

CHAPTER TWO: LITERATURE REVIEW

2.1 Introduction

“Are we now at the start of another mass extinction, similar in magnitude to the greatest ones of the past, but differing in being caused by humans?” (Diamond *et al.*, 1989)

The human race has been the cause of many biotic and ecological changes. Social, economic and technological advances are priority, whilst nature is constantly paying the price for careless actions and continuous development. Life on earth and its economies are dependent on natural capital which consists of resources (such as soil, water, air and minerals) and ecological services (such as biodiversity, nutrient recycling and pollution control) (Miller, 2005; NWDACE, 2008). Human activities and ignorance have been the main causes of major environmental- and resource problems such as biodiversity depletion, air-and water pollution, waste production and food supply problems (Daily, 1997; Miller, 2005) (Figure 2.1).

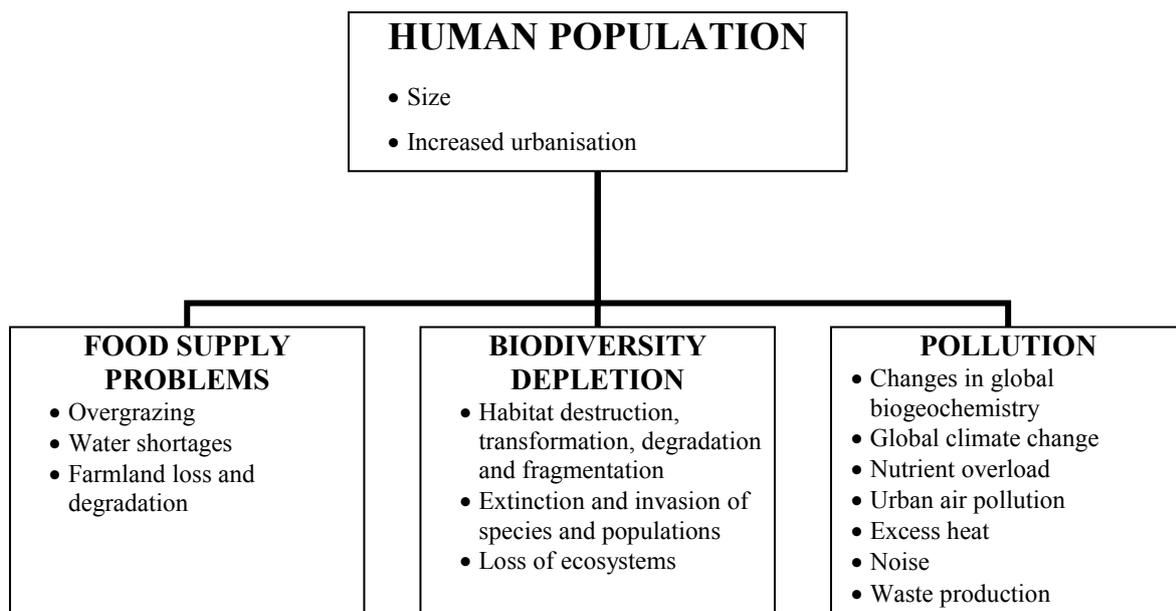


Figure 2.1: Major environmental problems representing the degradation of natural capital (adapted from Miller, 2005, and Vitousek *et al.*, 1997).

Sanderson *et al.* (2002) created a map of the ‘human footprint’ (influence of humans on the earth’s surface), and found that 83% of the world’s land surface has been influenced by human factors such as agriculture, industrialisation and urbanisation. The growing human population, and thus the increased requirement for basic human needs such as food and shelter, are driving substantial changes to the Earth’s ecosystems and their non-human inhabitants.

In this chapter literature from the various concepts involved in this study will be examined. Attention was focused on the following aspects:

- Urban ecology following a landscape ecological approach.
- Grasslands in South Africa, especially the Rand Highveld Grassland vegetation unit where this study was conducted.
- The characteristics of urban ecosystems and vegetation and the use of urbanisation gradients to study them.
- Landscape modification, fragmentation, and the influence of matrix characteristics on habitat remnants.
- Plant species diversity and plant functional diversity.
- Ecosystem functioning and fine-scale biogeochemical and biogeophysical functioning of landscapes.
- The relationships between plant species- and functional diversity and the functioning of ecosystems.

2.2 Urban ecology following landscape ecological principles

“Landscape ecology is uniquely poised to play a major role in tackling today's major conservation and land-use issues and in developing responses to the pressing problems arising as a result of human-induced global change” (Hobbs, 1997)

Urban ecological research has evolved into an interdisciplinary field where natural-and social sciences meet (Hobbs, 1997; Marzluff *et al.*, 2008; Niemelä *et al.*, 2009; Weiland & Richter, 2009 & 2012). Three main outlooks of urban ecology exist, namely 1) the ecology *in* cities from which the bio-ecology approach stemmed; 2) the ecology *of* cities as socioeconomic entities from which the socio-ecology approach is derived; and 3) the ecology *of* cities as ecosystems that resulted in the urban systems approach and the integrative urban ecosystems approach (Wu, 2008; Weiland & Richter, 2009). The bio-ecology approach emphasises the effects of urbanisation on flora and fauna dynamics, whilst the socio-ecology approach views cities as socio-economic entities where people interact with their urban surroundings (Wu, 2008; Weiland & Richter, 2009). The ecology of cities as ecosystems (urban systems- and integrative urban ecosystems approach) urban ecological outlook interprets cities as ecosystems constituting of both socioeconomic and biological components (Wu, 2008; Weiland &

Richter, 2009). In most of the different urban ecological approaches the landscape ecology perspective is widely used (Wu, 2008). Landscapes are mosaics of patches (McGarical and Marks, 1995; Cadenasso et al., 2003), considered to be scale-dependent, complex systems wherein processes, and spatial and temporal heterogeneity as main patterns, are integrated (Farina, 2007). Landscape ecology studies the composition, structure, function and change within landscapes (Turner, 1989), and is defined by Wu & Hobbs (2007) as *“the science and art of studying and influencing the relationship between spatial pattern and ecological processes across hierarchical levels of biological organisation and different scales in space and time.”* Urban morphology, spatial processes and socioeconomic undertakings may effect and are affected by the sustainability of cities and the regions beyond cities (Wu, 2008). With the recognition that humans are an integral part of ecosystems (McDonnell & Pickett, 1993), landscape ecological principles have been applied to human-dominated landscapes in order to identify urban ecological processes and patterns (Turner, 2005; Weiland & Richter, 2012). The study of urban-rural gradients has, for example, investigated the effects of landscape components (e.g. patch shape, size, and arrangement) on species composition and ecosystem processes (McDonnell & Pickett, 1990). Additionally landscape metrics may be used to quantify these urban-rural gradients (Du Toit, 2009; Hahs & McDonnell, 2006).

2.3 Grasslands and grassland ecology

“Grasslands in South Africa are both rich in biodiversity and important for providing a variety of ecosystem services.” (Egoh *et al.*, 2011)

Grasslands across the globe are currently under threat as this biome is undergoing habitat loss at an alarming extent and rate mainly due to human influences (Scholes & Biggs, 2005). Urbanisation and cultivation in grassland areas have long been resulting in transformed and fragmented landscapes, creating a greater need for conservation (Matsika, 2007; Scholes & Biggs, 2005). Grasslands in the urban environment are heavily modified by human actions such as mowing and alterations in the natural fire disturbance regime (frequency and magnitude) (Grobler *et al.*, 2006).

According to Gibson (2009) the fragmentation of grasslands leads to the rapid degradation of ecosystem structure and function. About 37% of grasslands on earth have been extensively fragmented (White *et al.*, 2000). The effects of habitat fragmentation hold dire consequences for native biodiversity, as a high diversity of exotic species are likely to invade these areas (Gibson, 2009).

The Grassland Biome of South Africa is one of the earth’s most diverse, productive and biologically richest terrestrial biomes (Gibson, 2009; Henwood, 1998), and nearly 30% of it has been transformed

by activities such as urbanisation, cultivation, mining, and forestry (Fairbanks *et al.*, 2000). According to Mucina and Rutherford (2006), the remaining untransformed grassland areas are fragmented to a critical extent. Consequently, the biodiversity in these grasslands is also drastically decreasing (Barnard *et al.*, 2007; Soulé, 1991). Grass species are adapted to withstand defoliation by grazing, but unsustainable grazing practices may have vast effects on plant species composition, density, size, life span, and production (Mucina & Rutherford, 2006). For instance, grazing may result in lower perennial grass cover (Drewa & Havstad, 2001), and may even affect soil and water functions which may lead to erosion (McIntyre & Tongway, 2005). Fire is an important factor in maintaining and determining the structure, distribution, ecological characteristics and plant species composition in grasslands (Bond, 2005; Mucina & Rutherford, 2006; O'Connor & Bredenkamp, 1997; White *et al.*, 2000). Without fire South African grasslands would be characterised by high woody tree species cover (Bond *et al.*, 2003).

2.3.1 The Rand Highveld Grassland

The Rand Highveld Grassland (Gm 11), which is the dominant vegetation unit in the Tlokwe Municipal area, consists of wide sloping plains and raised rocky outcrops at an altitude of 1 300m – 1635m (Mucina & Rutherford, 2006). Grasslands in South Africa have always been of great worth for agricultural development (Adamson, 1938), but agricultural activities (cultivation) and on-going urbanisation is leading to the fragmentation and transformation of the endangered Rand Highveld Grassland (of which a mere 1% is being conserved) (Mucina & Rutherford, 2006). The North-West Department of Agriculture, Conservation, Environment and Rural Development (NWDACERD, 2009) identifies the Rand Highveld Grassland as being vulnerable, as 49.8% of this vegetation type has been transformed, and 3.2% significantly degraded. Vulnerable ecosystems are defined by the National Environmental Management: Biodiversity Act (10 of 2004) as ecosystems that are at substantial risk of undergoing significant degradation of ecological structure, function or composition as a result of human intervention, but are not critically endangered or endangered ecosystems.

2.3.1.1 Climate

Annual rainfall for the Rand Highveld Grassland ranges between 570mm and 730mm, and the rainy season is predominantly in the summer months (October until March) (Mucina & Rutherford, 2006). The climate of this region is warm-temperate, with cold, dry winters when frost is prevalent (Adamson, 1938; Mucina & Rutherford, 2006).

2.3.1.2 Land type and soil

According to O'Connor and Bredenkamp (1997) the Bankenveld false grassveld type (an old classification which includes the Rand Highveld Grassland) is characterised by rocky ridges with shallow rocky soils, this is also confirmed by Mucina and Rutherford (2006) and the Soil

Classification Working Group (1991). The Tlokwe Municipal area is mainly situated in the Ba-land type characterised by red or yellow, dystrophic and/or mesotrophic (apedal) soil types (Land Type Survey Staff, 1984). The Rand Highveld Grassland supports shallow Glenrosa and Mispah soil forms (Mucina & Rutherford, 2006). Moderate to high erosion levels has been recorded in 7% of this vegetation unit (Mucina & Rutherford, 2006). Because the vegetation of the Ba-land type has been lost extensively due to agricultural activities, the representative vegetation communities are endangered (Bezuidenhout & Bredenkamp, 1991).

2.3.1.3 Vegetation

The grasslands of the South African high central plateau may be characterised by herbaceous vegetation with uncomplicated structure, predominantly grass species of the Poaceae family (Mucina & Rutherford, 2006). Adamson (1938) commented that the grasses of the “High Veld Grassland” rarely form a continuous turf, or dense tufts, but grows in low and spreading clumps. The structure is determined by climatic variables such as moisture availability and low temperatures; high altitudes; as well as anthropogenic processes such as grazing and the presence of fire (Acocks, 1988; Gibson, 2009; Mucina & Rutherford, 2006; O’Connor & Bredenkamp, 1997). According to Mucina and Rutherford (2006), these grassland plains are characterised by a great richness of wiry, sour grass species, the presence of shrubs on rocky ridges, and also a high diversity of herbaceous species from the Asteraceae family. The most common grasses in this vegetation unit belong to the *Themeda* (Adamson, 1938; Bezuidenhout & Bredenkamp, 1991; Mucina & Rutherford, 2006), *Eragrostis*, *Elionurus* (Bezuidenhout & Bredenkamp, 1991; Mucina & Rutherford, 2006), and *Heteropogon* genera (Mucina & Rutherford, 2006) (also see Table 2.1). Bezuidenhout (1988) described the vegetation as an *Eragrostis curvula*-*Themeda triandra* vegetation unit.

Table 2.1: Common grass, forb and woody species occurring in the Ba-land type (Bezuidenhout & Bredenkamp, 1991).

Grasses	Forbs	Trees
<i>Cynodon dactylon</i>	<i>Lactuca serriola</i>	<i>Acacia caffra</i>
<i>Elionurus muticus</i>	<i>Selago densiflora</i>	<i>Acacia karroo</i>
<i>Eragrostis curvula</i>		<i>Diospyros lycioides</i>
<i>Themeda triandra</i>		

2.4 Urban ecosystems

–Urban ecosystems differ from their „natural“ counterparts solely in the degree of man’s influence.” (Walbridge, 1997)

Pickett *et al.* (2011) defines urban ecosystems as systems of which the dominant land cover is infrastructure and built structures, and where the inhabitants live at high densities. Such systems are unique in that it does not consist of only plants and animals interacting with their environments, but it also contains humans and their socio-economic expressions (Pickett *et al.*, 2011).

2.4.1 Urbanisation

At the end of 2011 the world’s population reached a staggering 7 billion people, half of which lives in cities (United Nations Population Fund, 2011). Urbanisation is a global phenomenon defined by the creation of urban areas, thus land is transformed into modified urban environments (Alberti *et al.*, 2003; Collins *et al.*, 2000; Deng *et al.*, 2009; Grimm *et al.*, 2000; Niemelä, 1999b; Niemelä *et al.*, 2011; Ojima *et al.*, 1994; Pickett *et al.*, 2011; Williams *et al.*, 2005; Wu *et al.*, 2011). These altered environments create unique ecosystems which are characterised by increased human habitation, plants and animals that are domesticated, non-native or exotic species, impervious surfaces, artificial structures, and modified energy- and resource pathways (McDonnell & Pickett, 1990; Niemelä, 1999b; Pickett *et al.*, 2001). According to the United Nations (2011), the world’s current population of 7 billion will reach 10.1 billion in the following ninety years. Approximately half the people of the world currently reside in densely populated urban areas, due to rapid population growth and the migration of rural residents to cities (Miller, 2005; Yeh & Huang, 2009; Yu & Ng, 2006). Urbanisation is an on-going process where rural and ‘natural’ land cover is being transformed at an astonishing rate; it is not slowing down, and will most probably not slow down in the future.

2.4.2 The urban physical environment

“Future landscapes will be more human-dominated, with less extensive and more fragmented biotic communities, leading to disjunct species distribution.” (Noon & Dale, 2002)

Humans inflict a variety of change on their environment, creating unique human ecosystems. Human actions alter hydrology through built infrastructure and impervious surfaces (Groffman *et al.*, 2003; Kaye *et al.*, 2006; Niemczynowicz, 1999). They also have profound effects on species diversity (through changing habitat, succession and food cycles) (Diaz & Cabido, 2001; Ehrlich & Wilson, 1991; Loreau, 2000), and may change the magnitude, intensity and frequency of disturbances (Alberti, 2005, 2008).

Many scholars have dedicated their research on determining the intricate workings of urban environments in different parts of the world, and the effects of urbanised areas on flora (e.g. Bastin & Thomas, 1999; Cilliers & Bredenkamp, 2000; Hahs & McDonnell, 2007), soil (Craul, 1985; Effland & Pouyat, 1997; Pouyat *et al.*, 2007), atmospheric chemistry (Zhang *et al.*, 2005), and temperature (Alberti, 2005, 2008 & 2010; Zhang *et al.*, 2005; Zhou *et al.*, 2004) (see Table 2.2 for summary).

Urban components may influence soil formation processes (Chapin *et al.*, 2002), and the chemical, physical and biological attributes of soil (Pickett *et al.*, 2011). Soil modification includes physical disturbance (such as soil erosion), concealment by impervious surfaces, and increased water and chemicals (through irrigation and the use of fertilisers) (Pickett *et al.*, 2001; Zhao *et al.*, 2007; Wessolek, 2008), as well as soil compaction, limited aeration, water movement, and rooting space, disrupted nutrient cycling, and the presence of anthropogenic substances (Craul, 1985). Indirect effects consequently alter biotic and abiotic features which changes soil formation and ecological processes (Pickett *et al.*, 2001). This includes the urban heat island (Oke, 1995), and the introduction of exotic species (Ehrenfeld *et al.*, 2001). Thus urbanisation changes soils and therefore the substrate for vegetation, which may in turn affect the species composition and traits.

The urban physical environment, created through the process of urbanisation, results in a complex mosaic of high-density and lower-density built-up areas (Alberti, 2008). Habitat patches within urban environments are usually small and isolated, surrounded by a matrix (the most dominant land-cover or background in a landscape, which exerts a dominant role on ecological processes (Forman, 1995)) of built-up human environment (Niemelä, 1999b). Urban landscapes are also characterised by a rich spatial heterogeneity (Pickett *et al.*, 2011; Rebele, 1994; Savard *et al.*, 2000; Zipperer *et al.*, 2000). Heterogeneity is defined as the temporal and spatial arrangement or variability of patches across a landscape (Gaucherel, 2007; Zipperer *et al.*, 2000).

2.4.3 Urban vegetation

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

Vegetation in urban landscapes has been studied for many years, and has been the focus of ecological evaluation of urban spaces as it serves as an indicator of ecological processes and environmental conditions (Mucina, 1990). The land-use change that is associated with the development and expansion of urban areas modifies the composition, cover and diversity of vegetation (Cilliers & Siebert, 2011). Urban flora are characterised by species adapted to human-induced perturbation, and high non-native species diversity (Kowarik, 1995; Niemelä, 1999b; Pickett *et al.*, 2011; Pyšek, 1998).

Table 2.2: Literature summary of the effects of urbanisation.

Urbanisation effects	Literature
Abiotic	
Artificial structures	Hahs & McDonnell, 2006
Changes in disturbance regimes (such as fire and erosion)	Alberti, 2005, 2009 & 2010
Climatic conditions (such as increased heat)	Zhou <i>et al.</i> , 2004; Zhang <i>et al.</i> , 2005; Alberti, 2005, 2009 & 2010
Habitat degradation, fragmentation and loss	Alberti, 2003; Colding, 2006; Grime <i>et al.</i> , 2000; Yeh & Huang, 2009
Habitat/landscape transformation	Alberti, 2005 & 2010; Grime <i>et al.</i> , 2000; Sanderson <i>et al.</i> , 2002; Williams <i>et al.</i> , 2005;
Impervious surfaces	Hahs & McDonnell, 2006; Alberti, 2010; Niemczynowicz, 1999; Groffman <i>et al.</i> , 2003; Kaye <i>et al.</i> , 2006
Small, isolated habitat patches	Niemełá, 1999
Urban soils	Craul, 1985; Effland & Pouyat, 1997; Pouyat <i>et al.</i> , 2007
Water movement	Alberti, 2009
Biotic	
Easily invaded by exotic species	Niemełá, 1999; Gilbert, 1989
Loss of biota (local and global biodiversity)	Colding, 2006; Wilcox & Murphy, 1985; Yeh & Huang, 2009; Cilliers <i>et al.</i> , 2004
Species extinction	May & Tregonning, 1998
Ecosystem health and function	
Altered energy and nutrient pathways	Alberti, 2005; McDonnell & Pickett, 1990; Hahs & McDonnell, 2006; Yeh & Huang, 2009
Hydrolic, geomorphic, and biogeochemical processes	Alberti, 2009; Grime <i>et al.</i> , 2000
Nutrient cycling	Alberti, 2009
Primary production	Alberti, 2009
Anthropogenic	
Degradation of natural capital	Miller, 2005
Loss of ecosystem services	Colding, 2006; Alberti, 2005; Alberti, 2010

According to Gilbert (1989) and Grobler *et al.* (2006) many species are intentionally and unintentionally introduced into urban environments, for example horticultural species are most commonly the source of alien plant species in cities. This often leads to high alpha-diversity (species richness in single habitat patches) because many different species can persist in the unique urban environment (Niemelä, 1999b). According to Rebele (1994) the beta-diversity (diversity between habitat patches) in cities may also be high due to distinct habitat gradients observable in urban ecosystems. High species diversity in cities may be contributed to the variability in habitat, as urban areas may be extremely heterogeneous (Cadenasso & Pickett, 2008; Pickett *et al.*, 2011; Rebele, 1994; Savard *et al.*, 2000). On the other hand in exceedingly built-up areas species richness of fauna and flora may decrease due to degradation and destruction of available habitat (McKinney, 2008). Urban open spaces such as parks and road verges may be subjected to management by humans. These management practices primarily include mowing (Niemelä, 1999a; Rebele, 1994). Extensive management of vegetation due to human influences in urban environments, such as mowing, maintains grasslands in a sub-climax condition, decreasing the species diversity of the plant communities (Cilliers *et al.*, 1999; Niemelä, 1999b). Mowing is thus an important man-induced disturbance, affecting plant species composition, whilst natural disturbance of grasslands, such as burning, is highly restricted in urban areas (Cilliers *et al.*, 2008).

2.4.4 The urban-rural gradient approach

The urban-rural gradient approach in urban ecology has allowed scientists to study the effects of urbanisation pressures on patterns, processes, fauna and flora of complex urban ecosystems (McDonnell & Pickett, 1990). Urbanisation gradients have been subjectively determined based on geographical location in relation to urban cores (Cuevas-Reyes *et al.*, 2013; French *et al.*, 2008; Sadler *et al.*, 2006; Sun *et al.*, 2009). However, more recent quantification of urban-rural gradients involved the use of urbanisation measures that objectively and statistically define urbanisation gradients (Du Toit, 2009; Hahs & McDonnell, 2006; Lockaby *et al.*, 2005; Williams *et al.*, 2005). The urban-rural gradient approach is further discussed in *Chapter 4*.

2.5 Landscape change

“Habitat loss is the single greatest threat to biodiversity, followed by the spread of alien species.”
(Wilcove *et al.*, 1998)

McIntyre & Hobbs (1999) define habitat modification as the alterations to structure, biotic composition and ecological functioning of a landscape. Habitat loss is the process of land conversion from its current state to another land use or land cover type (Collinge, 2009), and usually occurs simultaneously with habitat fragmentation (Fahrig, 2003). Land is globally transformed and modified

by humans in order to provide for their basic needs (August *et al.*, 2002; Ojima *et al.*, 1994). The ecological integrity of ecosystems can be extensively compromised by human activities as it may consequently lead to the loss of native species, and alien invasions (Chapin *et al.*, 2002; Dunford & Freemark, 2004; Hooper *et al.*, 2005; Lindenmayer & Fischer, 2006; NWDACE, 2008; O'Neill *et al.*, 1997; Saunders *et al.*, 1991; Vitousek *et al.*, 1997; Wiens, 2002; With, 2004); declines in soil and water quality (Lindenmayer & Fischer, 2006; Saunders *et al.*, 1991); loss in spatial and structural complexity (August *et al.*, 2002; Chapin *et al.*, 2002; Gonzalez *et al.*, 2009); loss in species diversity (Diamond, 1989; Diaz & Cabido, 2001; Ehrlich & Wilson, 1991; Hobbie *et al.*, 1993; Krauss *et al.*, 2004; Loreau, 2000); and declines in ecosystem functioning (Diaz & Cabido, 2001; Vitousek *et al.*, 1997). According to Lindenmayer and Fischer (2006) the modification of landscapes leads to changes in the extent and spatial arrangement (horizontal patchiness and vertical structural complexity) of vegetation.

2.5.1 Fragmentation

“In landscapes and regions context is usually more important than content. That is, the surrounding mosaic has a greater effect on patch functioning and change than do the present characteristics within the patch.” (Forman, 1995)

The fragmentation of habitats is the disintegration of habitat, and the subsequent creation of smaller, isolated habitat patches (Bender *et al.*, 1998; Fahrig, 2003; Forman, 1995; Gutzwiller, 2002; Knight & Landres, 2002; McGarigal & Cushman, 2002; Wiens, 2002; Wilcove *et al.*, 1986), or “habitat islands” also known as remnants (Saunders *et al.*, 1991). These fragments differ in size and species richness (Fahrig, 2003). Fragmentation of habitat is not exclusively a man-induced disturbance that causes landscape change – glaciers, landslides, floods, fires and hurricanes may also cause discontinuity and isolation in landscapes (Collinge, 1996; Ewers & Didham, 2006). However, fragmentation of habitats caused by human activities is one of the main drivers of species extinction (Diamond, 1989; Murcia, 1995), as it causes the loss of habitats (Fahrig, 2003). Natural vegetation has been removed around the world, converting land for human use in order to provide for human needs such as food provision (agriculture) and shelter (urbanisation) (Collinge, 1996; August *et al.*, 2002). The result is remaining vegetation situated in fragmented patches positioned in a modified matrix of built-up areas or crops (Saunders *et al.*, 1991). Fragments created by humans are more symmetrical, have straighter, sharper boundaries, and contrasts with their surroundings more than naturally created patches (August *et al.*, 2002; Forman, 1995; Wiens *et al.*, 1993).

The fragmentation process increases the number and degree of isolation of patches within a landscape, and also decreases patch size (Collinge, 1996; Fahrig, 2003; Saunder *et al.*, 1991). The

species that remain in remnants are thus exposed to the new, altered conditions of the surrounding matrix (Jules & Shahani, 2003; Saunders *et al.* 1991).

Habitat may also be fragmented by roads. Andrews (1990) has written an extensive review concerning roads and habitat fragmentation. Roads subdivide natural areas into isolated fragments and create an edge effect (Andrews, 1990; Saunders *et al.*, 2002; Zhu *et al.*, 2006). The ecological impacts of roads include damage, loss and changes to habitats which extend beyond the edge of the road (Spellerberg, 1998; Carr *et al.*, 2002) and may also be considered as an adequate indicator of human presence (Saunders *et al.*, 2002). Habitat fragmentation caused by roads may have implications for the dispersal of fauna and flora and leads to the isolation of populations (Spellerberg, 1998).

Although the degree of isolation of grassland patches within our study area is not directly quantified, but grassland patches which are visually considered to be isolated from the surrounding grassland matrix are selected, it is still important to consider certain fragmentation concepts which may increase the understanding of vegetation and landscape function characteristics within grassland fragments.

Fragment size and edge effects

Many authors have found positive correlations between habitat area and species richness (for plants e.g. Iida & Nakashizuka, 1995; Krauss *et al.*, 2004; Peterken & Game, 1984), also confirming the validity of species-area relationships (Cain, 1938). According to Collinge (2009) larger fragments contain more species because the habitat is capable of supporting more species. When habitat is fragmented into smaller habitat remnants the border between the remnant and the matrix wherein it is situated, increases (Collinge, 1996). According to Matlack (1993), who studied the edge effects of forest fragments, the edge of a vegetation patch is the marginal zone of a fragment with different ecological conditions from that of the interior of the fragment. Irregularly shaped and small habitat fragments have a higher margin-to-area ratio (Collinge, 1996).

Connectivity and isolation

The degree of isolation of habitat fragments plays an important role in characterizing remnants, as it may determine the persistence of populations and communities, and the distribution of plants and animals within a landscape (Collinge, 2009). Isolation may be reduced through linear habitat strips or corridors that connect otherwise isolated habitat patches (Collinge, 2009).

2.5.2 Landscape context: the importance of the matrix

“...it is so important to know not only what a patch is, in terms of its size boundary length quality, and so on, but also where it is in terms of its adjacency to different kinds of neighbouring patches with different ecological properties.” (Wiens, 2002)

The spatial configuration of a landscape results in a unique combination of both intra- and inter-landscape patterns and ecological processes (Wiens, 2002). The environmental properties of the matrix habitat (i.e. exogenous disturbances) surrounding patches may be just as deterministic, possibly even more, of patch biota dynamics than intra-patch conditions (August *et al.*, 2002; Williams *et al.*, 2005; Wiens, 2002). Landscape context may be defined as the characteristics and effects of the landscape surrounding a habitat fragment (the matrix) on the ecological processes and patterns within a habitat fragment (Collinge, 2009). Ohlemüller *et al.* (2006) found in their study on the invasibility of indigenous forest fragments by alien species in New Zealand that the species composition of the surrounding matrix may have an effect on the species composition within the remnant, that is, alien species were lower in forest remnants surrounded by greater native vegetation cover. The idea of landscape context can also be applied to remnants enveloped in a matrix of urban development. Their urban surroundings apply unique pressures on them, differing from the pressures applied from natural or agricultural matrices (Collinge, 2009). Other studies have also found that the matrix habitat type and quality may affect avian species abundance and richness (Dunford & Freemark, 2004; Hamer *et al.*, 2006; Litteral & Wu, 2012); the local extinction possibility for grassland plants (Williams *et al.*, 2006); dispersal potential of grassland plant communities (Purschke *et al.*, 2012); plant species richness (Klimek, 2006; Marini *et al.*, 2008); weed plant species diversity (Gaba *et al.*, 2010; Gabriel *et al.*, 2005; Roschewitz *et al.*, 2005); and exotic plant species richness (Brady *et al.*, 2009).

2.6 Plant species– and functional diversity

“Understanding the role of biodiversity in ecosystem processes is important for practical reasons, because it has implications for how humans should respond to biodiversity loss.”(Begon *et al.*, 2006).

2.6.1 Plant species diversity

Plants act as the basis for maintenance of life on earth and provide an array of goods (i.e. food and shelter) and services (i.e. oxygen production through photosynthesis and maintenance of biogeochemical cycles) from which humans benefit daily (Henry, 2005). Diversity of biotic communities may be determined by local factors (e.g. abiotic condition, disturbance and competition) interacting with landscape structure (Hillebrand & Blenckner, 2002; Niemelä, 1999b). The most important and comprehensible plant species diversity measure is species richness, which may be used in association with other indices such as evenness, distribution, variation and abundance (Farinha-Marques *et al.*, 2011). The diverse characteristics of plant species contributes to ecosystem functioning which include resistance and resilience to disturbance (Chapin *et al.*, 1995; Loreau *et al.*,

2001; McNaughton, 1977; Pimm, 1984; Schulze & Mooney, 1993; Tilman *et al.*, 1998), and primary production (Loreau *et al.*, 2001; Reich *et al.*, 2004; Wilsey & Potvin, 2000).

2.6.2 Plant functional diversity

“Species diversity has functional consequences because the number and kinds of species present determine the organismal traits that influence ecosystem processes.” (Chapin *et al.*, 2000)

Functional composition (the presence of certain plant functional types or traits) and functional richness, rather than species richness, have been found to better reflect the rates and magnitudes of ecosystem processes (Diaz & Cabido, 2001). This approach may aid in the simplification of floristic complexity, and to understand the effects and responses of species within an ecosystem with regards to key ecological processes (Pla *et al.*, 2012). Functional diversity has been defined as the functional attributes of organisms, which includes the value, range, distribution and abundance of these attributes within a biological community (Diaz *et al.*, 2007; Hooper *et al.*, 2005). Tilman (2001) defines ecosystem function as *“the way in which an ecosystem operates”*, and functional diversity as *“those components of biodiversity that influence how an ecosystem operates or functions”*.

There has been a growing body of literature focusing on functional diversity instead of the traditional taxonomic diversity, and how functional diversity affects biota and ecosystem processes (Table 2.3). According to Mason *et al.* (2005), functional diversity is important for predicting the rate and consistency of ecological processes within biotic communities.

Table 2.3: Literature summary of some functional diversity studies.

Functional diversity effects	Reference
Disturbance (logging of tropical trees)	Baraloto <i>et al.</i> , 2012
Ecosystem processes (plant productivity)	Reich <i>et al.</i> , 2004; Roshcer <i>et al.</i> , 2012; Tilman <i>et al.</i> , 1997
Ecosystem services	Lavorel <i>et al.</i> , 2011
Estuarine fish communities	Villéger <i>et al.</i> , 2010
Impacts of land-use intensification	Pakeman, 2011
Plant communities	Tilman <i>et al.</i> , 2001; Walker & Langridge, 2002
Resilience to disturbance or invasion	Dukes, 2001
Soil processes	Heemsbergen <i>et al.</i> , 2004; Hooper & Vitousek, 1998; Sutton-Grier <i>et al.</i> , 2011

Measuring functional diversity can be quite complicated, therefore aspects (such as species richness) may be measured and used as correlates for functional diversity (Diaz & Cabido, 2001; Tilman, 2001). It is widely accepted that the functional diversity of a given ecosystem will be higher in the presence of more species, as these suite of species will contain a greater variety of traits (Tilman, 2001; Hooper *et al.*, 2005). Functional diversity may also be measured using the number of functional groups or types (see section 2.5.2.2), where species are grouped together based on similarities in their functional traits (Tilman, 2001). Greater functional type diversity should strongly reflect greater functional diversity (Tilman, 2001).

2.6.2.1 Plant functional traits

“When you look at vegetation, you can concentrate on the things you see (plants or species) or on the properties of these things (the traits of plants).” (Shipley, 2010)

In biology there has been much debate as to whether certain traits and their functions identified in species are the result of the species adapting to the environment, or merely a fabricated human concept; and on which scale or level of biological organisation beneficial properties and processes must be ascribed (Calow, 1987). 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). Species traits that have substantial effects on ecosystem processes are those that modify the flux of soil resources (such as nutrients and water), affect the trophic structure of communities, and influence the dynamics of disturbance regimes (Chapin *et al.*, 1997).

Violle *et al.* states in their 2007 paper *“Let the concept of trait be functional!”* that approaches based on the traits of species are a tool used extensively in ecological research. This approach is of increasing interest when ecological questions are to be answered at the biome, landscape, or ecosystem scale (Keddy, 1992). Such *“ecological questions”* may include concepts related to the response of vegetation to alterations in the environment (Cornelissen *et al.*, 2003). These alterations include changes in climate, natural disturbance regimes and land use.

Plant functional trait- and diversity research has been applied to urban areas (Aronson *et al.*, 2007; Duncan *et al.*, 2011; Knapp *et al.*, 2009; Knapp *et al.*, 2008; Knapp & Wittig, 2012; Schleicher *et al.*, 2011; Thompson & McCarthy, 2008; Williams *et al.*, 2005; Williams *et al.*, 2009). For example Aronson *et al.* (2007) investigated certain life history traits such as fruit type, life form, and origin of woody plant invaders in the New York metropolitan area. They found that the most successful plants in the urban landscape were alien deciduous shrubs, trees and broad-leaved vines with animal-dispersed fleshy fruits. These traits are characteristic of invaders in the unique urban environment of the New York metropolitan area, and are responsible for the increased distribution and persistence of these species in the altered urban landscape. Subsequently Aronson *et al.* (2007) could recommend that alien species possessing these traits should not be introduced to the city. Such species traits are defined as functional response traits – certain properties of a species resulting from a response to certain environmental elements, thus where function affects form (Gitay & Noble, 1997; Lavorel *et al.*, 1997; Lavorel & Garnier, 2002; Shugart, 1997; Walker *et al.*, 1999).

Additionally species properties may be regarded as having an effect on the functions within ecosystems (functional effect traits), where form affects function (Gitay & Noble, 1997; Lavorel *et*

al., 1997; Lavorel & Garnier, 2002; Shipley, 2010; Shugart, 1997). An example of this is the presence of nitrogen-fixing plants with the ability to access nitrogen in the atmosphere that may increase nitrogen availability in the soils of the ecosystem they inhabit (Levine *et al.*, 2003). For instance, Vitousek *et al.* (1987) found that in the presence of *Myrica faya*, an exotic nitrogen-fixing tree in Hawaii, the nitrogen availability was much greater in sites containing *Myrica faya* than in sites without it. In another study Angers & Caron (1998) found that the roots of plants are continuously forming macropores within soils, allowing for further root penetration, soil aeration and water storage and movement within soils, therefore plants affect soil properties and processes.

Another distinction within plant functional trait approaches is between ‘soft’ traits and ‘hard’ traits. Soft traits are traits that are easily quantified for a great number of sites and species, and include canopy height, dry matter content, flowering period, lateral spread (tufted or creeping), leaf dry weight, and specific leaf area (Hodgson *et al.*, 1999). Although soft traits are easily measured, they do not necessarily play a direct functional role in ecosystems. Hard traits, on the other hand, are much more difficult to measure, but have a distinct functional task, and reflect plant ecological response and effects more efficiently (Lavorel & Garnier, 2002). Soft traits are said to be effective correlates of harder traits (Figure 2.2), and are therefore usually recommended, due to quicker uncomplicated measurement (Cornelissen *et al.*, 2003), for use in studies on floristic change and ecological processes.

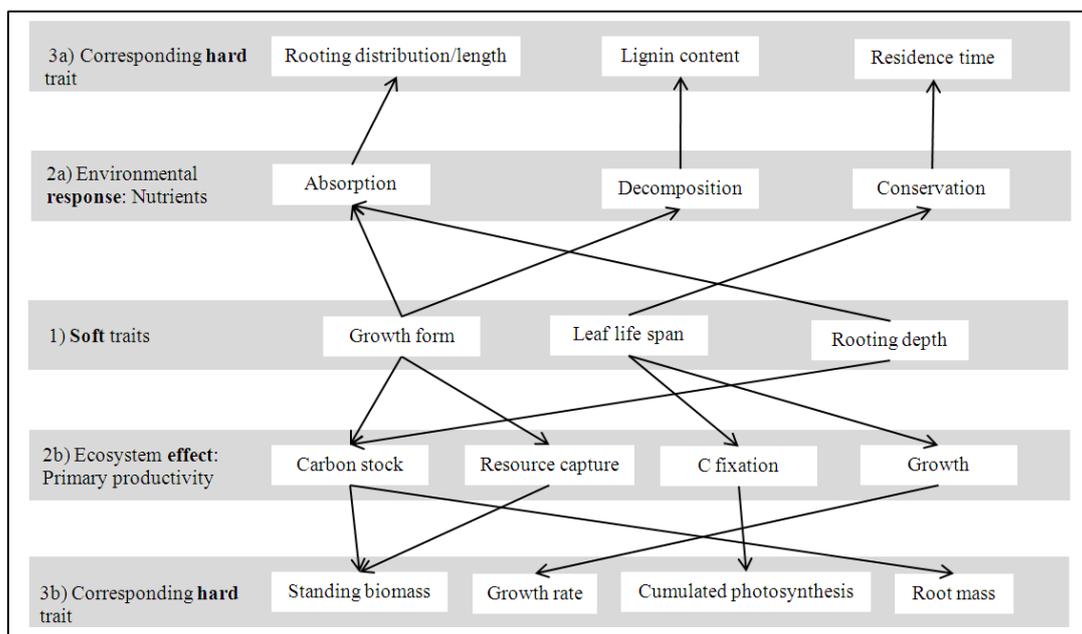


Figure 2.2: Soft traits (a) and their response to (2a) /effect on (2b) environmental conditions, as well as the correlating hard traits (3a & 3b) (adapted from Lavorel & Garnier, 2002).

Usually the focus of a functional approach is predominantly on the most abundant species or the species with the largest biomass, as these species will play the largest part in regulating ecosystem properties (Grime, 1998). But one must not forget that small, less abundant species may have substantial effects on the way an ecosystem functions. From this idea the concept of “keystone” species was developed. Keystone species are species that are ecologically unique (Chapin *et al.*, 2002), and that have a much larger effect on an ecosystem than was originally expected or predicted in regards to their biomass or abundance (Bond, 1993; Power *et al.*, 1996). An example of a plant keystone species would be nitrogen fixers, such as many legume plants, which are actively part of the nutrient pathways and rates.

2.6.2.2 Plant functional types (PFT's)

Non-phylogenetic classification of organisms when recording the structure and function of ecosystems has received increasing attention (Gitay & Noble, 1997; Solbrig, 1994). Species may be grouped together based on their shared biogeochemical abilities and attributes (Naeem *et al.*, 1995; Shugart, 1997; Vitousek & Hooper, 1994) to create functional groups or types (PFT's).

Plant species consist of various morphological and physiological traits, and in order to help simplify this complexity within species, PFT's may be identified (Tilman, 2001). The loss of such a functional group (such as nitrogen fixers) would alter important ecosystem function processes (Naeem *et al.*, 1995). Gitay and Noble (1997) define functional types as biotic elements of an ecosystem that possess similar traits, allowing them to fulfil similar functions within an ecosystem, or respond similarly to certain environmental conditions. According to Díaz and Cabido (1997) the identification of PFT's, as well as the estimation of their abundance is important for the ecosystem function assessment, as different PFT's fulfil different roles in the energy and matter fluxes within ecosystems.

Although defining PFT's has received much attention Petchey *et al.* (2009) proposed some major drawbacks of this approach: 1) intraspecific differences within a PFT may be overlooked, 2) functional group richness depends on the number of PFT's that have been identified (Petchey & Gaston, 2002), and 3) no method exists for deciding how dissimilar species should be classified into different PFT's. These challenges have given rise to the development of functional diversity metrics or indices.

2.6.2.3 Functional diversity indices

The most recent development in functional diversity research and the quantification of functional diversity is the use of functional diversity indices. These indices usually describe the extent and manner species fill a hypothetical functional niche space (Schleuter *et al.*, 2010). Many different indices of functional diversity have been proposed (Table 2.4). In this study functional diversity will

be quantified using functional diversity indices. Therefore this concept is described in detail in *Chapter 5*.

Table 2.4: Some functional diversity indices that have been proposed.

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 evenness	FEve	Villéger <i>et al.</i> , 2008
Functional divergence	FDiv	Villéger <i>et al.</i> , 2008
Functional dispersion	FDIs	Laliberté & Legendre, 2010
Functional specialisation	FSpe	Villéger <i>et al.</i> , 2010
Functional attribute diversity	FAD	Walker <i>et al.</i> , 1999

2.7 Landscape functionality

“Disturbances affect how well landscapes function to conserve resources and maintain biodiversity by degrading fine-scale patch structures and habitats, accelerating processes such as water- and wind-driven erosion (little things count).” (Ludwig, 2005).

It is important to define *landscape function* in the context of what is being studied and from which perspective. The terms *landscape function* and *ecosystem function* may be synonymous. Ecosystem function is used to describe the processes (services) and properties (goods) of ecosystems from which humans eventually benefit in some way or another, be it food and water production, waste management, nutrient cycling, climate control, amelioration of pollution, or biodiversity (Costanza *et al.*, 1997; Daily *et al.*, 2000; De Groot, 2006; NWDACE, 2008). The other definition of ecosystem function refers only to the internal processes occurring at specific scales within the ecosystem such as biogeochemical processes (nutrient cycling, infiltration, and maintaining the pathways of energy, material and species) (De Groot, 2006; Forman & Godron, 1986). For the purpose of this study the will focus on the latter definition of ecosystem function, and quantify it using Landscape Function Analysis (LFA) (Tongway & Hindley, 2004), which focuses on fine-scale biogeochemical landscape function. The aim is to investigate the possible changes that urbanisation inflict on the functioning of landscapes, specifically the landscapes of the Rand Highveld Grassland vegetation unit, and not to focus on the processes exclusively benefiting the human race.

An important characteristic of any landscape is that it is composed of a mosaic of patches at various scales (Cadenasso *et al.*, 2003; McGarical & Marks, 1995). LFA is concerned with fine-scale patchiness, where a patch may be defined as a discrete, identifiable unit differing from adjacent areas

in structure, position and function, and retains resources that pass through the system (Cadenasso *et al.*, 2003; Tongway & Hindley, 2004). An interpatch, on the other hand, may be defined as a unit between patches where vital resources, such as water, topsoil and plant litter are not retained, but transported away and may eventually be lost from the system (Tongway & Hindley, 2004). This gives rise to the concept of “critical fetch-length” within a landscape, which may be defined as the distance of unobstructed resource transport by water or wind through the system, where runoff occurs freely, and resources are lost from the system (Kakembo, 2009; Tongway & Ludwig, 1997). The “critical fetch-length” of a landscape can also be described as the value of interpatch length where the momentum of out-flowing resources is greater than the capacity of the patch system to regulate it. This will result in a “leaky” system that does not actively conserve resources.

2.7.1 The Trigger-Transfer-Reserve-Pulse Framework

To understand how a landscape functions, and why a landscape may be considered as being functional, knowledge about the processes taking place in landscapes (to enable it to function effectively as a biogeochemical or biophysical system) (Tongway & Hindley, 2004) must be obtained. Ludwig and Tongway (1997) presented the “Trigger-Transfer-Reserve-Pulse” (TTRP) framework (Figure 2.3), which is the basic conceptual framework underpinning Landscape Function Analysis (LFA). The two main aspects of this framework are (1) negative effects such as the pathways of loss of resources, for example erosion, and (2) the feedbacks such as the provision of goods and services and utilisation of resources to serve as a reserve, for example to secure seed pools, organic matter storage, and biomass production in the system.

The TTRP-framework considers landscapes to be temporally and spatially dynamic, interacting systems that function to retain vital resources (Ludwig & Tongway, 1997), and forms part of the LFA conceptual framework. The two main aspects of this framework are the loss of resources from the system and the utilisation of resources by the system. A system that loses vital resources is considered as a “leaky” or dysfunctional landscape that does not function optimally and sufficiently (Tongway & Hindley, 2003). Systems that are able to capture, retain, utilise and cycle vital resources may be considered healthy and functional. The four main processes that form the basis for this framework, namely trigger, transfer, reserve and pulse, are intertwined. Within and between each main element of the framework various processes operate.

A trigger event such as rainfall initiates the sequence of processes in the TTRP-framework (Tongway & Ludwig, 2006), and plays a substantial role in shaping landscapes (Hodgkinson & Freudenberger, 1997). Rainfall that does not infiltrate into the soil immediately will run off (3) and the resources that are absorbed into the system will form part of the “reserve” of the system (1) (Tongway & Hindley, 2004) (Figure 2.3). The capacity of the runoff is determined by the magnitude of the trigger event

(e.g. the volume of the rain). This, in turn, together with the slope steepness of the landscape, determines the severity of vital resources being eroded from the system (Ludwig & Tongway, 1997). A steeper slope will result in more loss from the system as the velocity of the runoff will prevent it from infiltrating.

The transfer component of the TTRP-framework involves that the runoff, that contains vital materials such as soil particles, litter, and nutrients, is consequently moved or transferred horizontally (1) across the landscape (Ludwig & Tongway, 1997; Tongway & Hindley, 2004) (Figure 2.3). Wind may also act as agent to transfer materials through a system. Patchiness in the landscape will obstruct the transfer of resources in the system. A trigger event, and the consequent transfer of runoff, may have detrimental effects on a system, resulting in poor infiltration, low stability of the soil and thus soil erosion.

Materials that form part of the reserve of the landscape is captured from runoff or infiltrated directly from the trigger event (Ludwig & Tongway, 1997) (Figure 2.3). The presence or absence of patches and interpatches will determine how much of the trigger substance will infiltrate the system (Tongway & Hindley, 2004). The more patches there are, the more rain is likely to infiltrate the system; whilst more interpatches will result in more runoff. The materials that have been captured within the system may once again be transferred out of the reserve of the system though factors such as rain, wind and erosion (3) or it may activate a pulse in the system (Ludwig & Tongway, 1997; Tongway & Hindley, 2004).

The pulse in the TTRP-framework may be defined as the response of fauna and flora to the trigger event such as rainfall (2) (Tongway & Hindley, 2004). The favourable conditions contained by the reserve of the system create a burst of life for vegetation and animals alike. From the pulse element the energy in the system may follow three pathways: back to the reserve (ploughbacks), back to creating patches (feedbacks) or be lost from the system entirely (Ludwig & Tongway, 1997). The resources in the system is cycled back and returned to the reserve though processes such as seed pool replenishment, the decomposition of dead material, and the concentration of resources by soil fauna (Hodgkinson & Freudenberger, 1997; Tongway & Hindley, 2004). This involves the ploughbacks (5), and the reserve of the system has been replaced by more resources. Tongway and Hindley (2004) describe the feedback (6) of the system as the materials that will once more be transferred in the system where it may be captured by, or lost, from the system (Figure 2.3). Therefore it may also create more patches which will cause obstruction and absorption processes (Hodgkinson & Freudenberger, 1997; Ludwig & Tongway, 1997; Tongway & Hindley, 2004). Materials that have already been utilised by the system and forms part of the pulse may be lost entirely (6) through herbivory, harvesting, fire, and deep drainage (Tongway & Hindley, 2004).

According to Tongway *et al.* (2003), a degraded landscape may also be characterised as a landscape in which the distribution and regulation of scarce resources has been reduced by a disturbance regime (e.g. unsustainable grazing). Such landscapes may be characterised by increased soil compaction or physical crusting, resulting in decreased infiltration and potential, including losses in organic matter (Snyman & Du Preez, 2005), among many other properties. Exploitation of natural resources and loss of spatial heterogeneity (fine-scale patchiness), as in urbanised areas, may permanently alter a landscape at different scales, creating a dysfunctional landscape that might not be able to return to its previous, more functional state.

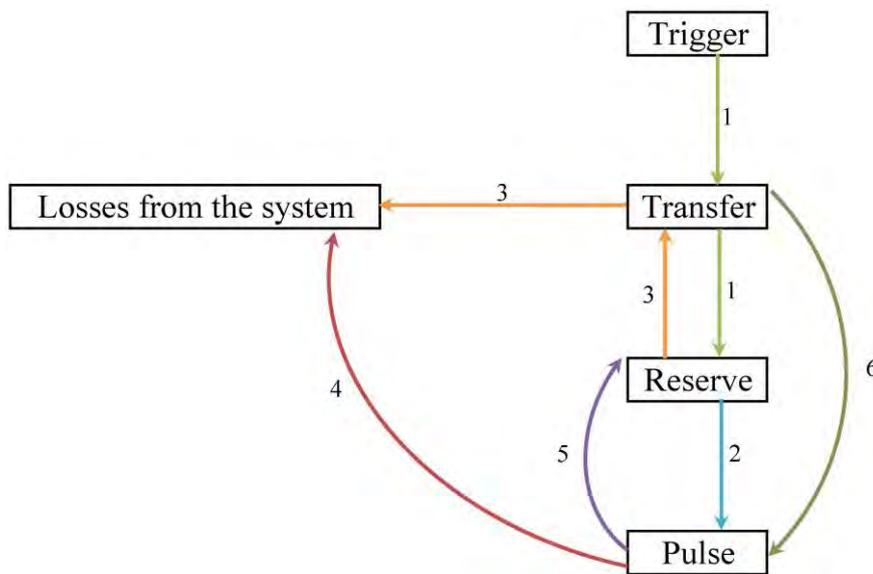


Figure 2.3: The “TTRP”-framework: processes representing the capture and loss of resources from a system (after Ludwig & Tongway, 1997; Tongway & Hindley, 2003; Tongway & Hindley, 2004). The arrows represent the flow of materials between the main components (Ludwig & Tongway, 1997).

2.7.2 The landscape functionality continuum

A continuum of landscape functionality exists with fully-functional landscapes on the one end of the continuum and dysfunctional landscapes on the other end (Freudenberger & Noble, 1997). Specific management objectives will determine where on the functionality continuum a landscape will occur. Functional landscapes can then be described as being “better” or “acceptable” for a specific land use, but underpinned by an objective analysis of its functional state. Tongway and Ludwig (1997) and Ludwig *et al.* (2005) described a functional landscape as having no or little losses from the system, thus being a conserving system. High fine-scale patchiness is an indicator of functionality, acting as the physical obstruction that captures resources for utilisation by the system. At the other end of the functionality spectrum dysfunctional landscapes have fewer, less connected patches to intercept,

capture and conserve vital resources needed for the landscape to function sufficiently (Ludwig *et al.*, 2005; Tongway & Hindley, 2004; Tongway & Ludwig, 1997; Tongway & Ludwig, 2006) and larger fetch length (average distance between two vegetated patches thus the length of unobstructed resource transport by water or wind (Kakembo, 2009; Tongway & Ludwig, 1997). Losses from such landscapes are excessive deeming them unable to sustain life. The ecological consequences of landscape dysfunction identified by Freudenberger *et al.* (1997) includes: (1) lower infiltration – less patches will result in less resources being captured, (2) increased loss of soil sediment through erosion, (3) loss of biodiversity – vegetation patches themselves enhance biodiversity, and serve as habitats for a wide variety of organisms

2.7.3 The importance of vegetated patches

Spatial patchiness over various scales has been recognised as extremely important in terrestrial ecosystems (Chapin *et al.*, 2002; Wu & Loucks, 1995). The fact that patches concentrate resources and prevents soil erosion is supported by a variety of previous studies such as Ludwig *et al.* (1999a, 1999b, 2005), Ludwig and Tongway (1995), Schlesinger *et al.* (1996), and Vásquez-Méndez *et al.* (2010).

Schlesinger *et al.* (1999) found during a rainfall simulation experiment that bare soil (interpatches) produced more runoff than grass patches, and that nutrient losses (specifically nitrogen) from systems with more bare soils were greater. Other authors also found similar results: for instance Reid *et al.* (1999) found that bare patches were characterised by most runoff generation and most severe erosion; also bare soils adjacent to vegetation patches (upslope) were less eroded. A patch will obtain resources from its surroundings and consequently expand and develop as to increase fertility in the region. The more the patch *‘develops’* the bigger it becomes and the more resources it will capture, creating a healthy, self-sustaining cluster. Vegetation patches trap excess water from rainfall for utilisation by the system. Organic matter, and soil nutrients and particles that is also transported by flowing water will also be captured by patches (Ludwig *et al.*, 1999b), creating *‘islands of fertility’* within a matrix of infertility (Ludwig *et al.*, 2001). The formation of these fertile units within a landscape will also attract fauna (such as soil biota) and other flora (Bastin *et al.*, 2002). Even mortality and decomposition of plants and animals associated with patches will be advantageous as they will enrich the soil with nutrients (Ludwig *et al.*, 1999b). Increased concentration of nutrients and water will create a microhabitat for the establishment of other plant species as patches also capture seeds in water runoff. Fine-scale patches thus maintain biological diversity in a landscape (Ludwig *et al.*, 1999a).

Patches on finer scales play an important role in preventing and controlling soil erosion. The velocity of runoff will determine the intensity of erosion (Fox & Bryan, 2000). Patches serve as obstructions to

slow the flow of water inhibiting natural resources and soil particles from being swept away, and thus preventing and mitigating the effects of soil erosion. Fine-scale patchiness of steeper slopes is extremely important as the increased slope gradient will increase the velocity of runoff and thus increase the severity of soil erosion, resulting in decreased landscape function indices (Rezaei *et al.*, 2006). The infiltrability of soil is also increased by the presence of vegetated patches through enhancing soil processes and biological activity (Ludwig *et al.*, 2005). Bare soil interpatches are thus the sources of runoff, and nutrient- and soil loss, whilst vegetated patches acted as sinks, capturing and conserving these resources. This has many implications for various processes characterising functional, resource conserving systems - vegetated patches encourages additional plant growth as more soil and water is being made available within the patch area (Ludwig *et al.*, 2005).

2.7.4 Landscape functionality in urban landscapes

Limited Landscape Function Analysis (LFA) studies have been performed in an urban context, but research has been done on various components of landscape functionality in urban landscapes that relate to the main LFA functionality parameters (stability, infiltration, and nutrient cycling). These components of landscape functionality are related to soil properties and processes, and fine-scale vegetation patchiness (Tongway & Hindley, 2004). The removal of vegetation may compromise resource-conserving fine-scale heterogeneity of urban environments resulting in reduced aerial cover, exposed soil susceptible to crust formation, erosion and compaction, which in turn also affects the infiltration capacity of the soil (Craul, 1985). Green *et al.* (2009) was the only study encountered in this literature review where LFA was performed in an urban environment in Australia. They quantified the urban landscape function in terms of infiltration capacity in order to determine and ameliorate flood risks (Green *et al.*, 2009).

Urban soils are often compacted and characterised by a soil surface crust which may be impervious resulting in limited infiltration of nutrients and water into the soil (Craul, 1985). The compaction of urban soils (be it mechanical or as a result of treading) reduces soil porosity and infiltrability of the soils which results in increased runoff and erosion (Sauerwein, 2011). This affects both the infiltration capacity and soil surface stability of urban landscapes. Zipperer and Gutenspergen (2009) found that trampling of urban woodland soils due to human activities resulted in increased erosion and reduced infiltration rates compared to rural woodlands. Decreased infiltration capacity in urban areas may increase the risk of floods (Green *et al.*, 2009).

The soil present in urban areas does not generally contain litter abundances, and may result in disrupted nutrient cycles (Craul, 1985). McDonnell *et al.* (1997) studied oak forests along an urbanisation gradient and found that leaf litter in urban forests were of poorer quality than their rural counterparts, but that the litter decomposed and nitrified at quicker rates.

2.8 Biodiversity and ecosystem functioning

“Will depauperate, but nevertheless intact, ecosystems (containing primary producers, consumers and decomposers) perform differently from the more species-rich systems from which they are derived?” (Naeem *et al.*, 1995).

The speedy loss of species has ignited a growing interest in the relationship between biodiversity and ecosystem stability. Hooper *et al.* (2005) states that: “when discussing effects of biodiversity on ecosystem functioning it is important to be specific about which components of biodiversity are affecting which components of functioning”. This section is commenced by defining various concepts relevant to biodiversity-ecosystem functioning relationships.

Alberti (2008) broadly defined *ecosystem function* in an ecological sense as the “ability of the Earth’s processes to sustain life over a long period of time”. The term ecosystem functioning may include ecosystem properties alone (Hooper *et al.*, 2005), or also include ecosystem services and goods (Costanza *et al.*, 1997; Christensen *et al.*, 1996; Daily *et al.*, 2000; De Groot, 2006). Ecosystem properties are the material and nutrient reserve (for example organic matter), as well as the processes within an ecosystem (such as decomposition) (Hooper *et al.*, 2005). Ecosystem goods are those ecosystem attributes which have an anthropogenic worth or market value (such as recreation or food) (Costanza *et al.*, 1997; Chapin *et al.*, 2002; Hooper *et al.*, 2005), whilst ecosystem services may be defined as conditions and processes within ecosystems which promotes human welfare (such as climate regulation, nutrient cycling, hydrologic and atmospheric cycles) (Christensen *et al.*, 1996; Daily, 1997). Although the variability of ecosystem attributes across ecosystems may be extensive, the properties are not by nature “good” or “bad” (Hooper *et al.*, 2005).

According to Naeem *et al.* (2009) biodiversity-ecosystem functioning is based on a framework (Figure 2.4) where biodiversity, ecosystem functioning, ecosystem services (ecosystem functions that benefit human), and human wellbeing are linked by causal relationships.

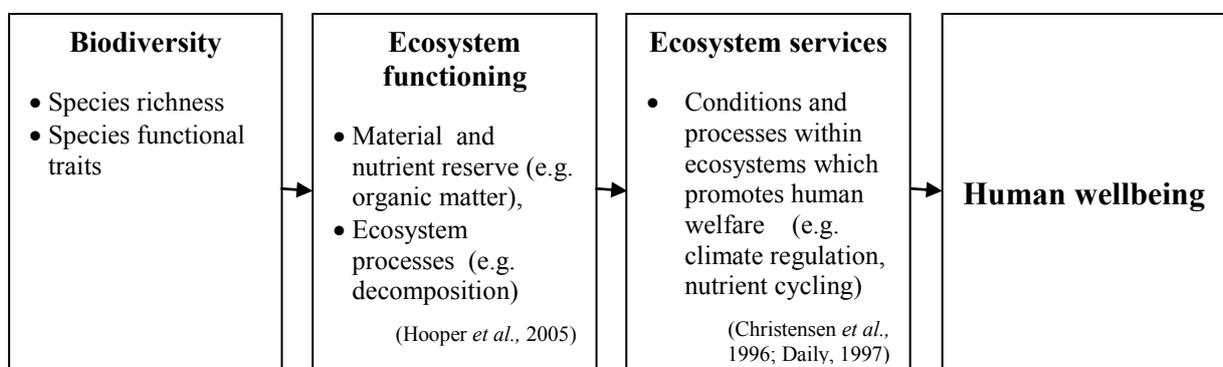


Figure 2.4: Biodiversity – ecosystem functioning framework (after the Millennium Ecosystem Assessment (2003) as well as Naeem *et al.* (2009)).

Early biodiversity-ecosystem function research (such as MacArthur 1955) focused on primary production as the most important and easiest quantifiable ecosystem function (Johnson *et al.*, 1996). Results suggested that a loss in biodiversity causes a loss in production, implying that human wellbeing would therefore also decrease (Naeem *et al.*, 2009). The fact that monocultures consisting of only a single or only a few species could have a higher production-output than a system that is very species rich, posed a problem to the findings of such research (Naeem *et al.*, 2009). It was also found that stability could be affected by a decline in biodiversity, and that biodiversity acts as species' insurance against ecological perturbation, keeping communities stable in the face of disturbance and environmental change (McNaughton, 1977; Pimm, 1984; Schulze & Mooney, 1993; Tilman *et al.*, 1998).

There are two opposing views in the "diversity-stability debate". On the one side is the concept that species are unique in their traits, and that the high variability of these traits in diverse ecosystems will provide the system with higher resistance to disturbance and alien invasions (Diaz & Cabido, 2001; Dukes, 2001; Elton, 1958; Pimm, 1984; Pokorny *et al.*, 2005). The other perspective regarding diversity-stability considers species to be similar in the roles they fulfil in ecosystems, therefore diversity does not determine ecosystem functioning.

Various authors have argued that the relationship between ecosystem functioning and biodiversity can be used as valid motivation for the conservation of biodiversity (Chapin *et al.*, 1997, 1998; Edwards & Abivardi, 1998). Schwartz *et al.* (2000) however states that in order for diversity-stability relationships to drive conservation practices, firstly a broad array of species must be responsible for maintaining ecosystem processes, entailing that to conserve ecosystem function is to conserve most of the species within the ecosystem. Secondly: ecosystem function should depend on native species, for if ecosystem processes may be maintained by conserving exotic species, the protection of native diversity would be nullified (Schwartz *et al.*, 2000).

There are several hypotheses concerning the functional role of species diversity on ecosystem processes and properties. The diversity-stability hypothesis, which states that species diversity stabilises properties of ecosystem functioning (Elton, 1958; McNaughton, 1977), became widely accepted. Other hypotheses such as the rivet hypothesis (Ehrlich & Ehrlich, 1981), the redundancy hypothesis (Walker, 1992), and the idiosyncratic hypothesis (Lawton, 1994) were introduced as alternatives for the diversity-stability hypothesis (Table 2.5).

Table 2.5: Hypotheses concerning the relationship between species diversity and ecosystem function.

Rivet hypothesis	Species are compared to the rivets keeping an aeroplane together. An undetermined loss of rivets may cause the aeroplane to crash, that is, loss of species may cause ecosystem collapse. (Ehrlich & Ehrlich, 1981).
Redundancy hypothesis	Species may be organised into functional groups. The role of a species that is lost may be fulfilled by a species with a similar functional purpose, that is, certain species may be expendable in terms of ecosystem continuation (Walker, 1992).
Idiosyncratic hypothesis	There might not be a relationship between ecosystem function and species diversity (Lawton, 1994).

2.8.1 Biodiversity and the stability of ecosystem functioning

“If biodiversity affects ecosystem properties, is there a point at which changes in properties might adversely influence human welfare?” (Hooper *et al.*, 2005).

Stability is defined by Tilman (2001) as the level of resistance and resilience to change due to disturbance, and the dynamics of returning to a pre-disturbance state. The concept of the diversity-stability hypothesis was first introduced by MacArthur (1955). He made three assumptions concerning the fluctuations of animal populations and a measure for community stability. These assumptions were: (1) that energy entering a community does not vary temporally, (2) that the time energy is retained by one species before being transferred to a next does not vary, and (3) that the variation within a population is dependent on the food energy availability (MacArthur, 1955). Because natural populations of species often fluctuate, one of these assumptions is not holding, and these fluctuations may be caused by phenomena such as predator-prey relations, or environmental variations (MacArthur, 1955). He states that *“In some communities the abundance of species tends to stay quite constant, while in others the abundances vary greatly. We are inclined to call the first stable and the second unstable”*. Thus: the more species interactions exist on the trophic level within a population, the greater the shared ability of a population to maintain its abundance post-disturbance (Johnson *et al.*, 1996).

McCann (2000) states that diversity does not necessarily drive the diversity-stability relationship, but an ecosystem’s ability to contain species that react differently to environmental conditions and change, may determine the stability of that system. The results of the Tilman and El Haddi’s (1992) long-term study on the effects of drought on grasslands supported the diversity-stability hypothesis. They found that species rich plots were more resistant to drought, because the probability of such plots containing drought-resistant species was higher. They also concluded that species-poor plots were less resilient; requiring more time to recover to the state it was in before the drought. Similar

results were also found by Tilman and Downing (1994). Thus: a diverse suite of species, having unique effects on ecosystem processes, may help to improve ecosystem resistance to environmental variation (Chapin *et al.*, 2002) as one species compensates for the loss of another (Petchey *et al.*, 2009).

2.9 Summary

Even though areas that have been extensively modified by humans may be small and degraded, they are the remains of a once productive landscape, and may still be very important for conservation, despite their small size and poor condition (Cilliers *et al.*, 2008; Lindenmayer & Fischer, 2006).

The following aspects with reference to the elements that will be examined in this study were explored in this literature review chapter:

- Urban- and landscape ecological concepts
- Grasslands in South Africa, especially the Rand Highveld Grassland vegetation unit where this study was conducted.
- The characteristics of urban ecosystems and vegetation and the use of an urbanisation gradient approach to study them.
- Landscape modification, fragmentation, and the influence of matrix characteristics on habitat remnants.
- Plant species diversity and plant functional diversity.
- Ecosystem functioning and fine-scale biogeochemical and biogeophysical functioning of landscapes.
- The relationships between plant species- and functional diversity and the functioning of ecosystems.

In the current study on grassland fragments in the Tlokwe Municipal area, all the above mentioned aspects will be addressed. From the literature reviewed in this chapter it is clear that extensive research has been done on the various concepts relevant to this study. The challenge is to draw connections between these concepts and synthesise them into a complex whole.

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