PATTERNS AND DETERMINENTS OF SPECIES RICHNESS IN MESIC TEMPERATE GRASSLANDS OF SOUTH AFRICA

D.B. HOARE

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PATTERNS AND DETERMINENTS OF SPECIES RICHNESS IN MESIC TEMPERATE
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By

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In accordance with Rule G4.6.3, I hereby declare that the above-mentioned treatise/dissertation/thesis is my own work and that it has not previously been submitted for assessment to another University or for another qualification.

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SUMMARY

The aim of this study is to gain a predictive understanding of the patterns and determinants of plant biodiversity in temperate, mesic grasslands of South Africa with a primary focus on the geographical area of the Eastern Cape. From a review of the literature on hypotheses explaining diversity (Chapter 2) it was possible to formulate a number of hypotheses that could be tested to explain species richness patterns in Eastern Cape grasslands. This thesis is organised so that each main chapter deals with a specific body of theory concerning the explanation of diversity patterns.

A detailed description of the study area is provided (Chapter 3), including environmental variation and a description of major vegetation patterns. A summary is provided of grassland plant community patterns, as determined by phytosociological studies in the study area. A multivariate analysis of environmental variables was undertaken to determine which variables contributed the most towards explaining environmental variation in the study area and to determine whether any variables co-vary, a possible problem for any multivariate analysis in later chapters. Altitude produced one of the strongest gradients in the study area. There were a number of variables that were correlated with altitude, most notably temperature. Rainfall co-varied partially with altitude, but there was also a strong rainfall gradient perpendicular to the altitude gradient.

A description of species richness, diversity and evenness patterns at the plot scale within different grassland plant communities of the Eastern Cape is provided in Chapter 4. To determine whether the environment acts differently on different growth forms, the contribution to species richness by different major growth forms is analysed. Furthermore, since the majority of literature attempts to explain diversity in terms of environmental factors, it was necessary to analyse the relationship between species richness and various environmental variables. The results indicate that there is high variation in species richness both within and among grassland communities. Forbs make the most significant contribution to overall species richness per 100 m², followed by grasses. Variance in richness of all species together is not significantly related to environmental variables in mesic grasslands, but is significantly related to environmental variables in semi-arid grasslands. The result of greatest interest from this chapter is the fact that richness amongst different life-forms in the same place is explained by different environmental factors, indicating that the environmental factors that affect coexistence of species have a different effect on different life-forms.

A classification of all the species of the dataset into plant functional types using a multivariate approach based on functional traits was conducted (Chapter 5). The grass species were classified into 16 functional types and the forbs into 14 functional types. The functional type classification provided the opportunity for undertaking analyses to develop an understanding of
the contribution by niche differentiation towards promoting species richness (Chapter 6). The results provide evidence of niche differentiation in the grasslands of the study area and also that niche differentiation promotes species richness in the grasslands of the study area. It was found that higher rainfall grasslands are less structured by niche differentiation than semi-arid grasslands.

A regional / historical analysis is undertaken (Chapter 7) to investigate the relationship between the regional species pool and local richness, and the relationship between local richness and phytochorological diversity. Regional richness appears to have little effect in promoting local richness in grassland plant communities of the study area except at sites where there is high local richness. This provides an indication that regional richness only promotes local richness in the absence of local limiting factors. Phytochorological diversity promotes local richness, but mostly through diversity amongst species with narrow distribution ranges.

Some theories ascertain that seasonal uncertainty may provide opportunities to species that would otherwise be outcompeted and thereby promote local richness. The degree to which seasonal uncertainty and seasonality promote local richness in the Eastern Cape grasslands was therefore investigated (Chapter 8). A weak relationship exists between these variables and local species richness in grassland communities of the study area, indicating that they do not promote niche differentiation to a significant degree in the study area.

It is clear that in the grasslands of the Eastern Cape, environmental limiting factors are more important in semi-arid grasslands and species interactions are more important in mesic grasslands for structuring plant communities (Chapter 9, Discussion). Regional processes do not appear to be important in structuring local communities, but the analysis undertaken in this study shows that they may be significant when factors operating at the other two levels are overcome (species interactions and environmental limiting factors).

_key words_: plant functional types, niche partitioning, species pool, environmental heterogeneity, seasonality
CHAPTER 1: STUDY OUTLINE

Introduction

South Africa has a unique natural environment and biological diversity recognised at an international level to be outstanding. There are considered to be nine separate biomes represented in the country (Mucina & Rutherford 2006), the second largest of which is the Grassland Biome. The Grassland Biome is characterised by high overall species richness and often very high local richness. Highveld grasslands are home to almost 4000 species overall (Cowling et al. 1989), and a single 100 m² plot may contain anywhere from 8 to 60 species. Furthermore there are at least seven Centres of Endemism (van Wyk & Smith 2002, Clark et al. 2009) that occur entirely or partially within the Grassland Biome (Mucina et al. 2006a). Local richness, regional richness and endemism are not, however, evenly distributed across the Biome and it is clear that there are multiple evolutionary and ecological factors shaping these patterns. It is of both scientific and practical interest to describe and understand these patterns.

The Grassland Biome of southern Africa is part of the global Temperate Grassland Biome that is comprised of the Eurasian steppes and American prairies in the northern hemisphere, and the Argentinean pampas, Australian Alps and tussock grasslands of New Zealand in the southern hemisphere. The extent of the Grassland Biome in South Africa can be reasonably well defined on the basis of vegetation structure in combination with environmental factors. The effect of being situated at relatively high elevation in the interior plateau of the continent is important in defining the Grassland Biome. Moisture availability, minimum temperature and rainfall seasonality are three factors considered to be important in defining the distribution of the Grassland Biome (Rutherford & Westfall 1986) and distinguishing it from surrounding Biomes. The Grassland Biome can also be subdivided into Bioregions (Rutherford et al. 2006a) and vegetation types that reflect differences in environmental conditions within the Biome.

This thesis focuses primarily on the grassland vegetation of the Eastern Cape Province of South Africa, which is situated at the southern to south-western side of the Grassland Biome of South Africa. The Eastern Cape comprises an area of approximately 170,500 km². It is an area of extraordinary complexity and diversity, encompassing four areas of regional biodiversity concentration, the Albany, Pondoland, Sneueuberg and Drakensberg Centres of Endemism (van Wyk & Smith 2002, Clark et al. 2009). Environmental gradients in this area are very steep and complex leading to a rich mixture of floristic elements. A number of phytochorological zones (sensu Takhtajan 1986, McLaughlin 1994, White 1983) converge in the Eastern Cape (Goldblatt 1978; Werger 1978; Gibbs-Russell & Robinson 1981; White 1983; Cowling 1983a, 1983b; Lubke et al. 1986, 1988). This provides an ideal natural laboratory which should be taken advantage of for understanding patterns of biodiversity within the Grassland Biome. An
understanding of diversity patterns in the region can lead to an understanding of ecosystem structure and function, resulting in better management of the area, especially with respect to rangeland conservation planning and understanding the potential effects of global climate change. The region has vast economic potential from the perspectives of eco-tourism and agriculture (commercial and subsistence). Different management practices have an effect on species composition and thus diversity and it is important to understand this relationship in order to predict their effects on diversity patterns.

It is the intention of this study to investigate the factors that contribute to species richness in grasslands of the southern to south-western part of the Grassland Biome of South Africa, restricted to the mountains and surrounding plains of the Eastern Cape. There are a number of compelling reasons why the study of plant biodiversity patterns in the Eastern Cape should be undertaken, summarised as follows:

1. In spite of extraordinary complexity, diversity patterns in the Eastern Cape have never been adequately described or documented.
2. Descriptions of diversity patterns can enhance understanding of the way that ecosystems are structured and function in this area. It may be possible to extrapolate this knowledge to other grassland ecosystems in southern Africa.
3. Environmental gradients in this area are very steep and complex leading to a rich mixture of floristic elements. This provides an ideal system for understanding patterns across a variety of scales. Of particular interest are the steep productivity gradients in the study area, which provide an opportunity to concentrate on current diversity-productivity issues and make a contribution to debates on this topic.
4. An understanding of diversity patterns in the region can lead to more appropriate management of the area, especially with respect to setting adequate targets for different vegetation types for conservation planning purposes.
5. The region has economic potential from the perspectives of eco-tourism and agriculture (both commercial and subsistence). Different management practices have an effect on species composition and thus diversity and it is important to understand this relationship so that one can predict the effects of different management practices on diversity patterns.
6. A successful predictive description of diversity patterns can contribute to the international debate on the topic of diversity.

**Aim and objectives of study**

The aim of this study is to gain a predictive understanding of the patterns and determinants of plant biodiversity in temperate, mesic grasslands of South Africa with a primary focus on the geographical area of the Eastern Cape. A number of specific objectives include the following:
1. To describe diversity within vegetation complexes in Eastern Cape grasslands (conventional diversity measures) so as to identify areas or plant communities of exceptional diversity.

2. To gain a predictive understanding of the environmental factors controlling species richness within grassland vegetation in the Eastern Cape.

3. To gain a predictive understanding of the factors controlling species diversity (richness) across environmental gradients, and particularly to focus on the relationship between diversity and productivity within grassland vegetation in the Eastern Cape.

4. To determine the relationship between measures of diversity and plant functional attributes that promote niche differentiation within grassland vegetation in the Eastern Cape.

5. To investigate the effect of historical factors (phytogeographical and species pool) on species diversity within grassland vegetation in the Eastern Cape.

6. To determine the relationship between diversity and seasonal heterogeneity and seasonality within grassland vegetation in the Eastern Cape.

**Research questions to be addressed**

The study provides an opportunity to develop a better understanding of the potential effect of competitive interactions within grassland species, how limited resources are partitioned and how these interactions structure grassland plant communities. The objective of analyzing diversity data for the study area is to understand the relative roles of environmental factors, the outcomes of species interactions and resource partitioning, and the effect of historical processes in determining species richness at a local scale. Based on theoretical considerations and characteristics of the study area, the following hypotheses (research questions) have been listed for grasslands of the Eastern Cape:

**PATTERNS:**

1. Do species richness patterns differ between habitats or from one site to another?

**PRODUCTIVITY:**

2. Does species richness differ along environmental gradients representing productivity (favourableness)?
   3. In semi-arid grasslands, do increased moisture levels promote species richness?
   4. In moist grasslands, does reduced soil nutrient status promote species richness?

**HETEROGENEITY, SEASONALITY AND DISTURBANCE:**

5. Does habitat heterogeneity have any relationship with species richness?
6. Does seasonality (resource pulsing) have any effect on species richness or plant functional type composition?
7. Do disturbance and/or fire have any effect on species richness?

RESOURCE PARTITIONING / NICHE DIFFERENTIATION:

8. Does plant functional type richness have any relationship with species richness?
9. Does dominance of plant attributes associated with persistence have any effect on species richness?
10. Does dominance of plant attributes associated with niche differentiation have any effect on species richness?
11. Are evenness and richness correlated?
12. Does the relationship between diversity and environmental/historical factors change within different growth forms?

HISTORICAL FACTORS:

13. Does regional richness have any influence on local richness?
14. Is there a relationship between the biogeographical origins of species that occur in grassland communities and local richness?
15. Do environmental factors have any influence on species pool effects?
16. Is there a relationship between species turnover and the size of the regional species pool?

It would be ambitious to undertake to address all these questions in a single thesis—a manageable subset of these is listed below as the main focus areas of this study.

**Thesis structure**

This thesis begins by undertaking a brief review of the theoretical literature on the study of diversity and some of the controversies surrounding theories explaining diversity patterns. This is followed by a detailed description of the study area in the Eastern Cape and then a detailed description of diversity patterns at a local scale within grassland plant communities of the Eastern Cape. Following chapters each address a specific theoretical explanation for diversity patterns and use this background to attempt to explain diversity at a local scale within grassland plant communities of the Eastern Cape. The main focus areas are the following:

1. Niche differentiation and resource partitioning effects on local diversity, including a detailed analysis of diversity within different functional type groups,
2. How seasonal effects (seasonality and seasonal uncertainty) may promote floristic diversity in grasslands at a local scale,
3. How species pool effects may be important in determining species richness in grasslands at a local scale,

The final chapter discusses the findings of the various components of this thesis and provides a synthesis.

References:


CHAPTER 2: THE STUDY OF BIOLOGICAL DIVERSITY: A REVIEW

Introduction

Ecologists have been involved in the formal study of biological diversity for many decades, and continue to retain an enduring interest in the subject. At the beginning of the 19th century we knew little about diversity, but now we have a deeper understanding of how various factors affect diversity. The concept of diversity is at the core of understanding theoretical and applied ecology (Gaston 1996, Grime 1997, Lawton et al. 1998, Mouillot et al. 2000, Tilman et al. 1996, 1997), but one of the greatest challenges for modern science is to formulate a comprehensive unifying theory of biodiversity (Brown et al. 2002).

From an ecological point of view, understanding diversity is of interest due to the fact that it is an outcome of the forces that shape community structure. Understanding diversity patterns is therefore essential for understanding functional ecology and the relationship between plant community structure and ecological processes (Tilman et al. 1996, 1997). Diversity has also become an important measure for the evaluation and monitoring of ecosystems (Norse 1995). Ecologists have attempted to address the relationship between species richness and ecosystem function (Hooper & Vitousek 1997, Tilman 1996, 1997), but have failed to reveal an unambiguous causal effect (Huston 1997). There are, therefore, a number of reasons why an understanding of diversity patterns is of interest to researchers and land managers. Diversity is also important in its own right, especially in light of high modern extinction rates and the need to understand diversity before it is lost (Altesor et al. 1998, Turner & Gardner 1991). Biodiversity is important for human well-being because it provides economic benefits, protects human health and safety, and offers recreational or aesthetic enjoyment.

Diversity indices, relative abundance distributions and mathematical models are useful ways of presenting patterns of diversity, but understanding the underlying mechanisms leading to these patterns has generated much academic argument and debate. The following section summarizes the theoretical framework within which the study of diversity patterns have been historically undertaken and that have led to the formulation of predictions of factors that may be important in explaining diversity patterns.

The relationship of species richness to various factors: some observed patterns and hypotheses

Early descriptions of diversity were limited to a count of the number of species in a given area and led to the observation that the number of species increases as the area increases. Some early patterns of diversity that were recognized are those relating richness to area, latitude, productivity and isolation on islands, including the following:
1. There are more species at the equator than towards the poles.
2. The greater the variety of habitats, the greater the species diversity.
3. Diversity is greatest at intermediate levels of disturbance.
4. In small plots diversity decreases as productivity increases.
5. Diversity increases on larger islands and with proximity to mainland areas.

There are other such relationships. These have, in many cases led to the formulation of theories to understand the observed patterns, for example species-energy theory and the intermediate disturbance hypothesis. Some of the most commonly observed patterns are described in more detail below.

**Area**

One of the earliest diversity patterns to be recognised was the observation that the number of species increases as the area increases. Larger areas contain more individuals, more habitats, and more biomes or biogeographic provinces than do smaller areas (Rosenzweig 1995), which results in an increase in species richness. The two most common models that have been advanced to characterize the species-area relationship are the exponential or semilogarithmic function of Gleason (1922, 1925) and the power function of Arrhenius (1921, 1923a,b), although alternative models exist based on the random placement of individuals (Coleman 1981, Coleman et al. 1982). The species-area theory was applied in the derivation of the Theory of Island Biogeography (MacArthur & Wilson 1963, 1967).

**Latitude**

The oldest and one of the most fundamental patterns concerning life on earth is the increase in biological diversity from polar to equatorial regions (Brown & Lomolino 1998, Gaston 1996, Rosenzweig 1995, Willig 2001). This pattern has been described for most major groups, including terrestrial plants (Cowling & Samways 1995, Gentry 1988). The major exceptions to this pattern are associated with narrow latitudinal extents, which are a form of scale dependence, parasitic species, aquatic plants, some marine algae and fish (Willig et al. 2003).

The first hypothesis to explain latitudinal gradients of richness was provided by von Humboldt in the 18th century (Hawkins 2001). An early review of the hypothesis (Pianka 1966) proposed a number of factors to account for the latitudinal gradient, including climatic stability, competition, predation, productivity, spatial heterogeneity, and time hypotheses. Following earlier work, there was some expansion of existing hypotheses, but by the end of the 1980’s the list of explanatory hypotheses had grown to ten (Brown 1988, Brown & Gibson 1983) and by the 1990’s to thirty (Rohde 1992). A review of the hypotheses (Willig et al. 2003) reduced this to a few feasible possibilities, including the Geographic Area Hypothesis, the Productivity
Hypothesis, the Ambient Energy Hypothesis, the Rapoport Rescue Hypothesis, the Evolutionary Speed Hypothesis and the Geometric Constraints Hypothesis.

The Geographic Area Hypothesis was proposed by Terborgh (1973), and developed as a hypothesis by Rosenzweig (1995). The hypothesis states that the tropics support more species because they are composed of a larger area than the poles. Secondarily, the elevated productivity and enhanced zonal bleeding (increased emigration of species from adjacent zones) in the tropics interact with area effects to increase richness. There has been a lot of controversy surrounding this hypothesis (Rohde 1997, 1998; Rosenzweig & Sandlin 1997), which is focused not on whether area is important as a mechanism, but on the degree to which area is the dominant factor (Willig 2001).

The Productivity Hypothesis states that greater productivity begets greater diversity (Hutchinson 1959, Pianka 1966). This led to the development of the species-energy hypothesis (Wright 1983). According to the Productivity Hypothesis, annual input of solar radiation determines energy availability, productivity and biomass, which is tightly linked to latitude. Data indicates that there is a reasonably high relationship between tree richness in North America and actual evapotranspiration, a measure of productivity (Currie 1991). The relationship is, however, not always clear — it may be positive linear, negative linear, or modal (Mittelbach et al. 2001, Waide et al. 1999), but is considered to be scale dependent (Gross et al. 2000, Pastor et al. 1996, Scheiner et al. 2000, Scheiner & Jones 2002).

The Ambient Energy Hypothesis is based on the concept that environments at high latitudes have mean conditions farther from the optima for an organism (e.g., their thermal neutral zones) than do their low-latitude counterparts. In addition, high-latitude environments are thought to be more variable and seasonal than are those at low latitudes. High latitudes are therefore considered to be harsher for organisms. It has been found that harsh environments, which require special and costly adaptations for survival, are generally poorer in species (Brown 1988). There are some notable exceptions, for example, there is incredible diversity in the abyssal zone. Rohde (1992) considered the harshness hypothesis to be circular — the fact that some environments have many species is interpreted as that habitat being favourable and vice versa.

The Rapoport Rescue Hypothesis is based on Rapoport’s rule, a pattern in which the distributional ranges of species are inversely related to latitude (Rapoport 1975, Stevens 1989). At high latitudes where seasonal variation is high, natural selection favours organisms with broad climatic tolerance. This allows organisms to persist through unfavourable times, but also results in large ranges which encompass greater variability. In tropical organisms, their narrower tolerances cause the environment to appear to be more heterogeneous. They are more likely to disperse into areas that are, from their point of view, unfavourable. Species
richness in tropical areas is therefore augmented by the addition of species that are maintained or “rescued” by continual dispersal from nearby favourable areas. Evidence from modelling and empirical data suggests that the logic underlying the Rapoport Rescue Hypothesis is only applicable under restrictive circumstances (Rohde 1996). There are also many taxa that exhibit latitudinal gradients in richness but do not exhibit Rapoport’s rule (Willig et al. 2003).

The Evolutionary Speed Hypothesis (Rohde 1992) states that species richness increases toward the tropics because of temperature-induced increases in rates of speciation. Latitudinal increase in temperature results in shorter generation times, higher mutation rates, and accelerated selection pressure in the tropics, which combine to enhance rates of speciation, and as a consequence, species richness (Rohde 1992). There is little empirical evidence to support or refute this hypothesis. A recent quantitative analysis based on phylogenetically independent contrasts of rates of evolution in latitudinally separated pairs of bird species provided no support for the contention that rate of molecular evolution increases toward the tropics (Bromham & Cardillo 2003).

The Geometric Constraints Hypothesis is a radically different approach to understanding the latitudinal gradient (Willig et al. 2003). It is based on the concept of a bounded domain, which is an area circumscribed by a physical or physiological barrier. This barrier restricts the distribution of a species to a subset of the earth’s surface. Colwell and Hurtt (1994) suggested that “nonbiological” latitudinal gradients of species richness could be produced as a consequence of the random placement of species ranges within a bounded domain. Simulation models produce latitudinal gradients with peaks in richness at mid-domains. There is empirical support for the geometric constraints model and it also predicts that species whose distributions are wholly contained within any geographic domain should exhibit a mid-domain peak in richness (Willig et al. 2003). Some have considered the hypothesis to be flawed because the assumption that ranges exist independently of the environment or that ranges are randomly placed has no theoretical justification (Hawkins & Diniz-Filho 2002). The view is, however, that neutral and deterministic mechanisms can operate simultaneously to produce patterns (Hubbell 2001).

There are a number of commonalities between these various hypotheses. Except for the Geometric Constraints Hypothesis, all involve, to some extent, area, productivity and “favourableness”. Many of the mechanistic factors associated with different hypotheses are shared or correlated (Willig et al. 2003).

**Habitat heterogeneity**

Various studies have indicated that the greater the habitat variety, the greater the number of species (Rosenzweig 1995). The ‘habitat heterogeneity hypothesis’ is one of the cornerstones
of ecology (e.g. Simpson, 1949; MacArthur & Wilson, 1967; Lack 1969). It assumes that structurally complex habitats may provide more niches and diverse ways of exploiting the environmental resources and thus increase species diversity (Bazzaz 1975). This facilitates specialization and avoidance of competition through spatial segregation. Habitat heterogeneity increases the probability that a propagule from an invading species (one that does not already occur there) would find available resources within its required optimal range of resource conditions and it would, therefore, be more likely to establish itself there (Tilman 2004). Habitat heterogeneity increases diversity in one of two ways (Cramer & Willig 2005). Firstly, adaptations that enhance adaptability to one habitat may result in competitive inferiority in another habitat. Where such tradeoffs exist, it enhances compositional differences between habitats. These differences enhance beta diversity which, in turn, enhances compositional (gamma) diversity across the landscape (Whittaker 1972). Secondly, small habitat patches may increase habitat quality of a pervasive habitat type by supplying complementary resources.

The idea that habitat heterogeneity affects species diversity has been applied to successional (Bollinger 1995) and disturbed environments (Levey 1988), as well as to latitudinal (Willig 2001, Willig et al. 2003), elevational (Finch 1989), and humidity gradients (Daniels et al. 1992). It is most frequently applied to the study of animal diversity with vegetation structural diversity constituting the habitat, but the principles apply equally to plant species diversity.

**Disturbance**

Various studies have shown a unimodal relationship between disturbance and species richness, with the greatest richness occurring at intermediate levels of disturbance (Rosenzweig 1995). There are two hypotheses that postulate a causal relationship between disturbance and species diversity, the Intermediate Disturbance Hypothesis (Connell 1978) and the Dynamic Equilibrium Model (Huston 1979, 1994). Both hypotheses consider diversity to be the outcome of local extinction through a combination of competition and disturbance. In the Intermediate Disturbance Hypothesis inferior competitors are excluded from communities until disturbance creates gaps which they can colonize. Diversity then increases until competition re-establishes. Continuous disturbance is therefore required to promote diversity. In the Dynamic Equilibrium Model growth rates of competing populations play a role in determining the outcome of competition, with maximum potential growth rates being determined by local environmental conditions. Disturbance alters growth rates by altering resource availability or through density-dependent effects. This alters the intensity of competition between species and may allow the inferior competitor to temporarily increase its population size. For both hypotheses there is a level of disturbance at which loss of species through competition and loss of species through disturbance-induced mortality are balanced and diversity is at its highest. The Dynamic
Equilibrium Model also predicts that the effect of disturbance on diversity is mediated by inherent growth rates, which are determined by environmental effects on productivity.

Competition may affect adult survival and growth or propagule establishment. Periodic disturbance, resource pulses and other processes that allow species to overcome resource-dependent recruitment limitation would increase local species diversity (Tilman 2004).

**Productivity / resource availability / favourableness**

Favourableness refers to there being sufficient resources to ensure that productivity is not inhibited. This includes abundant water, energy and mineral nutrients. Favourableness and resource availability affect vegetation productivity, which in turn determines the amount of biomass. The Productivity Hypothesis (Hutchinson 1959, Pianka 1966) and species-energy theory (Wright 1983) examine the relationship between productivity and diversity.

The most commonly reported pattern of biomass and species richness is the hump-shaped relationship (Grime 1973, Mittelbach et al. 2001). Species richness usually peaks at relatively low biomass/productivity levels and then declines above a threshold (Tilman & Pacala 1993). A possible explanation for this pattern is that few species can tolerate regions of low favourableness (resource availability), whereas in areas with high favourableness highly competitive species dominate resources at the expense of other species. Lower resource levels decrease the probability of propagules surviving and thus limit local diversity through the inhibitory effects of resource use by established plants (Tilman 2004). A relationship between favourableness and species richness can therefore be interpreted as a system in which competition drives coexistence. This hump-backed relationship is, however, not consistent and different studies have found different patterns.

Cornwell and Grubb (2003) reviewed a number of studies and found that there was no consistent relationship between richness and productivity in grasslands. Regional gradients in grassland productivity were much more likely to be caused by moisture than nutrient availability, although these factors were found to co-vary frequently (Cornwell & Grubb 2003). Resource-based factors, including production (favourableness) may be linked to one another (may show co-variation). It is therefore possible that the relationship between favourableness and richness is masked by other factors. Furthermore, these authors found that high water availability often led to increased richness and high nutrient status to low richness. The following general observations were made by these authors with respect to the relationship between richness and productivity (Cornwell & Grubb 2003): on a regional scale there is a hump-backed relationship between soil nutrient-supply and richness, the peak in species richness for grasslands and wetlands occurs on nutrient-poor soils, whereas in forests the peak is on nutrient-rich soils. Overall it appears that, gradients in plant productivity controlled by different variables (moisture-energy, soil nutrients) have dissimilar effects on richness.
Scale has emerged as a prominent factor in determining the type of patterns observed (Cornwell & Grubb 2003). Productivity is thought to show a positive relationship to diversity at a regional scale and that no clear relationship exists at a local scale. Within a single community type, there is often no significant relationship between biomass and species richness (Moore & Keddy 1989, Guo & Berry 1998). If plots are sampled across a range of community types, a hump-shaped relationship often becomes evident (Waide et al. 1999). At a continental scale, a monotonically increasing relationship between productivity and species richness is the dominant trend (Pianka 1966). The major productivity factors should therefore be correlated with species turnover, not richness. A lack of clear patterns from different studies may also be due to the fact that these studies have measured richness on different parts of the resource “scale” and therefore show only part of the unimodal relationship. They would therefore be expected to be positive, negative or neutral, depending on which part of this relationship they represent.

**Explaining diversity patterns: ecological versus historical factors**

Assembly rules (Diamond 1975) are principles that constrain the way in which communities are put together (Wilson 1999). There are two alternative views on assembly rules, those based only on biotic interactions and those that include biotic and abiotic factors. The “biotic only” view is based on a categorical approach where frequencies of species or functional groups are analyzed as a method for finding assembly rules. Some ecologists view assembly rules as a combination of biotic and abiotic constraints on the species pool (Keddy 1992, Zobel 1992, Weiher & Keddy 1995, Diaz et al. 1999). They use the three main theories of community assembly over time, the deterministic, stochastic and alternative stable states theories, and a response approach over time to find assembly rules (Temperton et al. 2004). In the deterministic model, the development of a plant community is seen as the inevitable outcome of physical and biotic factors. Clements (1916) based his models on this approach and believed that communities would ultimately reach equilibrium with their environment. The stochastic model of community assembly (Gleason 1926) has also been called the carousel model (van der Maarel & Sykes 1993) and states that community composition and structure is essentially a random process. Community assembly depends on the availability of vacant niches and the order of arrival of propagules. The alternative stable states model (Sutherland 1974) is intermediate between the other two. According to this model there is some restriction to community structure and composition, but they can develop into alternative stable states due to elements of randomness that are inherent in all ecosystems. Community assembly is therefore the outcome of deterministic processes complicated by stochastic events (Bradshaw 1983).

Many of the hypotheses mentioned previously have eschewed “history” because of the preference for deterministic models. Vegetation dynamics has long been studied from a
deterministic perspective, leading to important concepts like climax, equilibrium and reversibility. Stochasticity has been more recently introduced into models while a few have acknowledged the role of idiosyncratic, historical events. In recent decades, the emergence of the theory of chaos has changed our vision of natural laws. New concepts such as non-equilibrium, heterogeneity, disturbance and irreversibility have increasingly become popular.

The scientific understanding of ecological diversity has, in fact, taken a century and a half of study to reach its contemporary state. Early descriptions of diversity were limited to a count of the number of species in a given area and led to the observation that the number of species increases as the area increases. Other early patterns to be recognized are patterns relating richness to latitude, productivity and isolation on islands. Explanations for many of these patterns were centred on processes occurring across large areas and operating over long time periods. This included the observation that temperatures are higher and more stable in the tropics than at the poles, which may have led to more rapid evolution of species in tropical environments (Fischer 1960).

The discipline of community ecology developed rapidly after the 1960s on the back of a long tradition of population biology that began in the 1920s and 1930s. The development of population models and microcosm experiments led to the principle of competitive exclusion, from which niche theory developed. Early theories dealing with the control of species richness in plant communities have been influenced by the fact that plant communities contain assemblages of species that all require the same basic resources, namely light, water, carbon dioxide and soil nutrients. Competition for space amongst plants was thought to be very important because those plants that hold space succeed in pre-empting resources required by other plants (Werner 1979). From this the theory of competition and limiting similarity was developed by MacArthur and Levins (1967). Assembly rules for communities were proposed by Diamond (1975) based on the idea that species interactions limit coexistence. Patterns of species diversity at a local scale could be explained by the idea that species interactions limited community membership, so-called local determinism.

A factor which was overlooked in the early development of diversity theory was that many deterministic models were based on closed systems (Roughgarden 1989). The view of Gleason (1926) that communities are open systems without absolute boundaries versus Clements, who viewed them as closed natural units, was eventually settled by R.H. Whittaker and others (Whittaker 1953, 1967, McIntosh 1985) in favour of them being open systems. Since then the modern view of communities has expanded greatly to accommodate observations that highlight the connections between communities and movement of individuals between habitats, including mass effects (Shmida & Wilson 1985), supply-side ecology (Roughgarden et al. 1987), source-sink relationships (Pulliam 1988), Rapoport’s rule (Stevens 1989), macroecology (Brown 1995, Maurer 1999, Gaston & Blackburn 2000), metapopulation...
dynamics (Hanski & Gilpin 1997) and landscape ecology (Turner et al. 2001). A further challenge for deterministic theories was the development of the equilibrium theory of island biogeography (MacArthur & Wilson 1963, 1967), which proposes a strong external influence (colonization from source areas) on patterns of island diversity.

Some authors argued that an understanding of species diversity in local assemblages required knowledge of processes operating at regional scales, including determinants of regional richness and species turnover (Caley & Schluter 1997). Regional and historical processes were thought to play an important role in determining local species richness (Caley & Schluter 1997, Cornell 1993, Cornell & Lawton 1992, Ricklefs 1987, Ricklefs & Schluter 1993, Westoby 1993). Local richness was thought to possibly be dependent on regional processes, such as speciation, extinction, dispersal and fluctuation in range (Collins et al. 2002; Cornell & Lawton 1992; Ricklefs & Schluter 1993) as opposed to local processes, such as competition, predation and disturbance. These processes were thought to determine the characteristics of the species pool from which local communities could be assembled.

Theories related to historical and regional processes can be divided into two main concepts that have been presented in the literature; taxonomic structure effects and species pool effects (including dispersal limitation). Some areas, possibly with long stable climates, have experienced potentially higher speciation rates or lower extinction rates. Historical factors may lead to the development of large regional species pools via dispersal and speciation. A large regional species pool may also arise from high beta diversity, which also results in a proportionally high area of inter-community contact zones (Cowling et al. 1989). Local richness may be influenced by the size of the regional species pool, especially if many of the organisms are well-dispersed generalists (Holt 1993, Westoby 1993). Alternatively, high regional richness of habitat specialists in heterogeneous regions will promote local richness (Cowling 1990).

A commonly used method for inferring the impact of regional factors on local richness is the comparison of species richness in local assemblages ($S_L$) with the total number of species in the region ($S_R$) (Hillebrand & Blenckner 2002). Linear relations between $S_R$ and $S_L$ are interpreted as an indication of a strong regional influence. This linear relationship is also interpreted as a concomitant weak influence of biotic interactions within local communities (Hillebrand & Blenckner 2002). Assembly within local communities can be conceptualized as species passing through a series of filters, which represent historical (e.g. dispersal, speciation) and ecological (e.g. competition, predation, disturbance, abiotic environmental factors) constraints on the arrival and survival of organisms at a certain locality (Zobel 1997; Lawton 1999). Local and regional diversity are considered to be related if processes connected to the dispersal of organisms are primarily responsible for the assembly of local communities (Hillebrand & Blenckner 2002).
The consistent relationship between the number of species and higher taxa across continents supports the assertions of some researchers that the number of higher taxa can be used as a predictor of species richness within local assemblages (Enquist et al. 2002). Taxonomic structure in woody plant communities is well-explained by a power function suggesting that the processes that promote ecological similarity within plant communities operate in a regular manner across broad geographical gradients and also reflect ecological and evolutionary processes that dictate local composition. The fact that the patterns are identical between extant and fossil communities has been suggested as evidence that these processes have operated in a consistent pattern for millions of years. This has led to some researchers suggesting that environment, history and other factors are of secondary importance in their influence on the patterns of local species coexistence (Enquist et al. 2002).

Diversity in local communities may be linearly dependent on regional species pool, in which case the local communities are thought to be unsaturated (Cornell 1985, Cornell & Lawton 1992). Factors that may promote non-saturation include non-interactive community structure, lottery competition for space, random colonization and extinction and disruption of competitive exclusion by disturbance. Alternatively, local communities may reach a ceiling above which diversity does not rise irrespective of an increase in the regional species pool, in which case the communities are considered to be saturated (Cornell 1985, Cornell & Lawton 1992). This may be due to a variety of factors, including biotic interactions in limited niche space, disturbance and dispersal limitation. In general, there have been few studies demonstrating local saturation of species (Caley & Schluter 1997). Understanding species diversity in local assemblages requires knowledge of processes operating at regional scales, including determinants of regional richness and species turnover (Caley & Schluter 1997).

Where regional processes are found to be the dominant factor promoting local richness, the dispersal ability of species, the biogeographic origin of species or the amount of turnover of species along environmental gradients may all contribute to promoting local richness. Where a number of phytogeographic regions merge there will potentially be a higher number of species available from different origins to contribute to local richness. Cowling (1983) argued that, at the merging of different phytogeographical regions, richness would be highest in those communities that can accommodate species from a high number of such regions, owing to a mass effect (Shmida & Wilson 1985). This is due to dissimilar habitats occurring adjacent to one another. Plant populations within different communities in close contact produce a rain of propagules that maintain species in habitats in which they would otherwise not occur. Thus, these communities are able to accept species from many different phytochoria. This mixing produces rich local floras. On the other hand, where conditions are such that there are restrictions on local membership (i.e. where phytochorological diversity is low), local richness will be low, owing to a smaller regional pool.
The historical processes that are thought to explain species richness at a local scale in plant communities include palaeo-historical factors that promote the evolution of habitat specialists (Shmida & Wilson 1985; Cowling et al. 1992), inherent biological properties of species lineages (Vrba 1980, Cowling & Holmes 1992) and the interaction between these traits and the physical environment (Cowling et al. 1992). Local richness may be highly dependant on regional processes, such as speciation, extinction, dispersal and fluctuation in range (Collins et al. 2002; Cornell & Lawton 1992; Ricklefs & Schluter 1993) as opposed to local processes, such as competition, predation and disturbance.

Plant ecological researchers have diverged in their approaches to the study of diversity: some researchers have proposed that species richness is determined by ecological factors (e.g. Whittaker 1977; Shmida & Wilson 1985; Brown 1988; Diamond 1988), while others have invoked historical factors to explain patterns (e.g. Shmida & Wilson 1985; Cowling et al. 1992; Vrba 1980; Cowling & Holmes 1992). Some researchers (e.g. Pausas & Austin 2001) have argued that ecological and historical explanations are mutually exclusive. Cornell and Lawton (1992) assume implicitly that species distribution is controlled by local biotic factors and that dispersal processes have little relevance. Over time, these two opposing (ecological and historical) viewpoints have led to the development of two main theoretical frameworks to try to provide a mechanistic understanding of the factors driving local species richness, niche theory and neutral theory. Both theories make assumptions about plant communities and provide specific predictions regarding community structure. Neither fully explains observed patterns in nature. Recently, Tilman (2004) proposed an alternative theory that he claims resolves many of the problems inherent in these two theories. Hubbell (2001) proposed a unified neutral theory of biodiversity, based on the theory of island biogeography (MacArthur & Wilson 1967), which also addresses many of the problems associated with earlier theories, but has generated much recent controversy and debate. The following sections examine these competing theories to explain local richness in plant communities.

Niche theory

Coexistence in diverse ecological communities has been thought to be due, in part, to life-history trade-offs involving allocation of resources (Tilman 1988; Ricklefs 1977; Grubb 1977; Denslow 1980; Williamson 1996; Hubbell et al. 1999; Enquist et al. 1999). Trade-offs may affect the spatial or temporal harvesting of resources between species. Niche differentiation is an equilibrium model that assumes that coexisting plant species are dissimilar enough for competitive exclusion to be avoided, i.e. resource partitioning promotes richness by reducing competition. In coexisting species niche differentiation is manifested as growth form (Cody 1986) or functional type variation. A strong relationship between heterogeneity and richness can be interpreted as a system in which niche differentiation permits coexistence. Competition is therefore not a strong factor because species become niche specialists. Communities in
which there are weaker interspecific interactions can support a larger number of species (May 1974, McCann et al. 1998). According to Tilman (2004), established species are expected to strongly inhibit establishment of functionally similar species. High species richness is therefore expected to be correlated with dissimilarity between species. There should be a positive relationship between plant functional type richness and species richness. The relative abundance of species depends on their traits: according to Tilman (2004), those species that are the best competitors for the most frequent conditions are abundant because they prevent establishment of species similar to themselves. There should therefore be a relationship between specific traits or species within specific functional groups and their overall abundance. Niche theory predicts that community similarity will be positively correlated with similarity in ecological conditions. Richness is therefore dependant on local deterministic factors. To a large extent niche theory does not account for stochasticity. Niche theory also does not predict an upper limit to richness and does not provide an explanation for species relative abundance.

Neutral theory

The neutral theory of biodiversity states that major patterns in the distribution and abundance of ecologically similar organisms can be explained by supposing that all individuals have the same probabilities of birth and death. This is sufficient to generate abundance distributions, species-area curves and range-abundance relationships closely resembling those of natural communities. A number of publications have attempted to explain coexistence and diversity using neutral models (Caswell 1976, Hubbell 1979, Goldberg & Werner 1983, Shmida & Ellner 1984). Hubbell (1997, 2001) formalised the Unified Neutral Theory of Biodiversity. Another notable proponent of the theory is Graham Bell (Bell 2000, 2001, 2005, Bell et al. 2006).

According to unified neutral theory (Hubbell 2001), the number of species is controlled by species extinction and immigration or speciation rates. Richness is therefore dependant on dispersal processes. It assumes that, as a starting point, species and individuals are ecologically similar in their responses to constraints and thus have no interspecific trade-offs. Hubbell’s theory assumes that the differences between members of an ecological community of trophically similar species are "neutral," or irrelevant to their success. Unified neutral theory predicts that similarity in communities is negatively correlated with distance between sites. The theory explains the log-normal distribution of abundance, the species-area law and species turnover between sites. Neutral theory predicts that no relationship exists between species traits and abundance, or among community composition and environmental conditions.

There are four main empirical objections to the unified neutral theory (Leigh 2007). Firstly, it assumes that all plants are identical, which seems highly improbable; for example, different species are adapted to different habitats and respond differently to environmental change. Secondly, some deductions from the unified neutral theory don’t make logical sense. For
example, the theory predicts that similarity in species composition should be negatively correlated with distance, i.e. sites close together should be more similar than sites further apart. However, forests in similar habitats have been observed to have similar species composition, irrespective of proximity. Thirdly, neutral theorists emphasize species abundance distributions, although it is notoriously difficult to fit data to specific abundance distributions. MacArthur (1966) was very sceptical of the usefulness of species abundance distributions and pointed out that data may often fit more than one distribution. It is therefore difficult to demonstrate neutrality using abundance fitting techniques. Some studies have attempted to criticize the unified neutral theory using abundance fitting (e.g. McGill 2003, McGill et al. 2006). Fourthly, data indicates that common species are shorter lived in an evolutionary sense than the theory predicts by at least an order of magnitude (Leigh 1981, Ricklefs 2003). Other critics point out that neutral theory cannot explain adaptive divergence or ecosystem function, which are aspects of ecology that are important to understand. Even the staunchest supporters of neutral ecology accept that the theory has limitations (Whitfield 2002). It only applies within one level of the food web and it breaks down on large spatial scales. A study on coral reef diversity (Dornelas et al. 2006) claims to refute the theory, but points out that using the theory as a null model was useful for understanding the real mechanisms behind coral reef diversity. Neutral theory can therefore stimulate more realistic theory.

**Stochastic niche theory**

Recently, Tilman (2004) provided an alternative theory, which he called stochastic niche theory, which resolves many of the differences between neutral and niche theory. In Tilman’s stochastic niche theory, invading species become established only if propagules can survive stochastic mortality while growing to maturity on resources left unconsumed by established species. It offers an explanation for diversity, species composition, relative abundance patterns and invasion dynamics in communities (Tilman 2004). Stochastic niche theory is based on three observations,

1. community assembly results from the success or failure of propagules of invading species that, because of their rarity, are potentially subject to loss by means of demographic stochasticity,
2. successful propagules must be able to grow sufficiently and survive long enough on the resources left unconsumed by established species to become reproductively successful adults, and
3. the probability of successful establishment should depend on the resource requirements of the invading species relative to those of established species (Tilman 2004).

Contrary to neutral theory, stochastic niche theory predicts that species traits and abundances should be correlated with environmental conditions. It is consistent with the observation that
species tend to have highest abundances at the centre of their distribution range and low abundances near range limits. Niche theory is not able to explain species relative abundances and therefore provides no limit to diversity. In contrast, stochastic niche theory provides a limit to similarity that causes convergence on a particular pattern of relative abundance that is determined mainly by environmental heterogeneity and the niche widths of species.

**Other recent viewpoints**

Ricklefs (2004) attempted to reconcile the different spatial and temporal scales of regional effects and local constraints. He explains that, according to niche-based models, local communities can become ecologically saturated, at which point diversity is capped (Diamond 1975, Terborh & Faaborg 1980). However, this is not necessarily true and species can be added to a community by reducing average niche breadth in response to invasion. The second component of Ricklefs’s argument is based on refuting the claim that local processes reach equilibrium rapidly compared to evolutionary processes. Ricklefs points out that models and microcosm experiments are based on closed systems (an unrealistic framework given that the Gleasonian view of communities is now accepted). In natural systems local interactions take much longer (by orders of magnitude) to equalize than in model systems. This is due to the fact that ecological interactions between species occur across heterogeneous habitats distributed within regions. Exclusion of species from a region can therefore only occur through long-term regional-scale environmental change. Model systems therefore give an unrealistic estimate of the time taken to reach ecological equalization. In the real world local and regional effects probably occur on the same time scale, which would establish a link between these different extremes (Ricklefs 2004).

More recent studies indicate combined influences of environmental and historical factors on species richness, especially at a regional to global level (e.g. Buckley & Jetz 2007). Some authors have suggested that local and regional processes are extremes of a single spatio-temporal scale (Hubbell 2001, Ricklefs 2004). The modern view therefore appears to be integrating spatial and temporal scales into a single framework, where ecological factors strongly affect local patterns, but regional diversity is driven by historical and dispersal factors, which in turn constrain local diversity. In the opinion of some scientists, the most important task in the future is to bridge the niche-assembly theory and the neutral theory, to add species differences to the neutral theory and more stochasticity to the niche theory (Zhou & Zhang 2008).

**Measuring biological diversity: a historical review of indices**

The first species-area relationship is attributed to H.C. Watson in 1859 based on a description of the flora of the British Isles (Watson 1859). A graph relating the number of species in
different sized nested areas within the British Isles, centred on Surrey, shows a linear increase in the log of the number of species as the log of the area increases (Figure 2.1, from Rosenzweig 1995, pp. 11). Species-area relationships have since been found to consist of four different patterns, each with its own scale of space and time (Rosenzweig 1995), but a better understanding of these only came later in the history of the study of diversity. The empirical relationship between area and richness is now well understood (Rosenzweig 1995), although explanation for this pattern remains controversial.

Robert Whittaker, an American vegetation ecologist active in the 1950s to the 1970s, had a large influence on the study and understanding of diversity. Whittaker (1972) attempted to organize the study of diversity into a general framework by proposing that diversity be divided into three main components: alpha diversity, which is defined as the species richness of a particular homogeneous habitat, beta diversity, which is defined as species turnover among different habitats in a landscape and gamma diversity, which is defined as the species richness of an entire landscape (Whittaker 1972). The terms local, landscape and macro-scale are also used to define the scale of a study (Whittaker et al. 2001). Of the three components proposed by Whittaker, alpha diversity (species richness) has been studied the most and a great variety

Figure 2.1: The world’s oldest known empirical example of an ecological pattern (from Rosenzweig 1995, pp. 11).
of measures have been developed to quantify it (see reviews by Peet, 1974, Pielou, 1975, Magurran, 1988, 2004, Colwell & Coddington, 1994, Leitner and Turner, 2001, Chao, 2005).

Simpson (1949) suggested that the number of taxa only represented one aspect of taxonomic diversity and that diversity also depends on the quantitative equilibrium between the taxa, termed evenness, which describes differences in the relative abundance of species. The approach to describing species abundances relative to one another as a component of diversity is based on the observation that “...rarity is the attribute of vast numbers of species in all classes...” (Darwin 1859). Relative species abundance refers to how common or rare a species is relative to other species in a defined location. It is considered to be one of the best-known and most-studied patterns in macroecology.

From the previous paragraphs it is clear that diversity consists of two separate components, the number of species and the relative abundance of species. Two basic types of information may, therefore, be considered for measuring diversity in ecological communities: species richness and evenness (Gaston, 1996). Evenness refers to differences in species abundance that lead to an unequal representation of species in a community. This measure is often referred to as equitability. Classic indices of diversity combine information of species richness and evenness into one concept called a heterogeneity index. These diversity or heterogeneity indices like the Shannon-Wiener (Shannon 1948) or the Simpson indices (Simpson 1949), derived from information theory, are very popular because they are relatively easy to compute (Krebs, 1999). The Simpson index was first proposed by the British statistician Edward H. Simpson in a paper in Nature in 1949 and the Shannon-Wiener index by Shannon in 1948 in his paper that founded information theory.

Historically, mathematical methods were proposed to attempt to understand abundance patterns and infer the underlying biological principles at work from model parameters. Relative species abundance plots were, in fact, one of the first graphical methods for describing diversity. Common models developed for describing species abundance plots were the geometric series (Motomura 1932), the log series (Fisher et al. 1943), the general log normal series (Preston 1948, 1962), the broken stick model (MacArthur 1957), the Zipf-Mandelbrot model (Zipf 1965, Mandelbrot 1977, Gray 1988) and the truncated negative binomial model (Pielou 1975). There are others and, recently, the Yule model (Nee 2003) was proposed, indicating that interest in such models has not diminished over time. The alpha diversity term proposed by Whittaker originates from one of the two Fisher constants (the dimensionless $\alpha$) described for the logseries model (Fisher et al. 1943).

The first of the mathematical models of relative abundance distributions (RADs) were deterministic, such as the geometric model (Motomura 1947) and the general log-normal model (Preston 1948, 1962). These models have since also been criticised as been restrictive
in their hypotheses and difficult to fit (Hughes 1986, Tokeshi 1993, Wilson 1991). Some models were derived from assumptions about modes of partitioning of niche space amongst species. It has, however, become clear that the same distribution can be derived from various underlying assumptions and consequently the distribution could not be used to support mechanistic assumptions of the models. Stochastic models of RADs were introduced by Tokeshi (1990, 1993, 1996a, b) such as the “random fraction model”, “dominance pre-emption model”, “dominance decay model” and “power fraction model”. These models are mathematically complex and difficult to use, which is probably why they have not been used much in ecological studies (Mouillot et al. 2000). New parametric RAD models have been proposed (Mouillot et al. 2000) based on the fractal theory of the ecological species accumulation process (Frontier 1994, Frontier & Pichod-Viale 1995). Fractal models are attractive because they are independent of scale (Mouillot et al. 2000). Recent parametric models have also been linked to theories of species accumulation and the model parameters are claimed to be independent of classical diversity and evenness measures (Mouillot et al. 2000). Ongoing research is taking place into methods of presenting diversity data and understanding the meaning thereof and the topic is far from stagnant.

Over the years a large number of diversity indices have been proposed (see for example Hill 1973, 1997, Camargo 1992, 1993a,b, Bulla 1994, Smith and Wilson, 1996). However, a number of authors have pointed out that diversity indices are not reliable and that the same value for a diversity index may arise from different combinations of richness and evenness (Ludwig & Reynolds 1988, Mouillot et al. 2000, Tothmérész 1995). Others have criticized indices for having limited ability to discriminate between communities (Burel et al. 1998, Cairns & Pratt 1993, Cairns et al. 1993, Cao et al. 1996). There are also sampling difficulties associated with collecting data in the field (Frontier 1985, Pielou 1969, Peet 1974, 1975, Spellerberg 1991). To counteract some of these criticisms, various authors have encouraged the use of graphical relative abundance distributions (RADs) (Frontier 1985, Tokeshi 1993, Gaston 1996, Wilson et al. 1996, Wilson 1999), k-dominance curves (Shaw et al. 1983, Platt et al. 1984, Tothmérész 1995, Rogers et al. 1999) or rank frequency diagrams (Frontier 1985, Fromentin et al. 1997, Mouillot and Leprêtre 2000).

Various new approaches to measure diversity have been developed and tested in the last two decades (Magurran, 2004). A big step in the search for better approaches to quantify diversity has been the difference between the number of species recorded in a set of samples, and the estimation of the total possible number of species in a community. Estimation methods are by far more appropriate than indices that measure the diversity of samples, given that, in ecology, the completeness of species inventories is practically an impossible goal. Recent literature has contributed to promote the use of estimation methods by providing or analyzing statistical procedures (Smith & van Belle, 1984; Chao, 1984, 1987, 2005; Soberón & Llorente, 1993; Brewer & Williamson, 1994; Colwell & Coddington, 1994; Lee & Chao, 1994; Chazdon et
al., 1998; Moreno & Halffter, 2000; Gotelli & Colwell, 2001; Leitner & Turner, 2001; Thompson & Withers, 2003; Thompson et al., 2003).

**Scale effects**

Two attributes of scale, grain (or focus) and extent, are particularly relevant to studies of ecological patterns, including species richness (Turner et al. 1989, Scheiner et al. 2000). Grain refers to the resolution of the data, i.e., the area represented by each data unit, whereas extent refers to the overall size of the study area (Turner et al. 1989). For this thesis the grain of the data is equivalent to the plot size of the floristic data, which is 100 m² (10 × 10 m). The extent is the study area, which is the portion of the Grassland Biome found in the Eastern Cape province of South Africa.

Scale of observation is of critical importance in interpreting the results of an ecological analysis (e.g., Allen & Starr 1982, Delcourt et al. 1983, O'Neill et al. 1986, Addicott et al. 1987; Meentemeyer & Box 1987; Morris 1987, Turner et al. 1989). The detection of pattern and the identification of causal mechanisms in ecology critically depend on considerations of spatial scale (Gardner et al. 2001, Levin 1992, Peterson & Parker 1998). Parameters and processes important at one scale are frequently not important or predictive at another scale (Turner et al. 1989, Meentemeyer & Box 1987). One mechanism that has been shown to be affected by spatial scale is the productivity–diversity relationship. A study on scale-dependent productivity–diversity patterns in ponds (Chase & Leipold 2002) revealed that when the data were viewed at a local scale (among ponds), the relationship was hump-shaped, whereas when the same data were viewed at a regional scale (among watersheds), the relationship was positively linear. The explanation for this relationship was that dependence on scale results because dissimilarity in local species composition within regions increased with productivity (Chase & Leipold 2002). Similar patterns have emerged from other studies.

Scale may also manifest itself through the effect of environmental factors on the landscape. Different environmental factors are important at different scales. For example, rainfall gradients often operate over great distances (from a plant community point of view), whereas substrate properties (e.g. soil texture, soil depth and rockiness) and hydrology may change over relatively short distances.

Ecological problems often require the extrapolation of fine-scale measurements for the analysis of broad-scale phenomena (Turner et al. 1989). Care must be taken to account for the scale effects and be aware of the effect of extrapolating from one scale to another. Using data collected in small plots is likely to detect only those patterns and mechanisms that are important at a local scale, for example ecological and niche effects. However, data can be combined in different ways to measure factors that are important at other scales.
Studies of biodiversity are expected to be strongly dependent on spatial scale because of the manner in which species richness increases with area. In any particular study, the exact way in which species richness increases with area determines the impact of scale on biological conclusions (Kolasa & Pickett 1991, Palmer & White 1994). Larger areas contain more individuals, more habitats, and more biomes or biogeographic provinces than do smaller areas (Rosenzweig 1995) and, as a consequence, species richness increases as well.

Although richness at the local and the regional scale is interdependent (Ricklefs & Schluter 1993), these scales represent distinct levels of biological organization (i.e., reflecting ecological mechanisms that operate within communities versus those ecological and historical mechanisms that affect turnover among communities in a region). Interspecific interactions or dispersal limitations are more important at the local level, whereas mechanisms related to speciation and extinction are more important at the regional level (Ricklefs & Schluter 1993).

According to some authors, there are universal patterns of biodiversity that are emergent properties of ecological organisation (e.g. Brown et al. 2002). Underlying mechanisms, including thermodynamics, conservation of mass and energy, atomic particles and chemical elements and evolution by natural selection, constrain ecological complexity and regulate biodiversity (e.g. Brown et al. 2002). One emergent ecological phenomenon is a fractal-like scaling relationship over a wide range of spatial and temporal scales. These can be mathematically characterized by a simple power function, $Y = Y_0 X^b$.

References:


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to describe the species accumulation process and relative abundance distribution


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CHAPTER 3: STUDY AREA

This thesis focuses on the grassland communities of the Eastern Cape that comprises the southern limit of the Grassland Biome (Figure 3.1). The Eastern Cape constitutes an area of approximately 170,500 km². It is an area of extraordinary topographic and climatic complexity and diversity, with very steep and complex environmental gradients leading to a rich mixture of floristic elements. Approximately 45% of the Eastern Cape is covered by grasslands. These constitute the study area.

The Grassland Biome

The Grassland Biome of southern Africa (latitude span of 25°–33° S, Figure 3.1) is part of the global Temperate Grassland Biome that is comprised of the Eurasian steppes and American prairies in the northern hemisphere, and the Argentinian pampas, Australian Alps and tussock grasslands of New Zealand in the southern hemisphere. The most extensive temperate grasslands in the northern hemisphere are the Eurasian steppes that occur from latitudes 45° to 60° N. The entire Midwest of North America, ranging from the central Canadian provinces of Alberta, Saskatchewan and Manitoba to the Gulf of Mexico (lat. 30°–55° N) is covered by prairies. The Argentinian pampas are the largest continuous area of temperate grass steppe in the southern hemisphere and occur between 32° and 38° S. The obvious latitudinal differences

![Figure 3.1: Grassland Biome of South Africa showing the study area in the Eastern Cape Province (darker shading).](image-url)
between the northern and southern hemispheres in terms of occurrence of the temperate grasslands can be ascribed to the larger land mass concentrated on the northern hemisphere and consequently to harsher (more continental) climates governing larger land stretches of North America and Eurasia as opposed to the more oceanic climates of the southern hemisphere. In terms of relative latitude north or south, the southern African grasslands are also more tropical in position than either other southern or northern hemisphere grasslands. However, the grasslands in southern and central Africa occur at higher elevations on an inland plateau (1500–2000m) and altitude thus compensates for latitude. The effect of altitude is to lower the temperature by approximately 1°C for every 220 m climb in elevation.

The extent of the Grassland Biome in South Africa can be reasonably well defined on the basis of vegetation structure in combination with environmental factors. The term grassland refers to a herbaceous vegetation of short stature and simple structure that is dominated by graminoids, usually of the family Poaceae. Woody plants are rare (usually low or mid-high shrubs) or absent or are confined to specific habitats, such as rock faces and rocky koppies. Grasslands within the Grassland Biome correspond with clearly defined climatic parameters, whereas those outside the Biome boundaries may arise due to local edaphic or topographic circumstances. The Grassland Biome in South Africa occurs mainly on the high central plateau (Highveld), the inland areas of the eastern seaboard and the mountainous areas of KwaZulu-Natal and the central parts of the Eastern Cape. The topography is mainly flat to rolling, but also includes mountainous regions and the escarpment. The effect of being at a high elevation in the interior of the continent is important in defining the Grassland Biome because this feature results in large temperature differences from one time of the year to another and a high frequency of frost. In winter the climate on the Highveld is very cold and dry.

The most important environmental factors determining the distribution of the Grassland Biome are temperature and water balance (Rutherford & Westfall 1986, Cowling et al. 1997, Mucina et al. 2006a). The Grassland Biome is characterised by having summer to strong summer rainfall and winter drought (i.e. strongly seasonal climate), cool temperatures in winter with high incidence of frost and a high lightning flash density (Rutherford & Westfall 1986). These factors will all be described in more detail below.

**Biogeographic patterns**

The Grassland Biome in South Africa includes three major phytochoria (White 1983), namely the Kalahari-Highveld Region (part of the Karoo-Namib Region, Takhtajan 1986), the Tongaland-Pondoland Region (part of the Uzambara-Zululand Region, Takhtajan 1986) and the Afromontane and Afro-alpine Region. All three of these phytochoria are found within the study area in the Eastern Cape. The mountainous landscapes along the eastern escarpment are within the Afromontane and Afro-alpine Region of White (1983). These areas also include the
most temperate components of the Biome, both floristically and climatically. Numerous studies have demonstrated the floristic linkages between the Fynbos Biome, the mountain regions of the Grassland Biome and Afromontane regions further northwards in Africa (e.g. Rourke 1980, Hartmann 1991, Linder 1983, Linder & Ellis 1990, Puff 1986, Weimarck 1934, 1940) through the so-called African track (Adamson 1958, Linder 1990, Weimarck 1936). The number of Cape species becomes less as the distance from the Fynbos biome increases and the number of Afromontane species increases.

The Grassland Biome contains three regions of floristic endemism that fall entirely within its boundaries, the Drakensberg Alpine Centre, the Wolkberg Centre (van Wyk & Smith 2001) and the Sneeuwberg Centre (Clark et al. 2009). There are also five regions of floristic endemism that overlap with the Grassland Biome, namely the Albany Centre, the Sekhukhuneland Centre, the Soutpansberg Centre, the Barberton Centre (van Wyk & Smith 2001) and the Midlands Centre (Mucina et al. 2006a). The Drakensberg Centre forms the core of the temperate (Afromontane) regions of endemism within the Grassland Biome and has a number of floristic links westwards towards the Cape Region and northwards via the escarpment towards the Chimanimani Mountains of Zimbabwe and Mozambique and to the eastern arc mountains of Africa. The Sneeuwberg and Wolkberg Centres form part of this greater escarpment and mountain region, one at each end of the eastern temperate part of the Grassland Biome.

The Albany Centre comprises the Great Fish River basin and overlaps with areas of the south-western part of the Grassland Biome, but includes many other vegetation types. The typical and most obvious vegetation associated with the Albany Centre is thicket and not grassland. The Albany Centre is considered to be a transitional area for genera centered in the Cape, Nama-karoo and Maputo–Pondoland regions.

The three northernmost centres are the Sekhukhuneland Centre, the Barberton Centre and the Soutpansberg Centre. The Sekhukhuneland and Soutpansberg Centres occur within a bushveld region (Savanna Biome) and the grassland component occurs at the summit of mountain ranges within these areas. The Sekhukhuneland Centre includes the Sekhukhuneland and Leolo Montane Grasslands within its boundary and the Soutpansberg Centre includes the Soutpansberg Montane Grassland, all three of which are Bushveld Summit Grasslands (Mucina & Rutherford 2006). The Barberton Centre also occurs in mountainous territory, but may be considered to be part of the northern escarpment region.

The Midlands Centre links the high-lying Drakensberg Centre to the coastal regions along the east coast of South Africa. It is a sub-component of the Maputaland-Pondoland Region (White 1983, Davis et al. 1994, van Wyk & Smith 2001) and includes a number of the mountain peaks within the Midlands region of KwaZulu-Natal and the Eastern Cape, for example, the Ingeli Mountain, which are recognised as having high levels of endemism.
It is clear from the preceding discussion that the Grassland Biome has many areas of high species endemism. It is significant that the core of the Grassland Biome contains no regions of endemism and all those regions of high endemism are in areas peripheral to the Biome. The core regions of the Grassland Biome are dominated by C4 grasses and are considered to be either relatively young and/or subject to recurrent climate change that may have caused repeated floral extinctions (Mucina et al. 2006a).

**Vegetation of the study area**

The part of the Eastern Cape covered by this study includes numerous vegetation types. Based on vegetation physiognomy these can be divided into grassland, xerophytic dwarf shrubland, savanna, thicket, forest and fynbos. Various researchers have described or mapped the vegetation of this region (Pole-Evans 1936, Adamson 1938, Keay 1959, Acocks 1953, Low & Rebelo 1996, Mucina, Rutherford & Powrie 2005). The mountains and inland regions are dominated by grasslands, the valleys by thicket, the lowland plains by grassland and savanna and the coastal forelands by a variety of vegetation types, including thicket, savanna and secondary grassland. Forest may be found in patches on southern escarpment slopes, fynbos extends into the region on the sandstone ridges of the Zuurberg and xerophytic dwarf shrubland of the Karoo dominates the plains westwards from approximately the 26° meridian.

**Broad vegetation types**

The major sub-divisions of the Grassland Biome are based on gradients of altitude and moisture with subdivisions made on the basis of correlating floristic and environmental factors (Mucina et al. 2006). The grassland vegetation types (Mucina, Rutherford & Powrie 2005) that occur in and are covered by this study are as follows (Figure 3.2):

- **Drakensberg Grassland**
  - Stormberg Plateau Grassland
  - Amathole Montane Grassland
  - Amatole Mistbelt Grassland
  - Southern Drakensberg Highland Grassland
  - Lesotho Highland Basalt Grassland

- **Dry Highveld Grassland**
  - Karoo Escarpment Grassland
  - Aliwal North Dry Grassland

- **Mesc Highveld Grassland**
• Zastron Moist Grassland

Sub-escarpment Grassland

• Drakensberg Foothills Moist Grassland
• Tsomo Grassland
• Queenstown Thornveld
• Bedford Dry Grassland

The vegetation-type diversity of the study area is high and, as can be seen from Figure 3.2, the vegetation types often form mosaics with one another. The ratio of the boundary distance to core area of these vegetation types is high, indicating that contact zones between vegetation types are long. The floristic influence of vegetation types on one another is therefore high.

Drakensberg grasslands are associated with the high altitude regions of the Great Escarpment and Drakensberg region and contain some of the highest elevation and steepest topography of southern Africa. Rainfall is generally relatively high and, although it falls mainly in summer, could occur any time of the year. Frost is common and snow may fall at high elevations. Dry

![Figure 3.2: Grassland vegetation types of the study area in the Eastern Cape Province (Mucina, Rutherford & Powrie 2005).](image-url)
Highveld grasslands occur on the extensive central plateau of South Africa within which an east to west gradient of decreasing rainfall is found. The dry Highveld grasslands occur towards the western side where annual rainfall is lower. The topography is generally flat to undulating, occasionally broken by small mountains or incised river valleys. Sub-escarpment grasslands are found within the rolling hills and plains of the foothills of the Drakensberg and northern Escarpment regions. There is a diversity of landforms in these areas, shaped by the rate at which the escarpment descends and the degree to which the landscape has been shaped by geomorphological forces. The orographic influence of these rising landscapes often results in a high incidence of mists, which supplement rainfall.

**Classification of plant community data**

Plant communities in the study area are based on a classification of floristic data undertaken in a previous study (Hoare 1997) and published elsewhere (Hoare & Bredenkamp 1999, 2001). For that study the area was stratified broadly using environmental attributes and then on a local scale in the field using topography, i.e. crest, scarp, mid- and footslopes and valley bottoms and where variations in surface rock-cover, slope, aspect and soil type occurred. Relevés were compiled for each sample plot, which included Braun-Blanquet cover / abundance values for all taxa present. A total of 400 relevés were compiled in the study area during the summer seasons of 1995 and 1996, although these included non-grassland vegetation. A total of 275 sites were within grassland vegetation. Sample sites were standardised at a size of 100 m\(^2\) in order to facilitate comparisons among them.

The classification of floristic samples was based on the Braun-Blanquet approach (Westhoff & van der Maarel 1978). A preliminary classification of the data was performed using TWINSPAN (Hill 1979a). The data was split into two tables based on species occurrence patterns which coincided with the first major division of the full data set generated by TWINSPAN. This resulted in semi-arid and mesic vegetation data sets. The phytosociological tables were then refined using Braun-Blanquet procedures (Mueller-Dombois & Ellenberg 1974) in order to generate the final community classification (Hoare 1997). A summary of the grassland plant communities in the study area, as derived from this study (Hoare 1997), is given in Table 3.1.

**Table 3.1: Floristically defined grassland plant communities occurring in the study area and the vegetation types (according to Mucina, Rutherford & Powrie 2005) within which they are found.**

<table>
<thead>
<tr>
<th>Syntaxon</th>
<th>Description</th>
<th>VegMap vegetation type</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mountain grasslands</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Eragrostio curvulae-Themedetum triandrae: eragrostietosum planae</td>
<td>Amatola southern watershed</td>
<td>Amathole Montane Grassland</td>
</tr>
<tr>
<td>Eragrostio curvulae-Themedetum triandrae: leyseretosum gnaphalodis</td>
<td>Amatola northern watershed</td>
<td>Amathole Montane Grassland</td>
</tr>
<tr>
<td>Helichrysum rugulosae-Themedetum</td>
<td>Stormberg plateau</td>
<td>Stormberg Plateau Grassland</td>
</tr>
<tr>
<td>Family Name</td>
<td>Genus, Specific Name</td>
<td>Grassland Type</td>
</tr>
<tr>
<td>-------------</td>
<td>----------------------</td>
<td>----------------</td>
</tr>
<tr>
<td>Themeda triandrae-Helichrysetum aurei</td>
<td>Amatola mistbelt</td>
<td>Amathole Mistbelt Grassland</td>
</tr>
<tr>
<td>Eragrostio chloromeladis-Festucetum caprinae</td>
<td>High altitude, steep slope</td>
<td>Southern Drakensberg Highland Grassland, Lesotho Highland Basalt Grassland</td>
</tr>
<tr>
<td>Andropogono appendiculati-Festucetum scabrae</td>
<td>Festuca scabra escarpment grassland</td>
<td>Azonal: Amathole Mistbelt Grassland, Karoo Escarpment Grassland, Stormberg Plateau Grassland</td>
</tr>
<tr>
<td>Not classified</td>
<td>Protea simplex escarpment grassland</td>
<td>Drakensberg Foothills Moist Grassland</td>
</tr>
<tr>
<td>Eragrostio curvulae-Miscanthetum capensis</td>
<td>Miscanthus capensis drainage line grassland</td>
<td>Amathole Montane Grassland</td>
</tr>
</tbody>
</table>

**Plains grasslands**

<table>
<thead>
<tr>
<th>Family Name</th>
<th>Genus, Specific Name</th>
<th>Grassland Type</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hermannio depressa-Eragrostietosum chloromeladis</td>
<td>Aliwal North semi-arid grassland</td>
<td>Aliwal North Dry Grassland</td>
</tr>
<tr>
<td>Hermannio depressa-Eragrostietosum chloromeladis</td>
<td>Queenstown semi-arid grassland</td>
<td>Queenstown Thornveld, Tsomo Grassland</td>
</tr>
<tr>
<td>Cymbopogono excavati-Digitarietum argyrograptae</td>
<td>Smaldeel semi-arid grassland</td>
<td>Bedford Dry Grassland</td>
</tr>
</tbody>
</table>

**Semi-arid mountain grasslands**

<table>
<thead>
<tr>
<th>Family Name</th>
<th>Genus, Specific Name</th>
<th>Grassland Type</th>
</tr>
</thead>
<tbody>
<tr>
<td>Elytroappo rhinocerotis-Merxmuelleretum distichae</td>
<td>Merxmuellera disticha grassland</td>
<td>Karoo Escarpment Grassland</td>
</tr>
</tbody>
</table>

**Physical environment of the study area**

**Topography, Geology, Soils and Moisture Availability**

The study area is situated in the mountains of the Great and Little Escarpment and lowlands between and south of these in the Eastern Cape. The area includes the Stormberg Plateau, Witteberg, Drakensberg, Winterberg, Amathole and Kologha Mountains (Figure 3.3). The lowlands vary in altitude from 600 to 900 m and are intersected by numerous river valleys. The mountains of the southern Little Escarpment vary in altitude from 1000–1200 m in the east and 1500–2200 m in the west with the highest peaks at Great Winterberg (2350 m) and Elandsberg (2016 m). The highest mountain peaks in the Great Escarpment are in the Witteberg and Drakensberg ranges at Ben McDhui (3001 m) and Ben Nevis (2882 m). The Stormberg Plateau varies from 1400–1800 m. The Queenstown Basin ranges from 900–1500 m and is interspersed by small mountain peaks, e.g. Mount Arthur (1860 m).

The mountain regions of the study area are dominated primarily by grassland, with large patches of forest on the southern aspects. The southern plains consist of a mixture of savanna and grassland with the main valley systems containing Albany Thicket (Hoare et al. 2006, Valley Bushveld, Acocks 1953). The northern slopes of the mountains approaching the
Queenstown Basin have semi-arid grassland, savanna patches and, towards the west, some karroid dwarf shrubland.

The dominant geological group in the study area is the sedimentary Beaufort Group of the Karoo Supergroup, comprising alternating bands of fine-grained sandstone, shale and mudstone (Maud 1996). Volcanic basalt lavas of the Drakensberg Group make up the highlands of Lesotho and the northern part of the Eastern Cape (Maud 1996). The Karoo sedimentary rocks are extensively intruded by dykes, sills and inclined sheets of dolerite (Johnson & Keyser 1976). There are limited instances where the main geological formation is overlain by Quaternary or Tertiary deposits, e.g. around Aliwal North. In the south-west part of the study area (around Grahamstown and westwards) formations of the Cape Supergroup may be found which form the backbone of the Zuurberg Mountains in this region.

Soil characteristics are dependent on land-form and geology. In this regard the soils in the study area may be divided into mountain and plain types, with local geological influences playing a part in soil characteristics. The soils of the mountain areas are generally shallow, weakly developed lithosols, except soils of the high rainfall areas of the Amatola Mountains are deep, freely-drained and highly weathered (Hartmann 1988). The soils of the southern

![Figure 3.3: Topography of the study area in the Eastern Cape Province showing main mountain ranges and plains areas.](image-url)
lowlands are formed from argillaceous sedimentary material and contain high proportions of fine sand and tend to be hard-setting when dry (Hartmann 1988). Soils in the Queenstown Basin are often shallow and poorly drained with high-clay subsoils. The black, vertic soils of the Queenstown Basin have a high percentage of montmorillonitic clay causing them to swell and shrink markedly in response to moisture changes. Soils of the plains around Aliwal North are mostly sandy loams containing many boulders and gravel (Werger 1980).

Moisture availability is the major factor which can be used to divide the grassland biome into two classes (Ellery et al. 1995). Moist grassland consists of sour grasses, leached and dystrophic soils and high canopy cover, high plant production and high fire frequency. Semi-arid grassland has sweet, palatable grasses, soils are less leached and are eutrophic and canopy cover, plant production and fire frequency are lower than in moist grasslands. The division between semi-arid and moist grassland can be made on the basis of annual rainfall with 500–700 mm rainfall marking the boundary. This corresponds to the semi-arid limit of 500 mm annual rainfall of the Argentinian pampas and is consistent with divisions of the grasslands in South Africa into sweet and sourveld (Bond 1997, Huntley 1984). Sour grasslands in South Africa are generally found at higher altitudes and sweet grasslands at

![Figure 3.4: Mean annual temperature of the study area in the Eastern Cape Province. The extent shown here is identical to that in Figure 3.3.](image-url)
lower altitudes.

**Current climate**

The Eastern Cape grassland region can be divided into two broad climatic regimes (Kopke 1988). The lowlands have warm summers and mild winters whereas the mean temperatures of the mountain region are generally lower (Figure 3.4). Frost is a common phenomenon in grasslands and the coldest periods (usually from June to August) are exacerbated by seasonal aridity or the incidence of frost increases with increasing elevation. Winter frost is common and especially severe at high altitudes. The average daily minima for the coldest months are below freezing for all weather stations in the study area. Three stations, Cradock, Graaff Reinet and Aliwal North, experience an average of one day of snow a year and Buffelsfontein an average of two. Winter frost and cold is therefore a potentially limiting factor for plant growth, especially at high altitudes.

Altitude has a strong influence on most climatic variables. Generally, an increase in altitude corresponds with a decrease in temperature and an increase in rainfall. Mountains also have an orographic influence on rainfall, escarpment zones usually experiencing increased rainfall and mists, depending on aspect, cause either an increase or decrease in mean daily insolation.
The temperate grasslands of Southern Africa occur where there is strong summer rainfall and winter drought. However, the grasslands in the Eastern Cape mountains occur in an area of climatic transition. The mountains experience an autumn maximum rainfall pattern, but strong bimodal pattern of rainfall exists across most of the rest of the study area with a high proportion of spring and autumn rainfall. Rainfall across the entire biome may vary from 400–2500 mm per year and corresponds to the amount of rainfall found in other parts of the world where similar vegetation is found. In the study area within the Eastern Cape the rainfall varies from 500–2000 mm per year (Weather Bureau 1996, Figure 3.5) and is therefore relatively representative of the biome. Hogsback in the Amatola Mountains receives over 2000 mm of rainfall per annum (Kopke 1988) and is therefore the wettest part of the study area. There is a strong rainfall gradient from east to west across the study area with a difference in annual rainfall of 1500 mm recorded across only 80 km.

Fog is found on the upper slopes of the Great Escarpment and seaward scarps along the entire east and south-east boundary of the Grassland Biome, including the Eastern Cape mountains, and these areas support hygrophilous mistbelt vegetation. Dohne and Somerset East weather stations in the Eastern Cape, both on the southern side of the coastal mountain range, receive significant amounts of fog every year (average 113 and 71 days respectively). This not only supplements rainfall, but reduces mean insolation levels.

The biome, including the study area, has high lightning flash densities, which makes the incidence of lightning-induced fire a high likelihood (Schulze 1984). The number of days of thunder varies from one weather station to another, but ranges from 3 days (Buffelsfontein) to 60 days (Aliwal North), a decreased likelihood occurring towards the west and south-west.

**Land use**

The land use of the study area in the Eastern Cape is divided into communal and freehold tenure systems: communal tenure areas are heavily populated (56 people per km$^2$) whereas in regions characterised by freehold tenure, where commercial farming generally takes place, population density is lower (3–6 people per km$^2$) (Palmer et al. 1999). In communal areas livestock represents wealth and is a form of currency, and these areas are heavily stocked. In contrast, commercial farming systems in the freehold areas are characterised by land stocked at economically sustainable levels. The eastern part of the province has been under communal land ownership for in excess of 1000 years, whereas the westerly regions have been commercially farmed as stock ranches for close to 100 years. In the central regions there has been a recent shift from commercial to communal land ownership. In the communal area the major pressures on the landscape and on biodiversity are from intense herbivory, wood fuel harvesting and shifting cultivation.
Degradation of grasslands, including the spread of karroid shrublands into the Grassland Biome, has been blamed on high stocking rates of domestic livestock in commercial farming areas. Many communal grazing lands are commonly stocked at 3–4 times the recommended stocking rates for commercial farming and, although these areas appear to be degraded, they have remained in a stable and apparently productive state for decades. Heavy grazing in the communal areas of the Transkei appears to have reduced overall species richness (Hoare 2002) and changed species composition to less palatable grasses, especially on nutrient-poor soils (Owen-Smith & Danckwerts 1997).

**Seasonal patterns of vegetation productivity**

Studies of grassland vegetation activity from satellite data indicate that grasslands are strongly seasonal with a late summer maximum in vegetation activity and near complete termination of activity during the winter months (Hoare & Frost 2004). The area on the western side of the biome in the region that borders with Nama-karoo and arid savanna has highest vegetation activity in February, March and April. There is a correlation between increasingly late summer to autumn maximum vegetation activity and a changeover to the adjacent Nama-karoo and arid parts of the Savanna Biome (Hoare & Frost 2004). The temperate eastern half of the Grassland Biome has a period of maximum vegetation activity in January. Some of the steeper

![Figure 3.6: Seasonality (month of maximum NDVI) in the study area in the Eastern Cape Province. The extent shown here is identical to that in Figure 3.3.](image-url)
mountain regions within this eastern region are more active in December (Hoare & Frost 2004).

Within the study area in the Eastern Cape the season of maximum NDVI is summer, except for the Zuurberg in the south-west and the karoo vegetation in the west that tend to have late summer to autumn maximum NDVI activity (Hoare & Frost 2004). The high-lying parts of the study area tend to have mid-summer maximum NDVI, whereas the lowlands tend to have late-summer maximum NDVI (Figure 3.6). Most of the mountain areas have at least 6–7 months of high NDVI activity (> 210 days of activity, Figure 3.7), with isolated patches (forest patches and escarpment areas) active throughout the year (Hoare & Frost 2004). These areas also have a low co-efficient of variation in NDVI. In contrast, the lowland plains, especially of the Queenstown Basin, have high NDVI activity for 4–5 months with dryer patches having less than 3 months of high NDVI activity (< 90 days of activity, Figure 3.7) and much higher variability (Hoare & Frost 2004). The areas with the highest mean annual NDVI are within the Amathole Mountains. These are therefore the areas with the highest levels of vegetation production. There is a gradient of decreasing mean annual NDVI towards the west. Lowland areas have lower mean annual NDVI than upland areas.

**Figure 3.7:** Number of days of high NDVI in the study area in the Eastern Cape Province. The extent shown here is identical to that in Figure 3.3.
Analysis of environmental variables within study area

Species richness within communities (alpha diversity) may be influenced by a number of conditions, including ecological factors (Whittaker 1977; Brown 1988; Diamond 1988), and the number of available habitats (Shmida & Wilson 1985). It is important to consider which factors are likely to provide an explanation of diversity patterns and also to understand the way in which these vary within the study area.

The current study was undertaken at a local scale. Plot data used in the current analysis were collected for a floristic survey of the southern extreme of the Grassland Biome (Hoare 1997). A number of site variables were recorded in the field including aspect, slope inclination and surface rock cover. Additional variables were extracted from thematic maps of the study area or from surface response models (Dent et al. 1989). A list of variables for which values were obtained at each site is given in Table 3.2. The selection of variables is based on theoretical considerations of which variables may be important in explaining diversity patterns.

Of the environmental factors that may explain diversity patterns at a local scale, diversity may be explained in terms of primary environmental factors such as habitat heterogeneity, rainfall and available energy. These factors can be grouped into those describing resource availability and those describing heterogeneity, both in habitat and in terms of the supply of resources. Favourableness describes the absolute levels of the resources (availability) whereas heterogeneity applies to variability in the distribution or supply of the resources. Theoretical components of these factors are described in more detail in Chapter 4.

Table 3.2: Definition of environmental explanatory variables for diversity.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Abbreviation</th>
<th>Derivation</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>RESOURCE AVAILABILITY</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Favourableness:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean annual rainfall (mm)</td>
<td>MAR</td>
<td>Mean amount of rainfall per annum</td>
</tr>
<tr>
<td>Summer temperature regime (°C)</td>
<td>TMAX</td>
<td>Mean January maximum temperature</td>
</tr>
<tr>
<td>Winter temperature regime (°C)</td>
<td>TMIN</td>
<td>Mean July minimum temperature</td>
</tr>
<tr>
<td>Mean annual temperature (°C)</td>
<td>TEMP</td>
<td>Mean annual temperature</td>
</tr>
<tr>
<td>Period of very low temperature (days)</td>
<td>FROST</td>
<td>Mean number of days of frost per year</td>
</tr>
<tr>
<td>Land type</td>
<td>LTYPE</td>
<td>Uniform unit with respect to soil, climate &amp; topography</td>
</tr>
<tr>
<td>Geology</td>
<td>GEOL</td>
<td>Major geological unit</td>
</tr>
<tr>
<td>Altitude (m)</td>
<td>ALT</td>
<td>Height above mean sea level</td>
</tr>
<tr>
<td>Slope (°)</td>
<td>SLO</td>
<td>Slope inclination</td>
</tr>
<tr>
<td><strong>Energy:</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Potential evaporation (mm)</td>
<td>APAN</td>
<td>Summations of 12 monthly A-pan equivalent values</td>
</tr>
<tr>
<td>Solar radiation</td>
<td>SRAD</td>
<td>Mean amount of solar insolation</td>
</tr>
<tr>
<td>Duration of growing season (days)</td>
<td>DUR</td>
<td>Number of days when NDVI exceeds median annual</td>
</tr>
</tbody>
</table>
Trends in environmental gradients and correlations between environmental variables were analysed using Principal Components Analysis (PCA) (ter Braak 1987a). PC-ORD version 4 (McCune and Mefford 1999) was used for the ordination analysis. The PCA analysis indicated that 99% of the variance in the environmental data from the sampled sites was captured within the first four axes. The results of the PCA of the environmental variables (Table 3.2) showed that Axis 1, which accounted for 74.8% of the variance in the environmental data, was positively correlated with ALT ($r = 0.962$) and MAR ($r = 0.151$), and negatively correlated with APAN ($r = -0.225$). This defined an elevation gradient that also shows an increase in rainfall with elevation and a decrease in evaporative water loss. The strong correlation with elevation (ALT) and the high amount of variance explained by this axis are an indication of the importance of elevation as an environmental variable in the study area.

Axis 2, which accounts for 19.9% of the variance in the environmental data, was positively correlated with MAR ($r = 0.630$) and negatively correlated with ALT ($r = -0.263$) and APAN ($r = -0.695$). This defined a moisture gradient that is partially attributed to a change in elevation, but largely independent. It appears to be a complex gradient, probably reflecting the east-west and coast-interior gradient where rainfall increases with decreasing altitude. Axis 3 accounts for only 3.9% of the variance in the environmental data and further axes each account for less than 1% of the variance. Elevation, moisture and other climatic variables account for most of
the environmental variation in the study area. Other factors, e.g. SLOP, ROCK, NDVI, DUR, are correlated with later axes that explain little of the environmental variation within the study area. However, these factors appear from the PCA analysis to be independent of the other major climate and elevation variables.

Table 3.3: Results of Principle Components Analysis, indicating the correlation between environmental variables and first six eigenvectors.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Eigenvector 1</th>
<th>Eigenvector 2</th>
<th>Eigenvector 3</th>
<th>Eigenvector 4</th>
<th>Eigenvector 5</th>
<th>Eigenvector 6</th>
</tr>
</thead>
<tbody>
<tr>
<td>MAR</td>
<td>0.1511</td>
<td>0.6302</td>
<td>0.7065</td>
<td>0.2154</td>
<td>0.1643</td>
<td>0.0033</td>
</tr>
<tr>
<td>TMAX</td>
<td>-0.0027</td>
<td>-0.0047</td>
<td>0.0063</td>
<td>-0.0009</td>
<td>0.0036</td>
<td>0.0075</td>
</tr>
<tr>
<td>TMIN</td>
<td>-0.0036</td>
<td>0.0042</td>
<td>0.0026</td>
<td>-0.0015</td>
<td>-0.0133</td>
<td>-0.0150</td>
</tr>
<tr>
<td>TEMP</td>
<td>-0.0036</td>
<td>0.0011</td>
<td>0.0043</td>
<td>-0.0014</td>
<td>-0.0058</td>
<td>-0.0021</td>
</tr>
<tr>
<td>SRAD</td>
<td>0.0002</td>
<td>-0.0037</td>
<td>0.0023</td>
<td>-0.0013</td>
<td>0.0018</td>
<td>0.0069</td>
</tr>
<tr>
<td>FROST</td>
<td>0.0388</td>
<td>-0.0551</td>
<td>-0.0546</td>
<td>-0.0174</td>
<td>0.1707</td>
<td>0.1705</td>
</tr>
<tr>
<td>GEOL</td>
<td>0.0000</td>
<td>-0.0059</td>
<td>-0.0236</td>
<td>-0.0147</td>
<td>-0.0035</td>
<td>-0.0115</td>
</tr>
<tr>
<td>ALT</td>
<td>0.9615</td>
<td>-0.2630</td>
<td>0.0480</td>
<td>-0.0317</td>
<td>-0.0248</td>
<td>-0.0011</td>
</tr>
<tr>
<td>SLOP</td>
<td>0.0062</td>
<td>0.0071</td>
<td>0.0048</td>
<td>-0.0266</td>
<td>-0.0586</td>
<td>-0.2589</td>
</tr>
<tr>
<td>ROCK</td>
<td>0.0036</td>
<td>-0.0042</td>
<td>0.0062</td>
<td>-0.0079</td>
<td>-0.0042</td>
<td>-0.9377</td>
</tr>
<tr>
<td>TGRAD</td>
<td>0.0002</td>
<td>0.0001</td>
<td>0.0007</td>
<td>0.0002</td>
<td>0.0003</td>
<td>-0.0016</td>
</tr>
<tr>
<td>TRANG</td>
<td>0.0002</td>
<td>0.0966</td>
<td>0.1350</td>
<td>-0.1508</td>
<td>-0.8924</td>
<td>0.0480</td>
</tr>
<tr>
<td>TOPDIV</td>
<td>0.0050</td>
<td>0.0105</td>
<td>0.0070</td>
<td>-0.0141</td>
<td>-0.0456</td>
<td>-0.1353</td>
</tr>
<tr>
<td>APAN</td>
<td>-0.2253</td>
<td>-0.6949</td>
<td>0.6794</td>
<td>-0.0444</td>
<td>0.0173</td>
<td>0.0053</td>
</tr>
<tr>
<td>DUR</td>
<td>0.0106</td>
<td>0.1592</td>
<td>0.1015</td>
<td>-0.9588</td>
<td>0.2037</td>
<td>0.0033</td>
</tr>
<tr>
<td>NDVI</td>
<td>0.0104</td>
<td>0.1123</td>
<td>0.0630</td>
<td>-0.0755</td>
<td>-0.3009</td>
<td>0.0473</td>
</tr>
<tr>
<td>RCONC</td>
<td>0.0002</td>
<td>0.0011</td>
<td>0.0009</td>
<td>-0.0017</td>
<td>-0.0032</td>
<td>0.0012</td>
</tr>
<tr>
<td>NCONC</td>
<td>-0.0013</td>
<td>-0.0022</td>
<td>-0.0116</td>
<td>-0.0158</td>
<td>-0.0066</td>
<td>0.0055</td>
</tr>
<tr>
<td>MONTH</td>
<td>0.0009</td>
<td>-0.0089</td>
<td>0.0037</td>
<td>0.0006</td>
<td>0.0169</td>
<td>0.0225</td>
</tr>
<tr>
<td>RCOV</td>
<td>-0.0033</td>
<td>-0.0142</td>
<td>-0.0151</td>
<td>0.0016</td>
<td>0.0108</td>
<td>-0.0005</td>
</tr>
<tr>
<td>NCOV</td>
<td>-0.0001</td>
<td>-0.0001</td>
<td>-0.0001</td>
<td>0.0001</td>
<td>0.0000</td>
<td>-0.0002</td>
</tr>
</tbody>
</table>

Environmental variables were often strongly correlated with one another (Table 3.4). Such correlations are problematic for multiple regression since multi-collinearity (when two or more predictor variables in a multiple regression model are highly correlated) may cause the model to not give valid results about any individual predictor, or about which predictors are redundant with others. Correlations between environmental variables that are of interest include the following:

1. A number of variables are strongly correlated with elevation (Table 3.4), including a number of variables associated with temperature, TEMP ($r = -0.904$), TMAX ($r = -0.527$), TMIN ($r = -0.791$), FROST ($r = 0.724$), TGRAD ($r = 0.261$) and TRANG ($r = 0.265$), reflecting the fact that temperature decreases with elevation, the number of days with frost increases and temperature variability and range increases. There are also moisture related variables that are correlated with elevation, including MAR ($r = 0.270$), RCONC ($r = 0.313$), APAN ($r = -0.380$), RCOV ($r = -0.233$) and NCOV ($r = -0.508$), indicating that rainfall increases with elevation, evapotranspiration decreases and variability in rainfall as well as rainfall driven production decreases. One remaining variable is correlated with elevation, namely TOPDIV ($r = 0.245$), indicating that topographic diversity increases with elevation, a reflection of the fact that lowlands are relatively flat and highlands are steeper and more topographically diverse.
2. NDVI and MAR are strongly positively correlated \((r = 0.808)\) indicating that production is highly dependent on the amount of rainfall. NDVI is also positively correlated with NCONC \((r = 0.879)\), indicating that high production is often concentrated into strongly seasonal periods, and negatively correlated with RCOV \((r = -0.778)\), indicating that increased rainfall variability reduces overall levels of production. Other factors correlated with NDVI are TMAX \((r = -0.515)\), TMIN \((r = 0.352)\), SRAD \((r = -0.538)\), FROST \((r = -0.399)\), RGRAD \((r = 0.734)\), TOPDIV \((r = 0.399)\), APAN \((r = -0.661)\), DUR \((r = 0.620)\), TRANG \((r = -0.667)\) and NCOV \((r = -0.682)\). Temperature is an obviously important factor in explaining production with both upper and lower extremes negatively affecting vegetation production. RCOV and NCOV are positively correlated \((r = 0.702)\) indicating that variability in production is strongly determined by variability in rainfall.

3. APAN is positively correlated with TMAX \((r = 0.864)\) and SRAD \((r = 0.617)\) and negatively correlated with MAR \((r = -0.708)\).

4. ALT and NDVI are not correlated.

5. Both SLOP \((r = 0.372)\) and ROCK \((r = 0.222)\) are weakly positively correlated with TOPDIV. All three factors are weakly positively correlated with ALT, indicating that there is a slight tendency for there to be steeper slopes, greater topographic variation and increased rock cover with increasing elevation. ROCK is also weakly positively correlated with SLOP indicating that steeper slopes often have higher rock cover.

6. GEOL is not correlated meaningfully with any other factors. There are some apparent correlations, e.g. with SRAD, TGRAD and RCONC, but these are weak and probably due to chance. Although there is a gradient in geological type in the Eastern Cape from Tarkastad Subgroup at low elevation, through Molteno, Elliot and Clarens Formations to Drakensberg Formation at the highest elevation, this correlation with elevation is not evident from the sample sites.

Due to the fact that a number of variables are strongly correlated with one another, it is necessary in subsequent analyses to select a minimum set of environmental variables within which there is minimum colinearity. This will avoid statistical issues with colinearity that may complicate interpretation of results.

**Table 3.4: Cross-correlation matrix indicating correlations between environmental variables.**

<table>
<thead>
<tr>
<th></th>
<th>MAR</th>
<th>TMAX</th>
<th>TMIN</th>
<th>TEMP</th>
<th>SRAD</th>
<th>FROST</th>
<th>LTYPE</th>
<th>GEOL</th>
<th>ALT</th>
</tr>
</thead>
<tbody>
<tr>
<td>MAR</td>
<td>1.000</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>TMAX</td>
<td>-0.561</td>
<td>1.000</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>TMIN</td>
<td>0.117</td>
<td>0.178</td>
<td>1.000</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>TEMP</td>
<td>-0.135</td>
<td>0.615</td>
<td>0.806</td>
<td>1.000</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SRAD</td>
<td>-0.496</td>
<td>0.600</td>
<td>-0.538</td>
<td>-0.078</td>
<td>1.000</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>FROST</td>
<td>-0.228</td>
<td>-0.171</td>
<td>-0.927</td>
<td>-0.792</td>
<td>0.527</td>
<td>1.000</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>LTYPE</td>
<td>-0.374</td>
<td>-0.124</td>
<td>-0.140</td>
<td>-0.182</td>
<td>0.002</td>
<td>0.197</td>
<td>1.000</td>
<td></td>
<td></td>
</tr>
<tr>
<td>GEOL</td>
<td>-0.121</td>
<td>0.150</td>
<td>-0.108</td>
<td>0.032</td>
<td>0.274</td>
<td>0.055</td>
<td>-0.069</td>
<td>1.000</td>
<td></td>
</tr>
<tr>
<td>ALT</td>
<td>0.270</td>
<td>-0.527</td>
<td>-0.791</td>
<td>-0.904</td>
<td>0.175</td>
<td>0.724</td>
<td>0.027</td>
<td>0.024</td>
<td>1.000</td>
</tr>
</tbody>
</table>
### References:


Hill, M.O. 1979a. TWINSPAN. A FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes. Cornell University, Ithaca, NY.


CHAPTER 4: PATTERNS AND ABIOTIC ENVIRONMENTAL DETERMINANTS OF SPECIES RICHNESS IN GRASSLANDS OF THE EASTERN CAPE

Introduction

There are a number of theories dealing with the control of species richness in plant communities, many of which have been influenced by the fact that plant communities contain assemblages of species that all require the same basic resources, namely light, water, carbon dioxide and soil nutrients. Species richness within communities (alpha diversity) may be influenced by a number of conditions, including ecological factors (Whittaker 1977; Brown 1988; Diamond 1988), the number of available habitats (Shmida & Wilson 1985), historical factors that promote the evolution of habitat specialists (Shmida & Wilson 1985; Cowling et al. 1992), inherent biological properties of species lineages (Vrba 1980; Cowling & Holmes 1992) and the interaction between these biological traits and the physical environment (Cowling et al. 1989, 1992). Many studies explain diversity in terms of primary environmental factors such as habitat heterogeneity, rainfall and available energy. These factors can be grouped into those describing favourableness and those describing heterogeneity. Favourableness describes the absolute levels of the resources (availability) whereas heterogeneity applies to variability of the supply of the resources.

Cowling et al. (1989) remarked that despite a long history of research in grasslands in South Africa, no data could be found on patterns and maintenance of species richness in grasslands. Diversity patterns in South African grasslands have never been adequately described. Available data indicate that species richness in South African grasslands is comparable to that for North American grasslands (Cowling et al. 1989) and Eurasian Steppe grasslands (Wenhong 2007) but lower than some European grasslands of low productivity (Bond 1983, Kull & Zobel 2009). At the 1000m² scale grasslands have the second highest mean plant diversity behind renosterveld for all vegetation types in South Africa (Cowling et al. 1989). Diversity patterns within grassland communities of the Eastern Cape, an area of extraordinary complexity in the south-western extremity of the Grassland Biome, have never been adequately described or documented. Species richness has been observed to differ from one site to another within South African grasslands, but no comprehensive description exists for how patterns of richness differ within and between plant communities. Environmental gradients in the Eastern Cape study area are very steep and complex leading to a rich mixture of floristic elements. There are a wide variety of different grassland types within the same geographical area. Of particular interest are the steep productivity gradients in the study area.

This chapter examines patterns of species richness in plant communities of grassland vegetation, primarily in the Eastern Cape, but also in comparison to other parts of the
Grassland Biome of South Africa. The scale at which species richness patterns are examined here is within single plots of 10 × 10 m. It is at the small plot scale that species interactions occur and are thought to contribute to determining species richness (Latham & Ricklefs 1993). This within-habitat scale is the scale that defines alpha diversity, as opposed to the regional scale of many previous studies of this type (e.g. Cowling et al. 1989).

Table 4.1: Species richness reported in pure primary grassland for a number of regions within the Grassland Biome of South Africa where a Braun-Blanquet approach was adopted using 100 m\(^2\) quadrats for sampling.

<table>
<thead>
<tr>
<th>Region</th>
<th>Plots</th>
<th>Species richness range</th>
<th>SD</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Newcastle: Escarpment</td>
<td>20</td>
<td>25.5                   *</td>
<td>*</td>
<td>Smit et al. 1992</td>
</tr>
<tr>
<td>Newcastle: Escarpment</td>
<td>17</td>
<td>20.4                   *</td>
<td>*</td>
<td>Smit et al. 1993</td>
</tr>
<tr>
<td>Newcastle: Foothills</td>
<td>18</td>
<td>29.0                   *</td>
<td>*</td>
<td>Smit et al. 1993</td>
</tr>
<tr>
<td>Eastern Free State: high altitude</td>
<td>156</td>
<td>27.9                   *</td>
<td>*</td>
<td>Eckhardt et al. 1996a</td>
</tr>
<tr>
<td>Northeastern escarpment: low altitude</td>
<td>100</td>
<td>18.4                   13-23</td>
<td>3.6</td>
<td>Eckhardt et al. 1993</td>
</tr>
<tr>
<td>North-western Free State: semi-arid</td>
<td>53</td>
<td>25.7                   17-46</td>
<td>5.9</td>
<td>Matthews et al. 1992</td>
</tr>
<tr>
<td>North-western Free State: semi-arid</td>
<td>105</td>
<td>25.9                   18-35</td>
<td>6.9</td>
<td>Kooij et al. 1990a</td>
</tr>
<tr>
<td>Northern KZN: low altitude plains</td>
<td>59</td>
<td>15.4                   14-33</td>
<td>6.4</td>
<td>Kooij et al. 1990b</td>
</tr>
<tr>
<td>Northern KZN: high altitude</td>
<td>96</td>
<td>21.5                   9-30</td>
<td>5.4</td>
<td>Eckhardt et al. 1996b</td>
</tr>
<tr>
<td>Witbank NR: Highveld</td>
<td>20</td>
<td>43.0                   23-62</td>
<td>11.4</td>
<td>Smit et al. 1997</td>
</tr>
</tbody>
</table>

* no values given in publication.

Species richness at a 100 m\(^2\) scale has been reported for a number of studies done within grasslands of South Africa (see Table 4.1 for a selection of these). Species richness values have usually been included within phytosociological floristic studies without any attempt to understand or explain the richness patterns observed. Reported mean richness patterns in various parts of the Biome vary primarily between 20 and 30 species per 100 m\(^2\) plot from areas as divergent as KwaZulu-Natal to the western Free State and from the escarpment to Highveld regions. The highest values reported in published accounts are approximately 46 species per plot at Witbank Nature Reserve (Smit et al. 1997, Table 4.1), which is found within the Highveld region. This richness within the Witbank Nature Reserve is exceptional and most grassland areas in South Africa have less species than this per plot.

Eastern Cape grassland plant communities have been found to contain a range of richness values from plot to plot and between plant communities. In general, these species richness values fall within the range of values reported from other parts of the Grassland Biome. The objectives of this chapter were as follows:

1. to describe species richness, diversity and evenness patterns at the plot scale within different grassland plant communities of the Eastern Cape;
2. to describe the differences in richness patterns between plant communities;
3. to analyze the contribution to species richness by different major growth forms;
4. to analyze the relationship between species richness and various environmental variables.

**Study area**

See Chapter 3 for detailed description of the study area.

**Ecological separation between high and low rainfall grasslands in the study area**

Grasslands in South Africa occur where there is a mean annual rainfall of mostly between 400 and 2000 mm. The vegetation of the Grassland Biome follows a rainfall gradient and can be broadly divided into sweet and sour grasslands (Tainton 1981). Sweet grasses occur in lower rainfall areas, have lower fibre content and maintain a higher above-ground nutrient level in winter. In sweetveld, carbon assimilation tends to be low relative to nutrient supply, whereas the converse is true for sourveld (Ellery *et al.* 1995). Areas with a mean annual rainfall of above 625 mm tend to be dominated by sour grasses, although the change-over can be anywhere between 500 and 700 mm (Rutherford & Westfall 1986). The soils in moist grasslands tend to be leached by higher rainfall and tend to be dystrophic, whereas soils in semi-arid grasslands are generally eutrophic. Dystrophic soils have high organic content, variable (often low) nutrient levels and are often low in oxygen, whereas eutrophic soils have high nitrate and phosphate levels. Semi-arid grasslands have lower canopy cover, lower primary production and less frequent fires.

The ecological difference between semi-arid and mesic grasslands constrains the analysis of diversity to some degree. Different factors may be expected to shape diversity patterns in different ways within these two moisture regimes. However, it provides an opportunity to compare resource-driven (semi-arid) and competitively constrained (mesic) plant communities and understand the differences between them. In specific cases, data is therefore separated to take advantage of this contrast.

**Methods**

**Data collection**

Plot data were collected during a floristic survey of the Eastern Cape, which constitutes the south-western extreme of the Grassland Biome (Hoare 1997). These were classified into vegetation communities according to Braun-Blanquet procedures (Mueller-Dombois & Ellenberg 1974) and have been published elsewhere (Hoare & Bredenkamp 1999, 2001). Only the data from those plant communities that are physiognomically recognised as grassland are included in this analysis, although other plant communities, e.g. shrubland on rocky outcrops, also occur within the matrix of grasslands in the study area. A total of 227 plots from the Eastern
Cape were used in the current analysis. In each plot the projected canopy cover of each species was estimated and converted to a class value according to Braun-Blanquet methods (Westhoff & Van der Maarel 1978). The grassland plant communities included in this study are listed in Table 4.2 and grouped into semi-arid or mesic grassland types, as outlined in the section above (“Study area”).

### Table 4.2: Plant communities of the study area.

<table>
<thead>
<tr>
<th>Plant community description</th>
<th>Plant community name</th>
<th>Moisture regime (annual rainfall, mesic = &gt; 500 mm; semi-arid = &lt; 700 mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Mountain grasslands</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Amatola southern watershed</td>
<td>Eragrostio curvulae-Themedetum triandrae: eragrostietosum planae</td>
<td>Mesic</td>
</tr>
<tr>
<td>Amatola northern watershed</td>
<td>Eragrostio curvulae-Themedetum triandrae: leyseretosum gnaphalodis</td>
<td>Mesic</td>
</tr>
<tr>
<td>Stormberg plateau</td>
<td>Helichrysum rugulosae-Themedetum triandrae</td>
<td>Mesic</td>
</tr>
<tr>
<td>Amatola mistbelt</td>
<td>Themedo triandrae-Helichrysetum aurei</td>
<td>Mesic</td>
</tr>
<tr>
<td>High altitude, steep slope</td>
<td>Eragrostio chloromeladis-Festucetum caprina</td>
<td>Mesic</td>
</tr>
<tr>
<td>Festuca scabra escarpment grassland</td>
<td>Andropogono appendiculati-Festucetum scabra</td>
<td>Mesic</td>
</tr>
<tr>
<td>Protea simplex escarpment grassland</td>
<td>Protea simplicae-Themedetum triandra</td>
<td>Mesic</td>
</tr>
<tr>
<td><strong>Mountain drainage line grassland</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Miscanthus capensis grassland</td>
<td>Eragrostio curvulae-Miscanthetum capensis</td>
<td>Mesic</td>
</tr>
<tr>
<td><strong>Plains grassland</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Aliwal North semi-arid grassland</td>
<td>Hermanno depressa-Eragrostietosum chloromeladis</td>
<td>Semi-arid</td>
</tr>
<tr>
<td>Queenstown semi-arid grassland</td>
<td>Hermanno depressa-Eragrostietosum chloromeladis</td>
<td>Semi-arid</td>
</tr>
<tr>
<td>Smaldeel semi-arid grassland</td>
<td>Cymbopogono excavati-Digitarietum argyrograptae</td>
<td>Semi-arid</td>
</tr>
<tr>
<td><strong>Semi-arid mountain grasslands</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Merxmuellera disticha grassland</td>
<td>Elytropappo rhinocerotis-Merxmuelleretum distichae</td>
<td>Semi-arid</td>
</tr>
</tbody>
</table>

A number of site variables were recorded in each plot in the field, including aspect, slope inclination and surface rock cover. Additional information for each plot was extracted from thematic maps using the latitude and longitude co-ordinates of the plot obtained from a global positioning system. Species were categorised into life-form categories: woody trees and shrubs, dwarf shrubs, geophytes, graminoids and forbs. These life-forms were used as surrogates for functional types to determine whether there were differences in the diversity patterns of these groups in relation to environmental factors.

**Diversity indices**

Species richness ($S$) is defined as the number of species per site. There are a number of alpha diversity indices that require counts of the numbers of individuals in samples in order to calculate the index, for example, Margalef’s $D$ (Clifford & Stephenson 1975), McIntosh’s $D$ (McIntosh 1967), the Berger-Parker dominance index (Berger & Parker 1970), the Brillouin HB index (Pielou 1969, 1975), Fisher’s alpha index (Fisher et al. 1943), the Q statistic (Kempton &
Taylor 1976), Menhinick’s Dmn index (Whittaker 1977) and Strong’s Dw dominance index (Strong 2002). The data set used here contained percentage cover values for each species without counts of individuals. These alternative indices were not therefore used to describe diversity in this study.

Many different measures of evenness have been proposed, the most common approach being to scale one of the heterogeneity measures relative to its maximum value (Krebs 1989), i.e. by estimating the ratio between observed heterogeneity and maximum possible heterogeneity. Peet (1974) terms these heterogeneity indices because they include evenness and richness in a single measure. These indices are also considered to be non-parametric since they make no assumptions about the shape of the underlying species abundance distribution (Southwood 1978). There are two types of non-parametric indices (Magurran 1988), those derived from information theory and include the Shannon index (H'), and those termed dominance measures that include Simpson’s (1949) index (D). This second group of indices is weighted towards the abundances of the commonest species (Magurran 1988).

Mixed diversity, or heterogeneity measures, which combine richness and evenness, was calculated using the Shannon-Wiener index $H'$ (Shannon & Weaver 1949):

$$H' = -\sum p_i \ln p_i,$$

$p_i$ being the proportional importance of the ith species, and:

$$D = 1-\lambda \text{ where } \lambda = \sum p_i^2,$$

which is a variant of the Simpson index $D$ (Simpson 1949; Berger & Parker 1970; Peet 1974; Smith & Wilson, 1996), which is expressed in this format (1-$\lambda$) to vary directly with evenness rather than inversely, as is the case with the original formula ($\lambda$). This formula is also for an infinite sample and has been adjusted for sample size using the formula $N^2/(1-(1/S))$. Peet (1978) based species importance, using this method, on percentage cover. The Shannon-Wiener index $H'$ (Shannon & Weaver 1949) is an expression of equitability, whereas the Simpson index $D$ expresses relative concentration of dominance (Whittaker 1965, 1972; Peet 1974). The Shannon-Wiener index $H'$ is a popular index to use, but is considered to be “an insensitive measure of the character of the S:N relationship and is dominated by the abundant species” (Southwood & Henderson 2000). The value of the Shannon-Wiener Index usually lies between 1.5 and 3.5 for ecological data and rarely exceeds 4.0 in value. If species follow a log normal abundance distribution the sample must hold 100,000 species for $H'$ to be greater than 5.0 (May 1975). It is considered that this index often gives little more insight than species number, but does integrate richness and evenness.
May (1975) has shown that, where the number of observations > 10, the Simpson index $D$ is strongly influenced by the underlying distribution. Simpson's index is considered to be heavily weighted towards the most abundant species in the sample and less sensitive to species richness (Magurran 2004). However, Magurran (2004) also claims that the Simpson index is one of the most meaningful and robust diversity measures available, because it captures the variance of the species abundance distribution. Other earlier studies comparing diversity indices also support the Simpson index (e.g. Mouillot & Lepretre 1999). For both these heterogeneity-diversity measures the percentage canopy cover was used to give importance values for species (Peet 1978; Cowling 1983).

To measure beta diversity within communities (as a measure of within-community heterogeneity) Whittaker's (1972) function was used:

$$\beta_w = (S/\alpha)^{-1}$$

where $S$ (also expressed as $\gamma$) is the total number of species recorded in the system, and $\alpha$ is the average number of species per sample. This is defined more precisely by Vellend (2001) as the variation in species composition among localities, which distinguishes it from species turnover along gradients. The measure is independent of the distribution of species on spatial or environmental gradients (Vellend 2001), is useful for describing how total species diversity is partitioned within and among samples and can also be used to test for relationships between environmental and compositional heterogeneity (Vellend 2001). Wilson and Schmida (1984) assessed a number of beta diversity indices according to the criteria: ability to detect change, additivity, independence of $\alpha$ and independence of sample size. They concluded that $\beta_w$ (Whittaker 1972) performed the best, followed by Schmida and Wilson's own measure, 'T'.

**Explanatory variables**

Parameters that have a direct impact on plant growth were considered (nutrients, water, light, temperature) as well as several indirect variables (elevation, slope) that may affect local environmental conditions. Species richness and productivity (estimated from NDVI data) were correlated to determine whether there was a relationship between them. The effect of increasing area, biotic interactions, dispersal, speciation history and regional species pools are considered in other chapters.

Following Cowling *et al.* (1997), the environmental parameters are considered under the broad headings of environmental heterogeneity, favourableness, energy, seasonality and irregularity with various variables available to describe each of these (see Chapter 3, Table 3.2). Cowling *et al.* (1997) review hypotheses that fall within each of these sub-headings and they are not discussed further here. The selection of variables includes both the level of the environmental
variables as well as its heterogeneity, an essential consideration for distinguishing between these two types of parameters (Pausas & Austin 2001).

Data for explanatory variables was obtained from measurements taken in the field, a digital elevation model, various thematic maps (e.g. geology, land type), climatic surfaces (Dent et al. 1988), and from processed multidate satellite imagery to derive seasonal characteristics of vegetation growth (Hoare & Frost 2003). Geology was used as a surrogate for soil nutrient status (lowest nutrients = Cape Witteberg quartzites, highest is dolerite/basalt).

Table 4.3: Environmental explanatory variables used in the multiple regression for the analysis of the relationship between diversity and environment. The complete set of environmental variables is given in Chapter 3, Table 3.2. The list provided here is a reduced set of variables identified from Principle Components Analysis as representing the least amount of colinearity between variables.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Abbreviation</th>
<th>Transformation</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>RESOURCE AVAILABILITY</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Favourableness:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean annual rainfall (mm)</td>
<td>MAR</td>
<td>logarithmic</td>
</tr>
<tr>
<td>Geology</td>
<td>GEOL</td>
<td>None, converted to dummy variables</td>
</tr>
<tr>
<td>Altitude (m)</td>
<td>ALT</td>
<td>None</td>
</tr>
<tr>
<td>Slope (°)</td>
<td>SLO</td>
<td>arcsine (p’ = arcsin √p+0.5)</td>
</tr>
<tr>
<td><strong>Energy</strong>:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Potential evaporation (mm)</td>
<td>APAN</td>
<td>None</td>
</tr>
<tr>
<td>Duration of growing season (days)</td>
<td>DUR</td>
<td>Square root</td>
</tr>
<tr>
<td><strong>RESOURCE HETEROGENEITY</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Environmental heterogeneity:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Topographic diversity (%)</td>
<td>TOPDIV</td>
<td>None</td>
</tr>
<tr>
<td>Surface rockiness (%)</td>
<td>ROCK</td>
<td>arcsine (p’ = arcsin √p+0.5)</td>
</tr>
</tbody>
</table>

Multivariate analyses of environmental variables using PCA (see Chapter 3) indicates that there is strong correlation between some variables, most notably between elevation and various climatic variables (mostly temperature) and between rainfall and NDVI (a remote-sensed measure of production). In order to avoid issues with colinearity of variables during multiple regression modelling, it was therefore decided to use only those variables with the highest correlation with the first few axes of the PCA analysis, namely elevation (ALT), rainfall (MAR), potential evapotranspiration (APAN), duration of growing season (DUR) and surface rock cover (ROC) (see Chapter 3, Table 3.3) as well as those variables that were found to be not correlated with other variables, including geology (GEOL), slope inclination (SLO) and topographic diversity (TOPDIV). This selection process ensures that the most important variables are considered (in terms of variation in the study area) and that correlating variables are not included. The final list of environmental variables used in the analysis is given in Table 4.3. Due to covariation, it must be borne in mind that some of these variables may be surrogates of additional variables, e.g. elevation (ALT) represents changes in a number of climatic conditions, primarily temperature related variables.
Data analysis

Mean richness values were calculated for each grassland plant community. A one-way ANOVA was performed on the data from different plant communities to establish whether mean richness was significantly different between plant communities (to test the null hypotheses that the samples from all of the grassland communities belong to the same population). The one-way ANOVA assumes that data are sampled from populations with Gaussian distributions. A Kolmogorov-Smirnoff test was undertaken to test this assumption of normality. The one-way ANOVA also assumes that data are sampled from populations with equal standard deviations. A Bartlett test was undertaken to test this assumption of equal standard deviations. Where assumptions are violated, a non-parametric test (Kruskal-Wallis test = non-parametric ANOVA) replaced one-way ANOVA. A Tukey-Kramer multiple comparisons test was run post hoc in order to assess which groups are significantly different from which other groups in terms of diversity measures.

Multiple regression was used to test for contributions by independent variables on richness values (effect of environmental variables on richness and contribution to richness by different life-forms). In all multiple regression analyses, data for semi-arid and mesic grasslands were analyzed separately. Multiple regression was performed using life forms as independent variables against each of the diversity variables in order to test the degree to which different life-forms contributed towards overall richness. All life-form variables (counts of species in different life-forms) were square root transformed. This transformation is applicable when group variances are proportional to the means, which usually occurs when samples are taken from a Poisson distribution, i.e. when the data consists of counts of objects (Zar 1999).

For analyzing the contributions by environmental factors on diversity, multiple regression was performed using variables in Table 4.3 as independent variables against each of the diversity variables. Variables were transformed, depending on the type of data. This is due to the fact that there is an assumption of multiple regression models that data have a normal distribution. There were three types of data, continuous, percentage and counts. The continuous data, e.g. rainfall and elevation, was not transformed. Percentages or proportions form a binomial rather than normal distribution. The square root of each percentage value was transformed to its arcsine \( p' = \arcsin \sqrt{(p + 0.5)} \). This provides data with an almost normal distribution (Zar 1999). Count data, e.g. number of days (DUR), was square-root transformed. This transformation is applicable when group variances are proportional to the means, which usually occurs when samples are taken from a Poisson distribution, i.e. when the data consists of counts of objects (Zar 1999).

Minimum sets of explanatory variables were selected manually by a process of backward elimination. The multiple regression was performed with all the variables given in Table 4.3.
The variable with the highest p-value was then removed. The process was repeated iteratively removing one variable at a time (the least significant variable each time) until all variables remaining had a p-value below the threshold of 0.05 and were independent of one another. Analyses were performed separately on total species richness and on richness within growth forms.

**Results**

**Richness patterns**

There is high variation in species richness both within and among grassland communities. The values observed were, however, all within the overall range of values observed in other parts of the Grassland Biome (see Table 4.1). Within plant communities the richness varied substantially between plots with anything between 8 and 57 species per plot across all grassland community types. This causes the standard deviation in richness to vary within plant communities from 5.8 to 11.4 (Table 4.4).

Patterns of alpha diversity of plots in the grassland communities of the study area showed considerable variation (Table 4.4). Mean species richness per 100 m² plot (S) varied from 20.4 in *Miscanthus capensis* drainage line grasslands to 32.3 in *Protea simplex* escarpment grassland and Smaldeel Plains grassland. One-way ANOVA indicated that mean richness between grassland community types was significantly greater than expected by chance (p<0.0001). Richness data from different plant communities all passed a normality test (Kolmogorov-Smirnoff test, p>0.10). The assumption that the data was sampled from populations with equal standard deviations was not violated (Bartlett test). A post hoc Tukey-Kramer multiple comparisons test indicated that, for most pair-wise comparisons, the Amathole northern watershed grasslands (mean richness of 22.3 species per 100 m² plot) and *Miscanthus capensis* drainage line grasslands (mean richness of 20.4 species per 100 m² plot) had significantly lower mean richness than the remaining grassland plant communities (Table 4.4). Mean richness within remaining plant communities were not significantly different from one another.

Patterns of mixed diversity and internal heterogeneity of plots in the grassland communities of the study area also showed considerable variation (Table 4.4). Evenness data from different plant communities all passed a normality test (Kolmogorov-Smirnoff test, p>0.10). However, Bartlett’s test indicated that the standard deviations were significantly different between plant communities, a violation of the assumptions of one-way ANOVA. A Kruskall-Wallis (non-parametric) test was therefore performed to test for differences between means. This test indicated that variation in evenness between grassland types was significantly greater than expected by chance (p<0.0001). Mean mixed evenness/diversity was therefore considered to
be different between plant communities. Within the mountain grasslands the Amathole (southern and northern watershed) grasslands have the lowest values of $D$ and thus the most dominance by single species (Table 4.4). The plant communities with the highest values of $D$, and therefore the least dominance by single species, were within the *Merxmuellera disticha* semi-arid mountain grasslands (Table 4.4). According to a *post hoc* Tukey-Kramer multiple comparisons test, these differences are significant.

Heterogeneity ($H'$) data from different plant communities all passed a normality test (Kolmogorov-Smirnoff test, $p>0.10$). However, Bartlett’s test indicated that the standard deviations were significantly different between plant communities, a violation of the assumptions of one-way ANOVA. A Kruskall-Wallis (non-parametric) test was therefore performed to test for differences between means. This test indicated that variation in heterogeneity between grassland types was significantly greater than expected by chance ($p<0.0001$). Heterogeneity diversity ($H'$) was therefore considered to vary significantly between plant communities. Mean values of 0.16 to 0.61 were recorded. The lowest values were recorded in *Merxmuellera disticha* semi-arid mountain grasslands (Table 4.4) and the highest in *Miscanthus capensis* drainage line grasslands. However, the range of values overlapped for major physiographic regions. A *post hoc* Tukey-Kramer multiple comparisons test indicated that, for all pair-wise comparisons, the *Merxmuellera disticha* semi-arid grassland had significantly lower values of $H'$ than in other grassland communities and, for most comparisons, the *Protea simplex* escarpment grassland and Queenstown semi-arid grassland had significantly higher values of $H'$. The high altitude, steep slope grassland and Stormberg plateau grassland had significantly higher values of $H'$ than the Amathole southern watershed grasslands.

**Richness patterns within different growth-forms**

Diversity values differ between major growth forms in the study area. Table 4.5 shows the number of species of different life forms in grassland communities of the study area. Forbs make the most significant contribution to overall species richness per 100 m$^2$, followed by grasses (Table 4.5). This pattern was relatively consistent across plant communities (Table 4.5), although some trends can be observed. Within plains grasslands, the mean number of graminoids increases northwards from 9.3 in Smaldeel grasslands to 12.0 in Queenstown grasslands to 14.6 in Aliwal North grasslands. This trend is also evident in mountain grasslands with there being 7.7-8.3 graminoids per plot in the Amathole-Winterberg grasslands, which are further south, to 10.5-11.7 graminoids per plot in the Stormberg-Drakensberg grasslands. This appears to indicate more graminoids with closer proximity to the core of the Grassland Biome as well as more graminoids on lowland plains than within mountain areas. This pattern is possibly due to a species-energy relationship (Wright 1983), with altitude and latitude being surrogates for energy.
Forb richness varied substantially between plant communities with the highest richness values recorded within the Amathole mistbelt.

For mesic grasslands (n = 156), a multiple regression analysis indicated that for diversity ($H'$) amongst different growth forms, only forbs made a significant contribution to overall richness. For this analysis, the response variable is total richness and the explanatory variables are growth form diversity using the Shannon-Wiener index. A model containing richness amongst forbs explained only 4.1% of the variance in overall richness ($R^2 = 0.041$, $p < 0.0147$). The correlation between overall richness and diversity ($H'$) amongst graminoids was highest ($r^2 = 0.808$), followed by forbs ($r^2 = 0.710$), dwarf shrubs ($r^2 = 0.491$), geophytes ($r^2 = 0.119$) and trees/shrubs ($r^2 = 0.075$). There was some colinearity in diversity ($H'$) amongst different growth forms, primarily between grasses and forbs. A further multiple regression analysis indicated that diversity ($H'$) amongst all growth forms together explained only 12.9% of the variance in overall richness ($R^2 = 0.129$, $p < 0.0001$).

For semi-arid grasslands (n = 119), a multiple regression analysis indicated that for diversity ($H'$) amongst different growth forms, only forbs and geophytes made a significant contribution to overall richness. For this analysis, the response variable is total richness and the explanatory variables are growth form diversity using the Shannon-Wiener index. A model containing richness amongst forbs and geophytes explained 33.6% of the variance in overall richness ($R^2 = 0.336$, $p < 0.0001$). The correlation between overall richness and diversity ($H'$) amongst graminoids was highest ($r^2 = 0.963$), followed by dwarf shrubs ($r^2 = 0.834$), trees/shrubs ($r^2 = 0.584$), forbs ($r^2 = 0.578$) and geophytes ($r^2 = 0.310$). There was no colinearity in richness amongst different growth forms. A further multiple regression analysis indicated that diversity ($H'$) amongst all growth forms together explained only 0.4% of the variance in overall richness ($R^2 = 0.004$, $p < 0.5782$).

**Explanatory variables for richness**

**Mesic grasslands**

The results from the multiple regression (Table 4.6) indicate that variance in richness of all species together (ALL) in mesic grasslands is not significantly related to environmental variables. The same is the case for graminoids and forbs, the two dominant life-forms in mesic grasslands. However, there was a significant relationship between environmental explanatory variables and richness amongst geophytes, dwarf shrubs and trees/shrubs in mesic grasslands.

Within mesic grasslands, the relationship between richness of different life-forms (TREE, DWARF, GEOPH) and environmental variables differed for each life-form (Table 4.6). The results of the GEOPH multiple regression indicate that the model explains 11.9% of the variance in GEOPH and the variables that best explain variance in richness are DUR, MAR,
APAN and ROC (Table 4.6). According to the model, geophyte richness in mesic grasslands is therefore favoured by higher rainfall and a longer growing season and tends to be higher in areas with higher rock cover. The multiple regression for TREE explains 15.6% of the variance in TREE and the variables that best explain variance in richness are ROC, ALT and MAR (Table 4.6). The DWARF multiple regression explains 34.1% of the variance in DWARF and the variables that best explain variance in richness are ROC, ALT, SLO and TOPDIV (Table 4.6). Within TREE and DWARF, variables that best contributed to explaining both models are ROC and ALT, with tree/shrub richness declining with elevation and dwarf shrub richness increasing. Richness of both increased with increasing rock cover. The models otherwise indicate that richness within each life-form may be driven by different environmental variables.

**Semi-arid grasslands**

The results from the multiple regression (Table 4.7) indicate that variance in richness of all species together (ALL) in semi-arid grasslands is significantly related to environmental variables. The results of the ALL multiple regression indicate that the model explains 17.6% of the variance in ALL and the variables that contribute most towards explaining this variance are ROC and MAR (Table 4.7). Within semi-arid grasslands, the relationship between richness of different life-forms (GRASS, FORB, TREE, DWARF, GEOPH) and environmental variables differed for each life-form (Table 4.7). The results of the GRASS multiple regression indicate that the model explains 18.0% of the variance in GRASS and the variables that best explain variance in richness are MAR and APAN (Table 4.7). The results of the FORB multiple regression indicate that the model explains 12.6% of the variance in FORB and the variables that best explain variance in richness are ROC and MAR (Table 4.7). The results of the GEOPH multiple regression indicate that the model explains 9.4% of the variance in GEOPH and the variable that best explains variance in richness is SLO (Table 3.6). The multiple regression for TREE explains 28.3% of the variance in TREE and the variables that best explain variance in richness are ALT and TOPDIV (Table 4.7). The DWARF multiple regression explains 26.4% of the variance in DWARF and the variables that best explain variance in richness are ROC, ALT and MAR (Table 4.7).

Within GRASS, FORB, DWARF as well as in ALL, the one variable that features is MAR (Figure 4.1). Rainfall therefore appears to have a strong influence on richness within the dominant life-forms within semi-arid grasslands. The variable, ROC, also features prominently, with increasing richness of forbs and dwarf shrubs associated with increasing rock cover. The models otherwise indicate that richness within each life-form may be driven by different environmental variables. Graminoid richness is also linked to APAN, a surrogate for available energy, and indicates that increased production may favour higher richness within this life-form.
Evenness patterns and explanatory variables

EVEN and EQU were weakly correlated with environmental factors and the factors explaining these indices were different in mesic and semi-arid grasslands. Within mesic grasslands, the results from the multiple regression indicate that the model comparing EVEN and environmental variables explains only 7.6% of the variance in EVEN. The only environmental variable that explains significant variation in EVEN in mesic grasslands is MAR. For EQU within mesic grasslands, the results from the multiple regression indicate that the model comparing EQU and environmental variables explains only 8.8% of the variance in EQU. The environmental variable that explains significant variation in EQU in mesic grasslands are MAR and APAN, although APAN is poorly correlated with EQU (Table 4.6).

Within semi-arid grasslands, the results from the multiple regression indicate that the model comparing EVEN and environmental variables explains 11.4% of the variance in EVEN. The environmental variables that explains significant variation in EVEN in semi-arid grasslands are MAR and ROC. For EQU within semi-arid grasslands, the results from the multiple regression indicate that the model comparing EQU and environmental variables explains 15.4% of the variance in EQU. The environmental variable that explains significant variation in EQU in semi-arid grasslands are MAR, ROC, ALT and SLO, although ALT and ROC are poorly correlated with EQU (Table 4.7).

Discussion

Patterns of species richness in grassland plant communities

That species richness differs from one community to another is not surprising. It was the focus of many early studies on diversity to demonstrate that such patterns existed. The most extraordinary pattern revealed here is that richness amongst different life-forms in the same place is driven by different environmental factors. Any multivariate analysis of richness-environment relationships with all species together thus reveals only a small part of the true complexity of these ecosystems. Clearly, the factors that determine coexistence of species do not operate uniformly on all species or life-forms.

Grasslands consist of a single herbaceous layer dominated by grasses. Amongst the grasses occur a rich variety of forbs that seldom occur as more than a few individuals, except in rare cases where they may dominate in single patches in the landscape. Such simple structure does not seem to be the recipe for great variability and these apparently uniform grasslands do not appear to have a wide range of species richness values. The lowest mean values are around 23 species per plot and the highest only 35 species per plot per community, whereas individual plots may differ from having as few as eight to as many as 57 species. The range of richness
values overlaps significantly across all grassland communities and appears to reflect patterns in the Grassland Biome as a whole.

Graminoids and forbs contribute the majority of species to overall richness. However, richness amongst forbs contributes more significantly and richness amongst graminoids contributes less significantly towards overall richness in mesic than semi-arid grasslands. Richness amongst trees/shrubs and dwarf shrubs contributes more significantly towards overall richness in mesic than semi-arid grasslands.

**Relationship between species richness and environmental variables**

The environmental variables that best explain species richness in grasslands of the study area are MAR (rainfall) and ROC (surface rockiness). Although the multiple regression models indicate that there are a number of variables that are significant in terms of explaining richness, rainfall makes the largest contribution towards explaining richness in the entire dataset and richness within semi-arid grasslands. With an increase in rainfall, there is a slight increase in species richness (Figure 4.1), although the correlation is different amongst the two life-forms that contribute most to richness. Furthermore, richness amongst forbs has a stronger relationship with rainfall and a more obvious decline at higher rainfall levels. The relationship is not strong enough to indicate whether the relationship is linear or unimodal, but a polynomial regression provides a slightly better fit to the data than a linear regression (Figure 4.1). Theoretical considerations also suggest that richness should decline at higher resource levels. The relationship with surface rockiness (a heterogeneity measure) supports the notion that habitat variety in equal-area plots is positively related to species diversity (Harner & Harper 1976, MacArthur 1964) and that many of the species would be expected to be habitat specialists. Variables describing environmental favourableness also appear to promote higher total species richness across the study area.

In examining the relationship between species richness and environmental variables, the linear regression explains only 10.7% of the variation in species richness in the dataset, implying that almost 90% of the variation still needs to be explained by other factors. The analysis provides a simple indication of the identity of the environmental factors that explain species richness. Identifying these factors is critical in determining the underlying environmental factors that may structure these grassland plant communities. Environmental and resource variables, e.g. nutrients, water, light and temperature, may determine species occurrence, growth and competitive interactions, whereas parameters related to environmental heterogeneity tend to affect coexistence (Pausas & Austin 2001). The analysis suggests that both these factors are important to different degrees in different parts of the study area.
The identical explanatory variables are significant in semi-arid grasslands as for the study area as a whole. However, for mesic grasslands, the multiple regression of richness versus environmental parameters was not significant, indicating that environmental variables used in this study are not important in explaining species richness in these higher rainfall areas. The response of species richness in the study area to resource gradients appears to saturate at high resource levels, as would be expected if competition was excluding species at high resource levels (Grime 1979). Any interpretation must take into account the fact that forbs make the largest contribution by far to species richness in the study area, followed by graminoids (Table 4.5), whereas it is the grasses that influence species evenness (or dominance) to the greatest extent. It is predicted that richness of plant functional types will be correlated with species richness in the study area and that there are not high numbers of species in the same functional guilds, where competition would be expected to be more intense, except amongst the dominant grasses.

Figure 4.1: Relationship between rainfall and richness in the study area: annual rainfall is correlated with richness.

Soil properties were not investigated in this study. The geological types were used as a surrogate for soil nutrient status with Cape sandstones and quartzites categorized as having low nutrient status and dolerites and basalts as having high nutrient status. The geology of most the study area (mostly sandstones, mudstones, etc., interspersed with dolerites outcrops) does not appear to generate soils of sufficiently different nutrient levels to affect local richness significantly. Many studies have found a hump-backed relationship between
species richness and soil nutrient levels, with intermediate levels of soil nutrients producing the highest number of species (Grime 1973). At high nutrient levels a few highly competitive species dominate the resources as opposed to nutrient-poor soils where no species have an opportunity to become dominant and many more species are thus able to co-exist (Grime 1979). The high dominance in many grasslands of the study area supports this observation. In the Mpumalanga area, where a greater variety of substrates are found, it has been noted in the field that sandy soils (with low nutrient status) support the most number of species within grassland vegetation (pers. obs.).

Different environmental variables have an influence at different scales in the landscape. Climate generally varies across regional scales and, except for topographic influences, is unlikely to vary significantly at a localised or landscape scale. For example, rainfall is unlikely to vary over short distances and, in the study area, varies over a distance of 100 to 200 km. It is therefore unlikely that climatic (rainfall and temperature) effects will be detectable within single plant communities or even along gradients within semi-arid versus mesic grasslands at a landscape scale. This is evident from the current data set, where some climatic and productivity variables were only able to weakly explain variation in diversity indices when the entire dataset (semi-arid and mesic) was combined. Other variables, such as surface rock cover and topographic diversity, which may vary at the scale of the sample sites or their immediate surroundings, tended to explain more variation in diversity indices within more localised data sets. Species interactions, species pool effects and habitat heterogeneity are probably able to have an influence at this scale (if they are important). Habitat heterogeneity is fractal-like in that it has an influence over multiple scales and may influence diversity at a range of scales.

**Species richness of graminoids**

Within all grasslands, the primary environmental factors explaining graminoid richness are rainfall, topographic diversity, potential evapotranspiration and surface rock cover. In semi-arid grasslands, only rainfall and potential evapotranspiration were significant. Within mesic grasslands environmental factors fail to explain graminoid richness. This indicates that, on a landscape scale, increasing rainfall and energy promote graminoid richness, but once high rainfall areas are reached, rainfall and energy are no longer a factor. This implies that environmental factors may manifest their influence at different scales in the landscape and also at different values of the environmental variable. There is also an indication that increased productivity promotes graminoid richness below a critical rainfall level, after which other factors become important.

The fact that multiple regression explains graminoid richness best with measures of favourableness (MAR), energy (APAN) and heterogeneity (ROC and TDI) indicates that the
graminoids consist of species that compete for space and resources or, according to niche differentiation theory (Ricklefs 1977; Grubb 1977, Shmida & Ellner 1984, Cody 1986; Crawley 1986, Tilman 1988, 1990, Leibold 1995;), are niche specialists to some degree. Rainfall (MAR) relates directly to resource availability and the importance of this factor in the analysis suggests that there may be conditions in which strong competition for resources occur. Habitat heterogeneity promotes coexistence without competition because species may be limited by the number of niches available and the strong gradient in rainfall availability provides closely spaced dissimilar niches. Seasonality enables species with different physiological niches, e.g. C3 versus C4 grasses, to coexist (Monson et al. 1983) and therefore also promotes coexistence without competition. There is a weak positive relationship between DUR and richness indicating that a long growing season corresponds with higher richness. The longer season may allow less long-lived species to utilize the extremes of the growing season when competition is less severe.

The grasses in the study area have a wide variety of growth-form variation, including large, tussock-forming grasses that are likely to be dominant in competition for resources as well as smaller species with low abundance that occupy gaps between larger plants. The correlation of graminoid richness with the wide range of environmental variables is therefore consistent with the variety in grass functional types that occur in the study area. A positive relationship between graminoid functional type richness and species richness is therefore expected. A more comprehensive analysis of the functional syndromes amongst the grass species is necessary to also determine whether richness within particular functional syndromes is correlated with particular environmental variables. This is undertaken in Chapter 6.

There appears to be increasing richness of graminoids in open grasslands with distance northwards in the study area that would correspond to being closer to the core of the Grassland Biome. This richness corresponds with an increase in the number of species that belong to the Chloridoideae and Panicoideae (Andropogoneae) that are the dominant grass sub-families in the core of the Grassland Biome. This pattern may reflect a species-energy relationship within graminoids (Wright 1983), with altitude and latitude being surrogates for energy.

**Species richness of forbs**

The primary environmental factors explaining forb richness are rainfall and surface rock cover. This relationship is true for all grasslands or semi-arid grasslands on their own. Within mesic grasslands environmental factors fail to explain forb richness. This indicates that, on a landscape scale, increasing rainfall and rock cover promotes forb richness, but once high rainfall areas are reached, rainfall and rock cover are no longer a factor. As with graminoids, this provides further evidence that environmental factors may manifest their influence at
different scales in the landscape. As with graminoids, there is also a suggestion that increased productivity (for which rainfall is a surrogate) promotes forb richness up to a critical rainfall level, after which other (non-environmental) factors become important.

Forbs have a stronger relationship between richness and environmental variables linked to habitat heterogeneity (which promotes niche differentiation) than grasses, including topographical diversity (TOPDIV), surface rock cover (ROC) and length of growing season (DUR). This indicates that they exploit a variety of niches rather than competing for resources. This corresponds with the plant communities in which high forb richness was found, namely the mountain grasslands, except for the majority of the Amathole mountains and Queenstown semi-arid grasslands. The high richness within forbs indicates that there may be a high functional type richness within this group and it is likely that a variety of strategies to ensure persistence occurs amongst forbs. Of particular interest in the study area is the extreme richness within the Asteraceae, particularly of the genera Helichrysum and Senecio.

**Species richness of geophytes**

There was a low richness of geophytes in the grasslands of the study area. This may be partially due to the season of survey: most geophytes emerge early in the season, whereas the grassland survey was conducted primarily during the height of the growing season. However, previous studies suggest that low geophyte richness is due to competition with grasses and that the dryer parts of the country with lower grass cover have higher geophyte richness (le Maitre & Midgley 1992). This is not evident from the current study and the mean number of geophytes is lower in the arid areas than in the high rainfall mountain areas (Table 4.5). The plant community with the highest geophyte richness is Protea simplex escarpment grassland, a mesic grassland type (see Table 4.1).

A significant amount (14.4%) of the variance in richness amongst geophytes could be explained by environmental variables, of which MAR and ROC showed the best correlation (Table 3.7). Geophyte richness shows an increase with increase in rainfall, which is an environmental variable measuring favourableness. In mesic grasslands both these variables are statistically important in explaining geophyte richness, along with APAN and DUR, which are variables measuring energy. Whether these are acting directly in promoting geophyte richness or through effects on the dominant life-forms (graminoids and forbs) is not known. Higher rainfall may promote increased production in geophytes or else it is an indirect effect of there being more fires in grasslands with higher production, thus providing more opportunities for geophytes to appear. In semi-arid grasslands, geophyte richness increases with increasing slope inclination. Steeper slopes tend to provide a more favourable (cooler and more moist) environment, thus providing shelter from harsher (drier, hotter and more exposed) environmental conditions within semi-arid grasslands.
Geophyte richness is also correlated with a variable that measures heterogeneity (ROC) in both semi-arid and mesic environments. Habitat heterogeneity ensures that the likelihood of a favourable habitat existing is increased. Habitats with higher rock cover also tend to have lower dominance by graminoids, thus providing less competition to other life-forms.

**Species richness of dwarf shrubs**

Dwarf shrub richness was highest in any plant community with a karroid influence (Table 4.5), for example *Mermuellera* grassland, as well as in grasslands at high altitudes where the environment is more extreme. The dwarf shrub habit is a response to rainfall uncertainty and/or regular drought conditions, whether climatically or physiologically induced. The negative relationship of dwarf shrub richness with MAR and DUR is a manifestation of this trend, since this defines areas of low energy and low rainfall predictability. There is an increase in richness within the dwarf shrub growth form with decreasing rainfall that indicates movement from the Grassland Biome into the Karoo Biome. The reduced rainfall is not able to support high graminoid cover thus providing a competitive opportunity to dwarf shrubs that are able to persist under these more extreme conditions. Dwarf shrubs are able to persist in extreme conditions and then respond rapidly to favourable periods when they occur.

Dwarf shrub richness is primarily linked to an increase in rock cover, which both increases habitat heterogeneity and reduces grass cover. There is also a lower tendency for fires to occur within rocky habitats, due to the lower grass fuel loads. There is also a strong positive relationship between dwarf shrub richness and steep slopes, high elevation and high rock cover, all conditions that occur in the more extreme (drier) habitats of the study area.

**Species richness of woody species (trees and shrubs)**

There is a relatively strong relationship between tree and shrub species richness and surface rock cover (ROC), which is not surprising since areas of high rock cover are the only habitat within the mountain grasslands that support woody species. Higher vegetation structural diversity in areas of high rock cover contributed in general to higher species richness relative to the surrounding open grasslands. For example, in both the Amathole and Stormberg areas, shrublands occur in rocky areas embedded within the grasslands. Rocky areas tend to have shallow soils that are not able to support herbaceous vegetation due to low water availability in shallow soils. Shrubs and trees are, however, able to extend their roots deeper into the substrate to access water that is unavailable to herbaceous plants. The lower herbaceous cover, especially that of grasses, provides little fuel for regular fires so that shrub-dominated rocky areas tend to burn at a lower frequency than surrounding grasslands. Woody plants that occur within open grassland often have thick, fire-resistant bark, e.g. *Cussonia* and *Protea*. Fire effects on grassland vegetation are discussed further in Chapter 7.
Tree and shrub richness is positively correlated with an increase in rainfall and a decrease in elevation. Elevation is a surrogate variable for a number of temperature-related variables. Increased elevation therefore represents lower temperatures, increased frosts and more extreme minimum temperatures. The combination of decreased rainfall and increased likelihood of winter frost is the combination of environmental conditions that distinguishes savanna and grassland areas and is thought to contribute towards the general lack of trees in the Grassland Biome outside of specialised habitats (Rutherford & Westfall 1986). Tree species richness is also known to increase along production gradients (Currie 1991), which is related to both rainfall and energy.

**Species evenness**

Evenness is the outcome of resource supply and demand and the relative competitive abilities of species to utilize and dominate those resources. It depends on environmental and biological factors. Species evenness is the measure that gives the best indication of the level of competition for resources taking place in the plant communities of the study area. Where evenness is high species share resources relatively evenly, no species are dominating resources and intense competition is therefore not taking place. With less evenness some species are beginning to dominate space and resources at the expense of others and there is therefore more intense competition taking place.

Difference in evenness between sites in the grasslands of the study area can be explained by a combination of rainfall and topographic diversity, although rainfall explains a far greater amount of the variation in evenness. The open grasslands in areas of low topographic variability of the mountain regions have the lowest equitability scores, especially the Amathole region, which may contribute to the lower species richness. On a landscape scale, evenness increases at higher rainfall levels (Figure 4.2), although the relationship is less clear at higher rainfall levels. Within mesic grasslands, rainfall still has an effect, but much more weakly indicating that some other factor promotes evenness at a more local scale. In semi-arid grasslands, surface rock cover promotes evenness, probably by creating habitat diversity in which niche specialists can occur: rocky areas tend to have low dominance by grasses, which are the life-form that tends to contain the highest relative biomass.
The escarpment region has nutrient-poor, leached soils. Perennials need to protect "resource capital" (c.f. Grime 1977) in order to persist or must be able to compete effectively for resources after a disturbance. In the escarpment zone competition is continuous since the season never entirely stops: water is often available even when the rest of the landscape is dry and orographic mists tend to keep escarpment slopes moist. In the central part of the Grassland Biome the seasonal climate "resets" competition every winter (dry, cold). Persistence within species therefore includes attributes such as low palatability. Low evenness may be the logical outcome of a high proportion of persistence traits in species. This should be detectable from more detailed functional type analysis.

The relationship between species evenness and environmental variables revealed a discontinuity in the evenness scores above MAR = 500 mm and below APAN = 1900. This demonstrates the effect of resource availability on species coexistence. Above 500 mm rainfall water tends to no longer be a limiting resource and competitive species can dominate the available space. Below 500 mm rainfall the rainfall is insufficient to permit such dominance and competition for space is not so intense.
Concluding remarks

Diversity (richness, evenness and heterogeneity) varies significantly between different plant communities in the study area. This variation falls within the range of richness values found in other parts of the Grassland Biome, as reported from published phytosociological studies.

This study has shown that environmental variables explain richness to varying degrees, depending on the life-forms and whether it is semi-arid or mesic grassland. Environmental variables do not explain richness in mesic grasslands as well as in semi-arid grasslands. Co-existence in semi-arid grasslands appears to be limited by environmental factors to some degree, whereas in mesic grasslands, where environmental models do not provide significant explanations for diversity patterns, it appears that species interactions or other factors may be more important in structuring plant communities. Environmental variables explain more variation in richness patterns amongst trees and dwarf shrubs than amongst other life-forms. Environmental variables explain very little of the variation in richness amongst grasses and forbs, the two dominant life-forms in grasslands that dominate and shape community structure and composition. Disturbance, for example regular fires, species interactions, dispersal and historical factors are likely to explain significant amounts of variation in diversity within different grassland types, although the strength of these factors in shaping diversity patterns within plant communities is likely to vary between semi-arid and mesic grasslands. Species evenness patterns suggest that species interactions shaping competition for resources are likely to be more significant within mesic than semi-arid grasslands.

Different life-forms contribute to different degrees towards overall richness in grasslands. In general, forbs contribute the highest number of species to overall richness, followed by grasses. Geophytes, dwarf shrubs and woody plants (trees and shrubs) contribute small numbers of species to overall richness, depending on habitat, but this varies from semi-arid to mesic grasslands. Grasses and forbs have the anatomical and physiological adaptations to promote survival under the environmental conditions that predominate in grassland areas. Physical environmental conditions were covered in this study, but other factors important in shaping grassland vegetation structure include regular fires, grazing and strong seasonality. Regular defoliation is probably more important than general environmental conditions in limiting species occurrence in grasslands. Diversification amongst taxa with adaptations to these conditions is likely to have provided the species pool from which selection has occurred in local plant communities. Co-occurrence of overlapping guild members is likely to provide equal or greater insights into factors promoting diversity than environmental factors on their own. This is addressed in the chapter that follows.
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Table 4.4: Comparative diversity measures (all species combined) in 100 m² samples from the study area.

<table>
<thead>
<tr>
<th></th>
<th>n</th>
<th>( S )</th>
<th>( S' ) range</th>
<th>( H' )</th>
<th>( D ) range</th>
<th>( \beta_\omega )</th>
<th>Total species in combined samples</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mountain grasslands</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Amatola southern watershed</td>
<td>15</td>
<td>23.7</td>
<td>9–43</td>
<td>0.54</td>
<td>0.47–2.46</td>
<td>0.53</td>
<td>116</td>
</tr>
<tr>
<td>Amatola northern watershed</td>
<td>24</td>
<td>22.3*</td>
<td>11–43</td>
<td>0.47</td>
<td>0.74–2.55</td>
<td>0.60</td>
<td>172</td>
</tr>
<tr>
<td>Stormberg plateau</td>
<td>32</td>
<td>31.4</td>
<td>12–55</td>
<td>0.28</td>
<td>0.92–2.36</td>
<td>0.72</td>
<td>252</td>
</tr>
<tr>
<td>Amatola mistbelt</td>
<td>16</td>
<td>31.7</td>
<td>16–57</td>
<td>0.26</td>
<td>1.10–2.18</td>
<td>0.70</td>
<td>210</td>
</tr>
<tr>
<td>High altitude, steep slope</td>
<td>12</td>
<td>30.5</td>
<td>11–50</td>
<td>0.45</td>
<td>0.78–2.39</td>
<td>0.71</td>
<td>157</td>
</tr>
<tr>
<td>Festuca scabra grassland</td>
<td>10</td>
<td>31.6</td>
<td>8–45</td>
<td>0.44</td>
<td>0.89–2.21</td>
<td>0.68</td>
<td>153</td>
</tr>
<tr>
<td>Protea simplex grassland</td>
<td>19</td>
<td>32.3</td>
<td>20–45</td>
<td>0.30</td>
<td>1.39–2.54</td>
<td>0.77</td>
<td>153</td>
</tr>
<tr>
<td>Mountain drainage line grassland</td>
<td>15</td>
<td>20.4*</td>
<td>8–35</td>
<td>0.61</td>
<td>0.41–2.47</td>
<td>0.69</td>
<td>151</td>
</tr>
<tr>
<td>Plains grassland</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Aliwal North semi-arid grassland</td>
<td>14</td>
<td>30.9</td>
<td>15–47</td>
<td>0.24</td>
<td>1.36–2.23</td>
<td>0.74</td>
<td>117</td>
</tr>
<tr>
<td>Queenstown semi-arid grassland</td>
<td>17</td>
<td>31.2</td>
<td>19–48</td>
<td>0.45</td>
<td>1.13–2.89</td>
<td>0.77</td>
<td>180</td>
</tr>
<tr>
<td>Smalldeel semi-arid grassland</td>
<td>13</td>
<td>32.3</td>
<td>15–59</td>
<td>0.24</td>
<td>1.42–1.98</td>
<td>0.76</td>
<td>63</td>
</tr>
<tr>
<td>Semi-arid mountain grasslands</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Merxmuellera disticha grassland</td>
<td>47</td>
<td>25.8</td>
<td>13–51</td>
<td>0.16</td>
<td>0.19–0.81</td>
<td>1.03</td>
<td>231</td>
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</table>
Table 4.5: Mean species richness amongst different life-forms in vegetation communities of the study area.

<table>
<thead>
<tr>
<th>Community</th>
<th>Trees/shrubs</th>
<th>Dwarf shrubs</th>
<th>Graminoids</th>
<th>Forbs</th>
<th>Geophytes</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Mountain grasslands</strong></td>
<td></td>
<td></td>
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<td></td>
<td></td>
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<tr>
<td>Amatola southern watershed</td>
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<td>1.5</td>
<td>8.3</td>
<td>12.5</td>
<td>1.3</td>
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<tr>
<td>Amatola northern watershed</td>
<td>0.2</td>
<td>1.9</td>
<td>8.0</td>
<td>11.3</td>
<td>1.0</td>
</tr>
<tr>
<td>Stormberg plateau</td>
<td>0.6</td>
<td>1.9</td>
<td>11.1</td>
<td>16.6</td>
<td>1.1</td>
</tr>
<tr>
<td>Amatola mistbelt</td>
<td>0.2</td>
<td>2.6</td>
<td>7.7</td>
<td>19.5</td>
<td>1.7</td>
</tr>
<tr>
<td>High altitude, steep slope grasslands</td>
<td>0.8</td>
<td>3.3</td>
<td>10.5</td>
<td>13.8</td>
<td>1.8</td>
</tr>
<tr>
<td>Festuca scabra escarpment grassland</td>
<td>0.2</td>
<td>1.8</td>
<td>11.7</td>
<td>16.3</td>
<td>1.6</td>
</tr>
<tr>
<td>Protea simplex escarpment grassland</td>
<td>1.2</td>
<td>1.8</td>
<td>11.1</td>
<td>14.3</td>
<td>3.9</td>
</tr>
<tr>
<td><strong>Mountain drainage line grassland</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Miscanthus capensis grassland</td>
<td>1.3</td>
<td>1.2</td>
<td>7.7</td>
<td>9.5</td>
<td>0.7</td>
</tr>
<tr>
<td><strong>Plains grassland</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Aliwal North semi-arid grassland</td>
<td>0.9</td>
<td>1.4</td>
<td>14.6</td>
<td>13.3</td>
<td>0.9</td>
</tr>
<tr>
<td>Queenstown semi-arid grassland</td>
<td>0.8</td>
<td>1.7</td>
<td>12.0</td>
<td>15.5</td>
<td>1.2</td>
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<tr>
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<td>1.3</td>
<td>2.2</td>
<td>9.3</td>
<td>8.8</td>
<td>1.0</td>
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<tr>
<td><strong>Semi-arid mountain grasslands</strong></td>
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<tr>
<td>Merxmuellera disticha grassland</td>
<td>0.7</td>
<td>3.7</td>
<td>9.6</td>
<td>10.4</td>
<td>1.0</td>
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</table>
Table 4.6: Results of multiple regression of mesic grassland data and environmental variables, including a selected list of explanatory variables (see text). ALL = richness of all species together, GRASS = richness amongst graminoids only, FORB = richness amongst forbs only, GEOPH = richness amongst geophytes only, DWARF = richness amongst dwarf shrubs only, TREE = richness amongst woody trees and shrubs only, EVEN (D) = Simpson’s evenness index, including all species, EQU (H) = equitability, including all species.

<table>
<thead>
<tr>
<th>Diversity variable</th>
<th>p</th>
<th>Sum of squares</th>
<th>SD of residuals</th>
<th>R²</th>
<th>Adjusted R²</th>
<th>F</th>
<th>Model (based on minimum set of explanatory variables)</th>
<th>Correlations</th>
</tr>
</thead>
<tbody>
<tr>
<td>ALL (mesic)</td>
<td>0.0816</td>
<td>13577</td>
<td>9.578</td>
<td>0.0805</td>
<td>0.0370</td>
<td>1.8517</td>
<td>Model not statistically significant</td>
<td>ROC (0.2104), MAR (0.1550), DUR (0.1427)</td>
</tr>
<tr>
<td>GRASS</td>
<td>0.2029</td>
<td>43</td>
<td>0.5436</td>
<td>0.0628</td>
<td>0.0184</td>
<td>1.4161</td>
<td>Model not statistically significant</td>
<td>TOPDIV (-0.1429)</td>
</tr>
<tr>
<td>FORB</td>
<td>0.5827</td>
<td>122</td>
<td>0.9094</td>
<td>0.0368</td>
<td>-0.0088</td>
<td>0.8070</td>
<td>Model not statistically significant</td>
<td>ROC (0.1089)</td>
</tr>
<tr>
<td>GEOPH</td>
<td>0.0007</td>
<td>75</td>
<td>0.7061</td>
<td>0.1188</td>
<td>0.0955</td>
<td>5.0890</td>
<td>[GEOPH] = -3.301 + 0.0099*[ROC] + 0.0012*[MAR] + 0.0014*[APAN] + 0.0802*[DUR]</td>
<td>DUR (0.2278), MAR (0.2245), ROC (0.1812)</td>
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<tr>
<td>DWARF</td>
<td>&lt;0.0001</td>
<td>60</td>
<td>0.6318</td>
<td>0.3414</td>
<td>0.1866</td>
<td>8.6622</td>
<td>[DWARF] = -3.188 + 0.0183*[TOPDIV] + 0.0109*[ROC] + 0.0007*[ALT] + 0.0018*[APAN]</td>
<td>ALT (0.2981), TOPDIV (0.2478), ROC (0.2425), SLO (0.2186)</td>
</tr>
<tr>
<td>TREE</td>
<td>&lt;0.0001</td>
<td>41</td>
<td>0.5222</td>
<td>0.1561</td>
<td>0.1395</td>
<td>9.3727</td>
<td>[TREE] = 0.1961 + 0.0103*[ROC] + 0.0012*[MAR] - 0.0004*[ALT]</td>
<td>MAR (0.2422), ROC (0.2318), ALT (-0.1829)</td>
</tr>
<tr>
<td>EVEN(D)</td>
<td>0.0005</td>
<td>44</td>
<td>0.5388</td>
<td>0.0758</td>
<td>0.0698</td>
<td>12.6262</td>
<td>[EVEN] = 0.4745 + 0.0013*[MAR]</td>
<td>MAR (0.2753), TOPDIV (0.1743), MAR (0.2447), SLO (-0.1455)</td>
</tr>
<tr>
<td>EQU(H)</td>
<td>0.0008</td>
<td>4</td>
<td>0.1551</td>
<td>0.0884</td>
<td>0.0765</td>
<td>7.4187</td>
<td>[HET] = -0.2812 + 0.0004*[MAR] + 0.0004*[APAN]</td>
<td></td>
</tr>
</tbody>
</table>
Table 4.7: Results of multiple regression of semi-arid grassland data and environmental variables, including a selected list of explanatory variables (see text). ALL = richness of all species together, GRASS = richness amongst graminoids only, FORB = richness amongst forbs only, GEOPH = richness amongst geophytes only, DWARF = richness amongst dwarf shrubs only, TREE = richness amongst woody trees and shrubs only, EVEN (D) = Simpson’s evenness index, including all species, EQU (H) = equitability, including all species.

<table>
<thead>
<tr>
<th>Diversity variable</th>
<th>p</th>
<th>Sum of squares</th>
<th>SD of residuals</th>
<th>R²</th>
<th>Adjusted R²</th>
<th>F</th>
<th>Model (based on minimum set of explanatory variables)</th>
<th>Correlations</th>
</tr>
</thead>
<tbody>
<tr>
<td>ALL (semi-arid)</td>
<td>&lt;0.0001</td>
<td>7762</td>
<td>8.216</td>
<td>0.1764</td>
<td>0.1621</td>
<td>12.3145</td>
<td>[ALL (semi-arid)] = 9.757 + 13.403*[ROC] + 0.0331*[MAR]</td>
<td>ROC (0.3033), MAR (0.2488), SLO (0.2289), DUR (0.2000), TOPDIV (0.1653)</td>
</tr>
<tr>
<td>GRASS</td>
<td>&lt;0.0001</td>
<td>31</td>
<td>0.5198</td>
<td>0.1802</td>
<td>0.1661</td>
<td>12.7527</td>
<td>[GRASS] = -0.1412 + 0.0038*[MAR] + 0.0008*[APAN]</td>
<td>MAR (0.3944), DUR (0.1869)</td>
</tr>
<tr>
<td>FORB</td>
<td>0.0004</td>
<td>73</td>
<td>0.7943</td>
<td>0.1255</td>
<td>0.1104</td>
<td>8.3201</td>
<td>[FORB] = 1.738 + 0.8573*[ROC] + 0.0031*[MAR]</td>
<td>MAR (0.2689), DUR (0.2066), ROC (0.1973), APAN (-0.1965)</td>
</tr>
<tr>
<td>GEOPH</td>
<td>0.0007</td>
<td>47</td>
<td>0.6325</td>
<td>0.0941</td>
<td>0.0863</td>
<td>12.1466</td>
<td>[GEOPH] = 0.5615 + 1.563*[SLO]</td>
<td>SLO (0.3067), ROC (0.2191)</td>
</tr>
<tr>
<td>DWARF</td>
<td>&lt;0.0001</td>
<td>40</td>
<td>0.5872</td>
<td>0.2643</td>
<td>0.2451</td>
<td>13.7713</td>
<td>[DWARF] = 1.794 + 0.9252*[ROC] - 0.0026*[MAR] + 0.0006*[ALT]</td>
<td>ROC (0.3706), MAR (-0.2711), ALT (0.2334), SLO (0.2028), TOPDIV (0.1963), APAN (0.1715)</td>
</tr>
<tr>
<td>TREE</td>
<td>&lt;0.0001</td>
<td>41</td>
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<td>0.2834</td>
<td>0.2710</td>
<td>22.7425</td>
<td>[TREE] = 2.281 + 0.0241*[TOPDIV] - 0.0010*[ALT]</td>
<td>ALT (-0.5100), MAR (-0.2281), APAN (0.2123)</td>
</tr>
<tr>
<td>EVEN(D)</td>
<td>0.0009</td>
<td>4</td>
<td>0.1778</td>
<td>0.1136</td>
<td>0.0984</td>
<td>7.4365</td>
<td>[EVEN] = 0.5400 + 0.2552*[ROC] + 0.0004*[MAR]</td>
<td>ROC (0.2905), DUR (0.1762)</td>
</tr>
<tr>
<td>EQU(H)</td>
<td>0.0007</td>
<td>2</td>
<td>0.1307</td>
<td>0.1537</td>
<td>0.1240</td>
<td>5.1741</td>
<td>[HET] = 0.6962 + 0.2029*[ROC] + 0.0003*[MAR] - 0.0001*[ALT] - 0.2565*[SLO]</td>
<td>ALT (-0.2091), ROC (0.1792), DUR (0.1748)</td>
</tr>
</tbody>
</table>
Table 4.8: Results of multiple regression of all grassland data and environmental variables \( (n = 275) \), including a selected list of explanatory variables (see text). ALL = richness of all species together, GRASS = richness amongst graminoids only, FORB = richness amongst forbs only, GEOPH = richness amongst geophytes only, DWARF = richness amongst dwarf shrubs only, TREE = richness amongst woody trees and shrubs only, EVEN (D) = Simpson’s evenness index, including all species, EQU (H) = equitability, including all species.

<table>
<thead>
<tr>
<th>Diversity variable</th>
<th>p</th>
<th>Sum of squares</th>
<th>SD of residuals</th>
<th>R²</th>
<th>Adjusted R²</th>
<th>F</th>
<th>Model</th>
<th>Correlations</th>
</tr>
</thead>
<tbody>
<tr>
<td>ALL (mesic + semi-arid)</td>
<td>&lt;0.0001</td>
<td>190</td>
<td>0.8383</td>
<td>0.1068</td>
<td>0.1002</td>
<td>16.2083</td>
<td>[ALL] = 0.8685 + 1.115*[ROC] + 1.550*[MAR]</td>
<td>ROC (0.2724), SLO (0.1566), MAR (0.1737)</td>
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<tr>
<td>GRASS</td>
<td>0.0002</td>
<td>75</td>
<td>0.5268</td>
<td>0.0779</td>
<td>0.0642</td>
<td>5.7030</td>
<td>[GRASS] = -2.447 - 0.0201*[TOPDIV] + 0.3458*[ROC] + 1.690*[MAR] + 0.0006*[APAN]</td>
<td>TOPDIV (-0.1398)</td>
</tr>
<tr>
<td>FORB</td>
<td>&lt;0.0001</td>
<td>191</td>
<td>0.8389</td>
<td>0.0926</td>
<td>0.0860</td>
<td>13.8846</td>
<td>[FORB] = -2.495 + 0.6566*[ROC] + 2.195*[MAR]</td>
<td>MAR (0.2563), DUR (0.2397), SLO (0.1752), APAN (-0.2340), TOPDIV (0.1744)</td>
</tr>
<tr>
<td>GEOPH</td>
<td>&lt;0.0001</td>
<td>58</td>
<td>0.4626</td>
<td>0.1436</td>
<td>0.1341</td>
<td>15.1447</td>
<td>[GEOPH] = -2.654 + 0.5378*[ROC] + 1.518*[MAR] - 0.0002*[ALT]</td>
<td>MAR (0.2654), ROC (0.2159)</td>
</tr>
<tr>
<td>DWARF</td>
<td>&lt;0.0001</td>
<td>57</td>
<td>0.4599</td>
<td>0.2531</td>
<td>0.2392</td>
<td>18.2325</td>
<td>[DWARF] = 2.633 + 0.0141*[TOPDIV] + 0.6622*[ROC] - 1.050*[MAR] + 0.0004*[ALT] + 0.0006*[APAN]</td>
<td>ROC (0.3427), MAR (-0.1998), ALT (0.2230), SLO (0.1548), TOPDIV (0.1501), APAN (0.1653), DUR (-0.1901)</td>
</tr>
<tr>
<td>TREE</td>
<td>&lt;0.0001</td>
<td>38</td>
<td>0.3750</td>
<td>0.2856</td>
<td>0.2724</td>
<td>21.5130</td>
<td>[TREE] = 1.026 + 0.0091*[TOPDIV] + 0.4371*[ROC] - 0.0005*[ALT] + 0.0005*[APAN] - 0.0292*[DUR]</td>
<td>ALT (-0.3924), MAR (-0.2634), APAN (0.3576), ROC (0.2184), DUR (-0.2039)</td>
</tr>
<tr>
<td>EVEN(D)</td>
<td>&lt;0.0001</td>
<td>4</td>
<td>0.1172</td>
<td>0.2765</td>
<td>0.2711</td>
<td>51.9672</td>
<td>[EVEN] = -1.524 + 0.0029*[TOPDIV] + 0.6106*[MAR]</td>
<td>MAR (0.5120), TOPDIV (0.3099), DUR (0.3156), APAN (-0.3794), SLO (-0.1552), ROC (0.1684)</td>
</tr>
<tr>
<td>EQU(H)</td>
<td>&lt;0.0001</td>
<td>6</td>
<td>0.1466</td>
<td>0.0981</td>
<td>0.0848</td>
<td>7.3456</td>
<td>[HET] = -0.7411 + 0.1510*[ROC] + 0.3811*[MAR] - 0.1653*[SLO] + 0.0002*[APAN]</td>
<td></td>
</tr>
</tbody>
</table>
CHAPTER 5: CLASSIFICATION OF GRASSLAND SPECIES OF THE EASTERN CAPE INTO PLANT FUNCTIONAL TYPES

Introduction

The classification of plants into functional types has been undertaken in many parts of the world for a variety of reasons. One of the main reasons for studying functional types has been to understand the effect of species richness on ecosystem function (Diaz et al. 2003, 2007, Diaz & Cabido 2001, Hooper et al. 2002). Another reason for studying plant functional types is in order to understand plant community response to various ecological factors, including grazing (Hadar et al. 1999, Landsberg et al. 1999, Diaz et al. 2001, 2007, McIntyre & Lavorel 2001, Sternberg et al. 2000), environmental gradients (Diaz et al. 1999a, b), fire (Lavorel & Cramer 1999, Lavorel et al. 1997, 1999, McIntyre et al. 1995, 1999, Diaz et al. 2002, Pausus & Lavorel 2003) and climate change. There are obvious advantages to using plant functional types in ecological studies rather than taxonomic groupings, primarily due to the limitations of using taxonomic classifications to understand vegetation responses to the environment and the reciprocal effect of vegetation on environmental parameters. Many ecologists have realised that classifying plants into functional types provides a useful means for understanding these interactions (Cornelissen et al. 2003).

Plant functional types can be defined as groups of plant species that share similar responses to the environment and have similar roles and/or effects on ecosystems. These similarities are based on the fact that the species within a group share key functional traits (Grime & Hunt 1975, Thompson et al. 1993, Noble & Gitay 1996, Diaz & Cabido 1997, Grime et al. 1997, Weiher et al. 1999, McIntyre & Lavorel 2001, Lavorel & Garnier 2002, Pausus & Lavorel 2003). The identification of which traits are important and the measurement of these traits has been the focus of a large number of studies, the most recent of which attempt to list a global list of traits that can be used for functional assessments (e.g. McIntyre et al. 1999, Weiher et al. 1999, Diaz et al. 2002, Cornelissen et al. 2003, Diaz et al. 2007). There have also been a number of reviews concerning functional type classifications (e.g. Box 1981, Chapin et al. 1996, Lavorel et al. 1997, McIntyre et al. 1999, Semenova & van der Maarel 2000, Grime 2001, Hooper et al. 2002, Lavorel & Garnier 2002, Diaz et al. 2007).

The primary aim of this chapter was to classify the grassland plant species of the Eastern Cape into plant functional types based on functional traits. Life form is often used as an easily recognisable plant functional type, but most previous studies have found that life form alone is too broad a classification to determine the relative sensitivity to environmental variability (Kelly 1996). Broad life forms that occur in the grasslands of the Eastern Cape are primarily woody trees.
and shrubs, dwarf shrubs, geophytes, graminoids and forbs. The graminoids and forbs contribute the most to overall species richness in the grasslands (see Table 3.4, Chapter 3). It has also been noted that these two life-forms have apparently high numbers of co-existing species (Cowling et al. 1989). It is therefore of primary interest to classify these life forms into functional groups. McIntyre et al. (1999) adopted an heirarchical approach in which species are first divided into major life forms, e.g. grasses and forbs, before scoring them for traits.

**Study area**

See Chapter 2 for detailed description of the study area.

**Methods**

**Data collection**

The species to be classified into plant functional types were compiled from floristic plot data collected in the study area. Plot data used in the current analysis were collected for a floristic survey of the south-western extreme of the Grassland Biome (Hoare 1997). Plots were classified into vegetation communities (Hoare & Bredenkamp 1999, 2001). Further fieldwork in the Eastern Cape supplemented this data set. Only the data from those plant communities that are physiognomically recognised as grassland are used here, although other plant communities, e.g. shrubland on rocky outcrops, also occur within the matrix of grasslands in the study area. A total of 275 plots were used in the current analysis. From these plots, a total of 866 plant species were extracted.

**Classification of species into plant functional types**

Forbs and grasses occurring in the grasslands of the Eastern Cape were classified into plant functional types using the approach of McIntyre et al. (1999). Shrubs, dwarf shrubs and geophytes were not classified into functional types in this study since they occur at low frequencies in open grasslands. Where they occur they are treated simply as growth forms and not divided further into functional types.

A list of all forbs and grasses occurring in the grassland dataset of the Eastern Cape was compiled. It has been suggested (Cornelissen et al. 2003) that only the most dominant species should be analysed since they contribute most of the biomass to a community, but the objective of this study was to be able to compare functional type richness with species richness. It was therefore necessary to include all the species in the dataset.
The heirarchical approach of McIntyre et al. (1999) was followed in which species are first divided into grasses and forbs before scoring them for traits. Each species was scored for the traits suggested by Campbell et al. (1999) and Cornelissen et al. (2003), as listed in Table 5.1.

The objective was to identify traits that would explain the distribution of species along environmental as well as management gradients and would be useful for explaining species co-existence. The result was a matrix with species vs. plant functional attributes. One matrix was produced for grasses and one for forbs. Following Lavorel et al. (1999), this matrix was analysed to extract a set of PFT’s that best described functional syndromes.

**Data analysis**

Correlations between species for functional traits were analysed using Principal Components Analysis (PCA) (ter Braak 1987). PCA was used because it maximises the variance explained by successive axes, thus providing information on which traits best explain differences between species. A separate ordination was done on each of the matrices (grasses, forbs). PC-ORD version 4 (McCune & Mefford 1999) was used for all ordination analyses.

**Results**

**Grass functional types**

A PCA (correlation) ordination of the species by traits matrix for grass species captured 58% of the variation in the data in the first 6 ordination axes (Table 5.2). The grass traits were clumped, except for some outliers (Figure 5.1), indicating that many of the species share similar traits. The first axis was correlated with size traits, including life history, whether plants are tufted, leaf size and whether plants are erect or prostrate (Table 5.3). The second axis was correlated with growth and dispersal traits, including photosynthetic type, canopy height, lateral spread, above-ground cover density and dispersal type (Table 5.3). The third axis was correlated with clonal growth and grazing traits such as presence of rhizomes, uprooting potential, edibility, dispersal, leaf length, leaf length/width ratio and clonality (Table 5.3).

There were some correlations between traits:

1. Life-history (annual vs. perennial) was correlated with habit and uprooting potential: annual grass plants tend to be weak, upright plants with shallow roots.
2. Canopy height, leaf dimensions, lateral spread and above-ground cover density were positively correlated. For grass plants these are all measures of plant size—the longer the leaves, the taller the grass plant.
3. Following on from the previous observation, grass plant size tends to be correlated with photosynthetic type: bigger plants are mostly of the C4 photosynthetic type in the study area.

4. Habit (prostrate, decumbent or erect) is positively correlated with whether the grass plant is tufted, mat-forming or stoloniferous.

5. There was a negative correlation between being tufted and the uprooting potential of the plants. Tufted plants also tended not to be clonal.

6. All clonal grasses were rhizomatous and/or stoloniferous.

On the basis of the ordination, the grass species could be classified into 16 guilds. The species are described and characterised with respect to significant traits in Table 5.4. The two major divisions were between C3 and C4 species and between annuals and perennials. Further divisions were on

![Figure 5.1: Ordination plot of functional traits of grass species from grasslands of the Eastern Cape.](image)
the basis of the presence of rhizomes, whether the plants were tuft-forming (caespitose), the resprouting ability and fire-tolerance of species and the relative size of the plants.

**Forb functional types**

A PCA (correlation) ordination of the species by traits matrix for forb species captured 57% of the variation in the data in the first 6 ordination axes (Table 5.5). The first axis, which represents the greatest variation in attributes of the species in the data set, separates out the traits that are characteristic of the two basic functional syndromes amongst forbs in the study area. On one end of the axis are perennial rosette plants with basal, simple leaves of relatively high surface area and wind-dispersed seeds (Table 5.6, Figure 5.2). Many have prickles or hairs to protect them from grazing herbivores. At the other end of the axis are upright proto-rosettes, deciduous or

![Figure 5.2: Ordination plot of functional traits of forb species from grasslands of the Eastern Cape. See Table 5.1 for abbreviations used.](image-url)
annual with a large, soil-stored seed bank and relatively small leaves (Table 5.6), many of which are edible and/or easily uprooted. The axis represents a gradient from grazing avoiders on the negative end to grazing tolerators on the positive end. On axis 2 the biggest dichotomy is between upright and prostrate plants (Table 5.6). Traits associated with clonality are also correlated with axis 2. The third axis was correlated with grazing traits. At one end of axis 3 are upright plants with secondary compounds and high fecundity and at the other end are laterally spreading prostrate plants (Table 5.6).

There were some positive correlations between traits for forbs:

1. Leaf width and leaf length were positively correlated ($r=0.77$).
2. Nitrogen-fixing and leaf compounding were positively correlated ($r=0.95$).
3. Poisonous and partial rosette were positively correlated ($r=0.55$).
4. Basal branching and uprooting potential were negatively correlated ($r=-0.44$).
5. Wind dispersal was positively correlated with above-ground cover density ($r=0.53$), leaf length ($r=0.43$) and basal branching ($r=0.42$). Soil stored seed bank was negatively correlated with the same traits ($r=-0.50$, -0.41 and -0.38 respectively).
6. Clonality was negatively correlated with leaf deciduousness ($r=-0.49$) and positively correlated with mat-forming ($r=0.58$), rhizomatous ($r=0.50$) and stoloniferous ($r=0.35$).
7. Fecundity was positively correlated with the presence of secondary compounds ($r=0.40$).
8. Poisonous was positively correlated with milky latex ($r=0.58$).

On the basis of the ordination, the forb species were classified into 14 guilds. These are presented in Table 5.7 and characterised with respect to significant traits. The two major divisions were between rosettes and upright proto-rosettes. Further divisions were on the basis of the presence of a woody rootstock, clonality, edibility, succulence and the position of leaves and branches relative to the ground.

**Discussion**

In this study it was possible to classify forb and grass species into plant functional types that reflect morphological, life history, photosynthetic, storage and regeneration traits. The grass species found in the study area during field surveys (Hoare 1997) were classified into 16 functional types and the forbs into 14 functional types. Most of the traits were amenable to once-off assessment, except the number of seeds, seed size and dispersal vector. To some extent, these regeneration traits were assessed from literature sources and herbarium specimen information. Measurement of these traits was therefore less reliable than for directly measured
traits. Similar difficulties in measuring fecundity have been reported for other plant functional type assessments (Landsberg et al. 1999).

There were some moderate to weak correlations between some traits which led to some redundancy in measurements. This was especially true of leaf and plant height measurements. Correlations between other traits were, however, usually informative. All traits were therefore included and, where correlations occurred, these were interpreted biologically.

A characteristic of the ordination of forb species was the difficulty in grouping species on the basis of traits due to the fact that there was a large overlap of states and mixing of traits. This indicates that subtle combinations of traits are possible that result in a large number of species that are each slightly different to any others. This makes it difficult to classify species exactly into functional syndromes, but possibly shows that there is a diversity of species that utilize small divisions of niche space. Despite the overlap of traits between species, it was still possible to distinguish major functional syndromes amongst forbs that represent completely different approaches to survival. On one end of the spectrum are flat rosette plants and at the other end of the spectrum are upright plants. The rosette plants tended to have large, simple leaves and wind-dispersed seeds. They were strongly perennial, often clonal or with underground storage organs that facilitate rapid re-sprouting. Rosette plants are tolerant of strong grazing pressure and often increase in abundance under high grazing pressure regimes (Hoare 2002). The upright proto-rosettes were either deciduous with underground storage organs or they were annuals. They tend to have large soil seed banks and are either reseeders or resprouters. They may be edible or have secondary compounds to reduce edibility. However, most have small leaves and low above-ground cover density and do not, therefore, constitute important fodder for grazing animals.

Clonality emerged as an important trait in grassland forbs. Previous studies have concluded that clonal plants are more common in wet, cold and unproductive habitats (Groenendael et al. 1996). However, two types of clonals can be distinguished, those with short-lived, splitting connections between ramets and those with long-lasting, tightly packed, phalanx-like structures (Groenendael et al. 1996). The phalanx-like clonal species tend to be found in nutrient-poor, dry and open, unshaded conditions (Groenendael et al. 1996). In the current study clonality amongst forbs appears to be a grazing and disturbance response; many of the strongly clonal species are phalanx-like.

Grasslands may experience many disturbances in the form of fire, grazing animals and climatic irregularity and seasonality. Grazing pressure is an important constraint on species composition in grassland habitats. Studies have found that small plants with protected meristems and a prostrate habit are common in heavily grazed areas (Noy-Meir et al. 1989, Landsberg et al. 1999).
Approximately one out of every four forb species in the study area fit this description, indicating an influence of grazing on functional composition within the study area. Of equal importance is the fact that the remaining three out of four forbs is functionally adapted to constraints other than grazing.

Regular perturbations are expected to provide opportunities for early successional or r-selected species to colonize habitats. These r-selected plant species typically have a series of traits that provide them with the means to colonize and grow in new habitats, including high fecundity, long dispersal and rapid growth when resources are abundant (Rees et al. 2001). These attributes allow these species to colonize recently disturbed sites before the dominant competitors arrive (competition / colonization tradeoff, Tilman 1994) or to grow rapidly under resource-rich conditions allowing them to temporarily outperform late-successional species, even if both arrive simultaneously in a recently disturbed site (successional niche (Pacala & Rees 1998). In the study area, this does not appear to be the dominant case. There are many species in the study area (a large proportion of the richness) that fit neither r- or K-selected mode. Of the 548 species of forbs in the dataset, 340 (62%) have underground storage organs of some type (e.g. rhizomes, thickened tap-roots, woody underground stems or woody rootstocks) from which re-sprouting can occur (some examples are shown in Figure 5.3). These are traits that allow these species to survive fire and regular dry seasons. These species have a high frequency of occurrence in the study area, but low relative cover. They are therefore widespread and common, but of low

![Figure 5.3: Examples of underground storage organs from specimens collected in the grasslands of the Eastern Cape.](image)
importance in terms of landscape production. Such traits allow these species to maintain a presence in the landscape despite being less competitive than the dominant species. It is these species that make a significant contribution to local and regional richness in the study area.

A further 28 forb species (5%) are annuals, which may be considered to be r-selected. Of the remaining forb species, 110 (20%) are perennial re-seeders that branch above-ground, 40 (7%) are slow-growing succulents that occur in dryer habitats or habitats that are protected from fire, e.g. rocky areas, and 32 (6%) forb species contain milky latex or are poisonous and are therefore inedible to grazing animals. There are therefore a number of strategies for surviving conditions endemic to grassland areas.

An understanding of functional syndromes has important implications for conservation and management of grasslands. Anecdotal evidence indicates that previously cultivated areas, after many decades, do not develop a species composition containing the original forb composition. Many forb species do not re-colonize old fields even if they occur in adjacent natural grasslands. The classification of species into functional syndromes undertaken here indicates that this may be due to the fact that many of the forbs re-sprout from underground storage organs. Perhaps they do not re-seed very successfully and vegetative propagation is the primary mechanism of persistence. This may indicate that, although small, many of these plants may be relatively long-lived.

In conclusion, this study indicates that it is possible to classify species into functional syndromes using an *a priori* list of traits. The classification process provides useful insights into the functioning of local ecosystems and the manner in which species survive endemic conditions and perturbations. For the current study, it was the response of species to the environment that was of interest as well as to develop an understanding of why some life-forms appear to have high numbers of co-existing species: the functional type classification provides the opportunity for undertaking further analyses to develop this understanding further.

**References:**


<table>
<thead>
<tr>
<th>Table 5.1: Set of traits used in this study for identifying plant functional attributes (adapted from Campbell et al. 1999 and Cornelissen et al. 2003).</th>
</tr>
</thead>
<tbody>
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<td><strong>Trait type; traits</strong></td>
</tr>
<tr>
<td><strong>Life form</strong></td>
</tr>
<tr>
<td>Habit</td>
</tr>
<tr>
<td>Architecture</td>
</tr>
<tr>
<td><strong>Established phase traits</strong></td>
</tr>
<tr>
<td>Life history</td>
</tr>
<tr>
<td>Maximum canopy height</td>
</tr>
<tr>
<td>Lateral spreading</td>
</tr>
<tr>
<td>Above-ground cover density</td>
</tr>
<tr>
<td>Leaf measurements</td>
</tr>
<tr>
<td>Leaf shape</td>
</tr>
<tr>
<td>Photosynthesis type</td>
</tr>
<tr>
<td>N-fixation</td>
</tr>
<tr>
<td>Leaf longevity</td>
</tr>
<tr>
<td>Secondary thickening</td>
</tr>
<tr>
<td>Succulent</td>
</tr>
<tr>
<td><strong>Grazing &amp; disturbance persistence traits</strong></td>
</tr>
<tr>
<td>Spinescence</td>
</tr>
<tr>
<td>Forage quality</td>
</tr>
<tr>
<td>Leaf hairiness</td>
</tr>
<tr>
<td>Prickles, spines on leaves</td>
</tr>
<tr>
<td>Secondary compounds, milky latex</td>
</tr>
<tr>
<td>Poisonous</td>
</tr>
<tr>
<td>Flammability</td>
</tr>
<tr>
<td>Active bud position</td>
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<tr>
<td>Branching position</td>
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<tr>
<td>Leaf position</td>
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<tr>
<td>Resprouting</td>
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<tr>
<td><strong>Regeneration phase traits</strong></td>
</tr>
<tr>
<td>Clonality</td>
</tr>
<tr>
<td>Tuft-forming</td>
</tr>
<tr>
<td>Mat-forming</td>
</tr>
<tr>
<td>Stoloniferous</td>
</tr>
<tr>
<td>Rhizomatous</td>
</tr>
<tr>
<td>Below-ground storage</td>
</tr>
<tr>
<td>Dispersal</td>
</tr>
<tr>
<td>Fecundity</td>
</tr>
<tr>
<td>Seed size</td>
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Table 5.2: Variance extracted in the first 10 axes of the PCA for the analysis of grass traits.

<table>
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<tr>
<th>AXIS</th>
<th>Eigenvalue</th>
<th>% of Variance</th>
<th>Cum.% of Var</th>
<th>Broken-stick Eigenvalue</th>
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<tbody>
<tr>
<td>1</td>
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<td>14.640</td>
<td>3.962</td>
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<td>14.224</td>
<td>28.864</td>
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<tr>
<td>3</td>
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<td>9.810</td>
<td>38.673</td>
<td>2.462</td>
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<tr>
<td>4</td>
<td>2.537</td>
<td>8.749</td>
<td>47.423</td>
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<tr>
<td>5</td>
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<td>6.315</td>
<td>53.737</td>
<td>1.878</td>
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<td>6</td>
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<td>4.805</td>
<td>58.542</td>
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<td>7</td>
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<td>63.075</td>
<td>1.512</td>
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<td>8</td>
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<td>3.707</td>
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Table 5.3: Eigenvectors for the first 6 axes of the PCA analysis of grass species traits.

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<tr>
<th>Trait</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
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<th>6</th>
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</thead>
<tbody>
<tr>
<td>Annual</td>
<td>0.3470</td>
<td>0.0523</td>
<td>-0.1887</td>
<td>0.2484</td>
<td>-0.1158</td>
<td>0.0564</td>
</tr>
<tr>
<td>Perennial</td>
<td>-0.3470</td>
<td>-0.0523</td>
<td>0.1887</td>
<td>-0.2484</td>
<td>0.1158</td>
<td>-0.0564</td>
</tr>
<tr>
<td>Canopy height</td>
<td>0.0350</td>
<td>-0.3508</td>
<td>0.1820</td>
<td>0.2239</td>
<td>-0.0126</td>
<td>-0.0037</td>
</tr>
<tr>
<td>Lateral spread</td>
<td>-0.0989</td>
<td>-0.3194</td>
<td>0.0874</td>
<td>-0.0106</td>
<td>0.0360</td>
<td>0.1125</td>
</tr>
<tr>
<td>Above-ground cover density</td>
<td>-0.1470</td>
<td>-0.2343</td>
<td>0.0152</td>
<td>-0.1018</td>
<td>-0.1607</td>
<td>0.1871</td>
</tr>
<tr>
<td>Branching basally</td>
<td>-0.0282</td>
<td>0.0362</td>
<td>-0.1362</td>
<td>0.1519</td>
<td>0.1806</td>
<td>0.0082</td>
</tr>
<tr>
<td>Erect habit</td>
<td>-0.4096</td>
<td>0.0195</td>
<td>-0.0083</td>
<td>0.0352</td>
<td>-0.1065</td>
<td>-0.2243</td>
</tr>
<tr>
<td>Prostrate habit</td>
<td>0.4096</td>
<td>-0.0195</td>
<td>0.0083</td>
<td>-0.0352</td>
<td>0.1065</td>
<td>0.2243</td>
</tr>
<tr>
<td>Tufted</td>
<td>-0.2639</td>
<td>-0.2199</td>
<td>-0.1627</td>
<td>0.0282</td>
<td>-0.2561</td>
<td>0.0747</td>
</tr>
<tr>
<td>Mat-forming</td>
<td>-0.1818</td>
<td>-0.0283</td>
<td>-0.0451</td>
<td>0.3112</td>
<td>0.0106</td>
<td>-0.2711</td>
</tr>
<tr>
<td>Rhizomatous</td>
<td>-0.0633</td>
<td>-0.0076</td>
<td>-0.3367</td>
<td>0.2090</td>
<td>-0.1144</td>
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<tr>
<td>Stoloniferous</td>
<td>-0.1837</td>
<td>0.0217</td>
<td>-0.1212</td>
<td>0.3354</td>
<td>-0.1281</td>
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<tr>
<td>Leaves basal</td>
<td>-0.1802</td>
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<td>-0.0469</td>
<td>0.0560</td>
<td>0.2114</td>
<td>0.2643</td>
</tr>
<tr>
<td>Leaf length</td>
<td>-0.1551</td>
<td>-0.1317</td>
<td>0.2165</td>
<td>0.3170</td>
<td>0.2573</td>
<td>0.2646</td>
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<tr>
<td>Leaf width</td>
<td>0.2015</td>
<td>-0.1376</td>
<td>0.3008</td>
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<td>0.0504</td>
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<tr>
<td>Leaf length/width ratio</td>
<td>-0.2233</td>
<td>0.0498</td>
<td>-0.1085</td>
<td>0.0164</td>
<td>0.1469</td>
<td>0.4921</td>
</tr>
<tr>
<td>Leaf area</td>
<td>0.0313</td>
<td>-0.1524</td>
<td>0.3392</td>
<td>0.3755</td>
<td>0.2066</td>
<td>-0.0058</td>
</tr>
<tr>
<td>Photosynthetic type C3</td>
<td>-0.1037</td>
<td>0.3806</td>
<td>0.0387</td>
<td>0.2000</td>
<td>0.0937</td>
<td>0.1007</td>
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<tr>
<td>Photosynthetic type C4</td>
<td>0.1037</td>
<td>-0.3806</td>
<td>-0.0387</td>
<td>-0.2000</td>
<td>-0.0937</td>
<td>-0.1007</td>
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<tr>
<td>Below-ground storage organs</td>
<td>-0.0763</td>
<td>0.2113</td>
<td>0.1291</td>
<td>-0.0832</td>
<td>0.2285</td>
<td>-0.2335</td>
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<td>Secondary compounds</td>
<td>-0.0495</td>
<td>-0.2296</td>
<td>-0.0682</td>
<td>0.0031</td>
<td>0.2785</td>
<td>-0.0657</td>
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<tr>
<td>Leaf hairiness</td>
<td>0.0006</td>
<td>-0.1335</td>
<td>0.0508</td>
<td>0.0529</td>
<td>-0.2861</td>
<td>-0.1857</td>
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<tr>
<td>Uprooting potential</td>
<td>0.1952</td>
<td>0.1242</td>
<td>-0.2528</td>
<td>0.1589</td>
<td>0.1140</td>
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<td>Edible</td>
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<td>-0.2307</td>
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<td>0.2758</td>
<td>0.1300</td>
<td>-0.3687</td>
<td>0.1027</td>
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<td>Soil stored seedbank</td>
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<td>-0.2531</td>
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<td>0.3480</td>
<td>-0.0391</td>
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<tr>
<td>Plant functional type</td>
<td>Description</td>
<td>Examples</td>
<td></td>
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<td>-----------------------------------------------------------------------------</td>
<td>---------------------------------------------------------------------------</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Group 1. Annual C3 grasses</td>
<td>Annual and biennial grasses. Plants with single culms, usually of short stature (&lt; 1 m tall), limited lateral spread, low aerial cover density. Low fecundity, large seeds and rely on soil-stored seed banks to persist. Make use of small gaps between perennial plants and are not necessarily associated with disturbance.</td>
<td><em>Briza major, Helictotrichon hirtulum.</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Group 2-3. Non-tufted, small C3 graminoids</td>
<td>Same as group 1, but are perennial. Single culms, limited lateral spread and low aerial cover density. Can be separated into two groups on the basis of root strength (vulnerability to being uprooted) and seed size with the strong rooted, small seed-sized species being wetland specific, e.g. <em>Carex cognata</em>, whereas the other species are terrestrial.</td>
<td><em>Helictotrichon turgidulum, Schoenoxiphium sparteum, Carex cognata</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Group 4-5. Non-tufted rhizomatous C3 graminoids</td>
<td>Cool, temperate species that are strongly rhizomatous or clonal. Often have underground tubers which, when exposed, can form new plants vegetatively. Clonality imparts an advantage in the conquest of space and the utilization of resources through continuous “foraging” behaviour—invasion of new space using rhizomes. Species with tubers can be separated from those without tubers.</td>
<td>They are almost exclusively sedges (<em>Cyperaceae</em>).</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Group 6-9. Tufted C3 graminoids</td>
<td>This broad group can be divided into four groups on the basis of whether the species are fire-tolerant and resprouting or not, rhizomatous or not and whether they are short or tall (<em>PFT 6 = non-resprouting, non-fire-tolerant; PFT 7 = small, non-rhizomatous; PFT 8 = tall, non-rhizomatous; PFT 9 = tall, rhizomatous</em>). The tall members of this group (<em>PFT 8 and 9</em>) tend to be fire-tolerant with strong resprouting ability and have the ability to develop significant lateral spread.</td>
<td>All species from subfamily Arundinoideae (except the tribe Aristideae, which are C4) and subfamily Pooideae although some species from these two subfamilies are annual or weakly perennial. The group also included a number of <em>Cyperaceae</em>.</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Group 10. C4 Annual grasses</td>
<td>Decumbent or prostrate plants branching from the base. High fecundity and opportunistic weeds of disturbed areas, in many cases are listed as problem plants in South Africa (Bromilow 2001).</td>
<td><em>Chloris virgata and Urochloa panicoides</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
**Group 11. Weakly tufted C4 graminoids**
Relatively short-lived grasses (biennials or short-lived perennials) that branch from the base, are weakly tufted, have low aerial cover density and little lateral spread. They have low fire-tolerance and resprouting ability and rely on soil-stored seed banks to persist. Often weeds of disturbed or overgrazed places or are naturalized exotics.

* Aristida congesta and Paspalum dilatatum

**Group 12. C4 stoloniferous graminoids**
Strongly clonal C4 species, rhizomatous and mat-forming and do not form tufts. Are often good lawn grasses because of their tolerance of trampling, often known as “couch grass”, “swamp couch”, etc.

* Stenotaphrum secundatum and Cynodon dactylon

**Group 13-16. Tufted C4 graminoids**
Can be divided into four groups on the basis of whether the species are rhizomatous or not and whether they are short or tall (PFT 13 = short, non-rhizomatous; PFT 14 = tall, non-rhizomatous; PFT 15 = short, rhizomatous; PFT 16 = tall, rhizomatous). The tall members of this group (PFT 14 and 16) tend to be fire-tolerant with strong resprouting ability and have significant lateral spread. These are the tufted space dominators that have the ability to recover quickly after defoliation from fire or grazing.

All species from subfamilies Chloridoideae, Panicoideae and tribe Aristideae from the Arundinoideae although some species from these subfamilies are annual or weakly perennial. The Chloridoideae are arid summer rainfall species, the Panicoideae are moist summer rainfall species and the Aristideae are arid winter rainfall species.

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### Table 5.5: Variance extracted in the first 10 axes of the PCA for the analysis of forb traits.

<table>
<thead>
<tr>
<th>AXIS</th>
<th>Eigenvalue</th>
<th>% of Variance</th>
<th>Cum.% of Var</th>
<th>Broken-stick Eigenvalue</th>
</tr>
</thead>
<tbody>
<tr>
<td>2</td>
<td>3.986</td>
<td>8.857</td>
<td>23.721</td>
<td>3.395</td>
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<tr>
<td>3</td>
<td>3.353</td>
<td>7.450</td>
<td>31.171</td>
<td>2.895</td>
</tr>
<tr>
<td>4</td>
<td>2.975</td>
<td>6.611</td>
<td>37.782</td>
<td>2.562</td>
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<tr>
<td>5</td>
<td>2.397</td>
<td>5.326</td>
<td>43.108</td>
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</tr>
<tr>
<td>6</td>
<td>2.344</td>
<td>5.209</td>
<td>48.316</td>
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</tr>
<tr>
<td>7</td>
<td>1.777</td>
<td>3.948</td>
<td>52.265</td>
<td>1.945</td>
</tr>
<tr>
<td>8</td>
<td>1.749</td>
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<td>9</td>
<td>1.526</td>
<td>3.392</td>
<td>59.543</td>
<td>1.677</td>
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<tr>
<td>10</td>
<td>1.483</td>
<td>3.295</td>
<td>62.838</td>
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</table>

### Table 5.6: Eigenvectors for the first 6 axes of the PCA analysis of forb species traits.

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<th>Trait</th>
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<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
</tr>
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<tbody>
<tr>
<td>Canopy height</td>
<td>-0.0931</td>
<td>0.2597</td>
<td>0.0034</td>
<td>-0.1817</td>
<td>0.0345</td>
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</tr>
<tr>
<td>Lateral spread</td>
<td>-0.0123</td>
<td>-0.1249</td>
<td>-0.2273</td>
<td>-0.0684</td>
<td>-0.3168</td>
<td>-0.0829</td>
</tr>
<tr>
<td>Above-ground cover density</td>
<td>-0.2494</td>
<td>0.0112</td>
<td>0.1629</td>
<td>0.0987</td>
<td>0.0724</td>
<td>0.0262</td>
</tr>
<tr>
<td>Characteristic</td>
<td>Value1</td>
<td>Value2</td>
<td>Value3</td>
<td>Value4</td>
<td>Value5</td>
<td>Value6</td>
</tr>
<tr>
<td>----------------------------------------</td>
<td>---------</td>
<td>---------</td>
<td>---------</td>
<td>---------</td>
<td>---------</td>
<td>---------</td>
</tr>
<tr>
<td>Branching basal</td>
<td>-0.2457</td>
<td>-0.0949</td>
<td>0.0393</td>
<td>-0.0088</td>
<td>-0.0222</td>
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</tr>
<tr>
<td>Prostrate habit</td>
<td>-0.0987</td>
<td>-0.3415</td>
<td>-0.1581</td>
<td>0.0500</td>
<td>0.1423</td>
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</tr>
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<td>Decumbent habit</td>
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<td>-0.0011</td>
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<td>0.1402</td>
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<tr>
<td>Erect habit</td>
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<td>0.2450</td>
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<td>-0.0423</td>
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<td>Twining/scrambling habit</td>
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<td>-0.1788</td>
<td>-0.1108</td>
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<tr>
<td>Tufted</td>
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<td>0.0020</td>
<td>0.0912</td>
<td>-0.1030</td>
<td>-0.0141</td>
<td>-0.0056</td>
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<td>Mat-forming</td>
<td>-0.0870</td>
<td>-0.2772</td>
<td>0.0072</td>
<td>0.2973</td>
<td>-0.0448</td>
<td>-0.0511</td>
</tr>
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<td>-0.1398</td>
<td>0.1944</td>
<td>0.0815</td>
<td>-0.1966</td>
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</tr>
<tr>
<td>Stoloniferous</td>
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<td>-0.0542</td>
<td>0.2080</td>
<td>0.0399</td>
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</tr>
<tr>
<td>Active bud position basal</td>
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<td>-0.0187</td>
<td>0.1823</td>
<td>-0.0810</td>
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<tr>
<td>Succulent</td>
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<td>0.2335</td>
<td>0.0163</td>
<td>-0.0331</td>
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<td>Flat rosette</td>
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<td>0.0416</td>
<td>0.0138</td>
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<tr>
<td>Erect rosette</td>
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<td>0.0936</td>
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<td>0.1283</td>
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<tr>
<td>Proto-rosette</td>
<td>0.2813</td>
<td>0.0276</td>
<td>0.1523</td>
<td>0.0241</td>
<td>-0.1190</td>
<td>-0.0241</td>
</tr>
<tr>
<td>Partial rosette</td>
<td>-0.0938</td>
<td>0.2307</td>
<td>-0.1600</td>
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</tr>
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<td>Leaves positioned basally</td>
<td>-0.2202</td>
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<tr>
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<td>-0.2666</td>
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<td>-0.2050</td>
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<td>0.0067</td>
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<tr>
<td>Leaf width</td>
<td>-0.2329</td>
<td>0.0636</td>
<td>-0.2787</td>
<td>-0.0535</td>
<td>-0.0398</td>
<td>0.1495</td>
</tr>
<tr>
<td>Leaf length/width ratio</td>
<td>0.0032</td>
<td>0.0412</td>
<td>0.0877</td>
<td>-0.0953</td>
<td>0.1294</td>
<td>-0.1569</td>
</tr>
<tr>
<td>Leaf area</td>
<td>-0.2280</td>
<td>0.1051</td>
<td>-0.2082</td>
<td>-0.0777</td>
<td>-0.0375</td>
<td>0.1776</td>
</tr>
<tr>
<td>Leaves compound</td>
<td>0.1746</td>
<td>-0.1001</td>
<td>-0.0706</td>
<td>-0.1247</td>
<td>-0.0921</td>
<td>0.4225</td>
</tr>
<tr>
<td>Leaves divided</td>
<td>-0.0687</td>
<td>0.1490</td>
<td>-0.1893</td>
<td>0.1183</td>
<td>-0.0179</td>
<td>-0.0781</td>
</tr>
<tr>
<td>Swollen taproot</td>
<td>-0.0459</td>
<td>-0.0817</td>
<td>-0.1390</td>
<td>-0.1355</td>
<td>-0.0154</td>
<td>-0.2123</td>
</tr>
<tr>
<td>Woody rootstock</td>
<td>-0.0763</td>
<td>-0.1474</td>
<td>0.1772</td>
<td>-0.1800</td>
<td>-0.1308</td>
<td>0.3186</td>
</tr>
<tr>
<td>N-fixation</td>
<td>0.1757</td>
<td>-0.1080</td>
<td>-0.0619</td>
<td>-0.1252</td>
<td>-0.0478</td>
<td>0.4418</td>
</tr>
<tr>
<td>Secondary compounds</td>
<td>-0.0891</td>
<td>0.0813</td>
<td>0.2000</td>
<td>-0.1968</td>
<td>-0.1806</td>
<td>-0.2109</td>
</tr>
<tr>
<td>Leaf prickles</td>
<td>-0.1522</td>
<td>0.2030</td>
<td>-0.2375</td>
<td>0.1197</td>
<td>0.0268</td>
<td>0.1757</td>
</tr>
<tr>
<td>Leaf hairs</td>
<td>-0.1453</td>
<td>-0.0125</td>
<td>0.0887</td>
<td>0.0243</td>
<td>-0.0063</td>
<td>0.1508</td>
</tr>
<tr>
<td>Uprooting potential</td>
<td>0.1532</td>
<td>0.2570</td>
<td>-0.1294</td>
<td>0.1784</td>
<td>0.1055</td>
<td>0.0040</td>
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<tr>
<td>Edible</td>
<td>0.1254</td>
<td>-0.1876</td>
<td>0.1465</td>
<td>-0.0417</td>
<td>0.2602</td>
<td>-0.0140</td>
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<tr>
<td>Latex</td>
<td>-0.0060</td>
<td>-0.0121</td>
<td>-0.1159</td>
<td>-0.2121</td>
<td>-0.2853</td>
<td>-0.3181</td>
</tr>
<tr>
<td>Leaves deciduous</td>
<td>0.1799</td>
<td>-0.0647</td>
<td>-0.0091</td>
<td>-0.2760</td>
<td>0.2048</td>
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<tr>
<td>Resprouting</td>
<td>0.0159</td>
<td>-0.2102</td>
<td>0.0929</td>
<td>-0.2092</td>
<td>-0.2227</td>
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</tr>
<tr>
<td>Wind dispersal</td>
<td>-0.2841</td>
<td>0.0872</td>
<td>0.1470</td>
<td>-0.0211</td>
<td>-0.0789</td>
<td>0.0318</td>
</tr>
<tr>
<td>Seedbank</td>
<td>0.2759</td>
<td>-0.0481</td>
<td>-0.0917</td>
<td>0.0225</td>
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<tr>
<td>Animal dispersal</td>
<td>0.0261</td>
<td>-0.1053</td>
<td>-0.1492</td>
<td>-0.0033</td>
<td>-0.1547</td>
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<td>Clonality</td>
<td>-0.0897</td>
<td>-0.1836</td>
<td>0.1377</td>
<td>0.3307</td>
<td>-0.1501</td>
<td>0.0045</td>
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<td>Seed size</td>
<td>0.0590</td>
<td>-0.0788</td>
<td>-0.2172</td>
<td>-0.2139</td>
<td>0.1407</td>
<td>-0.0661</td>
</tr>
<tr>
<td>Fecundity</td>
<td>-0.1331</td>
<td>0.0599</td>
<td>0.2845</td>
<td>-0.0780</td>
<td>-0.2027</td>
<td>0.1026</td>
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<tr>
<td>Poisonous</td>
<td>0.0678</td>
<td>0.0255</td>
<td>-0.1097</td>
<td>-0.1187</td>
<td>-0.4037</td>
<td>-0.2008</td>
</tr>
<tr>
<td>Perennial</td>
<td>-0.1628</td>
<td>-0.1047</td>
<td>0.0925</td>
<td>-0.1732</td>
<td>0.2495</td>
<td>-0.0439</td>
</tr>
<tr>
<td>Annual</td>
<td>0.1628</td>
<td>0.1047</td>
<td>-0.0925</td>
<td>0.1732</td>
<td>-0.2495</td>
<td>0.0439</td>
</tr>
<tr>
<td>Plant functional type</td>
<td>Description</td>
<td>Examples</td>
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<td></td>
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</tr>
<tr>
<td>-----------------------------------------------------------</td>
<td>-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------</td>
<td>-----------------------------------------------------------------------------------------------</td>
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</tr>
<tr>
<td><strong>Group 1. Rosette plants, upright, non-clonal</strong></td>
<td>These are plants with the leaves radiating outwards from a short stem at ground level. In this group the leaves tend to grow <strong>upright from the stem</strong>. The growing point is at or near ground level. There is no branching. The plants within this PFT often have thickened tap-roots or similar underground storage organs from which re-sprouting can take place.</td>
<td>34 species. <em>Pelargonium reniforme</em>, <em>Ranunculus multifidus</em>, <em>Cynoglossum austro-africanum</em>, <em>Senecio erubescens</em></td>
<td></td>
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<tr>
<td><strong>Group 2. Rosette plants, flat, non-clonal</strong></td>
<td>These are plants with the leaves radiating outwards from a short stem at ground level. In this group the leaves tend to grow <strong>flat against the ground</strong>. The growing point is at or near ground level. There is no branching. The plants within this PFT often have thickened tap-roots or similar underground storage organs from which re-sprouting can take place.</td>
<td>35 species. <em>Hypochaeris radicata</em>, <em>Haplocarpha scaposa</em>, <em>Crabbea acaulis</em>, <em>Scabiosa columbaria</em>, <em>Sonchus dregeanus</em></td>
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<tr>
<td><strong>Group 3. Rosette plants, flat &amp; upright, non-clonal, with spines on leaves</strong></td>
<td>These are plants with the leaves radiating outwards from a short stem at ground level. In this group the leaves have <strong>spines or thorns</strong>. The growing point is at or near ground level. There is no branching. The plants within this PFT often have thickened tap-roots or similar underground storage organs from which re-sprouting can take place.</td>
<td>20 species. <em>Berkheya discolor</em>, <em>Berkheya bupthalmoides</em>, <em>Cirsium vulgare</em>, <em>Berkheya pinnatifida</em>, <em>Blepharis integrifolia</em></td>
<td></td>
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<tr>
<td>Group 4. Rosette plants, upright, clonal, with or without woody rootstock</td>
<td>These are plants with the leaves radiating outwards from a short stem at ground level. In this group the plants are clonal with upright leaves, often forming dense patches or tufts. They include primarily resprouting plants with woody rootstocks, but there are also non-resprouting species. The growing point is at or near ground level. There is no branching above-ground, but rhizomatous branching occurs.</td>
<td>27 species. <em>Helichrysum krebtsianum, Helichrysum nudifolium, Gazania krebtsiana, Conyza podocephala</em></td>
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<tr>
<td>Group 5. Rosette plants, flat on ground, clonal, with or without woody rootstock</td>
<td>These are plants with the leaves radiating outwards from a short stem at ground level. In this sub-group the plants are clonal with leaves flat on the ground, often forming dense mats or spreading carpets. Includes many species that are used as ground covers in gardens. The growing point is at or near ground level. There is no branching above-ground, but rhizomatous branching occurs. Thickened rhizomes or other underground storage organs are usually present.</td>
<td>12 species. <em>Arctotis arctotoides, Hermannia depressa, Centella asiatica, Diclis reptans, Falckia repens</em></td>
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<tr>
<td>Group 6. Annual proto-rosettes</td>
<td>Species with high fecundity and are opportunistic weeds of disturbed areas and, in many cases, are listed as problem plants in South Africa (Bromilow 2001). In most cases, they are exotic.</td>
<td>28 species. <em>Bidens pilosa</em> and <em>Conyza canadensis</em>.</td>
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<tr>
<td>Group 7. Small creeping, twining, decumbent or prostrate plants</td>
<td>Includes all plants in which the main stem is decumbent or creeping instead of upright. Leaves are all borne along the stem rather than at the base. This group consists primarily of small, relatively inconspicuous plants. All of these species have a thickened underground stem from which new above-ground parts sprout every season.</td>
<td>17 species. <em>Rhynchosia totta</em>, <em>Convolvulus sagittatus</em>, <em>Cucumis hirsutus</em>, <em>Cyphia sylvatica</em>, <em>Centella glabrata</em></td>
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<tr>
<td>Group 8. Large creeping, twining, decumbent or prostrate plants</td>
<td>Includes all plants in which the main stem is decumbent or creeping instead of upright. Leaves are all borne along the stem rather than at the base. This group consists primarily of large, relatively conspicuous plants.</td>
<td>25 species. <em>Acalypha caperonioides</em>, <em>Ipomoea crispa</em>, <em>Pentanisia angustifolia</em>, <em>Turbina oblongata</em></td>
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<tr>
<td>Group 9. Mat-forming, creeping, decumbent or prostrate plants</td>
<td>Includes all plants in which the main stem is decumbent or creeping instead of upright. The group consists primarily of multi-stemmed, spreading, mat-forming plants.</td>
<td>30 species. <em>Guilleminea densa</em>, <em>Gomphrena celosioides</em>, <em>Indigofera hedyantha</em>, <em>Lotononis laxa</em>, <em>Trifolium burchellianum</em>, <em>Hermannia depressa</em></td>
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<tr>
<td>Group 10. Non-clonal upright plants without woody rootstock (reseeders)</td>
<td>This group contains perennial forbs that branch basally (with leaves held above-ground) and those that branch above-ground. This group contains those without woody rootstock (reseeders).</td>
<td>102 species. <em>Geranium caffrum</em> and <em>Monsonia angustifolia</em>.</td>
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<tr>
<td>Group 11. Non-clonal upright plants with woody rootstock (resprouters)</td>
<td>This group contains perennial forbs that branch basally (with leaves held above-ground) and those that branch above-ground. This sub-group contains those with woody rootstock (resprouters).</td>
<td>141 species. <em>Felicia muricata</em>, <em>Kohautia amatymbica</em> and <em>Walafrida saxatilis</em></td>
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<tr>
<td>Group 12. Clonal upright plants (proto-rosettes)</td>
<td>tuft-forming upright plants that are strongly clonal. They include resprouting plants with woody rootstocks and non-resprouting plants.</td>
<td>5 species. <em>Helichrysum aureonitens</em>, <em>Helichrysum isolepis</em>, <em>Helichrysum rugulosum</em></td>
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<tr>
<td>Group 13. Succulents</td>
<td>herbaceous plants with succulent leaves</td>
<td>40 species. Various species of <strong>Crassulaceae</strong> and <strong>Mesembryanthemaceae</strong>, <strong>Haworthia</strong> species</td>
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<tr>
<td>Group 14. Poisonous or inedible upright plants</td>
<td>Any species that are strongly poisonous, inedible or irritant due to the presence of poisonous milky latex. Inedibility imparts an advantage on these plants that occur within a system dominated by grazing animals.</td>
<td>32 species. <strong>Adenocline pauciflora</strong>, <strong>Euphorbia striata</strong>, <strong>Sarcostemma viminale</strong>, <strong>Euphorbia striata</strong>, <strong>Pachycarpus vexillaris</strong>, <strong>Asclepias stellifera</strong></td>
<td></td>
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</tbody>
</table>
CHAPTER 6: THE EFFECT OF PLANT FUNCTIONAL TYPE RICHNESS ON SPECIES RICHNESS IN GRASSLAND VEGETATION OF THE EASTERN CAPE

Introduction

South Africa has a unique natural environment and its biological diversity is recognised at an international level to be outstanding (Takhtajan 1986, Cowling et al. 1989, 1997, van Wyk & Smith 2001). The Grassland Biome is characterised by high overall species richness and often very high local richness, despite having a simple structure. At a scale of 1000m$^2$, grasslands have the second highest mean plant diversity behind renosterveld for all vegetation types in South Africa (Cowling et al. 1989). Highveld grasslands, for example, are home to almost 4000 species (Cowling et al. 1989) and a single 100 m$^2$ plot may contain anywhere up to 60 species (Hoare, unpublished data). This high diversity is surprising in light of the apparent lack of structural complexity. The diversity of grasslands is enigmatic due to the fact that there appears to be coexistence amongst large numbers of species apparently occupying the same niche (Cowling et al. 1989). The question arises as to how so many ecologically similar species co-exist in the landscape.

Coexistence of different plant species in diverse ecological communities has been thought to be due, in part, to life-history trade-offs involving allocation of resources (Tilman 1988; Ricklefs 1977; Grubb 1977; Denslow 1980). Classical theories of competition ascertained that species occupy unique niches defined relative to limiting resources to which species respond differentially (MacArthur & Levins 1967; Diamond 1988). Under conditions where resources are strongly limited, each growth form is thought to represent a unique solution to survival (Cody 1989, 1991) and to occupy a distinct region on the resource axis. Resource partitioning amongst species, known as niche differentiation, is thought to promote species richness by reducing competition. The theory of niche differentiation assumes that coexisting plant species are dissimilar enough for competitive exclusion to be avoided. It follows, therefore that there should be a positive relationship between plant functional type richness and species richness.

Plant functional type diversity has been studied in many parts of the world for a variety of reasons. One of the main reasons for studying functional types has been to understand the effect of species richness on ecosystem function (Diaz et al. 2003, 2004, 2007, Diaz & Cabido 2001, Hooper et al. 2002). Another reason for studying plant functional types is in order to understand plant community response to various ecological factors, including grazing (Hadaar et al. 1999, Landsberg et al. 1999, Diaz et al. 2001, 2007, McIntyre & Lavorel 2001, Sternberg et al. 2000),
environmental gradients (Diaz et al. 1999), fire (Lavorel & Cramer 1999, Lavorel et al. 1997, 1999, McIntyre et al. 1995, 1999, Diaz et al. 2002, Pausus & Lavorel 2003) and climate change. There have been few studies linking functional diversity and species richness (Diaz & Cabido 2001); however this has the potential to provide insights into the relationship between niche differentiation, co-existence and species richness.

Functional diversity may be defined as the number of functional types (Cowling et al. 1994a). Taxa belonging to the same functional type are considered to be functional analogues. A classification of the species from the grasslands of the study area (Chapter 5) identified a number of functional types, each of which contained different numbers of species. It is not known, however, whether the species composition at a single site contains functional analogues or not. Functional redundancy occurs when there is more than one analogue at a site or in a community (Walker 1992). Where there is strong niche differentiation, it would be expected that there would be low levels of functional redundancy.

Cody (1989) used growth forms to explain strategies of resource utilization, but no studies have been published in which plant functional types have been used to explain diversity in grasslands. In South Africa, such studies have been undertaken in fynbos (Cowling et al. 1994a) and karoo vegetation (Cowling et al. 1994b). The current study focuses on the relationship between species richness and functional diversity in grassland plant communities. The premise upon which this study is based is that if the number of species at a site is the same as the number of plant functional types, then there is good evidence for niche differentiation; if there are more species than plant functional types then some factor other than niche differentiation via growth form differentiation must be at play.

Grasslands in South Africa occur where there is a mean annual rainfall of mostly between 400 and 2000 mm. The vegetation of the Grassland Biome follows a rainfall gradient and can be broadly divided into sweet and sour grasslands (Tainton 1981). Sweet grasslands occur in lower rainfall areas and carbon assimilation tends to be low relative to nutrient supply, whereas the converse is true for sourveld (Ellery et al. 1995). Areas with a mean annual rainfall of above 625 mm tend to be dominated by sour grasses, although the change-over can be anywhere between 500 and 700 mm (Rutherford & Westfall 1986). Different factors may be expected to shape diversity patterns in different ways within these two moisture regimes. This provides an opportunity to compare resource-driven (semi-arid) and competitively constrained (mesic) plant communities. In mesic grasslands canopy cover is usually saturated and there is more competition for space and resources. The expectation is therefore that there will be greater evidence of niche differentiation in semi-arid grasslands than in mesic grasslands, since mesic grasslands tend to be more competitively constrained.
The aim of this study is to analyse the relationship between plant functional type diversity and species richness in grassland communities in order to understand the factors that contribute towards determining species richness, specifically those factors that influence interactions of species with one another. The main questions to be addressed in this study are whether niche differentiation promotes species richness in grasslands of the Eastern Cape and whether there are differences between semi-arid and mesic grasslands with respect to niche differentiation.

It was expected that there would be a strong positive relationship between plant functional type richness and species richness at a local scale. Due to the fact that there are many hundreds of species in the study area and only 30 grass and forb plant functional types, it was expected that, at low levels of plant functional type and species richness, new species would be more likely to come from a new plant functional type (one not already represented in that site), whereas at high richness levels, any new species would be more likely to come from an existing plant functional type (one already represented at that site). The overall relationship between plant functional type richness and species richness was therefore expected to be approximately linear, but probably to more closely fit a power function. This would indicate that, as richness increases, species are more likely to be functionally similar so competition for niche space would be more intense.

For the comparison of plant communities in terms of the relationship between plant functional type richness and species richness, it is useful to use a linear function. The expectation is that the relationship will reflect the relative degree of niche differentiation—the greater the amount of niche differentiation, the closer the slope will approach a one to one relationship. A slope near unity indicates coexistence via strong niche differentiation; a slope much greater than unity indicates that some other mechanism contributes importantly to coexistence.

Specific objectives were as follows:

1. to determine whether there is a significant relationship between plant functional type richness and species richness at a local scale.
2. to determine whether the amount of mean annual rainfall affects the relationship between plant functional type richness and species richness.
3. to determine which plant functional types make the greatest contribution towards increased species richness at the plot scale.

**Study area**

See Chapter 2 for detailed description of the study area.
A list of the different plant communities in the study area is provided here (Table 6.1) to aid interpretation of the results.

**Table 6.1: Plant communities of the study area.**

<table>
<thead>
<tr>
<th>Location</th>
<th>Shortened phytosociological name</th>
<th>Annual rainfall, mesic = &gt; 500 mm, semi-arid = &lt; 700 mm</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Mountain grasslands</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Amatola southern watershed</td>
<td><em>Eragrostis plana</em> grassland</td>
<td>Mesic</td>
</tr>
<tr>
<td>Amatola northern watershed</td>
<td><em>Leysera gnaphalodis</em> grassland</td>
<td>Mesic</td>
</tr>
<tr>
<td>Stormberg plateau</td>
<td><em>Helichrysum rugulosum</em> grassland</td>
<td>Mesic</td>
</tr>
<tr>
<td>Amatola mistbelt</td>
<td><em>Helichrysum aureum</em> grassland</td>
<td>Mesic</td>
</tr>
<tr>
<td>High altitude, steep slope</td>
<td><em>Festuca caprina</em> grassland</td>
<td>Mesic</td>
</tr>
<tr>
<td>Main escarpment</td>
<td><em>Festuca scabra</em> grassland</td>
<td>Mesic</td>
</tr>
<tr>
<td>Sub-escarpment</td>
<td><em>Protea simplex</em> grassland</td>
<td>Mesic</td>
</tr>
<tr>
<td><strong>Mountain drainage line grassland</strong></td>
<td></td>
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<tr>
<td>Drainage lines</td>
<td><em>Miscanthus capensis</em> grassland</td>
<td>Mesic</td>
</tr>
<tr>
<td><strong>Plains grassland</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Aliwal North semi-arid grassland</td>
<td><em>Eragrostis gummiflua</em> grassland</td>
<td>Semi-arid</td>
</tr>
<tr>
<td>Queenstown semi-arid grassland</td>
<td><em>Hermannia depressa</em> grassland</td>
<td>Semi-arid</td>
</tr>
<tr>
<td>Smaldeel semi-arid grassland</td>
<td><em>Digitaria argyrograpta</em> grassland</td>
<td>Semi-arid</td>
</tr>
<tr>
<td><strong>Semi-arid mountain grasslands</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Karoo mountains / escarpment</td>
<td><em>Merxmuellera disticha</em> grassland</td>
<td>Semi-arid</td>
</tr>
</tbody>
</table>

**Methods**

**Data collection**

Plot data used in the current analysis were collected for a floristic survey of the south-western extreme of the Grassland Biome (Hoare 1997). Plots were classified into vegetation communities (Hoare & Bredenkamp 1999, 2001). Further fieldwork in the Eastern Cape supplemented this data set. Only the data from those plant communities that are physiognomically recognised as grassland are used here, although other plant communities, e.g. shrubland on rocky outcrops, also occur within the matrix of grasslands in the study area. A total of 275 plots were used in the current analysis.

**Classification of species into plant functional types**

Life form is often used as an easily recognisable plant functional type, but most previous studies have found that life form alone is too broad a classification to determine the relative sensitivity to environmental variability (Kelly 1996). Broad life forms that occur in the study area are primarily woody trees and shrubs, dwarf shrubs, geophytes, graminoids and forbs. The graminoids and forbs contribute the most to overall species richness in the grasslands (see Table 3.4, Chapter 3). It has also been noted that these two life-forms have apparently high numbers of co-existing species (Cowling et al. 1989).
Forbs and grasses occurring in the grasslands of the Eastern Cape were classified into plant functional types using the approach of McIntyre et al. (1999) (see Chapter 5). Shrubs, dwarf shrubs and geophytes were not classified into functional types in this study since they occur at low frequencies in open grasslands. Where they occur they are treated simply as growth forms and not divided further into functional types.

Data analysis

The following analyses were undertaken to address the objectives of this study:

1. In order to assess the relationship between species richness and plant functional type richness, the two variables were plotted against one another. Species richness ($S$) was defined as the number of species per site. The same index was used to describe plant functional type richness. I used a one-way ANOVA with Tukey post-hoc test to detect significant differences between plant communities in terms of the number of species per plant functional type. Plant functional type variables were square root transformed. This transformation is applicable when group variances are proportional to the means, which usually occurs when samples are taken from a Poisson distribution, i.e. when the data consists of counts of objects (Zar 1999).

2. In order to determine the extent to which mean annual rainfall influences niche differentiation, I plotted the number of species per plant functional type against annual rainfall. I used linear regression to determine the significance of this relationship.

3. Multiple regression was performed using diversity within the different plant functional types as independent variables against overall richness. In order to determine which plant functional types were making a significant contribution to overall richness, I tabulated the mean number of species per plant functional type in each community.

Results

Relationship between plant functional type richness and species richness

The mean species richness and plant functional type richness per plant community are presented in Table 6.2.

Table 6.2: Species and plant functional type richness in different plant communities in 100 m² samples from the study area.

<table>
<thead>
<tr>
<th>Shortened phytosociological name</th>
<th>n</th>
<th></th>
<th>SD</th>
<th>range</th>
<th>n</th>
<th>SD</th>
<th>range</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eragrostis plana grassland</td>
<td>15</td>
<td></td>
<td>23.7</td>
<td>10.0 9–43</td>
<td>13.4</td>
<td>3.44</td>
<td>7–18</td>
</tr>
<tr>
<td>Plant Community</td>
<td>PFT Number</td>
<td>Species Number</td>
<td>PFT Range</td>
<td>Species Range</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>-----------------------------------------------</td>
<td>------------</td>
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<td>------------</td>
<td>---------------</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Leysera gnaphaloidis</em> grassland</td>
<td>24</td>
<td>7.2</td>
<td>11–43</td>
<td>13.1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Helichrysum rugulosum</em> grassland</td>
<td>32</td>
<td>9.7</td>
<td>12–55</td>
<td>16.1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Helichrysum aureum</em> grassland</td>
<td>16</td>
<td>9.1</td>
<td>16–57</td>
<td>14.2</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Festuca caprina</em> grassland</td>
<td>12</td>
<td>11.4</td>
<td>11–50</td>
<td>13.8</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Festuca scabra</em> grassland</td>
<td>10</td>
<td>11.3</td>
<td>8–45</td>
<td>17.8</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Protea simplex</em> grassland</td>
<td>19</td>
<td>8.0</td>
<td>20–45</td>
<td>15.0</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Miscanthus capensis</em> drainage line grassland</td>
<td>15</td>
<td>8.7</td>
<td>8–35</td>
<td>12.3</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Eragrostis gummiflua</em> grassland</td>
<td>14</td>
<td>8.7</td>
<td>15–47</td>
<td>15.8</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Hermannia depressa</em> grassland</td>
<td>17</td>
<td>9.1</td>
<td>19–48</td>
<td>17.0</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Digitaria argyrograpta</em> grassland</td>
<td>13</td>
<td>5.8</td>
<td>15–59</td>
<td>14.8</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Merxmuellera disticha</em> grassland</td>
<td>47</td>
<td>6.8</td>
<td>13–51</td>
<td>13.9</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

The mean number of plant functional types per plot varies from 12.3 in *Miscanthus capensis* drainage line grassland to 17.8 in *Festuca scabra* escarpment grassland (Table 6.2). The two plant communities with the lowest mean number of plant functional types per plot are also the two plant communities with the lowest mean species richness values (Table 6.2), namely Amathole northern watershed (*Helichrysum aureum*) grasslands and *Miscanthus capensis* drainage line grasslands. There are four plant communities with a high mean number of species per plant functional type relative to the other plant communities: Amathole mistbelt (*Helichrysum aureum*) grassland, high altitude, steep slope (*Festuca caprina*) grassland, *Protea simplex* grassland and

![Figure 6.2: The relationship between plant functional type (PFT) richness and species richness in grassland phytosociological plots from the Eastern Cape.](image-url)
Smaldeel semi-arid (*Digitaria argyrograpta*) grassland.

The results of the comparison between plant functional type richness and species richness are presented in Figure 6.2. In all grassland plant communities combined, there is a significant relationship between plant functional type richness and species richness (Figure 6.2).

Where the relationship between plant functional type richness and species richness is plotted separately for each individual plant community, the slopes of the regressions between plant functional type richness and species richness for each community exceeds unity (Figure 6.3). However, the slopes were different for different plant communities and were generally steeper in mesic plant communities than semi-arid plant communities. The slope of the regression lines (plant functional type richness versus species richness) were between 1.7 and 2.9 in mesic grasslands where the $r^2$ value exceeded 0.2 (Figure 6.3a). Differences between these plant communities for this comparison were found to be significant ($p<0.0001$), but the differences were only significant for *Helichrysum aureum* grassland, where the slope was significantly greater than *Leysera gnaphalodis* grassland and *Eragrostis plana* grassland at $p<0.01$ and $p<0.05$ respectively (no other comparisons were significant). The plant communities with the steepest slopes were those with the most mesic conditions.

In semi-arid grasslands the relationship (plant functional type richness versus species richness) showed different patterns in different plant communities: two of the plant communities (*Eragrostis gummiflua* grassland and *Hermannia depressa* grassland) had slopes similar to those for mesic grasslands and two communities (*Digitaria argyrograpta* grassland and *Merxmuellera disticha* grassland) had slopes closer to unity (Figure 6.3b). Differences in means for these different plant communities were significant ($p=0.012$), but the differences were only significant for *Digitaria argyrograpta* grassland, where the slope was significantly less than the others at $p<0.05$ (no other comparisons were significant). The *Digitaria argyrograpta* grassland plant community was the driest in terms of mean annual rainfall in the entire study area and had the least functional redundancy.

**Effect of rainfall amount on the number of species per plant functional type**

There is a weak but positive relationship between the number of species per plant functional type and mean annual rainfall (Figure 6.4, $p=0.0016$, $r^2=0.0489$), and indicates that the number of species per plant functional type increases from 1.6 to 2.0 with a change in annual rainfall from under 400 to 1000 mm, the range of rainfall values found within the grasslands of the study area.
**Contribution to overall richness by different plant functional types**

There are specific plant functional types that make a significant contribution towards overall species richness. Within mesic grasslands the plant functional types that had high mean species richness were Forb 10 (non-clonal upright plants without woody rootstocks), Forb 11 (non-clonal upright plants with woody rootstock), Forb 2 (flat, non-clonal rosette plants), Forb 4 (upright, clonal rosette plants), Grass 13 (short, tufted C4 grasses), grass 14 (tall, non-rhizomatous, tufted C4 grasses), grass 16 (tall, rhizomatous, tufted C4 grasses), dwarf shrubs and geophytes (Table 6.3).

Within semi-arid grasslands, the plant functional types had high mean species richness were Grass 13 (short, tufted C4 grasses), grass 14 (tall, non-rhizomatous, tufted C4 grasses), grass 16 (tall, rhizomatous, tufted C4 grasses), Grass 11 (weakly tufted C4 grasses), Forb 11 (non-clonal upright plants with woody rootstock), Forb 10 (non-clonal upright plants without woody rootstocks), forb 4 (upright, clonal rosette plants) and geophytes (Table 6.3).

**Figure 6.4:** The relationship between species per plant functional type (PFT) and annual rainfall in phytosociological plots from grasslands of the Eastern Cape.
Discussion

The relationship between plant functional type richness and species richness provides evidence of niche differentiation in the grasslands of the study area. The prediction for this study was that, for the relationship between plant functional type richness and species richness, the slope of the relationship would reflect the relative degree of niche differentiation in a particular plant community; a slope near unity would indicate coexistence via strong niche differentiation and a slope much greater than unity would indicate that some other mechanism contributes in an important way to coexistence. It was found that the slope of the trendline was close to unity in semi-arid grasslands and steeper in mesic grasslands. This provides an indication that higher rainfall grasslands are less structured by niche differentiation than semi-arid grasslands. The contribution of functional type richness towards promoting species richness is therefore more important in semi-arid grasslands than mesic grasslands. The number of species per plant functional type was found to increase weakly with increasing rainfall, although the relationship is not very strong and there is overlap between semi-arid and mesic grasslands.

According to Diaz & Cabido (2001), the relationship between functional type richness and species richness is thought to only hold if there is a linear increase in coverage of niche space as species richness increases (Diaz & Cabido 2001). Theoretically this can only happen in two situations: random occupation of niche space or uniform occupation of niche space. However, aggregation and non-random assemblage of communities from the regional species pool are patterns more commonly observed in nature. Aggregation occurs when some plant functional types contain many species whereas others are represented by only a few species. Aggregated occupation of niche space may be related to strong convergence of different species into functional types. Within the study area, there is strong aggregation into some plant functional types (i.e. some plant functional types have high number of species whereas others are represented by only a few species). The relationship between plant functional type richness and species richness fitted a power function better than a linear function. This indicates that, as species richness increases, species are more likely to be from a functional type that already occurs at a site. With increasing richness species are more likely to be functionally similar so competition for niche space is more intense. This indicates random occupation of niche space at low species richness levels followed by increased aggregated coverage of niche space as species richness increases. This implies that functional redundancy is likely to increase with species richness.

Vegetation compositional changes along environmental gradients and selective clearing due to specific management actions can lead to change in species composition that may lead to impoverishment of functional types or a differential favouring of certain functional types. This can lead to an equitable or differential change in functional types, the latter being more common (Diaz
There are two strong characteristics of the study area in the Eastern Cape, the first being the existence of strong environmental gradients and the second being the fact that the grassland vegetation is used as natural rangeland for livestock production. Both of these factors can influence species richness, functional diversity and plant community composition. Where functional redundancy is high, these disturbance factors may promote species richness, which is the case in mesic grasslands in the study area.

In conclusion, this study indicates that there is evidence of niche differentiation in Eastern Cape grasslands and also that niche differentiation promotes species richness in these grasslands. The coexistence of large numbers of apparently functionally similar species is thus facilitated.

References:


Figure 6.3: The relationship between plant functional type (PFT) richness and species richness in phytosociological plots from semi-arid and mesic grassland communities of the Eastern Cape.
Table 6.3: Mean number of species per plant functional type (PFT) in plant communities of the study area. Plant communities are as in Table 5.1.

<table>
<thead>
<tr>
<th>PFT</th>
<th>Forb 1</th>
<th>Forb 2</th>
<th>Forb 3</th>
<th>Forb 4</th>
<th>Forb 5</th>
<th>Forb 6</th>
<th>Forb 7</th>
<th>Forb 8</th>
<th>Forb 9</th>
<th>Forb 10</th>
<th>Forb 11</th>
<th>Forb 12</th>
<th>Forb 13</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Erag</td>
<td>Leys</td>
<td>Heli</td>
<td>Heli</td>
<td>Fest</td>
<td>Fest</td>
<td>Prot</td>
<td>Misc</td>
<td>MEAN</td>
<td>MEAN</td>
<td>MEAN</td>
<td>MEAN</td>
<td>MEAN</td>
</tr>
<tr>
<td></td>
<td>plana</td>
<td>gnaph</td>
<td>rugus</td>
<td>aure</td>
<td>capra</td>
<td>scab</td>
<td>simp</td>
<td>cape</td>
<td>(mesic)</td>
<td>(all)</td>
<td>(all)</td>
<td>(all)</td>
<td>(all)</td>
</tr>
<tr>
<td>Erag</td>
<td>1.00</td>
<td>0.91</td>
<td>0.67</td>
<td>1.75</td>
<td>1.00</td>
<td>2.00</td>
<td>1.21</td>
<td>0.50</td>
<td>1.10</td>
<td>0.33</td>
<td>0.57</td>
<td>0.50</td>
<td>0.52</td>
</tr>
<tr>
<td>Leys</td>
<td>0.75</td>
<td>0.44</td>
<td>0.37</td>
<td>0.74</td>
<td>0.25</td>
<td>0.25</td>
<td>0.15</td>
<td>0.47</td>
<td>0.92</td>
<td>1.42</td>
<td>1.00</td>
<td>0.50</td>
<td>2.05</td>
</tr>
<tr>
<td>Heli</td>
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<td>0.33</td>
<td>0.25</td>
<td>0.37</td>
<td>0.25</td>
<td>0.15</td>
<td>0.47</td>
<td>0.92</td>
<td>1.42</td>
<td>1.00</td>
<td>0.50</td>
<td>2.05</td>
<td>1.65</td>
</tr>
<tr>
<td>Heli</td>
<td>0.50</td>
<td>0.47</td>
<td>0.50</td>
<td>0.52</td>
<td>1.57</td>
<td>3.13</td>
<td>1.62</td>
<td>1.48</td>
<td>1.88</td>
<td>5.14</td>
<td>3.67</td>
<td>3.24</td>
<td>3.91</td>
</tr>
<tr>
<td>Fest</td>
<td>0.33</td>
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<td>0.37</td>
<td>0.47</td>
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<td>0.34</td>
<td>0.25</td>
<td>0.00</td>
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<td>Prot</td>
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<td>0.15</td>
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<td>0.92</td>
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<td>1.00</td>
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<td>1.25</td>
<td>1.57</td>
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<td>0.14</td>
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</tr>
<tr>
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<td>1.00</td>
<td>0.50</td>
<td>0.50</td>
<td>1.57</td>
<td>1.62</td>
<td>1.48</td>
<td>1.88</td>
<td>3.91</td>
<td>5.14</td>
<td>3.24</td>
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</tr>
</tbody>
</table>

Table continues...
CHAPTER 7: SPECIES POOL EFFECTS ON LOCAL SPECIES RICHNESS IN GRASSLAND PLANT COMMUNITIES OF THE EASTERN CAPE

Introduction


Theories related to historical and regional processes can be divided into two main concepts that have been presented in the literature; taxonomic structure effects (Enquist et al. 2002) and species pool effects (including dispersal limitation). Some areas, possibly with long stable climates, have experienced potentially higher speciation rates or lower extinction rates. Historical factors may lead to the development of large regional species pools via dispersal and high speciation and/or low extinction rates. A large regional species pool may also arise from high beta diversity, which also results in a proportionally high area of inter-community contact zones (Cowling et al. 1989). High beta diversity may, in turn, arise as a consequence of a high regional species pool, high diversification rates or high environmental heterogeneity.

Where regional processes are found to be the dominant factor promoting local richness, the dispersal ability of species, the biogeographic origin of species or the amount of turnover of species along environmental gradients may all contribute to promoting local richness. Where a number of phytogeographic regions merge there will potentially be a higher number of species available from different origins to contribute to local richness. Cowling (1983b) argued that, at the merging of different phytogeographical regions, richness would be highest in those communities that can accommodate species from a high number of such regions, owing to a mass effect (Shmida & Wilson 1985). Thus, these communities are able to accept species from many different phytodiversity. This mixing produces rich local floras. Phytogeographic diversity should, therefore, promote local richness and a positive relationship between phytogeographic diversity and local richness is therefore expected.

Local richness may also be influenced by the size of the regional species pool. High regional richness is thought to provide a larger species pool from which species can invade local habitats. Where the relationship between local and regional richness is linear, local communities are thought to be non-saturated (Cornell 1985, Cornell & Lawton 1992). Where there is an absence of
interactions between species, niche space is not filled and colonizing species are more likely to find vacant niches to colonize. Factors that may promote non-saturation include noninteractive community structure, lottery competition for space, random colonization and extinction and disruption of competitive exclusion by disturbance (Cornell & Lawton 1992). The alternative situation is that there are strong interactions and local communities may reach a ceiling above which diversity does not rise irrespective of an increase in the regional species pool, in which case the communities are considered to be saturated (Cornell 1985, Cornell & Lawton 1992). Community saturation may be due to a variety of factors, including strong biotic interactions in limited niche space, dispersal limitation and disturbance. A commonly used method for inferring the impact of regional factors on local richness is the comparison of species richness in local assemblages (SL) with the total number of species in the region (SR) (Cornell & Lawton 1992, Lawton 1999, Srivastava 1999, Karlson et al. 2004). Linear relations between SR and SL are interpreted as an indication of a strong regional influence on local richness.

The aim of the current study was to determine the extent to which species pool and phytochorological effects are important in determining species richness amongst local assemblages within temperate grasslands of the Eastern Cape, South Africa. This can be expressed in the form of the following questions:

1. What is the influence of regional richness on local richness?
2. What is the influence of phytochorological diversity on local richness?

**Study area**

See Chapter 2 for detailed description of the study area.

The study area is situated in the Eastern Cape Province of South Africa. The Eastern Cape is an extremely complex area in which a number of phytochorological zones converge. Following White (1983), these phytochoria include the Cape Regional Centre of Endemism, the Karoo-Namib Regional Centre of Endemism, the Kalahari-Highveld Regional Transition Zone, the Afromontane Centre of Endemism and the Maputaland-Pondoland Regional Mosaic. The area also contains vegetation representing most of the major biomes that occur in South Africa, namely the Grassland, Nama-Karoo, Fynbos, Thicket, Forest, Savanna and Indian Ocean Coastal Belt Biomes. The occurrence of these phytochoria / biomes in close proximity has the effect of providing a high number of species that may invade individual habitats through mass effects (Shmida & Wilson 1985). Steep environmental gradients also result in the compression of vegetation types into small areas close to one another. These factors promote dispersal from one habitat to another and potentially high species richness in transitional zones.
Methods

Scale

The scale at which local communities are defined is considered an important issue to address when examining the relationship between local ($S_L$) and regional richness ($S_R$) (Hillebrand & Blenckner 2002). The scale at which local interactions (e.g. competition) occur should be used to define local habitat size, since it is these local interactions which are implicitly assumed to cause the non-linearity between $S_L$ and $S_R$ (Hillebrand & Blenckner 2002). It is at the small plot scale that species interactions contribute to determining species richness (Latham & Ricklefs 1993). For plant communities where competition for resources is expected this scale may be only a few square metres (Huston & De Angelis 1994). Sampling too small an area may result in undersampling of rare species and thus the artificial creation of a non-linear relationship between $S_L$ and $S_R$ (Hillebrand & Blenckner 2002), which has been called pseudosaturation (Caley & Schluter 1997; Karlson & Cornell 2002). The linearity of the relationship between $S_L$ and $S_R$ is expected to increase with increasing area of the local habitat as well as an increase in the ratio between the area of the local habitat to the area of the region (Hillebrand & Blenckner 2002).

Species area curves indicate that 10 × 10 m plots are sufficient size for capturing representative floristic information (including rare species) in grasslands in the study area (Hoare 1997). This plot size was therefore used in this study to depict local richness. A standardized plot size assists in overcoming some of the problems associated with regressions of $S_L$ and $S_R$.

Data collection

Plot data were collected during a floristic survey of the Eastern Cape, which constitutes the south-western extreme of the Grassland Biome (Hoare 1997). These were classified into vegetation communities according to Braun-Blanquet procedures (Mueller-Dombois & Ellenberg 1974) and have been published elsewhere (Hoare & Bredenkamp 1999, 2001). Only the data from those plant communities that are physiognomically recognised as grassland are included in this analysis, although other plant communities, e.g. shrubland on rocky outcrops, also occur within the matrix of grasslands in the study area. A total of 227 plots from the Eastern Cape were used in the current analysis. In each plot the projected canopy cover of each species was estimated and converted to a class value according to Braun-Blanquet methods (Westhoff & Van der Maarel 1978).
Determining the local and regional species pool

The delimitation of the regional species pool is an important factor in analyses of relationships between $S_L$ and $S_R$ (Dupré 2000). Due to the fact that particular ecological conditions associated with a community will allow only a portion of the total regional flora to colonize local habitats, it is important to define the regional species pool carefully (Dupré 2000). The regional species pool should, therefore, include the reservoir of species that are potentially able to occur in the plant community (Dupré 2000). In the current study the regional species pool is defined for each plant community as the combined species tally in all 10 × 10 m plots for the community from which the sample site was obtained. All sample sites have been classified into plant communities according to Braun-Blanquet procedures (Hoare 1997, Hoare & Bredenkamp 1999, 2001). Regional species pools therefore constitute a predicted richness value based on the combined species list of all the sample plots from a particular classified plant community. The assumption of the classification philosophy is that each plant community has a unique set of environmental conditions that can be used to explain the floristic composition of that community (Mueller-Dombois & Ellenberg 1974; Westhoff & van der Maarel 1978, Keddy 1992). Any species found within that plant community therefore has the potential to occur at any of the sites classified into that plant community.

According to Hillebrand and Blenckner (2002), most studies used an arbitrarily chosen large area (Caley and Schluter 1997) or an area delimited by natural geography (Oberdorff et al. 1998). The regional pool should include a list of all species that are able to invade the local site. This integrates a component of dispersal ability and a component of time. However, all species able to reach a site may not necessarily be able to survive there. A correction for the suitability of the habitat therefore needs to be done (Pärtel et al. 1996). For the current study, the process of classifying sites into plant communities assumes that environmental conditions favour a particular species composition and, therefore, that any species within the combined checklist for the plant community should have an equal chance of occurring at a site within that plant community. The classification process therefore provides the habitat suitability correction.

A wide range of statistical estimation methods have been proposed in the literature to estimate the total richness of a community based on sample data (Colwell & Coddington 1994). These estimators rely on many different approaches: the maximum likelihood, the jackknife method, the bootstrap method, log-linear or generalized log-linear models, Bayesian methods, mixture models, sample coverage procedures, and martingale estimating functions (Seber 1982, Swarz & Seber 1999, Chao 2001). These can be grouped into three distinct classes: extrapolation of species accumulation curves, fitting data on the relative abundance distribution of species in a single sample to a non-parametric distribution, and non-parametric estimators. Bunge and FitzPatrick (1993) reviewed estimation techniques and concluded that nearly all of the estimators reviewed
have drawbacks that are significant enough to raise reasonable doubts about their conclusions. Their provisional choice of an estimator is a nonparametric Chao estimator (the so-called Chao 2 estimator, Chao 1984, 1987). Longino et al. (2002) reviewed three different types of estimation methods and found that the performance of all three estimators was disappointing, as they were all demonstrated to be strongly dependent on sample size and fairly unstable (i.e., estimates were not predictable). O’Hara (2005) did a comparative study of several estimators and concluded that unless the actual number of species is known (in which case an estimator is not required) or the form of the underlying sampling distribution is known, the estimators cannot be relied upon. Despite these misgivings, it was considered useful to provide an estimation of total species richness. For this study, estimators based on species incidence (presence/absence) were required since numbers of individuals are unknown for the current dataset. Estimators based on singletons/doubletons (e.g. Chao 1) are sensitive to patchiness in species distribution and the Bootstrap method (Smith & van Belle 1984) was not used due to its reported poor performance for vegetation data (Chazdon et al. 1998). For data from South Africa, the Bootstrap method also consistently provides the lowest estimate of true species number (Desmet & Cowling 2004). Two other commonly used methods, ACE and ICE, require data about numbers of individuals in sample plots, information which is not available from the current data set.

Three non-parametric estimators were used, the Chao2 incidence-based estimator (Chao 1987), the first order Jackknife estimator (Burnham & Overton 1978, 1979, Smith & van Belle 1984, Heltshe & Forrester 1984) and the second order Jackknife estimator (Burnham & Overton 1978, 1979, Smith & van Belle 1984, Palmer 1991), as follows:

\[
S_{Chao2} = S_{obs} + (Q_1^2/2Q_2) \\
S_{jack1} = S_{obs} + Q_1(m-1/m) \\
S_{jack2} = S_{obs} + [Q_1(2m-3/m) - Q_2((m-2)^2/m(m-1))] 
\]

where \( Q_1 = \) number of unique species/singletons (occur in single sites only)

\( Q_2 = \) number of duplicate species/doubletons (occur in two sites only)

\( m = \) total number of quadrats.

The average value of the three estimates was used as the estimate of regional species richness (\( S_R \)). Local richness (\( S_L \)) was taken as the mean richness for all sites within a particular plant community.
Allocating species to phytochorological groups

Species were allocated to phytochorological groups, which are based on the distribution of taxa and represent recurring geographic distributions (Cowling 1983a). Sub-divisions of the region into phytogeographical zones are according to White (1976) with changes by Goldblatt (1978). Species were assigned to a phytogeographical zone on the basis of their distribution, as follows:

(i) Endemic to a phytochorion, including Cape, Afromontane, Tongaland-Pondoland, Kalahari-Highveld and Karoo-Namib taxa.
(iii) Widespread species, where they occurred in more than two phytochoria, they were classified as widespread.
(iv) Exotic species, naturalized exotic or alien invasive species.

Data analysis

Regression of local against regional richness

There are criticisms of the approach of comparing local and regional richness (Hillebrand & Blenckner 2002, Hillebrand 2005, Shurin & Srivastava 2005, related to statistical autocorrelation issues (Srivastava 1999), the definition of the two spatial scales for $S_L$ and $S_R$ (Loreau 2000, Shurin et al. 2000, Hillebrand and Blenckner 2002), and the effects of local interactions (Shurin and Allen 2001). The statistical problem of autocorrelation is considered to be implicit in the $S_L$ to $S_R$ regression; it becomes more important the larger the local area is relative to the regional area (Hillebrand & Blenckner 2002) and indicates that the two are not independent (Loreau 2000, Hillebrand 2005). These problems can be overcome by ensuring that the local area is small compared to the regional area, the size of the local area is standardized and the regional pool takes the dispersal ability of species into account, i.e. includes all species that could reach the local habitat. For the current study, the local area is defined as the plot size, which is 10x10 m. This is very small compared to the regional area (many square kilometres in size), and also provides a standardised local area. The classification of plots into plant communities using phytosociological methods assumes that any species in the combined checklist for the community could occur in any of the plots classified into that community. This ensures that all species that could reach the local habitat are included.
The approach adopted for the current study is to undertake an analysis where the regression between $S_R$ and $S_L$ is compared between mean and maximum local richness. The difference in slope between these two provides an indication whether extreme local richness is more dependent on regional richness than average local richness. The regression is first done using the mean species richness at a local scale against regional richness. This is then compared to maximum species richness at a local scale against regional richness. The first regression provides an indication of the average strength of the relationship between local and regional richness. The second regression provides an indication of whether this relationship is different at extreme levels of local richness, i.e. whether the nature of the relationship changes in order to promote higher local richness. The comparative approach is not dependent on the shape of the relationship, only the relative strength of the relationship.

Linear regression was performed using regional richness ($S_R$) as the independent variable against local richness ($S_L$). The data was first tested for normality. Richness variables were square root transformed. This transformation is applicable when group variances are proportional to the means, which usually occurs when samples are taken from a Poisson distribution, i.e. when the data consists of counts of objects (Zar 1999).

Phytochorological effects

Species richness was correlated with an index of phytochorological diversity (PHD, Cowling 1983a), where

$$PHD = - \sum p_i \ln p_i$$

in which $p_i$ is the number of species in a phytochorological group expressed as a fraction of the total number of species in the plot (Cowling 1983a).

Linear regression was performed using phytochorological diversity (PHD) as the independent variable against local richness ($S_L$). The richness variable was square root transformed. The PHD variable was not-transformed.

The analysis was first performed using all species to determine whether PHD is a significant contributor to local richness. The analysis was then repeated excluding all widespread and exotic species. The purpose was to evaluate whether local richness is promoted more by habitat specialists or habitat generalists.
Results

Estimates of regional richness

Counts and estimates of the total species richness in combined plots for each plant community is given in Table 7.1. Total species richness varied from 63 to 252 across the different plant communities. Estimates of species richness varied, depending on the estimate measure used. The Jacknife 1 estimate of species richness was always lower than the other two estimates, and the Jacknife 2 estimate was always the highest (Table 7.1). The mean value for the three estimates provided a range of richnesses of 107 to 355 species per plant community (Table 7.1).

Relationship between regional and local richness

A graphic of the comparative relationship between $S_L$ and $S_R$ is shown in Figure 7.1. The bottom graph shows the relationship between regional species richness and mean local richness and the top graph shows the relationship between regional richness and maximum local richness.

![Figure 7.1: Plot of regional richness ($S_R$) versus local richness ($S_L$) in grassland communities of the Eastern Cape. The lower graph is mean local richness and the upper graph maximum local richness.](image-url)
There was a weak, non-significant \((p=0.3319)\) linear relationship between regional and mean local richness. Linear regression analysis indicated that regional richness is not a significant contributor to mean local richness. The model explained 10.5% of the variance in local richness \((R^2 = 0.105, F=1.05)\).

There was a significant \((p=0.0144)\) and moderately strong linear relationship between regional richness and maximum local richness (the maximum richness value of all plots within each plant community). Linear regression analysis indicated that regional richness is a significant contributor to maximum local richness. The model explained 50.4% of the variance in maximum local richness \((R^2 = 0.504, F = 9.15)\).

**Effect of phytochorological diversity on local richness**

There was a marked difference in the phytochorological makeup of different plant communities (Table 7.2). For all plant communities, widespread species were the most dominant and the remaining species were predominantly Kalahari-Highveld-Afromontane linking species or species originating from a single phytochorion.

A plot of the relationship between phytochorological diversity (PHD) and local species richness is

![Figure 7.2: Plot of species richness per sample versus phytochorological diversity (PHD) in grassland communities of the Eastern Cape.](image-url)
shown in Figure 7.2. This indicates that there is a moderately strong positive linear relationship between phytochorological diversity (PHD) and local species richness.

Linear regression analysis indicated that PHD is a significant contributor to local richness ($R^2 = 0.386$, $p<0.0001$). The analysis therefore indicated that phytochorological diversity has a significant positive influence on species richness. This correlation is even more strongly positive when all widespread (WID) and exotic (EX) species are excluded from the analysis ($R^2 = 0.69$, $p<0.0001$). Amongst the grasses 92 of the 102 species in the family belong to this group of widespread species.

**Discussion**

Species pool effects have a weak impact on local richness in grassland plant communities of the Eastern Cape, but phytogeographical effects on local richness are significant.

**Relationship between local and regional richness**

No significant relationship was found between local and regional species richness in the study area in the Eastern Cape. This is contrary to what has been found for a variety of taxa in other parts of the globe, including plants (Pärtel et al. 1996, 2000, Caley & Schluter 1997, Zobel & Liira 1997). The pattern is so widespread that it has been suggested that it is a general law in community ecology (Lawton 1999) and has found its way into ecology textbooks (Ricklefs & Miller 2000, Krebs 2002, Nentwig et al. 2004).

In the study area, the poor relationship between local and regional richness indicates that the regional species pool has little influence on local species richness and composition. The relationship is only shown to be positive if the maximum richness value is used to represent local richness instead of using mean richness. This suggests that, on average, there is little species pool effect, but high richness may be due to some regional effect taking place. Local richness therefore appears to be limited mostly by local interactions, whereas the availability of suitable species within the regional species pool may promote richness only in some sites.

There are a few extreme circumstances in which the patterns observed from this study would be expected to be observed. Firstly, uniform upper limits to local diversity would have to constrain all habitats in a region (Hillebrand 2005). Even extreme competition is thought to be unlikely to produce such a constraint (Hillebrand 2005). Uniform grazing pressure over a wide area may, however, limit local richness to a pool of species capable of surviving these conditions (Landsberg et al. 1999, Diaz et al. 2001, 2007, McIntyre & Lavorel 2001). This may reduce local richness.
even if species are available in the species pool to colonize a particular local habitat. This could potentially lead to a non-linear relationship between $S_L$ and $S_R$.

Defining too small an area for $S_L$ may result in pseudosaturation due to undersampling of rare species and a resultant non-linear pattern (Caley & Shluter 1997, Karlson & Cornell 2002). The plot size used in this study was thought to be adequate to detect rare species, a number of which are found in the dataset. A large difference in the area of the local habitat in proportion to the region may also introduce a non-linear relationship (Hillebrand & Blencker 2002). The smaller the local area is relative to the region, the more it is influenced by local interactions (Hillebrand & Blencker 2002, especially if these are relatively strong. It is quite possible that this was a factor influencing the patterns observed in this study. However, using small sized local areas in relation to the regional area is recommended as a way of eliminating autocorrelation effects (Loreau 2000) and has been used effectively in the past to achieve this very end (Cornell & Karlson 1996; Karlson & Cornell 2002). It may be surmised that there is limited influence of auto-correlation in the current analysis. A further factor that may produce non-linear patterns is if many of the organisms have comparatively high dispersal ability. Many of the species could therefore occur in local plots irrespective of regional richness, which would tend to flatten the slope of the relationship. In the current study, on average more than 60% of the recorded species per plot are classified as widespread.

The feasible explanations for the observed patterns are, therefore, local constraints due to competition or grazing, too small an area of $S_L$ relative to $S_R$, and high dispersal ability of many of the species in the regional pool.

**Relationship between phytochorological diversity and local richness**

The results from this study show that local richness increases with phytochorological diversity within the grasslands of the Eastern Cape. This indicates that local richness is likely to be higher when there is a greater number of species available from diverse phytogeographical origins. The availability of species from diverse phytogeographical origins increases the likelihood of species being available to occupy unused niche space.

Immigration through mass effects, especially at biome boundaries, results in high numbers of species being available in the species pool from different phytochoria. Immigration depends on the dispersal properties of individual species as well as the right set of environmental conditions in order to favour dispersal and promote persistence in new habitats.
Cowling (1983b) argued that, where different phytogeographical regions converge, richness would be highest in those communities that can accommodate species from diverse phytogeographical origins, owing to a mass effect (Shmida & Wilson 1985). This observation is supported in the current study where local richness is highest in those habitats with high numbers of species from different phytogeographical zones.

Cowling (1990) argued that high regional richness of habitat specialists in heterogeneous regions will promote local richness. The results of the current analysis indicate that the geographical range of species has an influence on the relationship between phytochorological diversity and local richness. This provides evidence that the evolution of habitat specialists in the region is more likely to increase local richness than dispersal of widespread species into local habitats.

Conclusions

Regional richness appears to have little effect on local richness in grassland plant communities of the Eastern Cape. The exception is that, at sites where there is high local richness, regional richness may contribute towards promoting local richness. This provides an indication that regional richness promotes local richness in the absence of local limiting factors.

Although phytogeographical diversity promotes local richness, it is primarily through diversity amongst species with narrow distribution ranges. Possible reasons for these observed patterns are that local effects (competition, abiotic environmental factors, and disturbance) limit the diversity of widespread species and regional effects (speciation, climatic history) promote the diversity of species with narrow distribution ranges. Widespread species that are common in other parts of the Grassland Biome compete strongly with one another to occupy common niche space and other species with low dispersal ability have evolved to occupy less common niches or niches that are unique to the study area.

References:


Table 7.1: Estimates of total species richness from temperate grassland communities in the Eastern Cape.

<table>
<thead>
<tr>
<th>Community</th>
<th>Total number of species in combined plots</th>
<th>Estimate of total species richness</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Chao2</td>
<td>Jack1</td>
</tr>
<tr>
<td>Moist mountain grasslands</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Eragrostietosum planae (Amathole south)</td>
<td>158</td>
<td>243</td>
<td>233</td>
</tr>
<tr>
<td>Leyseretosum gnaphalodis (Amathole north)</td>
<td>172</td>
<td>292</td>
<td>246</td>
</tr>
<tr>
<td>Helichrysum rugulosae (Stormberg plateau)</td>
<td>252</td>
<td>357</td>
<td>312</td>
</tr>
<tr>
<td>Helichrysetum aurei (Amathole mistbelt)</td>
<td>210</td>
<td>372</td>
<td>314</td>
</tr>
<tr>
<td>Festucetum caprinae (Storm high altitude)</td>
<td>157</td>
<td>194</td>
<td>182</td>
</tr>
<tr>
<td>Festucetum scabrae (escarpment slope)</td>
<td>153</td>
<td>256</td>
<td>227</td>
</tr>
<tr>
<td>Proteo simplicis (Elliot sub-escarpment)</td>
<td>153</td>
<td>218</td>
<td>208</td>
</tr>
<tr>
<td>Plains grassland</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Eragrostietosum gummifluae (Aliwal North)</td>
<td>117</td>
<td>160</td>
<td>144</td>
</tr>
<tr>
<td>Hermannio depressae (Queenstown)</td>
<td>180</td>
<td>302</td>
<td>258</td>
</tr>
<tr>
<td>Digitarietum argyrograptae (Smaldeel)</td>
<td>63</td>
<td>121</td>
<td>91</td>
</tr>
<tr>
<td>Semi-arid mountain grasslands</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Merxmuelleretum distichiae (Karoo mountains)</td>
<td>231</td>
<td>273</td>
<td>215</td>
</tr>
</tbody>
</table>

Table 7.2: Proportion of species from different phytochorological groups present in plot data from temperate grassland communities in the Eastern Cape. For phytochorological linking species, the KH-AF group is the largest, representing the Highveld region and is shown separately, whereas all other linking species are combined into one column.

<table>
<thead>
<tr>
<th>Community</th>
<th>Widespread and exotic species (%)</th>
<th>Phytochorological group Linking species (%)</th>
<th>One phytochorion All groups (%) (incl. KH-AF)</th>
<th>KH-AF (%)</th>
<th>KH (%)</th>
<th>Eastern Cape endemics (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Moist mountain grasslands</td>
<td></td>
<td></td>
<td>All groups (%) (incl. KH-AF)</td>
<td>9.4</td>
<td>8.8</td>
<td>0.6</td>
</tr>
<tr>
<td>Eragrostietosum planae (Amathole south)</td>
<td>65.6</td>
<td>25.0</td>
<td>9.4</td>
<td>8.8</td>
<td>0.6</td>
<td>0.6</td>
</tr>
<tr>
<td>Leyseretosum gnaphalodis (Amathole north)</td>
<td>70.4</td>
<td>20.1</td>
<td>8.0</td>
<td>8.4</td>
<td>1.0</td>
<td>1.0</td>
</tr>
<tr>
<td>Helichrysetum aurei (Amathole mistbelt)</td>
<td>45.9</td>
<td>37.4</td>
<td>15.6</td>
<td>13.7</td>
<td>0.2</td>
<td>3.0</td>
</tr>
<tr>
<td>Festucetum caprinae (Storm high altitude)</td>
<td>58.3</td>
<td>28.9</td>
<td>14.6</td>
<td>11.0</td>
<td>0.0</td>
<td>1.8</td>
</tr>
<tr>
<td>Festucetum scabrae (escarpment slope)</td>
<td>59.2</td>
<td>21.4</td>
<td>11.2</td>
<td>18.7</td>
<td>0.0</td>
<td>0.7</td>
</tr>
<tr>
<td>Proteo simplicis (Elliot sub-escarpment)</td>
<td>49.6</td>
<td>35.4</td>
<td>20.7</td>
<td>13.7</td>
<td>0.0</td>
<td>1.3</td>
</tr>
<tr>
<td>Plains grassland</td>
<td></td>
<td></td>
<td>All groups (%) (incl. KH-AF)</td>
<td>9.4</td>
<td>8.8</td>
<td>0.6</td>
</tr>
<tr>
<td>Eragrostietosum gummifluae (Aliwal North)</td>
<td>77.8</td>
<td>17.6</td>
<td>4.2</td>
<td>4.6</td>
<td>3.9</td>
<td>0.0</td>
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<tr>
<td>Hermannio depressae (Queenstown)</td>
<td>76.8</td>
<td>17.4</td>
<td>6.0</td>
<td>5.7</td>
<td>3.0</td>
<td>0.2</td>
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<tr>
<td>Digitarietum argyrograptae (Smaldeel)</td>
<td>74.8</td>
<td>20.6</td>
<td>5.3</td>
<td>3.1</td>
<td>0.0</td>
<td>1.5</td>
</tr>
<tr>
<td>Semi-arid mountain grasslands</td>
<td></td>
<td></td>
<td>All groups (%) (incl. KH-AF)</td>
<td>9.4</td>
<td>8.8</td>
<td>0.6</td>
</tr>
<tr>
<td>Merxmuelleretum distichiae (Karoo mountains)</td>
<td>61.9</td>
<td>32.1</td>
<td>8.8</td>
<td>5.6</td>
<td>2.4</td>
<td>0.4</td>
</tr>
</tbody>
</table>
CHAPTER 8: THE EFFECT OF SEASONALITY AND SEASONAL UNCERTAINTY ON SPECIES RICHNESS IN GRASSLAND VEGETATION OF THE EASTERN CAPE

Introduction

There are a number of theories concerning the factors determining species richness in plant communities (see Chesson 2000 for a review). Some researchers have proposed that species richness is determined by local ecological factors, i.e. deterministic explanations, for example Whittaker 1977; Shmida & Wilson 1985; Brown 1988; Diamond 1988, while others have invoked regional historical factors (e.g. Caley & Schluter 1997, Cornell 1993, Cornell & Lawton 1992, Collins et al. 2002, Freestone & Harrison 2006, Hubbell 2001, Ricklefs 1987, 2004, 2007, Ricklefs & Schluter 1993, Stohlgren et al. 2008, Harrison & Cornell 2008, Westoby 1993). Many of the deterministic theories have been influenced by the fact that plant communities contain assemblages of species that all require the same basic resources, namely light, water, carbon dioxide and soil nutrients. It is thought that competition for resources may influence the number of species that can coexist at a local scale and that mechanisms that reduce direct competition are important for promoting coexistence and thus richness (Bengtsson et al. 1994).

The idea that environmental variability promotes long-term coexistence of ecologically similar species through ‘time-sharing’ of niches was first proposed by Hutchinson in 1961 (Ellner 1987). Many models of species co-existence (niche models) assume that the environment is at stable equilibrium, i.e. no environmental fluctuations. Natural systems are, however, variable, and different systems may differ substantially in the amount of spatial and/or temporal variability in the availability of resources. If environmental conditions change regularly then different species are favoured at different times and competitive exclusion is avoided, thus promoting coexistence (Hutchinson 1961, Pake & Venable 1995, 1996). This is a non-equilibrium model of co-existence (Caceres 1997).

Coexistence in fluctuating environments is facilitated by the ‘storage effect’ (Chesson 1982) whereby resources are stored during favourable periods to be used to survive unfavourable periods. Storage may be in the form of a seed bank or long-lived adults which can survive stressful periods through inactivity, i.e. through quiescence in which adults respond directly to adverse conditions. Coexistence is promoted by a trade-off between the capacity to maximise gains during favourable periods and the capacity to minimise losses during unfavourable periods (Ellner 1987). Co-existence is thought to be most favoured at intermediate levels of variability or intermittent stress (Ellner 1987).
For the storage effect to have a positive effect on species coexistence, three conditions need to be met (Adler et al. 2006): species must have long lifespans to buffer their populations during unfavourable periods, species must differ in their response to climate variation and the effect of competition must be more severe on species during favourable periods than during unfavourable periods. If any of these conditions do not hold then climate variability can have neutral or negative effects on coexistence (Adler et al. 2006).

The climate of grasslands in the study area is largely seasonal, although inter- and intra-seasonal variability is typical (Hoare & Frost 2004). The study area occurs at the interface between summer and autumn/spring maximum rainfall. The season may therefore be relatively unpredictable in the study area for any given date from one year to the next. In addition to differences in seasonality, there is a strong rainfall gradient in the study area in an east-west direction. Mean annual rainfall (and productivity) is strongly negatively correlated with rainfall (and production) variability (Hoare & Frost 2004, Figure 8.1). These climatic factors combine to create differences in seasonality as well as climatic uncertainty and provide an opportunity to study the effects of climatic variability on local species richness.

Grasslands in South Africa occur where there is a mean annual rainfall of mostly between 400 and 2000 mm. The vegetation of the Grassland Biome follows a rainfall gradient and can be broadly divided into sweet and sour grasslands (Tainton 1981). Sweet grasslands occur in lower rainfall areas and carbon assimilation tends to be low relative to nutrient supply, whereas the converse is true for sourveld (Ellery et al. 1995). Areas with a mean annual rainfall of above 625 mm tend to be dominated by sour grasses, although the change-over can be anywhere between 500 and 700 mm (Rutherford & Westfall 1986). Different factors may be expected to shape diversity patterns in different ways within these two moisture regimes. This provides an opportunity to compare resource-driven (semi-arid) and competitively constrained (mesic) plant communities and understand the differences between them.

The effect of increased climatic variability may be a change in growth form composition without any change in local richness. Some growth forms, e.g. dwarf shrubs, are thought to be an adaptation to uncertain environments. Increased environmental variability is also thought to lead to an increased tendency for plants to adopt lower risk strategies to survival, including stress resistance (‘S’ strategy of Grime 1977). It would therefore be expected that there may be differential effects of seasonal variability on richness within different major growth forms.

The main objective of this chapter was to examine the way in which seasonality and seasonal uncertainty in grasslands affects plant species richness at a local scale. The specific question addressed in this study is as follows:
1. What is the relationship between local species richness and measures of seasonal variability? Does this relationship differ for high- (sour) and low- rainfall (sweet) grasslands

**Study area**

See Chapter 2 for detailed description of the study area.

**Methods**

**Data collection**

Plot data used in the current analysis were collected for a floristic survey of the south-western extreme of the Grassland Biome (Hoare 1997). Plots were classified into vegetation communities (Hoare & Bredenkamp 1999, 2001). Further fieldwork in the Eastern Cape supplemented this data set. Only the data from those plant communities that are physiognomically recognised as grassland are used here, although other plant communities, e.g. shrubland on rocky outcrops, also occur within the matrix of grasslands in the study area. A total of 275 plots were used in the current analysis. The plot size was 10 × 10 m.

**Diversity indices**

Species richness \((S)\) is defined as the number of species per site.

**Explanatory variables**

Seasonal uncertainty was examined using climate data and time-series satellite data for the study area. In summer rainfall areas vegetation production is usually well-correlated with periods of rainfall. Rainfall therefore provides a good surrogate for variables describing seasonality. A better set of variables for describing seasonal uncertainty can be derived from the Normalized Difference Vegetation Index (NDVI) satellite data, which provides a direct measure of vegetation growth (Tucker & Sellers 1986). It therefore provides an index of the outcome of variation in all environmental variables that affect plant growth. NDVI represents production in plant communities, whereas rainfall is one of the factors that affects production

A list of variables for which values were obtained at each site are given in Table 8.1. Variables describing seasonality and irregularity (sensu Cowling et al. 1997) are used in the analysis done here (Table 8.1).
Table 8.1: Environmental explanatory variables used in multiple regression of richness and seasonality.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Abbreviation</th>
<th>Derivation</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Seasonality variables</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rainfall concentration (%)</td>
<td>RCONC</td>
<td>Monthly rainfall as proportion of annual rainfall combined by using evenness measure: ( \Sigma p_i \ln p_i ), where ( p_i ) is proportion of annual value</td>
</tr>
<tr>
<td>Duration of growing season (days)</td>
<td>DUR</td>
<td>Number of days when NDVI exceeds median annual NDVI less 1 SD. This is a calculation that detects any period when NDVI exceeds minimum levels.</td>
</tr>
<tr>
<td>NDVI seasonality (%)</td>
<td>NSEAS</td>
<td>Intra-annual coefficient of variation in NDVI</td>
</tr>
<tr>
<td><strong>Variability variables</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>NDVI variability (%)</td>
<td>NCOV</td>
<td>Inter-annual co-efficient of variation in NDVI</td>
</tr>
<tr>
<td>Rainfall reliability (%)</td>
<td>RCOV</td>
<td>Coefficient of variation in annual rainfall for wettest consecutive 3 months.</td>
</tr>
</tbody>
</table>

Data for NDVI-derived explanatory variables was obtained from processed multidate satellite imagery to derive seasonal characteristics of vegetation growth (Hoare & Frost 2003). NDVI data were obtained from the National Oceanic and Atmospheric Administration's (NOAA) Advanced Very High Resolution Radiometer (AVHRR) using the standard NDVI ratio of bands (Hoare & Frost 2003). Justice et al. (1985) demonstrated that the AVHRR data were a valuable tool for monitoring seasonal dynamics of vegetation primarily due to the relationship of the NDVI to several important vegetation properties, for example primary production (Tucker & Sellers 1986).

Rainfall data were obtained from climate models for South Africa (Dent et al. 1989), which provide an extrapolation of climate data from rainfall station sites to all areas in between using surface response models. Extrapolated climate data can therefore be obtained for any point in the study area and was extracted for each sample plot locality.

Data analysis

**Relationship between richness and seasonal variability**

For analyzing the contributions by seasonal uncertainty factors on diversity, multiple regression was performed using variables in Table 8.1 as independent variables against each of the diversity variables. Variables were transformed, depending on the type of data. This is due to the fact that there is an assumption of multiple regression models that data have a normal distribution. There are three types of data, continuous, percentage and counts. Percentages or proportions form a binomial rather than normal distribution. The square root of each percentage value was transformed to its arcsine (\( p' = \arcsin \sqrt{p + 0.5} \)). This provides data with an almost normal distribution (Zar 1999). Count data, e.g. number of days (DUR), was square-root transformed. This transformation is applicable when group variances are proportional to the means, which usually occurs when samples are taken from a Poisson distribution, i.e. when the data consists of counts of objects (Zar 1999).
Minimum sets of explanatory variables were selected manually by a process of backward elimination. The multiple regression was performed with all the variables given in Table 8.1. The variable with the highest p-value was then removed. The process was repeated iteratively removing one variable at a time (the least significant variable each time) until all variables remaining had a p-value below the threshold of 0.05 and were independent of one another. Analyses were performed separately on total species richness and on richness within different growth forms.

In order to assess the effect of amount of rainfall on the relationship between richness and seasonal variability, the analyses were performed separately for semi-arid grasslands and mesic grasslands.

**Results**

Richness data from different plant communities and data for explanatory variables (after transformation) all passed a normality test (Kolmogorov-Smirnoff test, $p>0.10$). The assumption that the data was sampled from populations with equal standard deviations was therefore not violated (Bartlett test).

**Relationship between overall richness and seasonal variability**

Multiple regression analysis indicated that seasonal uncertainty and seasonality variables explain a significant but small amount of the variation in richness in both mesic and semi-arid grasslands (Tables 8.2). The significance of this relationship is greater in mesic than semi-arid grasslands.

**Table 8.2: Results of multiple regression of species richness versus environmental variables representing seasonal variability. ALL = richness of all species together.**

<table>
<thead>
<tr>
<th>Diversity variable</th>
<th>$p$</th>
<th>Sum of squares</th>
<th>SD of residuals</th>
<th>$R^2$</th>
<th>Adjusted $R^2$</th>
<th>$F$</th>
<th>Model (based on minimum set of explanatory variables)</th>
</tr>
</thead>
<tbody>
<tr>
<td>ALL (mesic)</td>
<td>0.0004</td>
<td>13021.0</td>
<td>9.348</td>
<td>0.1149</td>
<td>0.0971</td>
<td>6.4498</td>
<td>[ALL] = $-105.63 + 0.66 \times [RCONC] + 14.20 \times [NSEAS] + 0.76 \times [RCOV]$</td>
</tr>
<tr>
<td>ALL (semi-arid)</td>
<td>0.0030</td>
<td>8582.7</td>
<td>8.602</td>
<td>0.0954</td>
<td>0.0798</td>
<td>6.1180</td>
<td>[ALL] = $137.01 - 9.94 \times [NSEAS] - 1.65 \times [RCOV]$</td>
</tr>
</tbody>
</table>

In mesic grasslands, the variables that contribute significantly towards explaining richness are NSEAS, RCOV and RCONC (Table 8.2). The relationship is positive for all three variables, indicating that an increase in uncertainty in environmental parameters that affect plant growth and an increase in seasonality leads to a slight increase in local species richness in mesic
grasslands. The model explains just under 12% of the variation in species richness in mesic grasslands. The correlation coefficients for the relationship between richness and the explanatory variables are below 0.10, except for RCONC, which is 0.25.

For semi-arid grasslands, the variables that contribute significantly towards explaining richness are NSEAS and RCOV (Table 8.2). The relationship is negative, indicating that increased uncertainty has a negative effect on local richness in semi-arid grasslands. This result, in combination with that for mesic grasslands (previous paragraph) implies a non-linear relationship across the whole study domain. The model explains just under 10% of the variation in species richness in semi-arid grasslands. The correlation coefficients for the relationship between richness and the explanatory variables are below 0.10.

Discussion

Effect of seasonality and seasonal uncertainty on richness

This study identified a relatively weak relationship between seasonal uncertainty and seasonality variables and local species richness in grassland communities of the Eastern Cape. The relationship between seasonal uncertainty and seasonality and species richness was stronger within mesic than semi-arid grasslands. In mesic grasslands the relationship was positive, indicating that increased seasonality and seasonal uncertainty promotes richness, whereas the opposite is the case for semi-arid grasslands. The ecology of mesic grasslands tends to be more competitively constrained than the ecology of dryer grasslands. It would therefore be expected that increased competition in mesic grasslands would lead to increased niche differentiation. The evidence from this study does not, however, support this hypothesis, as is explained as follows:

1. In the study area, increased seasonality is due to an increase in the proportion of summer rainfall. The Grassland Biome is strongly seasonal with most rainfall falling during the summer months (Rutherford & Westfall 1986), whereas the study area falls within a climatic transition zone between strong summer rainfall and autumn / spring maximum rainfall. It would be expected that increased seasonality would therefore favour the occurrence of increased numbers of summer rainfall species originating from the core of the Grassland Biome, but on the other hand, less concentrated rainfall may permit the coexistence of species from different phytochoria which would enhance richness (see Chapter 7)

2. Another variable that explains a significant amount of variation in species richness in mesic grasslands is RCOV (co-efficient of variation in rainfall). A strong relationship between richness and this variable would lead to the conclusion that ‘time-sharing’ of niches was taking place. It
was expected that seasonal uncertainty would lead to some promotion of niche differentiation (Hutchinson 1961, Ellner 1987), which would favour co-existence and thus increase local species richness. However, although significant, the relationship between richness in mesic grasslands and the variable RCOV is relatively weak.

The relationship between RCOV and species richness is negative in semi-arid grasslands. An increase in RCOV is coupled with a decrease in the amount of rainfall (Figure 8.1). The lower species richness associated with increased RCOV is interpreted as a general change in growth-form composition with increased aridity. Dryer grasslands have less forb and geophyte species per plot, but more dwarf shrubs and trees and shrubs. This may be due to an increase in the number of species that are so-called ‘S’ strategists (Grime 1977), that have higher stress resistance, in which there is higher adult survivorship and lower reproductive effort. Dwarf shrubs typically represent such a strategy, being relatively long-lived and resistant to periods of harshly unfavourable conditions (Pake & Venable 1995). The ecology of dryer grasslands tends to be more resource-driven than in mesic grasslands. The harsher climatic conditions thus cause increased growth form turnover along an aridity gradient rather than increased niche differentiation within existing growth forms.

In conclusion, the relationship between seasonal uncertainty and seasonality variables and species richness in grassland communities of the Eastern Cape was found to be quite weak, which indicates that promotion of niche differentiation due to seasonal uncertainty does not occur to a great extent in the study area. Variables representing uncertainty have generally low explanatory power in the study area.

References:


Figure 8.1: Relationship between median annual rainfall and the coefficient of variation in rainfall for plots in grassland communities of the Eastern Cape. Data from climate surfaces (Dent et al. 1989).
CHAPTER 9: GENERAL DISCUSSION

This study set out to develop a predictive understanding of the patterns and determinants of plant biodiversity in temperate, mesic grasslands of South Africa with a primary focus on the geographical area of the Eastern Cape. The principal conclusions about patterns and determinants of grassland diversity are of great significance in understanding ecosystems of a sector of South African’s rich biodiversity.

Initially, diversity patterns were described in different plant communities of the study area. Measures of richness, evenness and heterogeneity were found to vary significantly from one plant community to another, with variation falling within the range of richness values found in other parts of the Grassland Biome (Chapter 4).

Despite the fact that grasslands are dominated by grass species, forbs contribute the highest number of species to overall richness, followed by grasses. Geophytes, dwarf shrubs and woody plants (trees and shrubs) contributed small numbers of species to overall richness per site. There were differences in proportions of different life-forms from one community to another and between mesic and semi-arid grasslands. This raised the question as to why there is variation in richness amongst different life forms, and what factors contributed to the changing richness patterns between life forms. The plant functional type investigations (Chapter 6) attempted to address these questions. The major conclusions from this investigation are given below.

There are a number of deterministic theories of species diversity that invoke environmental factors as explanations of local species richness (Hutchinson 1959, Pianka 1966, Wright 1983). To address this body of theory, it was necessary to ascertain whether environmental factors were important determinants of diversity (Chapter 4). Environmental variables explain richness to varying degrees in different plant communities, but multiple regression models indicate that environmental variables do not explain richness in mesic grasslands. Environmental variables that are significant in terms of explaining richness explained less than 11% of the variation in richness in the whole dataset (mesic and semi-arid grasslands together). Rainfall contributes most towards explaining richness in the entire dataset and richness within semi-arid grasslands. Surface rockiness also significantly explained richness patterns in the entire dataset and within semi-arid grasslands.

To determine whether environmental factors act uniformly on all species, the relationship between environmental factors and richness within life forms was investigated in Chapter 4. Environmental variables explained variation in richness patterns differently within different life-forms. A positive
relationship was found between tree and shrub species richness and surface rock cover and rainfall. The interpretation of this is that areas of high rock cover are moderately protected from fire, thus providing a protected habitat in which woody plants can survive—rocky areas are therefore more likely to have woody species than other areas. Woody trees and shrubs have been found to increase in richness with increasing rainfall (O’Brien 1993, Currie 1991) as predicted in the Productivity Hypothesis (Wright 1983).

Environmental variables were more useful for explaining variation in richness amongst grasses and forbs in semi-arid grasslands than mesic grasslands. Increased productivity (for which rainfall is a surrogate) promotes forb and grass richness up to a critical rainfall level, after which other (non-environmental) factors become important. Forbs were found to have a stronger relationship than grasses between richness and environmental variables linked to habitat heterogeneity (which promotes niche differentiation).

One of the stated objectives of this thesis was to study the relationship between diversity and productivity within grassland vegetation in the Eastern Cape. The analysis of the relationship between richness and measures of productivity (primarily rainfall) indicated that there was a positive relationship overall, but that above a critical rainfall level some other factor becomes more important. The influence of rainfall is therefore critical in understanding diversity relationships in grasslands, although it may not provide high predictive power for predicting local richness.

At this stage of the study, it was apparent that environmental variables were only of moderate importance in understanding variation in local richness patterns. Species evenness patterns provided an indication that species interactions or niche differentiation were potentially important for shaping richness patterns. Further steps in this study were therefore aimed at understanding niche differentiation patterns and the effect of this on species richness (Chapter 6). In light of the recent importance attributed to regional effects on local richness, it was also important to investigate this aspect in more detail, which was done in Chapter 7.

A detailed study was undertaken to classify plant species into plant functional types (Chapter 5). For the current study, it was important to develop an understanding of why some life-forms appear to have high numbers of co-existing species. The plant functional type classification was used to determine whether niche differentiation was an important factor shaping grassland plant communities of the study area (Chapter 6). The analysis revealed that semi-arid grasslands were less structured by niche-differentiation than mesic grasslands. It also showed that the number of functionally equivalent species increases with increasing rainfall. The functional type analysis in combination with the previous analyses of environmental relationships reinforced the
understanding that environmental factors are more likely to shape richness patterns within semi-arid grasslands and species interactions more likely to shape richness patterns within mesic grasslands.

An analysis of species pool effects indicated that regional richness has little effect on local richness in grassland plant communities of the Eastern Cape (Chapter 7). However, sites with very high local richness appear to be positively influenced by a high regional species pool. This suggests that either environmental factors or species interactions may limit local richness for the most part, but that a high regional species pool can promote local richness if these limiting factors can be overcome.

The final analysis undertaken was to analyse the degree to which seasonal variability and uncertainty promotes local richness (Chapter 8). The premise was that temporal variability in the supply of resources may promote richness through ‘time-sharing’ of niches or that, in the presence of regular environmental variability, different species are favoured at different times and competitive exclusion is avoided, thus promoting coexistence (Hutchinson 1961, Pake & Venable 1995, 1996). The relationship between seasonal uncertainty and seasonality and species richness in grassland communities of the Eastern Cape was found to be quite weak, which indicates that promotion of niche overlap due to seasonal uncertainty does not occur to a great extent in the study area.

A general framework was sought that could be used to interpret the patterns observed from this study. Ecological theory provides two opposite interpretations for mechanisms that promote and maintain diversity, neutral-based and niche-based concepts. This is a modern dichotomy with many parallels to the historical individualistic-organisinal conflict. Although the latter was eventually settled largely towards the individualistic view (Whittaker 1953), there are many species interactions that indicate that communities are not entirely individualistic. Many studies have shown that both the positive interactions of facilitation (Bertness & Callaway 1994, Callaway 1995, Hunter & Aarssen 1988, Bruno et al. 2003) and the negative interactions of competition (Callaway & Aschehoug 2000, Levine 1999, Li & Wilson 1998, Miller 1994, Wilson & Keddy 1986) are important in structuring plant communities, especially when multiple trophic levels are considered. Species within natural plant communities can therefore function either individually or interdependently depending on synergism among: (i) stochastic processes, (ii) the abiotic tolerances of species, (iii) positive and negative interactions among plants, and (iv) indirect interactions within and between trophic levels (Lortie et al. 2004). These factors have been used to explain the limits to the geographic ranges of species and propose generalised filters for the distribution of species (Krebs 2001, Grime 1998, Laakso, et al. 2001) (Figure 9.1).
Random processes, such as dispersal (the first process depicted in Figure 9.1) can initially determine who arrives at a particular point in space (Hubbell 2001). The second level (environment) can change over time or from season to season. This level also includes disturbance factors (herbivory, fire, etc.). Factors operating at this level could, therefore, modify the species establishment history of a site (Dornelas et al. 2006). Relatively non-random processes, such as species interactions (positive and negative) determines which species persist at a site (Lortie et al. 2004) (the third process depicted in Figure 9.1). Community structure is therefore a function of several additive processes.

From the analyses undertaken in this thesis, it is probable that, in the study area, second level processes (environmental limiting factors) are more important in semi-arid grasslands and third level processes (species interactions) are more important in mesic grasslands for structuring plant communities. Although first level processes did not appear, from the analysis, to be important in structuring local communities, they are probably weak compared to processes at the other two levels, but do nevertheless play an important role. The analysis undertaken in this study shows that species pool effects are significant when factors operating at the other two levels are

![Figure 9.1: Geographical filters limiting species occurrence.](image-url)
There were some factors that, according to theory, are known to affect local diversity, but which were not adequately addressed in this study. The relationship between species richness and disturbance factors was not adequately addressed in this study. There was insufficient data to describe disturbance regimes (grazing and fire) in the study area to specifically test the effects of these factors. Anecdotal evidence suggests that both of these may have an influence on local richness in the study area (Hoare 2002, 2003).

The relationship between productivity and species richness was also not adequately addressed. It would have been useful to have more detailed information on soil nutrient properties, soil texture, soil depth and hydrological status for each site in order to test this theory more comprehensively. The reliance on broad rainfall values, as obtained from surface response models, was not adequate to understand local effects of these factors. It is, however, time-consuming and expensive to collect this additional information. It would only be possible to collect this information for a carefully selected number of sites.

Habitat heterogeneity at a plot scale was not collected during the field survey of vegetation. The percentage cover of surface rock was used as a surrogate for habitat heterogeneity, but does not provide direct information on plot-scale heterogeneity. The factors that define plot-scale habitat heterogeneity need to be carefully defined and appropriate data collected during field studies. Appropriate information may include some measure of soil depth variation, soil texture variation and/or variation in rockiness within each 10 × 10 m plot that can be summarised into an appropriate index to represent habitat variation per plot that can be compared to species richness.

This study did provide information that could be fruitfully expanded in future studies. For example, the classification of plant species into plant functional types provides opportunities to understand diversity and ecosystem function in the study area in more detail. A potentially productive analysis could be to model the number of species per plant functional type in terms of environmental variables. This may provide a more in-depth insight into the environmental factors that promote richness within particular functional syndromes.

References:


