# The Phytogeography of Southern Mistbelt Forests of the Eastern Cape, South Africa

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# Dedication

This thesis is dedicated to my mother, Nobuhle Abegail, a God fearing woman. Thank you for all your support, prayers, and unconditional love.

“Ngokuba akukho nanye into eya kumnqabela yena uThixa”

Luke 1:37

“Qengela kuYehova izenzo zakho, Zizimaseke iingcinga zakho”

Proverbs (Imizekeliso) 16:3

# Abstract

In the Eastern Cape, a moisture gradient (from west to east) exists along the Escarpment where patches of Southern Mistbelt Forests (SMF) occur. There is a notable profusion of plants in these forests, but the factors that drive plant species composition and abundance in these patches is poorly understood and such knowledge is critical if we are to address or mitigate the problems imposed by global change. Many of our ideas on plant community assembly are based on the premise that species differ in their environmental requirements for successful regeneration, especially when young.

The aims of this study were to document the floristic diversity of poorly known patches of Southern Mistbelt Forests in the Eastern Cape and identify the environmental factors that influence plant community composition in these forest patches.

Twenty six forest patches across the Eastern Cape were sampled. In each forest 400$m^2$ circular plots were constructed. The diameter at breast height and stem counts for the tree species was taken and the % cover of the herbaceous species was recorded. General collections were also made to supplement the plot data in order to obtain a comprehensive flora for each forest patch. All sampling was done during the summer season of 2013 and 2014.

Using plot data, Hierarchal Cluster Analysis and Multidimensional Scaling Analysis were done to compare similarities between patches. Plots from the same forest patch clustered which indicated that the species composition in each forest patch was unique. However, this pattern went down when only tree species were considered. Plant diversity also varied between patches; with those located in the east being generally more diverse than those in the west are.

Clustering patterns in fragmented communities and differences in species diversity indicate evidence of species “nestedness”. Analysis of nestedness indicated that these forest patches were significantly nested.

To identify which environmental variables might be correlated with both species diversity and nestedness, twelve environmental variables was selected for analysis using Canonical Correspondence Analysis and Principal Component Analysis. Results show that Mean Annual Precipitation, Mean Annual Potential Evapotranspiration, and percentage of Organic Matter of the soil were most strongly correlated with the patterns of diversity observed in these forest patches. Regression analysis indicated that Mean Annual Precipitation accounted for most of the variation in species diversity, especially for the herbaceous species. The herbaceous species thus show a greater sensitivity to “climate filtering” as a consequence of rainfall gradients.

With the implementation of suitable monitoring programs, changes in abundance or even local extinction of these species can act as an early warning indicator of the possible long-term effects of climate change on forest communities.

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# Chapter 1: Introduction to forest biodiversity in South Africa

Forests cover approximately 30-40% of the Earth's land surface (Waring and Running 2007), of which 17% is found in Africa (FAO 2011). Nemani and Running (1995) estimated that global forest distribution was 49% tropical, 29% temperate and 22% boreal. These forests and woodlands can be classified into nine general groups including tropical rain forests, tropical moist forest, tropical dry forests, tropical shrubs, tropical mountain forests, subtropical humid forests, subtropical mountain forests, and plantations (Sebukeera *et al.* 2006). Ecological studies indicate that forests are major contributors to a range of biosphere processes (Vitousek 1994). Forests are home to a profusion of plant and animal communities and local communities depend heavily on forests and their products; they provide shelter, food, protection, and are a source of income (Pearce and Pearce 2001). Many of these forests are highly fragmented due to clearance for agricultural land, urban areas, and over exploitation (Meyer and Turner 1994; Sebukeera *et al.* 2006). Future distribution of forests will be controlled by changes in climate, forest response to elevated $CO^2$, and land cover changes caused by human activities (Waring and Running 2007).

Historically, forests have been one of the most poorly understood biotas of our planet. However, over the past twenty years, there has been an increasing research interest in them. Pioneering ecologists had very few datasets, and their work was individually designed (Nadkarni *et al.* 2004). Research has since changed from descriptive and process oriented to predictive in nature (Nadkarni *et al.* 2004).

The driving forces behind both animal and plant diversity of forests are still not yet understood partly due to the structural and microclimate complexities that can exist in a forest (Nadkarni *et al.* 2004). However, many assemblage theories in fragmented communities have been proposed including niche theory, species co-existence and habitat specialization models, filtering theory, and nestedness to mention a few.

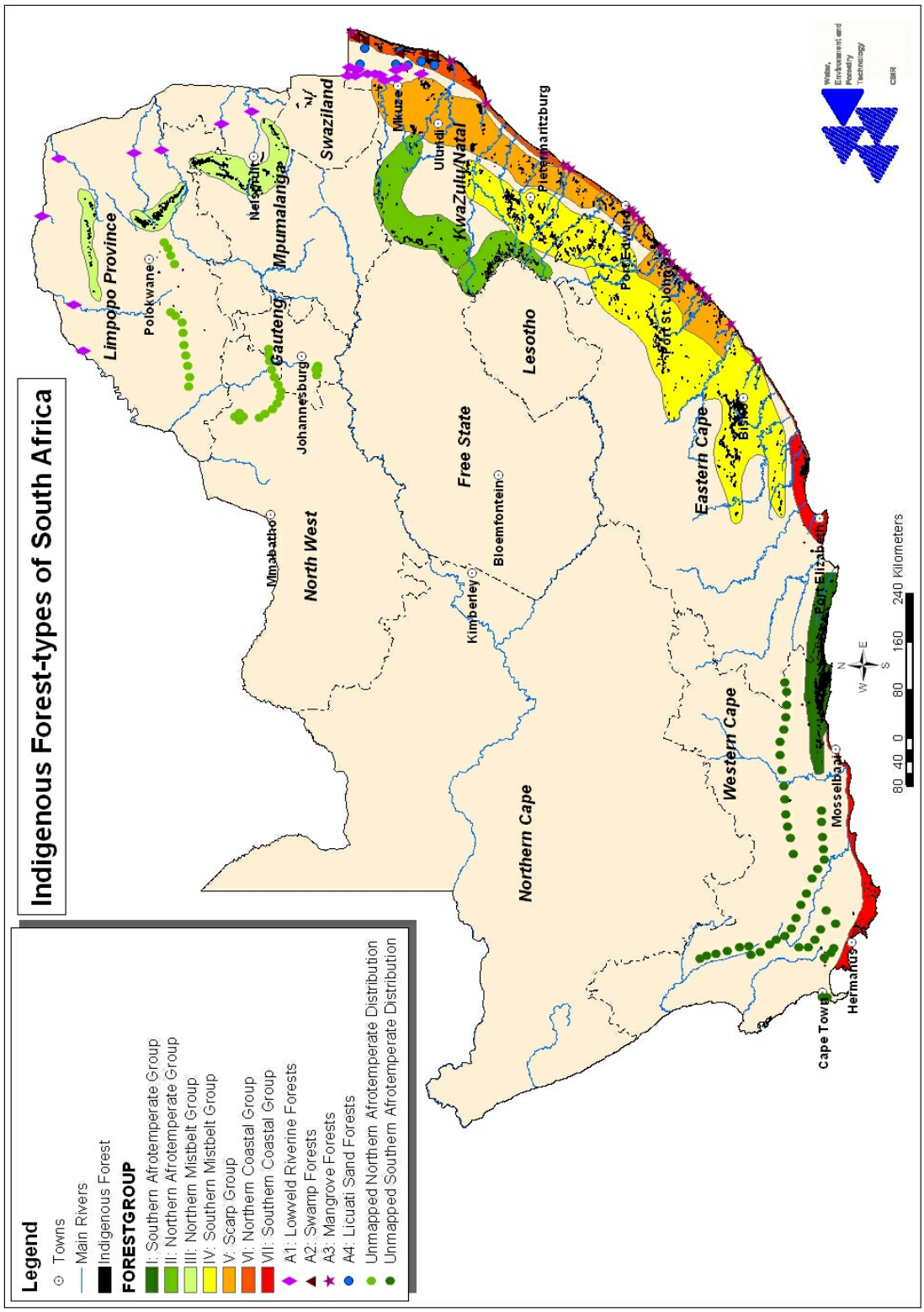


**Figure 1: Forest groups in South Africa (Sourced from Mucina and Geldenhuys (2006))**

## 1.1. Forests in South Africa

In South Africa indigenous forests are defined as "a general multi-layered vegetation unit dominated by trees (largely evergreen or semi-deciduous, whose combined strata have overlapping crowns, i.e. the crown cover is 75% or more), and where graminoids in the herbaceous stratum (if present) are generally rare" (Shackleton *et al.* 1999). This definition is the same as the one used by von Maltitz *et al.* (2003) who also added that "fire does not normally play a major role in forest function and dynamics except at the fringes". All indigenous forests are classified as evergreen and the forests differ in the surrounding ecotone (e.g. fynbos, grassland, thicket etc.). The stand height can range from 3 metres (m) in scrub forests and up to 30m in high forests (Mucina and Geldenhuys 2006). South African forests are relatively rare and represent the smallest biome (Kruger *et al.* 1997). Indigenous forests cover only 0.56% of the total land cover in South Africa (Lawes *et al.* 2004a). However, forests are considered the second richest biome containing 7.1% of indigenous vascular plant species (Geldenhuys 1992).

The forest biome extends along the southern and eastern seaboards, and occurs on the south- and southeast-facing slopes in the midlands of the Eastern Cape and KwaZulu-Natal provinces and along the Drakensberg escarpment as far north as Limpopo province (Figure 1; Lawes *et al.* 2004a). These forests are highly fragmented, ranging in area from less than 1 hectare (ha) to 25,706 ha (the Knysna-Tsitsikamma Forest in the southern Western Cape province) (Geldenhuys 1991). In the Eastern Cape the Pirie Forest block, which is located on the Amathole Escarpment, is 3173 ha in area (Lawes *et al*. 2004) and is the second-largest forest block in South Africa (Geldenhuys 1991).

Indigenous forests are usually limited to areas of high water availability (Mucina and Geldenhuys 2006). Precipitation (in the form of rainfall and mist), evapotranspiration, availability of groundwater, soil structure, and seasonality of precipitation are major factors influencing the availability of water to forest vegetation (Mucina and Geldenhuys 2006). The present-day distribution patterns of forest-dwelling plants and animal species in southern Africa are assumed to have been influenced by climatic changes that occurred during the Quaternary (Lawes *et al.* 2007, 2004a).

Five million hectares of the forests are state owned and protected (DAFF 2011) with a few privately owned or on communal land (Geldenhuys 1991). Conserved forests in South Africa are privately owned, in conservancies and natural heritage sites, and forests patches in nature reserves and wilderness areas proclaimed under the Forest Act (Geldenhuys and MacDevette 1989).

Some forest patches occur in areas of high population density. These areas may range from rural communities to more affluent societies (Geldenhuys 1999), where forests are used for different

purposes. Forests are a safety net in rural communities providing medicine, food, fuel wood and building material (Lawes *et al.* 2004b; Mulenga *et al.* 2011; Ros-tonen and Wiersum 2003); whereas in some affluent areas forests contribute towards, recreation, ecotourism, high-quality furniture and biodiversity conservation.

Pressures on forests including high intensity farming, growing human needs, economic pressures, mining of forested dunes along the coast, harvesting for wood for crafts, furniture and the development of infrastructure (Mucina and Geldenhuys 2006; DWAF 1997). Unfortunately, there is insufficient information to determine the assessment of deforestation (DWAF 1997).

### *1.1.1. Classifications of South African forests*

Numerous classifications of South African indigenous forests have been developed by previous authors (e.g. Sim 1907; Laughton 1937; Story 1952; Acocks 1953; Edward 1967; Van der Schijf and Schoonraad 1971; Scheeper 1978; Von Breitenbach and Von Breitenbach 1983; White 1983; Cawe 1986; Cooper and Swart 1992; Everard and Hardy 1993; Cawe 1996; von Maltitz *et al.* 2003; Mucina and Geldenhuys 2006), but no one classification has been adopted nationally (Lawes *et al.* 2004; von Maltitz *et al.* 2006). The classification of indigenous forests in South Africa is highly subjective because methods of data collection, level of sampling intensity, and data reliability varies substantially among forests sampled and the objectives addressed. Some previous classifications were based on timber quality (e.g. Laughton 1937), whereas the focus for other classifications was typically too narrow for their wider application in the Southern African context (e.g. Edwards 1967; White 1983; Cooper and Swart 1992).

By using Cluster Analysis and Non-metric Multidimensional Scaling (NMDS), Lötter *et al.* (2014) proposed 14 forest subtypes for the poorly known Mpumalanga Province, namely: Mariepskop Mistbelt, Blyde Canyon Dry Afromontane, Long Tom Mistbelt, Foothills Mistbelt, Barberton Mistbelt, Eastern dry Afrotemperate, Northern Highveld Kloof, Lydenburg Kloof, Wakkerstroom Midlands, Mapulaneng Scarp, Blyde Scarp, Barberton Scarp, Legogote Scarp, and Escarpment Riverine (Lötter *et al.* 2014). These forest subtypes belong to the Mpumalanga Mistbelt subgroup. Both the Mpumalanga and Limpopo Mistbelt Forest subgroups are classified under the Northern Mistbelt Forest Group (Mucina and Rutherford 2006). This work addresses the importance of forest classifications at a provincial level, which gives a detailed contribution of the different forest subtypes in the national forest classification system.

The indigenous forests of the Eastern Cape, especially the area formerly known as the Transkei, have been subject to several classifications. Sim (1907) provided the earliest account of these forests, but

Acocks' (1953) 'Veld Type' classification is the most well-known among scholars. Acocks (1953) classified these indigenous forests into two types, tropical forests and temperate forests. Tropical forests were classified into five groups: Typical Coast-Belt, Dune Forest, Pondoland Coastal Plateau, Ngongoni Veld, and Eastern Province Thornveld. The Temperate forest types were classified into two groups: Dohne Sourveld and Highland Sourveld. Acocks' (1953) classification, although well known, has often been criticised. For example, Cowling (1984) pointed out that "Acocks criteria for distinguishing veld types are never fully defined and often incorporate vague and untestable statements on history, utilization and dynamics. He completed his major work at a time when the assumptions of Clementsian dynamics were largely accepted. This allowed for the groupings of structurally and floristically unrelated types into a single veld type, based on assumed successional relationships."

Other notable classifications include that of Von Breitenbach and Von Breitenbach (1983) who acknowledged the contrast between Subtropical and Afrotemperate forests but, unlike Acocks (1953), their forest types occupied geographically distinct areas. Cawe (1986) recognised four additional types of Afrotemperate forests but these were not spatially differentiated into discrete geographical units. Cooper and Swart (1992) classified forest groups based on woody plants in various forest types adopted from Acocks' (1953) classification with some modifications and recognised two Subtropical and three Afrotemperate forest types.

With an interest in newer methods of classification, Cawe (1996) attempted to classify the indigenous forests of the Transkei. Using floristic data (for woody plants) collected from 86 forests in both the Afrotemperate and subtropical regions of Transkei by Cooper and Swart (1992), Cawe (1996) classified two forest types (Subtropical and Afrotemperate) with four units in each. The Subtropical Forest Types consisted of Moist Subtropical Forest, Medium Moist Subtropical Forest, Dry Subtropical Forest, and Subtropical Dune Forest. The four units of the Afrotemperate Forest Types were Mistbelt Afrotemperate Forest, Moist Afrotemperate Forest, Middle Altitude Afrotemperate Forest, and High Altitude Afrotemperate Forest.

A recent floristic–biogeographic classification of indigenous forests of South Africa by von Maltitz *et al.* (2003) recognised 26 forest types grouped into eight zonal groups and one azonal group. The nine Forest Groups (as well as underlying forest types) were derived on the basis of quadrat data, whereby the floristic composition, biogeographic relationship as well as climate, substrate, and water dynamics were taken into consideration. Mucina and Geldenhuys (2002) give details on the procedures that led to the classification of indigenous forests into forest types. The following Forest Groups were included in the classification: Southern Afrotemperate, Northern Afrotemperate, Southern Mistbelt, Northern Mistbelt, Scarp, Northern Coastal, Southern Coastal, Tropical Dry

Forest, Lowveld Riverine Forest, Swamp Forest, and Mangrove Forest (von Maltitz *et al.* 2003). Five of these Forest Groups occur in the Eastern Cape with the Southern Mistbelt Forest Group forming most of the inland forest patches.

The most recent classification of indigenous forests of South Africa is that of Mucina and Rutherford (2006), and is based on work done by Mucina and Geldenhuys (2006) and von Maltitz et al. (2003). In this classification the Vegetation Units of Mucina and Geldenhuys (2006) generally correspond with the Forest Groups of von Maltitz *et al.* (2003) but differ from the latter in that the Tropical Dry Forest Group is divided into the Sand Forest and Ironwood Dry Forest vegetation units. The treatment is unique in that it emphasises evolutionary and historical explanations of the current biogeographical patterns (Chrtek and Pergi 2008).

Most classification schemes applied to South African forests recognise White's (1983) broad spectrum classification of forests into two phytochoria, namely the Afromontane archipelago-like centres of endemism (now termed Afrotemperate forests) and the Tongaland–Pondoland regional mosaic (referred to as the Indian Ocean Coastal Belt Forests) as the biogeographic basis of forest classification in South Africa (Lawes *et al.* 2004a). The Afrotemperate forests were thought to be the oldest and most persistent of the two, being present in the region before the Last Glacial Maximum (c. 18 000 BP), whereas the Indian Ocean Coastal Belt Forest is believed to have extended southwards less than 8000 years ago (Lawes *et al.* 2004a). The Afrotemperate forests have been impacted the most by paleoclimatic events; because they pre-date the Last Glacial Maximum, they experienced more than one extinction filtering event (Lawes *et al.* 2004a). These have acted as significant distribution and extirpation filters of fauna and flora in the region. According to Lawes (1990) and Eeley *et al.* (1999) there is no evidence suggesting that the forests were any larger or more extensive in the last 20 000 years, apart from recent reductions caused by anthropogenic activities. It is likely that forest groups and types belonging to the Afrotemperate phytochorion are 'naturally' small in area. Lawes *et al.* (2000) suggested that past events influenced the ecology in these forest patches so that the communities they contained were likely resilient to many disturbances.

### *1.1.2. Economic Value of southern African forests*

Traditionally, many economic planners have valued forests in terms of their contribution to commercial timber supply (Emerton 2001) but this has changed over the years. Prior to the 1940s forests had been over exploited through various activities such as logging ventures. King (1941) reported that 52% of the forests in the Transkei had been over exploited for timber. Forests play a vital role in people's livelihood and contribute largely to the South African Gross Domestic Product

(GDP) (Kwakwa 2014). Humans are dependent on forests for a variety of products, services, and benefits. They have been sourced for food, wood, construction material, fuel and energy, and non-timber forest products (NTFPs) (Kwakwa 2014). These NTFPs include a variety of biological groups (herbaceous plants, insects, birds, mammals, etc.) as well as thousands of species all with different and specialised biological and ecological characteristics (Shackleton and Gumbo 2010), many of which are collected and purchased for their spiritual and cultural significance and value (Cocks 2006).

Southern African forests provide more than 35% of the rural household income (Lawes *et al*. 2004b), and natural resources necessary for their survival (Cocks *et al.* 2011; Cocks and Wiersum 2003). For example, almost three-quarters of the households in rural villages in the Eastern Cape utilized forest plant species for cultural rituals representing 58% of the total non-cash value of NTFPs use (Shackleton and Pandey 2014). However, the forest biome holds the highest proportion of restricted species in South Africa of which several are endangered (Castley and Kerley 1996). Some species such as *Ocotea bullata* and *Warburgia salutaris* have come close to the brink of extinction as a consequence of overharvesting and habitat destruction (Lawes *et al.* 2004b).

### *1.1.3. Species diversity and composition*

Two structural characteristics have been commonly used to characterize forest stands, namely course-grained and fine-grained forests, reflecting the different environmental and structural components responsible for their formation. Course-grained forests are those that show spatial heterogeneity in species composition due to large-scale gap dynamics (Von Maltitz 2004). In a coarse grained forest the size class distribution of various species would differ according to their position in the hierarchy of competition for light (degree of shade tolerance) (Everard *et al.* 1995). In a fine-grained forest, the species occupying the canopy are also present in the sub-canopy, would be relatively shade tolerant, and the tree stand would be dominated by small trees and few large trees (Everard *et al.* 1995).

Disturbance and recovery are integral ecological processes in the dynamics and level of biodiversity of all forests (Geldenhuys 2002). Forest communities experience many disturbances, varying in extremity that causes clearings (gaps) of various sizes on the forest floor. These disturbances are as a result of tree falling, fire or an extreme climatic event. In most forests, trees die 'on their feet' and new trees grow in their place without formation of an obvious gap in the canopy (Grubb 1977). These disturbances are considered to be important factors that structure communities; depending on the intensity, there could be an increase in species richness in old-growth forest communities (Connell 1978; Sheil 1999).

Differences in species composition, diversity and structure in South African forests are poorly understood but are more apparent at a local scale. Similarly, the origin of these differences is unclear: edaphic qualities of the landscape, past and present land use, anthropogenic disturbances, and paleoclimate filtering (Lawes *et al.* 2004a) have all been implicated. However, Johnson and Stinchcombe (2007) hypothesized that evolution within populations could lead to dynamic ecological changes in the structure, composition, and diversity of communities. The appreciation that evolution might be an important factor affecting the structures of communities over shorter time scales was acknowledged recently (Whithman *et al.* 2003; Johnson and Stinchcombe 2007), driving ecological changes in communities at a rate comparable to ecological mechanisms (Hairston *et al.* 2005; Ezard *et al.* 2009). According to von Maltitz (2006), understanding the processes that drive a system is imperative for making wise management decisions as it relates to the degree to which forest types will be resilient to different types of disturbances (i.e. ecological, environmental, and anthropological).

Species distribution patterns between and within sites have been studied to explain composition assemblages in sites (Austin 1982; Bazzaz 1987). The role of plant diversity in ecosystem functioning has been highly debated (Hodgson *et al.* 1998; Lawton *et al.* 1998; Huston *et al.* 2000). Studies have shown that a variety of factors influence differences in plant species composition and diversity between forest patches. These factors include historical land use (Geldenhuys 1997; Brown and Boutin 2009), fragment size (Curtis and Cottam 1956), seed sources, invasive species (Siderhurst *et al.* 2012), herbivory (Holmes and Webster 2011), disease (Geldenhuys 1993), distance from other fragments (Curtis and Cottam 1956; D'Orangeville *et al.* 2008), and topography (Yang *et al*. 2008). Most of these factors are highly forest- or species- specific and vary between forests. Questions on species diversity, composition and functioning of plant communities have interested ecologists for a long time. Clement (1916) regarded the community as a well-organized assemblage of particular species. However, Gleason (1926) considered communities as random assemblages of species occurring together at the same place and time.

While some research has been conducted on the effects of forest fragmentation on biodiversity (Castley and Kerley 2006; Fahrig 2003; Lawes *et al.* 2007; Lawes *et al.* 2004; Lawes *et al.* 2000), little research has been done to address plant species (herbaceous and woody) composition and diversity patterns in South African forest patches. There is a notable profusion of plants in these forests, but understanding the factors that drive plant species composition and abundance in these patches is poorly understood and is still critical if we are to address or mitigate the problems imposed by global change. Using the Southern Mistbelt Forests in the Eastern Cape as an example, this study has the following objectives:

1. **To document the floristic diversity of poorly known patches of Southern Mistbelt Forests (SMF) in the Eastern Cape.** As noted above, many forests in South Africa are poorly known, and this work contributes to our greater understanding of forest diversity, species distributions and phytogeographic knowledge. This aspect is addressed in Chapter 2. Using floristic data, the following in particular will be investigated:
    a. Assess whether there are differences in species diversity of different forest patches, and if this correlates to distance between forests.
    b. Assess whether there are differences in tree and herbaceous species composition between forest patches
    c. Test whether there is any merit in the classification by Von Maltitz *et al.* (2003) that there are different forest types within the SMF vegetation unit.

2. **To determine if there is any evidence for "species nestedness" in the Southern Mistbelt Forests.** The fragmented nature and extensive distribution range of these patches make them ideal to test for nested subsets. This will be investigated in Chapter 3.

3. **To assess the influence of environmental variables on forest patch diversity (Chapter 4).**

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# Chapter 2: Floristics, Classification and Diversity of Southern Mistbelt Forests

## 2.1. Introduction

Originally classified as Undifferentiated Afromontane Forest (White 1983), the Southern Mistbelt Forest is the most extensive forest vegetation type in the Eastern Cape. The forest patches occur on the south- and southeast-facing slopes located along the Great Escarpment, spanning from Somerset East, the Amathole Mountains, scarps of Transkei and the KwaZulu-Natal Midlands as far as Ulundi (Mucina and Geldenhuys 2006). Patches of forests belonging to this vegetation unit are also found in the Baviaanskloof Mountains, Zuurberg, and in the Grahamstown and King Williams Town region (Palmer, 2004). This group comprises the last remaining 'traditional' Mistbelt forests after separation of the Scarp Forest vegetation unit.

Mistbelt forests represent a southern extension of the Afromontane forest of tropical Africa. In these forests the forest floor has a wealth of juvenile canopy trees and woody shrubs and herbs supplemented with ferns. On the Great Escarpment (Amathole and Transkei Escarpments) the trees are tall (15–20 m) and multi-layered (canopy and subcanopy, a dense shrub layer, and a well-developed herbaceous layer) and the trees found on low-altitude scarps are low (3-10 m) (Palmer 2004; Mucina and Geldenhuys 2006). Most of these forests occur at altitudes between 1200m and 1400m, but may extend as low as 560 m or as high as 1720 m (Geldenhuys 1993a).

Southern Mistbelt Forests cover 0.56% of the total land area of South Africa but contain 5.355 % of South Africa's plant species (Luft 2007). These forests have a relatively high species richness of 0.58 species $km^{-2}$, exceeding that of the Grassland biome with 0.25 species $km^{-2}$ (Lötter and Beck, 2004). In the Eastern Cape, 8% of the forests are statutorily conserved (including forest under DAFF jurisdiction, including the Boschberg Nature Reserve, Addo Elephant National Park (AENP), Hogsback, Khologha, Isidenge, Kubusi, Katberg and Nabakyu State Reserve) with a provincial conservation target of 30% (DWAF, 2011). Before colonialism the forests were larger and more numerous, and many may have been contiguous (Adie *et al.* 2013). Adie *et al.* (2013) stated that, "The forest patches function in unison as a single ecological unit, and the whole is worth a great deal more than the sum of its parts". Von Maltitz *et al.* (2003) divided SMF into three subgroups; Eastern Mistbelt Forests, Transkei Mistbelt Forests, and the Amathole Mistbelt Forests. While the Eastern Mistbelt forests are not included in this study here, the existence of the other two forest types can be tested.

There is a notable profusion of plant species within these forests, but understanding and predicting the factors that drive plant species composition and abundance in these patches is poorly understood and is critical if we are to address or mitigate the problems imposed by global change. The present work contributes to a greater understanding of forest diversity, species distributions, and phytogeographic and floristic knowledge of this forest type. Using floristic data, the following questions will be investigated:

1. Are there differences in species diversity among forest patches, and if so, are differences correlated with distance between forest patches?

2. Are there differences in the diversity and composition of tree and herbaceous species between forest patches?

3. Is the classification by Von Maltitz *et al.* (2003) of the SMF forests into finer categories supported?

## 2.2. Materials and Methods

### *2.2.1. Study site*

The study was conducted in twenty-six forest patches throughout the Eastern Cape which belong to the Southern Mistbelt Forest Group (Figure 2). These patches occupy two sections of the Great Escarpment (Winterberg-Amatole and Transkei Escarpment) (Clark *et al.* 2014, 2011; Shaw and Escott 2011).

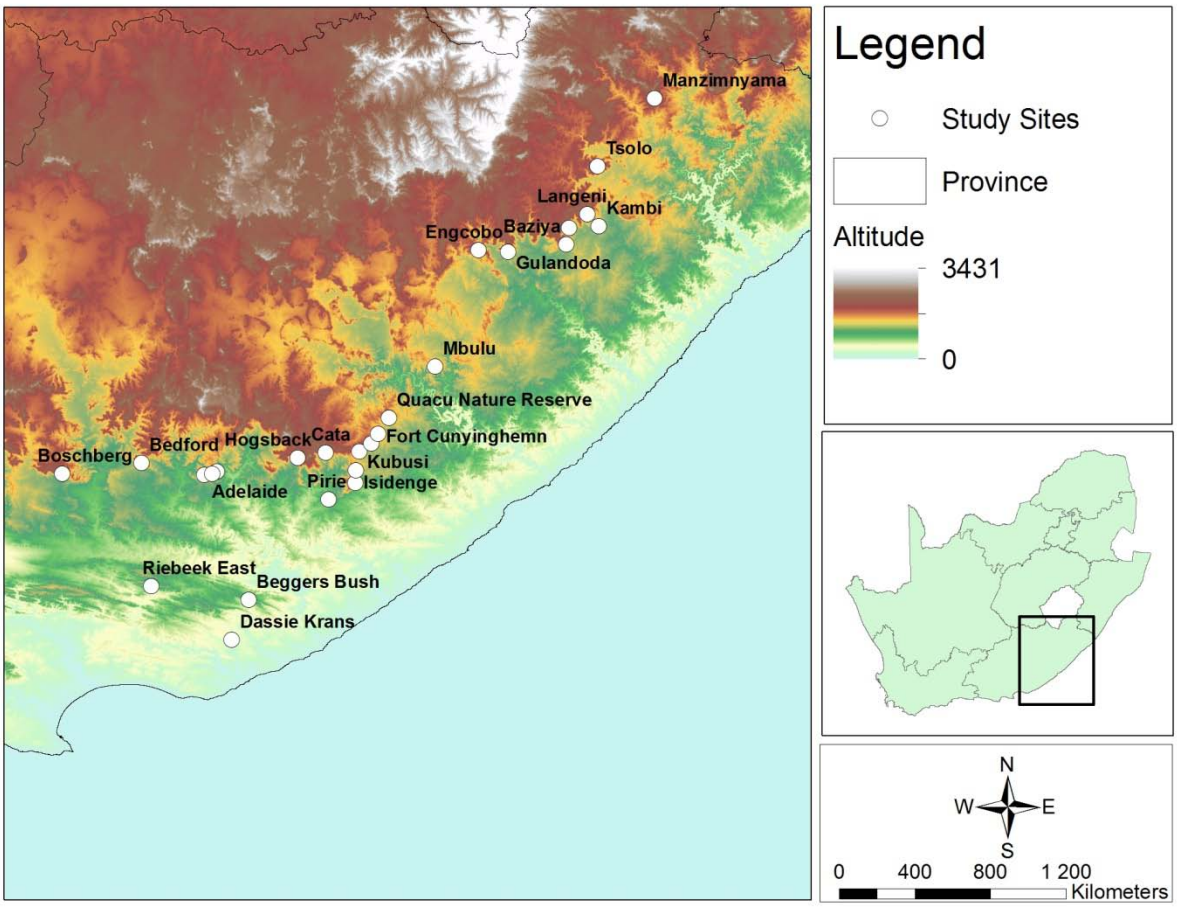


**Figure 2: Map showing the location of the study sites in the Eastern Cape. The circles indicate the location of the forest patches in which the study was conducted.**

#### 2.2.1.1. Geology and Soils

The geology of the twenty six study areas is characterised as Karoo Super group (Hattingh 1996). The Karoo Super group covers two thirds of the country and is made up of the Dwkye, Ecca and Beaufort Groups; this formation contains dolerite, sandstone, mudstone, and claystone (Hattingh 1996).

### 2.2.1.2. Climate

A subtropical climate prevails over the mountains, with rainfall peaking in the summer season (DWAF 2007). In the Eastern Cape, a moisture gradient (from west to east) exists along the Escarpment where patches of Southern Mistbelt Forests occur, with the eastern region being predominately wetter. Winds and altering cold and warm fronts results in a variable climate throughout the year. January and February are characterised by thunder storms caused by the frequent bergwinds. The annual average temperature is 15°C with a range of maxima and minima of 40°C and -6°C in summer and winter respectively (DWAF 2007). Thick blankets of mist often cover these mountains and are characteristic in these patches hence the term "Mistbelt Forest".

## *2.2.2. Acquisition of Floristic data*

The flora of each forest was assessed using two approaches: general botanical collecting, and use of plots to sample composition, abundance and environmental factors. The former method entailed the collection of as many specimens as possible from each forest patch, while the latter was a standard technique modified from Gentry (1982), Lorence and Sussman (1988), and Geldenhuys (unpublished). This method comprised a circular plot of 400 $m^2$ area, with a radius of 11.3 m. A rope of length 11.3 m with a knot at the midpoint was used to divide the plot into two distinguishable circles, a smaller inner circle of 100 $m^2$ and the outer circle of 400 $m^2$. The plots were at least 100 m apart and selected randomly. The number of plots constructed per forest varied because of differences in patch size, the time available to sample at each site, and prevailing weather conditions. The plots were placed arbitrarily; slope, boundary, canopy gaps and accessibility restrictions were taken into account when placing plots.

Trees within the 400 $m^2$ circular plot were sampled as follows: All trees with a diameter of 5 cm or more had the trunk circumferences measured using a measuring tape. All such measurements were done at standard diameter at breast height (DBH=1,3m). These measurements were only recorded for trees, shrubs and lianes. The stem count was then recorded for each tree for which the circumference was measured. All measurements were replicated at each study area. If a tree was forked below breast height, the diameter of the main trunk below the fork was measured. The DBH of a trunk growing vertically on a slope was taken on the upper side of a slope. The DBH of trees that possessed buttresses was measured just above the buttress. Herbaceous species were only sampled within the smaller 100 $m^2$ circle. The percentage cover of all herbaceous plants was estimated visually. The sampling method was repeated at all study sites and was used to assess the composition and abundance of species at the 26 forest sites.

Sampling was carried out in the summer months (January to April) for both study years (2013 and 2014; Table 1). GPS readings were taken in each sampled area. All plant specimens collected were pressed and later identified in the Selmar Schonland Herbarium, Albany Museum, Grahamstown.

**Table 1: Study area matrix with sampling date and number of plots sampled.**

| Study site | GPS | Sample Date (yr/m/dd) | No.Plots |
|---|---|---|---|
| Adelaide | 32°41'32.1926",26°28'21.2141" | N/A | 4 |
| Baziya | 31°33'26.8769",28°25'13.1045" | 2013/03/06 and 2014/03/09 | 9 |
| Bedford | 32°38'52.2778",26°04'14.2295" | 2013/01/20 and 2014/04/18 | 9 |
| Beggars Bush | 33°17'29.4630",26°41'20.3964" | 2013/08/02 and 2014/06/18 | 5 |
| Boschberg | 32°41'45.6934",25°37'28.2245" | 2014/10/08 | 6 |
| Cata | 32°34'53.7705",27°06'17.1585" | 2014/04/14 | 5 |
| Dassie Krans | 33°20'10.0246",26°35'23.0040" | 2014/06/19 | 6 |
| Engcobo | 31°35'45.6066",27°56'00.0673" | 2013/03/05 | 3 |
| Fort Cunyingham | 32°29'10.0445",27°23'51.4570" | 2014/04/25 | 5 |
| Fort Fordyce_North | 32°40'27.0225",26°29'55.7599" | 2014/06/29 | 5 |
| Fort Fordyce_South | 32°41'29.6771",26°30'02.6254" | 14/03/21-22; 14/06/28; 14/06/30 | 11 |
| Gulandoda | 31°36'03.3306",28°05'54.0565" | 2014/04/28 | 4 |
| Hogsback | 32°36'34.3229",26°57'03.4641" | 2013/01/24 and 2013/01/25 | 5 |
| Isidenge | 32°39'41.7555",27°16'37.8574" | 2014/04/20 | 5 |
| Kambi | 31°27'51.6814",28°35'58.9653" | 2014/03/09 | 5 |
| Khologha | 32°32'01.3750",27°21'36.2943" | 2014/04/21 | 5 |
| Kubusi | 32°34'15.0005",27°17'43.9739" | 2014/04/22 | 5 |
| Langeni | 31°28'23.5767",28°26'06.7195" | 2013/03/07 and 2014/03/08 | 5 |
| Maden Dam | 32°43'16.9320",27°16'35.5138" | 2014/04/16 and 2013/04/17 | 8 |
| Manzamnyama | 30°50'51.5542",28°53'03.6459" | 2014/03/07 | 4 |
| Mbulu | 32°09'19.9903",27°42'35.4405" | 2014/04/26 | 3 |
| Mhlahlane (Langeni) | 31°24'33.1319",28°32'03.4329" | 2013/03/04 and 2014/03/08 | 13 |
| Pirie | 32°48'15.7998",27°07'36.6921" | 2013/01/27 and 2013/04/15 | 10 |
| Quacu Nature Reserve | 32°24'28.2553",27°27'27.1027" | 2014/04/25 | 5 |
| Riebeek East | 33°14'01.8973",26°08'06.6549" | 2013/03/21 | 4 |
| Tsolo | 31°10'45.9115",28°34'53.6727" | 2014/03/05 | 3 |
| **Total** | | | **152** |

### *2.2.3. Caveat: Possible biases in Sampling and data*

In studies such as these it is important to note that the term “total number of species” does not represent the entire species composition of the patch but refers to the total number of species collected in the forest patch during the study. Two of the patches (Fort Fordyce North and Boschberg) were not surveyed during the main sampling season and therefore the species diversity and composition may not be as well represented at these sites. In addition, the number of plots sampled in each forest patch also varied as a consequence of weather conditions and available time.

## 2.3. Analysis of plot data

### *2.3.1. Cluster Analysis and Multidimensional Scaling*

*Plymouth Routines in Multivariate Ecological Research* (PRIMER) was used to analyse species and sample abundances (Clarke and Gorley 2006). It contains multivariate routines including grouping, comparisons, and diversity, dominance and distribution calculations (Clarke and Gorley 2006). In order to determine whether there were differences in species composition between the sampled forest patches, two analytic routines were used in this study: hierarchical cluster analysis (CLUSTER) and an ordination method (multidimensional scaling; MDS). These were applied to three different data sets: 1) All species data, 2) only tree species, and 3) only herbaceous species (Data provided in Appendix A).

A spreadsheet of the species compiled from the plot data was generated in which "1" represented the presence of a plant species in a plot and "0" its absence. The spreadsheets were then individually imported into *PRIMER 6.* The data were pre-treated using the "Absence and Presence" transformation option. Presence/absence transformation enables less abundant species to be given the same weight as abundant ones. After transformation, a resemblance analysis was performed using Bray–Curtis resemblance (Bray and Curtis 1957) to produce a dissimilarity matrix, which was then subjected to hierarchical clustering using the "group average" mode in *PRIMER 6*. All other options were set at default. Cluster analysis groups the samples (i.e. plot data) into clusters and constructs a dendrogram with branch length proportional to the degree of dissimilarity.

The same dissimilarity matrices were used for the 2-dimentional MDS analysis. A minimum stress value of 0.01 and a Kruskal fit scheme of two were selected together with the default values for other options. The MDS routine represents the samples as points in low-dimensional space such that points of high similarity are placed in close proximity. It also produces a "stress" value, which is a measure of the authenticity of the relationships among the samples displayed in the multidimensional space. However, Clarke and Gorley (2005) warned that this value should be interpreted with caution, especially when analysing large data sets.

### *2.3.2. Geographic distance and species diversity*

In order to determine the relationship between species diversity and geographical distance, a correlation analysis was performed. A dissimilarity matrix based on transformation data (absence and presence) of the total number of species sampled was generated with *PRIMER 6* (Clarke and Gorley 2005) using Bray–Curtis resemblance (Bray and Curtis 1957). The geographical distance data were obtained with the aid of satellite images (*Google Earth*).The "Ruler" and "path" options were selected to measure the distance between the multiple points on the ground and GPS coordinates were recorded for each measurement location (Table 1; Appendix B).

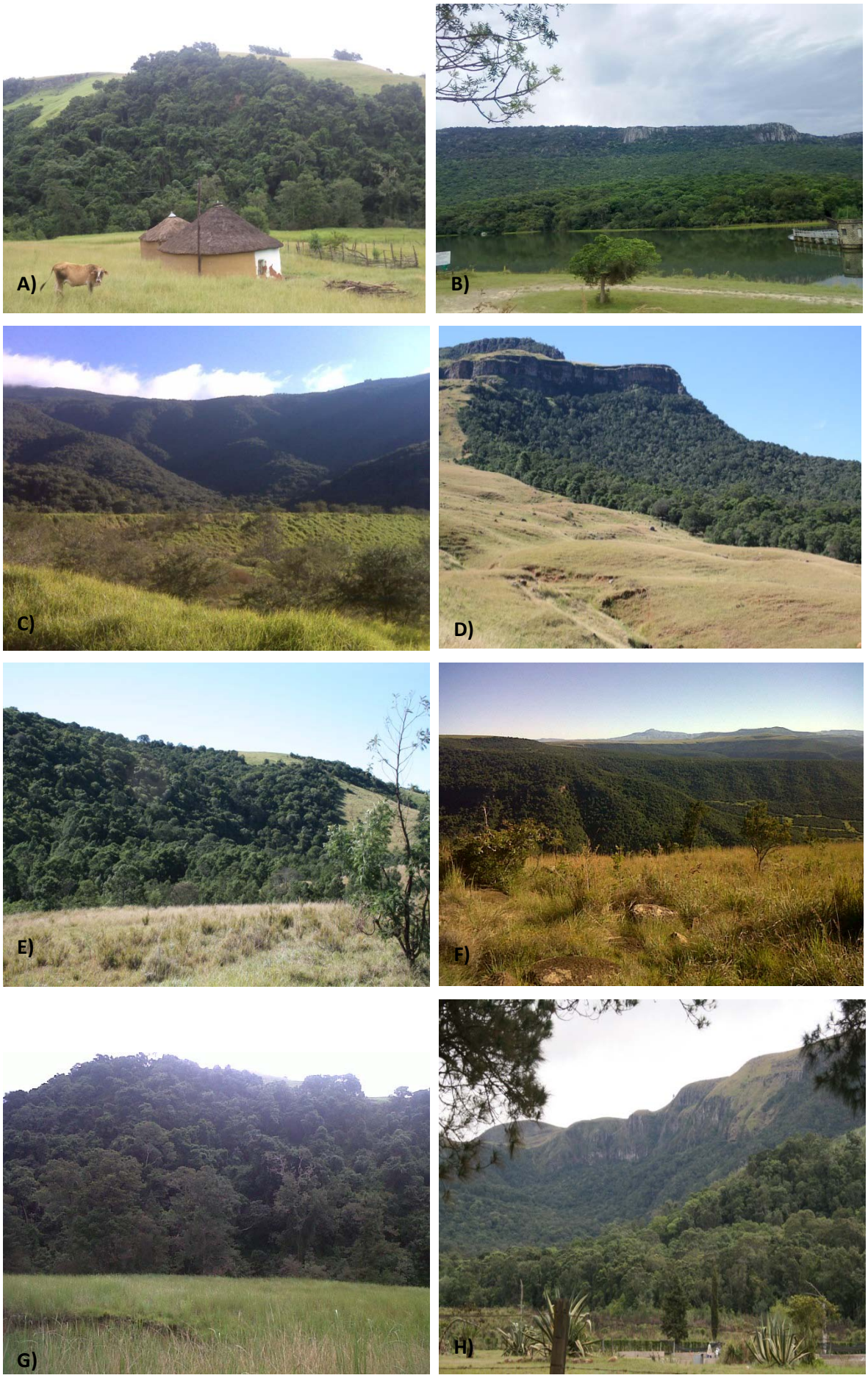


**Figure 3: Images selected from forest patches sampled in the study. A) Tsolo, B) Maden Dam, C) Boschberg, D) Gulandoda, E) Quacu, F) Fort Fordyce North, G) Manzamnyama, and H) Mhlahlane.**

## 2.4. Results and Discussion

### *2.4.1. Floristic comparison of forest patches*

A total of 152 plots were surveyed in the 26 study areas (Table 2; Appendices C and D). The number of plots surveyed per site ranged from 3-13. Engcobo, Mbulu and Tsolo had the least number of plots (three each) and Mhlahlane had the most recorded number of plots (13 in total) (Table 2).

**Table 2: Study area matrix showing number of sampled species from plots (in brackets) and the total number of species from plot and general collections for each floristic group.**

| | Study site | Total Species | Trees | Herbs | No. Plots |
|---|---|---|---|---|---|
| 1 | Adelaide | (47) 62 | (18) 19 | (29) 43 | 4 |
| 2 | Baziya | (112) 175 | (36) 38 | (76) 137 | 9 |
| 3 | Bedford | (83) 99 | (44) 48 | (39) 51 | 9 |
| 4 | Begger Bush | (65) 84 | (26) 45 | (39) 39 | 5 |
| 5 | Boschberg | (50) 55 | (17) 27 | (23) 28 | 6 |
| 6 | Cata | (69) 112 | (23) 42 | (46) 80 | 5 |
| 7 | Dassie Krans | (51) 100 | (27) 48 | (24) 52 | 6 |
| 8 | Engcobo | (46) 73 | (13) 18 | (33) 55 | 3 |
| 9 | Fort Cunyingham | (71) 102 | (41) 43 | (30) 59 | 5 |
| 10 | Fort Fordyce_North | (52) 68 | (25) 42 | (17) 26 | 5 |
| 11 | Fort Fordyce_South | (71) 99 | (30) 43 | (41) 56 | 11 |
| 12 | Gulandoda | (67) 103 | (31) 33 | (36) 70 | 4 |
| 13 | Hogsback | (59) 125 | (22) 35 | (37) 90 | 5 |
| 14 | Isidenge | (67) 139 | (27) 65 | (40) 74 | 5 |
| 15 | Kambi | (89) 179 | (49) 50 | (40) 129 | 5 |
| 16 | Khologha | (66) 86 | (30) 36 | (36) 50 | 5 |
| 17 | Kubusi | (67) 125 | (30) 37 | (37) 88 | 5 |
| 18 | Langeni | (80) 180 | (38) 51 | (42) 129 | 5 |
| 19 | Maden Dam | (87) 191 | (32) 87 | (55) 104 | 8 |
| 20 | Manzamnyama | (68) 120 | (23) 28 | (45) 92 | 4 |
| 21 | Mbulu | (50) 71 | (23) 29 | (27) 42 | 3 |
| 22 | Mhlahlane (Langeni) | (149) 295 | (48) 121 | (101) 174 | 13 |
| 23 | Pirie (Ntabakandoda) | (102) 152 | (45) 57 | (57) 95 | 10 |
| 24 | Quacu Nature Reserve | (58) 97 | (23) 28 | (35) 69 | 5 |
| 25 | Riebeek East | (50) 69 | (20) 29 | (30) 40 | 4 |
| 26 | Tsolo | (56) 111 | (16) 29 | (40) 82 | 3 |
| **Totals** | | **(1832) 3072** | **(757) 1128** | **(1055) 1954** | **152** |

The number of species sampled per plot across the 26 forest patches ranged from 7 to 21 for the tree species and 10 to 35 for the herbaceous species (Appendices C and D respectively). The presence of a high number of species in a few quadrats indicated that there was an uneven distribution of species within and between forest patches. This unevenness could be a result of niche specialization and differing ecological requirements among plant species, as well as also habitat and environmental heterogeneity.

A total of 2352 specimens were collected representing 589 identified species (Appendix E) of which 206 were tree species and 383 were herbaceous species. By augmenting species lists from the plots with species found using general collecting approaches, a comprehensive species list was generated for each of the individual forest patches (Appendix E). The total number of species for each forest patch is given in Table 2. Mhlahlane forest had the highest number of species (295) (but also had the most quadrats, 13), followed by Maden Dam (191), Langeni (180) Kambi (179), and Baziya (175) (Table 2). Boschberg had the least number of species (55), which were dominated by almost equal numbers of herbaceous (28) and tree species (27) (Table 2). With the exception of Beggars Bush, trees (45) species were more diverse than herbaceous (39) (Table 2).

The number of species recorded from each forest using the plots was considerably lower than the overall diversty obtained once the general collecting had been included. Of the plant species collected in Mhlahlane only 50% of the total number of species collected were sampled in the plots (Table 2). Less than 50% of the total number of herbaceous species were sampled in the plots assembled at Hogsback, Kambi, Kubusi, Langeni, and Manzamnyama (Table 2). This suggests that the quadrat sampling procedure used greatly underestimated diversity, and that a greater number of plots is required to obtain a more realistic representation of the floristic diversity in each forest patch.

In general, there was a notable increase in species diversity (species number) recorded in the eastern forest patches compared with the western patches (Figure 4). Geldenhuys (1997a, b) reported a similar decrease in species number in the Southern Cape forest patches from east to west and from south to north. At a continental scale, Linder (2014) also noted the contrast in species diversity between the eastern and western parts of Africa but failed to give the mechanisms responsible for this distribution. A rainfall gradient exists in the escarpement where these patches are located and could be driving the plant species diversity patterns stated previously. This will be explored in detail in chapter 4.

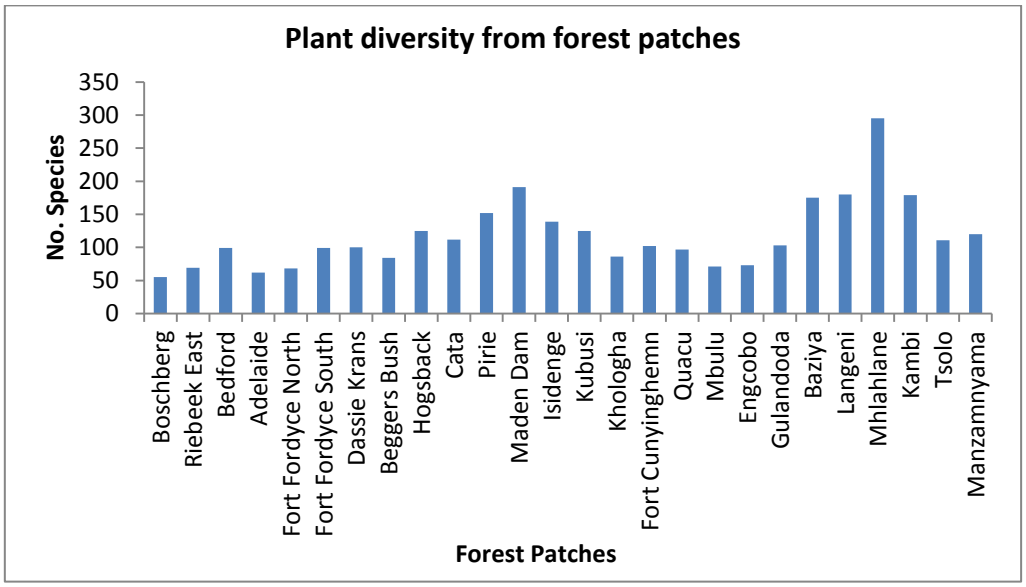


**Figure 4: Total diversity of forest patches ordered from West to East.**

### *2.4.1. Multivariate analysis of forest diversity*

Cluster and NMDS analysis was performed using data from 152 plots. The data set contained presence / absence data for 408 species.

#### *2.4.1.1. Analysis of full species data set*

The dendrogram generated from the full species dataset indicated that in general the species composition in each forest patch was unique, as plots from the same patch tend to cluster together (Figure 5). However, there were 16 plots that were not placed with other plots from the same forest. These include plots from Maden Dam (Q14), Kambi (Q125), Kubusi (Q137, Q138), Hogsback (Q3, Q5), Mhlahlane (Q60, Q64), Baziya (Q74, Q75), Isidenge (Q101, Q102 Q103, Q104, 105), and Gulandoda (Q149). Isidenge was the only forest patch for which most of the plots were not clustered together, and were instead grouped with plots from Tsolo, Fort Fordyce South, and Fort Cunyingham.

Similarly, the NMDS analysis of the full data set indicated that plots from the same forest patch tended to cluster (Figure 6), and patches of similar floristic composition were clustered in an overlapping manner.

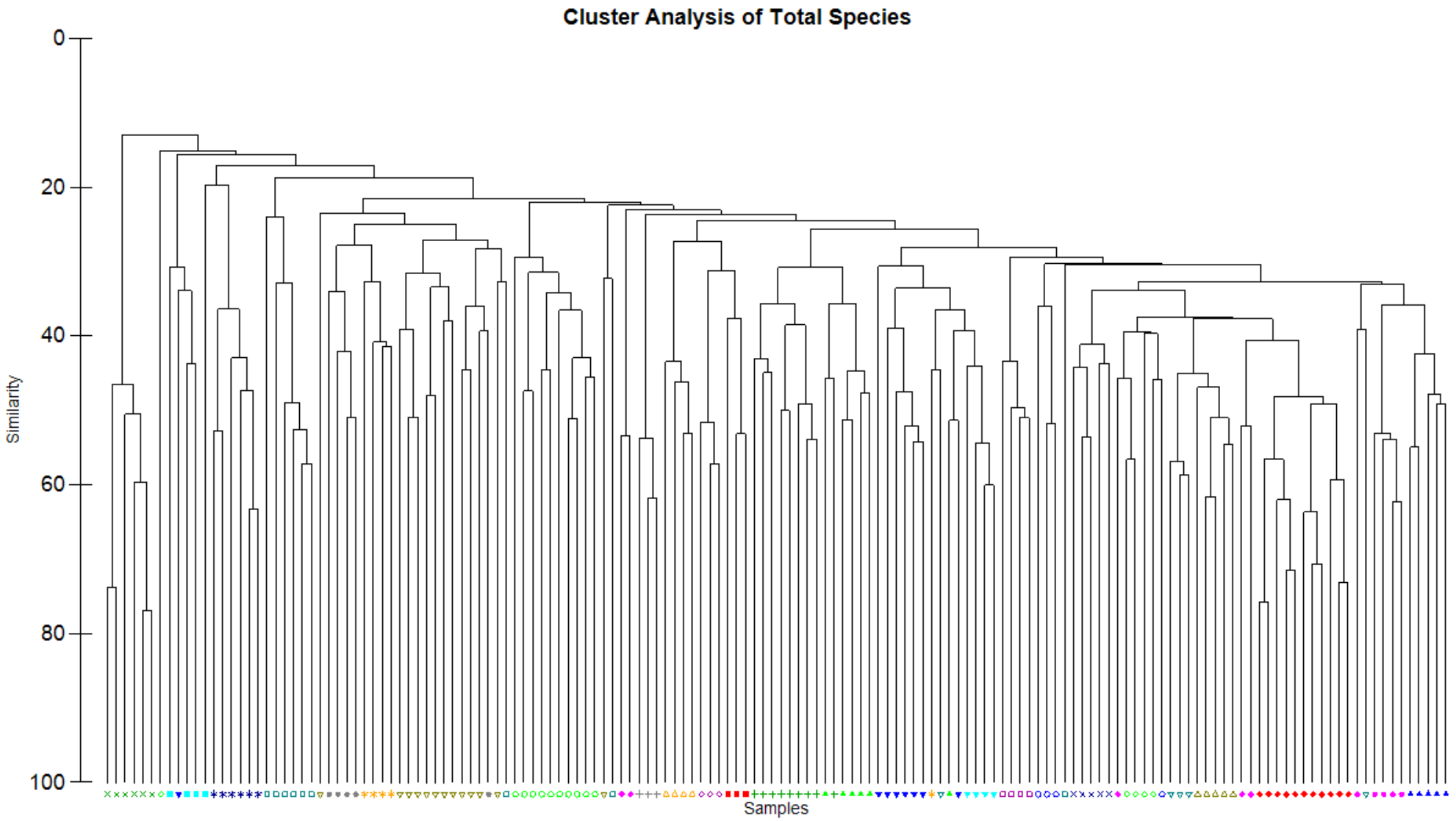


**Figure 5: Cluster analysis result of species composition of combined species plots. Plots from the same forest patch have the same colour and shape codes as shown in Figure 6.**

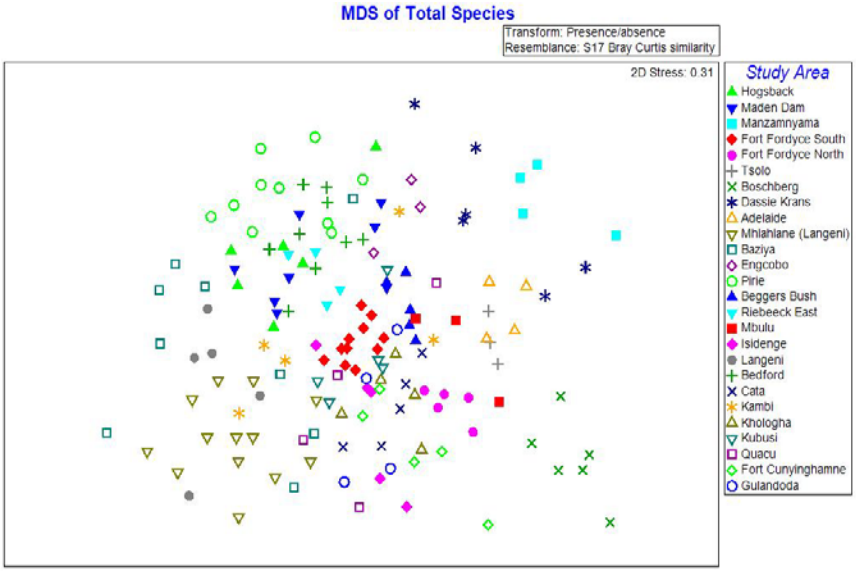


**Figure 6: 2D NMDS plot results of species composition of Total number of species sampled in plots surveyed**

### *2.4.1.2. Analysis of the tree species data set*

Similar to other studies the results showed trends for homogenisation in tree species composition in fragmented forests (McKinney 2006; Holmes and Webster 2011) analysis of tree species composition data provided no evidence of forest-specific tree composition, with the exception of plots from Boschberg, which were grouped in a forest-specific cluster (Figure 7). Similarly, the NMDS analysis of the tree data set showed no clustering of patch-specific plots (Figure 8).

These results suggest that tree species diversity is relatively uniform across patches of Southern Mistbelt Forests. This supports Geldenhuys and Golding (2008) who found there to be similarities among plots from the Amatole Mistbelt Forests but these differed in tree species composition from Eastern Mistbelt Forests, with only a single common quadrat between the vegetation units.

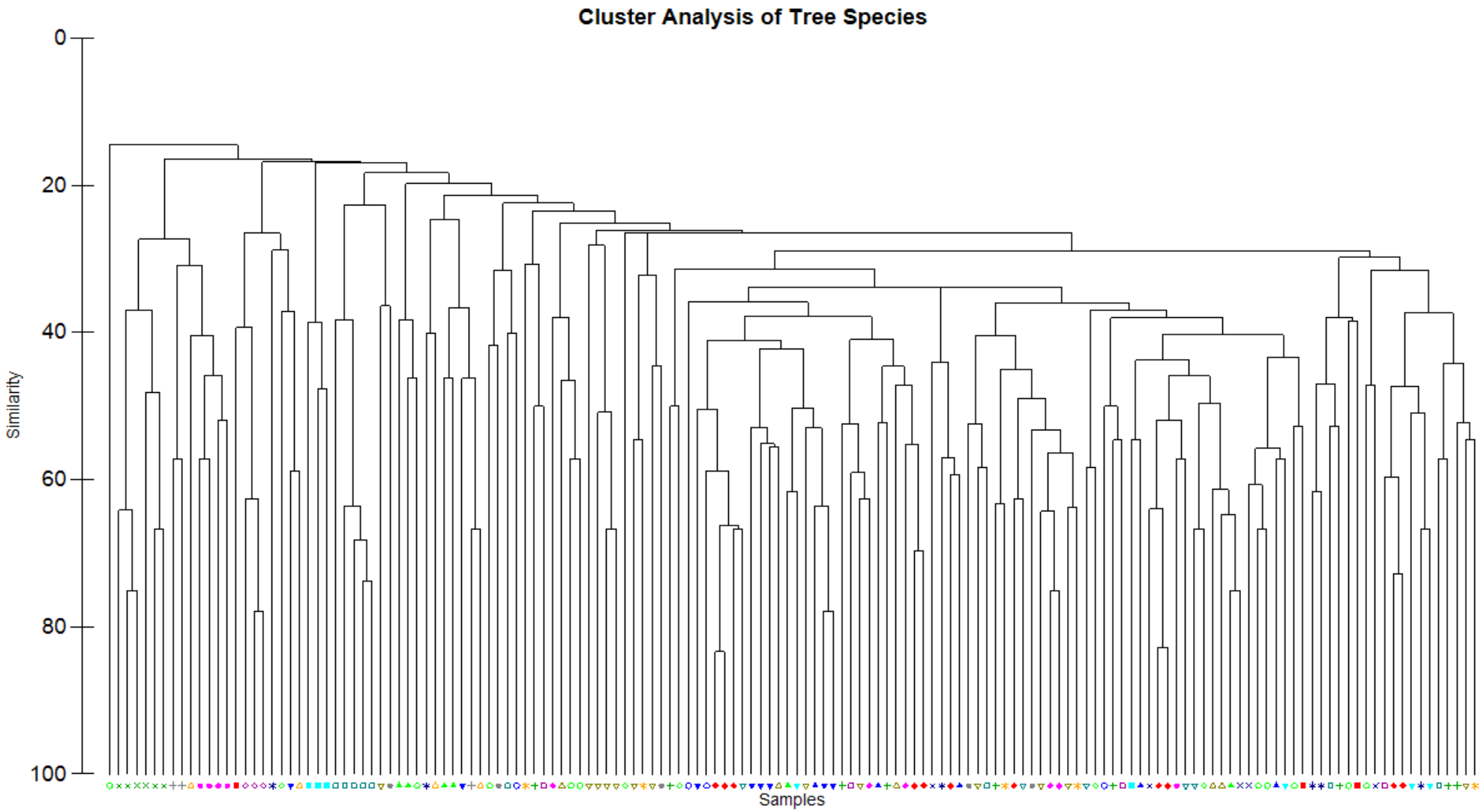


**Figure 7: Cluster analysis results of species composition of tree species in sampled plots. Plots from the same forest patch have the same colour and shape codes as shown in Figure 8.**

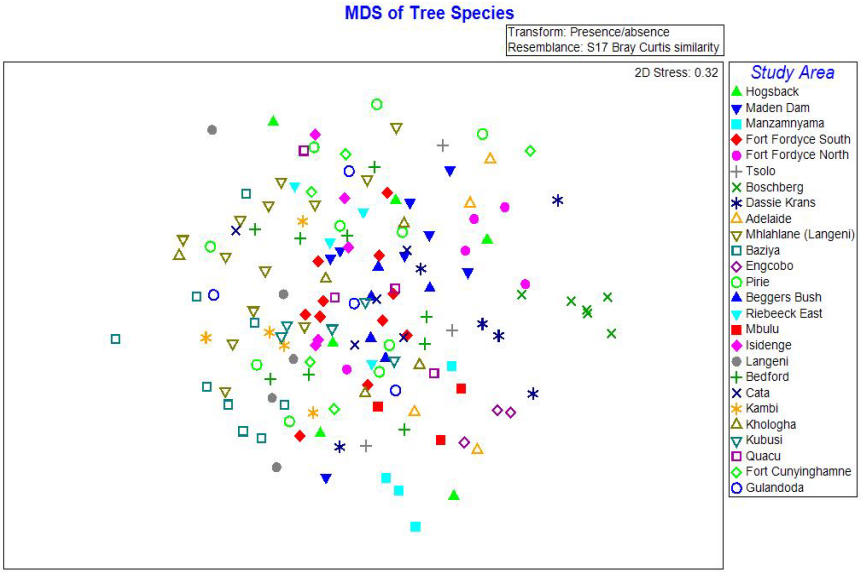


**Figure 8: 2D NMDS ordination from Tree species data collected from sampled plots**

### *2.4.1.2. Analysis of the herbaceous species data set*

Cluster analysis of the herbaceous species (including herbs and ferns) data set provided evidence for forest-specific species composition (Figure 9) as plots from each individual forest tended to cluster together. The NMDS analysis provided a similar result, with plots from the same forest patch grouped together. Although there was overlap in species composition in some forest patches (Figures 6 and 10), which was expected because a few common species were shared among the forest patches, the dendrograms (Figures 5 and 9) indicated that species composition was unique in each forest patch. Thus the pattern obtained for the total species data set is a consequence of patch-specific differences in the diversity of the herbaceous species, and not the tree species.

It must be noted that in the NMDS analysis, the 2D stress values were 0.3, 0.32, and 0.31, for the total, tree and herbaceous data sets respectively (Figure 6, 8, 10). These values are high and could be interpreted as indicating the results are insignificant. A 2D stress value of 0.1 is considered to be the value that confirms significance for dimensional scaling between the plots. The higher stress values obtained here could have been a consequence of differences in the number of plots between the forest patches and also the differences in recorded abundances within plots. However, NMDS stress values also tend to be distorted by a large number of samples (Clarke and Warwick 2001), such as in the present study. Hence these results must be interpreted with due caution.

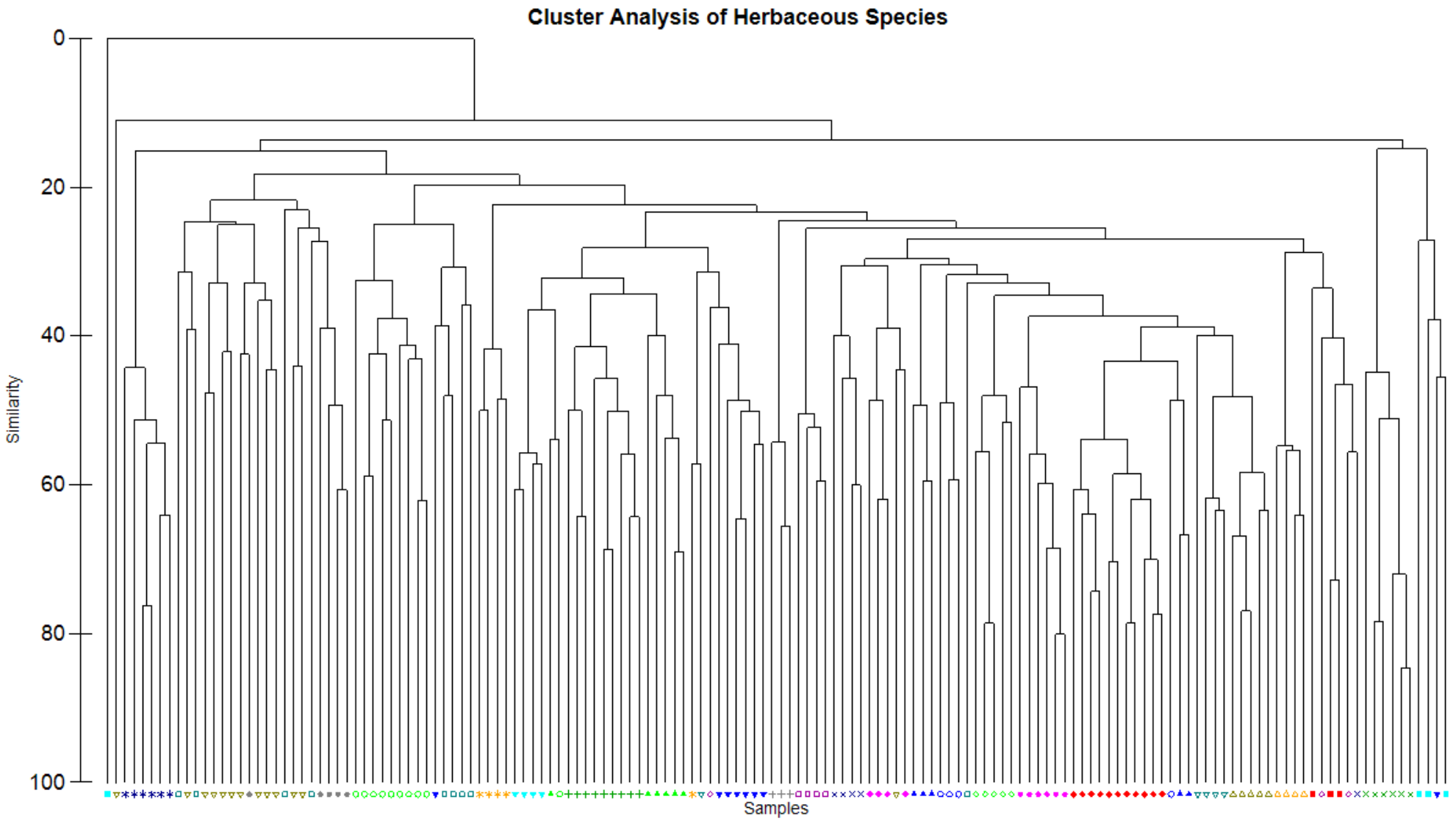


**Figure 9: Cluster analysis results of herbaceous species composition in sampled plots. Plots from the same forest patch have the same colour and shape codes as shown in Figure 10.**

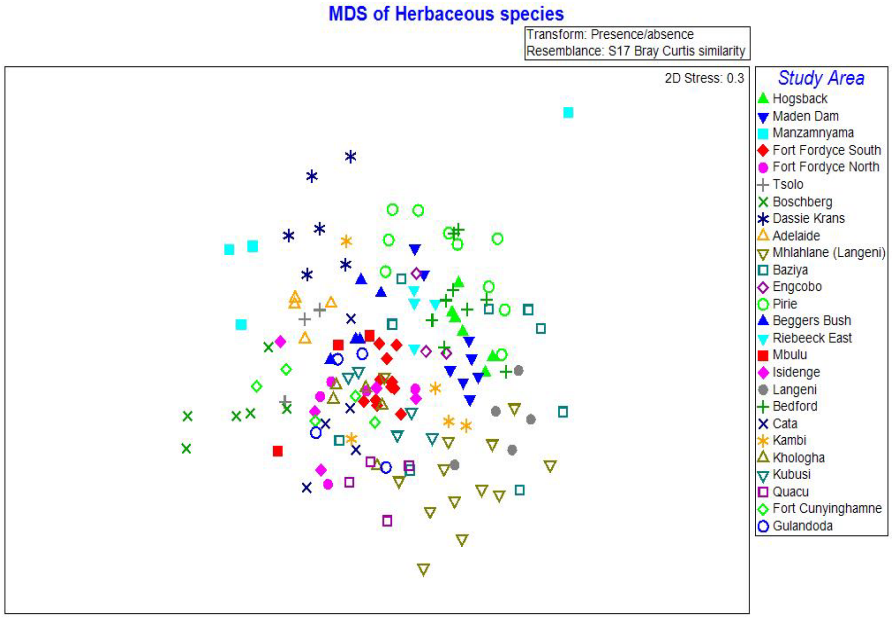


**Figure 10: 2D NMDS of Herbaceous species collected from the sampled plots.**

### *2.4.2. Correlation between Geographic distance and species diversity*

The correlation analysis between species diversity (expressed as Bray Curtis similarity) and geographic distance showed that species diversity and geographic distance in Southern Mistbelt Forests was not correlated ($R^2$ = 0.2776; Figure 11A), as was the case for herbaceous and tree data sets ($R^2$ = 0.2428 and 0.0922, respectively; Figure 11 B and C respectively). Also all three plots were also not significant at a 95% significant confidence level (p-values=1.32, 2.33, and 2.77 for Figure 11A, 11B and 11C respectively; Appendix B). The regression line in Figure 11B (tree species) does not deviate significantly from the horizontal line, but deviates significantly for the other two plots (Figure 11A and 11C). These results indicated that geographic distance has at best a minor effect on the species diversity of the forest patches for the total number of species and herbaceous species. All three figures suggest that there could be a problem with heteroscedasticity; this was confirmed by the relatively large F-statistics (124.09, 32.81, 103.57; Figure 11A, 11B, and 11C respectively; Appendix B. According to Williams (2015) heteroscedasticity can occur when there are population differences (i.e. some areas over sampled), and errors may occur as the value of the independent variable increases. Williams (2015) also states that the presence of heteroscedasticity does not necessarily produce biased results although the standard errors would be highly suspect. However, there was a gradual decline in Bray-Curtis similarly with increasing distance between patches. This result is pertinent because most studies show that many forest plants have low dispersal capacities

(e.g. Matlack 1994; Bossuyt *et al.* 1999). The distances between forest patches thus affects inter-patch dispersal and this has a strong impact on forest community structure, and neighbouring forest patches share more common species than distant patches (Geldenhuys 1993b, c). Indeed, few studies have investigated the role of dispersal in structuring local forest plant community composition and reported evidence for dispersal-assembled forest plant communities (Butaye *et al.* 2001; Honnay *et al.* 2001).

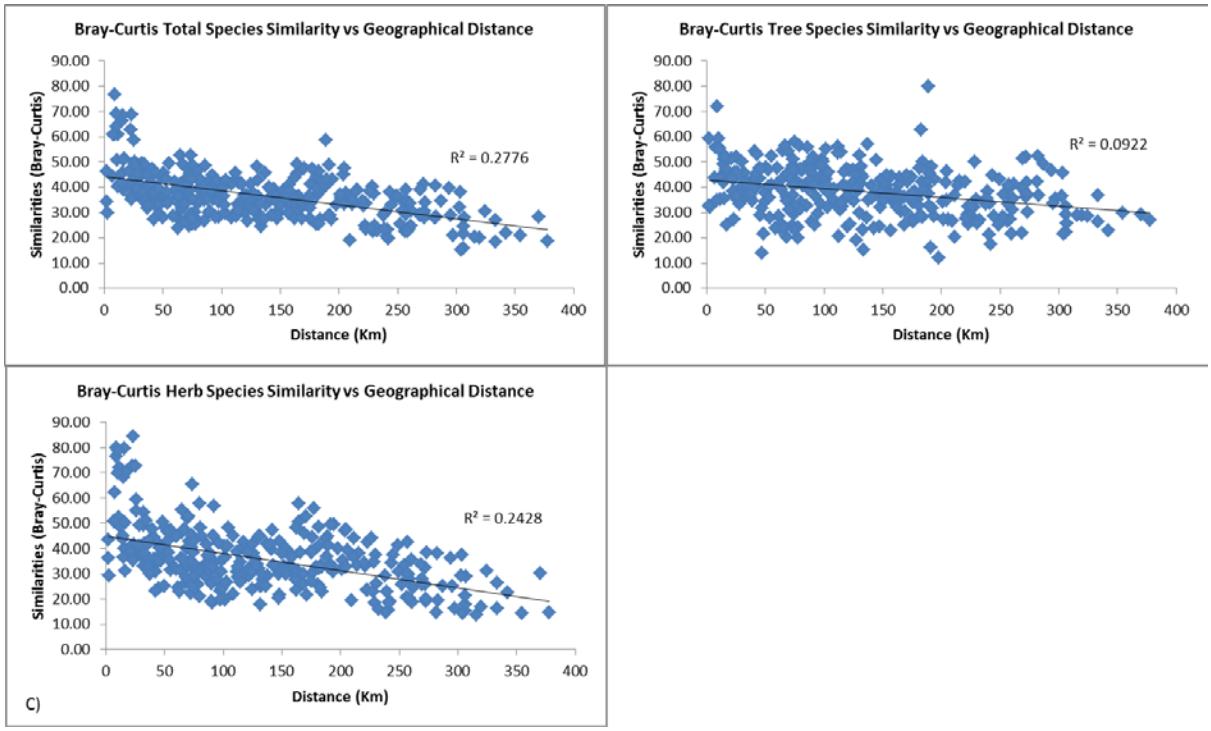


**Figure 11: Bray–Curtis Similarities in A) total number of species, B) tree, and C) herbaceous correlated with geographic distance.**

### *2.4.3. Ecology of Southern Mistbelt Forest plant species layers*

To date the ecology of understory species (especially herbaceous species) has received little attention (Newbery *et al.* 1999). As shown in the present study, the herbaceous layer plays a significant role in forest patch composition and structure (Figures 5 and 6). The ecology of the understory should receive greater attention given that there is potential for understory species to help us in understanding juvenile tree ecology (Boudreau *et al.* 2005). They represent the regeneration potential and affect the future patterns of ecological succession and species

composition of these plant communities (Sagar *et al.* 2007). The composition of the understory of forest patches may provide clues as to the nature and degree of mechanisms or resources that structure herbaceous species in these communities and also help in formulating hypothesis about the relevant processes (Scheller and Mladenoff, 2002). The discrete nature of the herbaceous species in SMF forest patches (Figure 9) suggests that there are elements that are patch-specific. This could be as a result of both ecological and environmental filtering by area-specific climatic variables which exclude most species without the appropriate traits to survive in those conditions. This will be discussed further in Chapter 4.

According to Toniato and de Oliveria-Filho (2004), larger forest fragments located closer to other fragments tend to be richer in tree species than smaller isolated patches. Similarly, in the present study, forest fragments located closer to each other in the Transkei (e.g. Mahlahlane, Langeni, Baziya, and Kambi) and Amatole (e.g. Maden Dam, Pirie, Isidenge, Kubusi, and Khologha) were more diverse (Table 2). However, the species composition between the forest patches was unique (Figures 5 and 9).

Comparisons of species composition or other facets (species diversity and richness) of different forests is challenging because of all the inconsistencies of the available data. There is a wealth of data for tree species, both in South Africa and internationally (e.g. Everard 1992; Geldenhuys 1991, 1993a, 1993b, 1994a, 1994b, 1996; Everard *et al.* 1995; Geldenhuys and Golding 2008; Aiba and Kitayama, 1999; Giliba *et al.* 2011; Lü *et al.* 2010; Omoro *et al.* 2010), but very few data for the herbaceous species on the forest understory (e.g. Mukhia et al. 2011). The present study has shown the significant contribution of herbaceous species to the floristic composition and diversity of forest patches, and there is a need for additional studies of this nature.

### *2.4.4. Testing von Maltitz et al. (2003) classification*

Von Maltitz *et al.* (2003) classified the Southern Mistbelt Forest Group into three subgroups: Amathole Mistbelt; Transkei Mistbelt; and Eastern Mistbelt. Unfortunately, in the present study Eastern Mistbelt Forests were not sampled, but no clear clustering of the plots was noted for the Amathole and Transkei Mistbelt Forest subgroups (Figure 5) although there was forest specific clustering (Figure 5 and 9). Moreover, plots sampled from Manzamnyama Forest, which is located a few kilometres from Ngeli Forest (Eastern Mistbelt Forest; Geldenhuys and Golding 2008), showed similar tree species composition to Adelaide, Baziya, and Beggars Bush (Figure 5). However, unlike

the present study, the von Maltitz *et al.* (2003) classification was based solely on woody species composition and no herbaceous species information was sourced. Their classification was based on floristic resemblance patterns using absence and presence data and frequency- abundance data. However, in some cases biogeographically motivated adjustments were introduced. Nonetheless, the woody species (Figure 7 and Figure 8) analysed in the present study did not cluster or form discrete regional groups (i.e. Amathole and Transkei), suggesting that the classification by von Maltitz *et al.* (2003) has no floristic validity. The plot analysis indicates homogeneity between plots in single forest, but not necessarily the relationship between patches.

#### *2.4.4.1. Comparison of Von Maltitz et al. (2003) Classification using whole forest data set*

Results from clustering and NMDS analyses based on the presence / absence data at a whole forest patch level are indicated in Figure 12 and 13. Results indicate there is some form of signal as the forest types to tend to a grouping. Forest patches from the Amathole Mistbelt are grouped together so are patches from the Transkei Mistbelt (Figure 12), which could be construed as support for the classification of Von Maltitz *et al.* (2003). However some of the forest patches from the Amathole Escarpment form a separate cluster. These are referred to here as “Dry Forest” patches because they occur in areas that receive the least amount of moisture as compared to the other patches. Hogback is the only forest from the Amathole Mistbelt group that is similar to forest patches in the Transkei Mistbelt group (Figure 13). Adelaide and Engcobo forest patches were the only outliers (Figure 13).

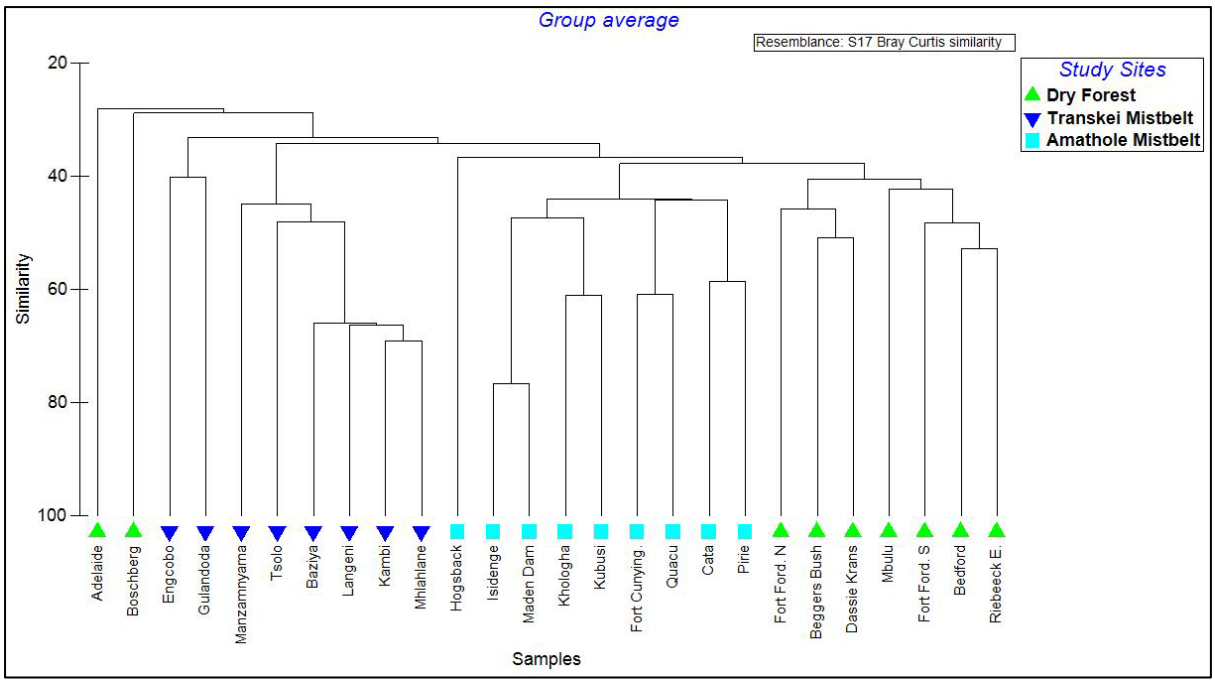


**Figure 12: Dendogram using the whole forest species data from all the forest patches. Same coloured symbols correspond to different forest groups.**

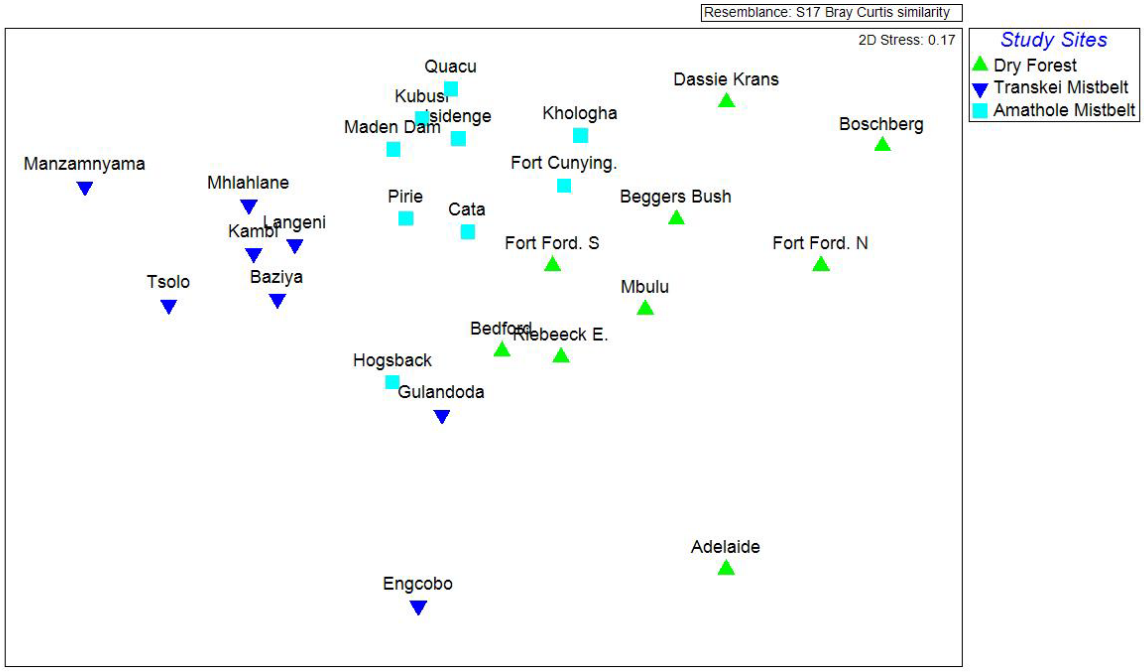


**Figure 13: 2D NMDS ordination plot from the total plant species collected at each forest patch.**

The analysis was repeated using only tree species data (Figure 14 and Figure 15). These results are not as clear as indicated for the full species analysis, as indicated by the cluster analysis (Figure 14) which does not group forests patches from each of the Amathole and Transkei Mistbelt together. The NMDS plot (Figure 15) is a little clearer in this regard.

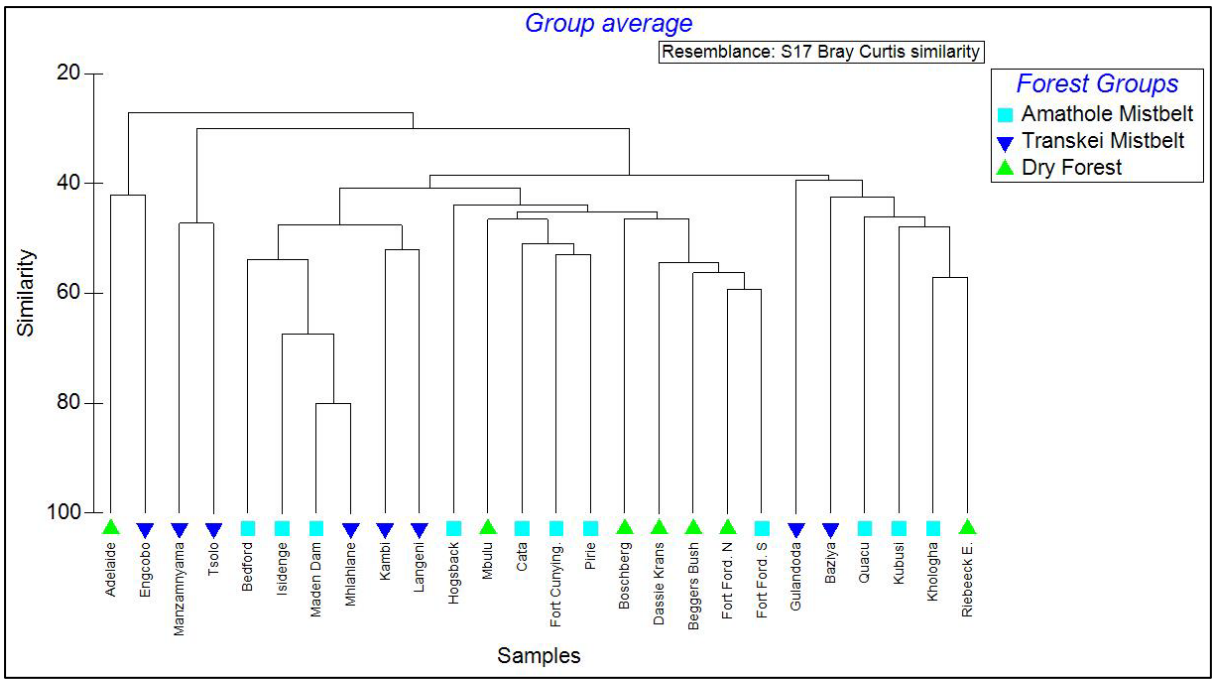


**Figure 14: Dendogram using tree species data sampled from the different forest patches. Coloured symbols correspond to forest group/type**

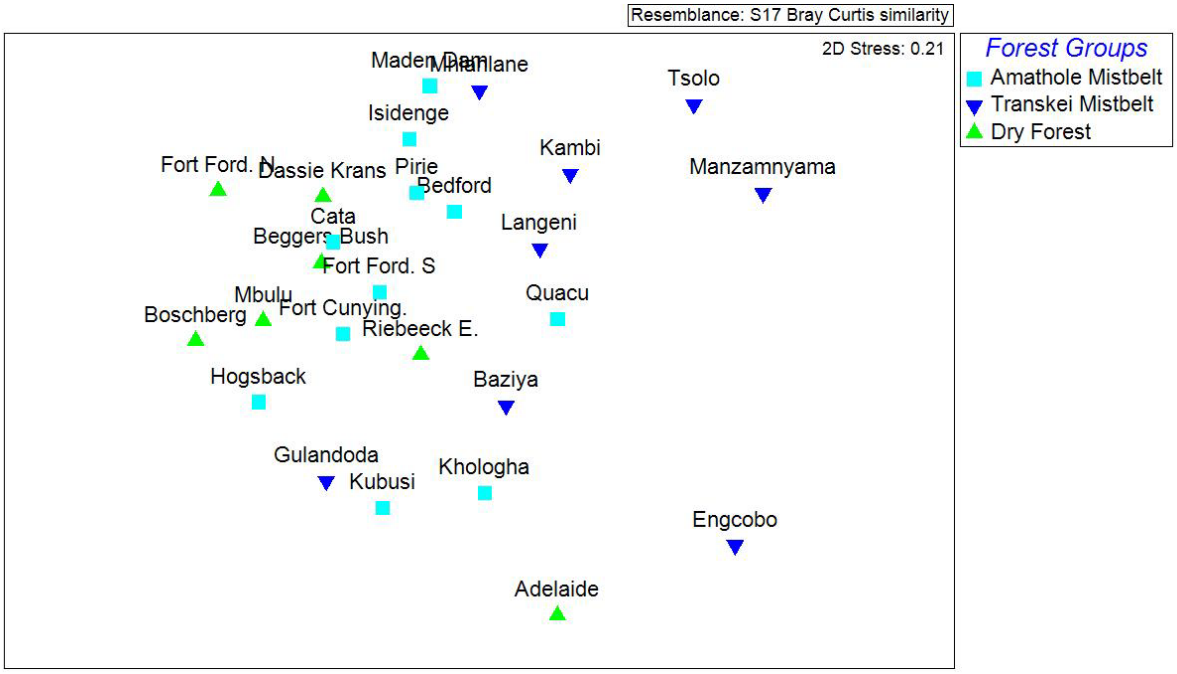


**Figure 15: 2D NMDS ordination plot from the total number of tree species collected at each forest patch**

When only herbaceous species are considered, the clustering analysis (Figure 16) indicated that there was some evidence favouring the recognition of the two forest types. Engcobo and Gulandoda were the only exceptions as they shared similar herbaceous species diversity with forest patches from Amathole Mistbelt group. This result is mirrored in the NMDS analysis (Figure 17).

The Von Maltitz *et al*. (2003) classification is thus partially supported only when using the full species data set, but these data suggest an additional vegetation type comprising Dry Forests.

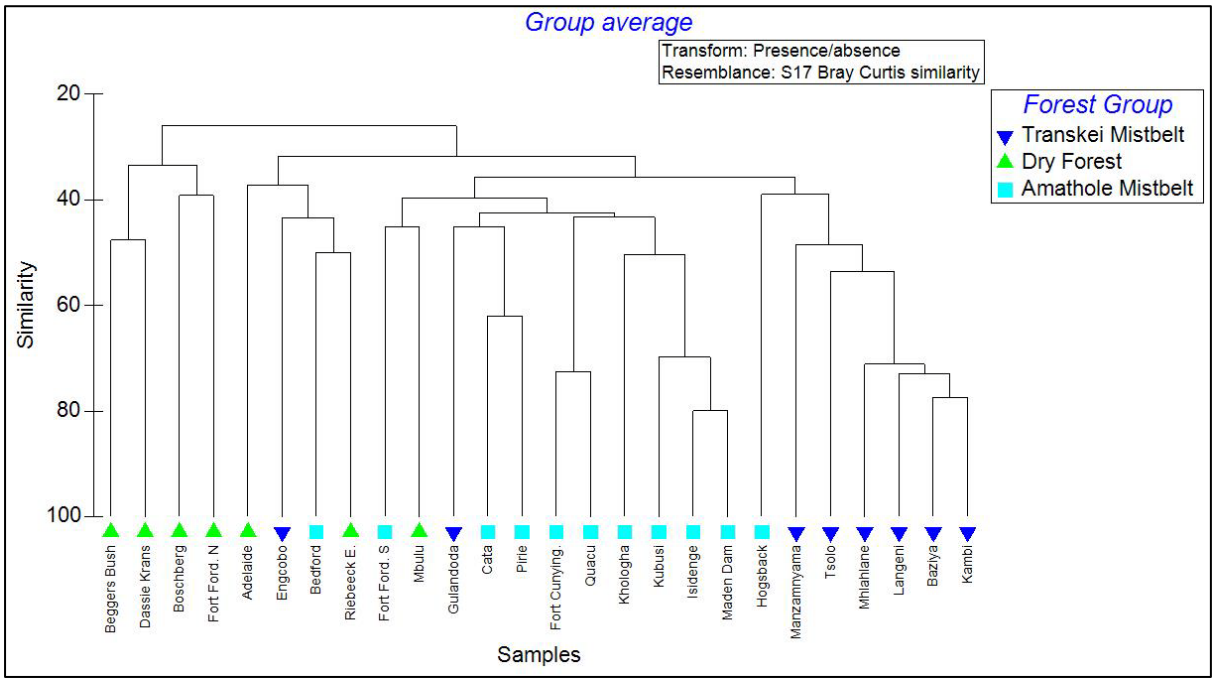


**Figure 16: Dendogram plot for the total number of herbaceous species sampled from the different forest patches. Different coloured shapes represent the different forest groups.**

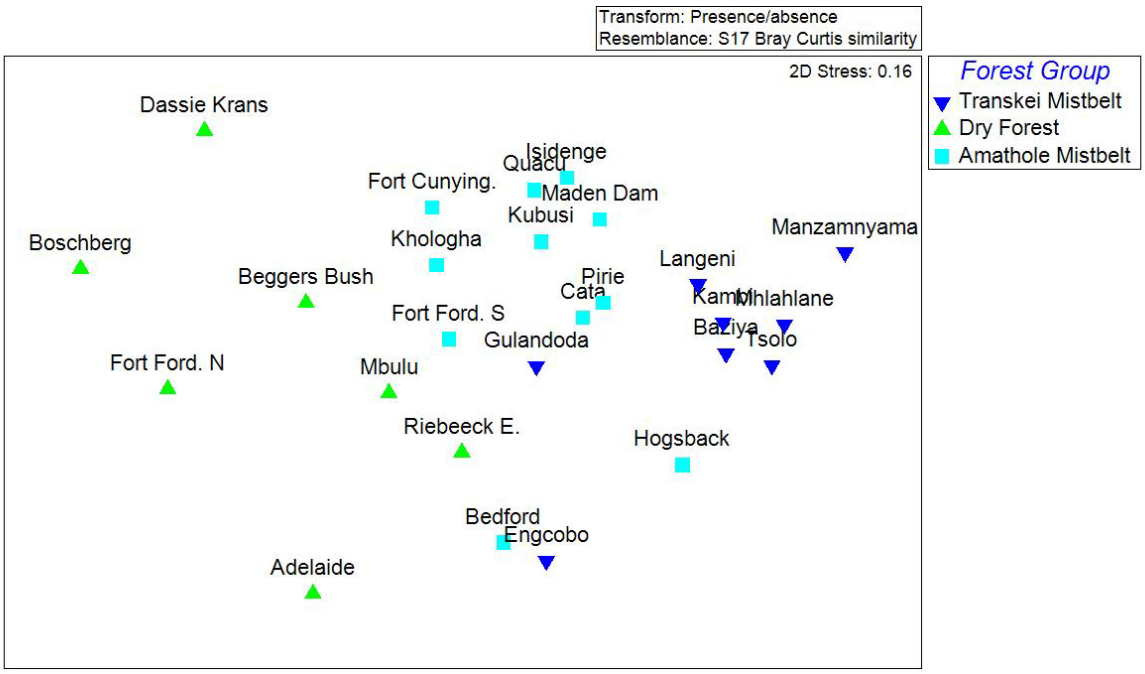


**Figure 17: 2D NMDS ordination plot from the total number of herbaceous species sampled from the different forest patches.**

### *2.4.5. Diameter at Breast Height Analysis*

The mean DBH of the individual forest patches indicated that the tree species in the different forest patches are small (Table 3; Figure 18 and 19). Beggers Bush and Mhlahlane forest had the smallest and largest means, 13cm and 27 cm respectively (Table 3). Most forests have very skewed plots showing a bias towards smaller trees. Exceptions are Hogsback, Isidenge, Quacu, and Khologha. These forests may have been protected for a long time, similarly they occur in wetter regions and therefore able to possibly recover faster. However it must be noted that not much can be concluded about the regeneration patterns of these forest patches as the data on younger individuals of tree species is lacking (only plants with stem diameters of 5cm or more were sampled). However; methods could be modified for a future study to incorporate stem diameters that are less than 5cm by subsampling within the existing plots.

DBH recorded were then grouped into eleven classes and the number of stems in each class was counted and recorded in Appendix F. Bedford, Kubusi, Khologha, Engcobo, Baziya, Langeni, and Mhlahlane were the only forest patches with DBH records above 100cm (Appendix F; Figure 18 and 19), indicating that some of the big trees survived historical timber harvests.

The top ten species in each forest patch are listed in Appendix G. The results indicate that there is a considerable variation in the top ten most frequent species of the different forest patches. *Podocarpus latifolius, Olea capensis* and *Trichocladus ellipticus* are the three most common tree species in the Southern Mistbelt Forests. *Scutia myrtina* occurred in the Amathole Mistbelt, *Ocotea bullata* and *Podocarpus henkelii* occurred within the Transkei Mistbelt however; a sample of *Ocotea bullata* was recorded in Fort Fordyce South (Appendix C).

**Table 3: Summary of DBH analysis showing diversity in tree sizes in Southern Mistbelt Forest patches.**

| Forest | Mean DBH (cm) | Total stems | Max DBH (cm) | Min DBH (cm) | SD of DBH |
|---|---|---|---|---|---|
| **Adelaide** | 16 | 125 | 94 | 5 | 16 |
| **Baziya** | 23 | 383 | 145 | 5 | 20 |
| **Bedford** | 17 | 343 | 125 | 5 | 16 |
| **Beggers Bush** | 13 | 276 | 61 | 5 | 9 |
| **Boschberg** | 16 | 194 | 76 | 5 | 10 |
| **Cata** | 16 | 252 | 84 | 5 | 13 |
| **Dassie Krans** | 15 | 177 | 74 | 5 | 12 |
| **Engcobo** | 23 | 82 | 139 | 5 | 18 |
| **Fort Cunyingham** | 13 | 205 | 66 | 5 | 7 |
| **Fort Fordyce North** | 14 | 180 | 58 | 5 | 10 |
| **Fort Fordyce South** | 21 | 682 | 81 | 5 | 15 |
| **Gulandoda** | 17 | 171 | 95 | 5 | 13 |
| **Hogsback** | 19 | 331 | 92 | 5 | 13 |
| **Isidenge** | 18 | 243 | 97 | 5 | 13 |
| **Kambi** | 20 | 232 | 105 | 5 | 18 |
| **Khologha** | 18 | 201 | 135 | 5 | 18 |
| **Kubusi** | 20 | 214 | 110 | 5 | 16 |
| **Langeni** | 25 | 228 | 150 | 5 | 22 |
| **Madem Dam** | 19 | 372 | 90 | 5 | 13 |
| **Manzamnyama** | 21 | 144 | 96 | 5 | 20 |
| **Mbulu** | 18 | 95 | 96 | 5 | 20 |
| **Mhlahlane** | 27 | 660 | 179 | 5 | 28 |
| **Pirie** | 20 | 334 | 96 | 6 | 16 |
| **Quacu** | 22 | 142 | 83 | 5 | 17 |
| **Riebeeck East** | 19 | 150 | 64 | 5 | 14 |
| **Tsolo** | 19 | 120 | 93 | 5 | 18 |
| **Total** | **489** | **6536** | **2584** | **131** | **405** |

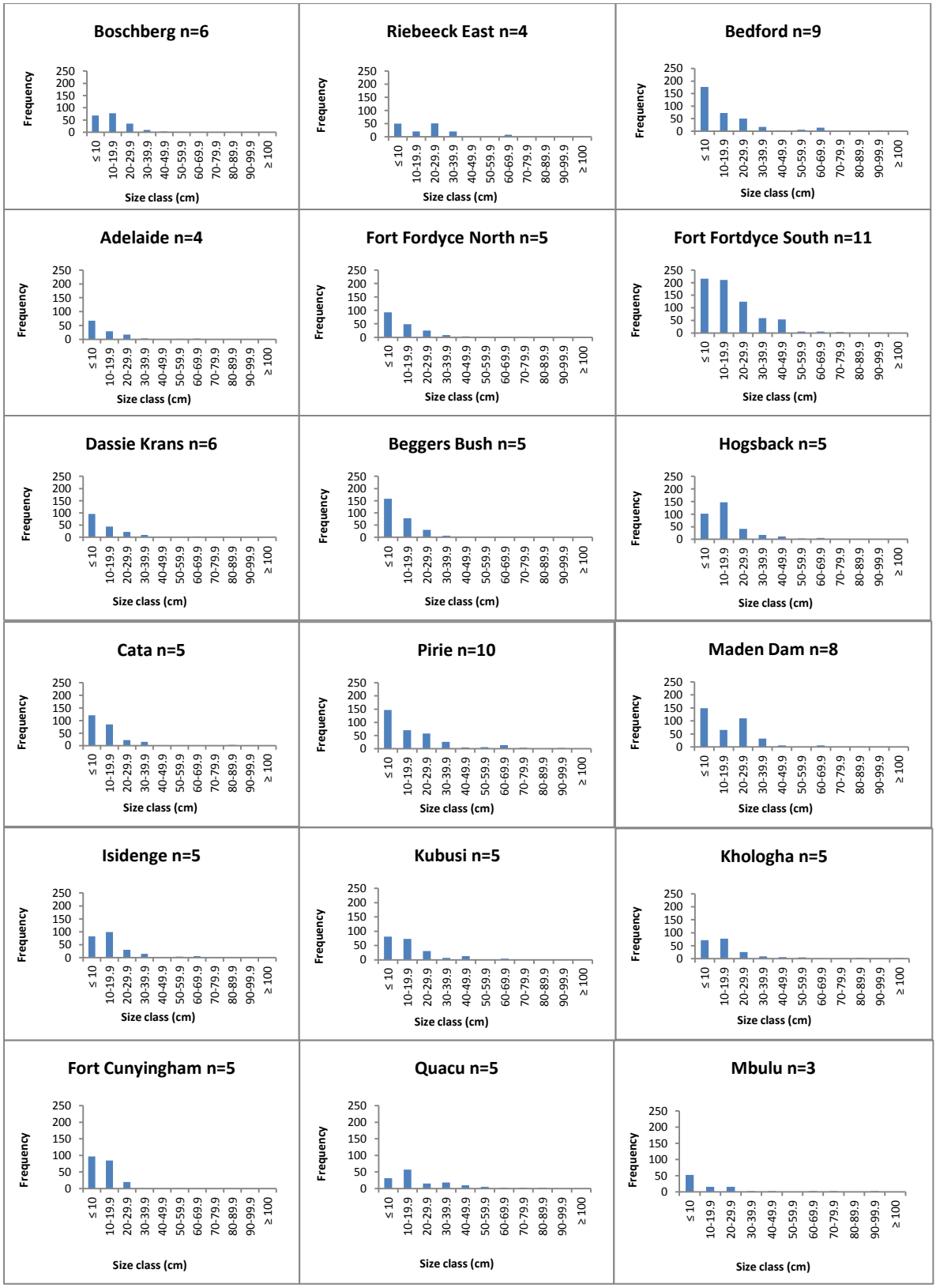


**Figure 18: The population structure of the tree species sampled in the Amathole Mistbelt Forests. X axis represents size class and Y the number of plants in each class. The number next to each heading represents the number of plots sampled from each forest patch.**

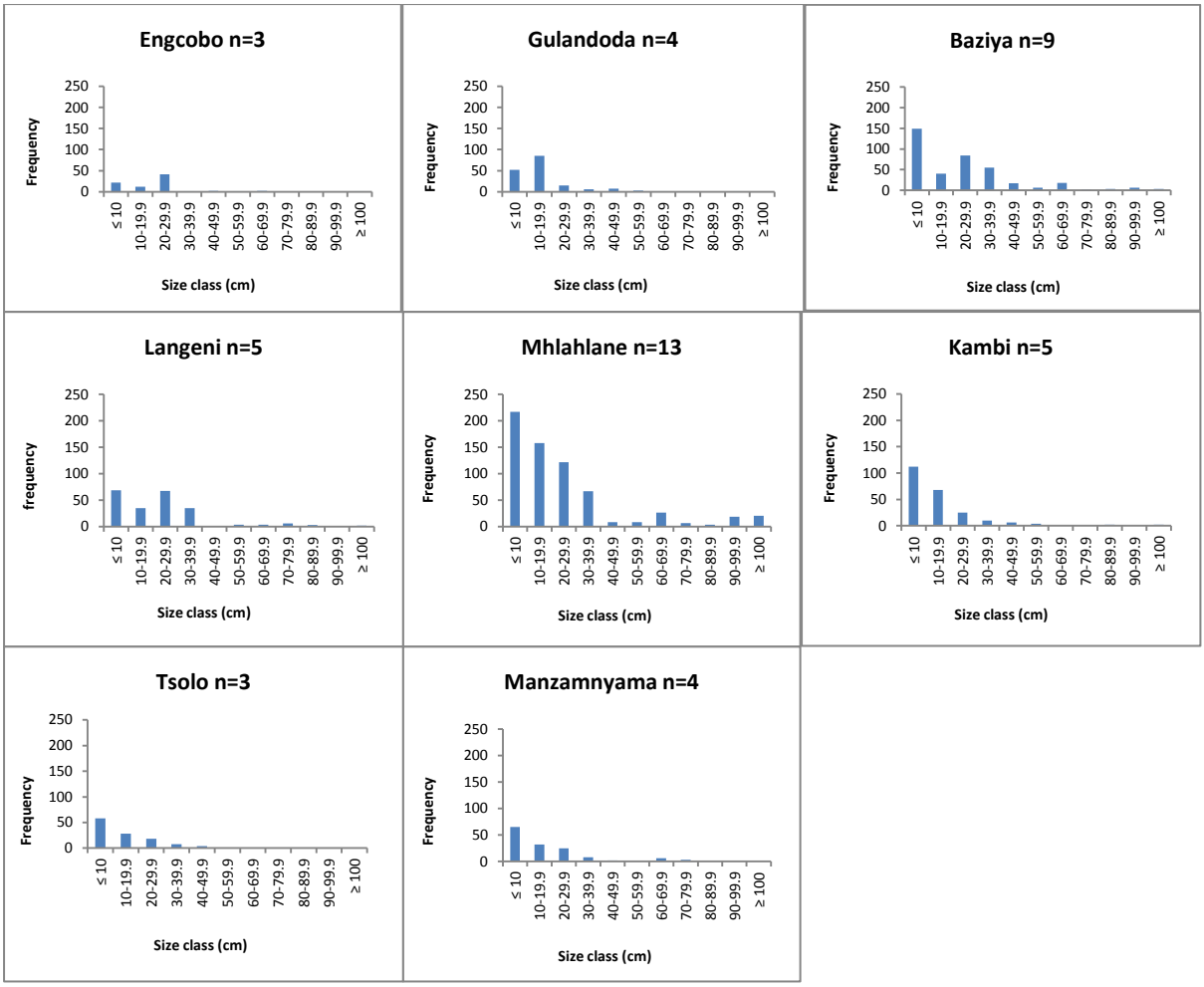


**Figure 19: The population structure of the tree species sampled in the Transkei Mistbelt Forests. X axis represents size class and Y the number of plants in each class. The number next to each heading represents the number of plots sampled from each forest patch.**

## 2.5. Conclusion

The analysis of floristic data from the plots indicated that there were more herbaceous species collected per plot than tree species. The presence of a high number of species in a few plots indicated that there was an uneven distribution of species within and between forest patches.

The Southern Mistbelt Forest patches showed discrete forest-specific composition (Figure 5 and 9). This was more obvious when examining herbaceous species diversity. Geographical distance and species diversity were not correlated, but a trend of decreasing similarity between forest patches with increasing distance for the herbaceous species and the total number of species was observed. Forest patches in the east were more diverse than patches situated in the western part of the escarpment. Patch-specific clustering may show evidence of nestedness in fragmented sites, and this will be investigated in the following chapter.

Additional studies are needed to determine whether the patterns observed in the present study occur in other forest types in South Africa, and how specific ecological and environmental factors shape diversity and composition. Such studies will help with establishment of conservation priorities for forests in these landscapes.

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# Chapter 3: Is there evidence of Species Nestedness in Southern Mistbelt Forest patches?

## 3.1. Introduction

Species-area relationships have been used to describe patterns of species distribution (e.g. Gilpin and Diamond 1976 and Lomolino 1990) and also study the patterns of richness within fragmented habits (e.g. Lomolino *et al.* 1989 and Blake 1991). The most notable of these studies is MacAuthur and Wilson's (1967) "The Theory of Island Biogeography". The theory hypothesized that the number of species on islands was the result of extinction and colonization events such that as island size decreased, extinction rate increased, and colonization rates increased when islands are closer to the mainland (MacAuthur and Wilson 1967). As a result islands further away from the mainland would contain the least amount of species. Although The Theory of Island Biogeography was the most popular approach taken to address ecological studies regarding species distribution, there remain a number of alternative approaches that have been suggested by scholars. These theories include random placement (Coleman 1981), disturbance (McGinness 1984), habitat diversity (Abbott 1974), and nested subsets (Patterson and Atmar 1986). The latter is the most popular in ecological community assemblage descriptive studies. Nested subset of species are considered very important in conservation biology because if smaller islands contain few common species and only larger islands are species rich, this would indicate the need to preserve larger islands (Patterson 1987).

### *3.1.1. Nestedness*

Whittaker (1992) questioned "whether the species composition of isolated communities is primarily the result of random processes, or is structured by ecological processes". If species of smaller communities (i.e. those with fewer species) form subsets of species in larger communities (i.e. those with higher species richness) this pattern is referred to as nestedness (Patterson and Atmar 1986; Patterson 1987; Lomolino 1996). This pattern of composition has received considerable attention and many efforts have been made to test hypotheses about ecological processes that may lead to nestedness (e.g. Lomolino 1996).

Patterson and Atmar (1986), Wright *et al.* (1998), and Fleishman and Murphy (1999) are amongst some who have studied and compared species composition in isolated and fragmented communities of different sizes to provide evidence that they were "nested". Several methods of nestedness analyses have been used to evaluate the patterns of species distribution for a variety of taxa (including birds, mammals, fish, insects, parasites, fungi and plants) within a fragmented system of either forest patches or islands (Cam *et al.* 2000; Martinez-Morales 2005; Wethered and Lawes 2005; Dobrovolski *et al.* 2012; Olivier and van Aarde 2014; Lehman 2006; Menezes and Fernandez 2013; Novack *et al.* 2011; Miyazono and Taylor 2013; Kusch *et al.* 2005; Berglund and Jonsson 2003; Norton *et al.* 2004; Matthews 2004; Spyreas and Matthews 2006; Page *et al.* 2009; Hu *et al.* 2011). When used in conjunction with measures relating species diversity to area, nestedness analyses provide information on the extent of rare species and their distributional patterns among patches of different sizes (e.g. Kadom 1995; Cook and Quinn 1995; Weiher *et al.* 1998; Honnay *et al.* 1999).

Nestedness is measured using absence and presence matrices, where 1 represents the presence of a species on an island and 0 its absence. Each column in the matrix represents a species, and is ordered in decreasing occurring frequency on the islands. The islands are arranged in rows from top to bottom in decreasing order of species diversity (i.e. number of species on each island). Common species on the most species diverse island are placed on the left hand corner of the matrix. The matrices are assessed for "gaps" where there is an absence of the species distribution; these gaps are considered to be the result of extinction events and cause deviation from a perfectly nested arrangement within the system (Culter 1991). However, this could also be as a result of inadequate sampling effort. The number of gaps may differ from individual species represented in the matrices.

Perfect nestedness (from area A to E with E being the smallest, Figure 20A) exists when the species of one island (the smaller island) is an exact subset of all assemblages with higher species richness (Patterson and Atmar 1986; Brualdi and Sanderson 1999; Roberts 2002). In Figure 20A the matrix is highly nested, only two species pairs (10 and 7, 10 and 9) form checkerboard distributions and species 1 through 9 form a perfectly nested pattern. Most systems, however, show some divergence from perfect nestedness. Maximal nestedness (Figure 20B) occurs if unexpected absences exist within the distributions of one or more species (discrepancies within a continuous species distribution), yet a reordering of islands with equal species richness will not produce a smaller number of deviations from perfect nestedness (Atmar and Patterson 1993). Figure 20B is the typical product of passive sampling from a metacommunity having a lognormal species abundance distribution (Ulrich and Gotelli 2007). Figure 20C is a typical product of a sampling from an equiprobable distribution (Ulrich and Gotelli 2007). The matrix in Figure 20D has nearly the

maximum number of checkerboards without any exclusive species combinations; it is highly disordered (Ulrich and Gotelli 2007). Checkerboard distributions (Figure 20C and 20D) and missing species combinations are attributed to species competition, environmental filters, unique habitat associations, limited dispersal, and also historical or evolutionary processes (Ulrich and Gotelli 2007; Ulrich 2004; Peres-Neto *et al.* 2001; Gotelli *et al.* 1997).

A

| | A | B | C | D | E |
|---|---|---|---|---|---|
| 1 | 1 | 1 | 1 | 1 | 1 |
| 2 | 1 | 1 | 1 | 1 | 0 |
| 3 | 1 | 1 | 1 | 1 | 0 |
| 4 | 1 | 1 | 1 | 1 | 0 |
| 5 | 1 | 1 | 1 | 0 | 0 |
| 6 | 1 | 1 | 1 | 0 | 0 |
| 7 | 1 | 0 | 0 | 0 | 0 |
| 8 | 1 | 1 | 0 | 0 | 0 |
| 9 | 1 | 0 | 0 | 0 | 0 |
| 10 | 0 | 1 | 0 | 0 | 0 |

B

| | A | B | C | D | E |
|---|---|---|---|---|---|
| 1 | 1 | 1 | 1 | 1 | 1 |
| 2 | 1 | 1 | 1 | 1 | 1 |
| 3 | 1 | 1 | 1 | 1 | 0 |
| 4 | 0 | 1 | 1 | 1 | 0 |
| 5 | 1 | 1 | 1 | 0 | 0 |
| 6 | 1 | 1 | 0 | 1 | 0 |
| 7 | 1 | 0 | 1 | 0 | 1 |
| 8 | 0 | 1 | 0 | 0 | 0 |
| 9 | 1 | 0 | 0 | 0 | 0 |
| 10 | 1 | 0 | 0 | 0 | 0 |

C

| | A | B | C | D | E |
|---|---|---|---|---|---|
| 1 | 1 | 1 | 0 | 1 | 1 |
| 2 | 1 | 0 | 1 | 0 | 1 |
| 3 | 1 | 0 | 1 | 1 | 0 |
| 4 | 0 | 1 | 0 | 1 | 1 |
| 5 | 1 | 1 | 1 | 0 | 0 |
| 6 | 1 | 0 | 0 | 1 | 0 |
| 7 | 1 | 0 | 1 | 0 | 0 |
| 8 | 1 | 1 | 0 | 0 | 0 |
| 9 | 0 | 1 | 1 | 0 | 0 |
| 10 | 0 | 1 | 0 | 1 | 0 |

D

| | A | B | C | D | E |
|---|---|---|---|---|---|
| 1 | 1 | 0 | 1 | 0 | 1 |
| 2 | 0 | 1 | 0 | 1 | 0 |
| 3 | 1 | 0 | 1 | 0 | 1 |
| 4 | 0 | 1 | 0 | 1 | 0 |
| 5 | 1 | 0 | 1 | 0 | 1 |
| 6 | 0 | 1 | 0 | 1 | 0 |
| 7 | 1 | 0 | 1 | 0 | 1 |
| 8 | 0 | 1 | 0 | 1 | 0 |
| 9 | 1 | 0 | 1 | 0 | 0 |
| 10 | 0 | 1 | 0 | 0 | 0 |

**Figure 20: Four presence and absence matrices with ten species and five sites (Source: Ulrich and Gotelli 2007).**

Most species communities are nested to some degree (Patterson 1990; Cook 1995), with analyses showing a high degree of significance (e.g. p<< 0.001; Roberts 2002). Wright *et al.* (1998) showed that most species-by-site matrices that sampled at different scales revealed strong amounts of nestedness for a number of taxa in a variety of different geographical regions. Nested species assemblages which are thought to be caused by a diverse number of biotic and abiotic interactions including extinctions and colonisations (Hecnar *et al.* 2002; Matthews 2004). For example, in a fragmented habitat where a species-area relationship created a nested pattern, the first species to go extinct are the vulnerable ones (i.e. habitat dependent) although they will survive for longer in the larger species rich sites (Ricotta 2007). Colonisation probably decreases with increasing isolation, where isolated biotas contain only highly mobile species (Matthews 2004).

Extinction and colonization are the two primary mechanisms cited in literature responsible for structuring species distributions in fragmented systems. Both extinction and colonisation have different influences on the fragmented habitats. For example extinctions are area related whereas colonisations are related to the degree of isolation (Roberts 2002). Abundant species have a higher probability of being represented in a given community than rare species. This is referred to as passive sampling (Connor and McCoy 1979) and could result lead to a nested structure (e.g. Bolger *et al.* 1991; Cutler 1991; Andren 1994; Fischer and Lindenmayer 2002; Higgins *et al.* 2006). Other causes of nestedness include nested habitat types where sites containing common and rare habitat types may contain habitat generalists and specialists (Sasaki *et al.* 2012), disturbance regimes, and

patterns of hierarchical niche overlap are also supposed to create nested distributions (Kolasa 1996; Wright *et al.* 1998; Honnay *et al.* 1999; Patterson and Atmar 2000).

Critics of nestedness state that there are many uncertainties regarding mechanisms, low predictive power, and an inability to provide unambiguous recommendations regarding key issues in reserve design and management (Boecklen 1997). However, nested subset analyses can provide important descriptive information about community structure (Worthen 1996). This can be used to determine whether non-random patterns exist in natural communities, and used to determine what factors might be contributing to composition patterns within a community (Worthen 1996).

The fragmented nature and extensive distribution range of Southern Mistbelt Forest patches make them an ideal example to test for nested subsets. Using the nestedness software, *NeD*, the species diversity data for 26 forest patches of SMF obtained as outlined in the previous chapter were assessed for nestedness.

## 3.2. Methods and Material

To investigate whether there was evidence of nestedness in Southern Mistbelt Forests a nestedness analysis was conducted with the software *Nestedness for Dummies* (*NeD*; Strona and Fattorini 2014a).

*NeD* is a user friendly open source application available online. It was developed to handle different matrix formats and has outputs that can easily be copied and pasted to a spreadsheet (Strona and Fattorini 2014b). Unlike previous software *NeD* can sort data and organise it so it can be easily analysed by the application. *NeD* differs from other available software in that is allows the user to decide whether to keep or exclude empty rows and columns (Strona and Fattorini 2014b). *NeD* also provides graphic representation of the matrix under examination and the corresponding maximally packed matrix (Strona and Fattorini 2014b). It uses the three most recommended and generally used metrics in the literature which can be used with different null models. These metrics include Matrix temperature (MT) (Atmar and Patterson 1993), Brualdi and Sanderson discrepancy (BR), and the nestedness measure based on overlap and decreasing fills (NODF) (Ulrich and Gotelli 2007). MT has been used as the standard measure of nestedness in ecological studies for species distribution between sites. It measures the rate of occurrence in the matrix as it departs from perfect nestedness (Atmar and Patterson 1993). The rows and columns are re-ordered using Euclidean distances so that nestedness is maximized. BR is the count of the minimum number of discrepancies, i.e. the number of absences and presences that must be modified to produce a perfectly nested matrix (Strona and Fattorini 2014b). NODF based on presence and absence metric and abundance data, calculates the nestedness metrics for distinctive species and sites (Strona and Fattorini 2014b).

The matrices are constructed using the 'proportional row and column total' algorithm, which is considered to be the most biologically realistic (Bascompte *et al*. 2003) and recommended by Strona and Fattorini (2014c). The way a matrix is packed can significantly influence the outcome of the nestedness results. *NeD* reorders the original matrix according to row and column totals which is a default method in all the available nestedness programs. The null model thus functions as a standard statistical null hypothesis for detecting pattern, in contrast to a scientific hypothesis, which is a mechanism to explain the pattern (Strona and Fattorini 2014b). *NeD* provides three null models that assess the significance of the selected metrics (MT, BR, and NODF). A null model is "a pattern-generating model that is based on randomization of ecological data, certain elements of the data are held constant and others are allowed to vary stochastically. The randomization is designed to produce a pattern that would be expected in the absence of a particular ecological mechanism"

(Gotelli and Graves 1996). Null models are developed to analyze for example, species-area relationship, phylogenetic diversity within communities, nestedness, and species co-occurrence (Srivastava 2010).

According to Strona and Fattorini (2014c) the program can implement five null model algorithms namely: 1) Equiprobable row totals, equiprobable column totals (EE) maintains the total number of species occurrences in the matrix. 2) CE (proportional row totals, proportional column totals) assigns to each matrix cell a probability to be occupied proportional to the corresponding row and column totals. 3) Equiprobable row totals, fixed column totals (EF) maintains observed column totals but allows row totals to vary randomly, thus preserving the species richness per site (column totals) and allows species occurrence (row totals) to vary randomly. 4) FE (fixed row totals, equiprobable column totals) maintains observed row totals (i.e. species occurrence frequencies) but allows column totals (species richness per site) to vary randomly. 5) FF (fixed-fixed) matrices created this way have the same row and column totals as the original.

Most scholars (e.g. Bascompte *et al.* 2003; Nielsen and Bascompte 2007; Krishna *et al.* 2008; Carstensen and Olesen 2009; Graham *et al.* 2009) tend to favour the CE null model analysis because "the statistical power of the FF null model decreases as matrices tend towards perfect nestedness, because the number of possible alternative configurations of a given matrix with fixed row and column sums decreases with matrix nestedness (being 0 for a perfect nested matrix)" (Staniczenko *et al.* 2013). FF is more prone to type II errors, known as a "false negative", the error of not rejecting a null hypothesis when the alternative hypothesis is the true state of nature (Gotelli 2000; Ulrich and Gotelli 2012; Strona and Fattorini 2014). Therefore, CE should be considered as the preferable null model algorithm for nestedness analysis.

*NeD* also calculates *Z* values to assess significance of the measured nestedness. For the NODF metric, *Z* values > 1.64 indicate significance at $p$=0.05, while BR and MT Z values < -1.64 indicate significance at $p$=0.05 (Strona and Fattorini 2014). *NeD* is the only available software that computes values of relative nestedness (RN). Different combinations of nestedness measures and null models may lead to inconsistent outcomes. The number of null matrices is set to 50 by default, but it can be expanded up to 999 matrices. On the one hand, the larger the better, but on the other hand the larger the higher the probability of getting a low p value, which is not good (keeping in mind that the computation time increase linearly with the number of null matrices) (Strona and Fattorini 2014a).

### *3.2.1. Test for Nestedness*

The source of the data set used in this analysis was the total number of species in all the forest patches which represented the diversity of whole patches. This was obtained from the entire quadrat data from Chapter 2 including the supplementary species from the general collections. The data set was also in presence and absence format where "1" represented the presence of a plant species in a forest patch and "0" its absence (Appendix H).

The analysis was conducted by calculating a nestedness measure based on overlap and decreasing fills (NODF) and temperature matrices. The spreadsheet was ordered such that plant species were arranged in rows and the forest patches in columns. All three metrics (MT, BR, and NODF) were selected to compute nestedness. *Z*, RN and p values were obtained by generating 100 null matrices and the data matrix rearrangement rule selected was CE, for reasons provided above (and as per personal communication with G. Strona, Institute for Environment and Sustainability, Italy).

## 3.3. Results

The presence and absence matrix revealed significant nestedness: NODF Z value was 8.862 which was greater than 1.64 with significance at $p<0.001$. BR and MT Z values were -14.258 and -11.26 respectively with significance at $p<0.001$ (Table 4; Appendix I).

Strona and Fattorini (2014b) stated that nestedness values should be standardized to avoid errors associated with null models. For example the Temperature index (Atmar and Patterson, 1993) is negetively correlated with the size and fill of the matrix (Ulrich and Gotelli, 2007), thus a large matrix is expected to have a low temperature independently from the way species are distributed among areas (Strona and Fattorini, 2014b). NODF is affected by the matrix fill but not the matrix size and shape (Almeida-Neto et al. 2008). This is particularly important for this study because the results are not biased by the fact that the matrix was large.

**Table 4: Summary results of nestedness from the forest dataset using CE null models algorithm and selected metrics.**

| | | Nestedness Measures: | | | |
|---|---|---|---|---|---|
| **Null Model** | **Fill %** | **METRIC** | **INDEX** | **Z-SCORE** | **NESTED?** |
| CE (Forests) | 15.1 | NODF | 25.266 | 8.862 | Yes (p<0.001) |
| Appendix I | 15.1 | NODF_row | 25.203 | 8.767 | Yes (p<0.001) |
| | 15.1 | NODF_col | 45.116 | 25.91 | Yes (p<0.001) |
| | 15.1 | T | 26.285 | -11.26 | Yes (p<0.001) |
| | 15.1 | BR | 901 | -14.258 | Yes (p<0.001) |

## 3.4. Discussion

The CE null model produced significantly nested results (Table 4). Species of less diverse communities (i.e. those with fewer species) form subsets of species in more diverse communities (i.e. those with more species) (Patterson and Atmar 1986; Patterson 1987; Lomolino 1996). By observing the Packed Column and Row Order in Appendix I it was observed that area did not influence the nestedness structure of plant species in these forest patches because it would have been expected that forest patches with the greatest area (usually associated with higher diversity) would be packed first. However that was not the case. The results suggest that although there was evidence of nestedness, species occurring at less diverse forest patches are always present in a more species-rich patches, whereas plant species absent from a more diverse forest patch never occured in a less species-rich one. Therefore, columns packed first (Mhlahlane) have more species than those packed last (Boschberg).

Kadmon (1995) showed that communities (with respect to woody plant communities) were nested with respect to isolation but not island size suggesting that species dispersal abilities were critical and that species with limited dispersal abilities were strongly nested. This explains how nestedness analysis could be used to answer questions regarding the factors affecting community structure (Worthen 1996). Generalist species should be found in most fragmented patches whereas specialists will be limited to areas where their minimum requirements are met. Large areas usually have the greater functional diversity than smaller areas thus leading to the assumption that communities with nested niches show the strongest relationship between nestedness, richness and area (Worthen 1996). However, in these communities nestedness is a result of habitat variability among these systems (Worthen 1996). For example, if these communities vary then they contain different specialists which create a strong species-area relationship even if the communities are not nested (Patterson and Brown 1991). Differences in species colonisation rates have also been acknowledged as potential causes for nested subsets (Darlington 1957; Diamond and May 1976; Diamond and Gilpin 1982; Patterson and Atmar 1986). Species with the greatest dispersal mechanisms are usually found in isolated fragments and those with poorer dispersal mechanisms should be found close to the mainland (Worthen 1996).

For most nested communities extinction and colonisation probabilities have usually been attributed to subset structure (Schoener and Schoener 1983; Jones *et al.* 1985; Patterson and Atmar 1986; Roughgarden 1979; Bolger *et al*. 1991; Newmark 1991; Patterson and Brown 1991; Soule *et al.* 1992). Little attention has been given to other potential explanations of nested structures that are as

important, if not more, than the traditional proposed probabilities. Lawes *et al.* (2007) suggested that these forests (including Southern Mistbelt Forests) were affected most by climatic extinction filtering events but their study focused on faunal exclusions in these forest patches. Nonetheless, the concept also applies to the flora of these patches.

Honnay *et al.* (1999) suggested that neither extinction nor colonization structured plant distributions in forest habitat patches in Belgium. Instead, habitat diversity within each patch was the key factor influencing species distributions, with area or isolation having little impact. Honnay *et al.* (1999) suggested that if it is assumed that only differential colonisation played a role, then one would expect a nested species pattern with respect to the degree of patch isolation. Honnay *et al.* (1999) concluded that forest-core plant species occurance was not dominated by colonization and/or extinction processes. Nested structures were as a result of patch specific ecological habitat dynamics resulting in species with particular traits occupying certain forest patches leading to the nested structure in forest patches. Selective environmental tolerances imposed by environmental harshness and species environmental tolerances (Driscoll 2008) can also form nested subsets. Communities with relatively harsh environmental conditions can include less species than sites with relatively benign environmental conditions due to environmental sorting (Sasaki *et al.* 2012). Habitat rich patches will support nearly all species whereas habitat poor patches will support generalists (Honnay *et al.* 1999). Nestedness is therefore generated by differences in habitat specializations where species persistance may be the occurance of local adaptation in isolated plant communities. This will be discussed further in the next chapter (Chapter 4) in which the variability in environmental data for the forest patches is assessed.

It is unfortunate that the software used here does not identify species that contribute to nestedness patterns in SMF, because analysis of their life history traits would be most enlightening. Saavedra *et al.* (2011) stated that nestedness contributors are more prone to extinctition under environmental and ecological stress compared to those that contribute less, which makes these species a priority for conservation in this changing climate.

## 3.5. Conclusion

The Southern Mistbelt Forests in the Eastern Cape are significantly nested. The size (area) of the forest patch did not play a role in the nested structure of these forest patches because the more diverse forest patches were not the ones with the greatest area, suggesting that smaller forest patches should be prioritised in conservation and management as they are biodiversity contributors.

The analysis of SMF forest patches and the majority of previous studies suggested that most fragmented biotas are significantly nested (Atmar and Patterson 1993; Wright *et al.* 1998). Species extinction patterns are highly predictable in these nested biotas (Atmar and Patterson 1993). These patterns are thus important to conservation biology and related practises. However, there is considerable variation in nestedness among species distributions in fragmented patches, some of which could be related to physical and historical background of these patches (Roberts 2002). The more nested a fragmented biota is, the more likely it is that a single large patch would preserve more species (Boecklen 1997). By considering the SLOSS (Single Large or Several Small) debate, the results obtained in this study suggest that SS (Several Small) fragments always have higher diversity than SL (Single Large) fragments of the same area. This contradicts the assumption that significant internal nestedness implies that groups of small patches support less species than one large patch of the same total size (Wright and Reeves 1992). However, nestedness is a poor predictor of SLOSS, as the vast majority of archipelogoes support a strategy of several small reserves, even though almost all of them are significantly nested (Boecklen 1997). This is important with regard to Southern Mistbelt forests in South Africa as the biggest forest patches are given more prioritised even though all forests are protected under the Forest Act. This study shows the importance of smaller forest patches and their key contribution to South Africa's forest biodiversity.

Although extinction and colonisation probabilities have long been used as key explanations of nestedness, ecological and environmental factors have also been suggested but not as often. In the following chapter we will attempt to address this gap by trying to explain the nestedness pattern observed in this study using environmental factors.

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# Chapter 4: Can patch diversity and nestedness be explained by climate filtering?

## 4.1. Introduction

The constraints to community assembly have been debated for centuries by ecologists, but are not properly resolved even in the present day and these questions still need to be answered (Temperton and Hobbs 2004). Some ecologists suggest that interactions between the environment and species and also organisms with each other restrict a community's development and structure (Temperton and Hobbs 2004). Keddy (1992) suggested that given a regional species pool and certain set of environmental conditions, one could predict which subset of organisms would occur in a particular habitat. If the regional pool of species consists of species with traits sorted along some environmental gradient, then the environmental conditions within any locality will favour different sets of species (Chase and Leibold 2003). That is, along an environmental gradient, we are essentially exploring how changing resource or stress supply would alter the species composition along that gradient (Chase and Leibold 2003). This is known as "Climate Filtering" and refers to the removal of species along a gradient due to their inability to survive in increasingly extreme conditions (Barker *et al.* 2013). Environmental variables will produce different sets of species combinations in different local communities (e.g. forest patches) (Chase and Leibold 2003).

Differential rates of local colonization and extinction are the main factors used to explain nested subset distributions (Lomolino 1996). Using environmental surrogates of extinction and colonisation to evaluate nestedness makes it possible to evaluate the causes of nestedness patterns (Heino *et al*. 2010). Relatively few studies on forest plant species assemblages (trees or vascular plants studies separately) reported positive nestedness results but failed to examine potential mechanisms causing the nested subset distribution pattern.

Several mechanisms such as passive sampling (Cutler 1998), selective extinction (Rosenzweig 1995; Wright *et al.* 1998), colonization (Kadmon 1995; Lomolin 1996), habitat characteristics (Honnay *et al.* 1996; Fleishman *et al.* 2007), and nested habitats (Wright *et al.* 1998; Honnay *et al.*1999) have all been linked in the production nested subset distribution pattern. Habitat characteristics, particularly

that of the environmental tolerances and structure, have received little attention in terms of their effects on nestedness despite many studies on plants, birds and invertebrates showing its importance (Honnay *et al*. 1999; Calme and Desrocher 1999; McAbendroth et al. 2005; Heino 2009, 2010). Mutairi *et al.* (2012) suggested that differences in environmental tolerances among species may interact with nested habitats to produce nestedness. This hypothesis suggests that species-rich sites are those that contain the greatest habitat heterogeneity and/or have environmental conditions tolerable to the largest number of species (Cook 1995; Honnay *et al.* 1999). Species distributions along environmental gradients have been studied since the 1950's. Whittaker (1956) discussed whether species were replaced by other species, or new species were added but few were lost (nested subsets). According to Mutairi *et al.* (2012) differential nestedness among groups of species (e.g. taxonomic groups or guilds) that vary in sensitivity to a particular environmental variable may determine how the variable contributes to the general pattern of species nestedness.

A number of studies have been done in South Africa to identify the drivers of forest communities but most of them are based on animal studies and a few are available on plant species (e.g. Geldenhuys 1993a, b). This chapter provides insights into the drivers of Southern Mistbelt forest patch vegetation patterns which will improve our understanding of the community structures of forests. The aim of this chapter was to determine whether nestedness could be explained by climate filtering by assessing the influence of environmental variables on forest patch diversity by using the canonical correspondence multivariate ordination methods.

## 4.2. Materials and Methods

Various environmental variables were measured and incorporated into analyses to assess their effect on or correlation with plant diversity. These variables were obtained as follows:

### *4.2.1. Climate data*

The South African Atlas of Climatology and Agrohydrology (SAACA) was used to obtain climate variables. These variables included mean annual precipitation (MAP), mean annual temperature (MAT), mean annual potential evapotranspiration (MAPE) and mean annual humidity (MAH).

SAACA is a data base which provides detailed spatial and temporal environmental data for South Africa and its neighbouring countries (Schulze *et al.* 2007). It provides a broad picture of climate parameters (e.g. precipitation, temperature etc.) in South Africa. Although some of the data provided is site specific, some of the information in based on statistical analysis and simulation modelling (Schulze *et al.* 2007).

As a consequence of the manner in which the SAACA data is calculated, iButton data loggers were used to obtain the exact temperature and humidity readings of the selected forest patches which were then compared to SAACA data. iButtons were placed in six forest patches (Beggers Bush, Bedford, Hogsback, Pirie, Maden Dam, and Mhlahlane(Langeni)). The number of iButtons placed in a forest depended on the size of the patch. In larger patches (Bedford, Maden Dam, and Mhlahlane) 2 iButtons were placed. The iButtons were programed to record temperature and humidity every two hours, these were logged during the the initial sampling trips in 2013 (January-March). The logged data was than downloaded every 6months, the devices were then recalibrated and restarted. When all the data was collected from the individual patches and exported as CSV (*csv) files (Appendix J), the data was then used to produce temperature and humidity graphs on *Microsoft Excel,* and compared to SAACA data.

In order to determine whether the SAACA data was reliable a number of iButtons were placed in selected forest patches across the Amathole and Transkei Escarpments. iButtons were glued in plastic bottles with perforations and open mouth, covered with shade cloth and hung upside down from a branch at breast height and placed in the interior of the forest patch. The iButtons were distributed arbitrarily.

*4.2.2. Soil data sampling and analysis*

In order to obtain the soil variables (pH, organic matter, p

500g each) were collected from each forest patch. These standard variables were selected in order to obtain soil characterists of the the different forest patches. Soil samples were collected within the sampled plots. For the forest patches with less than 5 plots, additional samples were collected randomly during general plant collections within the forest patch. The ground was first cleared of leaf debris, a hole was dug using a hand shovel and the top soil was sampled. The depth of the hole depended on the amount of root obstruction at the surface and beneath the ground. These samples were then kept in ziplock bags which were then stored in the freezer at the Botany Department, Rhodes University for further analysis in the labotarory, as follows:

4.2.2.1. Organic Matter (Weight Loss-on-Ignition)

To obtain the amount of organic matter present from the soil samples, ten grams of sediment was weighed in porcelian crucibles using an eletronic scale balance. The sample was then placed in a drying oven at 105°C for 24 hours to remove the moisture content (Black 1965). The sample was then re-weighed (to two decimal places) and heated at 360°C in a muffle furnace for 5 hours and re-weighed after the sample had cooled to room temperatue (Briggs 1977). This sampling procedure was used to estimate soil organic matter by the loss of weight in a sample heated at temperatures high enough to burn organic matter but not so high to decompose inorganic carbonates. The advantage of this method was that no reagents were used which could alter the intergrity of the sample. The average organic content was taken from five samples from each study area and the data was reported as " % Organic Matter". The percentage of weight loss-on-ignition (LOI) was calculated as (Briggs 1977):

$$LOI = \frac{(wt.\ at\ 105°C) - (wt.\ at\ 360°\ C)}{Wt.\ at\ 105°\ C} \times 100$$

4.2.2.2. Soil pH

The soil samples were removed from the ziplock bag and added to distilled water, after which the pH was measured using a pH probe glass electrode (Metter Toledo InLab 407) that was calibrated with pH 4.0 and 7.0 (Black 1965; Middleburg *et al.* 1996; Marchand *et al.* 2004). This was done for all the 130 samples and the data was recorded as the average soil pH for each forest patch.

4.2.2.3. Soil Electrical Conductivity (EC)

EC is the ability of the soil sample to conduct an electric current measured in units of milliSiemens per meter (mS/m) (Grisso 2009). EC can also indicate the absence or presence of salts but it does not indicate which salts could be present in the sample. The conductivity of a sample can vary depending on the amount of moisture the particles hold. Sands, silts and clays all have varying conductivities, ranging from low, medium, and high respectively (Grisso 2009).

Two hundred and fifty grams of each sample was measured on a balance and placed in a beaker. Fifty millilitres (ml) of distilled water was added and mixed into the sample to make 'paste'(Ferreira et al. 2007). The amount of distilled water mixed with the sample varied with soil texture. The mixture was then left for an hour to allow for slow soluble constituents to dissolve. The paste was filtered through Whatman No. 41 paper and the extracted solution was collected in a test tube. This was done to remove soil and debris from the solution. An Electrical Conductivity Meter calibrated in 0.005M KCL solution was used to measure conductivity. All the soil analysis are recorded in Appendix K.

4.2.2.4. Soil Particle Size Analysis

Soil particle size distribution was obtained with the use of a Mastersizer 3000 particle sizing instrument. This technology delivers rapid and reliable results for dry and wet samples, and it can detect particles sizes in the nanometre range (Malvern Instruments 1997).

The samples were sieved using a 1mm sieve because the particle sizes of interest were small. Approximately 5 grams of the seived sample was placed in a 100ml beaker and mixed with 30% hydrogen peroxide to remove organic matter. The hydrogen peroxide solution was placed in a freezer for 24 hours to decrease the rate of reaction (at room temperature the samples reacted vigorously to the hydrogen peroxide and resulted in sample spilling over and volume loss).

The sample was then poured into a solution which consisted of 500ml distilled water and 0.1% dispersant of sodium hexametosphate (HMP). The exact amount of dispersent needed to prevent

flocculation was dependent on the soil type. The ultrasonic dispersion option was selected to measure particle size, which enabled the soil particles to be dispersed evenly in the solution. The results were recorded as the volume distribution percentage of the different particles in the sample.

Three important particle diameter readings were recorded; D10, D50, and D90 for the separate forest patches . These represented 10%, 50%, and 90% cummulative percentile value of the grain in microns. The most valueable of these, in terms of this research, was the D50 parameter also known as the Median diameter or Medium value of particle diameter. It was one of the key parameters that represented the characteristics of the particles of the measured sample. For a sample, if D50=5µm for example, there are 50% particles larger than 5µm and 50% smaller than 5µm (Malvern Instruments 1997). This was used as the main representative of particle size in a sample. There are no guidelines as to which size distribution to use, it all depends on what you are trying to communicate (Malvern Instruments 1997). These sample readings (D50) were all recorded in Table 4 and contributed to study area matrix that was used for other analysis.

The percentage of all the different soil textures (clay, sand, and silt) of the different forest patches were also obtained from the Mastersizer 3000 and recorded in Table 4. Using Wentworth's (1922) particle size scale and terminology; clay particle size was considered to be less than 3.91µm, silt was less than 62.50µm, and sand was greater than 62.50µm. The particle size scale was also used to obtain the actual soil texture for individual patches using ternary software from the *Precision Ag.* website. It simulated the percentages of the different textures obtained from a sample and produced a soil texture triangle which highlighted the spectrum characteristic of the tested sample. This occurred when all the three points intercepted.

### 4.2.3. *Area and Altitude*

The area in square metres and altitude, of the different forest patches was obtained using *Google Earth*.

### *4.2.4. Multivariate and Statistical Analysis*

All variables were recorded in an *EXCEL* Spreadsheet. To determine which environmental variables correlated with the different forest patches a PCA (Principal Component Analysis) was performed using *PRIMER 6*. The protocol for this analysis was as follows: A data - area matrix (Table 6) was compiled using the environmental variables measured above and from SAACA for the different forest patches. The data set was normalized in order to reduce statistical errors. The PCA option was then selected with a default of five maximum PCs.

#### 4.2.4.1. CANOCO

A unimodal method, canonical correspondence analysis (CCA, Ter Braak 1986) was performed to test niche dependency of the samples from the study areas. A CCA analysis is a method for exploring biological assemblages of species on their environmental factors (Leps and Smilauer 2003). It identifies major environmental gradients and plots ordination diagrams (Leps and Smilauer 2003).

Using the total number of species obtained from each forest patch (plot data and general collections; Appendix L) to analyse the data the following protocol was used: Hill scaling with a focus on inter-species distance in the unimodel scaling options was selected. No transformation was done to the data as it was already in absence and presence format and rare species were not downweighted. A Monte Carlo Permutations test was selected with 499 permutations for the full model.

The data was then further separated according to life forms (herbaceous and tree species; Appendix L) from each forest patch, presented as absence/presence data, and the different matrices were analysed using the above method.

#### 4.2.4.2. Regression model

In order to assess which environmental variable accounted for the most variation in these forest communities, *XLSTAT* (Addinsoft 2015), a statistical analysis add-on for *Microsoft Excel* was used to perform Multiple Regression Models. A multiple regression attempts to explain or model two or

more explanatory variables (X) and a response variable (Y) by fitting a linear equation to the data. *Excel* (*XLSTAT*) was used to model the relationship of the two life forms (tree and herbaceous species) with all the important environmental variables indicated by the CCA and test the significance of the three models.

### *4.2.5. Rank and DBH Correlations*

To determine whether individual species were affected by climate filtering a Rank analysis was conducted using species that were recorded at least five times in the different forest patches; the data was then correlated with MAP. The top ten species were ranked in descending order where the species with the most recorded number of stems was placed first (Appendix G). The rank of the species was then correlated with MAP.

In order to determine whether tree species were filtered by DBH size structure in the Southern Mistbelt Forest, the mean DBH of tree species that were common in all the forest patches were correlated with MAP and MAPE.

## 4.3. Results

### *4.3.1. Climatic variables*

Boschberg received the least amount of MAP (363mm) and also subsequently had the highest MAPE reading (1926mm), Mhlahlane had the highest (1275mm). Maden Dam had the lowest MAT and Isidenge the highest reading (10 and 17 °C respectively). Langeni had the lowest MAPE whereas Boschberg had the highest reading (1598 and 1926mm respectively). Manzamnyama reached 1543 m above sea level (a.s.l.) and Dassie Krans peaked at 695 m a.s.l. these forests were subsequently located at the highest and lowest altitude (Table 6).

The results from the iButtons placed in four forest patches is shown in Figures 21 (temperature) and Figure 22 (Humidity). Unfortunately the iButtons from Maden Dam and Bedford Forest were stolen while in the field. These results show a decrease in temperature in June for both the years (2013 and 2014), which then increased again in January corresponding (not surprisingly) to winter and summer seasonal patterns. The humidity trends were similar in all the patches, with an exeption of Mhlahlane that recorded relatively high humidity readings. Varience was high for both Temperature and Humidity readings (Table 5). Despite the high variance, the averages for both humidity and temperature were not that different from the values for these forest patches obtained from the SAACA, indicating that the SAACA data can be used as a reliable source for environmental data for these forest patches.

**Table 5: iButton summary output compared to Shultz Atlas output data.**

| | Forest | Average | Variance | SAACA |
|---|---|---|---|---|
| Temperature | Mhlahlane | 14.18 | 26.27 | 15 |
| | Hogsback | 13.82 | 29.62 | 13 |
| | Pirie | 14.23 | 29.1 | 14 |
| | Fort Fordyce | 14.91 | 30.03 | 15 |
| Humidity | Mhlahlane | 80.27 | 405.87 | 80 |
| | Hogsback | 75.3 | 586.67 | 77 |
| | Pirie | 93.45 | 594.73 | 93 |
| | Fort Fordyce | 91.37 | 553.73 | 90 |

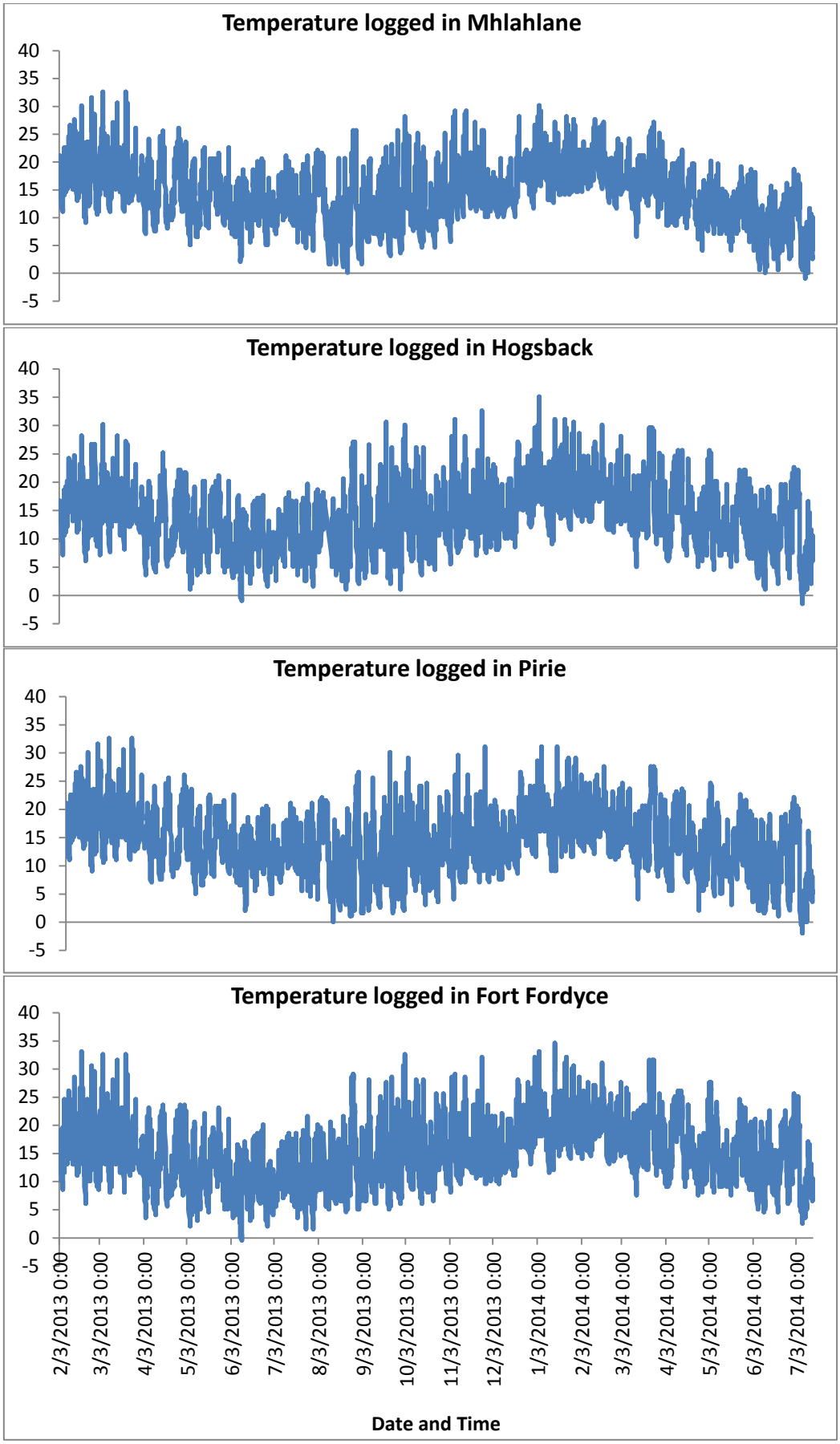



**Figure 21: Temperature readings logged at different forest patches.**

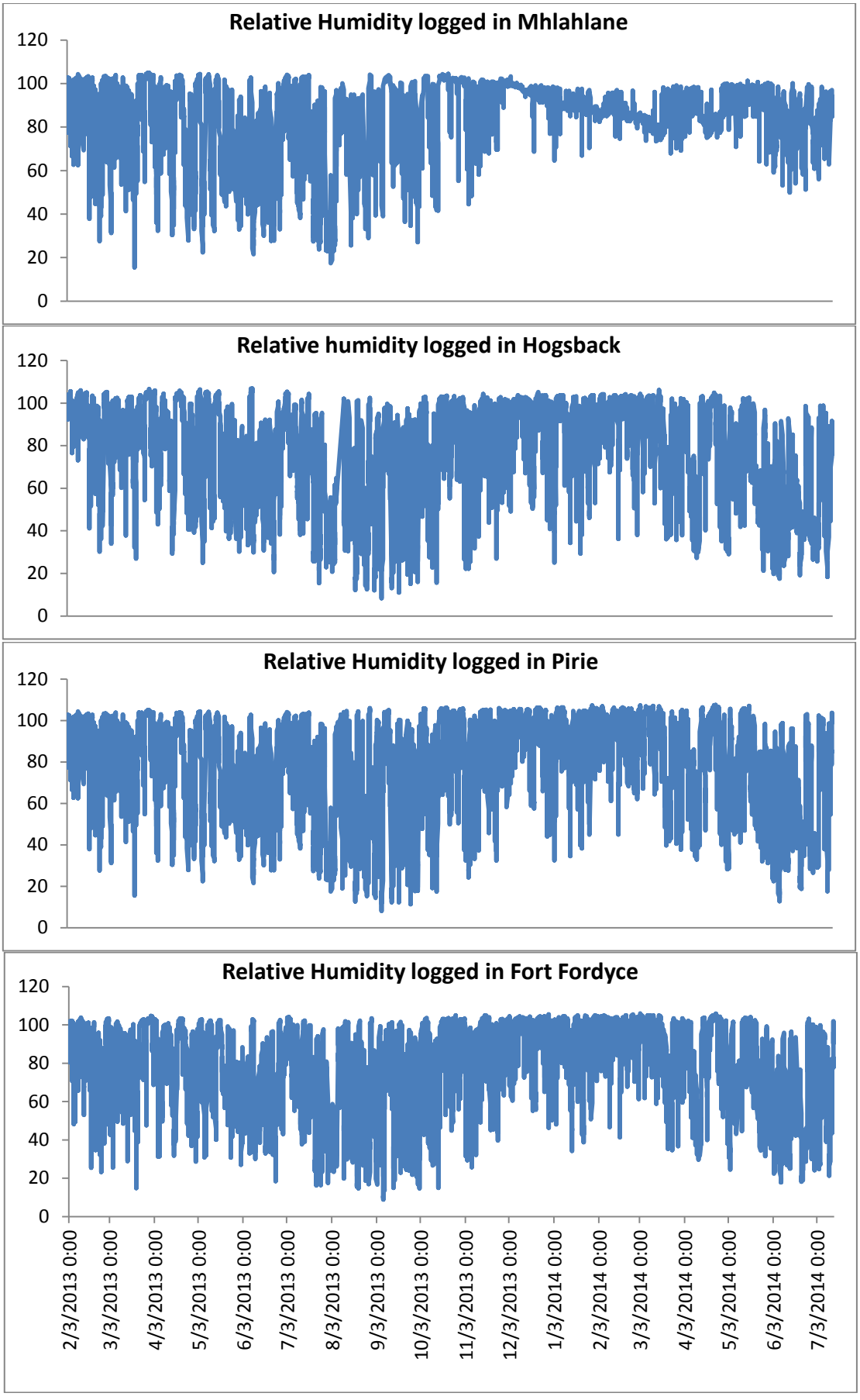



**Figure 22: Relative Humidity readings logged at different forest patches.**

#### 4.3.1.1. Soil Analysis

From Table 6 it was noted that the organic matter was relatively high throughout. Hogsback had the highest percentage of organic matter (33.65 %) followed by Baziya (33.27 %) and Quacu Nature Reserve had the least (8.88 %). All forest patch soils were slightly acidic, with Baziya and Mbulu recording the highest and lowest acidities, 4.76 and 6.93 respectively. Conductivity readings were low, the lowest conductivity reading was 0.22 mS (Cata) and the highest was 3.22 mS (Langeni). The range in standard deviation readings suggests that the soil samples conductivity, pH, and organic content readings are not homogeneous between the forest patches. Maden Dam had the lowest organic content standard deviation reading (1.08) and Langeni had the highest (20.60); Engcobo had the lowest pH standard deviation (0.04) and Fort Fordyce North the highest (1.20); and Beggers Bush had the lowest conductivity standard deviation (0.01) whereas Boschberg recorded the highest (0.23).

Median particle diameters of all the samples ranged from 8.71µm (Baziya) to 55.3µm (Cata) which showed that the soils from the different forest patches were mostly composed of silt particles. All particle size analysis for each of the patches results were recorded in Appendix M.

The ternary plots presented in Appendix N subdivided soil samples into different groups according to the percentages of each texture recorded at each forest. Each figure number corresponds to a forest patch on Table 6. For example, the majority of the patches were classified with ‘silty loam’ soils. Four forest patches were characterised by ‘silty clay loam’ soils and those were Baziya, Bedford, Gulandoda and Riebeeck East (Figure 2, 3, 12, and 25 respectively). Three forest patches were characterised by ‘loam’ soils, those were Boschberg, Langeni and Mhlahlane. Maden Dam was the only forest patch with ‘clay loam’ soils.

**Table 6: Study site matrix with all the measured environmental variables**

| | | Area($km^2$) | Altitude(m) | MAP(mm) | MAT(°C) | MAPE(mm) | OC % | SD | pH | SD pH | EC | SD EC | Median PS | %Clay | %Silt | %Sand |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | Adelaide | 4.48 | 1135 | 578 | 15 | 1723 | 14.84 | 7.67 | 6.346 | 0.48 | 0.708 | 0.07 | 24.8 | 14.07 | 51.6 | 34.33 |
| 2 | Baziya | 0.77 | 1479 | 1168 | 16 | 1601 | 33.27 | 10.43 | 4.764 | 0.32 | 0.4334 | 0.03 | 8.71 | 32.79 | 57.9 | 9.31 |
| 3 | Bedford | 4.68 | 1302 | 750 | 17 | 1810 | 11.58 | 8.85 | 5.564 | 0.22 | 0.226 | 0.03 | 11.1 | 31.67 | 54.3 | 14.03 |
| 4 | Begger Bush | 0.67 | 769 | 495 | 17 | 1743 | 10.39 | 6.05 | 6.216 | 0.45 | 0.286 | 0.01 | 18.3 | 16.41 | 57 | 26.56 |
| 5 | Boschberg | 0.84 | 1331 | 363 | 17 | 1926 | 13.75 | 3.36 | 6.576 | 0.39 | 2.8142 | 0.23 | 18 | 19.27 | 44.6 | 36.17 |
| 6 | Cata | 2.32 | 1495 | 770 | 17 | 1723 | 19.59 | 12.13 | 6.486 | 0.25 | 0.2232 | 0.02 | 55.3 | 7.67 | 47.6 | 44.71 |
| 7 | Dassie Krans | 1.20 | 695 | 576 | 17 | 1776 | 13.74 | 7.88 | 6.712 | 0.43 | 0.523 | 0.05 | 19 | 18.08 | 51.3 | 30.65 |
| 8 | Engcobo | 0.21 | 1372 | 883 | 13 | 1724 | 16.75 | 4.12 | 6.506 | 0.04 | 1.4502 | 0.11 | 27.4 | 14.45 | 59.3 | 26.25 |
| 9 | Fort Cunyingham | 0.96 | 1314 | 943 | 12 | 1728 | 12.50 | 1.30 | 6.586 | 0.19 | 0.4976 | 0.02 | 27.5 | 13.49 | 59.7 | 26.8 |
| 10 | Fort Fordy_North | 1.76 | 1096 | 578 | 19 | 1856 | 26.14 | 1.98 | 6.022 | 1.20 | 0.2884 | 0.06 | 18.1 | 20.97 | 54.6 | 24.39 |
| 11 | Fort Fordy_South | 2.22 | 1171 | 694 | 17 | 1753 | 13.51 | 2.74 | 6.192 | 0.78 | 0.2488 | 0.03 | 26.1 | 23.47 | 52.6 | 23.95 |
| 12 | Gulandoda | 3.32 | 1519 | 823 | 14 | 1679 | 12.25 | 3.20 | 6.732 | 0.13 | 0.4506 | 0.04 | 8.9 | 32.93 | 50.5 | 16.54 |
| 13 | Hogsback | 3.26 | 1202 | 1006 | 12 | 1681 | 33.65 | 12.29 | 6.3 | 0.17 | 1.38 | 0.19 | 19.9 | 20.25 | 58.1 | 21.62 |
| 14 | Isidenge | 13.83 | 1124 | 1087 | 17 | 1643 | 11.88 | 3.48 | 6.492 | 0.31 | 0.5188 | 0.02 | 20.8 | 19.9 | 62.4 | 17.74 |
| 15 | Kambi | 2.53 | 1161 | 1190 | 12 | 1690 | 12.86 | 1.35 | 5.756 | 0.68 | 0.3872 | 0.01 | 14.4 | 21.63 | 68 | 10.33 |
| 16 | Khologha | 13.21 | 1368 | 1059 | 15 | 1694 | 15.64 | 2.91 | 6.87 | 0.31 | 0.295 | 0.01 | 19.9 | 17.78 | 67.2 | 15.06 |
| 17 | Kubusi | 3.61 | 1433 | 1068 | 11 | 1678 | 11.15 | 6.95 | 6.612 | 0.49 | 0.2302 | 0.03 | 18.4 | 17.49 | 54.2 | 28.29 |
| 18 | Langeni | 1.27 | 1464 | 1103 | 12 | 1598 | 32.06 | 20.60 | 6.638 | 0.55 | 3.2154 | 0.24 | 11.9 | 29.72 | 46.3 | 24.01 |
| 19 | Maden Dam | 28.67 | 1125 | 1096 | 10 | 1666 | 11.82 | 1.08 | 5.954 | 0.35 | 0.6086 | 0.11 | 30.6 | 13.09 | 60.8 | 26.08 |
| 20 | Manzamnyama | 0.29 | 1543 | 729 | 11 | 1687 | 23.76 | 7.68 | 6.436 | 0.16 | 0.4334 | 0.04 | 15 | 21.69 | 58.5 | 19.79 |
| 21 | Mbulu | 1.09 | 1144 | 747 | 16 | 1793 | 17.33 | 4.35 | 6.926 | 0.23 | 0.4444 | 0.06 | 18.8 | 19.96 | 48.4 | 31.6 |
| 22 | Mhlahlane | 1.84 | 1529 | 1275 | 13 | 1698 | 24.19 | 2.60 | 5.2 | 0.36 | 0.6872 | 0.03 | 14.5 | 26.4 | 55 | 18.6 |
| 23 | Pirie | 5.03 | 935 | 1021 | 15 | 1627 | 19.02 | 2.30 | 6.544 | 0.24 | 1.618 | 0.39 | 12.3 | 27.59 | 55.2 | 17.2 |
| 24 | Quacu | 2.77 | 1314 | 954 | 17 | 1699 | 8.88 | 3.49 | 6.892 | 0.22 | 0.4398 | 0.01 | 13.7 | 24.68 | 63.5 | 11.84 |
| 25 | Riebeek East | 1.03 | 853 | 433 | 15 | 1742 | 13.30 | 9.13 | 5.74 | 0.21 | 1.1238 | 0.09 | 15.2 | 30.35 | 61.3 | 8.38 |
| 26 | Tsolo | 0.06 | 1172 | 1068 | 14 | 1629 | 12.13 | 3.06 | 6.758 | 0.52 | 0.9066 | 0.04 | 21.5 | 12.84 | 68.7 | 18.47 |

#### 4.3.1.2. Geographic data

The forest patch areas varied in size, Tsolo had the smallest area and Maden Dam had the largest area (0.06 and 28.67 $km^2$ respectively; Table 6). In terms of altitude, Dassie Krans at 695m above sea level and Mhlahlane was 1529m above sea level are the lowest and highest forests.

### *4.3.5. Principal Component Analysis*

The PCA (Figure 23) showed which environmental variables affected the different forest patches, the summary output was presented in Table 7. There was some level of clustering where the drier forests (Fort Fordyce South and North, Dassie Krans, Mbulu,Beggers Bush) were located at the bottom right and the wetter forests (Kambi, Khologha, Isidenge, Tsolo, Kubusi) at the top left. The results showed that the 2-d PCA was not a good indictor of structure; eigenvalue of 3.4 indicated that PC1 accounted for much of the variability (28.4%) and PC2 the remainder (20 %), and 48.4 % between them which is relatively low (Table 7). However, The ordination results showed that MAP, Median Particle size, MAPE, and percentage clay were important variables (Figure 23) because of the long vector lengths. Cata, Maden Dam, Boschberg and Baziya were all outliers. Boschberg was unusual because it is very dry, Maden Dam was located in a very wet area and also had the largest forest patch, Baziya had the highest organic matter percentage, and Cata had the largest Median Particle size and percentage of sand.

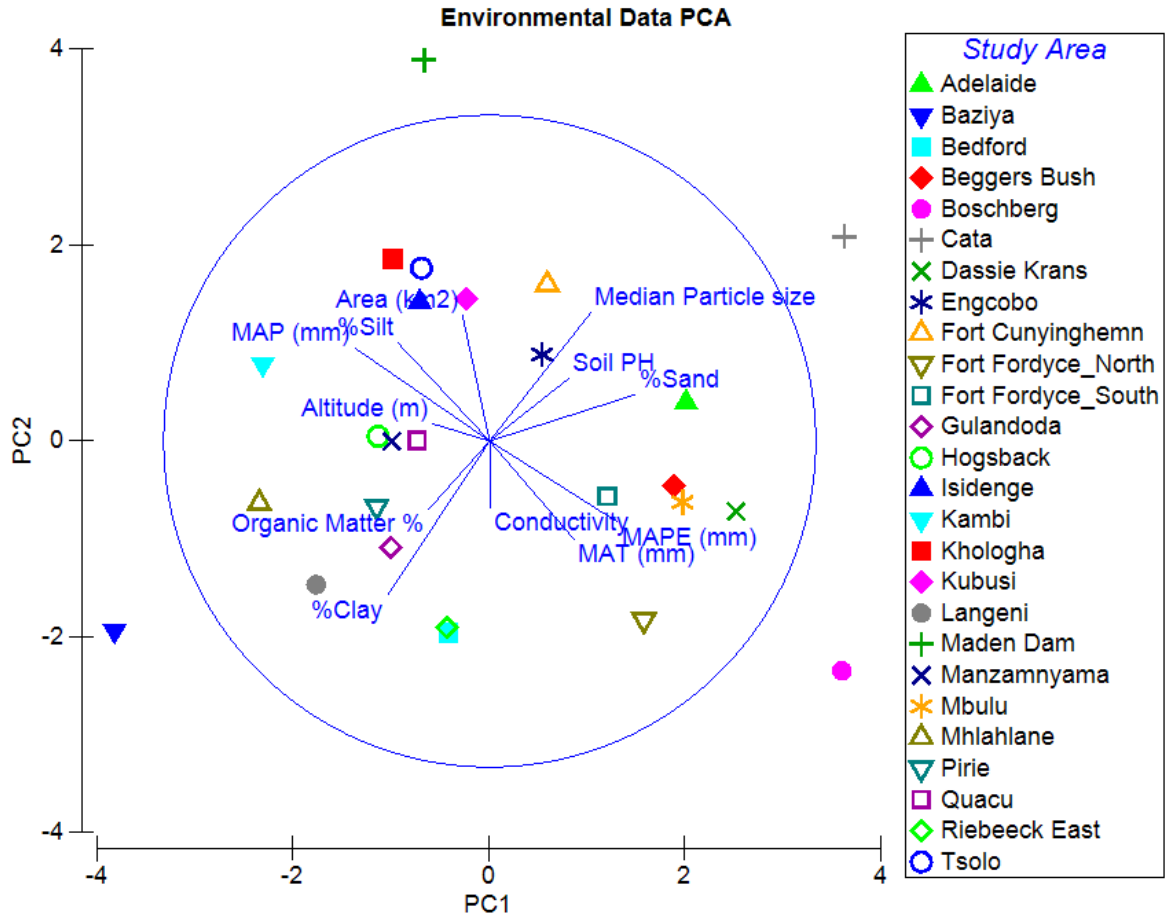



**Figure 23: PCA ordination diagram of the 26 forest patches showing axis 1 and 2. The lines indicate environmental variables and shapes represent a particular forest patch.**

**Table 7: Summary of PCA analysis**

| **Eigenvectors** | | |
|---|---|---|
| **Variable** | **PC1** | **PC2** |
| Area (km2) | -0.083 | 0.385 |
| Altitude (m) | -0.175 | 0.053 |
| MAP (mm) | -0.415 | 0.286 |
| MAT (mm) | 0.259 | -0.301 |
| MAPE (mm) | 0.393 | -0.249 |
| Organic Matter % | -0.187 | -0.209 |
| Soil PH | 0.244 | 0.193 |
| Conductivity | 0 | -0.205 |
| Median Particle size | 0.312 | 0.396 |
| %Clay | -0.312 | -0.472 |
| %Silt | -0.282 | 0.301 |
| %Sand | 0.447 | 0.143 |
| **Eigenvalues** | 3.4 | 2.4 |
| **%Variation** | 28.4 | 20 |

### *4.3.6. Canonical Correspondence Analysis*

The results of all three CCA ordinations are shown in Figure 24. Three ordination plots were produced, one for the total number of species (Figure 24 A), the second for the total number of tree species (Figure 24B), and the last one was for the total number of herbaceous species (Figure 24C). Some of the forest patches formed clusters; Winterberg-Amathole patches were situated on the right and the Transkei patches were positioned on the left (Figure 24A and 24C). However, there was no distinct pattern for the tree species (Figure 24B). There were also a number of outliers; Figure 24A had four outliers (forest patch 20, 13, 10, and 7), Figure 24B had five (forest patch 12, 20, 21, 7, and 10), and Figure 24C had six outliers (forest patch 10, 21, 4, 5, 7, and 19).

The summary output are presented in Table 8. The summary for the total number of species was as follows: The first axis is very well correlated with the environmental data (r = 0.976), the second axis is more highly correlated (r = 0.982) and the correlation for the other axes were also high but lower compared to the first two axes. This suggests that the whole data set is governed by multiple gradients. MAP, MAPE, organic matter percentage, and area were the most important environmental factors explaining species variation, because they tend to be represented by longer arrows than less important enviromental variables (Ter Braak 1986). The Monte-Carlo test of significance indicated that the measured variables accounted for a significant amount of variation, for the first canonical axes (p-value = 0.0020) and for all canonical axes (p-value = 0.0020). The cumulative percentage variation of species for the total number of species was low (7.9 %). The cumulative percentage variation of species-environment relation was also relatively low (17.3 %). However, the explained variability also depends on the number of species and sites, with large data and multiple factors the cumulate percentage is usually small. This does not mean that the results are not reliable. Hobbs and Norton (2004) suggested that many restrictions played a role in a plants establishment in a site. For example if we are to consider abiotic filters, moisture might be a determining factor for one species but another species may be excluded because of unfavourable light and soil structure conditions. Abiotic filters may be the major barrier to the reappearance of certain species (Hobbs and Norton 2004).

The summary for the tree species was similar to that of the previous analysis. All the axes correlated with the environmental data, with the second axis accounting for much of the variation (r = 0.974). The Monte-Carlo test of significance indicated that the measured variables accounted for a significant amount of variation, for the first canonical axes (p-value = 0.0020) and for all canonical

axes (p-value = 0.0020). The summary output for the herbaceous species was also similar to the first two outputs. All axes correlated with the environmental variables, however, the first axis was higher than the second was (r = 0.969). The Monte-Carlo test of significance indicated that the measured variables accounted for a significant amount of variation, for the first canonical axes (p-value = 0.0020) and for all canonical axes (p-value = 0.0020).

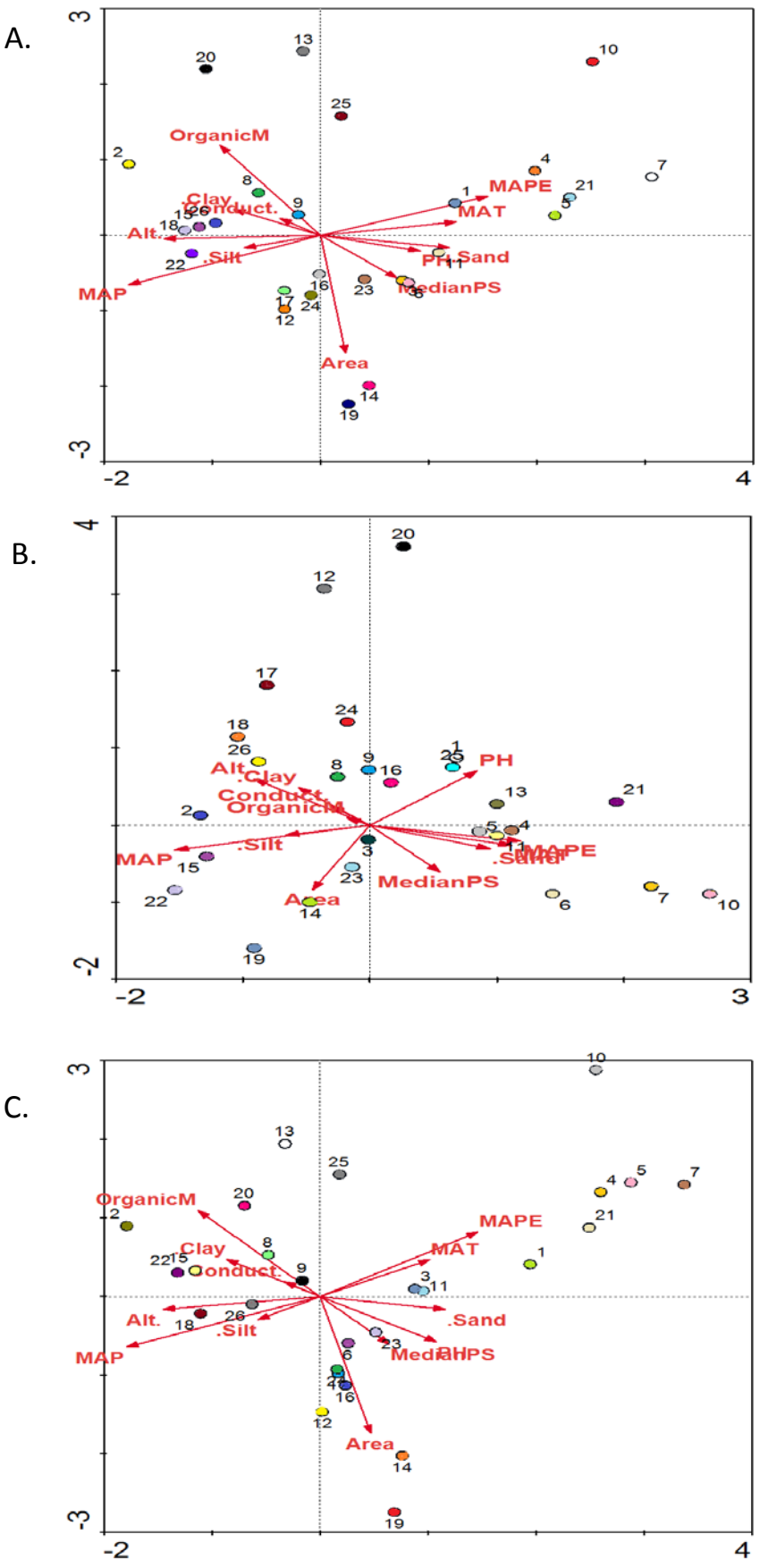



**Figure 24: CCA ordination diagrams of the 26 forest patches for A) Total species B) Trees C) Herbaceous species showing axis1 and axis 2. The arrows indicate environmental variables and the different coloured and numbered dots represent a forest patch. Each number corresponds to a forest patch listed on table 6.**

**Table 8: Summary of outputs for CCA ordinations for the different plant groups in Figure 12**

| | | | | | | |
|---|---|---|---|---|---|---|
| **Total Species** | **Axes** | **1** | **2** | **3** | **4** | **Total** |
| | Eigenvalues : | 0.326 | 0.245 | 0.222 | 0.184 | |
| | Species-environment correlations : | 0.976 | 0.982 | 0.979 | 0.977 | |
| | Cumulative percentage variance | | | | | |
| | of species data : | 7.9 | 13.8 | 19.1 | 23.6 | |
| | of species-environment relation: | 17.3 | 30.3 | 42 | 51.8 | |
| **Tree Species** | | | | | | |
| | Eigenvalues : | 0.272 | 0.232 | 0.208 | 0.182 | |
| | Species-environment correlations : | 0.965 | 0.974 | 0.96 | 0.948 | |
| | Cumulative percentage variance | | | | | |
| | of species data : | 7.1 | 13.2 | 18.7 | 23.4 | |
| | of species-environment relation: | 15.4 | 28.5 | 40.2 | 50.5 | |
| **Herbaceous Species** | | | | | | |
| | Eigenvalues : | 0.363 | 0.274 | 0.222 | 0.195 | |
| | Species-environment correlations : | 0.969 | 0.961 | 0.958 | 0.981 | |
| | Cumulative percentage variance | | | | | |
| | of species data : | 8.4 | 14.8 | 19.9 | 24.5 | |
| | of species-environment relation: | 18.6 | 32.7 | 44.2 | 54.2 | |

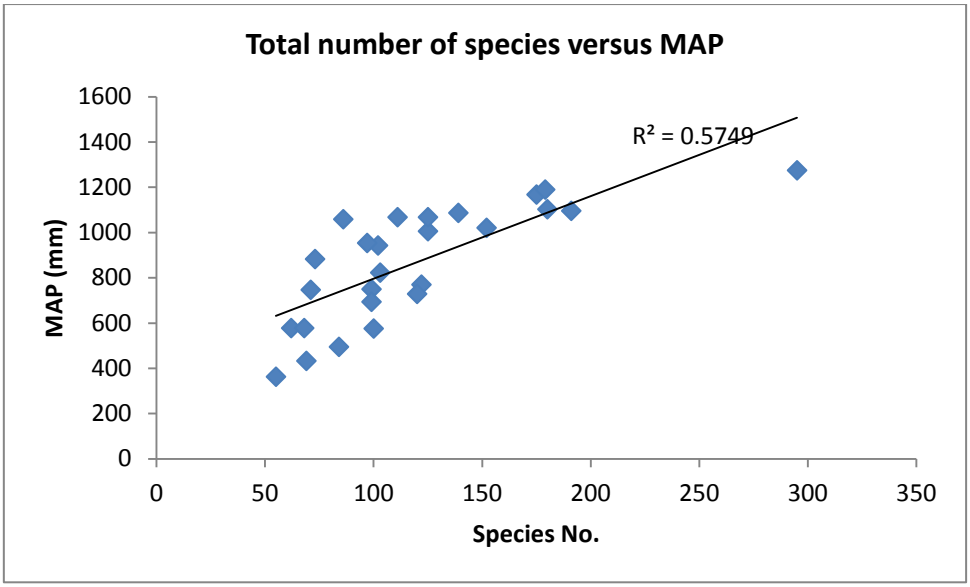
### *4.3.7. Regression Model*

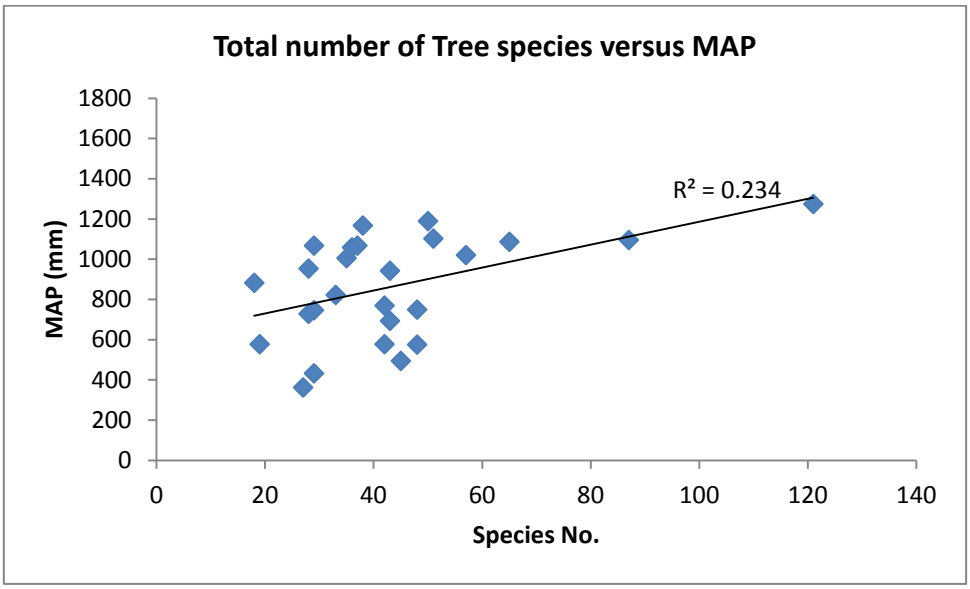
In order to assess which of the four important environmental variables presented in the previous analysis significantly influenced plant species diversity in these forest patches regression models were fitted for all growth forms. The full statistic output results for the total number of species, total number of trees and total number of herbaceous species are presented in Appendix O, P, and Q respectively. For the first model, total number of species, MAP was the only significant variable (p-value = 0.0031; Table 9) at 5% level of significance. The regression analysis for the total number of tree species showed that MAP was significant at a 5% level of significance (p-value = 0.031; Table 9). Total number of herbaceus species results MAP was the only significant variable and was significant at a 5% level of significance (p-value = 0.0013; Table 9). All three regression models consisted of 4 Degrees of Freedom, the Test statistic further confirms the significance of MAP as in all three models the p-values for MAP are lower than the T-statistic (Table 9).

Using *Microsoft Excel* scatter plots were produced to assess the relationship between species diversity in each forest patch and MAP. When comparing diversity against the climatic variables, it was found that the total species diversity and the herbaceous species correlated with Mean Annual Precipitation ($R^2$= 0.5687 and $R^2$ = 0.6426 respectively; Figure 25), whereas tree species diversity did not ($R^2$= 0.2339; Figure 25). The herbaceous species thus show a greater sensitivity to climate filtering, as driven by annual rainfall. In contrast, tree species are not so dependent on annual rainfall, possibly due to their deep root systems. However, extreme events such as prolonged drought (Geldenhuys 1993a) and frost (Hiratsuka and Zalasky 1993; Hänninen 2006) have been known to cause local extinctions. This filtering of tree species due to some extreme enviromental event could also explain the composition patterns observed in some of these forest patches. Geldenhuys (1993a) observed that evergreen trees were replaced by decidious trees after an extreme drought event. Trees dieback due to drought will enable the new stand to withstand such an event if it ever occurred again. The results support the concept that forest patchs composition is as a result of site specific environmental pressures and vegetation in Southern Mistbelt Forests are mainly influenced by rainfall gradients.

**Table 9: Summary output from multiple regression models for the different species groups**

| | Variables | P-value | Degrees of freedom | Test statistic |
|---|---|---|---|---|
| **Total Species** | Area (km2) | 0.630913 | 4 | 0.48756 |
| | MAP (mm) | **0.003136** | | 3.335837 |
| | MAPE (mm) | 0.738963 | | 0.337671 |
| | Organic M. % | 0.246717 | | 1.191585 |
| **Tree Species** | Area (km2) | 0.088363 | 4 | 1.787113 |
| | MAP (mm) | **0.031267** | | 2.308102 |
| | MAPE (mm) | 0.171044 | | 1.417363 |
| | Organic M. % | 0.554617 | | 0.600473 |
| **Herbaceous Species** | Area (km2) | 0.445862 | 4 | -0.77693 |
| | MAP (mm) | **0.001355** | | 3.691685 |
| | MAPE (mm) | 0.515295 | | -0.6618 |
| | Organic M. % | 0.134959 | | 1.554703 |



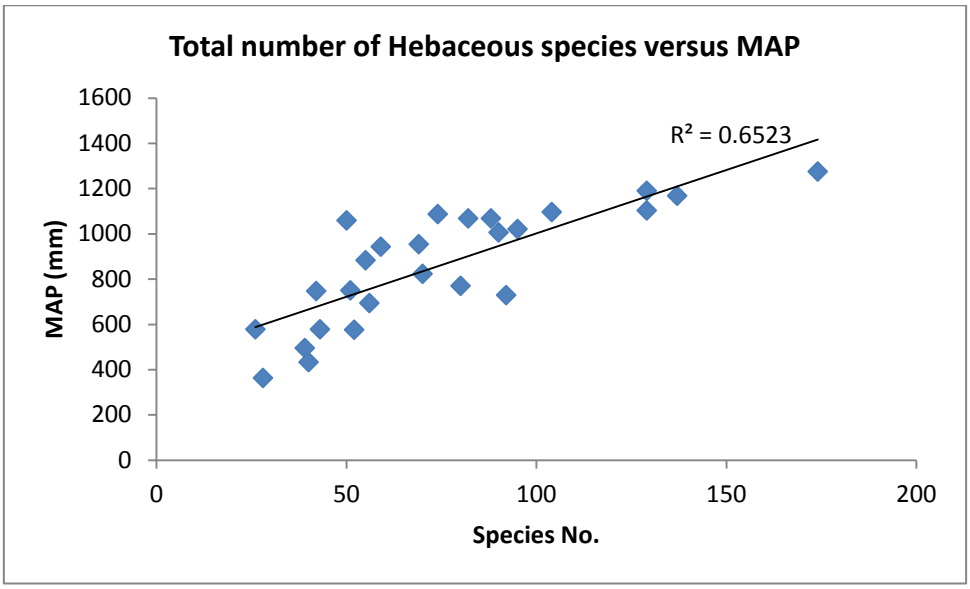




**Figure 25: Regression analysis between the different plant groups and MAP.**

### *4.3.8. Rank and DBH Correlations*

The results are presented in Appendix R and Figure 26. The species were ranked in descending order (i.e. species with the most recorded stems). From Appendix R it was observed that ten tree species were recorded at least five times or more in the different forest patches. These included: *Diospyros whyteana, Podocarpus latifolius, Olea capensis, Scolopia mundii, Rapanea melanophloeos, Curtisia dentata, Trichocladus ellipticus, Scutia myrtina, Xymalos monospora, and Podocarpus falcatus.* Of these, only *Curtisia dentata* and *Scutia myrtina* were the only two species that showed a correlation between DBH and MAP ($R^2$ = 0.5442 and $R^2$ = 0.6029 respectively; Figure 26). These results suggest that these two species may be susceptible to MAP and could be filtered out in the drier Southern Mistbelt Forests, as their frequency (expressed as rank) in the forest patches declines with decreasing MAP.

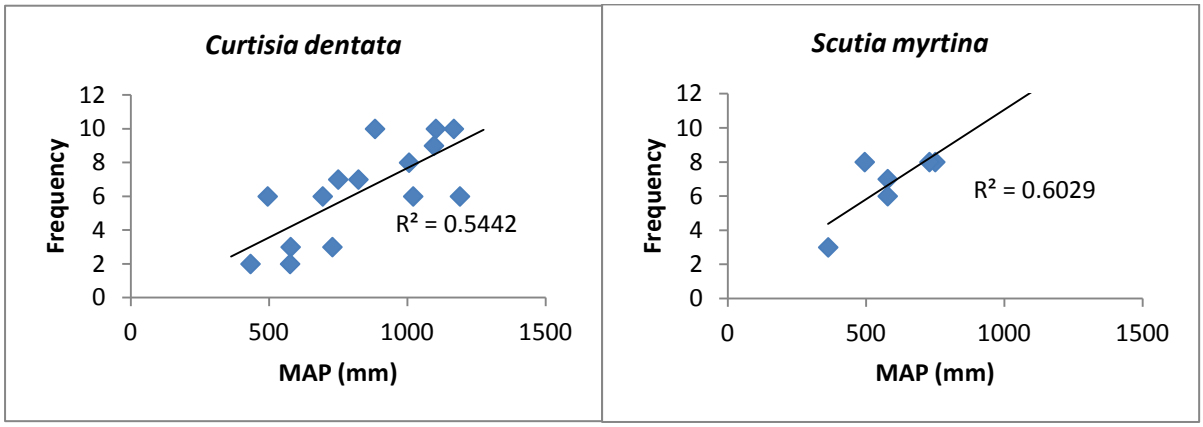



**Figure 26: Rank Correlation of Curtisia dentata and Scutia myrtina. Both species correlated with MAP.**

*Podocarpus latifolius, Olea capensis,* and *Trichocladus ellipticus* were the only species common to most if not all forest patches. The average DBH analysis of these three species showed no correlation with MAP and MAPE (Figure 27 and 28). This indicated that MAP and MAPE did not have an effect on the size structure of tree species in different forest patches.

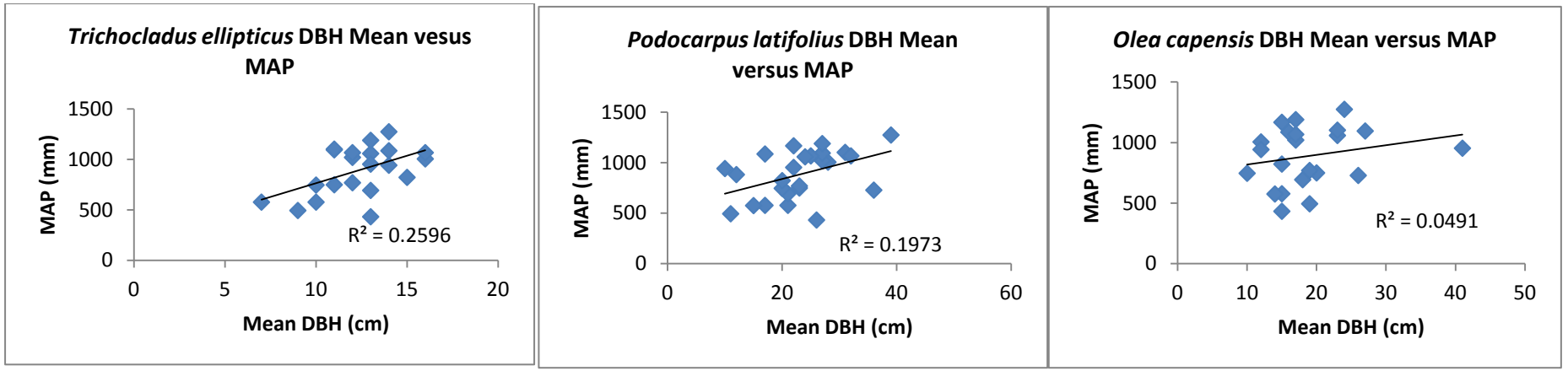



**Figure 27: Mean Diameter at Breast Height for the top three common species correlated with Mean Annual Precipitation. A) Trichocladus elliptica B) Podocarpus latifolius C) Olea capensis**

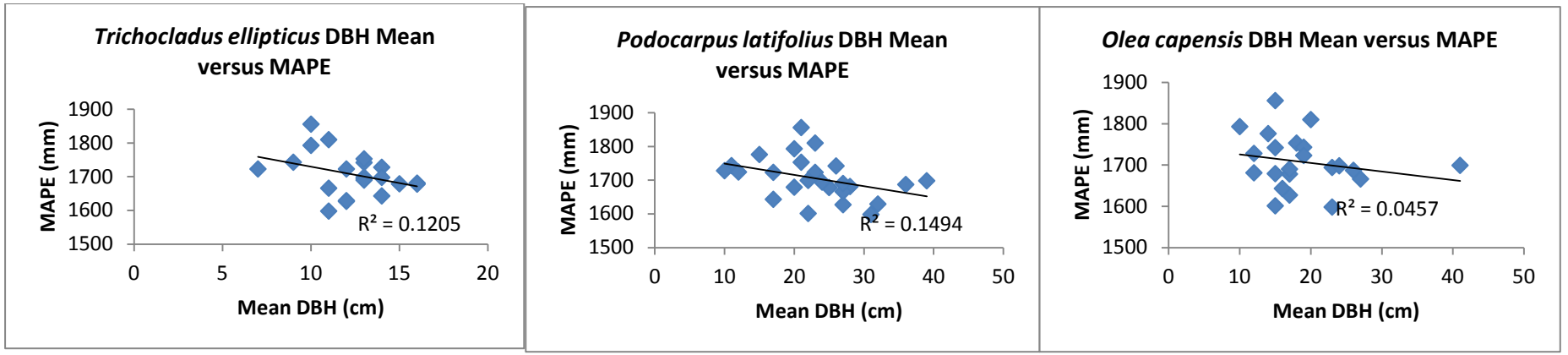



**Figure 28: Mean Diameter at Breast Height for the top three common species correlated with Mean Annual Potential Evapotranspiration. A) Trichocladus elliptica B) Podocarpus latifolius C) Olea capensis**

## 5. Discussion

The finding obtained here that herbaceous species diversity is correlated with MAP and MAPE reflects previous findings. In assessing the influence of environmental variables on forest patch diversity, climate appeared to play a key role in filtering forest plant species along a rainfall gradient based on their biological traits (Diaz *et al.* 2007). Traits include morphological, physiological, and life history traits such as growth, dispersal, seed production, photosynthetic pathway, life span, reproduction, and life form (Fattorini and Halle 2004). Very few assembly studies include environmental data in their analysis. Most of these studies are done at species level and analyse functional traits of species that determine the general community assembly. Work done by Engelbrecht *et al.* (2007), Kraft *et al.* (2008), Shipley *et al.* (2006), and Vile *et al.* (2006) on community assembly level studies analysed functional traits and species abundance showed that niche-related processes do play a role in community assembly even in tropical forests and that a community level approach has a highly predictive value. However, these studies do not include environmental data in their analysis. Lebrija-Trejos *et al.* (2010) states that "the inclusion of environmental factors is needed to obtain a more comprehensive mechanistic understanding of the role of functional traits in community assembly and to establish the precise links between filtering factors and functional traits in a system. "

The herbaceous community thus comprises an important component of the Southern Mistbelt Forest ecosystem, but are studied far less than tree species. Therefore, our knowlegde of the physiology of these species and predictive abilities along environmental gradients is limited. Relationships between functional groups (clustering) of plant species and environmental gradients can provide evidence of environmental filtering, particularly when traits suggest an advantage in the associated environment (McGill *et al.* 2006). For example, in many forest herbs ecological stategies may differ (i.e. reproductive periods and dispersal mechanisms; Whigham 2004). The diversity of ecological strategies suggests the potential for niche differentation along environmental gradients (Tilman 1990; Gilbert and Lechowicz 2004; Ozinga *et al.* 2005; Gotelli and McGill 2006). This was shown in the analysis of the plot data (Figure 5 Chapter 2) where quadrats formed patch-specific clusters. This result may explain the strong nestedness obtained in the *NeD* analysis (previous chapter). The relationships of nested subsets to environmental variables suggests that, at least in some forest patches, plant species show nested niche structure with regard to their responses to environmental gradients (Heino *et al.* 2010) . These environmental relationships are highly region-specific, however, suggest strong context-dependency in nested subset patterns (Heino *et al*. 2010).

Herbaceous species are susceptible to climate filtering shown by their comparative abundance in areas of high precipitation. These species can thus provide clues or act as indicators of the possible long-term effects of climate change on forest communities. “Adaptive species traits and their impacts on population dynamics, ecological adaptations and colonization are main keys to deciphering the relative importance of these factors on community patterns which remains the subject of controversy (e.g. neutral versus niche assembly theories)” (Hardy *et al.* 2012). These traits determine how the forest plant species will respond to the resources in the given patch defined by the impact of ecological factors on the species in the given community. In forest communities, species without traits that are suitable in moist conditions will be excluded in drier forest patches. Species with the required traits are successful, and as a result, the species community is homogenous with respect to these traits when compared to the regional pool. Herbaceous species of forest communities which includes herbs, ferns and shrubs is an important component of Southern Mistbelt Forests.

Chase and Leibold (2003) mentioned three main predictions of how species sorting influence the distribution of species along environmental gradients: 1) Species should distribute themselves along an environmental gradient in direct relation to their relative requirements for the factors of interest. 2) Species should exist in fewer sites than they could potentially occupy as a result of competition exclusion by other species. 3) Along a simple environmental gradient the range of environmental conditions that one species uses should not be nested within that of another species, or the species with the narrower range would be competitively excluded. Nestedness is maintained when the community structure is organised according to an environmental gradient (Joppa and Williams 2011). Rainfall is more likely to affect nestedness; Tilman and Pacala (1993) stated that the resource (i.e. rainfall) should determine which group of species are found in an area. Thus, forests that vary in rainfall should have a predictable composition of species. Lebrija-Trejos *et al.* (2010) suggested that if environmental filters and species traits were relevant for community structure, then under different environmental conditions communities would possess particular combinations of traits. It would thus have been useful to identify the species responsible for nestedness patterns in Southern Mistbelt forests and use the data to perform a CCA which would directly link nestedness with these results.

## 4.4. Conclusion

Climatic variables, notably MAP and MAPE, correlate with plant diversity. Forest plant species may thus be filtered along a rainfall gradient based on their biological traits and the herbaceous species are particularly suspectable to filtering. This may also result in the positive nestedness analysis result obtained in the previous chapter. Climatic variables can be good indicators of species occurances and have been overlooked for many years. This study has shown the importance of such variables and the potential impact they may have in the community structure of forest patches in South Africa.

It must be noted that light was not considered as a variable in this study. However, it could to be influencing the small scale spatial patterning of the herbaceous species communities. The importance of light gradients may be restricted to stands with canopy gaps created by the fall of old, large trees (Dahir and Lorime, 1996; Gillian *et al.* 1995). It is also possible that the herbaceous species communities in younger forest stands respond to variation in light intensities induced by variation in leaf phenology among tree species early in the growing season (Lopez *et al.* 2008). Alternately, current instruments used in measuring light intensity may not be sensitive enough to detect subtle variation in light levels in deeply shaded forests (Tobin and Reich 2009).

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# Chapter 5: Synthesis and Implications

The findings in this study can be summarised as follows:

- The floristic composition is unique in Southern Mistbelt Forests. The dendrogram generated from the full species and the herbaceous species dataset indicated that in general the species composition in each forest patch was unique, as plots from the same patch tend to cluster together. In contrast tree species showed trends uniform composition. Thus the pattern obtained for the total species data set is a consequence of patch differences in the diversity of herbaceous species and not the tree species.

- Von Maltitz *et al.* (2003) classification was not supported when using only plot data; however partially supported only when using the full species data set. These data also suggest an additional vegetation type comprising Dry Forests

- The Southern Mistbelt Forests in the Eastern Cape are significantly nested. The size (area) of the forest patch did not play a role in the nested structure of these forest patches because the more diverse forest patches were not the ones with the greatest area, suggesting that smaller forest patches should be prioritised in conservation and management as they are biodiversity contributors.

- Climate plays a key role in "filtering" herbaceous forest species in the patches of Southern Mistbelt Forest. Forest plant species may thus be filtered along a rainfall gradient based on their biological traits, particularly the herbaceous species. Herbaceous species are thus susceptible to climatic events such as drought, or gradual changes in rainfall linked with climate change. In contrast, tree species are not so dependent on annual rainfall, possibly due to their deep root systems. However, extreme events such as drought and frost have been known to cause local extinctions

Eeley *et al.* (1999) found several important variables that distinguished different forest types; these included mean annual precipitation, potential evapotranspiration, and mean annual temperature.

According to the South African Climate Change Response Strategy (2004) significant climate change is likely within the next 50 years and General Circulation Models (GCM) predicts an increase in MAT and a reduction in rainfall. While climate change predictions in South Africa are still highly debated, predictions indicate an increase in drier periods/seasons occurrences (South African Climate Change Response Strategy 2004). Plant species in Southern Mistbelt Forests would thus be at high risk for extinction, particularly those used to moist environments, as species without the necessary traits to survive in those new harsh environments would be filtered out.

Saavedra *et al.* (2011) stated in changing environments species responsible for nestedness patterns would be the first to go extinct and that fragmented areas might deviate from nested subset structure. This would be a huge biodiversity loss for South Africa. The identification of which species are most sensitive to filtering, and which may contribute to nestedness would be invaluable, as analysis of the traits possessed by these species would enable researchers to predict the exact effects of climate on these forest patches. These interpretations may assist in better decision making processes regarding the conservation of indigenous forests in South Africa.

The findings of this research have several implications for the conservation of the Southern Mistbelt Forest in South Africa:

1. The forest diversity of Transkei forest patches is higher than previously stated in earlier publications.
2. The conservation of many smaller forest patches than one big patch would be recommended.
3. Forest composition in SMF is unique; unfortunately these forest patches are not equally represented because scarp and coastal forests are better represented in conserved areas (Eeley *et al.* 2001).
4. Forest plant specialists are more vulnerable to extinction than generalist species in these climate changes.
5. The identification of species responsible for the nestedness pattern may be valuable in the identification of forest patches of high conservation priority. Conservation is of utmost concern to maintain the plant species diversity and composition in these forest patches over time.

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