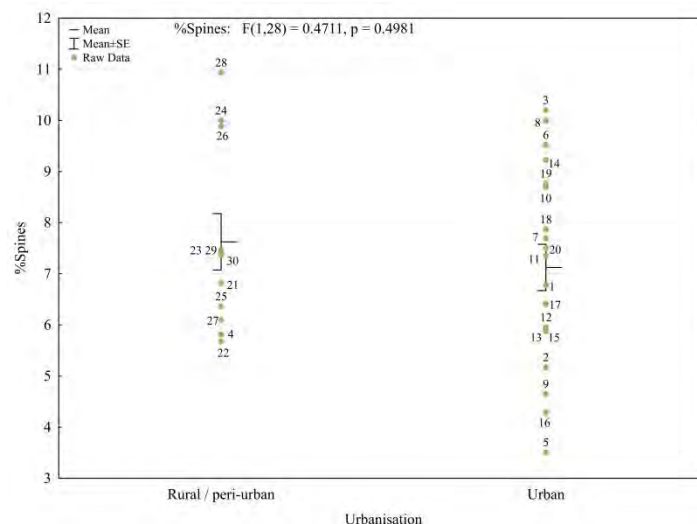


Figure 5.15: Spinescence – mean percentage plant species with spines for rural/peri-urban and urban grassland fragments. The green dots represent the percentage species possessing spines of the total species richness (raw data) for each selected grassland fragment.

7. Leaf periodicity

Leaf periodicity may reflect the growth rate, defence mechanisms, or nutrient conservation approaches of a species (Cornelissen *et al.*, 2003). The vegetation recorded in the Tlokwe Municipal area was primarily deciduous (Table 5.8 and Figure 5.16a) possibly to conserve nutrients and survive during the cold dry winters of this region (Mucina & Rutherford, 2006). Rural/peri-urban and urban grassland remnants had the same mean percentage deciduous, whilst urban grassland fragments had the lowest mean percentage evergreen (Figure 5.16b), and significantly higher mean percentage semi-evergreen (as indicated by similar symbols in Figure 5.16c; see Table H.2, Appendix H for complete

ANOVA results). Evergreen species recorded in the study area were mostly forbs such as *Aloe greatheadii*, *Cucumis zeyheri*, and *Berkheya* species, whilst most of the forbs documented in urban grassland fragments was semi-evergreen (Figure 5.16c) (e.g. *Anthospermum rigidum* and *Verbena officinalis*)

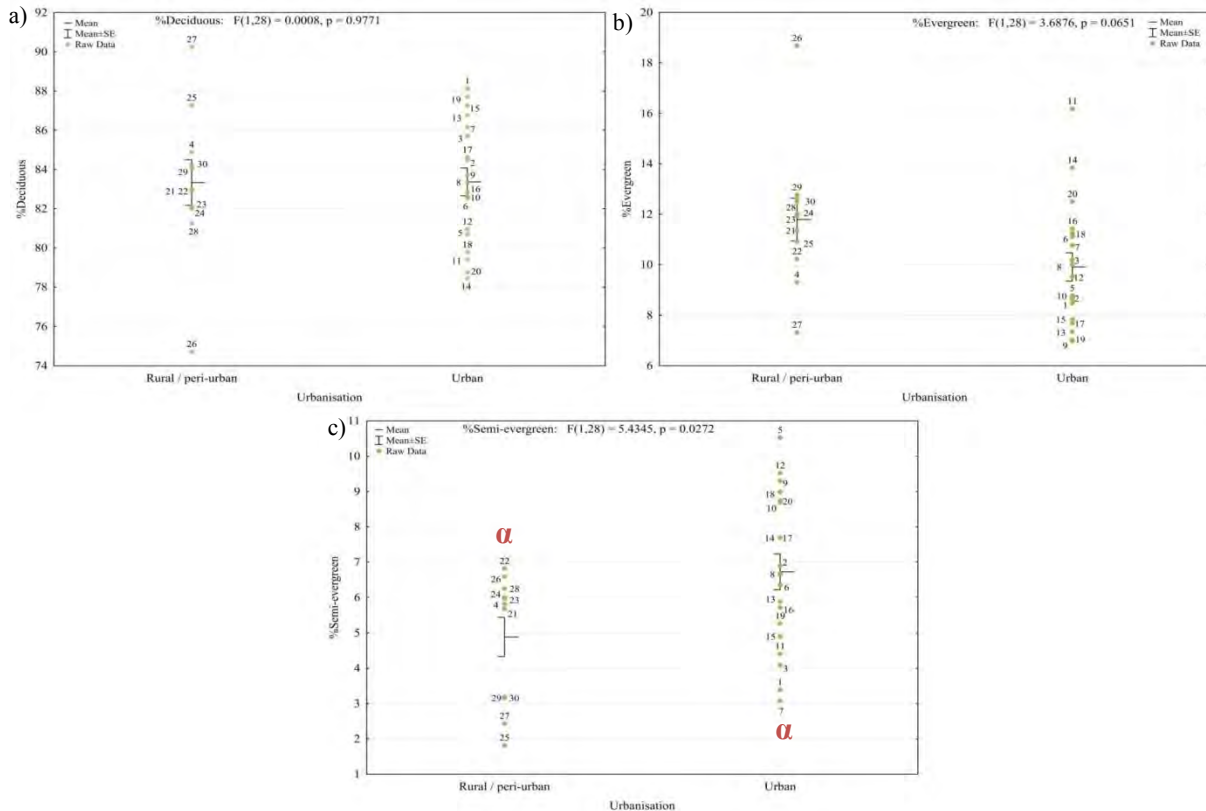


Figure 5.16: Leaf periodicity – mean percentage a) deciduous, b) evergreen, and c) semi-evergreen species for rural/peri-urban and urban grassland fragments. The green dots represent the percentage of each clonality type of the total species richness (raw data) for each selected grassland fragment. Symbols (α) indicate statistically significant differences between the mean percentage specific leaf periodicity for rural/peri-urban and urban grassland fragments ($p < 0.05$).

8. Primary dispersal mode

Rural/peri-urban grassland fragments had slightly lower mean percentage species that were characterised by unassisted seed dispersal (no morphological adaptation, e.g. hairs, wings, fleshy fruits (Leishman & Westoby, 1994)) (Figure 5.17a). The plant species characterised by unassisted seed dispersal were predominantly forbs (such as the *Indigofera* species). The most common dispersal mode for plants within the selected grassland fragments were unassisted dispersal and wind dispersal (Table 5.8 and Figure 5.17a and b). The abundance of grasses within the sites ascribes to wind as the dominant dispersal mode within the study area. The seeds of some plants were also adapted to be transported internally (e.g. the red berries of *Asparagus laricinus*) or externally (e.g. the prickly fruit of *Crabbea* species) by animals. Grasses (Cheplick, 1998) and some other species such as the exotic vine *Araujia sericifera*, and species belonging to the genera *Berkheya* and *Vernonia* are

predominantly dispersed by wind (see Appendix F for full species list and corresponding plant traits). The mean percentage wind dispersal of plant species in rural/peri-urban grassland fragments were higher (Figure 5.17b). Knapp *et al.* (2008) also found that urban areas were associated wind dispersed species. The mean percentage internal animal dispersal (by birds or herbivores) of rural/peri-urban and urban grassland remnants showed no significant variation (Figure 5.17c).

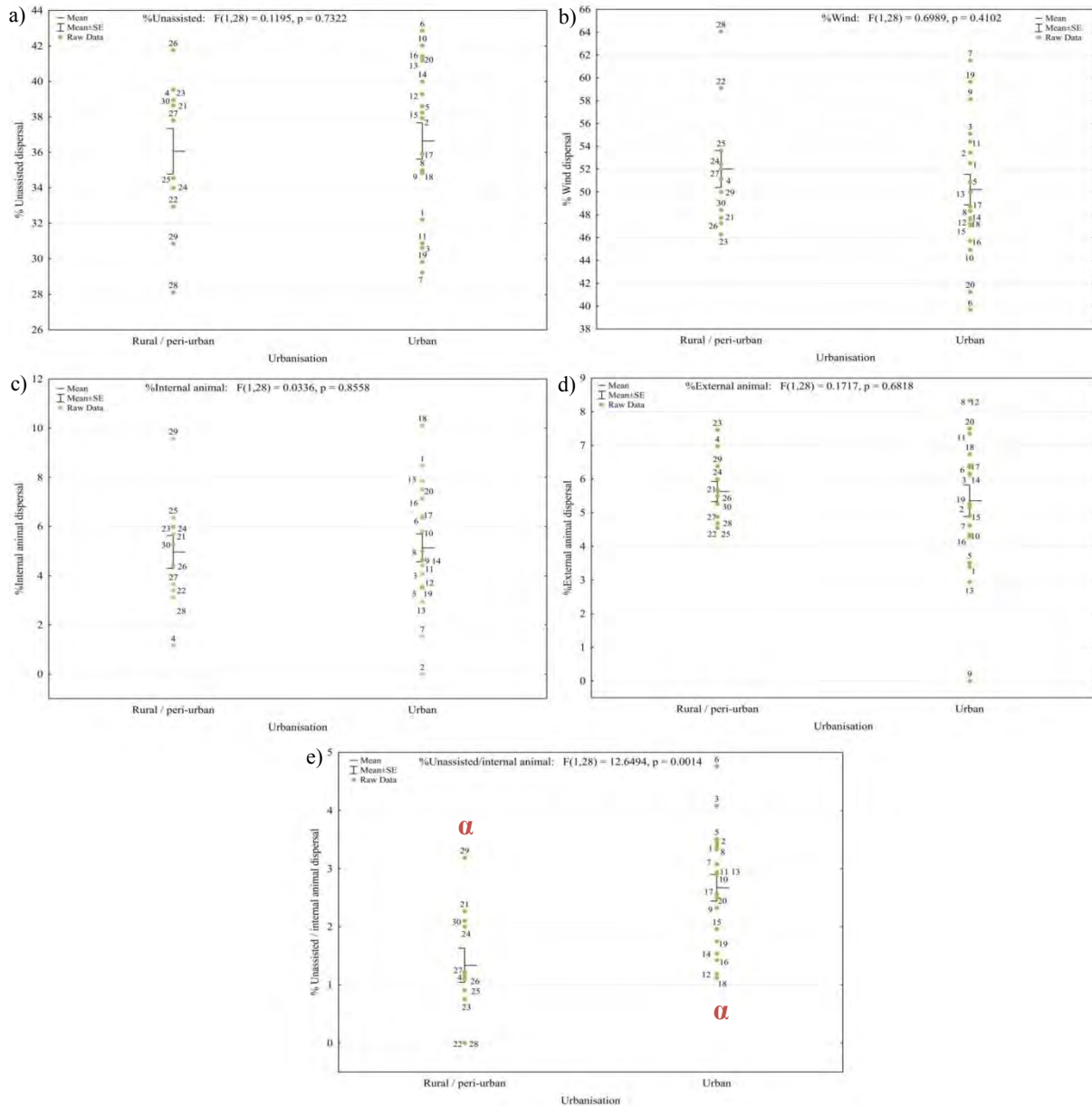


Figure 5.17: Dispersal mode – mean percentage a) unassisted, b) wind, and c) internal animal, d) external animal, and e) unassisted / internal animal dispersed plant species for rural/peri-urban and urban grassland fragments. The green dots represent the percentage of each dispersal type of the total species richness (raw data) for each selected grassland fragment. Symbols (α) indicate statistically significant differences between the mean percentage specific dispersal mode for rural/peri-urban and urban grassland fragments ($p < 0.05$).

Species that were characterised by internal animal transportation of seeds belong, amongst others, to *Asparagus*, *Celtis*, and *Ziziphus* genera. Grassland fragments in urban surroundings showed slightly

lower mean percentage external animal seed dispersal (Figure 5.17d), which is not consistent with the results of Knapp *et al.* (2008) who found that urban areas were more associated with plant dispersed by animals. Seeds or fruits of plant species may adhere to insects and animals with hooks, spines or barbs (Leishman & Westoby, 1994), and include some grass species such as *Aristida* species and forbs such as *Crabbea* species and *Guilleminea densa*. Species that have no morphological adaptations for dispersal, but have a chance to be dispersed by animals after ingestion belong to the *Acacia* (shrubs) and *Albuca* (forbs) genera, which were significantly more abundant in the urban landscape (as indicated by similar symbols in Figure 5.17e). See Table H.2, Appendix H for complete ANOVA results.

9. Primary pollination vector

Biotic pollination (by insects, birds, and animals) was the main pollination vector in the study area. Rural/peri-urban and urban grassland fragments were characterised by the same mean percentage biotic pollination (and therefore also the same mean percentage abiotic pollination) (Figure 5.18). This indicated that urbanisation does not determine the primary pollination vector for plant species in selected grassland fragments in the Tlokwe Municipal area. These results were contradictory to the findings of Knapp *et al.* (2008) who found that urbanised areas in Germany contained more plant species pollinated by wind (abiotic).

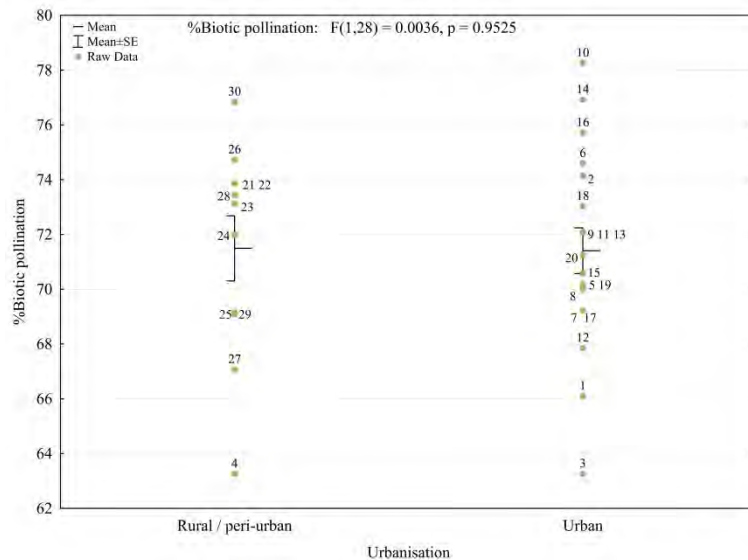


Figure 5.18: Pollination vector – mean percentage biotic pollination of plant species for rural/peri-urban and urban grassland fragments. The green dots represent the percentage biotic pollination of the total species richness (raw data) for each selected grassland fragment.

5.3.2.2 Quantification of plant functional diversity

The mean, median, minimum, and maximum values for available functional diversity indices are listed in Table 5.12. These values indicate the range of the functional diversity measures calculated for rural/peri-urban and urban selected grassland fragments in the Tlokwe Municipal area. The first consideration of the values in Table 5.12 indicated that the functional diversity indices did not vary much between rural/peri-urban and urban.

Table 5.12: Range of values for the various functional diversity indices calculated for rural/peri-urban and urban grassland fragments in the study area.

Functional diversity index	Mean	Median	Minimum	Maximum
Rural/peri-urban				
Functional richness (FRic)	7.97	8.2	5.18	10.19
Functional evenness (FEve)	0.48	0.48	0.44	0.54
Functional divergence (FDiv)	0.92	0.92	0.87	0.95
Functional dispersion (FDis)	1.16	1.15	0.92	1.4
Functional specialisation (FSpe)	1.82	1.82	1.76	1.92
Urban				
Functional richness (FRic)	7.62	7.48	5.32	10.63
Functional evenness (FEve)	0.53	0.53	0.47	0.62
Functional divergence (FDiv)	0.91	0.93	0.77	0.95
Functional dispersion (FDis)	1.18	1.21	0.87	1.53
Functional specialisation (FSpe)	1.8	1.78	1.68	1.93

Significant correlations were found between PURBLC, ED, PGRALC, and DESPEOP in the matrix surrounding selected grassland fragments and the functional evenness (FEve) functional diversity index for the grassland remnants (Table 5.13), but for none of the other functional diversity indices. This implies that FEve increased with higher percentage impervious surfaces, fragmentation, and human inhabitation and lower Rand Highveld Grassland habitat in the surrounding matrix. Biswas & Malik (2010) and Pakeman (2011) found that functional evenness may be higher at increased disturbance intensities. More disturbed plant communities contain species with similar abundances that are distributed regularly along functional trait gradients (Pakeman, 2011). This indicates that at lower levels of disturbance competition may shape community structure, and at higher disturbance intensities competition between species does not determine community structure (Pakeman, 2011). Refer to Table G.3, Appendix G for full multiple regression analysis results.

Table 5.13: Correlation matrix and multiple regression analysis results for functional diversity indices with the selected four urbanisation measures (representing pattern/process associated with urbanisation). Only significant correlations ($p < 0.05$) are indicated. Correlation directions are indicated in grey, moderate linear relationships ($0.1 < r^2 < 0.25$) in orange, and strong linear relationships ($r^2 \geq 0.25$) in red.

	PURBLC % Impervious surfaces	ED Fragmentation	PGRALC Habitat loss	DENSPEOP Urbanisation
FEve	+ 0.1785	+ 0.168569	- 0.314041	+ 0.227746

Differences in the various functional diversity indices between rural/peri-urban and urban areas will now be discussed.

1. *Functional richness (FRic)*

Sites 18 (urban; FRic = 10.63) and 23 (rural/peri-urban; FRic = 10.19) had the highest functional richness (Figure 5.19). Site 28 (rural/peri-urban) is the only selected grassland fragment that did not contain a keystone species (for a list of keystone species refer to Table 5.9), which may account for lower functional richness, as a functionally distinct species would have increased the Convex Hull volume of the trait space. High FRic values indicates that a site contains species with a combination of more extreme trait values and this fills a larger area in the hypothetical trait niche (Casanoves *et al.*, 2008). Rural/peri-urban grassland fragments had marginally higher mean FRic (Figure 5.19). High functional richness (diversity of functional traits) may provide a system with higher resistance to disturbance and invasion by alien species (Diaz & Cabido, 2001; Dukes, 2001; Elton, 1958; Pimm, 1984), as may be confirmed by the lower mean percentage exotic species in rural/peri-urban grassland fragments (16.74%) vs. the mean percentage exotic species of urban grassland remnants (29.46%). There were, however, no statistically significant differences between the mean FRic indices for the rural/peri-urban and urban grassland remnants (see Table H.3, Appendix H for complete ANOVA results).

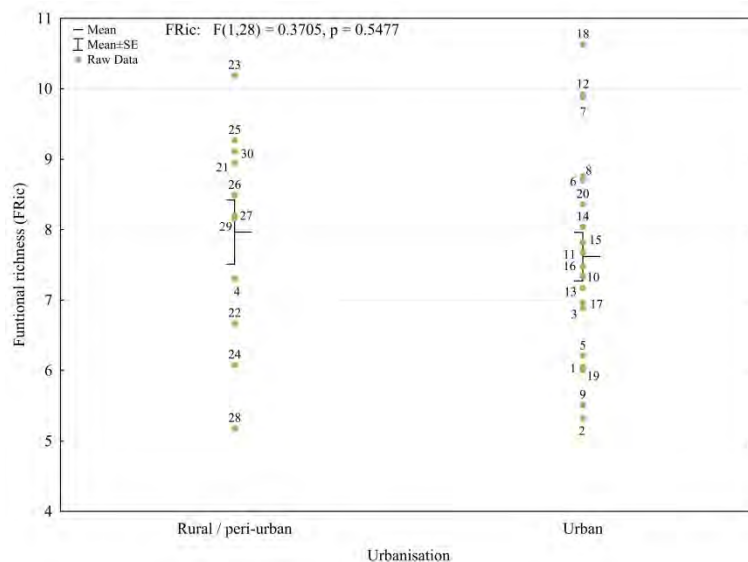


Figure 5.19: Mean functional richness (FRic) (Villéger *et al.*, 2008) functional diversity index for rural/peri-urban and urban grassland fragments. The green dots represent the FRic value (raw data) for each selected grassland fragment.

2. *Functional evenness (FEve)*

The plant species of urban sites 3 (FEve = 0.61) and 7 (FEve = 0.62) were most evenly distributed within the trait niche, whilst sites 4, 22 and 25 (rural/peri-urban) had the most irregular distribution of

species within the trait niche ($FEve = 0.44$), (Figure 5.20). Grassland fragments in more urbanised matrix areas had significantly higher mean $FEve$ values (as indicated by symbols in Figure 5.20; see Table H.3, Appendix H for complete ANOVA results). The implication of lower functional evenness is that all resources are not necessarily utilised by the species in the functional niche, resulting in underutilised areas that provide opportunity for biological invasion (Mason *et al.*, 2005; Pokorney *et al.*, 2005). Rural/peri-urban grassland fragments may be expected to be more vulnerable to exotic invasions, whilst the high $FEve$ of urban grassland remnants (Figure 5.20) may be ascribed to the possibility that exotic species are already occupying a great volume of trait space. The selected grassland fragments in urban surroundings contain a mean percentage exotic species of 29.46%. The exotic species may occupy a volume in the functional trait space that was previously underutilised by native species, and therefore exotic species appear to be more evenly distributed within the trait niche. Functional evenness may be higher at increased disturbance intensities, that is: more disturbed plant communities contain species with similar abundances that are distributed regularly along functional trait gradients (Biswas & Malik, 2010; Pakeman, 2011).

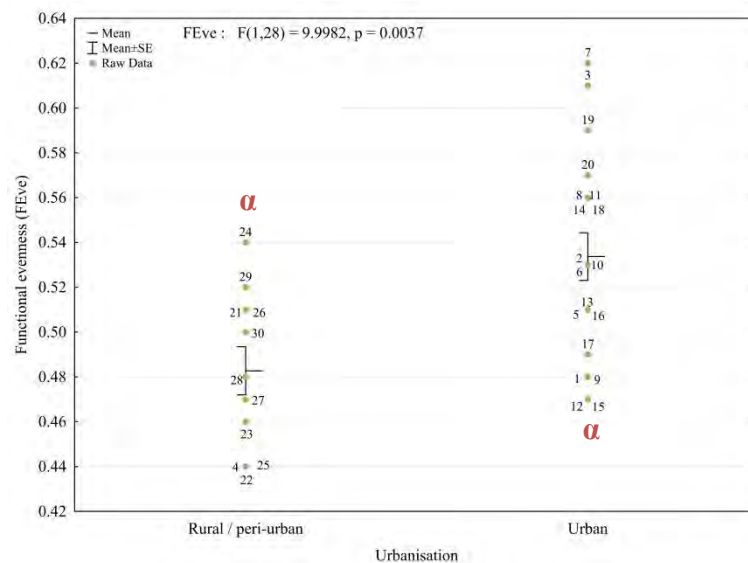


Figure 5.20: Mean functional evenness ($FEve$) (Villéger *et al.*, 2008) functional diversity index for rural/peri-urban and urban grassland fragments. The green dots represent the $FEve$ value (raw data) for each selected grassland fragment. Symbols (α) indicate statistically significant differences between the mean $FEve$ index for rural/peri-urban and urban grassland fragments ($p < 0.05$).

3. Functional divergence ($FDiv$)

There was little variability between the functional divergence ($FDiv$) index values of the selected grassland fragments (range $FDiv = 0.77 - 0.95$). Most sites had high functional divergence ($FDiv \geq 0.9$), whilst urban sites 1 ($FDiv = 0.86$), 10 ($FDiv = 0.77$), 12 ($FDiv = 0.82$) and rural/peri-urban site 23 ($FDiv = 0.87$) had the lowest $FDiv$ indices (Figure 5.21). Urban grassland fragments marginally had the lowest mean $FDiv$ due to the lowest $FDiv$ index values for sites 10 and 12 (Figure 5.21),

where resource competition between species should be expected to be high, shaping the plant community (Mason *et al.*, 2005). Functional divergence reflects the degree of niche differentiation and thus also the degree to which species must compete for resources (Mason *et al.*, 2003 & 2005). High functional divergence will indicate low resource competition between the most abundant species, thus the species that are present are functionally equipped to utilise a resource stratum that is unused / underutilised by another species (Mason *et al.*, 2003 & 2005). The mean FDiv of rural/peri-urban and urban selected grassland fragments did, however, not differ significantly (see Table H.3, Appendix H for complete ANOVA results).

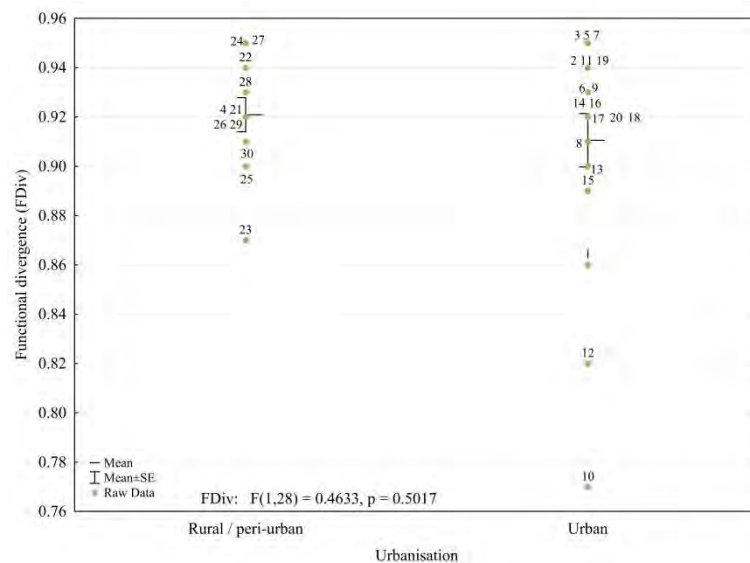


Figure 5.21: Mean functional divergence (FDiv) (Villéger *et al.*, 2008) functional diversity index for rural/peri-urban and urban grassland fragments. The green dots represent the FDiv value (raw data) for each selected grassland fragment.

4. Functional dispersion (FDis)

Site 9 (urban) had the highest functional dispersion (FDis = 1.53), whilst sites 2, and 3, 7, and 19 (urban), and 24 (rural/peri-urban) had the lowest functional dispersal with the FDis values ranging between 0.87 and 0.92 (Figure 5.22). Rural/peri-urban grassland fragments had slightly lower mean FDis (Figure 5.22). Lower functional dispersion indicates that the functional composition of a system contains species that are more functionally similar (Laliberté *et al.*, 2010), thus high FDis indicates that species that are functionally unique, and also not that abundant (possible keystone species), are present. Urban grassland remnants showed the most variability in FDis, containing grassland fragments with the highest (site 9) and lowest (site 19) FDis values. In site 9 species are scattered farther away from the centroid of all species and are functionally less similar than that of site 19 where species are closer together in the trait space (Laliberté, 2011). No significant differences were

evident between the mean FDis indices for rural/peri-urban and urban grassland fragments (see Table H.3, Appendix H for complete ANOVA results).

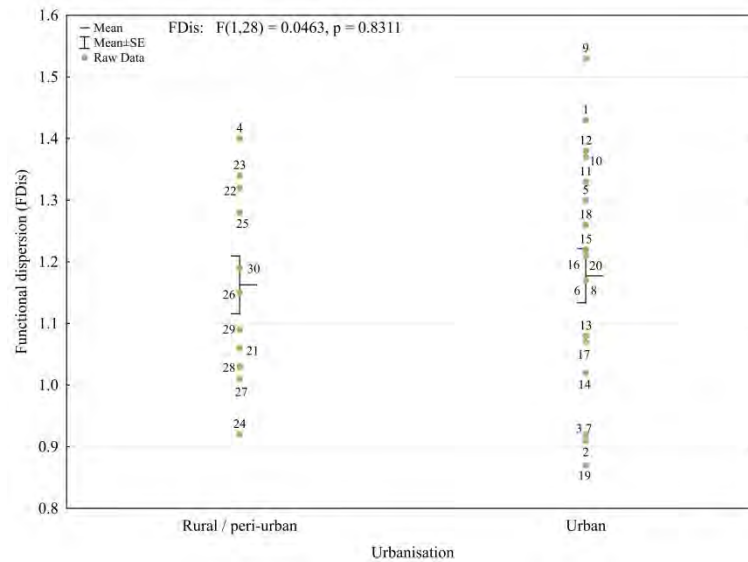


Figure 5.22: Mean functional dispersion (FDis) (Laliberté & Legendre, 2010) functional diversity index for rural/peri-urban and urban grassland fragments. The green dots represent the FDis value (raw data) for each selected grassland fragment.

5. *Functional specialisation (FSpe)*

Urban grassland fragments had the lowest mean FSpe (Figure 5.23). The functional specialisation index values of the selected grassland fragments did not show much variation between the sites, ranging from FSpe = 1.68 (site 1; urban) to FSpe = 1.93 (site 10; urban) (Figure 5.23) which indicates that there are not certain selected grassland fragments that contain one or more species that have very specialised functions. This may be due to the nature of the traits selected. Almost every site contains species that possess most combinations of traits. If more specialised functions (for example chemical traits such as nitrogen concentration (Cornelissen, 2003; Garnier *et al*, 2007)) were considered, the functional specialisation of the selected grassland fragments might have been higher and more varying. Such traits were not included for the purpose of this study because the traits had to be morphological, and therefore quick and easy to observe and measure. The mean FSpe indices for rural/peri-urban and urban grassland remnants did not differ significantly (see Table H.3, Appendix H for complete ANOVA results).

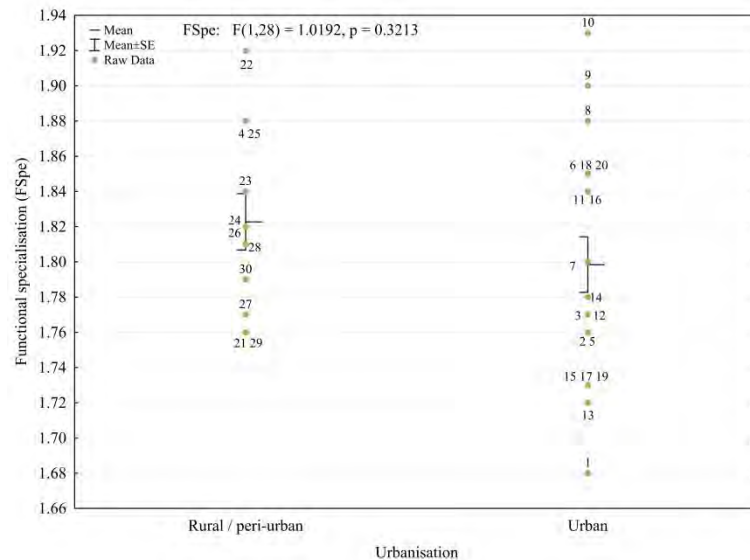


Figure 5.23: Mean functional specialisation (FSpe) (Villéger *et al.*, 2010) functional diversity index for rural/peri-urban and urban grassland fragments. The green dots represent the FSpe value (raw data) for each selected grassland fragment.

5.4 Summary and conclusions

One of the main concerns for biodiversity conservation is the invasion of exotic species. Many studies (Diaz & Cabido, 2001; Dukes, 2001; Elton, 1958; Pimm, 1984; Pokorny *et al.*, 2005) have shown that ecosystems that do not have high functional diversity are vulnerable to biotic invasions as there is a part of the trait niche that is underutilised or not utilised at all, providing a resource strata that may be exploited by an exotic species possessing the functional characteristics to do so (Lyons & Schwartz, 2001; Pokorny *et al.*, 2005). The aim of this chapter was to record the plant species existing in the selected grassland fragments within the Tlokwe Municipal area. Possible patterns of plant species richness and composition, and plant functional diversity across the urbanisation gradient (determined in *Chapter 4*) were also explored, and applied in determining whether the intensity of urbanisation has an effect on plant species- and functional diversity.

The results showed that the plant species richness, Shannon's diversity index and Pielou's evenness index varied greatly for the selected grassland fragments within the Tlokwe Municipal area. Urban grassland remnants had lower mean plant species richness, Shannon species diversity (significantly), and Pielou species evenness than rural/peri-urban grassland fragments. Usually urban areas are characterised by higher plant species richness (Deutschewitz *et al.*, 2003; Klotz, 1990; McKinney, 2002; Pyšek & Pyšek, 1990; Rebele, 1994; Stadler, *et al.*, 2000; Thuiller *et al.*, 2006), but the findings in this study is consistent with the results from Potchefstroom's neighbouring town Klerksdorp (Du Toit, 2009) where plant species richness was lower in urban areas than in rural areas. Therefore, the first hypothesis for this chapter that selected grassland fragments situated in matrix areas exposed to increased human impacts will have higher plant species diversity is not supported.

The urban grassland fragments had significantly higher mean percentage plant exotic species. Percentage native species correlated with PURBLC, ED, PGRALC, and DENSPEOP, implying that native species richness declined in grassland fragments situated in more urbanised and fragmented matrix areas with less Rand Highveld Grassland habitat. This was expected as urban areas are often characterised by many exotic invasions (Ehrenfeld *et al.*, 2001; Pickett *et al.*, 2001), and supports the second hypothesis for this chapter: that selected grassland fragments situated in matrix areas exposed to increased human impacts will contain more exotic species.

Both exotic and native keystone species were identified from all the species recorded during this study. Exotic keystone species (e.g. *Araujia sericifera*, *Melia azedarach*, and *Pinus* species), due to their unique suite of functional traits, have the ability to utilise resources in an ecosystem that are underutilised by other species, thus establish and persist as biotic invaders, possibly become invasive and eventually alter the functioning of these systems. *A. sericifera* (category 1 weed), *M. azedarach* (category 3 invader), and *Pinus* species (category 2 invader) are presently declared weeds and invaders in South Africa (Conservation of Agricultural Resources Act (43 of 1984); Henderson, 2001). Native keystone species (e.g. *Gomphocarpus fruticosus*, *Menodora africana*, and *Senecio venosus*) must be preserved as the loss of one of these species from the functional niche possibly provides opportunity for exotic species that can access the same resources, to establish.

There are several exotic species which are functionally similar to native species, which indicates that native and exotic species in the studied grasslands are in competition for the same resource strata (Funk *et al.*, 2008; Mason *et al.*, 2005). The questions that may arise from these results are:

- How long will the co-existence of such species persist before some of them is eradicated?
- Will it be the native or the exotic species that prevail?
- Which environmental factors contribute to the co-existence, persistence or possible eventual eradication of one of the two competing species?

Graminoids and forbs were the dominant growth forms within the Tlokwe Municipal area. Selected urban grassland fragments had less forbs, shrubs, and succulents, possibly due to the removal of aerial meristems by mowing which prevents the establishment and persistence of such growth forms (Flynn *et al.*, 2004). Trees and phanerophytes were more abundant in the urban areas possibly due to fire in rural areas (Bond *et al.*, 2003) and planting of trees in urban areas for aesthetic reasons. Hemicryptophytes and chamaephytes were the most abundant life forms in the study area. Geophytes correlated with PURBLC, ED, PGRALC, and DENSPEOP, and therefore seems to be sensitive to disturbances associated with urbanisation. Geophytes have also been found in other studies to be threatened by extinction in urbanised areas (Čepelová & Münzbergová, 2012; Williams *et al.*, 2005). Grassland remnants within the study area which were situated in the more urbanised matrix areas

were characterised by more annual plant species (therophytes). Annual plant species are often associated with built-up areas (Čepelová & Münzbergová, 2012; Kleyer, 1999; Pellissier *et al.*, 2008). Non-clonal plant species were most abundant in the Tlokwe Municipal area, with the highest percentage non-clonal species occurring in smaller grassland fragments situated in more urbanised areas. Clonal species will less likely persist in smaller habitat fragments (Robinson *et al.*, 1992). Less than 7% of all the species in the study area possessed spines. Species in urban areas may possess spines as an adaptation to heat stress (Cornelissen *et al.*, 2003) caused by the urban heat island effect (Oke, 1982). Most of the plant species recorded in the study area had deciduous leaves, possibly to conserve nutrients and survive during the cold dry winters of the Rand Highveld Grassland (Mucina & Rutherford, 2006). The seeds of plant species recorded in the Tlokwe Municipal area were predominantly dispersed by wind. Less than 27% of the plant species recorded undergone abiotic pollinations (e.g. wind pollination). Rural/peri-urban and urban grassland fragments had the same proportion species characterised by biotic/abiotic pollination, indicating that urbanisation does not affect the primary pollination vector for plant species in the selected grassland remnants.

Urban grassland remnants generally showed great variation in plant functional composition, often containing a suite of species that had the most and least abundance of certain plant traits. This may be ascribed to the habitat heterogeneity of urban areas (Pickett *et al.*, 2011; Rebele, 1994; Savard *et al.*, 2000). Although some statistically significant differences between rural/peri-urban and urban grassland fragments became evident, it cannot be confirmed that the degree of urbanisation / human impact in the matrix surrounding grassland fragments determines the occurrence or persistence of the types of plant species possessing certain functional attributes, based on the type of functional traits used.

The most recent development in functional diversity research and the quantification of function diversity is the use of functional diversity indices or metrics. These indices usually indicate the extent and manner species fill a hypothetical functional niche space (Schleuter *et al.*, 2010), and have been used in several functional diversity studies (Baraloto *et al.*, 2012; Barragán *et al.*, 2011; Laliberté, 2011; Lambdon *et al.*, 2008; Lepš *et al.*, 2006; Mouillot, *et al.*, 2011; Pakeman, 2011; Villéger *et al.*, 2010). The functional diversity index values did not show much variation between rural/peri-urban and urban grassland fragments. This may be due to the nature of the traits selected in that every site may contain species that possess most combinations of traits. Rural/peri-urban grassland fragments had slightly higher functional richness (FRic) than urban grassland remnants (no significant difference). High functional richness (FRic) may be able to provide a system with higher resistance to disturbance and invasion by alien species (Diaz & Cabido, 2001; Dukes, 2001; Elton, 1958; Pimm, 1984). Low functional evenness (FEve) implies that all resources are not necessarily utilised by the species in the functional niche, resulting in underutilised areas that provide opportunity for biological invasion (Mason *et al.*, 2005; Pokorney *et al.*, 2005). Grassland fragments in more urbanised matrix

areas had significantly higher mean FEve values. The FEve index also showed a significant positive correlation with PURBLC, ED, PGRALC, and DENSPEOP in the matrix area surrounding the grassland fragments, which implies that FEve is increased in grassland remnants situated in urbanised areas. Functional evenness has been found to be higher at increased disturbance intensities (Biswas & Malik, 2010; Pakeman, 2011). Urban grassland fragments marginally had the lowest mean functional divergence (FDiv) due to the very low FDiv index values for sites 10 and 12 where resource competition between species should be expected to be high, shaping the plant community (Mason *et al.*, 2005). High functional divergence indicates low resource competition between the most abundant species, thus the species that are present are functionally equipped to utilise a resource stratum that is unused / underutilised by another species (Mason *et al.*, 2003 & 2005). Grassland fragments in the rural/peri-urban landscape matrix had the lowest mean functional dispersion (FDis). Lower functional dispersion indicates that the functional composition of a system contains functionally similar species (Laliberté *et al.*, 2010). The little variability between the mean functional specialisation (FSpe) index values for the rural/peri-urban and urban grassland remnants indicated that no selected grassland fragment contained species that have very specialised functions. This may be a result of the traits selected for the purpose of this study. Almost every site contains species that possess most combinations of traits. Duncan *et al.* (2011) found in a meta-analysis of eleven cities in three continents (North America, Asia, and Australia) that urbanisation did not lead to the extinction of native plants with certain traits. This may be a reason for limited variability in plant functional traits and functional diversity indices for urban and rural/peri-urban grassland fragments in this study. It cannot be expected that species possessing certain traits have undergone extinction in the urban areas, but continue to exist in the rural/peri-urban areas.

The third hypothesis for this chapter states that selected grassland fragments situated in matrix areas exposed to increased human impacts will have higher plant functional diversity. Only the FEve and FDis values for urban grassland fragments were higher than that of rural/peri-urban grassland fragments, whilst FRic, FDiv, and FSpe were lower for urban than rural/peri-urban grassland fragments. None of these differences in rural/peri-urban and urban grassland fragments were statistically significant (except for FEve), and therefore the third hypothesis is not supported. The degree of urbanisation in the matrix area surrounding grassland fragments did not determine the plant functional diversity (based on the selected traits) in the Tlokwe Municipal area.

In this chapter the aim was to present the plant diversity and plant functional diversity data obtained for the selected grassland fragments in the Tlokwe Municipal area, and to explore possible patterns of plant species composition and plant functional diversity across an urbanisation gradient. This was applied in determining whether the intensity of urbanisation has an effect on plant species- and functional diversity.

5.5 References

- Aronson, M.F.J., Handel, S.N. & Clemants, S.E. 2007. Fruit type, life form and origin determine the success of woody plant invaders in an urban landscape. *Biological Invasions*, 9(4): 465-475.
- Baraloto, C., Hérault, B., Paine, C.E.T., Massot, H., Blanc, L., Bonal, D., Molino, J.-F., Nicolini, E.A. & Sabatier, D. 2012. Contrasting taxonomic and functional responses of a tropical tree community to selective logging. *Journal of Applied Ecology*, 49(4): 861-870.
- Barragán, F., Moreno, C.E., Escobar, F., Halffter, G. & Navarrete, D. 2011. Negative impacts of human land use on dung beetle functional diversity. *PLoS ONE*, 6(3): 1-8.
- Basilevsky, A. 1994. Statistical factor analysis and related methods, theory and applications. NY: John Wiley & Sons.
- Begon, M., Townsend, C.R. & Harper, J.L. 2006. Ecology: from individuals to ecosystems. 4th ed. Blackwell Publishing.
- Bellwood, D.R., Wainwright, P.C., Fulton, C.J. & Hoey, A.S. 2006. Functional versatility supports coral reef biodiversity. *Proceedings: Biological Sciences*, 273(1582): 101-107.
- Biswas, S.R. & Malik, A.U. 2010. Disturbance effects on species diversity and functional diversity in riparian and upland plant communities. *Ecology*, 91(1): 28-35.
- Bond, W.J. 1993. Keystone species. (In Schulze, E.-D. & Mooney, H.A., eds. 1993. Biodiversity and ecosystem function. *Ecological Studies* 99, Berlin: Springer-Verlag. p. 237-253).
- Bond, W.J., Midgley, G.F. & Woodward, F.I. 2003. What controls South African vegetation – climate or fire? *South African Journal of Botany*, 69(1): 79-91.
- Botta-Dukát, Z. 2005. Rao's quadratic entropy as a measure of functional diversity based on multiple traits. *Journal of Vegetation Science*, 16: 533-540.
- Brase, C.H. & Brase, C.P. 1999. Understandable statistics: concepts and methods. 6th ed. Boston: Houghton Mifflin Company
- Casanoves, F. 2012a. FDiversity software: categorical traits [e-mail]. 3 Sept. 2012.
- Casanoves, F. 2012b. Transformation on categorical trait data set [e-mail]. 16 Nov. 2012.
- Casanoves, F., Di Rienzo, J.A. & Pla, L. 2008. User Manual FDiversity: Statistical software for the analysis of functional diversity. 1st ed.

- Casanoves, F., Pla, L., Di Rienzo, J.A. & Diaz, S. 2010. FDiversity: a software package for the integrated analysis of functional diversity. *Methods in Ecology and Evolution*, 2: 233-237.
- Čepelová, B. & Münzbergová, Z. 2012. Factors determining the plant species diversity and species composition in a suburban landscape. *Landscape and Urban Planning*, 106(4): 336-346.
- Chapin, F.S., III, Lubchenco, J. & Reynolds, H.L. 1995. Biodiversity effects on patterns and processes of communities and ecosystems. (In Watson, R.T. *et al.*, eds. Global biodiversity assessment. Cambridge: Cambridge University Press. p.289-301.
- Chapin, F.S., III, Matson, P.A. & Mooney, H.A. 2002. Principles of terrestrial ecosystem ecology. Springer-Verlag.
- Chapin, F.S., III, Sala, O.E., Burke, I.C., Grime, J.P., Hooper, D.U., Laurenroth, W.K., Lombard, A., Mooney, H.A., Mosier, A.R., Naeem, S., Pacala, S.W., Roy, J., Steffen, W.L. & Tilman, D. 1998. Ecosystem consequences of changing biodiversity. *BioScience*, 48(1): 45-52.
- Chapin, F.S., III, Zavaleta, E.S., Eviner, V.T., Naylor, R.L., Vitousek, P.M., Reynolds, H.H., Hooper, D.U., Lavorel, S., Sala, O.E., Hobbie, S.E., Mack, M.C. & Diaz, S. 2000. Consequences of changing biodiversity. *Nature*, 405: 234-242.
- Cheplick, G.P. 1998. Seed dispersal and seedling establishment in grass populations. (In Cheplick, G.P., ed. Population biology of grasses. Cambridge: Cambridge University Press. p.84-105.)
- Cilliers, S.S. & Bredenkamp, G.J. 2000. Vegetation of road verges on an urbanisation gradient in Potchefstroom, South Africa. *Landscape and Urban Planning*, 46: 217-239.
- Cilliers, S.S., Williams, N.S.G., & Barnard, F.J. 2008. Patterns of exotic plant invasions in fragmented urban and rural grasslands across continents. *Landscape Ecology*, 23: 1243–1256.
- Conservation of Agricultural Resources Act **see** South Africa.
- Cornelissen, J.H.C., Lavorel, S., Garnier, E., Diaz, S., Buchmann, N., Gurvich, D.E., Reich, P.B., Ter Steege, H., Morgan, H.D., Van der Heijden, M.G.A., Pausas, J.G. & Poorter, H. 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany*, 61: 335-380.
- Cornwell, W.K., Schwilk, D.W. & Ackerley, D.D. 2006. A trait-based test for habitat filtering: convex hull volume. *Ecology*, 87: 1465-1471.
- Dethier, M.N., Graham, E.S., Cohen, S. & Tear, L.M. 1993. Visual versus random-point percent cover estimations: „objective“ is not always better. *Marine Ecology Progress Series*, 96: 93-100.

- Deuschewitz, K., Lausch, A., Kühn, I. & Klotz, S. Native and alien plant species richness in relation to spatial heterogeneity on a regional scale in Germany. *Global Ecology and Biogeography*, 12: 299-311.
- Di Rienzo J.A., Casanoves F., Balzarini M.G., Gonzalez L., Tablada M., Robledo C.W. 2012. InfoStat versión 2012. Grupo InfoStat, FCA, Universidad Nacional de Córdoba, Argentina. [Web:] <http://www.infostat.com.ar>. Date of access: 24 Nov. 2012.
- Díaz, S. & Cabido, M. 2001. Vive la difference: plant functional diversity matters to ecosystem processes. *Trends in Ecology and Evolution*, 16(11): 646-655.
- Díaz, S., Cabidon, M. & Casanoves, F. 1998. Plant functional traits and environmental filters at regional scale. *Journal of Vegetation Science*, 9: 113-122.
- Du Toit, M.J. 2009. Grassland ecology along an urban-rural gradient using GIS techniques in Klerksdorp, South Africa. Potchefstroom: NWU. (Thesis – MSc). <http://hdl.handle.net/10394/4197>.
- Dukes, J.S. 2001. Biodiversity and invasibility in grassland microcosms. *Oecologia*, 126: 563-568.
- Duncan, R.P., Clemants, S.E., Corlett, R.T., Hahs, A.K., McCarthy, M.A., McDonnell, M.J., Schwartz, M.W., Thompson, K., Vesk, P.A. & Williams, N.S.G. 2011. Plant traits and extinctions in urban areas: a meta-analysis of 11 cities. *Global Ecology and Biogeography*, 20: 509-519.
- Ehrenfeld, J.G., Kourtev, P. & Huang, W. 2001. Changes in soil functions following the invasions of exotic understory plants in deciduous forests. *Ecological Applications*, 11(5): 1287-1300.
- Ellis, S. 2013. R, p, and r^2 values. [E-mail]. *NWU Statistical Consultation Service*. 16 Apr. 2013.
- Elmqvist, T., Folke, C., Nyström, M., Peterson, G., Bengtsson J., Walker, B. & Norberg, J. 2003. Response diversity, ecosystem change and resilience. *Frontiers in Ecology and the Environment*, 1(9): 488-494.
- Elton, C.S. 1958. The ecology of invasions of animals and plants. London: Chapman Hall.
- Everitt, B.S. & Dunn, G. 1992. Applied multivariate data analysis. NY: Oxford University Press.
- Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, 34: 487-515.

- Fédoroff, E., Ponge, J.-F., Dubs, F., Fernández-González, F. & Lavelle, P. 2005. Small-scale response of plant species to land-use intensification. *Agriculture, Ecosystems and Environment*, 105: 283-290.
- Flora Zambesica. 2012. eFloras - Flora Zambesica. Facilitated by the Royal Botanic Gardens, Kew. [Web:] <http://apps.kew.org/efloras/search.do>. Date of access: 16 August, 2012.
- Folke, C., Carpenter, S., Walker, B., Scheffer, M., Elmqvist, T., Gunderson, L. & Holling, C.S. 2004. Regime shifts, resilience, and biodiversity in ecosystem management. *Annual Review of Ecology, Evolution and Systematics*, 35: 557-581.
- Funk, J.L., Cleland, E.E., Suding, K.N. & Zavaleta, E.S. 2008. Restoration through assembly: plant traits and invasion resistance. *Trends in Ecology and Evolution*, 23(12): 695-703.
- Fynn, R.W.S., Morris, C.D. & Edwards, T.J. 2004. Effects of burning and mowing on grass and forb diversity in a long-term grassland experiment. *Applied Vegetation Science*, 7: 1-10.
- Garnier, E., Lavorel, S., Ansquer, P., Castro, H., Cruz, P., Dolezal, J., Eriksson, O., Fortunel, C., Freitas, H., Golodets, C., Grigulis, K., Jouany, C., Kazakou, E., Kigel, J., Kleyer, M., Lehsten, V., Leps, J., Meier, T., Pakeman, R., Papadimitriou, M., Papanastasis, V. P., Quested, H., Quétier, F., Robson, M., Roumet, C., Rusch, G., Skarpe, C., Sternberg, M., Theau, J., Thébaud, A., Vile, D., and Zarovali, M. P. 2007. Assessing the effects of land-use change on plant traits, communities and ecosystem functioning in grasslands: a standardized methodology and lessons from an application to 11 European sites. *Annals of Botany*, 99(5): 967-985.
- Germishuizen, G., Meyer, N.L., Steenkamp, Y. & Keith, M. eds. 2006. A checklist of South African plants. Southern African Botanical Diversity Network Report No. 41. Pretoria: SABONET.
- Gibson, D.J. 2009. Grasses and grassland ecology. NY: Oxford University Press Inc.
- Gilbert, O.L. 1989. The ecology of urban habitats. Chapman and Hall.
- Grobler, C.H., Bredenkamp, G.J. & Brown, L.R. 2006. Primary grassland communities of urban open spaces in Gauteng, South Africa. *South African Journal of Botany*, 72: 367-377.
- Hanley, T.A. 1978. A comparison of the line-interception and quadrat estimation methods of determining shrub canopy coverage. *Journal of Range Management*, 31(1): 60-62.
- Henderson, L. 2001. Alien weeds and invasive plants. Plant Protection Research Institute Handbook No. 12. Pretoria: Agricultural Research Council.

- Henry, R.J. 2005. Importance of plant diversity. (In Henry, R.J. ed. Plant diversity and evolution: genotypic and phenotypic variation in higher plants. CAB international. p.1-6).
- Hillebrand, H. & Blenckner, T. 2002. Regional and local impact on species diversity – from pattern to process. *Oecologia*, 132: 479-491.
- Hooper, D.U., Chapin, F.S., III, Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Hawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A.J., Vendermeer, J. & Wardle, D.A. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs*, 75(1)3-35.
- Kent, M. 2012. Vegetation description and data analysis. Wiley & Sons, Ltd.
- Kleyer, M. 1999. Distribution of plant functional types along gradients of disturbance intensity and resource supply in an agricultural landscape. *Journal of Vegetation Science*, 10(5): 697-708.
- Klotz, S. 1990. Species/area and species/inhabitants relations in European cities. (In Sukopp, H. et al., eds. Urban ecology: plants and plant communities in urban environments. The Hague: SPC Academic Publishing. p. 99-103).
- Knapp, S., Kühn, I., Bakker, J.P., Kleyer, M., Klotz, S., Ozinga, W.A., Poschlod, P., Thompson, K., Thuiller, W. & Römermann, C. 2009. How species traits and affinity to urban land use control large-scale species frequency. *Diversity and Distributions*, 15: 533-546.
- Knapp, S., Kühn, I., Wittig, R., Ozinga, W.A., Poschlod, P. & Klotz, S. 2008. Urbanisation causes shifts in species' trait state frequencies. *Preslia*, 80: 375-388.
- Kowarik, I. 1995. On the role of alien species in urban flora and vegetation. (In Pyšek, P. et al., eds. Plant invasions - general aspects and special problems. Amsterdam: SPB Academic Publishing. p. 15-38).
- Laliberté, E. 2011. Land-use intensification in grazing systems: plant trait responses and feedbacks to ecosystem functioning and resilience. Christchurch: UC. (Thesis – PhD).
- Laliberté, E. & Legendre, P. 2010. A distance-based framework for measuring functional diversity from multiple traits. *Ecology*, 91(1): 299-305.
- Laliberté, E., Wells, J.A., DeClerck, F., Metcalfe, D.J., Catterall, C.P., Cibeles Queiroz, C., Aubin, I., Bonser, S.P., Yi Ding, Y., Fraterrigo, J.M., McNamara, S., John W. Morgan, J.W., Sánchez Merlos, D., Vesk, P.A. & Mayfield, M.M. 2010. Land-use intensification reduces functional redundancy and response diversity in plant communities. *Ecology Letters*, 13: 76-86.

- Lambdon, P.W., Lloret, F. & Hulme, P.E. 2008. Do non-native species invasions lead to biotic homogenisation at small scales? The similarity and functional diversity of habitats compared for alien and native components of Mediterranean floras. *Diversity and Distributions*, 14: 774-785.
- Lavorel, S., Grigulis, K., McIntyre, S., Williams, N.S.G., Garden, D., Dorrough, J., Berman, S., Quétier, F., Thébault, A. & Bonis, A. 2008. Assessing functional diversity in the field – methodology matters! *Functional Ecology*, 22: 134-147.
- Leishman, M.R. & Westoby, M. 1994. Hypotheses on seed size: tests using the semiarid flora of Western New South Wales, Australia. *The American Naturalist*, 134(5): 890-906.
- Lepš, J., De Bello, F., Lavorel, S. & Berman, S. 2006. Quantifying and interpreting functional diversity of natural communities: practical considerations matter. *Preslia*, 78: 481-501.
- Lindenmayer, D.B. & Fischer, J. 2006. Habitat fragmentation and landscape change: an ecological and conservation synthesis. Island Press.
- Lyons, K.G. & Schwartz, M.W. 2001. Rare species loss alters ecosystem function – invasion resistance. *Ecology Letters*, 4: 358-365.
- Mason, N.W.H., MacGillivray, K., Steel, J.B. & Wilson, J.B. 2003. An index of functional diversity. *Journal of Vegetation Science*, 14: 571-578.
- Mason, N.W.H., Mouillot, D., Lee, W.G. & Wilson, J.B. 2005. Functional richness, functional evenness and functional divergence: the primary components of functional diversity. *Oikos*, 111: 112-118.
- Mayfield, M.M., Boni, M.F., Daily, G.C. & Ackerly, D. 2005. Species and functional diversity of native and human-dominated plant communities. *Ecology*, 86(9): 2365-2372.
- McIntyre, S., Lavorel, S. & Tremont, R.M. 1995. Plant life-history attributes: their relationship to disturbance response in herbaceous vegetation. *Journal of Ecology*, 83(1): 31-44.
- McKinney, M.L. 2002. Urbanisation, biodiversity, and conservation. *BioScience*, 52(10): 883-890.
- McKinney, M.L. 2008. Effects of urbanisation on species richness: a review of plants and animals. *Urban Ecosystems*, 11: 161-176.
- McNaughton, S.J. 1977. Diversity and stability of ecological communities: a comment on the role of empiricism in ecology. *The American Naturalist*, 111(979): 515-525.

- Mouillot, D., Villéger, S., Sherer-Lorenzo, M. & Mason, N.W.H. 2011. Functional structure of biological communities predicts multifunctionality. *PLoS ONE*, 6(3): 1-9.
- Mucina, L. & Rutherford, M.C., eds. 2006. The Vegetation of South Africa, Lesotho and Swaziland. Strelitzia 19. Pretoria: South African National Biodiversity Institute.
- Niemelä, J. 1999a. Ecology and urban planning. *Biodiversity and Conservation*, 8: 119-131.
- Niemelä, J. 1999b. Is there a need for a theory of urban ecology? *Urban Ecosystems*, 3: 57-65.
- NWDACE (North West Department of Agriculture, Conservation and Environment). 2008. North West Province environment outlook. Mmbatho: North West Department of Agriculture, Conservation and Environment.
- Odum, E.P. 1983. Basic ecology. Saunders College Publishing.
- Oke, T.R. 1995. The heat island of the urban boundary layer: characteristics, causes and effects. (In Cermak, J.E., ed. Wind and climate in cities. Netherlands: Kluwe Academy. p. 81-107).
- Pakeman, R.J. 2011. Functional diversity indices reveal the impacts of land use intensification on plant community assembly. *Journal of Ecology*, 99: 1143-1151.
- Peet, R.K. 1974. The measurement of species diversity. *Annual Review of Ecology and Systematics*, 5: 285-307.
- Pellissier, V., Rozé, F., Aguajdad, R., Quénot, H. & Clergeau, P. 2008. Relationship between soil seed bank, vegetation and soil fertility along an urbanisation gradient. *Applied Vegetation Science*, 11: 325-334.
- Petchey, O.L. 2003. Integrating methods that investigate how complementarity influences ecosystem functioning. *Oikos*, 101: 323-330.
- Petchey, O.L. & Gaston, K.J. 2002. Functional diversity (FD), species richness and community composition. *Ecology Letters*, 5: 402-411.
- Petchey, O.L. & Gaston, K.J. 2006. Functional diversity: back to basics and looking forward. *Ecology Letters*, 9: 741-758.
- Petchey, O.L., O’Gorman, E.J. & Flynn, D.F.B. 2009. A functional guide to functional diversity measures. (In Naeem *et al.*, eds. Biodiversity, ecosystem functioning and human wellbeing. Oxford University Press. p.49-59).

- Pickett, S.T.A., Cadenasso, M.L., Grove, J.M., Boone, C.G., Groffman, P.M., Irwin, E., Kaushal, S.S., Mashall, V., McGrath, B.P., Nilon, C.H., Pouyat, R.V., Szlavecz, K., Troy, A. & Page, W. 2011. Urban ecological systems: scientific foundations and a decade of progress. *Journal of Environmental Management*, 92: 331-362.
- Pickett, S.T.A., Cadenasso, M.L., Grove, J.M., Boone, C.G., Groffman, P.M., Irwin, E., Kaushal, S.S., Mashall, V., McGrath, B.P., Nilon, C.H., Pouyat, R.V., Szlavecz, K., Troy, A. & Page, W. 2011. Urban ecological systems: scientific foundations and a decade of progress. *Journal of Environmental Management*, 92: 331-362.
- Pielou, E. C. 1975. Ecological diversity. NY: Wiley.
- Pimm, S.L. 1984. The complexity and stability of ecosystems. *Nature*, 307: 321-326.
- Pla, L., Casanoves, F. & Di Rienzo, J.A. 2012. Quantifying functional biodiversity. Springer.
- Pla, L., Casanoves, F., Di Rienzo, J.A., Fernandez, F. & Finegan, B. 2008. Confidence intervals for functional diversity indices considering species abundance. XXIV International Biometric Conference. Dublin, 2008.
- Pokorney, M.L., Sheley, R.L., Zabinski, C.A., Engel, R.E., Svejcar, T.J. & Borkowski, J.J. 2005. Plant functional group diversity as a mechanism for invasion resistance. *Restoration Ecology*, 13(3): 448-459.
- Power, M.E., Tilman, D., Estes, J.A., Menge, B.A., Bond, W.J., Mills, L.S., Daily, G., Castilla, J.C., Lubchenco, J. & Paine, R.T. 1996. Challenges in the quest for keystones. *BioScience*, 46(8): 609-620.
- PRIMER-E. 2012. PRIMER software v6. PRIMER-E ltd.
- PROTA. 2012. Protabase published species. Plant Resources of Tropical Africa. [Web:] <http://database.prota.org/publishedspeciesEn.htm>. Date of access: 16 August, 2012.
- Pyšek, P. 1998. Alien and native species in Central European urban floras: a quantitative comparison. *Journal of Biogeography*, 25(1): 155-163.
- Pyšek, P. & Pyšek, A. 1990. Comparison of vegetation and flora of West Bohemian towns. (In Sukopp, H. *et al.*, eds. Urban ecology: plants and plant communities in urban environments. The Hague: SPC Academic Publishing. p. 105-112).

- Pyšek, P., Prach, K. & Šmilauer, P. 1995. Relating invasion success to plant traits: an analysis of the Czech alien flora. (In Pyšek, P. *et al.*, eds. Plant invasions - general aspects and special problems. Amsterdam: SPB Academic Publishing. p. 39-60).
- Quinn, G.P. & Keough, M.J. 2002. Experimental design and data analysis for biologists. Cambridge: Cambridge University Press.
- Raunkaier, C. 1937. Plant life forms. Oxford: Clarendon Press.
- Rebele, F. 1994. Urban ecology and special features of urban ecosystems. *Global Ecology and Biogeography letters*, 4(6): 173-187.
- Robinson, G.R., Holt, R.D., Gaines, M.S., Hamburg, S.P., Johnson, M.L., Fitch, H.S. & Martinko, E.A. 1992. Diverse and contrasting effects of habitat fragmentation. *Science*, 257(5069): 524-526.
- SANBI (South African National Biodiversity Institute). 2012. PlantzAfrica. [Web]: <http://www.plantzafrica.com/index.html>. Date of access: 14 August, 2012.
- Saunders, S.A., Hobbs, R.J. & Margules, C.R. 1991. Biological consequences of ecosystem fragmentation: a review. *Conservation Biology*, 5(1): 18-32.
- Savard, J.-P. L., Clergeau, P. & Mennechez, G. 2000. Biodiversity concepts and urban ecosystems. *Landscape and Urban Planning*, 48: 131-142.
- Schleuter, D., Daufresne, M., Massol, F. & Argillier, C. 2010. A user's guide to functional diversity indices. *Ecological Monographs*, 80(3): 469-484.
- Schulze, E.-D. & Mooney, H.A., eds. 1993. Biodiversity and ecosystem function. *Ecological Studies* 99. Berlin: Springer-Verlag.
- Schwartz, M.W., Bringham, C.A., Hoeksema, J.D., Lyons, K.G., Mills, M.H. & Van Mantgem, P.J. 2000. Linking biodiversity to ecosystem function: implications for conservation ecology. *Oecologia*, 122(3): 297-305.
- Shannon, C. & Weaver, W. 1949. The mathematical theory of communication. Urbana: University of Illinois Press.
- Simpson, E.H. 1949. Measurements of diversity. *Nature*, 163: 688.
- South Africa. 1983. Conservation of Agricultural Resources Act 43 of 1983.

- Stadler, J., Trefflich, A., Klotz, S. & Brandl, R. 2000. Exotic plant species invade diversity hotspots: the alien flora of Northwestern Kenya. *Ecography*, 23(2): 169-176.
- StatSoft, Inc. 2011. STATISTICA (data analysis software system). Version 10. Tulsa: USA.
- StatSoft, Inc. 2012. STATISTICA (electronic manual). Version 11. Tulsa: USA.
- Steyn, H.S. 2009. Manual: Effect size indices and practical significance. Potchefstroom: North-West University (Potchefstroom Campus). <http://www.nwu.ac.za/p-statcs/index.html>. Date of access: 27 May 2013.
- Steyn, F. 2012. R-squared values [e-mail]. *NWU Statistical Consultation Service*. 6 Sept. 2012
- Sudnik-Wójcikowska B. & Galera H. 2005. Floristic differences in some anthropogenic habitats in Warsaw. *Annales Botanici Fennici*, 42: 185-193.
- Thompson, K. & McCarthy, M.A. 2008. Traits of British alien and native plants. *Journal of Ecology*, 96: 853-859.
- Thuiller, W., Midgley, G.F., Rouget, M. & Cowling, R.M. 2006. Predicting patterns of plant species richness in megadiverse South Africa. *Ecography*, 29: 733-744.
- Tilman, D., Lehman, C.L. & Bristow, C.E. 1998. Diversity-stability relationships: statistical inevitability of ecological consequence? *The American Naturalist*, 151(3): 277-282.
- Van Oudtshoorn, F. 2006. Guide to grasses of Southern Africa. Briza.
- Van Wyk, B. & Malan, S. 1988. Field guide to the wild flowers of the Witwatersrand and Pretoria region. Struik Publishers.
- Vankat, J.L. & Roy, D.G. 2002. Landscape invasibility by exotic species. (In Gutzwiller, K.J., ed. Applying landscape ecology in biological conservation. Springer. p. 171-191).
- Villéger, S., Mason, N. & Mouillot, D. 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology*, 89(8): 2290-2301.
- Villéger, S., Miranda, J.R., Hernández, D.F. & Mouillot, D. 2010. Contrasting changes in taxonomic vs. functional diversity of tropical fish communities after habitat degradation. *Ecological Applications*, 20(6): 1512-1522.
- Violle, C., Navas, M.-L. Vile, D., Kazakou, E., Fortunel, C., Hummel, I., Garnier, E. 2007. Let the concept of trait be functional! *Oikos*, 116: 882-892.

- Vitousek, P.M., Mooney, H.A., Lubchenco, J. & Melillo, J.M. 1997. Human domination of Earth's ecosystems. *Science*, 277: 494-499.
- Vitousek, P.M., Walker, L.R., Whiteaker, L.D., Mueller-Dombois, D. & Matson, P.A. 1987. Biological invasion by *Marica faya* later ecosystem development in Hawaii. *Science*, 238(4828): 802-804.
- Walker, B., Kinzig, A. & Langridge, J. 1999. Plant attribute diversity, resilience, and ecosystem function: the nature and significance of dominant and minor species. *Ecosystems*, 2(2): 95-113.
- Wania, A., Kühn, I. & Klotz, S. 2006. Plant richness patterns in agricultural and urban landscapes in Central Germany – spatial gradients of species richness. *Landscape and Urban Planning*, 75: 97-110.
- WCSP. 2012. World Checklist of Selected Plant Families. Facilitated by the Royal Botanic Gardens, Kew. [Web:] <http://apps.kew.org/wcsp/>. Date of access: 13 August, 2012.
- Williams, J.A. & West, C.J. 2000. Environmental weeds in Australia and New Zealand: issues and approaches to management. *Austral Ecology*, 25: 425-444.
- Williams, N.S.G., Morgan, J.W., McDonnell, M.J. & McCarthy, M.A. 2005. Plant traits and local extinctions in natural grasslands along an urban-rural gradient. *Journal of Ecology*, 93: 1203-1213.
- Williams, N.S.G., Schwartz, M.W., Veski, P.A., McCarthy, M.A., Hahs, A.K., Clemants, S.E., Corlett, R.T., Duncan, R.P., Norton, B.A., Thompson, K. & McDonnell, M.J. 2009. A conceptual framework, for predicting the effects of urban environments on floras. *Journal of Ecology*, 97: 4-9.
- With, K.A. 2004. Assessing the risk of invasive spread in fragmented landscapes. *Risk Analysis*, 24(4): 803-815.