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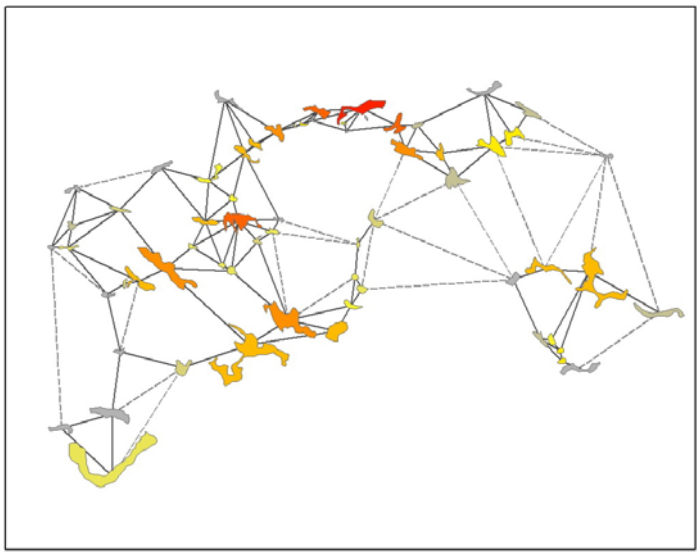
Indigenous forests of Mpumalanga Province (South Africa); patterns and processes for inclusion in a systematic conservation plan

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INDIGENOUS FORESTS OF MPUMALANGA PROVINCE (SOUTH AFRICA); PATTERNS AND PROCESSES FOR INCLUSION IN A SYSTEMATIC CONSERVATION PLAN

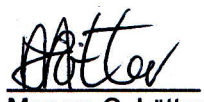


Mervyn Charles Lötter

A thesis submitted to the Faculty of Science, University of the Witwatersrand, Johannesburg, in fulfilment of the requirements for the degree of Doctor of Philosophy

Johannesburg, February 2014

I declare that this thesis is my own, unaided work. It is being submitted for the Degree of Doctor of Philosophy in the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination in any other University.



Mervyn C. Lötter

11 day of February 2014

ABSTRACT

Systematic conservation planning (SCP) relies fundamentally on spatial information about the distribution of biodiversity, and applying the principles of conserving a representative sample of biodiversity pattern that can persist over time, and the translation of conservation objectives into explicit quantitative targets. My thesis focuses on the development of appropriate data sets to include Mpumalanga Province's indigenous forests (South Africa) within a regional SCP. My aim is to investigate and describe forest pattern and ecological processes at appropriate scales to inform a provincial SCP assessment. A large data set consisting of 506 plots of 20 m x 20 m sampled the indigenous forests in and around Mpumalanga to inform the identification of SCP forest features and conservation targets. The current National Forest Classification (NFC) identifies forest types at a national scale, inappropriate for a regional assessment. I identified a hierarchy of forest subtypes, nested within the NFC based on Flexible beta ($\beta = -0.25$) clustering and Bray-Curtis resemblance measure. This classification procedure is selected after a detailed evaluation of available methods to identify a robust numerical classification technique, optimising on statistically identified faithful species. Fourteen forest subtypes are distinguished within three national forest types. I propose that the Wakkerstroom Midlands Forest Subtype be embedded within the Northern Highveld Forest Type, and not the Low Escarpment Mistbelt Forest Type as is currently recognised in the NFC. The proposed forest subtypes are described in terms of dominant plant families and genera, growth forms, seasonality or leaf retention characteristics, and the proportion of forest dependant species. A total of 125 plant families, 375 genera and 619 species are identified to occur in the Mpumalanga forests, with the most abundant species per family being Rubiaceae (33 plant species), Fabaceae (26), Celastraceae (25), Orchidaceae (23), Euphorbiaceae (22), Aspleniaceae (21) and Apocynaceae (20). 76% of all forest plant species are obligate forest species and 80% of all tree cover is evergreen. The identification and understanding of underlying ecological processes is informed by the analysis of three scales of environmental variables and geographic space on forest composition using variation partitioning and ordination. I propose the application of semivariogram analysis to categorise environmental variables into three scales of influence (local, regional and supra-regional scales). The largest fraction of variation is explained by the regional variables (45%), followed by the effects of supra-regional (21%) and local variables (19%). Using the full floristic data, both the environmental and geographic variable matrices accounted for 55% of observed variation. Geographic space (23%) partially explains the important role of dispersal in influencing variation in species patterns across all forest strata, even in the herbaceous stratum where the substantial contribution of dispersal is unexpected. My analysis provides insight into the relative contributions of environmental variables and the scale of their influence, and highlights the importance of dispersal in explaining forest vegetation patterns in Mpumalanga. The use of

ecological processes within SCP is still in its infancy, particularly in light of the threat of climate change. I propose a new method based on graph theory that incorporates dispersal distance to identify connectivity importance values for each forest patch based on their contribution towards landscape connectivity. Minimum patch distance is informed through a dispersal range ensuring 75% of flora can disperse between patches. The connectivity analysis supports resilience and persistence in SCP scenarios. Finally I needed to set quantitative targets for the pattern and process features for their inclusion within a SCP. With an overarching goal of ensuring that at least 75% of all species are represented by at least one individual within each forest subtype in a SCP, I utilised the Species Area Relationship (SAR) to determine the slope of the relationship and to estimate the proportion of area required to represent 75% of species. The number of plots in my data set was low for certain forest subtypes, which necessitated an approach of utilising highest values from estimators of species richness and integrating forest subtype targets with those for forest types of a higher level in the NFC. I integrate forest connectivity into pattern targets as a precautionary approach given the vulnerability of naturally disconnected forest patches and the importance of emigration and immigration of plant diaspores in maintaining forest composition across a network of small forest patches. The resulting forest pattern targets ranged between 24.9% and 49.7% for forest subtypes, with a mean value of 34.8%. I also propose forest process targets for more spatially fixed processes, such as the important forest patches supporting connectivity, as well as the spatially flexible buffers around each priority forest patch. Spatially fixed forest process targets are set at 100% and for spatially flexible forest processes the targets are set at 60% of original extent. Consideration also needs to be given to design criteria that can assist in developing a framework for prioritising conservation actions based on vulnerability and irreplaceability.

DEDICATION

I dedicate this work to my family and friends who have supported me while working on my thesis. My parents have always believed I could accomplish anything I really applied myself to. But most importantly, I would especially like to dedicate this thesis to my wonderful wife, Tracy, and my daughter, Amy, for their love and continuous support when I could have spent more time with them.

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ABBREVIATIONS

ASTER GDEM – Advanced Spaceborne Thermal Emission and Reflection Radiometer

C – Constant species

CA – Correspondence Analysis

CCA – Canonical Correspondence Analysis

DAFF – Department of Agriculture, Forestry and Fisheries

db-RDA – Distance-based Redundancy Analysis

BLM – Boundary Length Modifier, a value used within Marxan software to influence clustering of planning units so as to avoid high boundary costs

DBH – Diameter at breast height

DCA - Detrended Correspondence Analysis

DEAT – Department of Environmental Affairs and Tourism

Dg – Diagnostic species

Dm – Dominant species

Fb – Flexible beta clustering

ISAMIC – Indicator Species Analysis Minimising Intermediate Constancies

GDEM – Global Digital Elevational Model

GIS – Geographic Information Systems

MBCP – Mpumalanga Biodiversity Conservation Plan

MBSP – Mpumalanga Biodiversity Sector Plan (an update of MBCP)

MTPA – Mpumalanga Tourism & Parks Agency

NFC – National Forest Classification

NMDS (nMDS) – Non-metric Multidimensional Scaling

PCoA – Principal Coordinates Analysis

RM – Resemblance Measure

SAJB – South African Journal of Botany

SANBI – South African National Biodiversity Institute

SAR – Species Area Relationship

SCP – Systematic Conservation Planning

SD – Standard deviation

SDM – Species Distribution Modelling

T – Transformation (data may be transformed to remove noise)

TVE – Total Variation Explained

TWINSPAN - Two-way Indicator Species Analysis

CHAPTER ONE:
General Introduction

1.1. LITERATURE REVIEW

1.1.1. Introduction

At the heart of systematic conservation planning (*sensu* Margules and Pressey, 2000) lies the principles of planning for species representation (pattern) and persistence (process), and the translation of conservation objectives into explicit quantitative targets. These foundational principles inform the proposed PhD framework. However it is not the purpose of this thesis to run an actual SCP, but rather to develop the necessary input data layers and targets for inclusion within a SCP, which could also incorporate many other species and vegetation types (such as wetlands and grasslands) that are also of conservation concern. Furthermore, SCP is a process which can be broken into a systematic conservation assessment (*sensu* Knight et al., 2006), the development of conservation strategies, and the implementation of conservation actions. This thesis largely refers to the systematic conservation assessment.

1.1.2. Overview of Mpumalanga's indigenous forests

The Indigenous forest biome is the smallest, most widely distributed, and most fragmented biome in South Africa, estimated at 0.33% of the land surface area (von Maltitz and Fleming, 1999). Forests typically occur as a series of very small (<10 ha) to small patches (in most forests they are smaller than 100 ha in size) (Cooper, 1985; Geldenhuys, 1991; Mucina et al., 2006). These scattered patches form an intricate archipelago along the precipitation-rich eastern coast and inland escarpments, and in deep fire-sheltered kloofs in southern Africa (Mucina et al., 2007). The forest patches are relicts of past vegetation patterns and home to numerous habitat specialists. This pattern is mirrored in Mpumalanga Province where indigenous forests are estimated at 40 353 ha or 0.51% of the surface area. An analysis of forest patch data from the vegetation map of Mpumalanga (Chapter 5) reveals that 1914 forest patches have been mapped, ranging in size from 0.04 — 3790 ha, with a median patch size of 4.6 ha. The mean distance between nearest forest patches is 837 m (SD: 1660 m). Approximately 15% of South Africa's indigenous forests occur within Mpumalanga Province (Lötter et al., 2002).

The definition of a forest used in this thesis follows that of von Maltitz et al. (2003), which define forests as a multilayered vegetation unit dominated by trees whose combined strata have overlapping crowns and where graminoids in the herbaceous stratum are generally rare. Fire does not normally play a major role in forest function and dynamics, except at the fringes.

Considerable variation in climate, altitude and topography across the biome has over time resulted in a diversity of forest communities, many floristically unique and each contributing to the overall regional diversity. However, because of their patchy distribution, indigenous forests do not form a cohesive, contiguous biome in which this diversity can easily be conserved (Lawes et al., 2007). The small and fragmented nature of forests (Rutherford and Westfall, 1994) makes them vulnerable to disturbances or resource exploitation in the long-term (Adie and Goodman, 2000), and highlights the importance for their conservation and preservation (Morgenthal and Cilliers, 1999; von dem Bussche, 1991). Effective conservation and land use planning will not be possible without a sound knowledge of the different forest communities, their floristic composition, and the ecological drivers responsible for structuring these communities (Chytrý et al., 2011). An appropriately scaled and accurate forest classification is required in order to inform conservation priorities, where these priorities can be monitored, evaluated and protected (Geldenhuys and Mucina, 2006).

There are many different numerical classification techniques available to classify vegetation plot data, many of which may be conceptually appropriate but the resulting classifications may differ considerably (Tichý et al., 2009; Wolda, 1981). In forest management, selecting an appropriate vegetation classification tool is of practical importance. In recent years vegetation classifications have increasingly been used in nature conservation (de Cáceres et al., 2009; Ostermann, 1998), and particularly so in conservation planning (Chytrý et al., 2011; Ferrar and Lötter, 2007; Lombard et al., 2003; Margules and Sarkar, 2007), based on the assumption that ecosystem/habitat types serve as useful surrogates for species distributions (Bergeron et al., 2012; Lombard et al., 2003; Rouget et al., 2004).

1.1.3. Scale and importance of classifications as surrogates for biodiversity

Exhaustive biodiversity surveys are nearly always impractical or impossible (Colwell et al., 2012). Biodiversity surrogates can provide a practical, realistic and cost effective alternative to detailed and thorough biodiversity surveys that attempt to enumerate all species (Bergeron et al., 2012; Margules and Sarkar, 2007). The development of surrogate data can serve as a robust method to relate observed patterns in specific biodiversity groups to variation in other biodiversity groups, and does so in terms directly relevant to conservation planners.

Vascular plants and vertebrates are the species most frequently used in SCPs, whereas a large part of the diversity may actually be composed of fungi, invertebrates and microorganisms, many of which may be undescribed (Pressey et al., 2003). Biodiversity surrogates are a partial solution to the problem of planning for cryptic biodiversity. Applications of environmental and community-level classifications as surrogates in SCP have produced both encouraging and discouraging results (Arponen et al., 2008). But when applied correctly there is compelling scientific evidence that ecosystem-types correlate with observed biodiversity patterns for fauna, including cryptic groups such as invertebrates (Bergeron et al., 2012).

Identifying and mapping vegetation units that are more homogenous in terms of biodiversity would limit the potential for SCP to miss representing biodiversity within its selection of planning units required to meet targets (Desmet and Cowling, 2004). Mapping vegetation units at the appropriate scale contributes to the robustness of a SCP. The problem of scale is particularly important in large heterogeneous areas where targets framed as percentages for broad regions can be achieved even though they fail to protect the natural features most urgently in need of protection (Pressey et al., 2003). This is true even of regions with formal protection greater than 10% of the land surface area. Coarse-scale maps do not capture all communities, and even if the vulnerability of the region may be low, rare vegetation types or habitats can easily 'fall through the cracks'. These issues can be mitigated by mapping at finer-scales with improved mapping and classification techniques (Desmet and Cowling, 2004).

1.1.4. Overview of current forest classification in Mpumalanga

The classification of indigenous forests in Mpumalanga Province has previously either occurred at a local site-based scale for only a few parts of the province (Deal et al., 1989; Lötter and Beck, 2004; Morgenthal and Cilliers, 1999; Muller, 1994; Stalmans et al., 1999; van der Schijff and Schoonraad, 1971; von Breitenbach, 1990) or at a much broader national scale (Acocks, 1988; Cooper, 1985; Low and Rebelo, 1998; Geldenhuys and Mucina, 2006; Mucina et al., 2006; von Maltitz et al., 2003). Von Breitenbach's (1990) study of the south-eastern Transvaal is historically perhaps the most comprehensive forest survey attempted in Mpumalanga yet unfortunately only the data from the Kaapsehoop and Uitsoek forests were analysed and published and the author failed to complete the analysis of all the data collected from the former Transvaal and Kwa-Zulu Natal forests. This work amounted to some 600 field days conducting detailed floristic and structural forest surveys. In his first and only report, von Breitenbach (1990) stated that his study confirmed the general perception that Mpumalanga's forests required revising as distinct forest types. However, currently no forest classification exists at the provincial scale.

The Department of Agriculture, Forestry and Fisheries (DAFF), formerly known as the Department of Water Affairs and Forestry (DWAF), commissioned a national–scale forest type classification in 2003 (von Maltitz et al., 2003), which was the first comprehensive classification of forests across South Africa. A hierarchy of seven forest groups comprising 24 forest types were presented. This forest classification was updated in the revision of vegetation types of South Africa, Lesotho and Swaziland (Mucina and Rutherford, 2006). The proposed classification is appropriate at a national scale. Furthermore, during the von Maltitz et al. (2003) National Forest Classification (NFC) analysis, the project utilised relevé data collected by a variety of researchers for different purposes across South Africa, which resulted in large discrepancies in species identified and the structural strata sampled, as often only tree species with a stem diameter greater than 10 cm were historically sampled. Mucina et al. (2007)

assessed the impact of using incomplete floristic and strata data from various sources in a subtype forest analysis. They concluded that only full floristic data sets can be reliably used in a classification.

According to the DAFF NFC, of the 24 forest types occurring in South Africa, only four of these are represented within Mpumalanga, of which the Mpumalanga Mistbelt Forest Type is ascribed to 82% of all forests known to occur in the province. This large forest type extends along the escarpment from Mariepskop to Barberton, and is considered too broad for conservation planning purposes as it does not consider local levels of diversity. A forest classification describing floristic variability at levels below that of a Forest Type (*sensu* NFC) would be a more appropriate product for biodiversity planning and management (Mucina et al., 2007).

Both the Mpumalanga Tourism & Parks Agency (MTPA) and DAFF recognised this need for a more thorough forest classification suitable for use at a finer scale for the management or conservation of forest units. DAFF have since embarked on a systematic forest subtype classification starting with the Albany Coastal, Pondoland Scarp and Eastern Scarp forests (Mucina et al., 2007). The MTPA also saw it as a priority to complete forest subtype classifications of its indigenous forests before the review of it's Mpumalanga Biodiversity Conservation Plan (MBCP; Ferrar and Lötter, 2007).

1.1.5. Vegetation classification methods

Finding meaningful patterns in community composition is a persistent challenge in vegetation science (Schmidtlein et al., 2010), where vegetation ecologists rely on a variety of available classification techniques to disentangle complex structures to discover patterns in vegetation communities. To achieve this, vegetation surveys and classification provide the essential tools for defining vegetation types (Chytrý et al., 2011). The methodology and software available for the classification of vegetation communities has improved greatly over the years and has been aided with improved computing equipment. However, several recent or local vegetation classifications have continued to use an age-old approach of Two-way Indicator Species Analysis, more generally known as TWINSPAN (Hill, 1979a) to classify sample plot data (Eckhardt et al*.,* 1997; Geldenhuys and Mucina, 2006; Morgenthal and Cilliers, 1999) and Detrended Correspondence Analysis (DCA) (Hill, 1979b) as their ordination technique to interpret environmental gradients (Eckhardt et al., 1997; Mathews et al*.,* 2001; Morgenthal and Cilliers, 1999). These combined methodologies for phytosociological investigations are still very popular in South Africa and globally, even though these techniques have been heavily criticised (Belbin and McDonald, 1993; McCune and Grace, 2002; Minchin, 1987; van Groenewoud, 1992). TWINSPAN, DCA and Correspondence Analysis all make use of a similar correspondence analysis algorithm that is considered useful to extract the first environmental

gradient only and are reported to perform poorly when there is more than one important gradient and with large data sets.

Many classification techniques have been developed and are now available in many software packages (e.g. Belbin, 1993; Belbin and McDonald, 1993; Clarke and Warwick, 1994; Kindt and Coe, 2005; McCune and Mefford, 2006; Podani, 2001; Schmidtlein et al., 2010; Tichý, 2002). Each choice of classification (especially clustering) is usually accompanied by the difficult choice of selecting a resemblance measure (see Legendre and Legendre, 1998; Podani, 2001) and further complicated by the broad choice of transformations (Noy-Meir, 1975; Podani, 2001; van der Maarel, 1979). Wolda (1981) warns that classification results depend on the similarity index chosen, which suggests the dangerous possibility that one can choose an index to demonstrate whatever one wants the data to show, without necessarily being able to prove that this is indeed what it does show. Running any combination of these different methods may be mathematically correct and interpretable, but the results may not necessarily be as good as another alternative method. As vegetation classification is often exploratory in context, it is difficult to say which method is the correct/better method. Careful consideration needs to be given to the method used in the final classification (Tichý et al., 2009; Wolda, 1981).

1.1.6. Environmental variables or processes driving variation in species composition

The search for underlying drivers of vegetation patterns is often pursued through analysing the relationship between species distributions and environmental or spatial variables. Observed variation in vegetation patterns may be interpreted by means of various ecological and biogeographical theories, ranging from Diamond's (1975) community "assembly rules", or differences in assembly history (Chase, 2003) such as historic biogeography (i.e. glaciation) where the resulting flora was formed by environmental and ecological processes that may no longer exist. Current community composition may also be the result of either deterministic niche-based or stochastic neutral processes, where stochastic processes may result in chance colonisation or ecological drift. Dispersal limitation is a much debated process that may in fact influence both processes (Chase and Myers, 2011). Stochastic processes such as dispersal, seen as a sequence of random events, are also influenced by the size of available species pools (i.e. metacommunity; McGill et al., 2006) or "dark diversity" (Pärtel et al., 2011). Niche-based processes include both environmental (abiotic) filtering and biotic interactions but processes may also be affected or determined by morphological characteristics such as plant size, propagule pressure, availability of niches and niche competition, but all of these interact across a range of scales of environmental processes to inform community composition (Chase and Myers, 2011).

Ecologists occasionally use ordination and variation partitioning (Borcard et al., 1992; Legendre, 1990) to decompose and disentangle the variation in community composition according to current ecological theory. In particular, variation partitioning has been applied to

interpret the influences of neutral and niche-based theories (see Laliberté et al., 2009; Legendre et al., 2009), where it has generally been claimed that the portion attributable towards “space” directly represents the relative importance of “neutral processes” (*sensu* Hubbell, 2001), while that portion attributable to “environment” represents the relative importance of “niche-based processes” (Legendre et al., 2009).

But dispersal is not purely a neutral process (de Casas et al., 2012). In variation portioning models, dispersal would influence both geographic spatial structure as well as environmental control (Smith and Lundholm, 2010), and consequently the proportion of variation attributable to spatial and environmental variables may not identify the relative contribution of neutral and niche-based processes in shaping the community under study. Simulations with low migration rates (dispersal) and high mortality resulted in different species becoming dominant in cells with the same environmental values. As migration increases, exchange of individuals between adjacent cells produces a more invariant community associated with each value of the environmental variable. At high migration rates this consistency declines, as migrating individuals increasingly establish in cells with suboptimal habitat conditions, resulting in mass effects (Shmida and Wilson, 1985; Smith and Lundholm, 2010). The implication of the above is reiterated in that dispersal, or migration, informs both environmental as well as spatial variability and makes it difficult to distinguish between either using variation partitioning.

1.1.7. Dispersal and connectivity are important forest processes structuring communities

For most forest plant species, dispersal is the only mechanism to reach new localities and is therefore the primary means of habitat selection (de Casas et al., 2012). But dispersal probabilities say little about the likelihood that species will persist. At the community level, the influence of diaspore arrival (i.e. regional dispersal or immigration) on species patterns may depend on niche-based environmental filters and dispersal rates (Chase and Myers, 2011; Smith and Lundholm, 2010). Dispersal rates influence the similarity of local communities (Chase, 2003). Local diversity is typically higher in metacommunities where dispersal rates among localities are more frequent relative to those with less-frequent dispersal.

Dispersal and the associated colonisation of forest patches has been identified as an important process in the Drakensberg montane forests of South Africa. Small patch size and isolation can contribute directly to local extinction. A species’ dispersal ability will determine its likelihood of re-colonising a habitat patch and persisting within the landscape as part of a dynamic metapopulation (Lawes *et al.,* 2007). Stochastic population theory predicts that if there is no movement between patches, the inevitable fate of the overall population is extinction. Without dispersal populations with low density would not be ‘rescued’ by immigration (Benton and Bowler, 2012). In this sense dispersal is a key ecological process that maintains species and population diversity within naturally fragmented forest ecosystems. Dispersal by animals is particularly important in the tropics where up to 90% of tropical tree species have fleshy,

vertebrate-dispersed fruit (Jordano, 1992), and up to 75% of all species may be vertebrate dispersed (Bollen et al., 2004).

Landscape connectivity is defined as 'the degree to which the landscape facilitates or impedes movement among resource patches' (Taylor et al., 2006), where it determines what proportion of the total habitat area can be reached and is available for an organism located at a particular point in the landscape (Saura et al., 2011). Accounting for the effects of habitat connectivity and the importance of certain patches in maintaining connectivity, and contributing to habitat availability, is important for numerous reasons (Awade et al., 2012; Taylor et al., 2006). Connectivity should also be measured from a functional perspective, whereby not only is the spatial arrangement of the habitat considered (structural connectivity), but also dispersal distances and/or behavioural responses of focal species to the physical structure of the landscape (functional connectivity; Saura and Torné, 2009; Taylor et al., 2006). There is general consensus that connectivity is species-specific and hard to implement across multiple species or communities (Nicholson et al., 2006).

Loss in connectivity contributes towards a decrease in habitat availability in fragmented landscapes (Awade et al., 2012). For a habitat to be easily available for an animal population, it should be both abundant and well connected (Saura and Torné, 2009). Habitat availability across fragmented landscapes is governed by the availability of reachable natural vegetation of suitable cover (Pascual-Hortal and Saura, 2006; Saura et al., 2011).

Driven by a desire for a more functional approach to landscape quantification, landscape ecologists are increasingly using graph theory to examine patterns of connectivity, identify potential dispersal pathways, and prioritize habitat patches for conservation (Kupfer, 2012). Graph theory offers a very efficient method to assess connectivity by representing the landscape as a series of nodes (patches) and links representing the potential ability of an organism to directly disperse between two habitat nodes (Cook et al., 2009). However this approach requires knowledge of species inter-patch movement, information that is difficult to obtain (Taylor et al., 2006), and detailed dispersal information is scarce for most species (Awade et al., 2012; Saura *et al.,* 2011).

1.1.8. Planning for persistence

Planning for pattern and processes in SCP (Margules and Pressey, 2000; Margules and Sarkar, 2007) are two of the key principles that distinguish it from many other planning approaches. If biodiversity is to persist in conservation area networks, then a variety of ecological and evolutionary processes need to be incorporated (Sarkar et al., 2006). Representivity is easier to define spatially than delineating ecological processes that may vary both spatially and temporally. Ecological processes are also exponentially more difficult to include in SCP and attempts to do so may at times detract from the scientific rigour of a SCP. Pressey et al. (2007) warn that planning only for biodiversity pattern (representivity) is likely to

jeopardize the persistence of many processes that require conservation management, yet there has been little progress towards implementing ecological processes (Groves et al., 2012). Studies that target both pattern and processes in one plan are rare (Klein et al., 2009). More effective conservation planning depends partly on science catching up with our ability to include both pattern and ecological processes (Pressey et al., 2007).

1.1.9. Setting targets for pattern and process features

SCP also requires the translation of explicit conservation goals into quantitative, operational targets (Margules and Pressey, 2000; Margules and Sarkar, 2007). The realisation of these goals require that targets be quantified, measured and progress assessed. Explicitly stated targets provide a clear purpose for conservation decisions, lending them accountability and defensibility (Pressey et al., 2003). Targets are generally required for both pattern and process to allow for the effective contribution that a selection of areas can make towards conservation goals. For biodiversity pattern, the historically popular target of 10% of area for countries or vegetation types has been criticized because it is too small to prevent the extinction of many species (Margules and Pressey, 2000). Such uniform targets are not based on information about the requirements for persistence of species or natural processes (Pressey et al., 2003). In fact protection of only 10% of Earth's ecosystems could make at least half of all terrestrial species vulnerable to extinction (Lawes et al., 2007). But then again targets of less than 100% are likely to miss some biodiversity, and even 100% targets cannot guarantee biodiversity persistence because of extinction debt (Pressey et al., 2003). A more rigorous application of a target setting approach based on the Species Area Relationship (SAR) of Desmet and Cowling (2004) for a community of species identified area targets of between 16% and 36% for vegetation types in South Africa (Rouget et al., 2004).

1.2. RATIONALE FOR THE STUDY

The lack of an appropriately scaled forest classification that could be used as a surrogate for forest biodiversity in the next revision of the SCP for Mpumalanga Province, nor the availability of spatially mapped forest process features to support the persistence of forest biodiversity, provided the initial motivation for this thesis. The revised SCP for Mpumalanga Province will be called the Mpumalanga Biodiversity Sector Plan (Lötter, 2013) which will be used to guide land-use planning as well as protected area expansion spatial priority areas. The indigenous forests will be incorporated into the SCP together with a multitude of other biodiversity features, such as Red Data Listed species, grassland habitats, wetlands, etc.. An appropriately scaled forest classification will serve as a "coarse filter" surrogate to represent the distribution of forest biodiversity (Rouget, 2003).

The identification of forest communities for use in SCP is best informed by a methodology that is able to decompose the gamma diversity into homogenous units that reflect floristic and habitat similarities. These similarities ideally should not be shared with other communities and should contain species that efficiently discriminate each community from one another. Such species are called diagnostic (Kent and Coker, 1994; Willner et al., 2009) or faithful species (Chytrý et al., 2002). Diagnostic species are those with a high fidelity to a particular cluster or community.

The identification of important forest processes that can be spatially mapped and used in a SCP requires investigation and interrogation by means of exploring and assessing the underlying drivers responsible for variation in species composition. From this analysis important ecological processes can be identified and prioritised for inclusion within a SCP. Lastly, for forest features to be incorporated within a SCP that uses optimization algorithms to identify conservation priorities, quantitative targets need to be established for both pattern and process features.

1.3. AIM AND OBJECTIVES

AIM

The aim of this study is to investigate and describe forest pattern and ecological processes at appropriate scales in the indigenous forests of the Mpumalanga Province, South Africa, to inform a provincial systematic conservation assessment.

OBJECTIVES

The objectives of this study are:

1. Evaluate the performance of various classification methods to determine the most robust classification technique appropriate for a regional classification.
2. To classify and appropriately describe and present the results of the forest classification in terms of floristic and physiognomic differences.
3. Use variation partitioning and ordination to explore the influence of geographic space and local, regional and supra-regional scales of environmental variables on forest composition. This will include identifying the main environmental variables and ecological processes driving variation in species composition.
4. Use dispersal distances to identify priority forest patches across a largely natural landscape that ensures a functionally connected forest network (i.e. dispersal abilities maintained), and which supports the persistence of ecological processes that maintains species diversity and composition.

5. Lastly, to establish quantitative pattern and process targets for the indigenous forests in Mpumalanga for their inclusion into a SCP.

1.4. STRUCTURE OF THESIS

The first chapter (this chapter) presents a general introduction to the need for an appropriately scaled analysis of forest communities (pattern) and ecological processes that will support their inclusion within a SCP for the province of Mpumalanga. It provides a brief overview of some of the ecological theory informing vegetation classification, the current state of vegetation classification within Mpumalanga, the need for SCP pattern and process features, the importance of dispersal, and the need for quantitative target setting. Chapter 2 establishes the most robust classification method appropriate for the data set collected throughout Mpumalanga. The performances of various techniques are evaluated and assessed. In Chapter 3, the most appropriate classification technique is applied to the data set and the resulting classification is presented within the nested hierarchy of the National Forest Classification. Here the focus is on forest subtypes that are described in terms of various floristic, growth form, forest dependency, and leaf retention characteristics. In Chapter 4, variation partitioning and ordination explores and identifies the main environmental drivers responsible for differences in species composition, also allowing for the validation and interpretation of new subtype classification. Specifically, this chapter explores the influence of geographic space and three scales of environmental variables (local, regional, and supra-regional) on forest composition, also across all strata (herbaceous, shrub, tree). This chapter identifies dispersal as a key ecological process that is analysed and quantified in greater detail in Chapter 5, which looks at using dispersal, connectivity, and graph theory to prioritise the individual connectivity values for each forest patch. Chapters 2 to 5 identify spatially explicit data layers that can be incorporated into a SCP. However, to be incorporated within a SCP, they require quantitative targets guided by the translation of conservation goals into explicit targets. Chapter 6 determines the quantitative targets for both pattern and process features identified during the study. The concluding chapter, Chapter 7, provides a synopsis of the thesis and identifies some further research needs. Figure 1 provides an overview of the sample plots used in this thesis to survey the indigenous forests as well as a summary of the geographic names used throughout the thesis.

Each research chapter in this thesis has been formatted as a research paper that has or will be submitted for publication in a peer-reviewed journal. Thus Chapters 2–6 are designed to stand alone and there may therefore be repetition in content and references throughout this thesis. To date, Chapter 2 has been published in *Community Ecology* in 2013 (14: 121–132), Chapter 3 has now been published in the *South African Journal of Botany* in 2014 (90: 37–51), Chapter 4 will be submitted to *Ecological Monographs*, Chapter 5 to *Ecology Letters* and Chapter 6 to *Conservation Biology*. The formatting and reference style employed in each

chapter differs according to the requirements of the various journals. The format of introductory and concluding chapters (Chapters 1 and 7) follows that of the *South African Journal of Botany*.

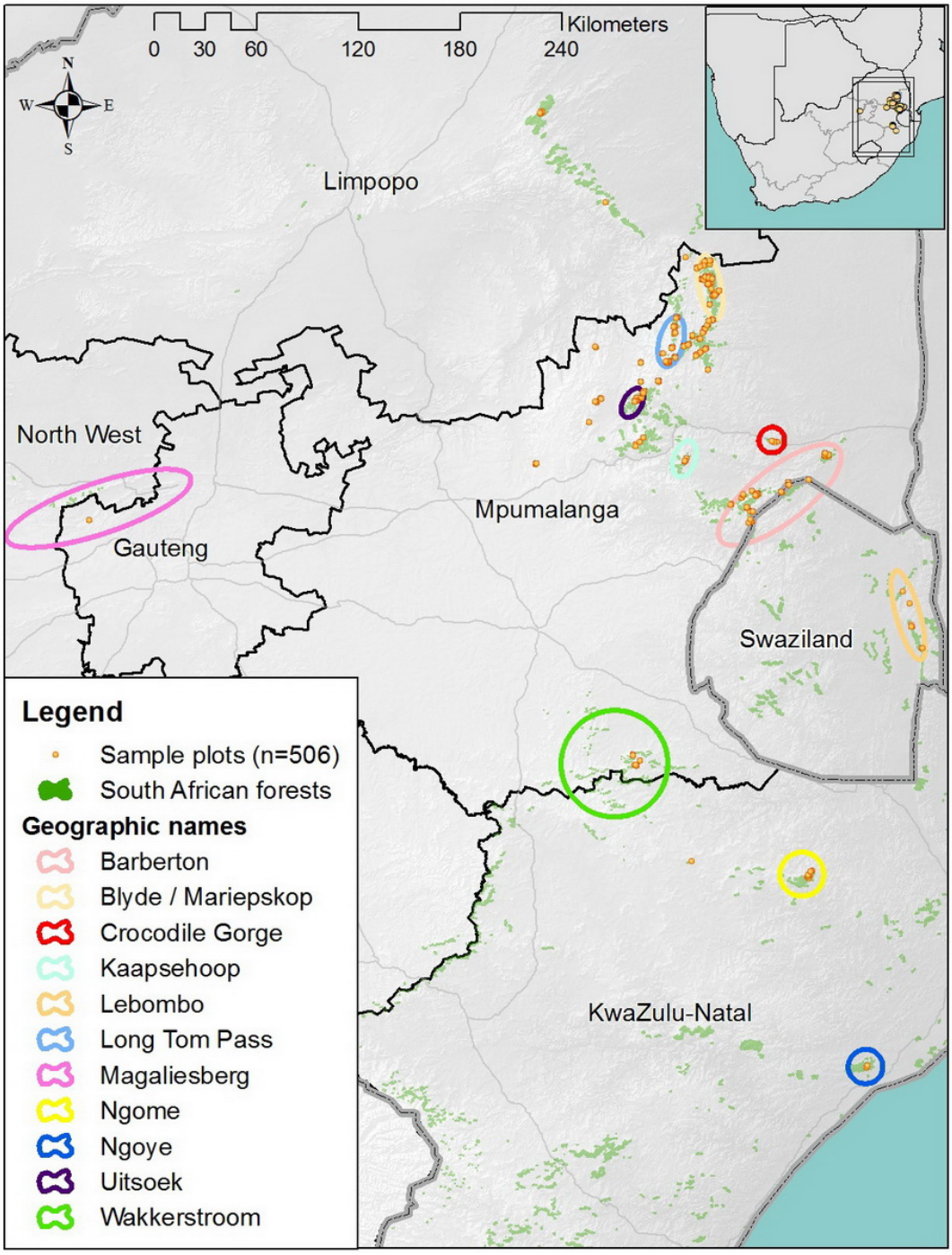


Fig. 1. Distribution of sample plots (n=506) and summary of some of the geographic names used in this thesis.

Throughout this thesis I make use of plot data as input into the various methodologies used in the various chapters (see Figure 1). The number of plots varies between the chapters according to the specific objectives of the chapter. In order to avoid confusion in the use of

different numbers of plots between the chapters, I provide an explanation below. In Chapter 2, I make use of the full floristic plot data set, which comprised 506 plot samples, each 0.04 ha (20 m x 20 m). This data set included samples from adjacent provinces. In Chapter 3, I limit this data set to only those forest subtypes (newly identified) occurring within Mpumalanga (n = 434), avoiding communities not occurring within Mpumalanga. In Chapter 4, I explore the contribution of the environmental variables towards explaining some of the observed variation. I therefore exclude four plots thought to be azonal at the time (thus n = 430 plots). In Chapter 5, I analyse dispersal characteristics of the Mpumalanga data set (n = 434) and finally in Chapter 6 I include an additional 4 plots (n = 438), collected subsequent to the classification, in the calculation of forest targets using species area curves, where I needed to try and increase the small number of sample plots for the Escarpment Riverine forest subtype.

In Chapters 2 to 5 I provide maps of the sample points or show the sample points classified according to the new forest classification (established in Chapter 3). In Chapter 6 I then provide a map wherein the spatial polygon data set for forests in Mpumalanga has been classified according to the new forest classification (n = 1914 forest polygons classified). I was required to classify the spatial data set according to the new forest subtype classification in order to calculate forest targets. The classification of the data set does not fall into the objectives of the paper (Chapter 6), hence it is not stated how I classified the data set in Chapter 6. I therefore briefly describe the process of doing so below. Based on the results of Chapter 4 (which provided an analysis of environmental variables explaining the differences in species composition), I collated GIS data of appropriate environmental variables which I then used to manually classify individual forest polygons into the new forest subtypes. I used the environmental variables to assist in classifying those polygons I was not familiar with.

REFERENCES

Acocks, J.P.H., 1988. Veld types of South Africa. Memoirs of the Botanical Survey of South Africa 57, 1–146.

Adie, H., Goodman, P.S., 2000. Forests, in: Goodman, P.S. (Ed), Determining the conservation value of land in KwaZulu-Natal. Draft Report. Biodiversity Division, KwaZulu-Natal Nature Conservation Service, Pietermaritzburg.

Arponen, A., Moilanen, A., Ferrier, S., 2008. A successful community-level strategy for conservation prioritisation. Journal of Applied Ecology 45, 1436–1445.

Awade, M., Boscolo, D., Metzger, J.P., 2012. Using binary and probabilistic habitat availability indices derived from graph theory to model bird occurrence in fragmented forests. Landscape Ecology 27, 185–198.

Belbin, L., 1993. PATN Pattern Analysis Package. Users Guide. Division of Wildlife and Ecology, CSIRO.

Belbin, L., McDonald, C., 1993. Comparing three classification strategies for use in ecology. Journal of Vegetation Science 4, 341–348.

Benton, T.G., Bowler, D.E., 2012. Linking dispersal to spatial dynamics, in: Clobert, J., Baguette, M., Benton, T., Bullock, J. (Eds.), Dispersal ecology and evolution. Oxford University Press, Oxford, pp. 251–265.

Bergeron, J.A., Blanchet, F., Spence, J.R., Volney, W.J.A., 2012. Ecosystem classification and inventory maps as surrogates for ground beetle assemblages in boreal forest. Journal of Plant Ecology 5, 97–108.

Bollen, A., Van Elsacker, L. Ganzhorn, J.U., 2004. Tree dispersal strategies in the littoral forest of Sainte Luce (SE-Madagascar). Oecologia 139, 604–616.

Borcard, D., Legendre, P., Drapeau, P., 1992. Partialling out the spatial component of ecological variation. Ecology 73, 1045–1055.

Chase, J.M., 2003. Community assembly: When should history matter? Oecologia 136, 489–498.

Chase, J.M., Myers J.A., 2011. Disentangling the importance of ecological niches from stochastic processes across scales. Philosophical transactions of the Royal Society of London, Series B 366, 2351–2363.

Chytrý, M., Tichý, L., Holt, J., Botta-Dukát, Z., 2002. Determination of diagnostic species with statistical fidelity measures. Journal of Vegetation Science 13, 79–90.

Chytrý, M., Schaminée, J.H.J., Schwabe, A., 2011. Vegetation survey: a new focus for Applied Vegetation Science. Applied Vegetation Science 14, 435–439.

Clarke, K.R., Warwick, R.M., 1994. Change in marine communities: an approach to statistical analysis and interpretation. Natural Environment Research Council, United Kingdom.

Colwell, R., Chao, A., Gotelli, N., Lin, S-Y., Mao, C.X., Chazdon, R.L., Longino, J.T., 2012. Models and estimators linking individual-based and sample-based rarefaction, extrapolation and comparison of assemblages. Journal of Plant Ecology 5, 3–21.

Cook, B., Puotinen, M.L., Borah, R., 2009. Ranking habitat patches by contribution to network connectivity: tradeoffs between processing time and spatial realization, in: 18th world IMACS/MODSIM congress, Cairns, 13–17 July 2009, pp. 1922–1928.

Cooper, K.H., 1985. The conservation status of indigenous forests in Transvaal, Natal and Orange Free State, South Africa. Wildlife Society of Southern Africa, Durban.

de Cáceres, M., Font, X., Vicente, P., Oliva, F., 2009. Numerical reproduction of traditional classifications and automatic vegetation identification. Journal of Vegetation Science 20, 620–628.

de Casas, R.R., Willis, C.G., Donohue, K., 2012. Plant dispersal phenotypes: a seed perspective of maternal habitat selection, in: Clobert, J., Baguette, M., Benton, T., Bullock, J. (Eds.), Dispersal ecology and evolution. Oxford University Press, Oxford, pp. 171–184.

Deal, G.B., Theron, G.K., Westfall, R.H., 1989. The vegetation ecology of the eastern Transvaal escarpment in the Sabie area. 2. Floristic classification. Bothalia 19, 69–89.

Desmet, P., Cowling, R., 2004. Using the species–area relationship to set baseline targets for conservation. Ecology and Society 9: 11. [online] URL: http://www.ecologyandsociety.org/vol9/iss2/art11

Diamond, J.M., 1975. Assembly of species communities, in: Cody, M.L., Diamond, J.M. (Eds.), Ecology and evolution of communities. Harvard University Press, Cambridge, Mass, pp. 342–444.

Eckhardt, H.C., van Rooyen, N., Bredenkamp, G.J., 1997. Plant communities of forests, woodlands and thickets in northern KwaZulu-Natal. Koedoe 40, 91–112.

Ferrar, A.A., Lötter, M.C., 2007. Mpumalanga Biodiversity Conservation Plan Handbook. Mpumalanga Tourism & Parks Agency, Nelspruit.

Geldenhuys, C.J., 1991. Distribution, size and ownership of the southern Cape forests. South African Forestry Journal 158, 51–66.

Geldenhuys, C.J., Mucina, L., 2006. Towards a new national forest classification for South Africa, in: Beentje, H., Ghazanfar, S. (Eds.), Taxonomy and ecology of African plants, their conservation and sustainable use, Royal Botanic Gardens, Kew, pp. 111–129.

Groves, C.R., Game, E.T., Anderson, M.G., Cross, M., Enquist, C., Ferdaña, Z., Girvetz, E., Gondor, A., Hall, K.R., Higgins, J., Marshall, R., Popper, K., Schill, S., Shafer, S., 2012. Incorporating climate change into systematic conservation planning. Biodiversity and Conservation 21, 1651–1671.

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

Hill, M.O., 1979b. DECORANA – a FORTRAN program for detrended correspondence analysis and reciprocal averaging. Cornell University, Ithaca, New York.

Hubbell, S.P., 2001. The Unified Neutral Theory of Biodiversity and Biogeography. Princeton University Press, Princeton.

Jordano, P., 1992. Fruits and frugivory, in: Fenner, M. (Ed.), Seeds: the ecology of regeneration in plant communities. CABI, Wallingford, United Kingdom, pp. 105–156.

Kent, M., Coker, P., 1994. Vegetation Description and Analysis – A Practical Approach. J. Wiley & Sons, Chichester.

Kindt, R., Coe, R., 2005. Tree diversity analysis. A manual and software for common statistical methods for ecological and biodiversity studies. World Agroforestry Centre (CRAF), Nairobi.

Klein, C.J., Wilson, K.A., Watts, M., Stein, J., Berry, S., Carwardine, J., Smith, M.S., Mackey, B.G., Possingham, H.P., 2009. Incorporating ecological and evolutionary processes into large–scale conservation planning. Ecological Applications 19, 206–217.

Knight, A.T., Cowling, R.M., Campbell, B.M., 2006. Planning for implementation: an operational model for implementing conservation action. *Conservation Biology* 20, 549–561.

Kupfer, J.A., 2012. Landscape ecology and biogeography: Rethinking landscape metrics in a post-FRAGSTATS landscape. Progress in Physical Geography 36, 400–420.

Laliberté, E., Paquette, A., Legendre, P., Bouchard, A., 2009. Assessing the scale-specific importance of niches and other spatial processes on beta diversity: a case study from a temperate forest. Oecologia 159, 377–388.

Lawes, M.J., Adie, H., Eeley, H.A.C., Kotze, D.J., Wethered, R., 2007. An assessment of the forests of the Maloti-Drakensberg transfrontier bioregion, with reference to important ecosystem processes. Forest Biodiversity Research Unit, School of Biological and Conservation Sciences, University of KwaZulu-Natal. URL: http://www.ukzn.ac.za/Biology/1156.aspx.

Legendre, P., 1990. Quantitative methods and biogeographic analysis, in: Garbary, D.J., South, R.G. (Eds.), Evolutionary Biogeography of the Marine Algae of the North Atlantic. Springer–Verlag, Berlin, pp. 9–34.

Legendre, P., Legendre, L., 1998. Numerical ecology. Elsevier, Amsterdam.

Legendre, P., Xiangcheng, M., Haibao, R., Keping, M., Mingjian, Y., Sun, I-F., Fangliang, H., 2009. Partitioning beta diversity in a subtropical broad-leaved forest of China. Ecology 90, 663–674.

Lombard, A.T., Cowling, R.M., Pressey, R.L., Rebelo, A.G., 2003. Effectiveness of land classes as surrogates for species in conservation planning for the Cape Floristic Region. Biological Conservation 112, 45–62.

Lötter, M.C., 2013. Technical Report for the Mpumalanga Biodiversity Sector Plan – MBSP 2013. Mpumalanga Tourism & Parks Agency, Nelspruit.

Lötter, M.C., Beck, H.T., 2004. Preliminary inventory and classification of indigenous afromontane forests on the Blyde River Canyon Nature Reserve, Mpumalanga, South Africa. BMC Ecology 2004, 4:9. (http://biomedcentral.com/1472-6785/4/9)

Lötter, M.C., Burrows, J., Emery, A.J., 2002. Phytochoria, Centres and regions of endemism: In: Emery, A.J., Lötter, M.C., Williamson, S.D. (Eds), Determining the conservation value of land in Mpumalanga, Report, Mpumalanga Parks Board, Nelspruit, pp. 48–59.

Lötter, M.C., Mucina, L., Witkowski, E.T.F., 2013. The classification conundrum: species fidelity as leading criterion in search of a rigorous method to classify a complex forest data set. Community Ecology 14, 121–132.

Lötter, M.C., Mucina, L., Witkowski, E.T.F., 2014. Classification of the indigenous forests of Mpumalanga Province, South Africa. South African Journal of Botany 90, 37–51.

Low, A.B., Rebelo, A.G., (Eds.) 1998. Vegetation of South Africa, Lesotho and Swaziland. A companion to the vegetation map of South Africa, Lesotho and Swaziland. Department of Environmental Affairs & Tourism, Pretoria.

Margules, C.R., Pressey, R.L., 2000. Systematic conservation planning. Nature 405, 243–253.

Margules, C.R., Sarkar, S., 2007. Systematic Conservation Planning. Cambridge: Cambridge University Press.

Mathews, W.S., van Wyk, A.E., van Rooyen, N., Botha, G.A., 2001. Vegetation of the Tembe Elephant Park, Maputaland, South Africa. South African Journal of Botany 67, 573–594.

McCune, B., Grace, J.B., 2002. Analysis of ecological communities. MjM Software, Gleneden Beach, OR.

McCune, B., Mefford, M.J., 2006. PC-ORD. Multivariate analysis of ecological data. Version 5.20. MjM Software, Gleneden Beach, OR.

McGill, B.J., Maurer, B.A., Weiser, M.D., 2006. Empirical evaluation of neutral theory. Ecology 87, 1411–1423.

Minchin, P.R., 1987. An evaluation of the relative robustness of techniques for ecological ordination. Vegetatio 69, 89–107.

Morgenthal, T.L., Cilliers, S.S., 1999. Vegetation analysis of Pedlar's Bush, Mpumalanga, and its conservation. South African Journal of Botany 65, 270–280.

Mucina, L., Geldenhuys, C.J., Rutherford, M.C., Powrie, L.W., Lötter, M.C., von Maltitz, G.P., Euston-Brown, D.I.W., Matthews, W.S., Dobson, L., McKenzie, B., 2006. Afrotemperate, subtropical and azonal forests, in: Mucina, L., Rutherford, M.C. (Eds.), The vegetation of South Africa, Lesotho and Swaziland, South African National Biodiversity Institute, Pretoria, pp. 584–615.

Mucina, L., Pienaar, E., van Niekerk, A., Lötter, M.C., Scott-Shaw, C.R., Meets, M., Seoke, L., Sekome, T., Siebert, S.J., Loffler, L., Cawe, S.G., Dold, A.P., Abbott, A., Kalwij, J., Tichý, L., 2007. Habitat-level Classification of the Albany Coastal, Pondoland Scarp and Eastern Scarp Forests. Unpublished Report for DWAF, Stellenbosch University, Matieland.

Mucina, L., Rutherford, M.C., (Eds) 2006. The vegetation of South Africa, Lesotho and Swaziland. South African National Biodiversity Institute, Pretoria.

Muller, D.J., 1994. Resultate van 'n voorraadsopname in die inheemse bos op Mariti, Oos Transvaal. South African Journal of Forestry 168, 27–31.

Nicholson, E., Westphal, M.I., Frank, K., Rochester, W.A., Pressey, R.L., Lindenmayer, D.B. Noy-Meir, I., Walker, D., Williams, W.T., 1975. Data transformations in ecological ordination. Journal of Ecology 63, 779–800.

Ostermann, O.P., 1998. The need for management of nature conservation sites designated under Natura 2000. Journal of Applied Ecology 35, 968–973.

Pärtel, M., Szava-Kovats, R., Zobel, M., 2011. Dark diversity: shedding light on absent species. Trends in ecology and evolution 26, 124–128.

Pascual-Hortal, L., Saura, S., 2006. Comparison and development of new graph-based landscape connectivity indices: towards the priorization of habitat patches and corridors for conservation. Landscape Ecology 21, 959–967.

Podani, J., 2001. SYN-TAX 2000. Computer Programs for Data Analysis in Ecology and Systematics. User's Manual. Scientia Publishing, Budapest.

Pressey, R.L., Cabeza, M., Watts, M.E., Cowling, R.M., Wilson, K.A., 2007. Conservation planning in a changing world. Trends in Ecology and Evolution 22, 582–592.

Pressey, R.L., Cowling, R.M., Rouget, M., 2003. Formulating conservation targets for biodiversity pattern and process in the Cape Floristic Region, South Africa. Biological Conservation 112, 99–127.

Rouget, M., 2003. Measuring conservation value at fine and broad scales: implications for a diverse and fragmented region, the Agulhas Plain. Biological Conservation 12, 217–232.

Rouget, M., Reyers, B., Jonas, Z., Desmet, P., Driver, A., Maze, K., Egoh, B., Cowling, R.M., Mucina, L., Rutherford, M., 2004. South African National Spatial Biodiversity Assessment Technical Report. Volume 1: Terrestrial Component. South African National Biodiversity Institute, Pretoria.

Rutherford, M.C., Westfall, R.H., 1994. Biomes of southern Africa: an objective categorization. Memoirs of the Botanical Survey of South Africa No 63.

Sarkar, S., Pressey, R.L., Faith, D.P., Margules, C.R., Fuller, T., Stoms, D.M., Moffett, A., Wilson, K.A., Williams, K.J., Williams, P.H., Andelman, S., 2006. Biodiversity conservation planning tools: present status and challenges for the future. Annual Review of Environment and Resources 31, 123–159.

Saura, S., Estreguil, C., Mouton, C., Rodríguez-Freire, M., 2011. Network analysis to assess landscape connectivity trends: application to European forests (1990–2000). Ecological Indicators 11, 857–860.

Saura, S., Torné, J., 2009. Conefor Sensinode 2.2: a software package for quantifying the importance of habitat patches for landscape connectivity. Environmental Modelling & Software 24, 135–139. www.conefor.org, accessed June 2012.

Schmidtlein, S., Tichý, L., Feilhauer, H., Faude, U., 2010. A brute-force approach to vegetation classification. Journal of Vegetation Science 21, 1162–1171.

Shmida, A. Wilson, M.V., 1985. Biological determinants of species diversity. Journal of Biogeography 12, 1–20.

Smith, T.W., Lundholm, J.T., 2010. Variation partitioning as a tool to distinguish between niche and neutral processes. Ecography 33, 648–655.

Stalmans, M., Robinson, E.R., Balkwill, K., 1999. Ordination and classification of the vegetation of Songimvelo Game Reserve in the Barberton Mountainland, South Africa, for the assessment of wildlife habitat distribution and quality. Bothalia 29, 305–325.

Taylor, P.D., Fahrig, L., With, K.A., 2006. Landscape connectivity: a return to the basics, in: Crooks, K.R., Sanjayan, M. (Eds.), Connectivity conservation. Cambridge University Press, Cambridge, pp. 29–43.

Tichý, L., 2002. JUICE, software for vegetation classification. Journal of Vegetation Science 13, 451–453.

Tichý, L., Chytrý, M., Hájek, M., Talbot, S., Botta-Dukát, Z., 2009. OptimClass: Using species-to-cluster fidelity to determine the optimal partition in classification of ecological communities. Journal of Vegetation Science 21, 287–299.

van der Maarel, E., 1979. Transformation of cover-abundance values in phytosociology and its effects on community similarity. Vegetatio 39, 97–114.

van der Schijff, H.P., Schoonraad, E., 1971. The flora of the Mariepskop Complex. Bothalia 10, 461–500.

van Groenewoud, H., 1992. The robustness of Correspondence, Detrended Correspondence, and TWINSPAN Analysis. Journal of Vegetation Science 3, 239–246.

von Breitenbach, F., 1990. Reports on indigenous forests. Part 1. Introduction and methods. South-eastern Transvaal forests. Kaapsehoop forests. Uitsoek forests. Department of Environmental Affairs and Tourism, Pretoria.

von dem Bussche, G.H., 1991. Indigenous high forests in the Transvaal with special reference to inventory and monitoring systems. South African Forestry Journal 158, 109–111.

von Maltitz, G., Fleming, G., 1999. Status of indigenous forests in South Africa, in: Seydack, A.H.W., Vermeulen, W.J., Vermeulen, C. (Eds.), Towards sustainable management based on scientific understanding of natural forests and woodlands. Proceedings: Natural Forests and Savanna Woodlands Symposium II, Knysna, South Africa, pp. 93–99.

von Maltitz, G., Mucina, L., Geldenhuys, C., Lawes, M., Eeley, H., Adie. H., Vink, D., Fleming, G., Bailey, C. 2003. Classification system for South African indigenous forests: an objective classification for the Department of Water Affairs and Forestry. Report ENV-P-C 2003-017, Environmentek, CSIR, Pretoria.

Willner, W., Tichý, L., Chytrý, M., 2009. Effects of different fidelity measures and contexts on the determination of diagnostic species. Journal of Vegetation Science 20, 130–137.

Wolda, H., 1981. Similarity indices, sample size and diversity. Oecologia 50, 296–302.

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CHAPTER TWO:

The classification conundrum: species fidelity as leading criterion in search of a rigorous method to classify a complex forest data set

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Abstract: We present a test involving a large number of data-analytical techniques to identify a rigorous numerical classification method optimising on statistically identified faithful species. The test follows a stepwise filtering process involving various numerical-classification tools. Five steps were involved in the testing: (1) evaluation of 322 classification tools using OptimClass 1; (2) comparison of 20 best performing methods by standardising the various performances across a range of fidelity values using OptimClass 1 and OptimClass 2, to assess the effectiveness of the agglomerative clustering and one divisive technique; (3) calculation and comparison of Uniqueness values and ISAMIC (Indicator Species Analysis Minimising Intermediate Constancies) scores of the resulting classifications; (4) comparison of different classifications by analysing the similarities of the resulting synoptic tables using faithful species, assuming that clusters with similar faithful species represent corresponding vegetation types, and (5) final selection of the single best method based on an expert review of non-geometric internal evaluators, NMDS ordinations and mapped classification solutions. A complex data set, representing many forest vegetation types and consisting of 506 relevés of 20 m × 20 m sampled in the indigenous forests of Mpumalanga Province (South Africa), was tested. Analysis of Uniqueness provided insight into which methods produced classifications that did not share faithful species. The analysis of synoptic table similarity showed that the classification results were at most 88% similar, while in the most divergent case similarity of only 50% was achieved. OptimClass eliminated poorly performing numerical-classification combinations and highlighted the best performing methods. Yet it was unable to reveal the single best performing method unequivocally across the range of fidelity values used. In such cases, we suggest the solution can be sought in relying on involving external data through expert opinion. Ordinal Clustering and TWINSPAN produced the most outlying classification results. Flexible beta clustering ($\beta = -0.25$) in combination with Bray-Curtis coefficient, standardised by sample unit totals, produced the most informative result for our data set when using informal expert-defined ecological and biogeographical judgement criteria. We recommend that the performance of a set of methods be tested prior to selecting the final classification approach.

Abbreviations: ISAMIC–Indicator Species Analysis Minimizing Intermediate Constancies, GIS–Geographical Information Systems, NMDS–Non-metric Multidimensional Scaling, PCoA–Principal Coordinates Analysis, TWINSPAN–Two-way Indicator Species Analysis, UPGMA–Unweighted Pair-Group Method using Arithmetic Averages.

1. Introduction

Vegetation scientists are commonly faced with the daunting task of finding the best performing, appropriate formal numerical-analytical tools to reveal the complex structures of their multivariate data sets. Advent of powerful computers and easy-to-use software packages has been a major technological catalyst for numerical data analysis in vegetation science over the past 20-30 years (e.g., Jongman et al. 1995, Kent and Coker 1994, McCune and Grace 2002, Mucina and van der Maarel 1989, Podani 2006). The field of vegetation classification witnessed rapid development of new tools and approaches whose application was further assisted by the release of software packages well tailored to the needs of vegetation scientists (e.g., Belbin 1993, Belbin and McDonald 1993, Clarke and Warwick 1994, Kindt and Coe 2005, McCune and Mefford 2006, Podani 2001, Tichý 2002). However, the great choice of options may result in new problems. Selection of a clustering method, for instance, involves complexity of selecting an appropriate resemblance measure (see Legendre and Legendre 1998, Podani 2001, Tamás et al. 2001) – a process which might be further complicated by the broad choice of transformations (Noy-Meir et al. 1975, Podani 2001, van der Maarel 1979). We call selecting the appropriate numerical classification approach when several valid alternatives exist, *the classification conundrum.*

Wolda (1981) warned against the danger of choosing a resemblance index to demonstrate whatever one wants the data to show, without necessarily being able to prove that this

is indeed what it does show. Best practice requires comparative assessment of a variety of available procedures in order to select the most rigorous classification procedure appropriate for a particular data set. Aho et al. (2008) suggested that classification methods should be examined and tested prior to vegetation classification. The choice of a classification technique is not a trivial procedure as results of numerical classification can vary greatly depending on the selected methodology and nature of the data sets (Aho et al. 2008, Belbin and McDonald 1993, Campbell 1978, Tichý et al. 2009).

Given the large number of numerical-analytic tools available, vegetation scientists need criteria with which to make their choice. The two approaches generally followed have been formal assessment tools of classification effectiveness, as developed for instance by Aho et al. (2008), or the pragmatic (albeit less formal) expert judgement based on ecological and biogeographical interpretability. Classification solutions can be evaluated using external or internal criteria (e.g., Gauch and Whittaker 1981). There are basically two groups of criteria used in judging effectiveness and plausibility of the achieved classification result, those involving *external criteria* and those involving *internal criteria*.

External criteria are variables measured on the classified objects but not used in the process of classification. If classification is based on species composition, environmental variables are appropriate external criteria. Discriminant analysis, for instance, could be used to evaluate the degree of differentiation between clusters based on values of external variables (Tichý et al. 2009). On the other hand, internal criteria use the characteristics of the clusters themselves to gauge effectiveness of classification (Aho et al. 2008). It is worth noting that internal and external criteria may contradict each other, such as when a transitional or disturbed area may lack faithful species but it is identified using external criteria.

There are two kinds of internal evaluators, namely *geometric* and *non-geometric evaluators*. Geometric evaluators concentrate on data set characteristics and evaluate classification effectiveness based on the relationship between the sampled plots. Non-geometric evaluators measure classification effectiveness based on species distributions and indicator species (Aho et al. 2008). Dale (1995) was critical of the use of geometric evaluators as they failed to assess what most vegetation scientists are interested in, namely the characterization of clusters based on indicator (faithful) species. External evaluators have generally been used to assess classification efficiency while the uses of internal evaluators have largely been ignored (Aho et al. 2008, Belbin and McDonald 1993, Gauch and Whittaker 1981). Practically, the use of internal evaluators is of more importance to vegetation scientists as external evaluation of classification solutions may be difficult for non-simulated data sets. Furthermore internal evaluation allows an assessment of the suitability of a particular classification method for a particular data set (Aho et al. 2008). In a way, using *expert opinion* as an assessment tool of classification effectiveness is a form of external evaluation analysis: synthetic knowledge (or experience) not previously involved in formal numerical analysis is used to make judgements.

In South Africa the progress in numerical analysis of vegetation data and in formal testing of the effectiveness of the classification in particular, remained largely ignored by practising vegetation scientists. Most vegetation-classification studies have continued to rely on TWINSPAN (Hill 1979), often followed by informal (and ill-specified) table hand-sorting to classify vegetation. TWINSPAN remains globally popular (Roleček et al. 2009) despite the numerous criticisms this technique has been rightly exposed to (Belbin and McDonald 1993, McCune and Grace 2002, Minchin 1987, van Groenewoud 1992).

The purpose of this paper is to provide a practical demonstration of selecting a rigorous data-analytical technique with the aim of advising the numerical classification methodology in achieving formally robust and ecologically/biogeographically informative classification of the forest vegetation of Mpumalanga Province (South Africa).

The following specific objectives will be targeted:

1. Evaluation of a variety of numerical-classification tools (combinations of various transformations, resemblances, and clustering/divisive algorithms) and filtering out poorly performing ones through a series of filters (steps) which consider faithful species as good indicators of classifications.

2. Comparison of identified top performing methods using Uniqueness values (Chytrý and Tichý 2003) and Indicator Species Analysis Minimizing Intermediate Constancies (ISAMIC) classification scores (Roberts 2010).

3. Comparison of the classification output of the top performing methods by using principal coordinate analysis of the similarity between the synoptic tables.

4. The selection of the most appropriate numerical-classification method from the final three rigorous yet dissimilar techniques based on expert interpretation of comparative assessment results, NMDS ordinations, and mapping the resulting classifications.

2. Materials and methods

2.1. The test data set

A data set comprising 506 relevés was compiled by original sampling of the indigenous forests of Mpumalanga Province and surrounding areas of Limpopo Province, KwaZulu-Natal Province (all South Africa) and the Kingdom of Swaziland. Indigenous forests make up 0.51% of Mpumalanga's vegetation cover and mostly occur in small fragments with an average patch size of 29 ha (Lötter et al. 2002). Altitude at which the forest patches occur varies between 251 m and 1974 m above sea level while mean annual rainfall ranges from 500 to 1635 mm. Mean annual temperature varies between 14°C and 22°C (according to modelled GIS data, based on Schulze 1997).

Plots of 20 m × 20 m (0.04 ha) were used to sample species composition. Cover-abundance values were recorded for each higher plant species according to the seven-class Braun-Blanquet cover-abundance scale (Mueller-Dombois and Ellenberg 1974). The plot data were stored in a database operated by Turboveg 2.0 software package (Hennekens and Schaminée 2001) and exported to JUICE 7 (Tichý 2002) where the data were code replaced into percentage values prior the numerical analyses. Only woody taxa (canopy trees, sub-canopy trees, shrubs, and woody lianas) were extracted and used for classifications because the herb layer tends to reflect finer-scale micro-habitat differences obscuring regional ecological patterns. A total of 457 woody plant taxa were recorded; this tally excludes 13 exotic taxa that were removed from the analysis. Average woody taxa richness per relevé was 33 (range of 9 to 72) and the mean Sørensen (applied as a measure of beta diversity) was 0.712. We also ran a Detrended Correspondence Analysis (Hill and Gauch 1980) with detrending by segments and Hill's scaling to measure species turnover and used the gradient length calculated in half-change units (Lepš and Šmilauer 2003) to provide an alternative estimate of beta diversity in our data set. The first DCA axis yielded a value of 7.076 HC (half change) units which is almost a double turnover of species composition based on 95% turnover of species for an axis 4 HC long (Oksanen and Tonteri 1995). This high turnover clearly suggests that our data set is very complex and it is highly improbable that only one single ecological factor controls the structuring of our vegetation data.

2.2. Classification methods tested

Nine agglomerative methods and one divisive method, Modified TWINSPAN (Roleček et al. 2009), were assessed. Eight of the agglomerative methods were tested using seven resemblances (1–7 in Table 1). Three resemblances specific to ordinal clustering where also tested (8–10 in Table 1). More information on resemblances 1–7 can be extracted from McCune and Grace (2002) and Podani (2000). The Bray-Curtis dissimilarity coefficient was applied to either raw data (also called Sørensen in PC-ORD 5.20; McCune and Mefford 2006) or data standardised by sample unit total (called Relative Sørensen in PC-ORD). Standardisation or relativisation by sample unit totals ensures each relevé contributes equally to the distance measure. Bray-Curtis and Jaccard resemblances were not considered in combination with Ward's method due to incompatibility. Besides Ordinal Clustering and Modified TWINSPAN, which used pseudospecies cut levels to transform cover-abundance data, the input cover-abundance data for the rest of the agglomerative methods were transformed after code replacement (see above) before analyses, or left untransformed (Table 1).

Some agglomerative clustering methods (Table 1: 1–8) were computed in PC-ORD 5.20, and one of them (Table 1: 9) was computed in SYN-TAX 2000 (Podani 2001). Resemblance measures 1–7 (see Table 1) were computed in PC-ORD 5.20, while those involved in Ordinal Clustering (Table 1: 8–10) were computed in SYN-TAX 2000.

The modified version of TWINSPAN (Roleček et al. 2009) was run by JUICE 7 (available at http://www.sci.muni.cz/botany/juice, Tichý 2002). The modified TWINSPAN first calculates the mean internal heterogeneity for each cluster using Sørensen (in our study) and then only the cluster with the highest value is divided using the divisive algorithm. The process is then repeated to calculate mean internal heterogeneity of all the clusters to assess which cluster should be divided next. This ensured the resulting clusters had a similar level of heterogeneity amongst them. Minimum group size for division was set to five.

The testing of classification methods was done within the JUICE 7 software package (Tichý 2002), where the comparative methods selected were mainly based on the use of statistically identified faithful (diagnostic) species.

2.3. Non-geometric evaluation algorithms

For evaluating the classification efficiency, OptimClass (Tichý et al. 2009) and standardisation of various solutions across a range of fidelity values, were applied to our data set. For comparison of top performing techniques, we applied Uniqueness values (Chytrý and Tichý 2003) and ISAMIC scores (Roberts 2010). All algorithms were computed using JUICE 7 (Tichý 2002).

2.3.1. OptimClass: assessing optimal number of clusters and classification performance. OptimClass is a powerful technique (Tichý et al. 2009) that evaluates quality of each set of different cluster levels of the same data set, based on the number of species that are faithful to the clusters in that particular cluster level. Faithful species are identified using Fisher's exact text for the right-tailed hypothesis. For each species and each cluster in each cluster level, this test compares the observed number of species occurrences within the cluster with the total number of occurrences in the entire data set, taking into account the number of relevés in the cluster and in the entire data set. Then it compares the observed pattern with the pattern of random distribution of species across the data set and calculates the probability *P* of the observed pattern under the null expectation of a random distribution of species across relevés. In this case, the *P* value of Fisher's exact test is used as a measure of positive fidelity (or faithfulness) of species clusters (Chytrý et al. 2002, Tichý et al. 2009). Lower P values result in higher species fidelity. In OptimClass, the user subjectively selects a P value that determines the thresholds for faithful species. Based on the concept of faithful species, Tichý et al. (2009) propose two new methods for detecting the optimum number of clusters and comparing classification performance.

OptimClass 1 measures the quality of each cluster level by the total count of faithful species across all clusters for that particular cluster level. A particular cluster level is evaluated as 'good' if most clusters have a high or moderate number of faithful species, but it also includes cases where a few clus-

Table 1. Summary of the clustering methods, resemblances and data transformations used in our analyses.

Clustering methods	*Resemblances*	*Data transformations*
1.Nearest Neighbour (=Single Linkage)	1. Bray-Curtis	1. No transformation
2. Farthest Neighbour (=Complete Linkage)	2. Bray-Curtis (data standardised by sample unit totals)	2. Presence/Absence
3. Median (=Gower's method)	3. Jaccard Similarity	3. Square root
4. Group Average (=UPGMA)	4. Euclidean Distance	4. Logarithmic
5. Centroid (=Weighted Group)	5. Chord Distance (= Relative Euclidean)	5. Ordinal scale 3 cut levels (0, 5, 25)
6. Ward's Method (=Incremental sum of squares)	6. Chi-square Contingent Similarity	6. Floating cut level derived by species data value
7. Flexible beta (β = -0.25)	7. Correlation	
8. McQuitty's Method	8. Goodman-Kruscal lambda*	
9. Ordinal Clustering	9. Kendall's tau*	
	10. Podani's Discordance*	

* Resemblances used only with Ordinal Clustering.

ters have many faithful species and some clusters have little or no faithful species (Tichý et al. 2009).

OptimClass 2 measures the quality of each cluster level by the count of clusters that contain at least *x* faithful species, where *x* is a subjectively selected minimum number of expected faithful species. With this method a cluster level is evaluated as 'good' if all or most of its clusters have at least the minimum number of expected faithful species (Tichý et al. 2009).

Tichý et al. (2009) determined that with OptimClass 1, cluster levels with a few large clusters may be evaluated as better than cluster levels with several small clusters. This is because with a large number of species many may be considered faithful species with a low (though often significant) fidelity. These species with low fidelity values increase the resulting summed value for larger but not for smaller clusters. Tichý et al. (l.c.) conclude that OptimClass 2 may be of more practical application if the purpose is to define core types of community typology that are easy to identify using faithful species. Several numerical classification techniques may be analyzed almost simultaneously where OptimClass will identify the optimal data-analytical technique and the optimal number of clusters.

2.3.2. OptimClass: averaged classification performance across the range of fidelity values. Different OptimClass *P* values may highlight different classification techniques as superior in determining the highest number of faithful species. This means that a particular fidelity threshold value will identify a certain classification method as the most efficient method. However, by changing the threshold value and recalculating OptimClass 1 or 2, it may identify a completely different classification method as superior with the highest number of faithful species. Because the hierarchy of a resulting classification is also of importance, and because the exact number of clusters is not always established until the output is interpreted by experts, it is difficult to accept one threshold value and one recommended number of clusters as the definitive answer to the classification conundrum. Hence a range of threshold values were assessed. Within a simple spreadsheet, the performance of each threshold *P* value was standardised against the highest value for that particular threshold (by converting values to percentages with the highest value equalling 100%). The percentage values were then averaged across a range of threshold values in an attempt to identify the classification techniques which consistently performed the best.

2.3.3. Uniqueness of classification. The concept of testing classifications using the highest cumulative number of faithful species occurrences is attractive but only if the faithful species are not shared with other vegetation units. JUICE 7 provides a procedure for testing the uniqueness of the resulting classification or clusters by assessing if any of its faithful species within a synoptic table are simultaneously faithful in other clusters. Uniqueness decreases if a cluster shares its faithful species with other vegetation clusters. We applied the phi fidelity (Φ) threshold value of 25 with $P \leq .01$ using Fisher's exact test to test for significance. Species with positive Φ values for particular clusters were then considered as faithful species for these clusters. The Uniqueness procedure is based on 12 clusters and a uniqueness value was calculated for each of the 12 derived clusters. These values were then averaged across the 12 clusters to obtain a mean uniqueness and standard deviation value for each classification method.

2.3.4. Average ISAMIC score of classification. The recently published Indicator Species Analysis Minimizing Intermediate Constancies (ISAMIC; Aho et al. 2008, Roberts 2010) was used to evaluate classification performance. ISAMIC assesses the degree to which species are either always present or always absent within clusters. High ISAMIC scores should indicate optimal clustering solutions.

2.4. Evaluation process

2.4.1. Optimal number of clusters. In order to evaluate the performances of the various classification techniques in the tests, a fixed number of clusters was required to assess methods on an equal basis and avoid bias towards any particular method (Schmidtlein et al. 2010). Mucina (1997) warned that the choice of the optimal number of clusters can never be fully objective. Even if highly formalised procedures are used there are many subjective choices to be made by the

classification users. Although we used OptimClass (Tichý et al. 2009) to determine an ideal number of clusters, our results are still subjective as the various user-defined threshold fidelity values generate different recommended numbers of clusters. Initial test runs using both OptimClass 1 and OptimClass 2 established that 10–14 clusters would be ideal. For the purposes of this study, the number of clusters was set to 12 when required for the comparative tests. A flow chart is provided in Fig. 1 summarising the steps and methodology followed in the evaluation process.

2.4.2. Step 1: Evaluating the wide array of numerical classification techniques. Using a *P* fidelity value of 12 (10^{-12}) in OptimClass 1, we assessed the performance of 322 combinations of classification methods to filter the availability of methods down to 20 acceptable solutions. These solutions included six resemblance measures, each with the 3 best combinations of clustering algorithm and data transformation, ordinal clustering and Modified TWINSPAN.

2.4.3. Step 2: Standardising OptimClass. Twenty acceptable solutions were run through multiple OptimClass procedures using a range of fidelity threshold values. The results were evaluated by standardising both OptimClass 1 and OptimClass 2 solutions. Fidelity threshold values ranged from (10^{-6} to 10^{-20}). For OptimClass 2, the minimum number of faithful species required for each individual cluster was set to three. Finally the best performing resemblance measure with its associated clustering and data transformation techniques could be selected for comparative analyses. Both Modified TWINSPAN and Ordinal Clustering were included regardless of performance.

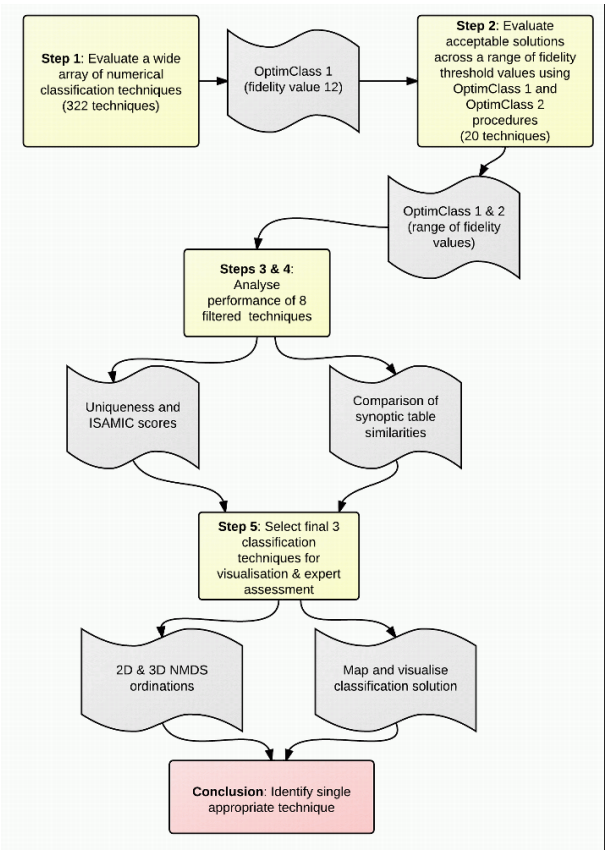


Figure 1. Flow chart summarising the evaluation procedure used to select the most appropriate methodology. Boxes indicate steps followed, while grey paper shapes indicate methods or processes followed.

2.4.4. Step 3: Uniqueness and ISAMIC classification scores. The eight filtered classification techniques were then compared using two algorithms for assessing the degree to which clusters do not share faithful species with other clusters. Uniqueness values, based on positive fidelity values, were determined for each of the 12 clusters, and then averaged across all 12 clusters. ISAMIC scores were calculated for cluster levels 2 to 12 for each of the classification techniques. Scores were averaged for the cluster levels.

2.4.5. Step 4: Comparison of different classifications using synoptic table similarities. Synoptic tables are useful to summarise the resulting data of the proposed classifications. Each community type is represented by a column in which each characterising species of each community is indicated by a value (Kent and Coker 1994). These values are usually a choice of dominance (as cover), or frequency, or fidelity values. In this study we used fidelity values in the synoptic table which highlight faithful species. We compared the similarity of the different synoptic tables derived from 12 clusters using each of the eight refined classification techniques. The purpose was to show how similar or different the classification solutions are. As in Knollová et al. (2005), we compared classifications through the similarity between sets of faithful species of particular columns within the synoptic tables, assuming that clusters with similar faithful species represent corresponding vegetation types. JUICE 7 was used to compare the similarity of two synoptic tables to find their total similarity by cross-tabulating the Euclidean distances between all pairs of synoptic columns (Tichý and Holt 2006). The synoptic tables were compared against all combinations to produce a synoptic table comparison matrix. This table was converted to a distance matrix and then analyzed using Principal Coordinates Analysis (PCoA) within the Ordin module of SYN-TAX 2000 (Podani 2001).

2.4.6. Step 5: Visualization and expert assessment of solutions. The final selection of the optimal classification technique was based on an expert review of classification evaluation results. John Burrows and Warren McCleland were approached and the various solutions were presented to them and the merits of each discussed. After consideration of comparative assessment results, we superimposed the classification solutions from three rigorous yet dissimilar methods onto two and three-dimensional NMDS ordination diagrams (based on Bray-Curtis) for visual assessment. Similarly the classification solutions were mapped using ArcView 3.3 (ESRI 2002) for geographical visualization and assessment. The final selection of the single most appropriate classification method involved the expert review of material, methods, and results in the above steps.

3. Results

3.1. Step 1: Evaluating the wide array of numerical classification techniques

A total of 322 different combinations of clustering, resemblance measures, and data transformation techniques (see Table 1) were applied to our data set using OptimClass 1 (results not shown). The selection of clustering method was unambiguous with Flexible beta (β = –0.25) or Ward's method outperforming the other methods. However, the selection of appropriate data transformation techniques was more subtle and therefore the three best performing techniques for each resemblance measure were selected for further assessment in Step 2. For Ordinal Clustering, Podani's Discordance was the most efficient resemblance measure.

3.2. Step 2: Standardising OptimClass

The performances of the 20 filtered data-analytical techniques were assessed across a range of fidelity values (Fig. 2) using OptimClass 1 and OptimClass 2. The relative performance of data transformation techniques varied considerably across fidelity values. Yet it was possible to discern the

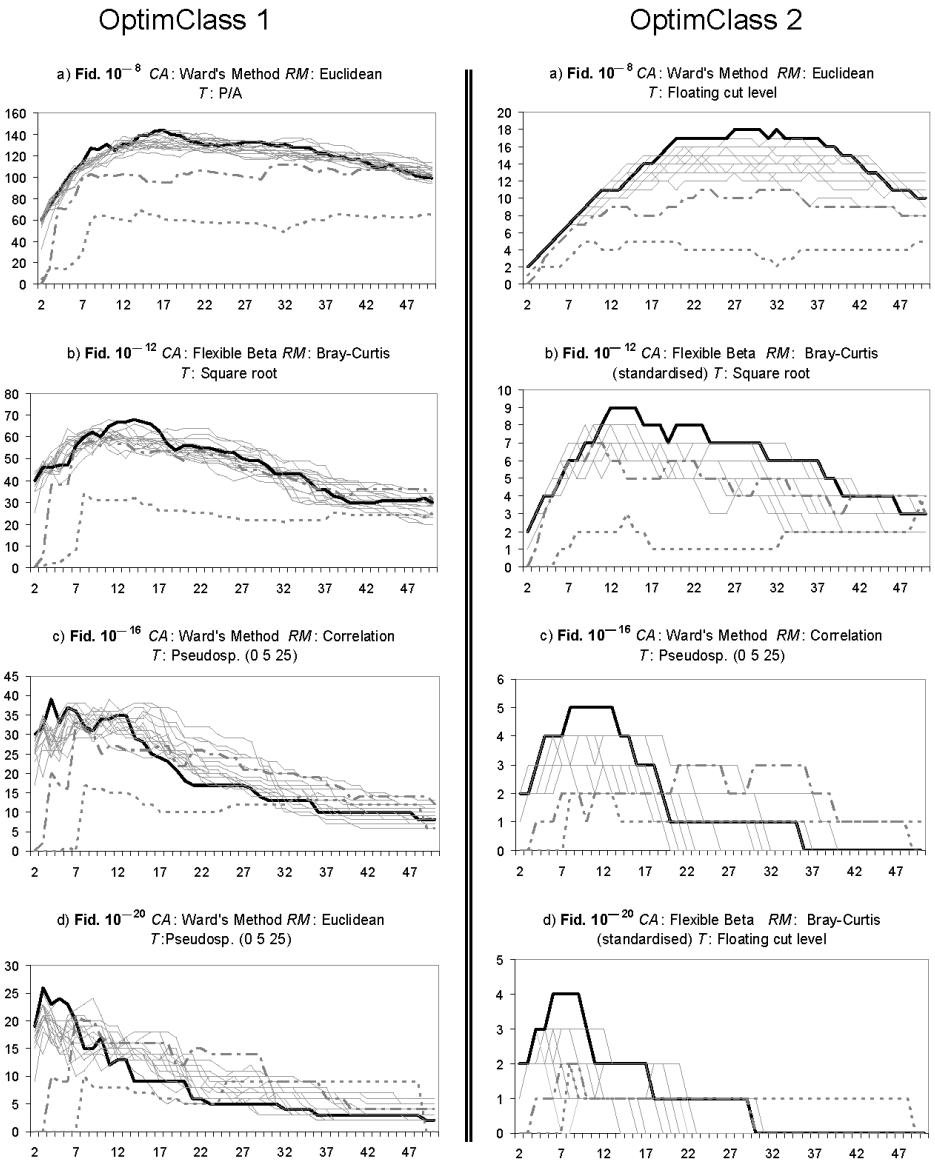


Figure 2. Results of OptimClass 1 and OptimClass 2 analyses applied to 506 forest relevés using four fidelity threshold P values. In OptimClass 1, the vertical axis represents the number of faithful species, the black solid line indicating the classification with the highest total number of faithful species for that particular fidelity value, which is also reflected in each graph title. In OptimClass 2, the vertical axis represents the number of clusters with more than three faithful species, the solid black line indicating the classification method with the highest number of clusters, the name of which is also reflected in the graph title. In both OptimClass 1 and OptimClass 2, the horizontal axis represents the numbers of cluster levels (or partitions). The dashed-dotted line follows the performance of the Modified TWINSPAN classification, while the dotted line follows the performance of Ordinal Clustering with Podani's Discordance. (CA: Classification algorithm, RM: Resemblance measure, T: Data transformation).

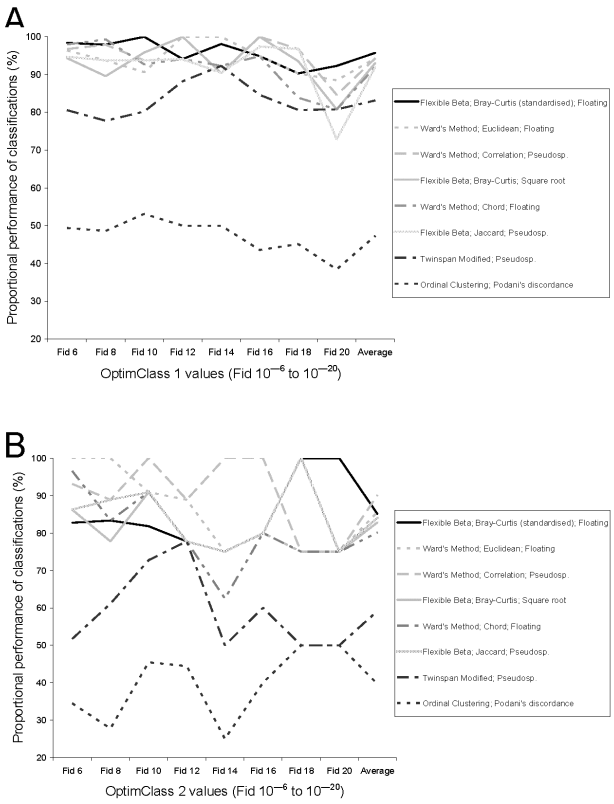


Figure 3. The proportional performance (%) of each refined classification technique for varying fidelity threshold values from 10^{-6} to 10^{-20} using JUICE 7 OptimClass 1 (A) and OptimClass 2 (B) procedures. The vertical axis, showing standardised percentage performance values, allows for comparison between OptimClass 1 (A) and OptimClass 2 (B) methods. On the x-axis, Fid 6-20 are JUICE 7 user settings that equate to the range of fidelity thresholds of 10^{-6} to 10^{-20} that were tested.

most constant techniques by means of averaging the relative performances across the range of fidelity values in both OptimClass 1 and OptimClass 2 (the eight best performing classification methods are shown in Fig. 3). No single method consistently performed well across the range of fidelity values.

Fig. 3 directly compares the performance of OptimClass 1 (graph A) and OptimClass 2 (graph B) for each classification technique. The highest averaged values for OptimClass 1 identified Flexible beta clustering ($\beta = -0.25$) with standardised Bray-Curtis and 'floating cut level by species data value' as best performer (96%). Floating cut level by species data value (henceforth referred to as *Floating cut levels*), is a new transformation method (Tichý 2002) where species abundances are converted to a value of 2 if values are equal or higher than the median value for that taxon, or 1 if the abundance is less than the median value. Ward's method with Pearson's Correlation coefficient (hereafter simply referred to as Correlation) and pseudospecies (cut levels of 0, 25, 50), and Ward's method with Euclidean distance and Floating cut levels came second (at 94%). Modified TWINSPAN (83%) and Ordinal Clustering (47%) were the least successful methods. The highest averaged values for OptimClass 2 identified Ward's method with Correlation and pseudospecies (90%), followed by Ward's method with Euclidean distance and Floating cut levels (86%), and Flexible beta clustering ($\beta = -0.25$) with standardised Bray-Curtis and Floating cut levels (85%). Again Modified TWINSPAN (59%) and Ordinal Clustering (40%) were the worst performers.

3.3. Step 3: Uniqueness and ISAMIC scores

Uniqueness assessed the degree to which communities shared faithful species with other communities. A value of 1 indicates that they share no species with any other community. Ordinal Clustering (0.84) and Modified TWINSPAN (0.81) were the best at identifying the most distinct classification of clusters. This was followed by Flexible beta with Bray-Curtis (0.75), Ward's method with Chord distance (0.74) and Flexible beta with standardised Bray-Curtis (0.74). Ward's Method and Correlation performed poorly (0.69) (see Table S1). However, the standard deviations show that Flexible beta with Bray-Curtis and Jaccard more consistently identified clusters with Uniqueness values that did not vary very far from the mean.

The range in the results from the averaged ISAMIC classification scores (Table S2) varied between 87.04 (Ordinal Clustering; cluster level 2) and 93.2 (Modified TWINSPAN; cluster level 2). At 12 clusters, Ordinal Clustering (90.57), Flexible beta with standardised Bray-Curtis (90.53), and Modified TWINSPAN (90.39) were the better performing methods. Flexible beta with Bray-Curtis (88.81) and Ward's method with Euclidean distance (88.66) were the weaker performing methods at 12 clusters. As the hierarchy is also of importance, the ISAMIC scores were averaged across hierarchical levels 2 to 12. The results show that Modified TWINSPAN (90.7), Ordinal Clustering (89.62) and Flexible beta with standardised Bray-Curtis (88.81) were the more consistent classifications that do not share many species with other clusters.

3.4. Step 4: Similarity comparison of synoptic tables

As the tested classification methods have been selected based on performance, and all performed well in the tests with similar numbers of faithful species, one might assume that they would produce relatively similar classifications. This was not, however, the case (Table S3 and Fig. 4). The most similar classification techniques showed 88% similarity, while the most divergent techniques were only 50% similar. Ordinal Clustering with Podani's Discordance was the most dissimilar method bearing little similarity to any of the other tested methods. The method most similar to it was standardised Bray-Curtis at 61%. Modified TWINSPAN was also dissimilar to most methods with the greatest similarity to Correlation with Ward's method (76%), and the greatest dissimilarity to Chord distance (=Relative Euclidean distance) with Ward's method (71%). The similarity between the three most rigorous methods (based on the averaged OptimClass 2 results, Fig. 3) all ranged between 79% and 81%, showing a weak measure of congruence.

3.5. Step 5: Visualisation and expert assessment of solutions

The selection of the single best classification method to apply to this data set was based on expert opinion and an assessment of the evaluation data. An assessment of the eight classification results by means of OptimClass, Uniqueness, and ISAMIC scores, failed to highlight any one particular method. Considering all information, Bray-Curtis coefficient standardised by sample unit totals with Flexible beta and Floating cut levels produced possibly the best classification solution. Its average to poor performance in the Uniqueness tests detracts from its obvious selection. However, it attained above average ISAMIC scores. The dissimilar synoptic tables, together with the strong performance of Modified TWINSPAN and Ordinal Clustering in the Uniqueness and ISAMIC algorithms, ensured that their solutions should be expertly assessed together with that of the standardised Bray-Curtis coefficient and Flexible beta. We superimposed their solutions on individual 2- and 3-dimensional NMDS ordinations (see Figure S1) calculated in JUICE 7 to visualise classifications and cluster overlap by creating envelopes around classification clusters. The classification solutions were also mapped using ArcView 3.3 for expert assessment. This expert interpretation was the final key to the adoption of a classification technique to be used to derive a proposed syntaxonomic classification of the Mpumalanga forests.

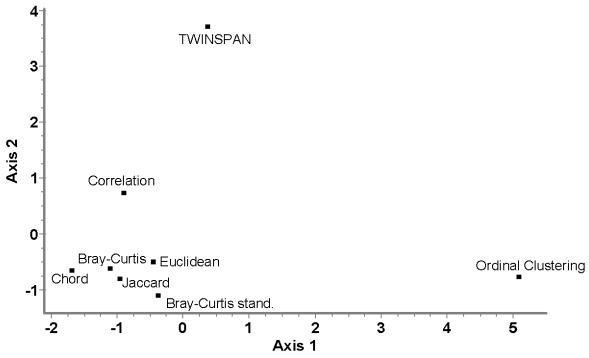


Figure 4. A PCoA ordination diagram of the cross tabulation of the Euclidean Distance matrix presented in Table S3. The diagram shows the similarity of the synoptic tables calculated for all classification techniques. Stand = standardised by sample unit totals.

4. Discussion

4.1. Cover-abundance transformations

Our data showed that the choice of a data transformation in most instances had a large impact on the resulting classifications. As assessed by OptimClass, no transformation generally resulted in poor classification solutions, but when used in combination with presence/absence based resemblances such as Sørensen (when applying Bray-Curtis coefficient to presence/absence data), they produced reasonable solutions where quantitative resemblances such as Euclidean distance performed very poorly. This could be attributed to the evaluating procedure being based on the presence-absence of species where Podani (1998) highlights that evaluating procedures need to be compatible with data-analytical techniques used in the classifications.

Conversion of percentage values into presence/absence data (resulting in "flattening" of the data) produced reasonable and interpretable results for most resemblance measures except for Chi-squared. Tichý's (2002) transformation involving *Floating cut levels by species data values* performed as well as any of the other data transformations in our data set. Any combination of logarithmic, square root, or transformation into ordinal classes performed well in terms of the interpretability of the classification, yet the performance depended on the type of transformation in conjunction with selected resemblance and clustering algorithms.

The automated nature and user-friendliness encourages users to handle software often as a 'black-box' (Podani 2006) which frequently results in the misapplication of mathematical operations. Podani (2005, 2006) correctly warned against pitfalls such as the use of ordinal (or mixed nominal/quasi-ordinal) scales such as the Braun-Blanquet cover-abundance scale containing categories r, +, 1 and partly also 2 (or 2m) which do not fit the definition of the ordinal values at all! Podani (l.c.) further argued that the nature of the ordinal scale precludes use of arithmetic operations such as multiplication, division, subtraction and addition. Van der Maarel (2007) in response to Podani (2006) concluded that numerical analyses of cover-abundance data may be permissible if: (1) a transformation (rather: 'code replacement') of these values is performed to approximate fairly a ratio scale (van der Maarel l.c. called the latter less appropriately a 'metric scale'), or (2) if for each plant species a frequency distribution of cover-abundance values and an 'optimal performance interval' can be interpreted, then the data can be reduced to 'metric' presence

(optimal) or absence (less than optimal) data. JUICE (Tichý 2002) contains such a customised floating cut level transformation whereby species abundances are converted into a value of 2 if values are equal to or higher than the median value for that taxon, or into a value of 1 if the abundance is less than the median value. In our opinion the use of floating cut levels does not invalidate its use of data originally collected in Braun-Blanquet cover-abundance values, and even less so if these data had been code-replaced by % values.

4.2. Resemblances

The choice of resemblance measure is a vital decision in any numerical analysis because it may exert decisive control over classification solutions (Huhta 1979, Mucina and van der Maarel 1989, Podani 2000, Wolda 1981). Literature abounds with many propositions to assess ecological resemblance, and the choice which one has to apply should follow logical rules (see Legendre and Legendre 1998, Tamás et al. 2001). Podani (2006) reminded that it is important to use resemblance measures appropriate for the measurement scales used to enumerate species. Our results support the findings of Tichý et al. (2009) that the application of metric resemblance measures to data originally recorded as Braun-Blanquet cover-abundances and then code-replaced with percentage values, performed as well as most methods, including that of ordinal clustering in the OptimClass evaluation. However the percentage data needed to be log-transformed before analysis. In our analyses metric measures performed better than ordinal clustering but where Tichý et al. (2009) found Podani's Discordance to identify the fewest number of faithful species for clusters, we found it to be the better of the three resemblance measures suited for ordinal clustering.

The good performance of the standardised Bray-Curtis coefficient has been highlighted in literature (Chase et al. 2010, D'Souza and Barnes 2008, Jüriado et al. 2011, Mlambo et al. 2011, Redman and Leighton 2009, Williams 2010). Faith et al. (1987) highlight that the standardised Bray-Curtis coefficient deserved more use after evaluation using simulated data, and McCune and Grace (2002) reported that the Bray-Curtis (called Sørensen index in PC-ORD) had repeatedly been shown to be the most effective measures of sample or species similarity.

Only a few of the resemblance measures performed poorly, such as the Chi-squared (data not shown). For each measure, OptimClass improved the associated clustering and data transformation methods whereby optimising the performance of the resemblance measure. Bray-Curtis, Correlation, Euclidean and Jaccard eventually performed well after optimization of data transformation (i.e., logarithmic) and group clustering methods. Resemblance measures considering mutual absences (i.e., Euclidean distance) occasionally performed well, however only in combination with appropriate transformations, such as normalisation (Wildi 2010) or data expressed in proportional abundances (Anderson et al. 2010) such as in our case.

4.3. Clustering methods

Both the Ward's method and Flexible beta clustering were usually the best performing algorithms across a range of resemblance measures. As found by Tichý et al. (2009), UPGMA performed well with large numbers of clusters, while Centroid, Median and Nearest Neighbour techniques performed less satisfactorily. UPGMA, Farthest Neighbour and McQuitty's method produced classifications with average to low numbers of faithful species for 12 clusters. Ordinal Clustering using three distances produced classifications with very few faithful species per cluster level. Of the distance measures tested, Podani's Discordance produced the best results. Conversely Ordinal Clustering produced the most unique classifications that did not share many faithful species with other clusters. Based on this performance it was included amongst the final three numerical-classification methods that were expertly assessed.

4.4. Modified TWINSPAN

Modified TWINSPAN identified unique clusters that shared the smallest number of faithful species with other clusters (ranking first in ISAMIC scores and second in Uniqueness). This fact should be perhaps understood in terms of this technique failing to identify clusters with a high number of faithful species. Tichý et al. (2009) has, however, reported that Modified TWINSPAN was efficient in identifying clusters rich in faithful species when the numbers of clusters were small. In Table S2 the ISAMIC scores for TWINSPAN are highest at few hierarchical levels and gradually decrease with increased clusters. This is contrary to performance of agglomerative methods, however still expected when comparing a divisive with an agglomerative algorithm. Modified TWINSPAN performed better in OptimClass 1 which sums the number of faithful species across all clusters. In OptimClass 2, its performance deteriorated as it was unable to identify many clusters with at least 3 faithful species.

When visualising the resulting classification on a map, the forest experts concluded that TWINSPAN failed to capture the differences in multidimensional floristic patterns present in the Mpumalanga forests. Flexible beta clustering (in combination with standardised Bray-Curtis) on the other hand appeared to exploit the floristic patterns and produce the most meaningful classification that was ecologically informative and spatially discrete. TWINSPAN's failure may be due to the fact that this study used a complex data set with several underlying gradients, while the nature of TWINSPAN classification is focused on recovery of a single (albeit dominant) floristic gradient – a feature criticised earlier by van Groenewoud (1992).

4.5. Comparing evaluators

An acceptable (informative) classification should identify clusters that are internally homogenous, yet distant from each other in multivariate resemblance terms. This dual property had been used as a criterion in the search for the optimal

number of clusters in partitioned clusterings by many authors in the past (Feoli and Lausi 1980, Hogeweg 1976, Mucina and Hauser 1993, Popma et al. 1983). The evaluation methods used in this study inherently identified classification techniques incorporating this dual property since they create clusters based on the between-site similarity in species composition (Podani 2000, Tichý et al. 2009). Additionally, any reasonable classification should produce clearly interpretable clusters, i.e. those rich in faithful species which can subsequently be used as diagnostic or indicator species for identification of the community types. While determining internally homogenous clusters is inherent to various classification methods, the identification of clusters rich in faithful species is evaluated by OptimClass (Tichý et al. 2009). In our data-analytical study, OptimClass quickly assessed the performance of 322 combinations of numerical-classification methods and the best performing methods were those containing a high number of faithful species.

The results of the OptimClass 1 and 2 analyses were largely similar, however the performance of Modified TWINSPAN differed the greatest between these two approaches. The application of both approaches was useful and both provide for greater insight into the performance of the various methods. Tichý et al. (2009) reported that OptimClass 1 may be the preferable approach where the user wants to accept cluster levels in which some clusters have many faithful species, while others have few or none. Such cluster levels are typical where some communities are comprised of ecological specialist species and other communities comprised of more generalist species, and both community types are expected from the data set. OptimClass 2 may be a more appropriate choice if the user prefers cluster levels in which each cluster has its own faithful species. Such cluster levels may be useful if the purpose of classification is defining clusters that are easy to identify using faithful species.

The degree to which species were shared among clusters was assessed by both Uniqueness and ISAMIC. The Uniqueness approach identified those methods that produced classifications which shared few faithful species among clusters. The standard deviation of the Uniqueness calculated across all clusters for each classification method assessed the consistency in identifying clusters which do not share faithful species. Although the results of the ISAMIC scores were informative, and in part supported the Uniqueness values, Aho et al. (2008) found that the ISAMIC scores favour single linkage classifications since this method continually isolates individual outlier clusters with relatively distinctive taxa as it chains together the rest of the data. This is possibly why the results could not be interpreted in a meaningful way and this may also explain why Modified TWINSPAN performed so well in this comparative test as the resulting NMDS ordinations shows the classification of outlier clusters (see Figure S1 in Supporting Information). The Uniqueness and ISAMIC results appear to contradict the results from the OptimClass tests. This may in part be a result of OptimClass undervaluing cluster levels containing small clusters with outlying relevés.

4.6. Comparison of classification outcomes using synoptic tables

Comparing the similarity between synoptic tables (based on fidelity patterns) resulting from different classification procedures highlighted that top performing methods differed remarkably in their classification solutions. In PCoA the first axis in the ordination diagrams represents the true distances in the distance matrix in the best possible way that can be achieved in one dimension (Lepš and Šmilauer 2003). Ordinal Clustering based on Chord (Relative/Normalised Euclidean) distance was found to be the most extreme in terms of classification output, with Ordinal Clustering showing little similarity to any other method (Fig. 4). Along Axis 2, Modified TWINSPAN is clearly separated from the other classification solutions. The three top performing methods in terms of OptimClass 1 and 2 were still rather dissimilar. The classification solutions offered by the Jaccard and Bray-Curtis (in combination with Flexible beta clustering) showed the highest similarity.

5. Conclusion

1. Through a series of steps, we applied several evaluation and comparative procedures to assist in selecting the best method suitable for the characteristics of our particular data set. We tested the appropriate procedures in JUICE 7, which offered several new and powerful data-analytical methods that assisted in selecting the appropriate numerical classification technique.

2. In essence, the procedure used to detect faithful species in OptimClass is based on Fisher's exact test, which has a presence/absence foundation. Therefore when assessing classifications based on quantitative input data, the results may not be as meaningful as when assessed using ordinal or ratio-based methods (see Podani 1998, 2006). Thus the performances of metric numerical-classification methods may be under-emphasised based on Fisher's exact test. What is required is that the evaluating criteria should be consistent with the optimizing criteria used during the clustering process. The future development of quantitative methods within the OptimClass approach is encouraged where the evaluation criteria can be compatible with the selected resemblance coefficient used in the classification.

3. Although our results supported Tichý et al. (2009) in that Modified TWINSPAN performed best at low cluster levels, they did differ in that the overall performance of Modified TWINSPAN was generally less than the agglomerative algorithms. Modified TWINSPAN failed to identify many clusters with faithful species, where some clusters had several and others very few or none.

4. Classifications made by different methods were very disparate. Comparing the results of different acceptable classification solutions is valuable and highlights the similarity/dissimilarity of the various classifications. Comparing synoptic tables based on fidelity and also plotting the results in GIS assisted

in conceptualising the impacts of classification choice and realising the extent of the differences in the results.

5. The selection of the classification method remains an informed subjective one. Expert input into interpreting classification outputs, and selecting the final methodology, is essential. Although the purpose of this paper was to describe procedures and not so much on the resulting classification, the most appropriate and rigorous classification technique for our data set was Bray-Curtis standardised by sample unit totals with Flexible beta clustering ($\beta = -0.25$) and data transformed using floating cut level by species data values. This methodology may also be appropriate in other vegetation studies, and the performance of this approach should certainly be assessed, but we recommend that the performance of a set of methods be tested prior to selecting the final classification approach.

6. The rigorous performance of Flexible beta clustering was not surprising due to earlier findings by Aho et al. (2008), Belbin and McDonald (1993), and Tichý et al. (2009). This technique also enjoys wide use (e.g., Knollová et al. 2005, Mucina et al. 2007). Its application in combination with both non-metric and semi-metric resemblance measures appears to be unchallenged and it performs well using metric resemblance measures as well (see Tichý et al. 2009).

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References

Aho, K., D.W. Roberts and T. Weaver. 2008. Using geometric and non-geometric internal evaluators to compare eight vegetation classification methods. *J. Veg. Sci.* 19: 549-562.

Anderson, M.J., T.O. Crist, J.M. Chase, M. Vellend, B.D. Inouye, A.L. Freestone, N.J. Sanders, H.V. Cornell, L.S. Comita, K.F. Davies, S.P. Harrison, N.J.B. Kraft, J.C. Stegen and N.G. Swenson. 2010. Navigating the multiple meanings of â diversity: a roadmap for the practicing ecologist. *Ecol. Lett.* 14: 19-28.

Belbin, L. and C. McDonald. 1993. Comparing three classification strategies for use in ecology. *J. Veg. Sci.* 4: 341-348.

Belbin, L. 1993. *PATN Pattern Analysis Package. Users Guide*. Division of Wildlife and Ecology, CSIRO.

Campbell, B.M., 1978. Similarity coefficients for classifying relevés. *Vegetatio* 37: 101-109.

Chase, J.M., A.A. Burgett and e.g., Biro. 2010. Habitat isolation moderates the strength 4 of top-down control in experimental pond food webs. *Ecology* 91: 637-643.

Chytrý, M., L. Tichý, J. Holt and Z. Botta-Dukát. 2002. Determination of diagnostic species with statistical fidelity measures. *J. Veg. Sci.* 13: 79-90.

Chytrý, M. and L. Tichý. 2003. Diagnostic, constant and dominant species of vegetation classes and alliances of the Czech Republic: a statistical revision. *Folia Facultatis Scientiarum Naturalium Universitatis Masarykianae Brunensis* 108: 1-231.

Clarke, K.R. and R.M. Warwick. 1994. *Change in Marine Communities: An Approach to Statistical Analysis and Interpretation*. Plymouth Marine Laboratory, Plymouth.

Dale, M.B. 1995. Evaluating classification strategies. *J. Veg. Sci.* 6: 437-440.

D'Souza, L.E. and P.W. Barnes. 2008. Woody plant effects on soil seed banks in a central Texas savanna. *Southwestern Naturalist* 53: 495-506.

ESRI. 2002. *ArcView 3.3*. Environmental Systems Research Institute, Redlands, CA.

Faith, D.P., P.R. Minchin and L. Belbin. 1987. Compositional dissimilarity as a robust measure of ecological distance. *Vegetatio* 69: 57-68.

Feoli, E. and D. Lausi. 1980. Hierarchical levels in syntaxonomy based on information functions. *Vegetatio* 42: 113-115.

Jüriado, I., J. Liira, D. Csencsics, I. Widmer, C. Adolf, K. Kohv and C. Scheidegger. 2011. Dispersal ecology of the endangered woodland lichen *Lobaria pulmonaria* in managed hemiboreal forest landscape. *Biodivers. Conserv.* 20: 1803-1819.

Gauch Jr., H.G. and R.H. Whittaker.1981. Hierarchical classification of community data. *J. Ecol.* 69: 537-557.

Hennekens, S.M. and J.H.J. Schaminée. 2001. TURBOVEG, a comprehensive database management system for vegetation data. *J. Veg. Sci.* 12: 589-591.

Hill, M.O. 1979. *TWINSPAN – a FORTRAN Program for Arranging Multivariate Data in an Ordered Two-way Table by Classification of the Individuals and Attributes*. Ecology & Systematics, Cornell University, Ithaca, NY.

Hill, M.O. and H.G. Gauch Jr. 1980. Detrended correspondence analysis, an improved ordination technique. *Vegetatio* 42: 47-58.

Hogeweg, P. 1976. Iterative character weighting in numerical taxonomy. *Computers in Biology and Medicine* 6: 199-211.

Huhta, V. 1979. Evaluation of different similarity indices as measures of succession in arthropod communities of the forest floor after clear-cutting. *Oecologia* 41: 11-23.

Jongman, R.H.G., C.J.F. ter Braak and O.F.R. van Tongeren. 1995. *Data Analysis in Community and Landscape Ecology*. Cambridge University Press, Cambridge.

Kent, M. and Coker, P. 1994. *Vegetation Description and Analysis – A Practical Approach.* Wiley, Chichester.

Kindt, R. and R. Coe. 2005. *Tree Diversity Analysis. A Manual and Software for Common Statistical Methods for Ecological and Biodiversity Studies.* World Agroforestry Centre (CRAF), Nairobi.

Knollová, I., M. Chytrý, L. Tichý and O. Hájek. 2005. Stratified resampling of phytosociological databases: some strategies for obtaining more representative data sets for classification studies. *J. Veg. Sci.* 16: 479-486.

Legendre, P. and L. Legendre. 1998. *Numerical Ecology*, second ed. Elsevier, Amsterdam.

Lepš, J. and P. Šmilauer. 2003. *Multivariate Analysis of Ecological Data Using CANOCO*. Cambridge University Press, Cambridge.

Lötter, M.C., A.J. Emery, and S.D. Williamson. 2002. Forests. In: Emery, A.J., M.C. Lötter, and S.D. Williamson (eds.), *Determining the Conservation Value of Land in Mpumalanga*. Mpumalanga Parks Board, Nelspruit, pp. 28-34.

McCune, B. and J.B. Grace. 2002. *Analysis of Ecological Communities*. MjM Software, Gleneden Beach, OR.

McCune, B. and M.J. Mefford. 2006. *PC-ORD. Multivariate Analysis of Ecological Data*. Version 5.20. MjM Software, Gleneden Beach, OR.

Minchin, P.R. 1987. An evaluation of the relative robustness of techniques for ecological ordination. *Vegetatio* 69: 89-107.

Mlambo, M.C., M.S. Bird, C.C. Reed, and J.A. Day. 2011. Diversity patterns of temporary wetland macroinvertebrate assemblages in the south-western Cape, South Africa. *Afr. J. Aquatic Sci.* 36: 299-308.

Mucina, L. 1997. Classification of vegetation: past, present and future. *J. Veg. Sci.* 8: 751-760.

Mucina, L. and E. van der Maarel. 1989. Twenty years of numerical syntaxonomy. *Vegetatio* 81: 1-15.

Mucina, L. and M. Hauser. 1993. A new method for determining optimal number of clusters in vegetation data. *Abstracta Botanica* 17: 147-153.

Mucina, L., E. Pienaar, A. van Niekerk, M. Lötter, C.R. Scott-Shaw, M. Meets, L. Seoke, T. Sekome, S.J. Siebert, L. Loffler, S.G. Cawe, A.P. Dold, A. Abbott, J. Kalwij and L. Tichý. 2007. *Habitat-level Classification of the Albany Coastal, Pondoland Scarp and Eastern Scarp Forests*. Unpublished Report for DWAF. Stellenbosch University, Matieland, ZA.

Mueller-Dombois, D. and H. Ellenberg. 1974. *Aims and Methods of Vegetation Ecology*. Wiley, New York.

Noy-Meir, I., D. Walker and W.T. Williams. 1975. Data transformations in ecological ordination. *J. Ecol.* 63: 779-800.

Oksanen, J. and T. Tonteri. 1995. Rate of compositional turnover along gradients and total gradient length. *J. Veg. Sci.* 6: 8 15-824.

Podani, J. 1998. Explanatory variables in classifications and the detection of the optimum number of clusters. In: Hayashi, C., N. Ohsumi, K. Yajima, Y. Tanaka, H.-H. Bock and Y. Baba, (eds.), *Data Science, Classification and Related Methods*. Springer, Tokyo, pp. 125-132.

Podani, J. 2000. *Introduction to the Exploration of Multivariate Biological Data*. Backhuys Publishers, Leiden, NL.

Podani, J. 2001. *Computer Programs for Data Analysis in Ecology and Systematics. User's Manual*. Scientia, Budapest.

Podani, J. 2005. Multivariate exploratory analysis of ordinal data in ecology: pitfalls, problems and solutions. *J. Veg. Sci.* 16: 497-510.

Podani, J. 2006. Braun-Blanquet's legacy and data analysis in vegetation science. *J. Veg. Sci.* 17: 113-117.

Popma, J., L. Mucina, O. van Tongeren and E. van der Maarel. 1983. On the determination of optimal levels in phytosociological classification. *Vegetatio* 52: 65-75.

Redman, C.M. and L.R. Leighton. 2009. Multivariate faunal analyses of the Turonian Bissekty Formation: variation in the degree of marine influence in temporally and spatially averaged fossil assemblages. *Palaios* 24: 18-26.

Roberts, D.W. 2010. Labdsv: ordination and multivariate analysis for ecology. R package version 1.4–1. http://CRAN.R-project.org/package=labdsv; accessed on 15 March 2010

Roleček, J., L. Tichý, D. Zelený and M. Chytrý. 2009. Modified TWINSPAN classification in which the hierarchy respects cluster heterogeneity. *J. Veg. Sci.* 20: 596-602.

Schulze, R.E. 1997. *South African Atlas for Agrohydrology and Climatology*. Water Research Commission, Pretoria, Report TT82/96.

Schmidtlein, S., L. Tichý, H. Feilhauer and U. Faude. 2010. A brute-force approach to vegetation classification. *J. Veg. Sci.* 21: 1162-1171.

Tamás, J., J. Podani and P. Csontos. 2001. An extension of presence/absence coefficients to abundance data: a new look at absence. *J. Veg. Sci.* 12: 401-410.

Tichý, L. 2002. JUICE, software for vegetation classification. *J. Veg. Sci.* 13: 451-453.

Tichý, L. and J. Holt. 2006. *JUICE, Program for Management, Analysis and Classification of Ecological Data. User's Manual*. Masaryk University, Brno.

Tichý, L., M. Chytrý, M. Hájek, S. Talbot and Z. Botta-Dukát. 2009. OptimClass: Using species-to-cluster fidelity to determine the optimal partition in classification of ecological communities. *J. Veg. Sci.* 21: 287-299.

van der Maarel, E. 1979. Transformation of cover-abundance values in phytosociology and its effects on community similarity. *Vegetatio* 39: 97-114.

van der Maarel, E. 2007. Transformation of cover-abundance values for appropriate numerical treatment – alternatives to the proposals by Podani. *J. Veg. Sci.* 8: 767-770.

van Groenewoud, H. 1992. The robustness of Correspondence, Detrended Correspondence, and TWINSPAN Analysis. *J. Veg. Sci.* 3: 239-246.

Wildi, O. 2010. *Data Analysis in Vegetation Ecology*. Wiley, Chichester, UK.

Williams, N.E. 2010. Restoration of nontarget species: bee communities and pollination function in riparian forests. *Restor. Ecol.* 19: 450-459.

Wolda, H. 1981. Similarity indices, sample size and diversity. *Oecologia* 50: 296-302.

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Electronic Appendix

Supplementary information in Figure S1 and Tables S1-S3 may be found in the online version of this article. The file may be downloaded from the web site of the publisher at www.akademiai.com.

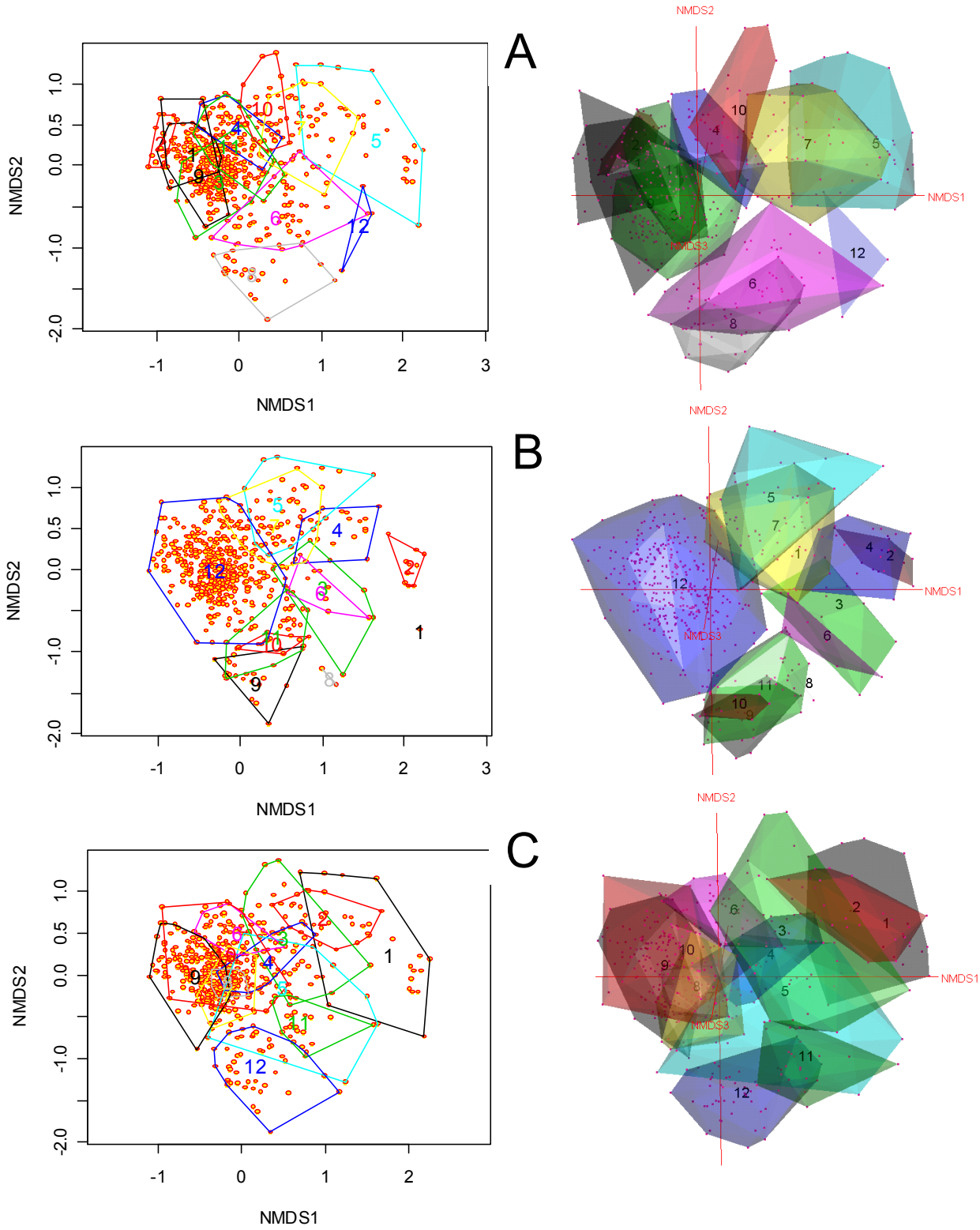


Figure S1
Results of the two- and three-dimensional NMDS ordinations on which the classifications of the final three rigorous yet dissimilar methods are superimposed. The three classifications are (A) Bray-Curtis standardised by sample unit totals with Flexible beta (β = –0.25) clustering and Floating cut levels transformation; (B) Modified TWINSPAN with pseudospecies cut levels of 0, 25, 50; and (C) Ordinal Clustering with Podani's Discordance.

Table S1
Comparing the uniqueness of the acceptable classifications (as determined in Fig. 3) across the 12 recommended clusters. The Uniqueness is determined for each cluster group, then averaged across all 12 clusters and the standard deviation calculated. Fb: Flexible beta (β = –0.25) clustering, W: Ward's Method; stand: standardised by sample unit totals.

Individual Clusters	*Jaccard (Fb)*	*Bray-Curtis stand. (Fb)*	*Bray-Curtis (Fb)*	*Euclidean (W)*	*Chord (W)*	*Correlation (W)*	*Ordinal Clustering*	*Modified TWINSPAN*
1	0.62	0.53	0.70	0.60	0.71	0.66	1.00	0.99
2	0.70	0.72	0.76	0.73	0.66	0.64	1.00	0.95
3	0.47	0.77	0.76	0.73	0.76	0.51	0.76	0.93
4	0.75	0.56	0.80	0.57	0.59	0.49	0.67	0.85
5	0.60	0.73	0.61	0.71	0.67	0.73	0.53	0.81
6	0.65	0.47	0.79	0.44	0.76	0.47	0.82	0.76
7	0.77	0.65	0.88	0.85	0.87	0.86	0.98	0.65
8	0.90	0.88	0.47	0.89	0.98	0.72	0.76	0.53
9	0.88	0.94	0.67	0.72	0.46	0.95	0.76	0.85
10	0.72	0.97	0.87	0.93	0.88	0.56	1.00	0.82
11	0.85	0.75	0.81	0.58	0.93	0.80	0.85	0.61
12	0.96	0.91	0.93	0.80	0.66	0.97	1.00	0.93
Average	*0.739*	*0.740*	*0.753*	*0.713*	*0.744*	*0.695*	*0.844*	*0.807*
St. Dev.	*0.14*	*0.17*	*0.13*	*0.15*	*0.15*	*0.17*	*0.15*	*0.15*

Table S2
Comparing the ISAMIC scores of the acceptable classifications (as determined in Fig. 3) across a range of hierarchical cluster levels (2 to 12 cluster levels/partitions). The ISAMIC scores are determined for each cluster level, then averaged across all 11 levels and the standard deviation calculated. Fb: Flexible beta (β = –0.25) clustering; W: Ward's Method; stand: standardised by sample unit totals. Numbers in bold represent the most extreme values.

Hierarchy (Cluster levels)	*Jaccard (Fb)*	*Bray-Curtis stand. (Fb)*	*Bray-Curtis (Fb)*	*Euclidean (W)*	*Chord (W)*	*Correlation (W)*	*Ordinal Clustering*	*Modified TWINSPAN*
Level 2	87.05	87.31	87.16	87.24	87.27	87.22	**87.04**	**93.20**
Level 3	87.25	87.65	87.39	87.24	87.78	87.60	89.62	91.67
Level 4	87.76	87.70	87.26	87.78	88.18	88.07	88.86	90.54
Level 5	88.25	88.24	87.89	88.79	88.80	88.79	89.12	90.52
Level 6	88.71	88.46	88.44	88.77	88.71	89.12	88.90	90.10
Level 7	89.17	88.90	88.70	88.92	88.85	89.14	90.48	90.02
Level 8	89.44	89.06	88.81	89.20	89.18	89.04	90.74	90.19
Level 9	89.56	89.11	89.00	89.28	89.08	89.35	90.22	90.48
Level 10	89.30	89.86	89.47	89.43	89.17	89.24	90.20	90.27
Level 11	89.37	90.13	89.51	89.38	89.37	89.44	90.11	90.31
Level 12	89.69	90.53	89.74	89.26	89.65	89.43	90.57	90.39
Average	*88.69*	*88.81*	*88.49*	*88.66*	*88.73*	*88.77*	*89.62*	*90.70*
St. Dev.	*0.96*	*1.06*	*0.94*	*0.84*	*0.72*	*0.78*	*1.09*	*0.94*

Table S3
Comparison of the synoptic tables using JUICE 7 cross tabulation of Euclidean Distances between all pairs of synoptic columns in two synoptic tables. The matrix compares the synoptic tables of 12 clusters between eight of the more rigorous classification techniques. Fb: Flexible beta (β = –0.25) clustering; W: Ward's Method; stand: standardised by sample unit totals. The most extreme values appear in bold.

	Jaccard (Fb)	*Bray-Curtis stand. (Fb)*	*Bray-Curtis (Fb)*	Euclidean (W)	Chord (W)	Correlation (W)	Modified TWINSPAN
Bray-Curtis stand. (Fb)	85.8	0	0	0	0	0	0
Bray-Curtis (Fb)	**88.2**	87.3	0	0	0	0	0
Euclidean (W)	85	*79.9*	78.7	0	0	0	0
Chord (W)	85.2	82.9	87.1	83.7	0	0	0
Correlation (W)	83.4	*78.9*	81.5	*80.9*	84	0	0
Modified TWINSPAN	72.7	71.4	73.8	71.6	70.7	76.1	0
Ordinal Clustering	57.9	61.4	56	59.4	**50.4**	55.4	56

CHAPTER THREE:

Classification of the Indigenous Forests of Mpumalanga Province, South Africa (*South African Journal of Botany* 90: 37–51)

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ABSTRACT

This paper presents a hierarchical system of forest communities of Mpumalanga Province (South Africa) compatible with the existing South African National Forest Classification (NFC). It describes and interprets floristic and physiognomic differences between the communities and the relevant higher-rank vegetation unit. A total of 434 relevés (rectangular plots, each 0.04 ha; listing all species in the plots in Braun-Blanquet cover-abundance scale), sharing 619 species, served as the basis of the classification. The data were classified using the Flexible beta clustering (β = –0.25) in combination with Bray-Curtis similarity measure. The proposed forest subtypes are described in terms of dominant plant families and genera, growth forms, seasonality or leaf retention characteristics, and the proportion of forest dependant species. Fourteen forest subtypes are distinguished within three national forest types, with no subtypes being recognised within the Lowveld Riverine Forest Type. We propose that the Wakkerstroom Midlands Forest Subtype be embedded within the Northern Highveld Forest Type, and not the Low Escarpment Mistbelt Forest Type as is currently recognised in the NFC. A total of 125 plant families and 375 genera were identified to occur in the Mpumalanga forests, with the most abundant species per family being Rubiaceae, Fabaceae, Celastraceae, Orchidaceae, Euphorbiaceae and Aspleniaceae. 76% of all forest plant species were obligate forest species and 80% of all tree cover is evergreen.

Key words: cluster analysis; floristics; forest classification; Mistbelt Forest; non-metric multidimensional scaling (NMDS); physiognomy; synoptic table.

Nomenclature: Germishuizen and Meyer (2003) with updates from online African Plants Database (version 3.3.4) at <http://www.ville-ge.ch/musinfo/bd/cjb/africa/.

1. INTRODUCTION

The first comprehensive, nation-wide classification of indigenous forest of South Africa was presented in a report by von Maltitz et al. (2003). This system, also known as the National Forest Classification (NFC), contains seven forest groups, comprising 24 forest types. This classification was updated by Mucina et al. (2006) and is being expanded by more detailed studies aimed at the habitat level of complexity (Mucina et al., 2007).

Classification of the forests of Mpumalanga Province is incomplete and patchy, despite numerous assessments at both a very fine-scale (Deal et al., 1989; Eckhardt et al., 1997; Lötter and Beck, 2004; Morgenthal and Cilliers, 1999; Muller, 1994; Stalmans et al., 1999; Van Der Schijff and Schoonraad, 1971; Von Breitenbach, 1990) and at a much broader national scale (Acocks, 1988; Cooper, 1985; Mucina et al., 2006; von Maltitz et al., 2003). According to von Maltitz et al. (2003), of the 24 forest types occurring in South Africa, only five are represented in Mpumalanga. The Mpumalanga Mistbelt Forest (a NFC forest type in von Maltitz et al., 2003), accounting for 82% off all indigenous forests in the Province, extends along the Mpumalanga Escarpment from Mariepskop to Barberton. However its circumscription was considered too broad for use in provincial conservation planning as it does not recognise floristic differences at the habitat-level. There is no classification that has assessed forest diversity at the provincial scale that would be suitable for conservation planning. Hence the Mpumalanga Tourism & Parks Agency (MTPA) and the Department of Agriculture, Forestry and Fisheries (DAFF) of the Government of South Africa identified the need for a comprehensive forest classification suitable for use at a local scale for the management and conservation of indigenous forests.

The aims of this study were to address the need for a more detailed, regional forest classification, in particular by (1) developing a hierarchical framework of forest subtypes, grouped into higher-rank categories embedded within the existing NFC system, and by (2) describing and interpreting floristic and physiognomic differences between these subtypes.

2. STUDY AREA

Mpumalanga Province is situated in the north-eastern part of South Africa and covers an area of 76 520 km², comprising a diversity of landscapes characteristic of the grassland, savanna and warm-temperate and subtropical forest biomes. Grasslands are most prevalent in Mpumalanga, making up 65% of the Province, while forests occupy only 0.51% of Mpumalanga's territory. Altitude varies between 110 m and 2328 m above sea level while mean annual rainfall ranges between 341 and 1933 mm. Mean annual temperature spans 10°C to 23°C (according to modelled data of Schulze, 1997). This topographic and climatic diversity is reflected by the fact that of South Africa's 438 mapped vegetation types (Mucina and Rutherford, 2006), 58 vegetation mapping units occur in Mpumalanga (Ferrar and Lötter, 2007).

The indigenous forests are largely confined to the north-south running Mpumalanga Escarpment.

3. METHODS

3.1. Vegetation sampling

A total of 434 vegetation relevés (plot samples) were collected throughout Mpumalanga and the immediate surrounding areas of Northern Province, KwaZulu-Natal Province (both South Africa) and the Kingdom of Swaziland. Relevés from neighbouring provinces, representing a forest type that straddled Mpumalanga's border, were incorporated in this data set. The relevés were initially pre-classified into the NFC forest groups and forest types (von Maltitz et al., 2003). Sampling involved selecting sites across a range of altitudes, landscapes, and climatic conditions. The sample sites were restricted to those forest patches with little evidence of recent human disturbance or where the floristic composition was natural (we avoided areas where invasive alien plant species were present). At each site several plots (minimum of 2) were preferentially located throughout the forest as far as accessibility allowed. Plots of 20 m x 20 m (0.04 ha) were used to sample species composition. Cover-abundance values were recorded for each higher plant species according to the seven-class Braun-Blanquet cover-abundance scale (Mueller-Dombois and Ellenberg, 1974). The relevés included a list of all vascular plant species stratified into woody or herbaceous layers. Plants were identified to species level or, to infraspecific level (subspecies or variety) wherever possible. The term 'species' is hereafter used to refer to the finest recognised taxonomic category. All relevés, except for 37 plots from Pedlar's Bush (Morgenthal and Cilliers, 1999) are original data, collected for the purposes of this study by the first author of this paper. Two relevés were placed by the first author within Pedlar's Bush to ensure comparability of taxonomy and species concepts with the 37 relevés surveyed in 1997. The relevé data were stored in a Turboveg 2.8 database (Hennekens and Schaminée, 2001) for ease of extraction and information management.

3.2. Classification procedures

A very detailed study targeting the performance of various classification methods (Lötter et al., 2013) established that the most appropriate method to classify our data set would be the Flexible beta clustering ($\beta = -0.25$), based on Bray-Curtis similarity. This procedure was identified as the most rigorous technique to produce an ecologically and biogeographically meaningful classification. The same study, using the OptimClass procedure in JUICE 7 (Tichý, 2002) and expert opinion during validation, established that the ideal number of clusters would be between 12 and 14. Few adjustments were done to the resulting numerical classification based on expert review. The cluster analysis was performed using the software package PC-ORD 5.20 (McCune and Mefford, 2006).

Ordination diagrams were also used to assist in the interpretation of the cluster analysis results. Two and three dimensional Non-metric Multidimensional Scaling (NMDS) ordinations on the full floristic data set, based on Bray-Curtis similarity and performed in JUICE 7 (Tichý, 2002), were produced.

As herbaceous vegetation often reflects changes in habitat at a local scale, the classification was done on two different data sets, (1) one including only woody species, and (2) the other including both woody and herbaceous species. Although there were no large differences between the results of these two classifications, the former was considered to be more biogeographically explicit and better represented the occurrence of forest subtypes during expert review.

3.3. Fidelity assessment

Floristic classification usually involves the arrangement of plant community units into hierarchically structured clusters, which are discriminated from each other by sets of *diagnostic species* (Braun-Blanquet, 1928; Kent and Coker, 1994; Willner et al., 2009). Diagnostic species are those with a high *fidelity* to a particular cluster (interpreted as a forest subtype). The statistical concept of diagnostic species, as defined by Chytrý et al. (2002) was followed. Using JUICE 7 (Tichý, 2002), we applied a phi fidelity (Φ) threshold value of 25, with $p<0.01$ using Fisher's exact test to test for significance. Species with positive Φ values for particular clusters were then considered as diagnostic or faithful species to these clusters.

Diagnostic species can also be used for sorting species in large phytosociological or synoptic tables. In these tables, diagnostic species for particular vegetation units are clustered into diagonally arranged blocks. Diagnostic species that are included in these blocks are defined as those exceeding a set threshold Φ value of 25 in JUICE 7. The threshold value was adjusted to yield an average 25 diagnostic species in each column. JUICE 7 was used to construct the synoptic table using fidelity values and to determine *Diagnostic*, *Constant* and *Dominant Species* (Tichý and Holt, 2006). Constant species are those which frequently occur in a particular unit and are identified when they have a relative frequency higher than a frequency threshold. Dominant species are species which frequently attain a high cover in particular vegetation units. These species must exceed both a cover threshold value as well as a frequency threshold value. Uniqueness value expresses the degree to which species within a particular unit are shared with other units. Values range between 0 and 1, with a value of 1 indicating that they share no species with any other units (Chytrý and Tichý, 2003).

3.4. Building a forest classification hierarchy

The syntaxonomic (vegetation-systematic) hierarchy adopted follows that of the NFC, which recognises *forest groups* and *forest types*, and more recently *forest subtypes* for selected

forest types (Mucina et al., 2007). A cluster dendrogram (McCune and Mefford, 2006) was created from the synoptic table columns using Bray-Curtis similarity measure standardised by sample unit totals, and Flexible beta clustering (β = –0.25). The cluster diagram was inspected to assist in interpreting the relationships between subtypes and between subtypes and types. From the dendrogram and the ordered synoptic table, artificial subtype groupings were recognised (numbered A–E in resulting dendrogram and synoptic table) to aid interpretation of linkages and relationships. The forest subtypes were superimposed on NMDS ordination planes, where envelopes were constructed around different hierarchical groupings that corresponded to those of the revised NFC types.

3.5. Description of communities

Two synoptic tables (see Westhoff and van der Maarel, 1978) are presented for the proposed forest subtypes. These tables explore species frequency and fidelity values and are sorted within particular subtypes. Each subtype is then described and defined in the body of the text according to its species composition, which is aimed at listing basic characteristics needed to recognise the subtype in the field. Species information is summarised into diagnostic, constant and dominant species. The subtypes are also described in terms of their taxonomic, structural and physiognomic characteristics.

The proposed forest subtypes are described in terms of broad taxonomic groups, dominant plant families and genera, growth forms, seasonality or leaf retention characteristics, and the proportion of forest dependant species. Growth forms and forest dependency is described in terms of species occurrences, unless indicated otherwise. As leaf retention or ‘evergreenness’ describes structure, structure should be described in terms of cover and hence leaf retention is presented in terms of summing all cover values (extrapolated from the cover-abundance values into percentage values) for each tree species occurrence and assessing the proportion of each leaf retention category. We distinguish two groups of species in relation to their dependence to a forest environment. Obligate forest species are those which are linked exclusively to forests (occur only in forest communities throughout their known distribution in the Province), while the facultative forest species are those which can be prevalent in the forests, however are also found in communities of non-forest vegetation (incl. grasslands and savanna).

We used the proposed growth form system of Mucina and Rutherford (2006, p. 26) to categorise all species. A MS Access database was created containing the following information: taxonomic position (family and high-rank taxa), leaf retention, forest dependency, plant longevity patterns, and growth form. This database was linked to the relevé data for querying and extraction of pertinent information.

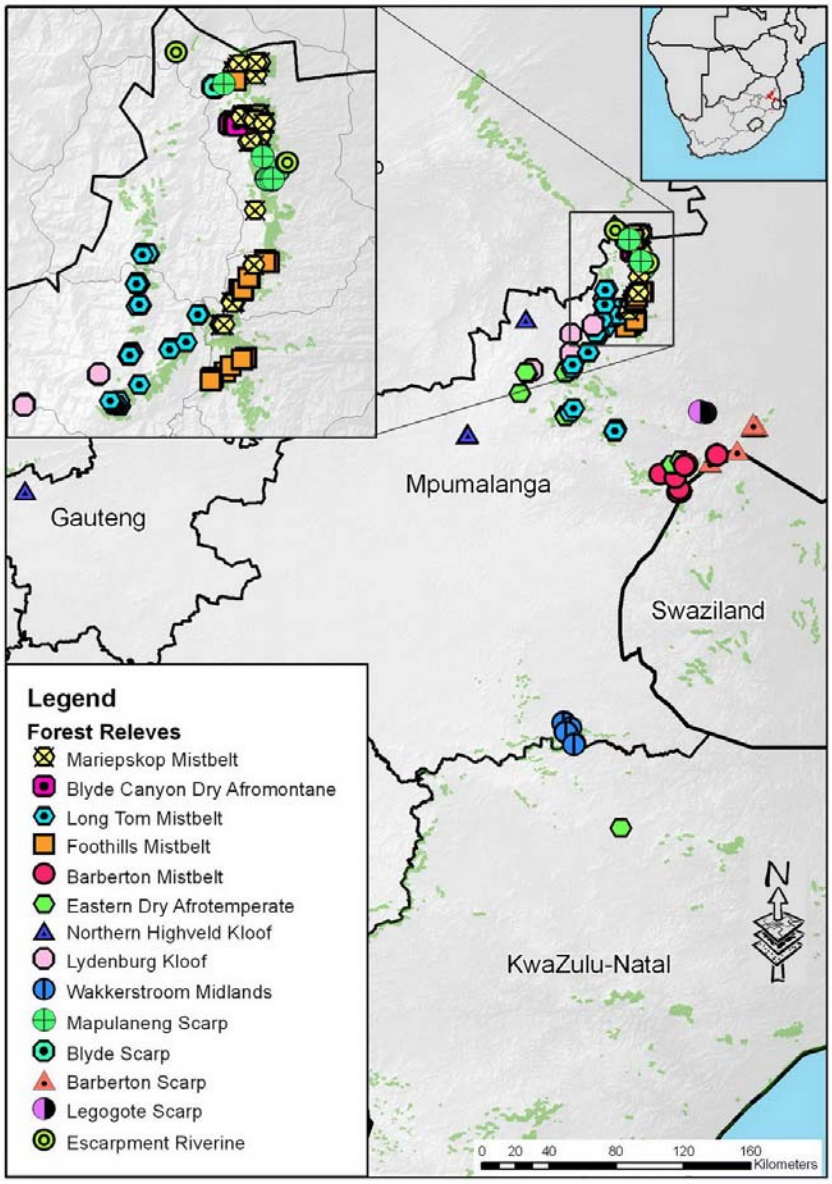


Fig. 1. Location and classification of the 434 forest relevés used to determine forest subtypes for Mpumalanga Province. Symbols represent the different proposed forest subtypes.

4. RESULTS

4.1. General patterns

4.1.1. Taxonomic overview of Mpumalanga forest flora

To describe the taxonomic diversity recorded, a total of 619 plant species were identified within the 434 relevés, which included 362 shrubs and trees. These counts exclude 13 alien species and 10 species that could not be identified beyond the genus level (usually sterile plants). We characterise the vegetation based on characteristics which refer to form (structural characteristics, physiognomy) and position in the taxonomic system (species composition,

families; Werger and Sprangers, 1982). From the data collected on the forests in Mpumalanga, a total of 125 plant families were identified. In descending order of abundance, the dominant families include: Rubiaceae (33 plant species), Fabaceae (26), Celastraceae (25), Orchidaceae (23), Euphorbiaceae (22), Aspleniaceae (21), Apocynaceae (20), Asteraceae (18) Lamiaceae (17) and Acanthaceae (14).

A total of 375 genera were identified, of which only two contained more than 10 plant species. The dominant genera are: *Asplenium* (21), *Searsia* (11), *Asparagus* (7), *Cheilanthes* (7), *Streptocarpus* (7), *Plectranthus* (7), *Solanum* (7), *Maytenus* (7), *Diospyros* (6), *Pavetta* (6), *Combretum* (6) and *Gymnosporia* (6). As many as 262 genera (70%) are represented by a single taxon only.

Just over half (51% of the 619 species) of all species identified are obligate forest species, but when assessed in terms of species occurrences recorded (out of a total of 19,434 records), the proportion of obligate forest species increases to 76% and the number of facultative forest species decreases to 24%. Leaf retention or leaf-fall is a common structural characteristic to distinguish evergreen and deciduous forests (Chytrý and Rafajová, 2003; Lötter and Beck, 2004; Mucina et al., 2006; Small and McCarthy, 2002; von Maltitz et al., 2003). An assessment of all forest relevé cover data revealed that 80% of the tree cover is evergreen (75% of all species occurrences), 14% is deciduous (16% of all occurrences), and 6% are semi-deciduous (9% of all occurrences). Semi-deciduous trees loose some of their leaves but not all at once so the tree is never totally without leaves.

4.1.2. Classification of the plot data

The classification created 14 forest subtypes nested within the existing NFC hierarchy. This hierarchy is presented in Table 1. Within the Northern Afrotemperate Group, four subtypes now occur within the Northern Highveld Forest Type, with the forest patches around Wakkerstroom, previously classified under Low Escarpment Mistbelt Forest Type, now also falling under the Northern Highveld Forest type. This is the only proposed change to the current NFC. Within the NFC Northern Mistbelt Group, five subtypes now occur within the Mpumalanga Mistbelt Forest Type. Within the Scarp Forest Group, five subtypes are recognised within the Eastern Scarp Forest Type, which include community concepts and nomenclature from the Eastern Scarp classification into subtypes (Mucina et al., 2007). No forest relevés were placed within the azonal Lowveld Riverine Forest Type.

Table 1 presents the proposed forest hierarchy which includes the proposed forest subtypes; Fig. 1 shows the location of the various forest subtypes. The relationships between the forest subtypes and the forest types is explored in terms of a dendrogram (Fig. 2) and a two-dimensional NMDS graph (Fig. 3). Visual analysis of both figures support the proposed classification.

Table 1 Syntaxonomic classification of Mpumalanga forests into subtypes, partly nested within the National Forest Classification (von Maltitz et al., 2003) and Eastern Scarp subtype classification (Mucina et al., 2007). Numbers in brackets correspond to subtypes in Figures 2-3, Table 2, and subtype descriptions.

II Northern Afrotemperate Group
II2 TYPE: Northern Highveld Forest
SUBTYPE GROUP A
SUBTYPE: Eastern Dry Afrotemperate Forest (**1**)
SUBTYPE: Wakkerstroom Midlands Forest (**2**)
SUBTYPE: Lydenburg Kloof Forest (**3**)
SUBTYPE: Northern Highveld Kloof Forest (**4**)

IV Northern Mistbelt Group
IV2 TYPE: Mpumalanga Mistbelt Forest
SUBTYPE GROUP B
SUBTYPE: Mariepskop Mistbelt Forest (**5**)
SUBTYPE: Long Tom Mistbelt Forest (**6**)
SUBTYPE: Barberton Mistbelt Forest (**7**)
SUBTYPE GROUP C
SUBTYPE: Blyde Canyon Dry Afromontane Forest (**8**)
SUBTYPE: Foothills Mistbelt Forest (**9**)
V Scarp Forest Group
V1 TYPE: Eastern Scarp Forest
SUBTYPE GROUP D
SUBTYPE: Mapulaneng Scarp Forest (**10**)
SUBTYPE: Barberton Scarp Forest (Mucina et al., 2007) (**11**)
SUBTYPE GROUP E
SUBTYPE: Blyde Scarp Forest (**12**)
SUBTYPE: Escarpment Riverine Forest (**13**)
SUBTYPE: Legogote Scarp (Mucina et al., 2007) (**14**)

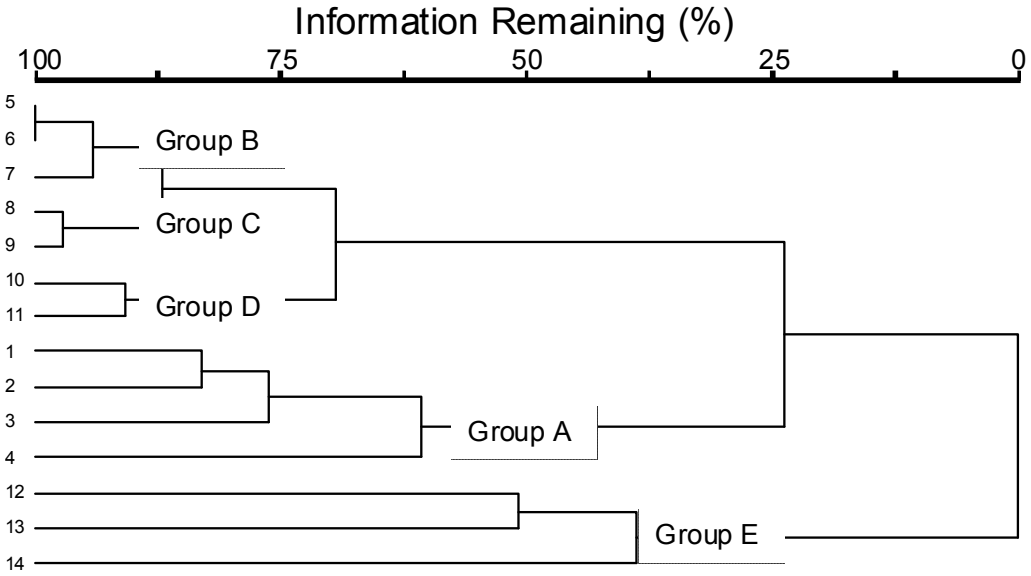


Fig. 2. Forest subtype cluster dendrogram where cluster numbers refer to the proposed subtypes: 1) Eastern Dry Afrotemperate Forest, 2) Wakkerstroom Midlands Forest; 3) Lydenburg Kloof Forest; 4) Northern Highveld Kloof Forest; 5) Mariepskop Mistbelt Forest; 6) Long Tom Mistbelt Forest; 7) Barberton Mistbelt Forest; 8) Blyde Canyon Dry Afromontane Forest; 9) Foothills Mistbelt Forest; 10) Mapulaneng Scarp Forest; 11) Barberton Scarp Forest; 12) Blyde Scarp Forest; 13) Escarpment Riverine Forest; and 14) Legogote Scarp Forest.

Synoptic tables are presented based on species frequency (Table 2) and fidelity values (Table S1 in Supplementary Material). Fidelity values informed diagnostic species which are in black font (Table 2) and only diagnostic species are included in Table S1, which are based on fidelity values. From the ordered synoptic table it is clear that diagnostic species can be recognised for both subtypes and subtype groupings, yet there is also clearly an overlap in species between these groups. The reasons for this are not further explored in this paper, however we anticipate that connectivity or adjacency, as well as biogeography may be responsible.

Uniqueness values (with a phi fidelity (Φ) threshold value of at least 25) indicate that the Escarpment Riverine and Legogote Scarp forests are the most unique, sharing few species with any of the other subtypes. Foothills Mistbelt forest is the least unique, sharing several species with other units. The units are considered to be sufficiently unique at the level of subtypes.

Table 2 Ordered synoptic table of the Mpumalanga forest subtype classification. Diagnostic species (Φ fidelity thresholds) are in black, non-diagnostic species are in grey. Species are clustered into artificial groups (A–E) to aid interpretation and relationships characterising the subtypes (ST1–ST14) and/or the clusters of subtypes. Species are ranked by decreasing values of frequency. Subtype (ST) identifiers refer to the proposed forest subtypes: 1 Eastern Dry Afrotemperate Forest, 2 Wakkerstroom Midlands Forest; 3 Lydenburg Kloof Forest; 4 Northern Highveld Kloof Forest; 5 Mariepskop Mistbelt Forest; 6 Long Tom Mistbelt Forest; 7 Barberton Mistbelt Forest; 8 Blyde Canyon Dry Afromontane Forest; 9 Foothills Mistbelt Forest; 10 Mapulaneng Scarp Forest; 11 Barberton Scarp Forest; 12 Blyde Scarp Forest; 13 Escarpment Riverine Forest; and 14 Legogote Scarp Forest. Growth form (GF) categories refer to C = Climber, E = Epiphyte, G = Graminoid, H = Herb, S = Shrub, T = tree. An * indicates a taxon described in Schmidt et al. (2002).

Forest Subtypes	**Groups**	**GF**	ST1	ST2	ST3	ST4	ST5	ST6	ST7	ST8	ST9	ST10	ST 11	ST 12	ST 13	ST 14
No. of relevés			36	17	14	10	68	118	59	10	35	14	36	5	4	8
No. of diagnostic species (Φ >25)			13	32	33	37	36	19	31	44	15	19	30	36	46	64
No. of species in synoptic columns (Φ > 2)			59	42	40	42	74	78	56	48	31	34	67	36	46	65
Average no. of species per relevé			45	41	33.5	34.4	43	48.8	45	70.2	38.6	48.9	41.8	44.4	42.3	44.6
Uniqueness for the fidelity cut level: (Φ >25)			0.6	0.8	0.74	0.85	0.7	0.63	0.8	0.68	0.41	0.55	0.63	0.66	0.91	0.9
New codes of the preliminary subtypes groups			**A**	**A**	**A**	**A**	**B**	**B**	**B**	**C**	**C**	**D**	**D**	**E**	**E**	**E**
Pachystigma macrocalyx	**A**	T	3	.	.	70	.	.	.	.	.	.	.	.	.	.
Pavetta gardeniifolia	**A**	S	3	.	.	70	.	.	.	.	.	.	.	.	.	.
Buddleja saligna	**A**	T	3	.	7	10	.	.	.	.	.	.	.	.	.	.
Blechnum australe	**A**	H	11	.	29	.	.	.	.	.	.	.	.	.	.	.
Acokanthera oppositifolia	**A**	S	3	.	.	10	.	.	.	.	.	.	.	.	.	.
Hypoestes triflora	**A**	H	6	6	.	.	.	.	.	.	.	.	.	.	.	.
Streptocarpus polyanthus	**A**	E	8	.	14	.	.	.	.	.	.	.	.	.	.	.
Acacia caffra	**A**	T	3	.	14	.	.	.	.	.	.	.	.	.	.	.
Solanum lichtensteinii	**A**	S	3	35	7	.	.	.	.	.	.	.	.	.	.	.
Leucosidea sericea	**A**	T	.	6	29	.	.	.	.	.	.	.	.	.	.	.
Gymnosporia buxifolia	**A**	T	.	6	14	.	.	.	.	.	.	.	.	.	.	.
Pteris dentata	**A**	H	.	6	7	30	.	.	.	.	.	.	.	.	.	.
Diospyros lycioides subsp. *guerkei*	**A**	S	.	.	21	40	.	.	.	.	.	.	.	.	.	.
Asplenium adiantum-nigrum var. *adiantum-nigrum*	**A**	H	.	.	21	20	.	.	.	.	.	.	.	.	.	.
Mystacidium capense	**A**	E	11	.	.	.	.	.	.	.	.	.	.	.	.	.
Aloe barberiae	**A**	T	6	.	.	.	.	.	.	.	.	.	.	.	.	.
Carex mossii	**A**	G	6	.	.	.	.	.	.	.	.	.	.	.	.	.
Senecio pleistocephalus	**A**	C	3	.	.	.	.	.	.	.	.	.	.	.	.	.
Commiphora harveyi	**A**	T	3	.	.	.	.	.	.	.	.	.	.	.	.	.
Zantedeschia albomaculata subsp. *albomaculata*	**A**	H	3	.	.	.	.	.	.	.	.	.	.	.	.	.
Littonia modesta	**A**	H	3	.	.	.	.	.	.	.	.	.	.	.	.	.
Elaeodendron zeyheri	**A**	T	3	.	.	.	.	.	.	.	.	.	.	.	.	.
Cyphostemma woodii	**A**	C	3	.	.	.	.	.	.	.	.	.	.	.	.	.
Buddleja dysophylla	**A**	S	.	41	.	.	.	.	.	.	.	.	.	.	.	.
Streptocarpus pentherianus	**A**	H	.	35	.	.	.	.	.	.	.	.	.	.	.	.
Diaphananthe caffra	**A**	E	.	18	.	.	.	.	.	.	.	.	.	.	.	.
Mystacidium flanaganii	**A**	E	.	12	.	.	.	.	.	.	.	.	.	.	.	.

Rubus rigidus	**A**	S	.	12	.	.	.	.	.	.	.	.	.	.	.	.	.
Huttonaea fimbriata	**A**	H	.	6	.	.	.	.	.	.	.	.	.	.	.	.	.
Polystachya pubescens	**A**	E	.	6	.	.	.	.	.	.	.	.	.	.	.	.	.
Ehrharta erecta var. *natalensis*	**A**	G	.	.	29	.	.	.	.	.	.	.	.	.	.	.	.
Sparrmannia ricinocarpa	**A**	S	.	.	14	.	.	.	.	.	.	.	.	.	.	.	.
Acacia karroo	**A**	T	.	.	7	.	.	.	.	.	.	.	.	.	.	.	.
Searsia dentata	**A**	S	.	.	7	.	.	.	.	.	.	.	.	.	.	.	.
Aeollanthus buchnerianus	**A**	H	.	.	.	30	.	.	.	.	.	.	.	.	.	.	.
Solanum retroflexum	**A**	S	.	.	.	30	.	.	.	.	.	.	.	.	.	.	.
Searsia pallens	**A**	T	.	.	.	30	.	.	.	.	.	.	.	.	.	.	.
Cyathula uncinulata	**A**	H	.	.	.	30	.	.	.	.	.	.	.	.	.	.	.
Solanum giganteum	**A**	S	.	.	.	30	.	.	.	.	.	.	.	.	.	.	.
Solanum pseudocapsicum	**A**	S	.	.	.	20	.	.	.	.	.	.	.	.	.	.	.
Searsia leptodictya	**A**	T	.	.	.	20	.	.	.	.	.	.	.	.	.	.	.
Searsia pyroides var. *pyroides*	**A**	T	.	.	.	20	.	.	.	.	.	.	.	.	.	.	.
Maytenus albata	**A**	T	.	.	.	20	.	.	.	.	.	.	.	.	.	.	.
Cussonia paniculata	**A**	T	.	.	.	20	.	.	.	.	.	.	.	.	.	.	.
Searsia gerrardii	**A**	S	.	.	.	10	.	.	.	.	.	.	.	.	.	.	.
Cyanotis lapidosa	**A**	H	.	.	.	10	.	.	.	.	.	.	.	.	.	.	.
Plectranthus hereroensis	**A**	H	.	.	.	10	.	.	.	.	.	.	.	.	.	.	.
Haemanthus humilis subsp. *hirsutus*	**A**	H	.	.	.	10	.	.	.	.	.	.	.	.	.	.	.
Disperis micrantha	**A**	H	.	.	.	10	.	.	.	.	.	.	.	.	.	.	.
Combretum erythrophyllum	**A**	T	.	.	.	10	.	.	.	.	.	.	.	.	.	.	.
Croton gratissimus var. *gratissimus*	**A**	T	.	.	.	10	.	.	.	.	.	.	.	.	.	.	.
Euphorbia ingens	**A**	T	.	.	.	10	.	.	.	.	.	.	.	.	.	.	.

Afrocanthium mundianum	**AE**	S	3	6	.	50	.	.	.	.	.	.	.	40	50	.
Plectranthus verticillatus	**AE**	H	11	.	14	.	.	.	.	.	.	.	.	.	25	.
Argyrolobium tomentosum	**AE**	S	6	6	.	.	.	.	.	.	.	.	.	.	25	.
Zanthoxylum capense	**AE**	T	11	.	.	10	.	.	.	.	.	.	.	20	.	.
Capparis fascicularis var. *fascicularis*	**AE**	C	6	.	.	10	.	.	.	.	.	.	.	40	.	13
Dovyalis zeyheri	**AE**	T	6	.	.	40	.	.	.	.	.	.	.	20	.	.
Diospyros natalensis subsp. *nummularia*	**AE**	T	3	.	.	.	.	.	.	.	.	.	.	.	.	100
Triumfetta pilosa	**AE**	S	3	.	.	.	.	.	.	.	.	.	.	20	.	.
Tacazzea apiculata	**AE**	C	3	.	.	.	.	.	.	.	.	.	.	.	25	.
Secamone filiformis	**AE**	C	3	.	.	.	.	.	.	.	.	.	.	40	.	13
Searsia pentheri	**AE**	T	3	.	.	.	.	.	.	.	.	.	.	20	.	.
Olea europaea subsp. *africana*	**AE**	T	6	.	.	.	.	.	.	.	.	.	.	.	25	.
Chaetachme aristata	**AE**	T	6	.	.	.	.	.	.	.	.	.	.	.	25	25
Asplenium cordatum	**AE**	H	8	.	.	.	.	.	.	.	.	.	.	.	.	13
Ziziphus mucronata subsp. *mucronata*	**AE**	T	.	6	.	.	.	.	.	.	.	.	.	20	.	.
Tetradenia riparia	**AE**	S	.	.	.	20	.	.	.	.	.	.	.	20	.	.
Ficus ingens	**AE**	T	.	.	.	20	.	.	.	.	.	.	.	20	25	25
Equisetum ramosissimum	**AE**	H	.	.	.	10	.	.	.	.	.	.	.	40	.	.
Dombeya rotundifolia	**AE**	T	.	.	.	20	.	.	.	.	.	.	.	20	.	.
Combretum molle	**AE**	T	.	.	.	10	.	.	.	.	.	.	.	20	.	75

Elaphoglossum acrostichoides	**B**	E	.	.	.	.	19	1	2	.	.	.	.	.	.	.
Polystichum macleae	**B**	H	.	.	.	.	10	15	5	.	.	.	.	.	.	.
Asplenium erectum var. *usambarense*	**B**	H	.	.	.	.	1	14	14	.	.	.	.	.	.	.
Streptocarpus micranthus	**B**	E	.	.	.	.	18	.	2	.	.	.	.	.	.	.
Elaphoglossum aubertii	**B**	E	.	.	.	.	28	2	.	.	.	.	.	.	.	.
Vittaria isoetifolia	**B**	E	.	.	.	.	13	1	.	.	.	.	.	.	.	.
Vaccinium exul	**B**	T	.	.	.	.	13	4	.	.	.	.	.	.	.	.
Asplenium friesiorum	**B**	H	.	.	.	.	10	1	.	.	.	.	.	.	.	.
Blotiella natalensis	**B**	H	.	.	.	.	9	2	.	.	.	.	.	.	.	.
Asplenium lunulatum	**B**	H	.	.	.	.	9	4	.	.	.	.	.	.	.	.
Asplenium lividum	**B**	H	.	.	.	.	1	2	.	.	.	.	.	.	.	.
Brownleea coerulea	**B**	H	.	.	.	.	4	1	.	.	.	.	.	.	.	.
Nothoperanema squamiseta	**B**	H	.	.	.	.	4	2	.	.	.	.	.	.	.	.
Elaphoglossum macropodium	**B**	E	.	.	.	.	21	.	.	.	.	.	.	.	.	.
Solenostemon latifolius	**B**	H	.	.	.	.	16	.	.	.	.	.	.	.	.	.
Rumohra adiantiformis	**B**	H	.	.	.	.	15	.	.	.	.	.	.	.	.	.
Ocotea bullata	**B**	T	.	.	.	.	13	.	.	.	.	.	.	.	.	.
Plectranthus rubropunctatus	**B**	H	.	.	.	.	9	.	.	.	.	.	.	.	.	.
Disperis fanniniae	**B**	H	.	.	.	.	9	.	.	.	.	.	.	.	.	.
Maytenus species A (Mariepskop)*	**B**	T	.	.	.	.	7	.	.	.	.	.	.	.	.	.
Huperzia dacrydioides	**B**	E	.	.	.	.	7	.	.	.	.	.	.	.	.	.
Drimia robusta	**B**	H	.	.	.	.	7	.	.	.	.	.	.	.	.	.
Cyathea capensis	**B**	T	.	.	.	.	7	.	.	.	.	.	.	.	.	.
Abrodictyum rigidum	**B**	E	.	.	.	.	4	.	.	.	.	.	.	.	.	.
Impatiens sylvicola	**B**	H	.	.	.	.	4	.	.	.	.	.	.	.	.	.
Huperzia verticillatum	**B**	E	.	.	.	.	4	.	.	.	.	.	.	.	.	.
Athyrium scandicinum	**B**	H	.	.	.	.	3	.	.	.	.	.	.	.	.	.
Polystachya fusiformis	**B**	E	.	.	.	.	3	.	.	.	.	.	.	.	.	.
Duvernoia adhatodioides	**B**	S	.	.	.	.	3	.	.	.	.	.	.	.	.	.
Polystachya transvaalensis	**B**	E	.	.	.	.	1	.	.	.	.	.	.	.	.	.
Olinia rochetiana	**B**	T	.	.	.	.	1	.	.	.	.	.	.	.	.	.
Streptocarpus fenestra-dei	**B**	E	.	.	.	.	1	.	.	.	.	.	.	.	.	.
Sphaerocionium capillare	**B**	E	.	.	.	.	1	.	.	.	.	.	.	.	.	.
Cynorkis kassneriana	**B**	H	.	.	.	.	1	.	.	.	.	.	.	.	.	.
Histiopteris incisa	**B**	H	.	.	.	.	1	.	.	.	.	.	.	.	.	.
Cheilanthes multifida	**B**	H	.	.	.	.	1	.	.	.	.	.	.	.	.	.
Cassine peragua	**B**	T	.	.	.	.	.	11	.	.	.	.	.	.	.	.

Hippocratea longipetiolata (forest form)	**B**	C	.	.	.	.	.	7	.	.	.	.	.	.	.	.	.
Arachniodes webbiana subsp. *foliosa*	**B**	H	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.
Buddleja pulchella	**B**	S	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.
Pilea rivularis	**B**	H	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.
Cyrtomium micropterum	**B**	H	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.
Psoralea pinnata	**B**	S	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.
Clutia affinis	**B**	S	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.
Polygala virgata var. *decora*	**B**	S	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.
Lycopodium clavatum	**B**	H	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.
Senecio panduriformis	**B**	S	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.
Seriphium sp. (escarpment form)*	**B**	S	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.
Cyathula cylindrica	**B**	H	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.
Asplenium preussii	**B**	H	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.
Aristea ecklonii	**B**	H	.	.	.	.	.	.	25	.	.	.	.	.	.	.	.
Memecylon natalense	**B**	T	.	.	.	.	.	.	10	.	.	.	.	.	.	.	.
Polystichum transkeiense	**B**	H	.	.	.	.	.	.	8	.	.	.	.	.	.	.	.
Clivia miniata	**B**	H	.	.	.	.	.	.	8	.	.	.	.	.	.	.	.
Cheilanthes bergiana	**B**	H	.	.	.	.	.	.	5	.	.	.	.	.	.	.	.
Pavonia burchellii	**B**	S	.	.	.	.	.	.	5	.	.	.	.	.	.	.	.
Leonotis ocymifolia	**B**	S	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.
Andrachne ovalis	**B**	S	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.
Salacia gerrardii	**B**	C	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.
Cassinopsis tinifolia	**B**	S	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.
Streptocarpus cyaneus subsp. *cyaneus*	**B**	E	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.
Jasminum abyssinicum	**BC**	C	.	.	.	.	47	80	.	20	29	.	.	.	.	.	.
Tylophora flanaganii	**BC**	C	.	.	.	.	6	42	2	10	3	.	.	.	.	.	.
Crepidomanes melanotrichum	**BC**	E	.	.	.	.	3	3	.	30	11	.	.	.	.	.	.
Asplenium sandersonii	**BC**	E	.	.	.	.	7	8	.	10	9	.	.	.	.	.	.
Loxogramme lanceolata	**BC**	E	.	.	.	.	12	3	.	10	3	.	.	.	.	.	.
Begonia sonderiana	**BC**	H	.	.	.	.	9	3	.	10	3	.	.	.	.	.	.
Hymenophyllum tunbrigense	**BC**	E	.	.	.	.	18	1	.	10	.	.	.	.	.	.	.
Elaeodendron croceum	**BC**	T	.	.	.	.	16	3	.	60	.	.	.	.	.	.	.
Selaginella mittenii	**BC**	H	.	.	.	.	3	4	.	20	.	.	.	.	.	.	.
Searsia tumulicola var. tumulicola	**BC**	T	.	.	.	.	12	2	.	10	.	.	.	.	.	.	.
Crepidomanes borbonicum	**BC**	E	.	.	.	.	6	.	.	10	.	.	.	.	.	.	.
Hymenophyllum capense	**BC**	E	.	.	.	.	6	.	.	.	6	.	.	.	.	.	.
Todea barbara	**BC**	T	.	.	.	.	3	.	.	10	.	.	.	.	.	.	.
Tectaria gemmifera	**BC**	H	.	.	.	.	.	1	.	.	6	.	.	.	.	.	.
Adenocline acuta	**BC**	H	.	.	.	.	.	2	.	10	.	.	.	.	.	.	.
Chlorophytum krookianum	**BC**	H	.	.	.	.	.	.	3	.	3	.	.	.	.	.	.
Syzygium gerrardii	**BCD**	T	.	.	.	.	96	72	71	60	94	14	36	.	.	.	.
Schefflera umbellifera	**BCD**	T	.	.	.	.	49	17	31	90	29	7	33	.	.	.	.
Pavetta inandensis	**BCD**	T	.	.	.	.	69	19	54	70	31	14	6	.	.	.	.
Streptocarpus wilmsii	**BCD**	E	.	.	.	.	31	24	32	10	9	7	6	.	.	.	.
Cephalanthus natalensis	**BCD**	S	.	.	.	.	9	8	.	.	29	29	14	.	.	.	.
Cnestis polyphylla	**BCD**	S	.	.	.	.	1	11	5	10	34	.	31	.	.	.	.
Ocotea kenyensis	**BCD**	T	.	.	.	.	3	2	22	.	3	.	19	.	.	.	.
Mackaya bella	**BCD**	S	.	.	.	.	7	.	7	.	6	7	14	.	.	.	.
Osyridicarpos schimperianus	**BCD**	S	.	.	.	.	.	1	2	20	.	.	3	.	.	.	.
Psychotria zombamontana	**BCD**	T	.	.	.	.	91	77	.	90	80	21	.	.	.	.	.
Vernonia wollastonii	**BCD**	S	.	.	.	.	50	25	8	40	20	7	.	.	.	.	.
Olinia radiata	**BCD**	T	.	.	.	.	63	.	46	20	3	7	.	.	.	.	.
Talbotia elegans	**BCD**	H	.	.	.	.	1	.	.	20	.	7	.	.	.	.	.
Plectranthus ciliatus	**BCD**	H	.	.	.	.	.	21	.	10	3	21	.	.	.	.	.
Asplenium gemmiferum	**BCD**	H	.	.	.	.	.	6	2	.	6	7	.	.	.	.	.
Morella pilulifera	**BCD**	T	.	.	.	.	.	4	.	.	3	7	.	.	.	.	.
Teclea natalensis	**BCD**	T	.	.	.	.	.	7	.	10	.	.	3	.	.	.	.
Ptaeroxylon obliquum	**BCE**	T	.	.	.	.	4	9	7	20	.	.	.	40	.	75	
Gymnosporia harveyana	**ABCD**	T	86	94	64	.	4	67	34	90	34	57	3	.	.	.	
Zanthoxylum davyi	**ABCD**	T	67	94	21	60	34	88	80	90	54	36	47	.	.	.	
Scolopia mundii	**ABCD**	T	67	71	71	.	7	50	12	100	.	.	11	.	.	.	
Carissa bispinosa subsp. *zambesiensis*	**ABCD**	S	69	82	36	.	7	76	86	100	77	57	47	.	.	.	
Rothmannia capensis	**ABCD**	T	36	29	7	90	69	51	68	40	20	7	17	.	.	.	
Allophylus africanus	**ABCD**	T	39	82	14	10	.	8	14	30	9	36	8	.	.	.	
Rhoicissus sp.1*	**ABCD**	C	50	53	14	20	.	24	3	80	3	7	3	.	.	.	
Combretum kraussii	**ABCD**	T	83	18	.	.	15	20	53	100	94	93	89	.	.	.	
Asplenium splendens	**ABCD**	H	64	6	.	50	46	66	68	80	80	50	31	.	.	.	
Asplenium rutifolium	**ABCD**	E	25	35	29	.	74	69	49	60	31	7	17	.	.	.	
Behnia reticulata	**ABCD**	C	47	47	.	.	74	94	68	100	66	36	42	.	.	.	
Rapanea melanophloeos	**ABCD**	T	11	35	21	.	57	69	46	30	9	14	8	.	.	.	
Pittosporum viridiflorum	**ABCD**	T	31	18	71	40	15	18	7	60	3	21	6	.	.	.	
Dryopteris inaequalis	**ABCD**	H	25	53	79	30	21	64	41	10	9	7	14	.	.	.	
Pterocelastrus rostratus	**ABCD**	T	22	.	50	40	62	57	36	80	40	21	17	.	.	.	
Peperomia retusa	**ABCD**	E	25	29	21	10	53	31	14	50	14	14	11	.	.	.	
Plectranthus fruticosus	**ABCD**	S	22	53	29	20	57	14	53	30	11	36	3	.	.	.	
Pteris catoptera	**ABCD**	H	33	47	.	40	13	56	63	20	43	57	19	.	.	.	
Maytenus acuminata var. *acuminata*	**ABCD**	T	31	12	14	.	49	58	12	90	11	.	17	.	.	.	
Choristylis rhamnoides	**ABCD**	S	8	35	14	.	6	20	.	10	3	14	6	.	.	.	
Xymalos monospora	**ABCD**	T	28	53	.	.	75	86	75	20	49	57	39	.	.	.	
Asplenium aethiopicum	**ABCD**	H	19	12	64	.	53	47	12	30	11	7	.	.	.	.	

Ilex mitis	**ABCD**	T	17	18	21	70	10	7	5	40	.	.	11	.	.	.
Clematis brachiata	**ABCD**	C	6	.	86	50	21	39	5	50	11	.	8	.	.	.
Maerua cafra	**ABCD**	T	17	6	7	40	.	3	.	20	3	7	11	.	.	.
Nuxia congesta	**ABCD**	T	6	.	7	70	12	8	7	.	49	21	19	.	.	.
Podocarpus latifolius	**ABCD**	T	8	88	.	.	69	64	61	70	11	.	.	.	.	.
Dovyalis rhamnoides	**ABCD**	T	11	59	.	.	.	.	32	70	.	7	.	.	.	.
Scutia myrtina	**ABCD**	C	44	65	.	.	6	36	8	80	.	14	.	.	.	.
Polypodium polypodioides	**ABCD**	E	19	18	.	.	26	42	29	30	11	7	.	.	.	.
Prunus africana	**ABCD**	T	11	6	.	10	.	13	8	.	6	.	6	.	.	.
Clutia pulchella var. *pulchella*	**ABCD**	S	14	.	14	10	.	1	27	10	3	.	6	.	.	.
Brachypodium flexum	**ABCD**	G	6	12	.	10	6	5	.	10	3	14	3	.	.	.
Clivia caulescens	**ABCD**	H	6	.	14	.	56	38	14	20	.	7	6	.	.	.
Robsonodendron eucleiforme	**ABCD**	T	8	12	43	.	28	16	14	30	6	.	11	.	.	.
Curtisia dentata	**ABCD**	T	22	6	.	.	13	37	19	30	6	21	3	.	.	.
Cryptocarya transvaalensis	**ABCD**	T	22	.	.	.	41	72	64	70	40	43	28	.	.	.
Eugenia natalitia	**ABCD**	T	17	.	.	.	25	10	17	100	71	50	22	.	.	.
Tricalysia capensis var. *transvaalensis*	**ABCD**	S	3	.	.	.	40	32	73	60	100	7	36	.	.	.
Asparagus falcatus	**ABCD**	C	8	.	.	.	.	3	2	40	23	79	33	.	.	.
Dracaena aletriformis	**ABCD**	T	17	.	.	.	.	2	7	20	23	64	33	.	.	.
Sclerochiton harveyanus	**ABCD**	S	17	.	7	.	71	51	2	90	29	7	.	.	.	.
Marattia fraxinea	**ABCD**	T	3	.	.	.	10	1	2	.	11	14	3	.	.	.
Combretum edwardsii	**ABCD**	C	6	.	.	.	53	39	37	40	20	21	3	.	.	.
Bersama tysoniana	**ABCD**	T	8	.	.	.	32	56	46	80	37	.	44	.	.	.
Trichocladus grandiflorus	**ABCD**	T	8	.	.	.	21	8	10	40	6	.	6	.	.	.
Peddiea africana	**ABCD**	S	8	.	.	.	84	86	73	90	89	100	67	.	.	.
Crocosmia aurea var. *aurea*	**ABCD**	H	8	71	.	.	10	28	3	20	23	64	11	.	.	.
Olea capensis subsp. *macrocarpa*	**ABCD**	T	6	.	.	.	82	64	78	100	17	7	14	.	.	.
Sanicula elata	**ABCD**	H	3	35	.	.	.	14	.	10	6	14	.	.	.	.
Cassipourea malosana	**ABCD**	T	8	.	.	.	90	60	80	50	57	14	.	.	.	.
Chionanthus foveolatus subsp. *major*	**ABCD**	T	3	.	.	.	44	54	66	10	.	7	6	.	.	.
Cyperus pseudoleptocladus	**ABCD**	G	6	.	43	.	43	45	2	20	29	14	3	.	.	.
Piper capense	**ABCD**	S	3	.	.	.	13	22	14	.	9	7	3	.	.	.
Cardamine africana	**ABCD**	H	3	6	.	.	9	19	.	20	9	7	.	.	.	.
Rubus pinnatus	**ABCD**	S	6	.	.	.	1	8	.	.	3	.	3	.	.	.
Ekebergia pterophylla	**ABCD**	T	6	.	.	.	6	.	8	.	14	7	8	.	.	.
Burchellia bubalina	**ABCD**	S	3	12	.	.	.	2	2	.	9	.	11	.	.	.
Justicia campylostemon	**ABCD**	S	6	.	.	.	.	.	22	20	9	.	19	.	.	.
Riocreuxia picta	**ABCD**	C	8	.	.	.	1	.	20	.	6	.	3	.	.	.
Prosphytochloa prehensilis	**ABCD**	C	6	.	.	.	9	10	63	.	9	.	25	.	.	.
Asplenium varians	**ABCD**	H	.	24	14	.	1	.	.	.	3	.	3	.	.	.
Chionanthus peglerae	**ABCD**	T	.	12	.	.	6	.	59	.	17	36	28	.	.	.
Ochna gamostigmata	**ABCD**	S	.	.	.	20	.	.	36	.	3	.	3	.	.	.
Carex zuluensis	**ABCD**	G	.	.	14	.	.	2	2	.	3	.	3	.	.	.

Celtis africana	**ABCDE**	T	67	59	14	100	6	31	17	70	14	71	69	100	25	50
Cyperus albostriatus	**ABCDE**	G	58	71	21	70	65	45	69	100	51	79	47	20	.	63
Clausena anisata	**ABCDE**	T	67	88	64	70	6	54	34	40	23	50	14	.	25	.
Trimeria grandifolia	**ABCDE**	T	69	29	29	.	12	46	19	50	14	64	14	20	.	.
Grewia occidentalis	**ABCDE**	T	58	29	.	.	.	9	25	40	6	43	19	20	25	.
Dioscorea cotinifolia	**ABCDE**	C	17	12	14	10	4	.	.	.	9	7	6	40	.	63
Rhoicissus rhomboidea	**ABCDE**	C	50	6	.	.	34	66	85	100	89	71	61	20	.	.
Asparagus virgatus	**ABCDE**	S	83	6	71	50	.	3	8	30	3	7	33	40	.	13
Oplismenus hirtellus	**ABCDE**	G	75	41	14	20	81	64	47	100	94	93	72	100	100	100
Apodytes dimidiata	**ABCDE**	T	53	6	21	.	25	33	5	40	34	57	11	20	.	13
Desmodium repandum	**ABCDE**	H	47	59	21	20	1	15	2	20	14	57	11	.	75	.
Diospyros whyteana	**ABCDE**	T	83	76	100	100	38	82	58	100	9	100	3	.	75	.
Asparagus setaceus	**ABCDE**	C	22	88	21	60	50	74	83	80	31	36	22	20	.	50
Dalbergia armata	**ABCDE**	C	64	.	.	.	.	3	10	40	63	57	89	100	25	88
Cussonia spicata	**ABCDE**	T	36	.	14	.	28	56	76	50	37	29	28	20	.	.
Ochna holstii	**ABCDE**	T	50	24	.	.	35	55	85	80	60	43	36	40	.	.
Strychnos henningsii	**ABCDE**	T	14	29	.	.	10	2	12	80	3	7	6	40	25	.
Scolopia zeyheri	**ABCDE**	T	28	6	21	10	1	.	10	60	.	7	25	.	.	25
Dietes iridioides	**ABCDE**	H	42	35	.	20	65	58	34	90	31	64	64	80	25	.
Halleria lucida	**ABCDE**	T	17	41	64	70	29	41	25	40	.	14	3	.	50	.
Euclea crispa subsp. *crispa*	**ABCDE**	T	39	6	50	.	1	10	.	40	3	14	6	20	.	.
Schoenoxiphium lehmannii	**ABCDE**	G	56	29	.	.	.	6	.	20	.	.	14	20	25	.
Searsia chirindensis	**ABCDE**	T	28	76	.	20	7	11	5	30	6	36	19	40	50	.
Cissampelos torulosa	**ABCDE**	C	50	53	29	10	9	26	12	70	14	21	19	60	75	.
Cheilanthes viridis var. *viridis*	**ABCDE**	H	50	6	21	60	59	68	39	90	80	93	36	40	.	.
Secamone alpini	**ABCDE**	C	69	71	21	50	40	73	54	90	37	86	25	20	.	.
Senecio tamoides	**ABCDE**	C	61	53	57	.	47	57	53	20	29	36	8	20	.	.
Adenopodia spicata	**ABCDE**	C	28	6	.	.	4	6	.	50	29	29	22	40	.	.
Impatiens hochstetteri	**ABCDE**	H	17	47	29	10	15	23	22	.	9	36	3	.	75	.
Canthium inerme	**ABCDE**	S	25	12	.	.	4	11	27	40	31	57	64	20	.	.
Euclea natalensis	**ABCDE**	T	39	6	.	.	.	.	5	60	.	7	36	20	.	88
Protorhus longifolia	**ABCDE**	T	22	12	.	.	6	.	8	70	34	93	64	60	25	.
Brachylaena transvaalensis	**ABCDE**	T	31	.	7	10	16	34	12	60	29	43	56	40	.	.
Ekebergia capensis	**ABCDE**	T	22	.	7	.	1	5	10	10	6	14	3	.	25	25
Maytenus peduncularis	**ABCDE**	T	47	.	43	.	4	55	10	90	11	50	39	40	.	.
Carex spicato-paniculata	**ABCDE**	G	22	.	.	30	.	3	3	.	31	.	6	.	75	.
Mimusops obovata	**ABCDE**	T	31	12	.	.	6	3	7	90	9	36	22	.	.	88
Rhoicissus tomentosa	**ABCDE**	C	39	.	.	10	1	3	.	30	6	86	53	100	75	88
Nuxia floribunda	**ABCDE**	T	14	.	.	10	31	8	3	30	6	57	17	60	.	.
Psychotria capensis (forest form)	**ABCDE**	T	8	6	.	.	87	71	42	60	94	79	8	.	25	.
Tricalysia lanceolata	**ABCDE**	S	6	41	.	.	.	.	2	30	14	64	8	100	25	.
Pyrenacantha grandiflora	**ABCDE**	C	3	18	.	.	.	9	2	.	9	14	25	20	.	25

Ficus craterostoma	**ABCDE**	C	6	35	.	.	18	8	31	10	17	7	8	.	25	.
Cyphostemma anatomicum	**ABCDE**	C	6	6	.	.	7	1	7	.	.	7	.	20	.	.
Trema orientalis	**ABCDE**	T	6	.	.	.	.	1	.	.	3	14	11	.	.	13
Syzygium cordatum	**ABCDE**	T	6	.	.	.	6	.	.	.	26	57	17	60	100	.
Englerophytum magalismontanum	**ABCDE**	T	6	.	.	10	4	.	8	20	80	79	86	80	25	.
Maesa lanceolata	**ABCDE**	T	.	.	7	10	4	8	7	10	9	14	3	.	75	13
Oxyanthus speciosus subsp. *gerrardii*	**ABCDE**	T	.	12	.	.	81	27	63	.	86	29	33	.	25	.
Setaria megaphylla	**ABCDE**	G	.	.	.	30	.	3	19	10	17	36	22	60	100	.
Schrebera alata	**ABCDE**	T	.	.	.	10	26	25	.	20	6	.	3	.	.	38
Rawsonia lucida	**CDE**	T	.	.	.	.	13	15	42	20	46	21	69	100	25	.
Englerophytum natalense	**CDE**	T	.	.	.	.	7	.	7	.	43	50	94	100	.	.
Smilax anceps	**CDE**	C	.	.	.	.	7	2	2	30	31	43	22	40	50	.
Selaginella kraussiana	**CDE**	H	.	.	.	.	9	9	5	.	6	29	3	.	50	.
Eugenia woodii	**CDE**	T	.	.	.	.	1	.	.	40	9	7	14	20	.	.
Rothmannia globosa	**CDE**	T	.	.	.	.	.	.	2	50	14	71	6	20	.	.
Drypetes gerrardii	**CDE**	T	.	.	.	.	.	.	14	.	3	14	11	20	.	.
Croton sylvaticus	**CDE**	T	.	.	.	.	.	.	10	.	43	36	72	80	.	.
Galopina circaeoides	**ABCE**	H	31	41	50	10	7	25	2	50	9	.	.	.	25	.
Vangueria infausta	**ABCE**	T	3	.	.	.	3	.	.	40	.	.	.	.	.	13
Podocarpus falcatus	**ABCE**	T	.	59	.	.	40	37	44	100	.	.	.	.	25	.
Dumasia villosa var. *villosa*	**ABCE**	C	.	.	.	20	.	2	.	10	.	.	.	20	.	.
Maytenus deflexa	**ABC**	T	31	18	86	30	29	42	24	50	.	.	.	.	.	.
Myrsine africana	**ABC**	S	28	6	43	70	6	3	.	20	6	.	.	.	.	.
Canthium kuntzeanum	**ABC**	S	22	35	57	.	34	64	.	80	6	.	.	.	.	.
Olinia emarginata	**ABC**	T	39	18	71	80	.	18	.	20	.	.	.	.	.	.
Dovyalis lucida	**ABC**	T	31	.	.	10	46	87	71	80	57	.	.	.	.	.
Lauridia tetragona	**ABC**	S	17	29	.	.	9	41	20	40	.	.	.	.	.	.
Psydrax obovata subsp. *elliptica*	**ABC**	T	11	6	.	60	53	30	3	80	14	.	.	.	.	.
Canthium ciliatum	**ABC**	S	6	29	.	.	4	22	20	80	43	.	.	.	.	.
Heteromorpha arborescens var. *abyssinica*	**ABC**	T	3	6	50	20	.	2	.	10	.	.	.	.	.	.
Blechnum punctulatum var. *atherstonei*	**ABC**	H	8	18	.	20	16	2	3	10	14	.	.	.	.	.
Calpurnia aurea	**ABC**	S	22	29	.	.	9	23	22	10	.	.	.	.	.	.
Polystichum luctuosum	**ABC**	H	11	12	7	.	.	10	.	10	.	.	.	.	.	.
Peperomia tetraphylla	**ABC**	E	11	6	14	.	32	11	2	10	6	.	.	.	.	.
Asplenium lobatum	**ABC**	H	11	12	.	.	24	44	7	.	11	.	.	.	.	.
Rhamnus prinoides	**ABC**	T	19	6	71	.	.	8	.	30	.	.	.	.	.	.
Searsia lucida forma. *lucida*	**ABC**	T	31	.	36	.	.	8	.	40	9	.	.	.	.	.
Strophanthus speciosus	**ABC**	C	6	24	.	.	3	21	15	.	9	.	.	.	.	.
Vepris lanceolata	**ABC**	T	14	6	.	.	.	.	34	30	.	.	.	.	.	.
Faurea galpinii	**ABC**	T	3	.	7	.	6	23	19	50	14	.	.	.	.	.
Senecio deltoideus	**ABC**	C	19	18	.	.	.	3	.	.	3	.	.	.	.	.
Ochna arborea var. *oconnorii*	**ABC**	T	3	.	.	.	74	32	.	30	20	.	.	.	.	.
Asplenium erectum var. *erectum*	**ABC**	H	.	6	.	.	19	36	.	.	11	.	.	.	.	.
Streptocarpus confusus subsp. *confusus*	**ABC**	E	3	.	.	.	.	3	22	.	9	.	.	.	.	.
Bowkeria cymosa	**ABC**	S	8	.	7	.	.	11	.	50	.	.	.	.	.	.
Pleopeltis macrocarpa	**ABC**	E	6	.	36	.	13	8	.	10	.	.	.	.	.	.
Pavetta cooperi	**ABC**	S	.	29	.	.	.	1	.	.	6	.	.	.	.	.
Lepisorus schraderi	**ABC**	E	3	.	.	.	6	.	.	.	3	.	.	.	.	.
Disperis lindleyana	**ABC**	H	.	6	.	.	.	4	.	.	6	.	.	.	.	.
Amauropelta bergiana	**ABC**	H	.	6	.	.	3	2	3	20	.	.	.	.	.	.
Micrococca capensis	**BD**	S	.	.	.	.	.	.	64	.	.	.	3	.	.	.
Cola greenwayi	**BD**	T	.	.	.	.	.	.	51	.	.	.	22	.	.	.
Garcinia gerrardii	**BD**	T	.	.	.	.	.	.	25	.	.	.	14	.	.	.
Aphloia theiformis	**BD**	T	.	.	.	.	.	.	24	.	.	.	17	.	.	.
Trichilia dregeana	**BD**	T	.	.	.	.	.	.	3	.	.	.	56	.	.	.
Asplenium anisophyllum	**BD**	H	.	.	.	.	10	1	7	.	.	.	3	.	.	.
Gymnanthemum mespilifolium	**BD**	C	.	.	.	.	.	1	7	.	.	.	3	.	.	.
Harveya silvatica	**BD**	H	.	.	.	.	.	3	.	.	.	7	.	.	.	.
Pteridium aquilinum	**BD**	H	.	.	.	.	.	1	.	.	.	7	.	.	.	.
Kiggelaria africana	**ABD**	T	14	53	50	20	10	35	17	.	.	14	8	.	.	.
Searsia pyroides var. *gracilis*	**ABD**	T	19	.	79	60	1	13	.	.	.	7	.	.	.	.
Pteris cretica	**ABD**	H	8	12	57	20	.	3	2	.	.	7	8	.	.	.
Dioscorea retusa	**ABD**	C	3	12	.	40	6	2	.	.	.	21	.	.	.	.
Clerodendrum glabrum	**ABD**	T	17	41	.	.	.	1	7	.	.	.	8	.	.	.
Blechnum attenuatum var. *giganteum*	**ABD**	H	.	6	21	40	18	6	3	.	.	.	6	.	.	.
Pavetta barbertonensis	**ABD**	S	3	.	.	.	.	.	76	.	.	.	39	.	.	.
Oricia bachmannii	**ABD**	T	8	.	.	.	.	.	47	.	.	.	14	.	.	.
Allophylus chaunostachys	**ABD**	T	3	.	.	.	.	.	24	.	.	.	6	.	.	.
Bersama lucens	**ABD**	T	8	.	.	.	.	1	22	.	.	.	19	.	.	.
Asparagus "robustus" sp. nov.)	**ABD**	C	3	.	29	.	1	.	.	.	.	7	.	.	.	.
Stenoglottis fimbriata	**ABD**	H	3	.	7	.	3	3	2	.	.	.	3	.	.	.
Begonia sutherlandii	**ABD**	H	6	.	7	.	7	.	7	.	.	.	11	.	.	.
Heteropyxis canescens	**ABD**	T	8	.	.	.	.	1	.	.	.	.	3	.	.	.
Gymnosporia grandifolia	**ABD**	T	8	.	.	.	.	.	14	.	.	.	3	.	.	.
Cyphostemma cirrhosum	**ABD**	C	.	.	.	40	.	1	.	.	.	.	3	.	.	.
Solanum terminale subsp. *terminale*	**ABD**	C	.	18	14	.	4	4	2	.	.	7	.	.	.	.
Chlorophytum comosum	**ABD**	H	.	18	.	.	1	2	2	.	.	14	3	.	.	.
Polystichum transvaalense	**ABD**	H	.	6	14	.	4	16	.	.	.	.	3	.	.	.

Scadoxus puniceus	**ABD**	H	.	12	7	20	.	1	.	.	.	14	3	.	.	.
Achyranthes aspera var. *aspera*	**ABDE**	H	47	.	86	70	.	.	3	.	.	21	3	.	.	63
Harpephyllum caffrum	**ABDE**	T	44	.	.	.	.	.	2	.	.	.	53	.	.	13
Keetia gueinzii	**ABDE**	S	11	.	.	.	.	2	63	.	.	21	61	.	50	.
Christella dentata	**ABDE**	H	3	.	.	.	.	.	3	.	.	36	11	60	75	13
Secamone parvifolia	**ABDE**	C	8	.	.	.	.	1	7	.	.	.	11	.	.	38
Cyrtorchis arcuata	**ABDE**	E	.	18	.	.	.	1	.	.	.	.	3	.	.	13
Ficus burkei	**ABDE**	T	3	.	.	10	1	.	.	.	.	7	.	40	.	.
Homalium dentatum	**BDE**	T	.	.	.	.	.	.	24	.	.	7	22	20	25	75
Acridocarpus natalitius var. *natalitius*	**BDE**	C	.	.	.	.	.	.	2	.	.	.	47	20	25	63
Stephania abyssinica	**BDE**	C	.	.	.	.	1	.	.	.	.	14	.	.	75	.
Ochna arborea var. *arborea*	**BDE**	T	.	.	.	.	1	.	.	.	.	.	11	40	.	.
Cassinopsis ilicifolia	**AB**	S	50	35	64	.	.	10	5	.	.	.	.	.	.	.
Calodendrum capense	**AB**	T	11	29	.	.	3	9	32	.	.	.	.	.	.	.
Buddleja auriculata	**AB**	S	11	12	57	70	.	8	.	.	.	.	.	.	.	.
Hypoestes aristata var. *alba*	**AB**	H	8	.	29	.	.	1	34	.	.	.	.	.	.	.
Lepisorus excavatus	**AB**	E	8	.	21	30	25	.	2	.	.	.	.	.	.	.
Pavetta kotzei	**AB**	T	6	6	57	.	10	58	.	.	.	.	.	.	.	.
Asplenium boltonii	**AB**	H	3	6	.	.	54	25	3	.	.	.	.	.	.	.
Asplenium theciferum	**AB**	E	14	6	.	.	6	1	3	.	.	.	.	.	.	.
Dais cotinifolia	**AB**	T	33	76	29	.	.	1	.	.	.	.	.	.	.	.
Adiantum poiretii	**AB**	H	17	12	71	.	.	1	.	.	.	.	.	.	.	.
Plectranthus grallatus	**AB**	H	8	53	14	.	.	3	.	.	.	.	.	.	.	.
Thalictrum rhynchocarpum	**AB**	H	3	47	14	.	.	3	.	.	.	.	.	.	.	.
Myrsiphyllum asparagoides	**AB**	C	6	.	14	.	1	.	.	.	.	.	.	.	.	.
Aloe arborescens	**AB**	T	3	.	7	50	7	.	.	.	.	.	.	.	.	.
Kalanchoe rotundifolia	**AB**	H	3	.	.	40	1	.	.	.	.	.	.	.	.	.
Scolopia oreophila	**AB**	T	.	41	.	.	.	7	.	.	.	.	.	.	.	.
Cheilanthes hirta var. *nemorosa*	**AB**	H	.	12	.	.	.	1	.	.	.	.	.	.	.	.
Greyia radlkoferi	**AB**	T	.	.	50	.	3	2	.	.	.	.	.	.	.	.
Pavonia columella	**AB**	S	3	12	.	.	.	2	.	.	.	.	.	.	.	.
Polystichum pungens	**AB**	H	3	12	7	.	.	4	.	.	.	.	.	.	.	.
Panicum monticola	**AB**	G	.	12	.	.	6	2	2	.	.	.	.	.	.	.
Asplenium monanthes	**AB**	H	.	.	21	.	13	5	.	.	.	.	.	.	.	.
Buddleja salviifolia	**AB**	S	.	.	7	10	1	3	.	.	.	.	.	.	.	.
Solanum anguivi	**AB**	S	8	.	.	.	.	3	.	.	.	.	.	.	.	.
Liparis bowkeri	**AB**	H	8	.	.	.	4	3	2	.	.	.	.	.	.	.
Faurea macnaughtonii	**AB**	T	3	.	.	.	7	3	12	.	.	.	.	.	.	.
Oleandra distenta	**AB**	E	.	.	.	10	6	.	.	.	.	.	.	.	.	.
Bulbophyllum sandersonii	**AB**	E	.	6	.	.	10	.	.	.	.	.	.	.	.	.
Coccinia palmata	**AB**	C	.	6	.	.	1	1	.	.	.	.	.	.	.	.
Tridactyle tricuspis	**AB**	E	.	6	.	.	1	.	.	.	.	.	.	.	.	.
Plectranthus laxiflorus	**AB**	H	.	6	.	.	1	3	2	.	.	.	.	.	.	.
Asplenium protensum	**AB**	H	.	6	.	.	.	2	.	.	.	.	.	.	.	.
Mikania capensis	**ABE**	C	.	.	.	20	.	3	.	.	.	.	.	.	25	.
Asparagus angusticladus	**ABE**	C	.	.	.	10	.	.	2	.	.	.	.	.	.	25
Laportea alatipes	**ABE**	H	.	.	14	.	.	1	.	.	.	.	.	.	50	.
Asparagus ramosissimus	**ABE**	C	.	.	14	.	6	3	.	.	.	.	.	20	.	.
Englerodaphne pilosa	**ABE**	S	3	.	.	.	.	2	.	.	.	.	.	.	.	.
Stegnogramma pozoi	**BE**	H	.	.	.	.	1	3	.	.	.	.	.	.	75	.
Microlepia speluncae	**BE**	H	.	.	.	.	.	1	.	.	.	.	.	.	75	.
Rubus apetalus	**BE**	S	.	.	.	.	.	2	.	.	.	.	.	20	.	.
Osmunda regalis	**C**	H	.	.	.	.	.	.	.	20	.	.	.	.	.	.
Commelina africana	**C**	H	.	.	.	.	.	.	.	20	.	.	.	.	.	.
Blechnum capense	**C**	H	.	.	.	.	.	.	.	10	.	.	.	.	.	.
Passerina montana	**C**	S	.	.	.	.	.	.	.	10	.	.	.	.	.	.
Gonioma kamassi	**C**	T	.	.	.	.	.	.	.	10	.	.	.	.	.	.
Gleichenia umbraculifera	**C**	H	.	.	.	.	.	.	.	10	.	.	.	.	.	.
Pluchea dioscoridis	**C**	S	.	.	.	.	.	.	.	10	.	.	.	.	.	.
Smithia erubescens	**C**	S	.	.	.	.	.	.	.	10	.	.	.	.	.	.
Strelitzia caudata	**C**	H	.	.	.	.	.	.	.	.	9	.	.	.	.	.
Costularia natalensis	**C**	G	.	.	.	.	.	.	.	.	6	.	.	.	.	.
Scleria transvaalensis	**C**	G	.	.	.	.	.	.	.	.	3	.	.	.	.	.
Stachys natalensis	**C**	H	.	.	.	.	.	.	.	.	3	.	.	.	.	.
Chionanthus foveolatus subsp. *foveolatus*	**ACDE**	T	69	29	.	.	.	.	.	.	3	.	.	.	.	100
Jasminum streptopus	**ACDE**	C	28	6	.	.	.	.	.	30	31	14	.	.	.	75
Acacia ataxacantha	**ACDE**	T	33	6	14	.	.	.	.	40	20	36	8	20	25	.
Cryptolepis capensis	**ACDE**	C	25	29	.	.	.	.	.	.	9	21	22	20	.	13
Hippobromus pauciflorus	**ACDE**	T	22	6	.	10	.	.	.	10	.	.	8	.	.	38
Ficus sur	**ACDE**	T	14	6	.	20	.	.	.	.	11	64	36	80	75	13
Erythroxylum emarginatum	**ACDE**	T	14	.	.	.	.	.	.	10	3	.	42	60	.	13
Toddalia asiatica	**ACDE**	S	8	.	.	.	.	.	.	20	3	.	8	20	50	.
Pachystigma bowkeri	**ACDE**	T	8	.	.	.	.	.	.	.	14	7	3	40	.	.
Tarchonanthus trilobus var. *galpinii*	**ACDE**	T	3	.	.	.	.	.	.	.	3	14	.	20	.	.
Heteropyxis natalensis	**ACDE**	T	3	.	.	.	.	.	.	.	3	7	.	20	.	.
Christella gueinziana	**ACD**	H	6	.	.	20	.	.	.	20	.	21	3	.	.	.
Abrus laevigatus	**ACD**	C	.	.	.	10	.	.	.	.	3	7	.	.	.	.
Olea capensis subsp. *enervis*	**AD**	T	.	.	7	.	.	.	.	.	.	.	3	.	.	.

Pleurostylia capensis	**AC**	T	22	6	.	.	.	.	.	30	.	.	.	.	.	.
Dicliptera clinopodia	**AC**	S	3	.	.	20	.	.	.	10	.	.	.	.	.	.
Ceropegia linearis subsp. *woodii*	**AC**	C	.	.	.	10	.	.	.	.	3	.	.	.	.	.
Rauvolfia caffra	**CDE**	T	.	.	.	.	.	.	.	.	14	.	14	20	100	13
Hyperacanthus amoenus	**CDE**	S	.	.	.	.	.	.	.	50	.	.	11	100	.	75
Adenia gummifera	**CDE**	C	.	.	.	.	.	.	.	.	3	7	8	.	25	13
Peperomia blanda	**CDE**	H	.	.	.	.	.	.	.	10	.	.	.	40	.	88
Monanthotaxis caffra	**CD**	S	.	.	.	.	.	.	.	.	80	71	100	.	.	.
Asplenium inaequilaterale	**CD**	H	.	.	.	.	.	.	.	.	6	.	3	.	.	.
Arthropteris monocarpa	**D**	E	.	.	.	.	.	.	.	.	.	21	6	.	.	.
Diospyros galpinii	**D**	S	.	.	.	.	.	.	.	.	.	7	.	.	.	.
Helichrysum splendidum	**D**	S	.	.	.	.	.	.	.	.	.	7	.	.	.	.
Hypolepis sparsisora	**D**	H	.	.	.	.	.	.	.	.	.	7	.	.	.	.
Isoglossa cooperi	**D**	H	.	.	.	.	.	.	.	.	.	7	.	.	.	.
Parinari curatellifolia	**D**	T	.	.	.	.	.	.	.	.	.	7	.	.	.	.
Phyllanthus nummulariifolius	**D**	S	.	.	.	.	.	.	.	.	.	7	.	.	.	.
Ranunculus meyeri	**D**	H	.	.	.	.	.	.	.	.	.	7	.	.	.	.
Pavetta galpinii	**D**	S	.	.	.	.	.	.	.	.	.	.	75	.	.	.
Tabernaemontana ventricosa	**D**	T	.	.	.	.	.	.	.	.	.	.	58	.	.	.
Cheilanthes pentagona	**D**	H	.	.	.	.	.	.	.	.	.	.	22	.	.	.
Pseuderanthemum subviscosum	**D**	S	.	.	.	.	.	.	.	.	.	.	22	.	.	.
Atalaya natalensis	**D**	T	.	.	.	.	.	.	.	.	.	.	14	.	.	.
Tiliacora funifera	**D**	C	.	.	.	.	.	.	.	.	.	.	14	.	.	.
Asparagus setaceus (Lebombo)	**D**	C	.	.	.	.	.	.	.	.	.	.	8	.	.	.
Margaritaria discoidea var. *fagifolia*	**D**	T	.	.	.	.	.	.	.	.	.	.	8	.	.	.
Maytenus sp nov. (= *Gymnosporia filiformis* ip.p.)	**D**	S	.	.	.	.	.	.	.	.	.	.	8	.	.	.
Sclerocroton integerrimus	**D**	T	.	.	.	.	.	.	.	.	.	.	8	.	.	.
Tragiella natalensis	**D**	S	.	.	.	.	.	.	.	.	.	.	8	.	.	.
Trilepisium madagascariense	**D**	T	.	.	.	.	.	.	.	.	.	.	8	.	.	.
Encephalartos paucidentatus	**D**	T	.	.	.	.	.	.	.	.	.	.	6	.	.	.
Nervilia crociformis	**D**	H	.	.	.	.	.	.	.	.	.	.	6	.	.	.
Oxyanthus pyriformis	**D**	T	.	.	.	.	.	.	.	.	.	.	6	.	.	.
Pentas micrantha	**D**	H	.	.	.	.	.	.	.	.	.	.	6	.	.	.
Rinorea angustifolia	**D**	S	.	.	.	.	.	.	.	.	.	.	6	.	.	.
Stylochiton natalensis	**D**	H	.	.	.	.	.	.	.	.	.	.	6	.	.	.
Tabernaemontana elegans	**D**	T	.	.	.	.	.	.	.	.	.	.	6	.	.	.
Albizia versicolor	**D**	T	.	.	.	.	.	.	.	.	.	.	3	.	.	.
Indigofera macrantha	**D**	S	.	.	.	.	.	.	.	.	.	.	3	.	.	.
Manilkara discolor	**D**	T	.	.	.	.	.	.	.	.	.	.	3	.	.	.
Oncinotis tenuiloba	**D**	C	.	.	.	.	.	.	.	.	.	.	3	.	.	.
Pneumatopteris unita	**D**	H	.	.	.	.	.	.	.	.	.	.	3	.	.	.
Synaptolepis kirkii	**D**	S	.	.	.	.	.	.	.	.	.	.	3	.	.	.
Thunbergia alata	**D**	H	.	.	.	.	.	.	.	.	.	.	3	.	.	.
Cryptocarya woodii	**AD**	T	22	65	.	.	.	.	.	.	.	21	42	.	.	.
Dombeya pulchra	**AD**	S	19	6	.	20	.	.	.	.	.	.	3	.	.	.
Laportea peduncularis	**AD**	H	3	24	.	.	.	.	.	.	.	.	6	.	.	.
Mystacidium venosum	**AD**	E	3	12	.	.	.	.	.	.	.	.	3	.	.	.
Aloe dyeri	**AD**	H	19	.	.	.	.	.	.	.	.	7	.	.	.	.
Polystachya ottoniana	**AD**	E	8	12	.	.	.	.	.	.	.	.	3	.	.	.
Cussonia sphaerocephala	**AD**	T	.	71	.	.	.	.	.	.	.	.	3	.	.	.
Syzygium species A*	**AD**	T	.	.	.	.	.	.	.	.	.	50	.	.	.	.
Anemia dregeana	**AD**	H	8	.	.	.	.	.	.	.	.	57	17	.	.	.
Conostomium natalense	**AD**	H	8	.	.	.	.	.	.	.	.	7	.	.	.	.
Crotalaria capensis	**AD**	S	6	.	.	.	.	.	.	.	.	7	3	.	.	.
Thunbergia natalensis	**AD**	H	3	.	.	.	.	.	.	.	.	7	.	.	.	.
Tephrosia subulata	**AD**	S	.	6	.	.	.	.	.	.	.	7	.	.	.	.
Helinus integrifolius	**AD**	S	.	6	.	10	.	.	.	.	.	.	6	.	.	.
Cyathea dregei	**AD**	T	.	.	.	10	.	.	.	.	.	.	3	.	.	.
Doryopteris concolor	**ADE**	H	50	.	.	20	.	.	.	.	.	.	3	.	.	13
Rhoicissus tridentata subsp. *cuneifolia*	**ADE**	S	3	.	29	30	.	.	.	.	.	7	.	20	.	75
Acalypha glabrata	**ADE**	S	3	.	.	20	.	.	.	.	.	7	3	80	25	50
Mimusops zeyheri	**ADE**	T	.	.	.	30	.	.	.	.	.	7	19	100	.	.
Gymnosporia rubra	**ADE**	S	17	.	.	.	.	.	.	.	.	.	44	80	.	.
Ochna natalitia	**ADE**	S	6	.	.	.	.	.	.	.	.	7	22	100	25	63
Obetia tenax	**ADE**	T	6	.	.	.	.	.	.	.	.	.	3	.	25	50
Sansevieria hyacinthoides	**ADE**	H	3	.	.	.	.	.	.	.	.	.	3	.	.	25
Rotheca myricoides	**ADE**	T	3	.	7	.	.	.	.	.	.	7	.	.	.	13
Dioscorea dregeana	**ADE**	C	6	.	.	.	.	.	.	.	.	.	6	.	.	.
Erythrina lysistemon	**ADE**	T	.	6	.	.	.	.	.	.	.	7	6	20	.	.
Bridelia micrantha	**DE**	T	.	.	.	.	.	.	.	.	.	86	31	60	100	13
Aneilema aequinoctiale	**DE**	H	.	.	.	.	.	.	.	.	.	29	.	.	75	38
Anthocleista grandiflora	**DE**	T	.	.	.	.	.	.	.	.	.	21	28	.	75	.
Pterolobium stellatum	**DE**	C	.	.	.	.	.	.	.	.	.	7	.	20	50	.
Shirakiopsis elliptica	**DE**	T	.	.	.	.	.	.	.	.	.	14	19	20	.	.
Antidesma venosum	**DE**	T	.	.	.	.	.	.	.	.	.	14	3	20	.	.
Gymnanthemum myrianthum	**DE**	S	.	.	.	.	.	.	.	.	.	29	.	.	75	.
Abrus precatorius	**DE**	C	.	.	.	.	.	.	.	.	.	.	6	80	.	50
Adenia digitata	**DE**	S	.	.	.	.	.	.	.	.	.	.	6	40	.	25
Breonadia salicina	**DE**	T	.	.	.	.	.	.	.	.	.	.	6	40	25	.
Kraussia floribunda	**DE**	S	.	.	.	.	.	.	.	.	.	.	19	.	.	13

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4.1.3. Physiognomic and taxonomic analysis of National Forest Types in Mpumalanga

An analysis of species richness, broad taxonomic groupings, forest dependency, leaf retention and diversity within families and genera for each of the 14 forest subtypes is presented in Table 3. The 17 most species rich plant families and genera are ranked in descending order of abundance. There was greater variation in the rankings of the genera than families, but the more consistently higher ranking genera included *Asplenium, Asparagus, Rhoicissus, Searsia, Maytenus* and *Ficus*. An analysis of the broad taxonomic groups highlighted the important contribution that ferns make towards species composition, with 53 species recorded within Mariepskop Mistbelt Forest, and 50 species within Long Tom Mistbelt Forest (25% and 21% of respective total species composition). All forest subtypes contained fern species. Across all forest types, the dicotyledonous plants are consistently the largest broad taxonomic grouping.

An analysis of forest dependent species for each forest type revealed that the highest proportion of obligate species is found in Barberton Mistbelt Forest (78%). This was closely followed by Long Tom Mistbelt, Mariepskop Mistbelt, and Foothills Mistbelt. The subtypes with the lowest proportion of obligate species were Legogote Scarp, Blyde Scarp, Northern Highveld Kloof, and Escarpment Riverine. A comparison of leaf retention revealed that Mariepskop Mistbelt has the highest proportion of evergreen tree cover at 90%, followed by Long Tom Mistbelt and Barberton Mistbelt. Legogote Scarp had the highest proportion of deciduous tree cover.

Fig. 4 summarises the broad forest growth form categories for each subtype as well as a summary across all subtypes (bottom right-hand graph). This enables each subtype to be compared with the mean of all forest subtypes. The general pattern expressed is relatively similar. The tree category dominates all forest subtypes with shrubs, climbers and herbs all similar in their occurrence values. The subtypes with a disproportionate number of growth form categories are: Mariepskop Mistbelt forest (epiphytes), Mpumalanga Escarpment Riverine forest (both graminoids and herbs), Blyde Canyon Dry Afromontane (trees), Blyde Scarp and Legogote Scarp forests (shrubs), Northern Highveld Kloof and Lydenburg Kloof forests (herbs).

In Figure S1 (in Supplementary Material), the mean value across all subtypes is presented in the right-hand most stacked bar. In descending order of abundance, the most dominant growth form subcategories are: small trees (31%), tall trees (16%), tall shrubs (11%), herbs (9%), woody climbers (8%), herbaceous climbers (6%), geophytic herbs (5%), graminoids (5%), epiphytes (3%), low shrubs (3%), soft shrubs (1.5%), succulent herbs (0.7%), succulent trees (0.5%), graminoid climbers (0.2%), aquatic herbs (0.2%) and tree-ferns (0.1%).

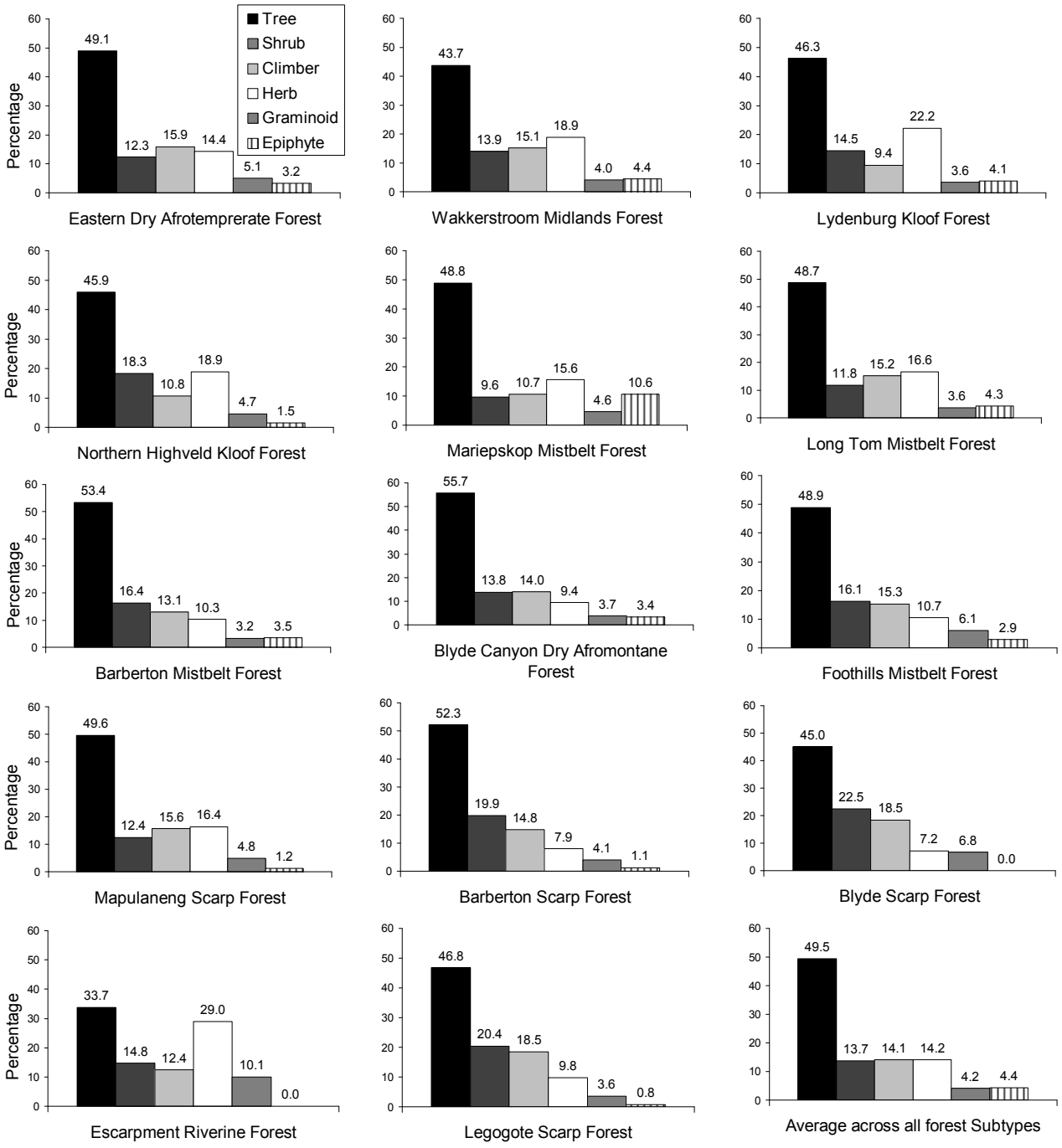


Fig. 4. Frequency distributions of growth form categories for each forest subtype, and averaged across all forest subtypes (bottom, right graph), represented as a percentage of all species occurrences.

4.2. Description of the subtypes

The forest subtypes are briefly described in terms of their distribution, taxonomy and physiognomy (Figs. 4 and Figure S1). Species highlighted in bold have exceeded one of several upper threshold limits. Diagnostic species/taxa are calculated based on a minimum fidelity threshold value of 25 and an upper threshold of 35 (bold highlighted text). Constant species/taxa are those species with a frequency occurrence of more than 65% (with upper threshold of 75%).

Dominant species/taxa are those species with a frequency occurrence of more than 10% and with a cover threshold of more than 15% (upper threshold of 25%). Dg stands for Diagnostic, Dm stands for Dominant, and C stands for Constant species.

A detailed taxonomic and physiognomic assessment for each forest subtype is provided in Table 3.

Table 3 Taxonomic and functional assessment of each forest subtype. An analysis of species richness, broad taxonomic groups, leaf retention of tree species, forest dependency, and 17 of the most species rich families and genera are provided for each forest subtype.

	Eastern Dry Afrotemperate	Wakkerstroom Midlands	Lydenburg Kloof	Northern Highveld Kloof	Mariepskop Mistbelt	Long Tom Mistbelt	Barberton Mistbelt	Blyde Canyon Dry Afromontane	Foothills Mistbelt	Mapulaneng Scarp	Barberton Scarp	Blyde Scarp	Escarpment Riverine	Legogote Scarp
Relevés (N)	36	17	14	10	68	118	59	10	35	14	36	5	4	8
No. of Species (S)	241	158	112	117	216	241	191	168	175	179	229	117	99	113
Average Species richness	44	41	34	34	43	49	45	70	39	49	42	44	42	45
Broad Taxonomic Groups (as % of species list)														
Pteridophyta	10%	15%	15%	13%	25%	21%	13%	13%	12%	9%	9%	3%	7%	4%
Gymnosperms	0%	1%	0%	0%	1%	1%	1%	1%	1%	0%	0%	0%	1%	0%
Monocotyledons	13%	15%	13%	14%	13%	11%	12%	9%	12%	12%	12%	12%	13%	11%
Dicotyledons	76%	69%	72%	74%	62%	68%	74%	77%	75%	78%	78%	85%	79%	85%
Forest Dependency (as % of species list)														
Facultative	40%	34%	51%	66%	28%	28%	22%	33%	31%	37%	34%	68%	64%	73%
Obligate	60%	66%	49%	34%	72%	72%	78%	67%	69%	63%	66%	32%	36%	27%
Seasonality of tree species (measured in terms of occurrence records)														
Deciduous	27%	22%	24%	30%	5%	12%	13%	15%	17%	29%	23%	36%	25%	44%
Evergreen	61%	67%	71%	65%	90%	80%	79%	76%	75%	57%	65%	47%	65%	49%
Semi-deciduous	12%	11%	6%	5%	5%	9%	8%	9%	7%	14%	12%	17%	11%	7%
Family														
Rubiaceae	19	13	4	6	14	16	14	14	17	13	19	9	7	4
Celastraceae	11	7	7	3	9	10	9	9	5	3	8	4	2	5
Aspleniaceae	7	9	5	2	15	17	9	4	9	4	5	0	0	1
Fabaceae	8	7	4	3	3	6	3	7	5	10	9	9	7	6
Apocynaceae	9	4	2	3	5	5	6	4	8	3	10	7	3	5
Flacourtiaceae	7	6	4	4	6	6	9	6	3	6	7	4	2	2
Asteraceae	5	2	2	2	3	8	4	4	5	8	3	6	4	0
Euphorbiaceae	2		1	4		3	5	2	3	7	11	7	4	6
Rutaceae	7	4	2	3	3	4	5	5	3	2	6	3	3	1
Pteridaceae	5	6	4	5	3	5	4	2	2	3	5	2	1	3

Anacardiaceae	6	2	3	6	4	4	3	4	3	3	3	3	2	3
Asparagaceae	5	2	5	3	4	4	4	3	3	4	4	3	0	3
Cyperaceae	5	2	3	2	2	5	4	3	6	2	5	3	4	1
Lamiaceae	5	4	4	4	4	5	4	2	3	4	2	2	2	2
Oleaceae	5	3	1	1	5	4	3	5	6	4	5	0	1	4
Poaceae	3	3	2	3	4	5	4	3	4	3	4	5	3	1
Orchidaceae	5	10	1	1	9	5	2	0	1	0	5	0	1	3
Acanthaceae	6	1	2	1	3	2	4	3	3	4	5	0	2	3
Ebenaceae	4	3	3	2	2	2	2	3	2	4	3	3	2	3
Vitaceae	4	2	2	3	2	3	2	3	3	4	3	3	1	3
Dryopteridaceae	3	4	4	1	5	8	3	2	1	1	2	0	0	0
Buddlejaceae	4	2	4	5	3	5	2	1	2	2	2	1	0	0
Myrtaceae	2	0	0	0	4	2	2	3	4	6	4	3	1	2
Sapotaceae	2	1	0	2	3	1	3	2	3	4	5	3	1	2
Moraceae	3	2	0	3	2	1	1	1	2	3	3	3	4	3
Piperaceae	3	2	2	1	3	3	3	3	3	2	2	1	0	1
Genera														
Asplenium	7	9	5	2	15	17	9	4	9	4	5	0	0	1
Asparagus	4	2	4	3	3	4	4	3	3	4	4	3	0	3
Rhoicissus	4	2	2	3	2	3	2	3	3	4	3	3	1	3
Searsia	4	1	3	6	3	4	1	3	2	2	1	2	1	1
Maytenus	3	2	3	2	4	3	3	3	2	1	3	2	1	1
Ficus	3	2	0	3	2	1	1	1	2	3	2	3	4	3
Ochna	3	1	0	1	3	2	2	2	3	2	4	3	1	1
Plectranthus	3	3	3	2	3	4	2	2	2	2	1	0	1	0
Canthium	3	3	1	0	3	3	2	3	3	1	1	1	0	0
Cyperus	2	1	2	1	2	2	2	2	2	2	2	2	1	1
Combretum	2	1	0	2	2	2	2	2	2	2	2	2	0	2
Peperomia	2	2	2	1	2	2	2	3	2	1	1	1	0	1
Pteris	2	3	2	3	1	2	2	1	1	2	2	0	1	0
Pavetta	3	2	1	1	2	3	2	1	2	1	3	0	0	0
Gymnosporia	3	2	2	0	1	1	2	1	1	1	3	1	0	2
Scolopia	2	3	2	1	2	2	2	2	0	1	2	0	0	1
Secamone	3	1	1	1	1	2	2	1	1	1	2	2	0	2

4.2.1. Northern Highveld forest subtypes

Four proposed forest subtypes (1−4) are recognised within the Northern Highveld Forest Type. These subtypes are represented by 77 relevés and 327 species.

1. Eastern Dry Afrotemperate Forest Subtype

Occurring in the eastern half of Mpumalanga in the rain shadow of the Mpumalanga escarpment, these forests are naturally drier than the Mistbelt forests and fall outside the mistbelt area. Elevation of relevé data ranges between 1160 and 1700 m above sea level. This unit has a high total flora list of 241 species, with intermediate relevé richness (45 species per relevé). Climbers make up 16% of growth forms. The proportion of obligate forest species is somewhat low (60%) while leaf retention values are 71% for evergreenness and 22% for deciduous plants. Dominant families include Rubiaceae, Celastraceae, Apocynaceae, Fabaceae, Aspleniaceae, Flacourtiaceae and Rutaceae. Dominant genera include *Asplenium, Asparagus, Rhoicissus, Searsia* and *Canthium.*

Diagnostic taxa: *Cassinopsis ilicifolia,* ***Chionanthus foveolatus* subsp. *foveolatus (C, Dm),*** *Grewia occidentalis, Gymnosporia harveyana (C, Dm),* ***Harpephyllum caffrum****, Ekebergia capensis, Pleurostylia capensis, Trimeria grandifolia (C);* ***Aloe dyeri, Asparagus virgatus (C), Doryopteris concolor,*** *Mystacidium capense,* ***Schoenoxiphium lehmannii,*** *Senecio deltoideus.*

Constant taxa: *Carissa bispinosa* subsp. *zambesiensis, Celtis africana (Dm), Chionanthus foveolatus* subsp. *foveolatus (Dg, Dm), Clausena anisata,* ***Combretum kraussii (Dm), Diospyros whyteana (Dm), Gymnosporia harveyana (Dg, Dm),*** *Scolopia mundii, Secamone alpini, Trimeria grandifolia (Dg), Zanthoxylum davyi;* ***Asparagus virgatus (Dg),*** *Oplismenus hirtellus (Dm).*

Dominant taxa: *Apodytes dimidiata, Celtis africana (C), Chionanthus foveolatus* subsp. *foveolatus (Dg, C), Combretum kraussii (C), Cryptocarya woodii, Diospyros whyteana (C),* ***Gymnosporia harveyana (Dg, C),*** *Olinia emarginata, Searsia lucida, Xymalos monospora;* ***Oplismenus hirtellus (C)****.*

2. Wakkerstroom Midlands Forest Subtype

Occurring in the higher altitudes of southern Mpumalanga escarpment, it has a flora list of 158 species with an average of 42 species per relevé. Elevation of relevé data ranges between 1400 and 1710 m above sea level. The tree growth form is the most abundant (44%), followed by herbs (19%) and climbers (15%). Although 66% of all species are obligate forest species, this forest subtype has the lowest proportion of evergreen canopy (59%) out of all the Mistbelt and Afrotemperate forest types. The dominant families are Rubiaceae, Orchidaceae, Aspleniaceae, Celastraceae and Fabaceae. Dominant genera include *Asplenium, Canthium, Plectranthus, Scolopia, Polystichum* and *Pteris.*

Diagnostic taxa: ***Allophylus africanus (C, Dm), Buddleja dysophylla,*** *Choristylis rhamnoides, Clausena anisata (C, Dm),* ***Clerodendrum glabrum, Cryptocarya woodii (Dm), Cussonia sphaerocephala (C, Dm), Dais cotinifolia (C), Dovyalis rhamnoides,*** *Gymnosporia harveyana (C, Dm), Kiggelaria africana,* ***Pavetta cooperi, Podocarpus latifolius (C, Dm),*** *Searsia chirindensis (C, Dm), Rubus rigidus, Scolopia mundii (C, Dm),* ***Scolopia oreophila,*** *Scutia myrtina,* ***Solanum lichtensteinii,*** *Zanthoxylum davyi (C); Asplenium varians, Cheilanthes hirta* var. *nemorosa,* ***Crocosmia aurea* var. *aurea (C),*** *Cyrtorchis arcuata,* ***Diaphananthe caffra, Laportea peduncularis,*** *Mystacidium flanaganii, Mystacidium venosum,* ***Plectranthus grallatus,*** *Sanicula elata,* ***Streptocarpus pentherianus, Thalictrum rhynchocarpum****.*

Constant taxa: ***Allophylus africanus (Dg, Dm), Carissa bispinosa* subsp. *zambesiensis, Clausena anisata (Dg, Dm),*** *Cussonia sphaerocephala (Dg, Dm),* ***Dais cotinifolia (Dg),***

Diospyros whyteana, Gymnosporia harveyana (Dg, Dm), Podocarpus latifolius (Dg, Dm), Searsia chirindensis (Dg, Dm), *Scolopia mundii (Dg, Dm), Secamone alpini,* ***Zanthoxylum davyi (Dg); Asparagus setaceus,*** *Crocosmia aurea* var. *aurea (Dg), Cyperus albostriatus.*
Dominant species: *Allophylus africanus (Dg, C),* ***Celtis africana,*** *Clausena anisata (Dg, C), Cryptocarya woodii (Dg), Cussonia sphaerocephala (Dg, C), Gymnosporia harveyana (Dg, C), Podocarpus latifolius (Dg, C),* ***Searsia chirindensis (Dg, C),*** *Scolopia mundii (Dg, C),* ***Xymalos monospora****.*

3. Lydenburg Kloof Forest Subtype

Situated in the cold and dry Lydenburg catchment area, this forest has one of the lowest flora lists (112 species) and lowest number of species recorded per relevé (34 on average). Elevation of relevé data ranged between 1550 and 1980 m above sea level. The tree growth form has the highest proportion of species at 46% and herbs 22% (higher than the average value of 14% across all subtypes). Lydenburg Kloof forest has a higher proportion of obligate forest species (49%) than closely related Northern Kloof forests (34%). The canopy is built by evergreen species (85%). Dominant families include Celastraceae, Asparagaceae, Lamiaceae and Buddlejaceae. Dominant genera include *Asplenium, Asparagus, Searsia, Maytenus* and *Plectranthus*.

Diagnostic taxa: *Acacia caffra,* ***Buddleja auriculata, Cassinopsis ilicifolia, Clematis brachiata (C),*** *Euclea crispa* subsp. *crispa (Dm),* ***Greyia radlkoferi,*** *Gymnosporia buxifolia,* ***Heteromorpha arborescens* var. *abyssinica,*** *Kiggelaria africana,* ***Leucosidea sericea, Maytenus deflexa (C, Dm), Olinia emarginata (C, Dm), Pavetta kotzei,*** *Pittosporum viridiflorum (C, Dm),* ***Rhamnus prinoides (C),*** *Searsia lucida,* ***Searsia pyroides* var. *gracilis (C),*** *Scolopia mundii (C, Dm);* ***Achyranthes aspera* var. *aspera (C), Adiantum poiretii (C),*** *Asparagus aethiopicus, Asparagus sp. nov. (A. robustus), Asparagus virgatus (C), Asplenium adiantum-nigrum* var. *adiantum-nigrum, Asplenium aethiopicum,* ***Blechnum australe,*** *Dryopteris inaequalis (C),* ***Ehrharta erecta* var. *natalensis,*** *Hypoestes aristata* var. *alba,* ***Pleopeltis macrocarpa, Pteris cretica, Sparrmannia ricinocarpa,*** *Streptocarpus polyanthus* subsp. *comptonii.*

Constant taxa: ***Clematis brachiata (Dg), Diospyros whyteana (Dm), Maytenus deflexa (Dg, Dm),*** *Olinia emarginata (Dg, Dm), Pittosporum viridiflorum (Dg, Dm), Rhamnus prinoides (Dg),* ***Searsia pyroides* var. *gracilis (Dg),*** *Scolopia mundii (Dg, Dm);* ***Achyranthes aspera* var. *aspera (Dg),*** *Adiantum poiretii (Dg), Asparagus virgatus (Dg),* ***Dryopteris inaequalis (Dg)****.*

Dominant taxa: ***Diospyros whyteana (C),*** *Euclea crispa* subsp. *crispa (Dg), Gymnosporia harveyana, Maytenus deflexa (Dg, C),* ***Maytenus peduncularis, Olinia emarginata (Dg, C),***

Pittosporum viridiflorum (Dg, C), Pterocelastrus rostratus, Rapanea melanophloeos, Scolopia mundii (Dg, C).

4. Northern Highveld Kloof Forest Subtype

This subtype occurs to the west of the Mpumalanga Escarpment and stretches across the cold highveld to the Magaliesberg. Elevation of relevé data ranged between 1320 and 1730 m above sea level. It has a low total flora list of 117 species with only 34 species per relevé on average. Only 34% of recorded flora are obligate forest species. Furthermore, only 69% of the canopy is evergreen. When compared to other forest types, however, the proportion of species in the herb layer is high (19%). Dominant families include Anacardiaceae, Rubiaceae, Buddlejaceae, Pteridaceae and Lamiaceae. Dominant genera include *Searsia, Pteris, Solanum, Buddleja* and *Ficus*.

Diagnostic taxa: ***Aloe arborescens, Buddleja auriculata (C), Afrocanthium mundianum,*** *Celtis africana (C, Dm),* ***Cussonia paniculata, Diospyros lycioides*** **subsp.** ***guerkei,*** *Dombeya rotundifolia,* ***Dovyalis zeyheri,*** *Halleria lucida (C),* ***Ilex mitis (C, Dm),*** *Maerua cafra,* ***Maytenus albata, Myrsine africana (C), Nuxia congesta (C), Olinia emarginata (C, Dm), Pachystigma macrocalyx (C), Pavetta gardeniifolia (C), Searsia leptodictya, Searsia pallens, Searsia pyroides*** **var.** ***gracilis, Searsia pyroides*** **var.** ***pyroides, Rothmannia capensis (C, Dm), Solanum giganteum, Solanum retroflexum,*** *Tetradenia riparia; Achyranthes aspera* var. *aspera (C),* ***Aeollanthus buchnerianus,*** *Asplenium adiantum-nigrum* var. *adiantum-nigrum,* ***Blechnum attenuatum*** **var.** ***giganteum, Cyathula uncinulata, Cyphostemma cirrhosum,*** *Dicliptera clinopodia,* ***Dioscorea retusa, Kalanchoe rotundifolia,*** *Mikania capensis,* ***Pteris dentata, Solanum pseudocapsicum****.*

Constant taxa: *Buddleja auriculata (Dg),* ***Celtis africana (Dg, Dm),*** *Clausena anisata (Dm),* ***Diospyros whyteana (Dm),*** *Halleria lucida (Dg), Ilex mitis (Dg, Dm), Myrsine africana (Dg), Nuxia congesta (Dg),* ***Olinia emarginata (Dg, Dm),*** *Pachystigma macrocalyx (Dg), Pavetta gardeniifolia (Dg),* ***Rothmannia capensis (Dg, Dm);*** *Achyranthes aspera* var. *aspera (Dg), Cyperus albostriatus (Dm).*

Dominant taxa: *Acalypha glabrata,* ***Celtis africana (Dg, C), Clausena anisata (C), Diospyros whyteana (C),*** *Ilex mitis (Dg, C), Maytenus deflexa, Mimusops zeyheri,* ***Olinia emarginata (Dg, C), Psydrax obovata*** **subsp.** ***elliptica,*** *Searsia chirindensis, Rothmannia capensis (Dg, C), Scolopia zeyheri;* ***Cyperus albostriatus (C),*** *Dietes iridioides*.

4.2.2. Mpumalanga Mistbelt forest subtypes

Five proposed forest subtypes (5-9) are recognised within the Mpumalanga Mistbelt Forest Type. These subtypes are represented by 290 relevés and 366 species.

5. Mariepskop Mistbelt Forest Subtype

This forest subtype occurs along the summit of the Graskop escarpment, coming up from the lowveld where it largely follows the Black Reef quartzite geological formation. Elevation of relevé data ranged between 1330 and 1830 m above sea level. This subtype has a total flora list of 216 species with 43 species per plot on average. Ferns account for 25% of all species surveyed. An analysis of growth forms reveals that this forest subtype also contains the highest proportion of epiphytes (11%). The number of obligate forest species is very high at 72% (value shared with Long Tom Mistbelt Forest). The tree layer is strongly evergreen (93%), which is higher than any other forest subtype. Dominant families include Aspleniaceae, Rubiaceae, Celastraceae, Orchidaceae and Flacourtiaceae. Dominant genera include *Asplenium, Asparagus, Maytenus, Hymenophyllum* and *Searsia*.

Diagnostic taxa: ***Cassipourea malosana (C, Dm),*** *Combretum edwardsii, Alsophila capensis, Jasminum abyssinicum, Maytenus sp. A,* ***Ochna arborea* var. *oconnorii (C), Ocotea bullata, Olea capensis* subsp. *macrocarpa (C, Dm), Olinia radiata, Oxyanthus speciosus* subsp. *gerrardii (C), Pavetta inandensis (C),*** *Podocarpus latifolius (C, Dm), Psychotria capensis (C),* ***Psychotria zombamontana (C, Dm), Sclerochiton harveyanus (C, Dm), Syzygium gerrardii (C, Dm),*** *Vaccinium exul,* ***Vernonia wollastonii; Asplenium boltonii,*** *Asplenium friesiorum, Asplenium rutifolium (C), Blotiella natalensis,* ***Clivia caulescens (Dm),*** *Disperis fanniniae, Drimia robusta,* ***Elaphoglossum acrostichoides, Elaphoglossum aubertii, Elaphoglossum macropodium,*** *Hymenophyllum tunbrigense, Huperzia dacrydioides, Peperomia tetraphylla, Plectranthus rubropunctatus,* ***Rumohra adiantiformis, Solenostemon latifolius, Streptocarpus micranthus,*** *Vittaria isoetifolia*.

Constant taxa: ***Cassipourea malosana (Dg, Dm),*** *Ochna arborea* var. *oconnorii (Dg),* ***Olea capensis* subsp. *macrocarpa (Dg, Dm), Oxyanthus speciosus* subsp. *gerrardii (Dg),*** *Pavetta inandensis (Dg),* ***Peddiea africana,*** *Podocarpus latifolius (Dg, Dm),* ***Psychotria capensis (Dg), Psychotria zombamontana (Dg, Dm),*** *Rothmannia capensis, Sclerochiton harveyanus (Dg, Dm),* ***Syzygium gerrardii (Dg, Dm),*** *Xymalos monospora (Dm); Asplenium rutifolium (Dg), Behnia reticulata,* ***Oplismenus hirtellus***.

Dominant taxa: *Cassipourea malosana (Dg, C), Olea capensis* subsp. *macrocarpa (Dg, C), Podocarpus latifolius (Dg, C), Psychotria zombamontana (Dg, C), Pterocelastrus rostratus, Sclerochiton harveyanus (Dg, C),* ***Syzygium gerrardii (Dg, C), Xymalos monospora (C)****; Clivia caulescens (Dg).*

6. Long Tom Mistbelt Forest Subtype

This unit occurs along the Long Tom Pass escarpment, from Pilgrim's Rest to the Kaapsehoop area. Elevation of relevé data ranged between 1300 and 1870 m above sea level. This forest subtype has 241 identified species, with 49 species per relevé on average. The analysis of broad taxonomic groups revealed that 21% of recorded plants were ferns. Unlike the Mariepskop Mistbelt Forest Subtype, only 4% of the flora are epiphytes, while 72% comprises obligate forest species. This forest subtype has the second highest value for evergreenness (87%). Dominant families include Aspleniaceae, Rubiaceae, Celastraceae, Asteraceae and Flacourtiaceae. Dominant genera include *Asplenium, Polystichum, Asparagus, Plectranthus* and *Searsia.*

Diagnostic taxa: *Canthium kuntzeanum, Cassine peragua, Chionanthus foveolatus* subsp. *major (Dm), Cryptocarya transvaalensis (C, Dm),* ***Dovyalis lucida (C),*** *Hippocratea longipetiolata,* ***Jasminum abyssinicum (C),*** *Lauridia tetragona, Maytenus acuminata* var. *acuminata,* ***Pavetta kotzei,*** *Psychotria zombamontana (C, Dm), Rapanea melanophloeos (C, Dm),* ***Tylophora flanaganii,*** *Xymalos monospora (C, Dm);* ***Asplenium erectum* var. *erectum, Asplenium lobatum,*** *Behnia reticulata (C), Dryopteris inaequalis*.

Constant taxa: ***Carissa bispinosa* subsp. *zambesiensis,*** *Cryptocarya transvaalensis (Dg, Dm),* ***Diospyros whyteana (Dm), Dovyalis lucida (Dg),*** *Gymnosporia harveyana (Dm),* ***Jasminum abyssinicum (Dg), Peddiea africana (Dm),*** *Psychotria capensis (Dm),* ***Psychotria zombamontana (Dg, Dm),*** *Rapanea melanophloeos (Dg, Dm), Rhoicissus rhomboidea, Secamone alpini, Syzygium gerrardii (Dm),* ***Xymalos monospora (Dg, Dm), Zanthoxylum davyi;*** *Asparagus setaceus, Asplenium rutifolium, Asplenium splendens,* ***Behnia reticulata (Dg),*** *Cheilanthes viridis* var. *viridis*.

Dominant taxa: *Brachylaena transvaalensis,* ***Chionanthus foveolatus* subsp. *major (Dg),*** *Cryptocarya transvaalensis (Dg, C), Curtisia dentata, Diospyros whyteana (C), Gymnosporia harveyana (C), Olea capensis* subsp. *macrocarpa, Peddiea africana (C), Psychotria capensis (C), Psychotria zombamontana (Dg, C), Rapanea melanophloeos (Dg, C), Sclerochiton harveyanus, Syzygium gerrardii (C),* ***Xymalos monospora (Dg, C)****.*

7. Barberton Mistbelt Forest Subtype

This subtype occurs along the high-lying forested areas of the Barberton Mountains. Elevation of relevé data ranged between 1220 and 1590 m above sea level. The total flora list has 191 species with 45 species per relevé on average. This forest subtype also contained the greatest proportion of obligate forest species (78%) with high leaf retention of 84% for evergreenness. Dominant families include Rubiaceae, Celastraceae, Flacourtiaceae,

Aspleniaceae, and Apocynaceae. Dominant genera include *Asplenium, Streptocarpus, Asparagus, Maytenus* and *Dovyalis.*

Diagnostic taxa: ***Allophylus chaunostachys,*** *Aphloia theiformis, Bersama lucens, Calodendrum capense, Cassipourea malosana (C, Dm),* ***Chionanthus foveolatus*** **subsp. *major (C), Chionanthus peglerae, Cola greenwayi (Dm),*** *Cussonia spicata (C), Dovyalis lucida (C),* ***Garcinia gerrardii, Keetia gueinzii,*** *Memecylon natalense,* ***Micrococca capensis (Dm), Ochna gamostigmata,*** *Ochna holstii (C), Ocotea kenyensis, Olea capensis* subsp. *macrocarpa (C, Dm), Olinia radiata,* ***Oricia bachmannii, Pavetta barbertonensis (C),*** *Pavetta inandensis, Tricalysia capensis* var. *transvaalensis (C, Dm), Vepris lanceolata;* ***Aristea ecklonii,*** *Clivia miniata,* ***Hypoestes aristata*** **var. *alba,*** *Polystichum transkeiense,* ***Prosphytochloa prehensilis,*** *Riocreuxia picta, Streptocarpus confusus* subsp. *confusus.*

Constant taxa: ***Carissa bispinosa*** **subsp. *zambesiensis, Cassipourea malosana (Dg, Dm),*** *Chionanthus foveolatus* subsp. *major (Dg),* ***Cussonia spicata (Dg),*** *Dovyalis lucida (Dg),* ***Ochna holstii (Dg), Olea capensis*** **subsp. *macrocarpa (Dg, Dm), Pavetta barbertonensis (Dg),*** *Peddiea africana,* ***Rhoicissus rhomboidea,*** *Rothmannia capensis, Syzygium gerrardii (Dm), Tricalysia capensis* var. *transvaalensis (Dg, Dm), Xymalos monospora (Dm),* ***Zanthoxylum davyi (Dm); Asparagus setaceus,*** *Asplenium splendens, Behnia reticulata, Cyperus albostriatus.*

Dominant taxa: *Cassipourea malosana (Dg, C), Cola greenwayi (Dg), Justicia campylostemon, Micrococca capensis (Dg), Olea capensis* subsp. *macrocarpa (Dg, C),* ***Syzygium gerrardii (C),*** *Tricalysia capensis* var. *transvaalensis (Dg, C), Xymalos monospora (C), Zanthoxylum davyi (C).*

8. Blyde Canyon Dry Afromontane Forest Subtype

This is a drier subtype that occurs at lower altitudes than the closely related Mariepskop Mistbelt Forest with several species indicating it is perhaps transitional to scarp or Afrotemperate forest. Elevation of relevé data ranges between 1180 and 1370 m above sea level. This subtype has a total floral list of 168 species with 70 species per 0.04 ha on average, higher than any of the other subtypes. Obligate forest species account for 67% of the flora. Canopy is 75% evergreen and 16% deciduous. Dominant families include Rubiaceae, Celastraceae, Fabaceae, Flacourtiaceae and Rutaceae. Dominant genera include *Asplenium, Peperomia, Rhoicissus, Canthium* and *Maytenus.*

Diagnostic taxa: *Adenopodia spicata,* ***Bersama tysoniana (C), Bowkeria cymosa, Canthium ciliatum (C), Canthium kuntzeanum (C),*** *Carissa bispinosa* subsp. *zambesiensis (C), Combretum kraussii (C),* ***Dovyalis rhamnoides (C), Elaeodendron croceum,*** *Euclea*

natalensis, ***Eugenia natalitia (C), Eugenia woodii, Faurea galpinii,*** *Gymnosporia harveyana (C, Dm),* ***Maytenus acuminata* var. *acuminata (C, Dm), Maytenus peduncularis (C, Dm), Mimusops obovata (C), Olea capensis* subsp. *macrocarpa (C), Osyridicarpos schimperianus, Pavetta inandensis (C),*** *Pittosporum viridiflorum,* ***Pleurostylia capensis, Podocarpus falcatus (C, Dm),*** *Protorhus longifolia (C, Dm),* ***Psychotria zombamontana (C), Psydrax obovata* subsp. *elliptica (C),*** *Rhoicissus rhomboidea (C, Dm),* ***Rhoicissus* sp. 1 *(C),*** *Searsia lucida, Rothmannia globosa,* ***Schefflera umbellifera (C), Sclerochiton harveyanus (C), Scolopia mundii (C, Dm), Scolopia zeyheri, Scutia myrtina (C), Strychnos henningsii (C), Trichocladus grandiflorus, Vangueria infausta; Commelina africana* var. *africana, Crepidomanes melanotrichum,*** *Cyperus albostriatus (C), Dietes iridioides (C, Dm),* ***Osmunda regalis, Talbotia elegans***.

Constant taxa: ***Bersama tysoniana (Dg), Canthium ciliatum (Dg), Canthium kuntzeanum (Dg), Carissa bispinosa* subsp. *zambesiensis (Dg),*** *Celtis africana (Dm),* ***Combretum kraussii (Dg),*** *Cryptocarya transvaalensis,* ***Diospyros whyteana (Dm), Dovyalis lucida,*** *Dovyalis rhamnoides (Dg),* ***Eugenia natalitia (Dg), Gymnosporia harveyana (Dg, Dm), Maytenus acuminata* var. *acuminata (Dg, Dm), Maytenus peduncularis (Dg, Dm), Mimusops obovata (Dg), Ochna holstii, Olea capensis* subsp. *macrocarpa (Dg),*** *Pavetta inandensis (Dg),* ***Peddiea africana, Podocarpus falcatus (Dg, Dm),*** *Podocarpus latifolius, Protorhus longifolia (Dg, Dm),* ***Psychotria zombamontana (Dg), Psydrax obovata* subsp. *elliptica (Dg), Pterocelastrus rostratus, Rhoicissus rhomboidea (Dg, Dm), Rhoicissus* sp. 1 *(Dg), Schefflera umbellifera (Dg), Sclerochiton harveyanus (Dg), Scolopia mundii (Dg, Dm), Scutia myrtina (Dg), Secamone alpini, Strychnos henningsii (Dg), Zanthoxylum davyi; Asparagus setaceus, Asplenium splendens, Behnia reticulata (Dm), Cheilanthes viridis* var. *viridis,*** *Cissampelos torulosa,* ***Cyperus albostriatus (Dg), Dietes iridioides (Dg, Dm), Oplismenus hirtellus***.

Dominant taxa: *Brachylaena transvaalensis, Celtis africana (C), Diospyros whyteana (C),* ***Gymnosporia harveyana (Dg, C),*** *Ilex mitis, Maytenus acuminata* var. *acuminata (Dg, C), Maytenus peduncularis (Dg, C), Podocarpus falcatus (Dg, C), Protorhus longifolia (Dg, C), Psychotria capensis, Rhoicissus rhomboidea (Dg, C),* ***Scolopia mundii (Dg, C);*** *Behnia reticulata (C), Dietes iridioides (Dg, C).*

9. Foothills Mistbelt Forest Subtype

This subtype occurs along the slopes and foothills of the Sabie/Graskop escarpment. It is considered to contain some subtropical forest elements although still Afrotemperate in nature. Subtropical elements occurring in this unit include *Monanthotaxis caffra, Cnestis polyphylla* and *Dracaena aletriformis*, primarily in the shrub stratum. The canopy is very Afrotemperate in character. Elevation of relevé data ranged between 1060 and 1330 m above sea level. The total flora list has only 175 species with a relatively low 39 species per relevé on average. The fern

flora constitutes only 12% of the species composition. Obligate forest species make up 72% of all occurrence records. The tree canopy is predominately evergreen (82%). Epiphytes comprise only 3% of the growth forms, indicating a drier climate outside the mistbelt. Dominant families are Rubiaceae, Aspleniaceae, Apocynaceae, Cyperaceae and Oleaceae. Dominant genera include *Asplenium, Ochna, Asparagus, Rhoicissus,* and *Canthium*.

Diagnostic taxa: *Cephalanthus natalensis, Cnestis polyphylla, Combretum kraussii (C, Dm), Englerophytum magalismontanum (C, Dm), Eugenia natalitia (C),* ***Monanthotaxis caffra (C),*** *Nuxia congesta,* ***Oxyanthus speciosus* subsp. *gerrardii (C),*** *Peddiea africana (C), Psychotria capensis (C, Dm), Psychotria zombamontana (C), Rhoicissus rhomboidea (C, Dm), Strelitzia caudata,* ***Syzygium gerrardii (C, Dm), Tricalysia capensis* var. *transvaalensis (C, Dm)****.*

Constant taxa: ***Carissa bispinosa* subsp. *zambesiensis, Combretum kraussii (Dg, Dm), Englerophytum magalismontanum (Dg, Dm),*** *Eugenia natalitia (Dg),* ***Monanthotaxis caffra (Dg), Oxyanthus speciosus* subsp. *gerrardii (Dg), Peddiea africana (Dg), Psychotria capensis (Dg, Dm), Psychotria zombamontana (Dg), Rhoicissus rhomboidea (Dg, Dm), Syzygium gerrardii (Dg, Dm), Tricalysia capensis* var. *transvaalensis (Dg, Dm); Asplenium splendens,*** *Behnia reticulata,* ***Cheilanthes viridis* var. *viridis, Oplismenus hirtellus****.*

Dominant taxa: *Apodytes dimidiata, Combretum kraussii (Dg, C),* ***Englerophytum magalismontanum (Dg, C),*** *Englerophytum natalense, Protorhus longifolia, Psychotria capensis (Dg, C), Pterocelastrus rostratus, Rhoicissus rhomboidea (Dg, C),* ***Syzygium gerrardii (Dg, C), Tricalysia capensis* var. *transvaalensis (Dg, C),*** *Xymalos monospora.*

4.2.3. Eastern Scarp forest subtypes

Five proposed forest subtypes (10-14) are recognised within the Eastern Scarp Forest Type. These subtypes are represented by 67 relevés and 412 species.

10. Mapulaneng Scarp Forest Subtype

Although an untested hypothesis, the Mapulaneng Scarp Forest is considered to be a moist subtropical forest subtype and may represent a relict forest type from a time when moist subtropical forests extended up the Mpumalanga Escarpment. Elevation of relevé data ranged between 800 and 1100 m above sea level. This forest subtype has a flora list of 179 species with 49 species per relevé on average. Only 63% of the flora are obligate forest species. This subtype has the lowest proportion of evergreen trees in the canopy at only 49%. Dominant families include Rubiaceae, Fabaceae, Asteraceae, Euphorbiaceae and Flacourtiaceae. Dominant genera include *Syzygium, Rhoicissus, Asplenium, Asparagus* and *Ficus*. Certain

unusual factors make this forest subtype of significant biogeographic importance. For instance, a yet not formally described *Syzygium*, referred to as *Syzygium* sp. A (Schmidt et al., 2002), found only in this forest type, may represent a geographic outlier of a tropical/subtropical species of *Syzygium*. In addition, although not recorded in relevé data, this forest type is the only locality in South Africa for *Adiantum lunulatum* var. *fissum*, a fern hitherto known from Zimbabwe. This forest subtype is also the southernmost limit of the distribution of the Black-fronted Bush-shrike (*Telophorus nigrifrons*), which occurs further north in Africa.

Diagnostic taxa: ***Asparagus falcatus (C), Bridelia micrantha (C, Dm),*** *Combretum kraussii (C, Dm),* ***Dracaena aletriformis,*** *Englerophytum magalismontanum (C), Ficus sur,* ***Monanthotaxis caffra (C),*** *Nuxia floribunda (Dm), Peddiea africana (C),* ***Protorhus longifolia (C, Dm),*** *Rhoicissus tomentosa (C),* ***Rothmannia globosa (C, Dm),*** *Syzygium cordatum (Dm),* ***Syzygium* sp. A,** *Tricalysia lanceolata;* ***Anemia dregeana, Arthropteris monocarpa,*** *Cheilanthes viridis* var. *viridis (C), Crocosmia aurea* var. *aurea.*

Constant taxa: ***Asparagus falcatus (Dg), Bridelia micrantha (Dg, Dm),*** *Celtis africana,* ***Combretum kraussii (Dg, Dm), Diospyros whyteana, Englerophytum magalismontanum (Dg),*** *Monanthotaxis caffra (Dg),* ***Peddiea africana (Dg), Protorhus longifolia (Dg, Dm), Psychotria capensis,*** *Rhoicissus rhomboidea,* ***Rhoicissus tomentosa (Dg),*** *Rothmannia globosa (Dg, Dm),* ***Secamone alpini; Cheilanthes viridis* var. *viridis (Dg), Cyperus albostriatus, Oplismenus hirtellus***.

Dominant species: *Brachylaena transvaalensis,* ***Bridelia micrantha (Dg, C), Combretum kraussii (Dg, C),*** *Cryptocarya woodii, Gymnosporia harveyana, Nuxia floribunda (Dg), Protorhus longifolia (Dg, C), Rothmannia globosa (Dg, C), Syzygium cordatum (Dg).*

11. Barberton Scarp Forest Subtype

This subtype occurs in the lower, frost-free areas around Barberton. Elevation of relevé data ranges between 480 and 1170 m above sea level. It has 229 species and 42 species per relevé on average. Tree growth form accounts for 52%, shrubs 20%, climbers 15% and herbs 8% of species. Epiphytes account for only 1%. Obligate forest species make up 66% of all species occurrences while 70% of the tree canopy is evergreen. Dominant families include Rubiaceae, Euphorbiaceae, Apocynaceae, Fabaceae, and Celastraceae. Dominant genera include *Asplenium, Asparagus, Ochna, Pavetta* and *Maytenus*.

Diagnostic taxa: *Acridocarpus natalitius* var. *natalitius,* ***Atalaya natalensis,*** *Canthium inerme, Cnestis polyphylla, Combretum kraussii (C, Dm),* ***Croton sylvaticus (C, Dm),*** *Cryptocarya woodii (Dm), Dalbergia armata (C, Dm),* ***Englerophytum magalismontanum (C, Dm), Englerophytum natalense (C, Dm),*** *Erythroxylum emarginatum, Gymnosporia rubra,*

Harpephyllum caffrum (Dm), Keetia gueinzii, *Kraussia floribunda, Margaritaria discoidea* var. *fagifolia, Maytenus* sp. nov. *(= G. filiformis),* ***Monanthotaxis caffra (C, Dm),*** *Pavetta barbertonensis,* ***Pavetta galpinii (C), Pseuderanthemum subviscosum,*** *Rawsonia lucida (C), Sclerocroton integerrimus,* ***Tabernaemontana ventricosa (Dm), Tiliacora funifera, Trichilia dregeana,*** *Trilepisium madagascariense; Asparagus setaceus (Lebombo form),* ***Cheilanthes pentagona,*** *Tragiella natalensis*.

Constant species: *Celtis africana,* ***Combretum kraussii (Dg, Dm),*** *Croton sylvaticus (Dg, Dm),* ***Dalbergia armata (Dg, Dm), Englerophytum magalismontanum (Dg, Dm), Englerophytum natalense (Dg, Dm), Monanthotaxis caffra (Dg, Dm),*** *Pavetta galpinii (Dg), Peddiea africana, Rawsonia lucida (Dg); Oplismenus hirtellus.*

Dominant species: *Anthocleista grandiflora,* ***Combretum kraussii (Dg, C),*** *Croton sylvaticus (Dg, C), Cryptocarya woodii (Dg), Dalbergia armata (Dg, C),* ***Englerophytum magalismontanum (Dg, C), Englerophytum natalense (Dg, C),*** *Harpephyllum caffrum (Dg),* ***Monanthotaxis caffra (Dg, C), Protorhus longifolia,*** *Schefflera umbellifera, Syzygium gerrardii, Tabernaemontana ventricosa (Dg), Xymalos monospora.*

12. Blyde Scarp Forest Subtype

Limited to the dry ravines at the base of Mariepskop, it has a small floral list of 117 species with 44 species per relevé on average. Elevation of relevé data ranged between 800 and 850 m above sea level. The tree growth form accounts for 45%, shrubs 23%, climbers 19% and herbs 7%. No epiphytes were recorded in this subtype. Only 32% of the flora is made up of obligate forest species, however as much as 67% of the tree canopy is evergreen. Dominant families include Fabaceae, Rubiaceae, Apocynaceae, Euphorbiaceae and Asteraceae. Dominant genera include *Rhoicissus, Ficus, Ochna, Asparagus* and *Canthium*.

Diagnostic taxa: ***Acalypha glabrata (C), Breonadia salicina,*** *Bridelia micrantha (Dm), Afrocanthium mundianum,* ***Capparis fascicularis* var. *fascicularis, Carissa edulis,*** *Celtis africana (C),* ***Croton sylvaticus (C), Dalbergia armata (C),*** *Englerophytum magalismontanum (C),* ***Englerophytum natalense (C, Dm), Erythroxylum emarginatum, Eugenia natalitia* (river form)*, Ficus burkei (Dm), Ficus sur (C), Gymnosporia rubra (C, Dm), Hyperacanthus amoenus (C), Maytenus undata (wood), Mimusops zeyheri (C, Dm), Ochna arborea* var. *arborea, Ochna natalitia (C), Pachystigma bowkeri, Rawsonia lucida (C, Dm), Rhoicissus tomentosa (C), Secamone filiformis,*** *Syzygium cordatum (Dm),* ***Tricalysia lanceolata (C), Vepris reflexa; Abrus precatorius (C), Adenia digitata, Christella dentata, Cyperus keniensis, Equisetum ramosissimum,*** *Peperomia blanda, Setaria megaphylla,* ***Telosma africana****.*

Constant species: ***Acalypha glabrata (Dg), Celtis africana (Dg), Croton sylvaticus (Dg), Dalbergia armata (Dg), Englerophytum magalismontanum (Dg), Englerophytum natalense (Dg, Dm), Ficus sur (Dg), Gymnosporia rubra (Dg, Dm), Hyperacanthus amoenus (Dg), Mimusops zeyheri (Dg, Dm), Ochna natalitia (Dg), Rawsonia lucida (Dg, Dm), Rhoicissus tomentosa (Dg), Tricalysia lanceolata (Dg); Abrus precatorius (Dg), Dietes iridioides, Oplismenus hirtellus***.

Dominant species: *Bridelia micrantha (Dg),* ***Englerophytum natalense (Dg, C),*** *Ficus burkei (Dg),* ***Gymnosporia rubra (Dg, C),*** *Mimusops zeyheri (Dg, C), Rawsonia lucida (Dg, C), Searsia chirindensis,* ***Syzygium cordatum (Dg),*** *Trimeria grandifolia.*

13. Escarpment Riverine Forest Subtype

This subtype occurs below the escarpment at altitudes between 400–800 m. It has 42 species per relevé on average. Only 36% of the flora are obligate forest species, yet as much as 76% of the trees are evergreen. Dominant families include Rubiaceae, Fabaceae, Thelypteridaceae, Asteraceae and Moraceae. Dominant genera included *Ficus, Acacia, Diospyros* and *Strychnos*.

Diagnostic taxa: ***Acacia robusta* subsp. *clavigera, Anthocleista grandiflora (C, Dm), Brachylaena huillensis, Bridelia micrantha (C, Dm), Afrocanthium mundianum, Capparis tomentosa, Diospyros mespiliformis, Dracaena transvaalensis, Ehretia obtusifolia,*** *Ficus sur (C, Dm),* ***Flueggea virosa, Hibiscus vitifolius, Karomia speciosa, Maesa lanceolata (C, Dm), Phoenix reclinata, Pterolobium stellatum, Rauvolfia caffra (C, Dm), Sesbania macrantha, Solanum americanum, Strychnos mitis, Syzygium cordatum (C, Dm), Toddalia asiatica, Gymnanthemum myrianthum (C); Aneilema aequinoctiale (C), Carex spicato-paniculata (C), Christella dentata (C), Commelina benghalensis (C), Crassula alsinoides (C), Cyclosorus interruptus (C, Dm), Cyperus sexangularis, Eulophia horsfallii, Hydrocotyle verticillata (C), Kyllinga odorata (C), Laportea alatipes, Microlepia speluncae (C, Dm), Persicaria decipiens, Phragmites mauritianus, Pteris friesii (C), Setaria megaphylla (C), Sida serratifolia, Stegnogramma pozoi (C, Dm), Stephania abyssinica (C), Thelypteris confluens (Dm), Urera sp. (C), Zehneria scabra***.

Constant taxa: *Anthocleista grandiflora (Dg, Dm),* ***Bridelia micrantha (Dg, Dm),*** *Diospyros whyteana, Ficus sur (Dg, Dm), Maesa lanceolata (Dg, Dm),* ***Rauvolfia caffra (Dg, Dm),*** *Rhoicissus tomentosa,* ***Syzygium cordatum (Dg, Dm),*** *Gymnanthemum myrianthum (Dg); Aneilema aequinoctiale (Dg), Carex spicato-paniculata (Dg), Christella dentata (Dg), Cissampelos torulosa, Commelina benghalensis (Dg), Crassula alsinoides (Dg), Cyclosorus interruptus (Dg, Dm), Desmodium repandum (Dm), Hydrocotyle verticillata (Dg), Impatiens hochstetteri (Dm), Kyllinga odorata (Dg), Microlepia speluncae (Dg, Dm),* ***Oplismenus hirtellus***

(Dm), *Pteris friesii (Dg),* ***Setaria megaphylla (Dg),*** *Stegnogramma pozoi (Dg, Dm), Stephania abyssinica (Dg), Urera sp. (Dg).*

Dominant species: *Anthocleista grandiflora (Dg, C), Breonadia salicina,* ***Bridelia micrantha (Dg, C), Ficus sur (Dg, C), Maesa lanceolata (Dg, C),*** *Rauvolfia caffra (Dg, C), Rawsonia lucida,* ***Syzygium cordatum (Dg, C); Cyclosorus interruptus (Dg, C),*** *Desmodium repandum (C),* ***Impatiens hochstetteri (C), Microlepia speluncae (Dg, C), Oplismenus hirtellus (C),*** *Selaginella kraussiana,* ***Stegnogramma pozoi (Dg, C),*** *Thelypteris confluens (Dg).*

14. Legogote Scarp Forest Subtype

Confined to the Crocodile Gorge area near Kaapmuiden, it has only 113 species, with a relatively high 45 species per relevé on average. Elevation of relevé data ranged between 420 and 530 m above sea level. Only 27% of the flora are obligate forest species (lowest of all subtypes), yet as much as 53% of the tree canopy is evergreen. Dominant families include Euphorbiaceae, Fabaceae, Celastraceae, Apocynaceae, Oleaceae and Rubiaceae. Dominant genera include *Rhoicissus, Ficus, Asparagus, Combretum*, and *Adenia*.

Diagnostic taxa: ***Acacia schweinfurthii,*** *Acalypha glabrata,* ***Acridocarpus natalitius* var. *natalitius, Asparagus angusticladus, Atalaya alata (C, Dm),*** *Barleria rotundifolia,* ***Berchemia zeyheri, Bridelia cathartica,*** *Chaetachme aristata,* ***Chionanthus foveolatus* subsp. *foveolatus (C, Dm), Combretum molle (C, Dm), Combretum* cf. *woodii, Commiphora mollis,*** *Dalbergia armata (C),* ***Diospyros natalensis* subsp. *nummularia (C, Dm), Dombeya cymosa (C), Duvernoia aconitiflora, Erythroxylum delagoense, Euclea natalensis (C), Euclea schimperi, Eugenia mossambicensis, Garcinia livingstonei, Grewia flavescens* var. *flavescens, Gymnosporia* sp. D *(= G. graniticola) (C), Hibiscus calyphyllus (C),*** *Hippobromus pauciflorus,* ***Hippocratea africana, Homalium dentatum (C, Dm), Hyperacanthus amoenus (C), Jasminum streptopus (C), Kirkia wilmsii (C, Dm), Maerua rosmarinoides, Mimusops obovata (C, Dm), Obetia tenax, Ochna natalitia, Olax dissitiflora, Ptaeroxylon obliquum (C, Dm), Rhoicissus tomentosa (C), Rhoicissus tridentata* subsp. *cuneifolia (C), Searsia* taxon C *(Moffett), Ruttya ovata (Dm), Secamone parvifolia, Spirostachys africana, Sterculia murex, Strychnos madagascariensis, Coptospermum supra-axillaris (C, Dm), Tecoma capensis, Terminalia phanerophlebia (C, Dm), Vitellariopsis marginata (C, Dm), Vitex obovata* subsp. *wilmsii; Abrus precatorius,*** *Achyranthes aspera* var. *aspera, Adenia digitata,* ***Adiantum incisum,*** *Aneilema aequinoctiale,* ***Cheilanthes viridis* var. *glauca (C), Cocculus hirsutus, Dioscorea cotinifolia, Drimia delagoensis, Marsdenia sylvestris (C), Momordica foetida, Peperomia blanda (C), Pupalia lappacea, Sansevieria hyacinthoides****.*

Constant taxa: *Atalaya alata (Dg, Dm),* ***Chionanthus foveolatus* subsp. *foveolatus (Dg, Dm),*** *Combretum molle (Dg, Dm),* ***Dalbergia armata (Dg), Diospyros natalensis* subsp. *nummularia (Dg, Dm),*** *Dombeya cymosa (Dg),* ***Euclea natalensis (Dg),*** *Gymnosporia* sp. D *(= G. graniticola) (Dg), Hibiscus calyphyllus (Dg), Homalium dentatum (Dg, Dm), Hyperacanthus amoenus (Dg), Jasminum streptopus (Dg),* ***Kirkia wilmsii (Dg, Dm), Mimusops obovata (Dg, Dm),*** *Ptaeroxylon obliquum (Dg, Dm),* ***Rhoicissus tomentosa (Dg),*** *Rhoicissus tridentata* subsp. *cuneifolia (Dg),* ***Coptospermum supra-axillaris (Dg, Dm), Terminalia phanerophlebia (Dg, Dm), Vitellariopsis marginata (Dg, Dm);*** *Cheilanthes viridis* var. *glauca (Dg),* ***Marsdenia sylvestris (Dg), Oplismenus hirtellus, Peperomia blanda (Dg)***.

Dominant taxa: *Atalaya alata (Dg, C), Bridelia micrantha,* ***Chionanthus foveolatus* subsp. *foveolatus (Dg, C),*** *Combretum molle (Dg, C),* ***Diospyros natalensis* subsp. *nummularia (Dg, C), Homalium dentatum (Dg, C), Kirkia wilmsii (Dg, C),*** *Mimusops obovata (Dg, C), Ptaeroxylon obliquum (Dg, C), Ruttya ovata (Dg), Syzygium guineense, Coptospermum supra-axillaris (Dg, C), Terminalia phanerophlebia (Dg, C),* ***Vitellariopsis marginata (Dg, C)***.

5. DISCUSSION

5.1. Linking the Mpumalanga subtype classification and the National Forest Classification

Our forest analysis builds on the current two tiered National Forest Classification hierarchy (von Maltitz et al., 2003), although our relevé data was restricted to Mpumalanga. Our data clearly shows that the indigenous forests in the Wakkerstroom area, previously thought to be Low Escarpment Mistbelt Forest Type, now need to be incorporated under the Northern Highveld Forest Type. No new forest types are proposed, and the hierarchical level directly below that of a forest type is used to distinguish new forest subtypes.

The three zonal forest groups, namely Northern Mistbelt, Northern Afrotemperate, and Scarp Forests, are clearly distinguished from one another, with the Northern Mistbelt and Northern Afrotemperate Forest Groups being the most similar. Two forest subtype groupings are recognised within the Eastern Scarp Forest Type. Group E is very distinct and characterises 'core' scarp forest (as representative of the subtropical forest biome; *sensu* Mucina et al., 2006), whereas there is an overlap of species between Group D and the Mpumalanga Mistbelt Forest Type (comprising Groups B & C; representative of the afrotemperate forest biome; *sensu* Mucina et al., 2006). This may lead to the sharing of species simply as a result of topographic proximity as nowhere else in South Africa do Scarp and Northern Mistbelt Forest Groups come so close to one another.

The Northern Mistbelt Forest Group is represented by the Mpumalanga Mistbelt Forest Type, which forms part of the afrotemperate forest biome (or afromontane forests *sensu* White, 1978). This forest type comprises a warm temperate flora that shares several genera and

species with the high mountainous forests to the north in south-central Africa. Two subtype grouping are recognised, one (Group B) which favours the wetter and higher altitude areas, and the other (Group C) which favours drier and lower areas and starts approaching the composition of scarp forest with an afrotemperate mix of species (Group D).

The Northern Afrotemperate Forest Group of forests either occur in the drier and colder highveld parts of the grassland plateaus or escarpment and small ravines, or in the dry rain-shadow valleys of the mountainous Mpumalanga Escarpment. This forest group is represented by the Northern Highveld Forest Type which shares many species with the cold highveld parts of South Africa. The Wakkerstroom Midlands Forest Subtype is now embedded within the Northern Highveld Forest Type.

The Eastern Scarp forest group is represented by the Eastern Scarp forest type, and then several scarp forest subtypes. Conventional thinking was that this forest type is transitional in nature between Afromontane and Coastal forests, however it is now considered to represent a subtropical forest with its own characteristic species (Geldenhuys and Mucina, 2006; Mucina et al., 2007). Our results showed that the Escarpment Riverine Forest is more Scarp than azonal and we suspect that azonality becomes more apparent at lower altitudes where Lowveld Riverine Forests (not studied) occur.

The Northern Highveld forests have been described as being the most “biogeographically eroded” forest type, as they contain only a very small portion of the typical Afrotemperate, or Afromontane, elements. They were probably once linked to the species-rich Afrotemperate forests found along the Mpumalanga escarpment (Geldenhuys and Mucina, 2006). Our research supports this statement that this forest type is probably the most species poor as average species richness per relevé is the lowest sampled (40.6). Obligate forest species make up only 52% of this forest flora, although as much as 75% of the tree canopy is evergreen.

The Barberton area is a recognised centre of plant endemism (van Wyk and Smith, 2001) and the identification and then division of the dry and moist Barberton forests into two unique subtypes is an example of how the proposed classification has, to a certain extent, managed to mirror this biogeographic classification. Similarly, the Wolkberg Centre of Endemism comprises two subcentres (Mathews et al., 1993), of which the Blyde Subcentre occurs south of the Olifants River in Mpumalanga. This subcentre is also circumscribed in what we propose as the Mariepskop Mistbelt Forest Subtype.

5.2. Further outlook

With the indigenous forests making up only 0.51% of Mpumalanga’s territory, it contains a unique suite of plant species (316 obligate forest taxa) not found in any other major vegetation type in the region. This result highlights the unique nature of indigenous forests and the need to conserve a representative sample of this biodiversity.

Although much attention was placed on surveying forest patches across a range of environmental conditions, the results show that the number of sample relevés per forest type and subtype varies considerably. This may have an impact on the resulting subtype classification. Future surveys should increase the number of relevés in the Lowveld Riverine forest types. In particular our current understanding of the Lowveld Riverine Forest Type is inadequate and incomplete, and comprehensive descriptions are required for the subtypes.

The data set used to develop the Mpumalanga subtype classification will be provided to the National Vegetation Database hosted by SANBI, where it will be made available for vegetation surveys and analyses in accordance with SANBI's policies. The database currently stores more than 48 000 relevés for over 1 million species records (Powrie et al., 2012).

The proposed forest classification presented here offers the basis for further studies aimed at identifying ecological and evolutionary drivers of the species composition and spatial variability of the indigenous forests in Mpumalanga. Such studies are underway (Chapter 4).

We suggest that further subdivision of forest types into subtypes is necessary for inclusion into conservation initiatives to be used at a provincial scale. The effective conservation of forest habitats is reliant on robust classifications at the appropriate scale. The resulting classifications need to be spatially explicit if they are to be of any value in conservation initiatives. In addition, inappropriate habitat classifications would result in wastage of time, money and resources. We present here a forest classification that is methodologically robust, biogeographically distinct and ecologically accurate. It is appropriate for use in conservation planning initiatives in Mpumalanga. Our proposed hierarchical floristic assessment is largely nested within the NFC (von Maltitz et al., 2003; Geldenhuys and Mucina, 2006; Mucina et al., 2006, 2007), and hence will facilitate comparisons between forests across the country, and ensure edge-match with additional subtype classifications that are produced for other areas.

The nature of our numerical analyses and the formalised definitions of the subtypes (containing formally defined lists of Diagnostic, Constant and Dominant species groups) allows, for the first time in the history of South African vegetation science, the building of an expert system for semi-automatic assignment (hence identification) of the vegetation field data into a pre-defined stable typological system (see Hill, 1989; Janišová and Dúbravková, 2010; Janišová et al., 2010 for examples in the world literature).

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REFERENCES

Acocks, J.P.H., 1988. *Veld types of South Africa. Memoirs of the Botanical Survey of South Africa* 57, 1–146.

Braun-Blanquet, J., 1964. *Pflanzensoziologie*. Grundzüge der Vegetationskunde. 3rd ed. Springer-Verlag, Wien.

Chytrý, M., Tichý, L., Holt, J., Botta-Dukát, Z., 2002. Determination of diagnostic species with statistical fidelity measures. *Journal of Vegetation Science* 13, 79–90.

Chytrý, M., Rafajová, M., 2003. Czech National Phytosociological Database: basic statistics of the available vegetation-plot. *Preslia* 75, 1–15.

Chytrý, M., Tichý, L., 2003. Diagnostic, constant and dominant species of vegetation classes and alliances of the Czech Republic: a statistical revision. *Folia Facultatis Scientiarum Naturalium Universitatis Masarykianae Brunensis* 108, 1–231.

Conservatoire et Jardin botaniques de la Villle de Genève & South African National Biodiversity Institute, Pretoria. African Plants Database (version 3.3.4). Retrieved January 2011, from <http://www.ville-ge.ch/musinfo/bd/cjb/africa/>.

Cooper, K.H., 1985. *The conservation status of indigenous forests in Transvaal, Natal and O.F.S., South Africa.* Wildlife Society of South Africa, Durban.

Deal, G.B., Theron, G.K., Westfall, R.H., 1989. The vegetation ecology of the eastern Transvaal escarpment in the Sabie area. 2. Floristic classification. *Bothalia* 19, 69–89.

Eckhardt, H.C., van Rooyen, N., Bredenkamp, G.J., 1997. Plant communities of the forests, woodlands and thickets in northern KwaZulu-Natal. *Koedoe* 40, 91–112.

Ferrar, A.A., Lötter, M.C., 2007. Mpumalanga Biodiversity Conservation Plan Handbook. Mpumalanga Tourism & Parks Agency, Nelspruit.

Geldenhuys, C.J., Mucina, L., 2006. Towards a new national forest classification for South Africa, in: Ghazanfar, S.A., Beentje, H.J. (Eds.), *Taxonomy and ecology of African plants, their conservation and sustainable use*, pp. 111–129. Royal Botanic Gardens, Kew.

Germishuizen, G., Meyer, N.L., 2003. *Plants of southern Africa: an annotated checklist*. National Botanical Institute, Pretoria.

Hennekens, S.M., Schaminée, J., 2001. TURBOVEG, a comprehensive data base management system for vegetation data. *Journal of Vegetation Science* 12, 589–591.

Hill, M.O., 1989. Computerized matching of relevés and association tables, with an application to the British National Vegetation Classification. *Vegetatio* 83: 18–194.

Janišová, M., Dúbravková, D., 2010. Formalized classification of rocky Pannonian grasslands and alpine Sesleria-dominated grasslands in Slovakia using a hierarchical expert system. *Phytocoenologia* 40: 267–291.

Janišová, M., Uhliarová, E., Ružičková, H., 2010. Expert system-based classification of semi-natural grasslands in submontane and montane regions of central Slovakia. *Tuexenia* 30: 375–422.

Kent, M., Coker, P., 1994. *Vegetation description and analysis - a practical approach*. John Wiley & Sons, Oxford.

Lötter, M.C., Beck, H., 2004. Preliminary inventory and classification of indigenous afromontane forests on the Blyde River Canyon Nature Reserve, Mpumalanga, South Africa. *BMC Ecology* 4, 9. [doi:10.1186/1472-6785-4-9]

Lötter, M.C., Mucina, L., Witkowski, E.T.F., 2013. The classification conundrum: species fidelity as leading criterion in search of the most robust method to classify a complex forest data set.

Matthews, W.S., Van Wyk, A.E., Bredenkamp, G.J., 1993. Endemic flora of the North- eastern Transvaal Escarpment, South Africa. *Biological Conservation* 63, 83–94.

McCune, B., Mefford, M.J., 2006. PC-ORD. Multivariate analysis of ecological data. Version 5.20. MjM Software, Gleneden Beach, OR.

Morgenthal, T.L., Cilliers, S.S., 1999. Vegetation analysis of Pedlar's Bush, Mpumalanga, and its conservation. *South African Journal of Botany* 65, 270–280.

Mucina, L., Rutherford, M.C., (Eds.) 2006. *The vegetation of South Africa, Lesotho and Swaziland*. South African National Biodiversity Institute, Pretoria.

Mucina, L., Geldenhuys, C.J., Rutherford, M.C., Powrie, L.W., Lötter, M.C., Von Maltitz, G.P., Euston-Brown, D.I.W., Matthews, W.S., Dobson, L., McKenzie, B., 2006. Afrotemperate, subtropical and azonal forests, in: Mucina, L., Rutherford, M.C. (Eds.), *The vegetation of South Africa, Lesotho and Swaziland*. pp. 584–615. South African National Biodiversity Institute, Pretoria.

Mucina, L., Pienaar, E., van Niekerk, A., Lötter, M.C., Scott-Shaw, C.R., Meets, M., Seoke, L., Sekome, T., Siebert, S.J., Loffler, L., Cawe, S.G., Dold, A.P., Abbott, A., Kalwij, J., Tichý, L., 2007. *Habitat-level Classification of the Albany Coastal, Pondoland Scarp and Eastern Scarp Forests*. Unpublished Report for DWAF, Stellenbosch University, Matieland, ZA.

Mueller-Dombois, D., Ellenberg, H., 1974. *Aims and methods of vegetation ecology*. J. Wiley & Sons, New York.

Muller, D.J., 1994. Resultate van 'n voorraadsopname in die inheemse bos op Mariti, Oos Transvaal. *South African Journal of Forestry* 168, 27–31.

Oliver, I., Broese, E.A., Dillon, M.L., Sivertsen, D., McNellie, M.J., 2013. Semi-automated assignment of vegetation survey plots within an a priori classification of vegetation types. *Methods in Ecology and Evolution* 4, 73-81.

Powrie, L.W., Rutherford, M.C., Mucina, L., Mangwale, K., 2012. National Vegetation Database of South Africa, in: Dengler, J., Oldeland, J., Jansen, F., Chytrý, M., Ewald, J., Finckh, M., Glöckler, F., Lopez-Gonzalez, G., Peet, R.K., Schaminée, J.H.J. (Eds.), Vegetation databases for the 21st century. *Biodiversity & Ecology* 4, 299–299. DOI: 10.7809/b-e.00096.

Schmidt, E., Lötter, M.C., McCleland, W., 2002. *Trees and shrubs of Mpumalanga and Kruger National Park*. Jacana, Johannesburg.

Schulze, R.E., 1997. *South African atlas for agrohydrology and climatology*. Water Research Commission, Pretoria.

Small, C.J., McCarthy, B., 2002. Spatial and temporal variation in the response of understory vegetation to disturbance in a central Appalachian oak forest. *Journal of the Torrey Botanical Society* 129, 136–153.

Stalmans, M., Robinson, E.R., Balkwill, K., 1999. Ordination and classification of the vegetation of Songimvelo Game Reserve in the Barberton Mountainland, South Africa, for the assessment of wildlife habitat distribution and quality. *Bothalia* 29, 305–325.

Tichý, L., 2002. JUICE, software for vegetation classification. *Journal of Vegetation Science* 13, 451–453.

Tichý, L., Holt, J., 2006. JUICE, program for management, analysis and classification of ecological data. Users Manual. Masaryk University, Brno.

Van Der Schijff, H.P., Schoonraad, E., 1971. The flora of the Mariepskop complex. *Bothalia* 10, 461–500.

Van Wyk, A.E., Smith, G.F., 2001. *Regions of floristic endemism in southern Africa. A review with emphasis on succulents*. Umdaus Press, Pretoria.

Von Breitenbach, F., 1990*. Reports on indigenous forests, Part 1. Introduction and methods, South-eastern Transvaal forests, Uitsoek forests*. DEA, Forestry Branch, Pretoria.

Von Maltitz, G., Mucina, L., Geldenhuys, C.J., Lawes, M., Eeley, H., Aidie, H., Vink, D., Fleming, G., Bailey, C., 2003. *Classification system for South African indigenous forests*. An objective classification for the Department of Water Affairs and Forestry. Report ENV-P-C 2003-017. Environmentek, CSIR, Pretoria.

Werger, M.J.A., Sprangers, J.T.C., 1982. Comparison of floristic and structural classification of vegetation. *Vegetatio* 50, 175–183.

White, F., 1978. The afromontane region, in: Werger, M.J.A. (Ed.), *Biogeography and ecology of southern Africa*, pp. 463–513. Dr. W Junk Publ., The Hague.

Willner, W., Tichý, L., Chytrý, M., 2009. Effects of different fidelity measures and contexts on the determination of diagnostic species. *Journal of Vegetation Science* 20, 130–137.

SUPPLEMENTARY MATERIAL

Supplementary data to this article can be found online at
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Table S1
Synoptic table of 434 relevés of the Mpumalanga forest subtype classification based on Φ fidelity thresholds to determine diagnostic species. They are ranked by decreasing values of Φ. Dashes in table indicate negative fidelity. Numbers in brackets refer to subtype numbering used in tables and NMDS graphs.

	Phi coefficient (Φ)													
Forest Subtypes	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**
No. of relevés	36	17	14	10	68	118	59	10	35	14	36	5	4	8
No. of diagnostic species (Φ >25)	13	32	33	37	36	19	31	44	15	19	30	36	46	64
No. of species in synoptic columns (Φ > 2)	59	42	40	42	74	78	56	48	31	34	67	36	46	65
Average no. of species per relevé	44.5	41.4	33.5	34.4	43.3	48.8	44.5	70.2	38.6	48.9	41.8	44.4	42.3	44.6
Diagnostic species of the vegetation unit: *Eastern Dry Afrotemperate Forest* (1)														
Doryopteris concolor	50.9	-	-	-	-	-	-	-	-	-	-	-	-	-
Schoenoxiphium lehmannii	36.9	-	-	-	-	-	-	-	-	-	-	-	-	-
Aloe dyeri	35.7	-	-	-	-	-	-	-	-	-	-	-	-	-
Mystacidium capense	32.2	-	-	-	-	-	-	-	-	-	-	-	-	-
Trimeria grandifolia	27.3	-	-	-	-	12.4	-	-	-	24.1	-	-	-	-
Grewia occidentalis	27	-	-	-	-	-	-	-	-	-	-	-	-	-
Senecio deltoideus	26.5	-	-	-	-	-	-	-	-	-	-	-	-	-
Diagnostic species of the vegetation unit: *Wakkerstroom Midlands Forest* (2)														
Cussonia sphaerocephala	-	81.3	-	-	-	-	-	-	-	-	-	-	-	-
Buddleja dysophylla	-	62.8	-	-	-	-	-	-	-	-	-	-	-	-
Dais cotinifolia	21.7	61.7	-	-	-	-	-	-	-	-	-	-	-	-
Streptocarpus pentherianus	-	58	-	-	-	-	-	-	-	-	-	-	-	-
Scolopia oreophila	-	57.6	-	-	-	-	-	-	-	-	-	-	-	-
Plectranthus grallatus	-	57.2	-	-	-	-	-	-	-	-	-	-	-	-
Thalictrum rhynchocarpum	-	54.7	-	-	-	-	-	-	-	-	-	-	-	-
Solanum incanum	-	50.3	-	-	-	-	-	-	-	-	-	-	-	-
Pavetta cooperi	-	47.1	-	-	-	-	-	-	-	-	-	-	-	-
Allophylus africanus	15.2	46.7	-	-	-	-	-	-	-	-	-	-	-	-
Clerodendrum glabrum	14.1	44.6	-	-	-	-	-	-	-	-	-	-	-	-
Mystacidium caffrum	-	40.7	-	-	-	-	-	-	-	-	-	-	-	-
Laportea peduncularis	-	39.5	-	-	-	-	-	-	-	-	-	-	-	-
Rhus chirindensis	-	34.7	-	-	-	-	-	-	-	-	-	-	-	-
Sanicula elata	-	34.6	-	-	-	10	-	-	-	-	-	-	-	-
Mystacidium flanaganii	-	33.2	-	-	-	-	-	-	-	-	-	-	-	-
Rubus rigidus	-	33.2	-	-	-	-	-	-	-	-	-	-	-	-
Asplenium varians	-	32	-	-	-	-	-	-	-	-	-	-	-	-
Cheilanthes hirta var. *nemorosa*	-	31.9	-	-	-	-	-	-	-	-	-	-	-	-
Clausena anisata	16.2	28.6	-	-	-	9.1	-	-	-	-	-	-	-	-
Cyrtorchis arcuata	-	27.5	-	-	-	-	-	-	-	-	-	-	-	-
Choristylis rhamnoides	-	27	-	-	-	12	-	-	-	-	-	-	-	-
Mystacidium venosum	-	26.4	-	-	-	-	-	-	-	-	-	-	-	-
Zanthoxylum davyi	-	25.6	-	-	-	22.3	17.6	-	-	-	-	-	-	-
Diagnostic species of the vegetation unit: *Lydenburg Kloof Forest* (3)														
Adiantum poiretii	10.2	-	69	-	-	-	-	-	-	-	-	-	-	-
Greyia radlkoferi	-	-	66	-	-	-	-	-	-	-	-	-	-	-

Rhamnus prinoides	9.3	-	58.2	-	-	-	-	-	-	-	-	-	-	-	-
Ehrharta erecta var. *natalensis*	-	-	52	-	-	-	-	-	-	-	-	-	-	-	-
Heteromorpha arborescens var. *abyssinica*	-	-	49.2	-	-	-	-	-	-	-	-	-	-	-	-
Pteris cretica	-	-	48.9	-	-	-	-	-	-	-	-	-	-	-	-
Leucosidea sericea	-	-	46.7	-	-	-	-	-	-	-	-	-	-	-	-
Clematis brachiata	-	-	46	-	-	13.5	-	-	-	-	-	-	-	-	-
Blechnum australe	13.8	-	43	-	-	-	-	-	-	-	-	-	-	-	-
*Asparagus sp. (*climbing form of *A.plumosus*)	-	-	42.8	-	-	-	-	-	-	-	-	-	-	-	-
Maytenus deflexa	-	-	42.6	-	-	13	-	-	-	-	-	-	-	-	-
Pleopeltis macrocarpa	-	-	38.3	-	-	-	-	-	-	-	-	-	-	-	-
Sparrmannia ricinocarpa	-	-	36.6	-	-	-	-	-	-	-	-	-	-	-	-
Acacia caffra	-	-	33	-	-	-	-	-	-	-	-	-	-	-	-
Asplenium aethiopicum	-	-	33	-	24.8	20.9	-	-	-	-	-	-	-	-	-
Gymnosporia buxifolia	-	-	29.9	-	-	-	-	-	-	-	-	-	-	-	-
Euclea crispa subsp. *crispa*	20.6	-	29.6	-	-	-	-	-	-	-	-	-	-	-	-
Myrsiphyllum asparagoides	-	-	28.9	-	-	-	-	-	-	-	-	-	-	-	-
Streptocarpus polyanthus	14.8	-	27.9	-	-	-	-	-	-	-	-	-	-	-	-
Diagnostic species of the vegetation unit: *Northern Highveld Kloof Forest* (4)															
Pavetta gardeniifolia	-	-	-	81	-	-	-	-	-	-	-	-	-	-	-
Pachystigma macrocalyx	-	-	-	81	-	-	-	-	-	-	-	-	-	-	-
Cyphostemma cirrhosum	-	-	-	58.9	-	-	-	-	-	-	-	-	-	-	-
Aloe arborescens	-	-	-	58.6	-	-	-	-	-	-	-	-	-	-	-
Kalanchoe rotundifolia	-	-	-	58.4	-	-	-	-	-	-	-	-	-	-	-
Rhus pallens	-	-	-	53.4	-	-	-	-	-	-	-	-	-	-	-
Cyathula uncinulata	-	-	-	53.4	-	-	-	-	-	-	-	-	-	-	-
Aeollanthus buchnerianus	-	-	-	53.4	-	-	-	-	-	-	-	-	-	-	-
Solanum retroflexum	-	-	-	53.4	-	-	-	-	-	-	-	-	-	-	-
Solanum giganteum	-	-	-	53.4	-	-	-	-	-	-	-	-	-	-	-
Diospyros lycioides subsp. *guerkei*	-	-	23.1	48.2	-	-	-	-	-	-	-	-	-	-	-
Myrsine africana	12.3	-	24.8	47.2	-	-	-	-	-	-	-	-	-	-	-
Dovyalis zeyheri	-	-	-	46.4	-	-	-	-	-	-	-	-	-	-	-
Ilex mitis	-	-	-	44.3	-	-	-	-	-	-	-	-	-	-	-
Solanum pseudocapsicum	-	-	-	43.4	-	-	-	-	-	-	-	-	-	-	-
Rhus leptodictya	-	-	-	43.4	-	-	-	-	-	-	-	-	-	-	-
Maytenus albata	-	-	-	43.4	-	-	-	-	-	-	-	-	-	-	-
Cussonia paniculata	-	-	-	43.4	-	-	-	-	-	-	-	-	-	-	-
Rhus pyroides var. *pyroides*	-	-	-	43.4	-	-	-	-	-	-	-	-	-	-	-
Pteris dentata	-	-	-	43.3	-	-	-	-	-	-	-	-	-	-	-
Dioscorea retusa	-	-	-	39.8	-	-	-	-	-	-	-	-	-	-	-
Blechnum attenuatum var. *giganteum*	-	-	-	35.4	11.3	-	-	-	-	-	-	-	-	-	-
Rothmannia capensis	-	-	-	35.4	22.8	-	22.1	-	-	-	-	-	-	-	-
Dicliptera clinopodia	-	-	-	32.4	-	-	-	-	-	-	-	-	-	-	-
Maerua cafra	8.6	-	-	32.3	-	-	-	-	-	-	-	-	-	-	-
Tetradenia riparia	-	-	-	28.5	-	-	-	-	-	-	-	-	-	-	-
Dombeya rotundifolia	-	-	-	28.5	-	-	-	-	-	-	-	-	-	-	-
Halleria lucida	-	-	22.2	25.8	-	7.7	-	-	-	-	-	-	-	-	-
Mikania capensis	-	-	-	25.4	-	-	-	-	-	-	-	-	-	-	-
Diagnostic species of the vegetation unit: *Mariepskop Mistbelt Forest* (5)															
Ochna arborea var. *oconnorii*	-	-	-	-	54.4	18.3	-	-	-	-	-	-	-	-	-
Asplenium boltonii	-	-	-	-	53.9	20.3	-	-	-	-	-	-	-	-	-
Elaphoglossum aubertii	-	-	-	-	49.8	-	-	-	-	-	-	-	-	-	-
Elaphoglossum macropodium	-	-	-	-	44	-	-	-	-	-	-	-	-	-	-

Elaphoglossum acrostichoides	-	-	-	-	39.5	-	-	-	-	-	-	-	-	-	
Solenostemon latifolius	-	-	-	-	39	-	-	-	-	-	-	-	-	-	
Clivia caulescens	-	-	-	-	38.7	23.3	-	-	-	-	-	-	-	-	
Streptocarpus micranthus	-	-	-	-	38.6	-	-	-	-	-	-	-	-	-	
Rumohra adiantiformis	-	-	-	-	37.1	-	-	-	-	-	-	-	-	-	
Ocotea bullata	-	-	-	-	35.2	-	-	-	-	-	-	-	-	-	
Vernonia wollastonii	-	-	-	-	35.2	-	-	-	-	-	-	-	-	-	
Vittaria isoetifolia	-	-	-	-	34	-	-	-	-	-	-	-	-	-	
Hymenophyllum tunbrigense	-	-	-	-	30.7	-	-	-	-	-	-	-	-	-	
Vaccinium exul	-	-	-	-	29.9	-	-	-	-	-	-	-	-	-	
Asplenium friesiorum	-	-	-	-	29.6	-	-	-	-	-	-	-	-	-	
Peperomia tetraphylla	-	-	-	-	28.8	-	-	-	-	-	-	-	-	-	
Plectranthus rubropunctatus	-	-	-	-	28.7	-	-	-	-	-	-	-	-	-	
Disperis fanniniae	-	-	-	-	28.7	-	-	-	-	-	-	-	-	-	
Combretum edwardsii	-	-	-	-	28.5	17.8	-	-	-	-	-	-	-	-	
Asplenium rutifolium	-	-	-	-	27.9	24.9	-	-	-	-	-	-	-	-	
Cyathea capensis	-	-	-	-	26.2	-	-	-	-	-	-	-	-	-	
Lycopodium dacrydioides	-	-	-	-	26.2	-	-	-	-	-	-	-	-	-	
Drimia robusta	-	-	-	-	26.2	-	-	-	-	-	-	-	-	-	
Maytenus species A	-	-	-	-	26.2	-	-	-	-	-	-	-	-	-	
Blotiella natalensis	-	-	-	-	25.9	-	-	-	-	-	-	-	-	-	
Diagnostic species of the vegetation unit: *Long Tom Mistbelt Forest* (6)															
Tylophora flanaganii	-	-	-	-	-	50	-	-	-	-	-	-	-	-	
Asplenium erectum var. *erectum*	-	-	-	-	-	39	-	-	-	-	-	-	-	-	
Asplenium lobatum	-	-	-	-	-	37.6	-	-	-	-	-	-	-	-	
Rapanea melanophloeos	-	-	-	-	24.2	32.3	-	-	-	-	-	-	-	-	
Cassine peragua	-	-	-	-	-	32.1	-	-	-	-	-	-	-	-	
Behnia reticulata	-	-	-	-	-	30	-	-	-	-	-	-	-	-	
Xymalos monospora	-	-	-	-	23.8	30	23.5	-	-	-	-	-	-	-	
Cryptocarya transvaalensis	-	-	-	-	-	28	23.2	-	-	-	-	-	-	-	
Lauridia tetragona	-	-	-	-	-	26	-	-	-	-	-	-	-	-	
Hippocratea longipetiolata	-	-	-	-	-	25.2	-	-	-	-	-	-	-	-	
Diagnostic species of the vegetation unit: *Barberton Mistbelt Forest* (7)															
Micrococca capensis	-	-	-	-	-	-	77.3	-	-	-	-	-	-	-	
Cola greenwayi	-	-	-	-	-	-	56.9	-	-	-	21.2	-	-	-	
Oricia bachmannii	-	-	-	-	-	-	54.2	-	-	-	-	-	-	-	
Prosphytochloa prehensilis	-	-	-	-	-	-	53.4	-	-	-	-	-	-	-	
Aristea ecklonii	-	-	-	-	-	-	49	-	-	-	-	-	-	-	
Ochna gamostigmata	-	-	-	-	-	-	42.3	-	-	-	-	-	-	-	
Chionanthus peglerae	-	-	-	-	-	-	42.2	-	-	-	-	-	-	-	
Allophylus chaunostachys	-	-	-	-	-	-	39.7	-	-	-	-	-	-	-	
Garcinia gerrardii	-	-	-	-	-	-	38	-	-	-	-	-	-	-	
Aphloia theiformis	-	-	-	-	-	-	34.5	-	-	-	22.8	-	-	-	
Streptocarpus confusus subsp. *confusus*	-	-	-	-	-	-	34.1	-	-	-	-	-	-	-	
Vepris lanceolata	-	-	-	-	-	-	32.7	-	-	-	-	-	-	-	
Cussonia spicata	-	-	-	-	-	18.3	31.1	-	-	-	-	-	-	-	
Memecylon natalense	-	-	-	-	-	-	30.8	-	-	-	-	-	-	-	
Calodendrum capense	-	-	-	-	-	-	30.4	-	-	-	-	-	-	-	
Riocreuxia picta	-	-	-	-	-	-	29.8	-	-	-	-	-	-	-	
Clivia miniata	-	-	-	-	-	-	28.1	-	-	-	-	-	-	-	
Polystichum transkeiense	-	-	-	-	-	-	28.1	-	-	-	-	-	-	-	
Ocotea kenyensis	-	-	-	-	-	-	28	-	-	-	24.1	-	-	-	

Ochna holstii	-	-	-	-	-	-	28	-	-	-	-	-	-	-
Bersama lucens	-	-	-	-	-	-	27.3	-	-	-	23.5	-	-	-
Diagnostic species of the vegetation unit: *Blyde Canyon Dry Afromontane Forest* (8)														
Elaeodendron croceum	-	-	-	-	12.6	-	-	65.1	-	-	-	-	-	-
Bowkeria cymosa	-	-	-	-	-	6.8	-	54.3	-	-	-	-	-	-
Podocarpus falcatus	-	24.9	-	-	-	10.4	15	52.6	-	-	-	-	-	-
Schefflera umbellifera	-	-	-	-	21.8	-	-	51.6	-	-	-	-	-	-
Canthium ciliatum	-	-	-	-	-	-	-	51.3	22.2	-	-	-	-	-
Vangueria infausta	-	-	-	-	-	-	-	49.8	-	-	-	-	-	-
Strychnos henningsii	-	-	-	-	-	-	-	47.9	-	-	-	-	-	-
Rhoicissus sp 1 (horny domatia)	22.7	24.8	-	-	-	-	-	44.1	-	-	-	-	-	-
Psydrax obovata subsp. *elliptica*	-	-	-	-	24.8	-	-	44.1	-	-	-	-	-	-
Commelina africana	-	-	-	-	-	-	-	43.4	-	-	-	-	-	-
Osmunda regalis	-	-	-	-	-	-	-	43.4	-	-	-	-	-	-
Faurea galpinii	-	-	-	-	-	14	-	40.7	-	-	-	-	-	-
Trichomanes melanotrichum	-	-	-	-	-	-	-	40.6	-	-	-	-	-	-
Bersama tysoniana	-	-	-	-	-	23	-	39.2	-	-	-	-	-	-
Maytenus peduncularis	-	-	-	-	-	16.8	-	38.4	-	-	-	-	-	-
Osyridicarpos schimperianus	-	-	-	-	-	-	-	37.9	-	-	-	-	-	-
Eugenia woodii	-	-	-	-	-	-	-	37.7	-	-	8.3	-	-	-
Scolopia zeyheri	11.2	-	-	-	-	-	-	37.1	-	-	9	-	-	-
Trichocladus grandiflorus	-	-	-	-	14.6	-	-	35.7	-	-	-	-	-	-
Talbotia elegans	-	-	-	-	-	-	-	35.2	-	-	-	-	-	-
Carissa bispinosa subsp. *zambesiensis*	-	-	-	-	-	17.1	22.7	30.3	-	-	-	-	-	-
Adenopodia spicata	9.7	-	-	-	-	-	-	26.8	10.3	-	-	-	-	-
Dietes iridioides	-	-	-	-	11.9	-	-	26	-	-	-	-	-	-
Cyperus albostriatus	-	-	-	-	-	-	-	25.5	-	-	-	-	-	-
Diagnostic species of the vegetation unit: *Foothills Mistbelt Forest* (9)														
Strelitzia caudata	-	-	-	-	-	-	-	-	28.3	-	-	-	-	-
Cephalanthus natalensis	-	-	-	-	-	-	-	-	25.6	-	-	-	-	-
Diagnostic species of the vegetation unit: *Mapulaneng Scarp Forest* (10)														
Syzygium species A	-	-	-	-	-	-	-	-	-	69.4	-	-	-	-
Anemia dregeana	-	-	-	-	-	-	-	-	-	60.5	12.7	-	-	-
Asparagus falcatus	-	-	-	-	-	-	-	-	-	53.1	16.3	-	-	-
Dracaena aletriformis	-	-	-	-	-	-	-	-	-	45	18.5	-	-	-
Arthropteris monocarpa	-	-	-	-	-	-	-	-	-	39.3	-	-	-	-
Nuxia floribunda	-	-	-	-	10.4	-	-	-	-	29.9	-	-	-	-
Cheilanthes viridis var. *viridis*	-	-	-	-	-	12.2	-	-	19	26.2	-	-	-	-
Diagnostic species of the vegetation unit: *Barberton Scarp Forest* (11)														
Pavetta galpinii	-	-	-	-	-	-	-	-	-	-	85.8	-	-	-
Tabernaemontana ventricosa	-	-	-	-	-	-	-	-	-	-	75.2	-	-	-
Trichilia dregeana	-	-	-	-	-	-	-	-	-	-	70.9	-	-	-
Cheilanthes pentagona	-	-	-	-	-	-	-	-	-	-	45.8	-	-	-
Pseuderanthemum subviscosum	-	-	-	-	-	-	-	-	-	-	45.8	-	-	-
Atalaya natalensis	-	-	-	-	-	-	-	-	-	-	36.1	-	-	-
Tiliacora funifera	-	-	-	-	-	-	-	-	-	-	36.1	-	-	-
Kraussia floribunda	-	-	-	-	-	-	-	-	-	-	31.9	-	-	-
Canthium inerme	-	-	-	-	-	-	-	-	-	24.8	29.4	-	-	-
Maytenus sp nov (aff. *G. filiformis)*	-	-	-	-	-	-	-	-	-	-	27.9	-	-	-
Trilepisium madagascariense	-	-	-	-	-	-	-	-	-	-	27.9	-	-	-
Tragiella natalensis	-	-	-	-	-	-	-	-	-	-	27.9	-	-	-
Sapium integerrimum	-	-	-	-	-	-	-	-	-	-	27.9	-	-	-

Asparagus setaceus (Lebombo form)	-	-	-	-	-	-	-	-	-	-	27.9	-	-	-
Margaritaria discoidea var. *fagifolia*	-	-	-	-	-	-	-	-	-	-	27.9	-	-	-
Diagnostic species of the vegetation unit: *Blyde Scarp Forest* (12)														
Mimusops zeyheri	-	-	-	16.6	-	-	-	-	-	-	7.3	78.2	-	-
Telosma africana	-	-	-	-	-	-	-	-	-	-	4.4	70.9	-	-
Eugenia natalitia (river form)	-	-	-	-	-	-	-	-	-	-	-	61.8	-	-
Mariscus keniensis	-	-	-	-	-	-	-	-	-	-	-	61.8	-	-
Equisetum ramosissimum	-	-	-	-	-	-	-	-	-	-	-	54.4	-	-
Ochna arborea var. arborea	-	-	-	-	-	-	-	-	-	-	10.7	52.9	-	-
Secamone filiformis	-	-	-	-	-	-	-	-	-	-	-	51.3	-	-
Ficus burkei	-	-	-	-	-	-	-	-	-	-	-	48.2	-	-
Carissa edulis	-	-	-	-	-	-	-	-	-	-	-	46.6	-	-
Vepris reflexa	-	-	-	-	-	-	-	-	-	-	-	45.4	-	-
Capparis fascicularis var. *fascicularis*	-	-	-	-	-	-	-	-	-	-	-	45.3	-	-
Breonadia salicina	-	-	-	-	-	-	-	-	-	-	-	44.3	-	-
Pachystigma bowkeri	-	-	-	-	-	-	-	-	11.4	-	-	43.6	-	-
Maytenus undata (woodland form)	-	-	-	-	-	-	-	-	-	-	-	41.8	-	-
Diagnostic species of the vegetation unit: *Escarpment Riverine Forest* (13)														
Kyllinga odorata	-	-	-	-	-	-	-	-	-	-	-	-	85.8	-
Commelina benghalensis	-	-	-	-	-	-	-	-	-	-	-	-	85.8	-
Thelypteris interrupta	-	-	-	-	-	-	-	-	-	-	-	-	85.8	-
Urera species	-	-	-	-	-	-	-	-	-	-	-	-	85.8	-
Hydrocotyle verticillata	-	-	-	-	-	-	-	-	-	-	-	-	85.8	-
Pteris friesii	-	-	-	-	-	-	-	-	-	-	-	-	85.8	-
Microlepia speluncae	-	-	-	-	-	-	-	-	-	-	-	-	85.3	-
Thelypteris pozoi	-	-	-	-	-	-	-	-	-	-	-	-	83.4	-
Crassula alsinoides	-	-	-	-	-	-	-	-	-	-	-	-	81.6	-
Stephania abyssinica	-	-	-	-	-	-	-	-	-	-	-	-	77.2	-
Rauvolfia caffra	-	-	-	-	-	-	-	-	2.4	-	2.1	-	77	-
Vernonia myriantha	-	-	-	-	-	-	-	-	-	22.4	-	-	71.6	-
Eulophia horsfallii	-	-	-	-	-	-	-	-	-	-	-	-	69.4	-
Sida serratifolia	-	-	-	-	-	-	-	-	-	-	-	-	69.4	-
Anthocleista grandiflora	-	-	-	-	-	-	-	-	-	-	18.4	-	64.5	-
Laportea alatipes	-	-	12.7	-	-	-	-	-	-	-	-	-	59.7	-
Maesa lanceolata	-	-	-	-	-	-	-	-	-	-	-	-	55.6	-
Pterolobium stellatum	-	-	-	-	-	-	-	-	-	-	-	-	54.1	-
Carex spicato-paniculata	8.5	-	-	-	-	-	-	-	16.3	-	-	-	53.2	-
Zehneria scabra	-	-	-	-	-	-	-	-	-	-	-	-	48.6	-
Polygonum salicifolium	-	-	-	-	-	-	-	-	-	-	-	-	48.6	-
Ehretia obtusifolia	-	-	-	-	-	-	-	-	-	-	-	-	48.6	-
Agrimonia procera	-	-	-	-	-	-	-	-	-	-	-	-	48.6	-
Phoenix reclinata	-	-	-	-	-	-	-	-	-	-	-	-	48.6	-
Dracaena transvaalensis	-	-	-	-	-	-	-	-	-	-	-	-	48.6	-
Hibiscus vitifolius	-	-	-	-	-	-	-	-	-	-	-	-	48.6	-
Solanum nodiflorum	-	-	-	-	-	-	-	-	-	-	-	-	48.6	-
Cyperus sexangularis	-	-	-	-	-	-	-	-	-	-	-	-	48.6	-
Acacia robusta subsp. *clavigera*	-	-	-	-	-	-	-	-	-	-	-	-	48.6	-
Phragmites mauritianus	-	-	-	-	-	-	-	-	-	-	-	-	48.6	-
Flueggea virosa	-	-	-	-	-	-	-	-	-	-	-	-	48.6	-
Brachylaena huillensis	-	-	-	-	-	-	-	-	-	-	-	-	48.6	-
Thelypteris confluens	-	-	-	-	-	-	-	-	-	-	-	-	48.6	-
Strychnos mitis	-	-	-	-	-	-	-	-	-	-	-	-	48.6	-

Karomia speciosa	-	-	-	-	-	-	-	-	-	-	-	-	48.6	-	
Sesbania macrantha	-	-	-	-	-	-	-	-	-	-	-	-	48.6	-	
Capparis tomentosa	-	-	-	-	-	-	-	-	-	-	-	-	48.6	-	
Diospyros mespiliformis	-	-	-	-	-	-	-	-	-	-	-	-	48.6	-	
Toddalia asiatica	-	-	-	-	-	-	-	-	-	-	-	-	43.6	-	
Diagnostic species of the vegetation unit: *Legogote Scarp Forest* (14)															
Marsdenia sylvestris	-	-	-	-	-	-	-	-	-	-	-	-	-	100	
Vitellariopsis marginata	-	-	-	-	-	-	-	-	-	-	-	-	-	100	
Diospyros natalensis subsp. nummularia	-	-	-	-	-	-	-	-	-	-	-	-	-	98.5	
Kirkia wilmsii	-	-	-	-	-	-	-	-	-	-	-	-	-	93.1	
Terminalia phanerophlebia	-	-	-	-	-	-	-	-	-	-	-	-	-	90.6	
Cheilanthes viridis var. *glauca*	-	-	-	-	-	-	-	-	-	-	-	-	-	85.8	
Dombeya cymosa	-	-	-	-	-	-	-	-	-	-	-	-	-	85.8	
Atalaya alata	-	-	-	-	-	-	-	-	-	-	-	-	-	85.8	
Gymnosporia sp. (= *D graniticola*)	-	-	-	-	-	-	-	-	-	-	-	-	-	85.8	
Hibiscus calyphyllus	-	-	-	-	-	-	-	-	-	-	-	-	-	85.8	
Tarenna supra-axillaris subsp. *barbertonensis*	-	-	-	-	-	-	-	-	-	-	-	-	-	82	
Tecomaria capensis	-	-	-	-	-	-	-	-	-	-	-	-	-	77.9	
Euclea schimperi	-	-	-	-	-	-	-	-	-	-	-	-	-	77.9	
Adiantum incisum	-	-	-	-	-	-	-	-	-	-	-	-	-	77.9	
Combretum molle	-	-	-	-	-	-	-	-	-	-	-	-	-	71.1	
Maerua rosmarinoides	-	-	-	-	-	-	-	-	-	-	-	-	-	69.4	
Olax dissitiflora	-	-	-	-	-	-	-	-	-	-	-	-	-	69.4	
Sterculia murex	-	-	-	-	-	-	-	-	-	-	-	-	-	69.4	
Eugenia mossambicensis	-	-	-	-	-	-	-	-	-	-	-	-	-	69.4	
Grewia flavescens var. *flavescens*	-	-	-	-	-	-	-	-	-	-	-	-	-	69.4	
Combretum sp woodii	-	-	-	-	-	-	-	-	-	-	-	-	-	59.8	
Garcinia livingstonei	-	-	-	-	-	-	-	-	-	-	-	-	-	59.8	
Cocculus hirsutus	-	-	-	-	-	-	-	-	-	-	-	-	-	59.8	
Vitex obovata s. wilmsii	-	-	-	-	-	-	-	-	-	-	-	-	-	59.8	
Bridelia cathartica	-	-	-	-	-	-	-	-	-	-	-	-	-	59.8	
Ptaeroxylon obliquum	-	-	-	-	-	-	-	-	-	-	-	-	-	56.4	
Ruttya ovata	-	-	-	-	-	-	-	-	-	-	-	-	-	55	
Rhoicissus tridentata subsp. *cuneifolia*	-	-	14.6	15.8	-	-	-	-	-	-	-	-	-	54.7	
Homalium dentatum	-	-	-	-	-	-	9.6	-	-	-	8.3	-	-	52.8	
Obetia tenax	-	-	-	-	-	-	-	-	-	-	-	-	-	51.6	
Jasminum streptopus	12	-	-	-	-	-	-	-	15	-	-	-	-	50.7	
Erythroxylum delagoense	-	-	-	-	-	-	-	-	-	-	-	-	-	48.6	
Berchemia zeyheri	-	-	-	-	-	-	-	-	-	-	-	-	-	48.6	
Momordica foetida	-	-	-	-	-	-	-	-	-	-	-	-	-	48.6	
Strychnos madagascariensis	-	-	-	-	-	-	-	-	-	-	-	-	-	48.6	
Commiphora mollis	-	-	-	-	-	-	-	-	-	-	-	-	-	48.6	
Duvernoia aconitiflora	-	-	-	-	-	-	-	-	-	-	-	-	-	48.6	
Spirostachys africana	-	-	-	-	-	-	-	-	-	-	-	-	-	48.6	
Pupalia lappacea	-	-	-	-	-	-	-	-	-	-	-	-	-	48.6	
Acacia schweinfurthii	-	-	-	-	-	-	-	-	-	-	-	-	-	48.6	
Rhus taxon C Moffett	-	-	-	-	-	-	-	-	-	-	-	-	-	48.6	
Urginea lydenburgensis	-	-	-	-	-	-	-	-	-	-	-	-	-	48.6	
Hippocratea africana	-	-	-	-	-	-	-	-	-	-	-	-	-	44.4	
Secamone parvifolia	-	-	-	-	-	-	-	-	-	-	-	-	-	43.5	
Sansevieria hyacinthoides	-	-	-	-	-	-	-	-	-	-	-	-	-	43.3	
Dioscorea cotinifolia	-	-	-	-	-	-	-	-	-	-	-	-	-	41	

Asparagus angusticladus	-	-	-	-	-	-	-	-	-	-	-	-	-	38.9
Hippobromus pauciflorus	17.2	-	-	-	-	-	-	-	-	-	-	-	-	34.1
Barleria rotundifolia	-	-	-	-	-	-	-	-	-	-	-	-	-	32
Chaetachme aristata	-	-	-	-	-	-	-	-	-	-	-	-	-	29.9
Common diagnostic species of two forest communities														
Olinia radiata	-	-	-	-	49.4	-	33.2	-	-	-	-	-	-	-
Cassipourea malosana	-	-	-	-	40.7	21.9	34.3	-	-	-	-	-	-	-
Syzygium gerrardii	-	-	-	-	38.1	24.1	-	-	37.3	-	-	-	-	-
Sclerochiton harveyanus	-	-	-	-	35.8	22	-	49.4	-	-	-	-	-	-
Oxyanthus speciosus subsp. *gerrardii*	-	-	-	-	35.4	-	23.8	-	38.5	-	-	-	-	-
Psychotria capensis	-	-	-	-	30.6	21.5	-	-	35	-	-	-	-	-
Jasminum abyssinicum	-	-	-	-	28.9	56.3	-	-	-	-	-	-	-	-
Podocarpus latifolius	-	38.7	-	-	26.7	23.2	21.6	-	-	-	-	-	-	-
Eugenia natalitia	-	-	-	-	-	-	-	51.7	32.7	-	-	-	-	-
Dovyalis rhamnoides	-	38.2	-	-	-	-	16.1	47.5	-	-	-	-	-	-
Maytenus acuminata var. *acuminata*	-	-	-	-	18.8	25	-	47.1	-	-	-	-	-	-
Mimusops obovata	6	-	-	-	-	-	-	46.1	-	-	-	-	-	44.4
Scutia myrtina	19	33.6	-	-	-	12.6	-	44.6	-	-	-	-	-	-
Canthium kuntzeanum	-	-	-	-	-	28.7	-	39.8	-	-	-	-	-	-
Pleurostylia capensis	25.1	-	-	-	-	-	-	35.9	-	-	-	-	-	-
Rothmannia globosa	-	-	-	-	-	-	-	33.2	-	51.7	-	-	-	-
Rhoicissus rhomboidea	-	-	-	-	-	13.8	24.3	32.9	26.5	-	-	-	-	-
Rhus lucida forma. lucida	21.4	-	26.5	-	-	-	-	30.7	-	-	-	-	-	-
Euclea natalensis	14.4	-	-	-	-	-	-	29.5	-	-	12.5	-	-	49.1
Pittosporum viridiflorum	-	-	34.8	-	-	-	-	27	-	-	-	-	-	-
Protorhus longifolia	-	-	-	-	-	-	-	25.8	-	39.9	22	-	-	-
Pavetta kotzei	-	-	44.3	-	-	44.8	-	-	-	-	-	-	-	-
Dovyalis lucida	-	-	-	-	-	37.4	27.4	-	-	-	-	-	-	-
Chionanthus foveolatus subsp. *major*	-	-	-	-	-	32.9	42.6	-	-	-	-	-	-	-
Dryopteris inaequalis	-	-	34.2	-	-	25.1	-	-	-	-	-	-	-	-
Tricalysia capensis var. *transvaalensis*	-	-	-	-	-	-	30.6	-	48	-	-	-	-	-
Cnestis polyphylla	-	-	-	-	-	-	-	-	30.9	-	26.8	-	-	-
Nuxia congesta	-	-	-	44.3	-	-	-	-	27.3	-	-	-	-	-
Peddiea africana	-	-	-	-	23.1	24.1	-	-	25.8	32.2	-	-	-	-
Pavetta barbertonensis	-	-	-	-	-	-	67.7	-	-	-	30.4	-	-	-
Keetia gueinzii	-	-	-	-	-	-	37.3	-	-	-	36.1	-	-	-
Hypoestes aristata var. alba	-	-	29.5	-	-	-	36.2	-	-	-	-	-	-	-
Chionanthus foveolatus subsp. *foveolatus*	43.5	-	-	-	-	-	-	-	-	-	-	-	-	67.6
Asparagus virgatus	37.6	-	29.9	-	-	-	-	-	-	-	5.5	-	-	-
Harpephyllum caffrum	37.4	-	-	-	-	-	-	-	-	-	45.9	-	-	-
Cassinopsis ilicifolia	32.9	20.2	45.2	-	-	-	-	-	-	-	-	-	-	-
Buddleja auriculata	-	-	40.1	51.4	-	-	-	-	-	-	-	-	-	-
Olinia emarginata	15.6	-	39.3	45.5	-	-	-	-	-	-	-	-	-	-
Rhus pyroides v. gracilis	-	-	54.6	39.2	-	-	-	-	-	-	-	-	-	-
Celtis africana	9.5	-	-	28	-	-	-	-	-	12.2	11.1	28	-	-
Asplenium adiantum-nigrum var. *adiantum-nigrum*	-	-	30.2	27.9	-	-	-	-	-	-	-	-	-	-
Kiggelaria africana	-	28.2	26	-	-	14.4	-	-	-	-	-	-	-	-
Cryptocarya woodii	10.3	48.4	-	-	-	-	-	-	-	-	27.8	-	-	-
Crocosmia aurea var. *aurea*	-	39.5	-	-	-	8	-	-	-	34.8	-	-	-	-
Tricalysia lanceolata	-	14	-	-	-	-	-	-	-	29.8	-	54.2	-	-
Abrus precatorius	-	-	-	-	-	-	-	-	-	-	-	65.9	-	37.8
Gymnosporia rubra	-	-	-	-	-	-	-	-	-	-	31.7	64.4	-	-

Ochna natalitia	-	-	-	-	-	-	-	-	-	-	4.8	63.8	-	35.4
Hyperacanthus amoenus	-	-	-	-	-	-	-	24.5	-	-	-	61.6	-	43.1
Acalypha glabrata	-	-	-	-	-	-	-	-	-	-	-	54.2	-	29.8
Englerophytum natalense	-	-	-	-	-	-	-	-	14.4	19.2	49.2	52.9	-	-
Rawsonia lucida	-	-	-	-	-	-	11	-	13.1	-	28.3	47.8	-	-
Croton sylvaticus	-	-	-	-	-	-	-	-	18.8	-	40.4	46.1	-	-
Erythroxylum emarginatum	-	-	-	-	-	-	-	-	-	-	29.1	46	-	-
Adenia digitata	-	-	-	-	-	-	-	-	-	-	-	44.3	-	25.3
Thelypteris dentata	-	-	-	-	-	-	-	-	-	16.9	-	36.2	48	-
Peperomia blanda	-	-	-	-	-	-	-	-	-	-	-	28.1	-	72.4
Setaria megaphylla	-	-	-	-	-	-	-	-	-	9.9	-	26.4	53.5	-
Acridocarpus natalitius var. *natalitius*	-	-	-	-	-	-	-	-	-	-	31.7	-	-	45.2
Aneilema aequinoctiale	-	-	-	-	-	-	-	-	-	17	-	-	59.8	25.3
Common diagnostic species of three forest communities														
Pavetta inandensis	-	-	-	-	35.6	-	25.1	36.2	-	-	-	-	-	-
Olea capensis subsp. *macrocarpa*	-	-	-	-	35.3	24	32.5	46.4	-	-	-	-	-	-
Scolopia mundii	24.1	26.5	27	-	-	13.8	-	44.7	-	-	-	-	-	-
Gymnosporia harveyana	27.4	32	-	-	-	16.4	-	29.6	-	-	-	-	-	-
Monanthotaxis caffra	-	-	-	-	-	-	-	-	44.8	38.6	59.3	-	-	-
Canthium mundianum	-	-	-	35.5	-	-	-	-	-	-	-	26.5	35.5	-
Achyranthes aspera var. *aspera*	17.9	-	44.2	33.5	-	-	-	-	-	-	-	-	-	28.3
Bridelia micrantha	-	-	-	-	-	-	-	-	-	44.6	6.8	27	54.4	-
Rhoicissus tomentosa	2.3	-	-	-	-	-	-	-	-	29.5	10.4	37.8	-	30.5
Ficus sur	-	-	-	-	-	-	-	-	-	27.4	8.8	37.8	34.5	-
Syzygium cordatum	-	-	-	-	-	-	-	-	4.5	26.5	-	28.5	56.6	-
Dalbergia armata	14.5	-	-	-	-	-	-	-	13.9	-	28.7	35.1	-	27.9
Common diagnostic species of four forest communities														
Psychotria zombamontana	-	-	-	-	41.6	32.6	-	40.8	34.5	-	-	-	-	-
Combretum kraussii	24.3	-	-	-	-	-	-	33.7	30.5	29.7	27.5	-	-	-
Englerophytum magalismontanum	-	-	-	-	-	-	-	-	31.7	30.8	35.5	31.7	-	-

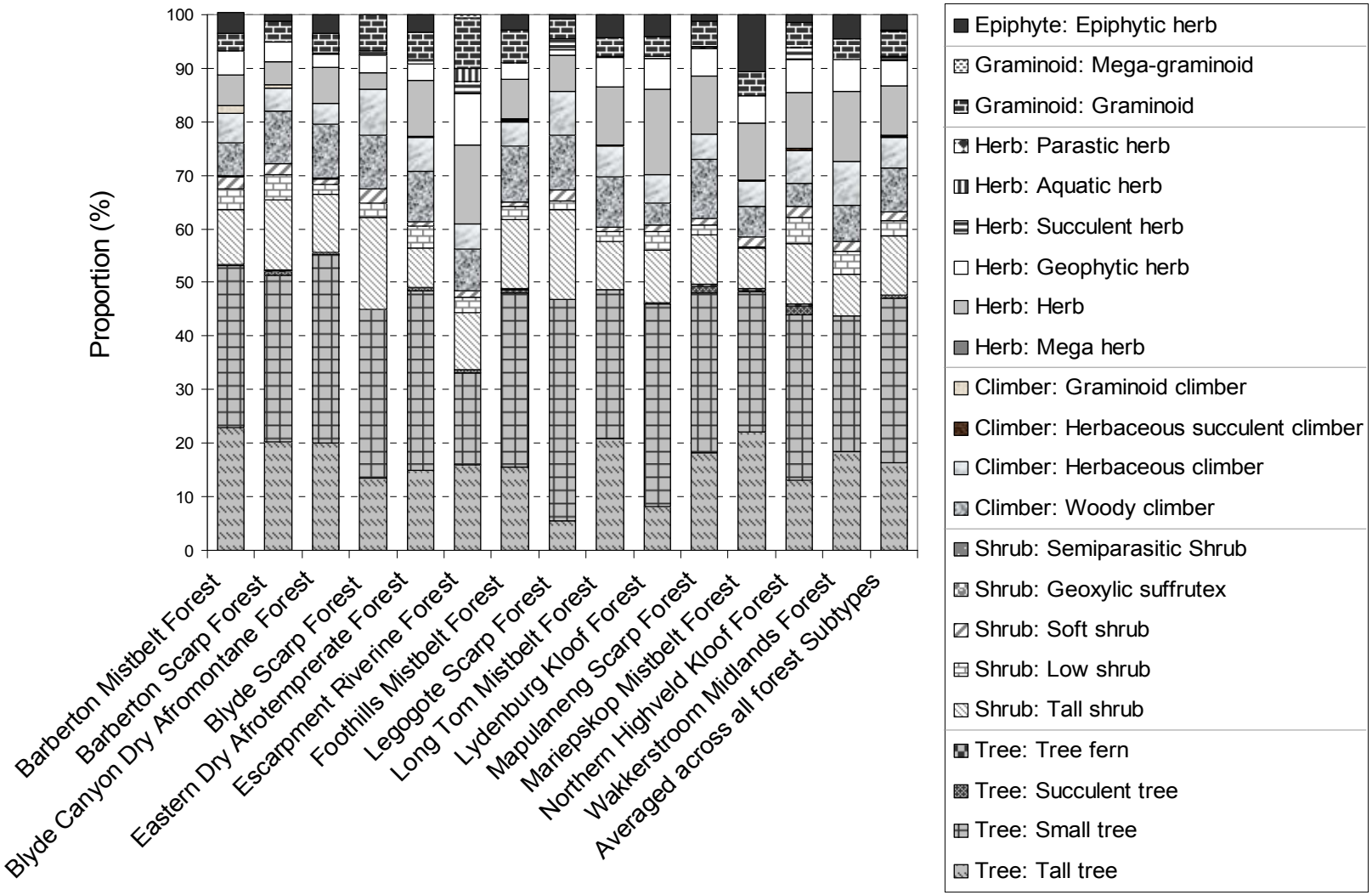


Figure S1
Proportional stacked bar graph of growth form subcategories for all forest subtypes. The values represent a proportion of all species occurrences.

CHAPTER FOUR:

Disentangling forest composition: scaling hierarchy of environmental and geographic variables controlling species patterns

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ABSTRACT

Aim The search for underlying drivers of vegetation patterns is often pursued through analysing the relationship between species distributions and environmental or spatial characteristics. In order to ascertain the effect of geographic space and different scales of environmental variables on forest composition, we addressed the following four questions: (1) What are the main environmental variables driving variation in species patterns and richness? (2) What is the influence of local, regional and supra-regional scaled environmental variables on species patterns? (3) To what extent can species-compositional gradients be interpreted in environmental and geographic space, and do they differ across forest strata? (4) Is dispersal an important driver of species patterns in forests?
Location Mpumalanga Province, South Africa.

Methods We applied the Bray-Curtis distance measure within db-RDA to interpret species–environment gradients. Constrained ordination and variation partitioning were used to explore the influence of three scales of environmental variables and geographic space on patterns in species composition. In addition to the full floristic complement, the data set was also separated into herbaceous, shrub and tree strata, and the influence of explanatory variables on individual forest strata interpreted. The scale at which the environmental variables vary over distance was established by means of semivariogram analysis, where each variable was categorised into one of three spatial scales (local, regional, and supra-regional) based on a visual inspection of the resulting nuggets, sills and range values. To investigate the influence of geographic space, we used a polynomial function of the geographic coordinates of the sampling sites to represent broad-scale spatial relationships, such as dispersal, to explain variation in vegetation patterns.

Results The db-RDA based on all environmental variables showed that 51% of total variability can be explained across all axes. The largest fraction of species–environment variation was

explained by the regional variable matrix (45%), followed by the effects of supra-regional (21%) and local variable matrices (19%).
Using the full floristic data, both the environmental and geographic variable matrices accounted for 55% of the observed variation. In addition, most (19%) of the spatial variation (23%), can be explained by spatially structured environmental variables. Only about 4% of the variation is attributed to pure geographic space. The results support our hypothesis that the geographic and environmental factors are interacting across a range of spatial and environmental scales, although regionally scaled environmental variables have the greatest influence on species composition. These factors have similar observed effects on the three forest strata, although most of the detected variation occurred in the shrub stratum.

Main conclusions Environmental gradients have a greater influence on species composition than geographic space. Geographic space partially explains the important role of dispersal in influencing variation in species patterns across all forest strata, even in the herbaceous stratum where the substantial contribution of dispersal was unexpected. We confirm that dispersal alters both environmental as well as spatial variability but it is difficult to distinguish between them using variation partitioning. Our model provides insight into the relative contributions of environmental variables and the scale of their influence, and geographic space on forest vegetation patterns in Mpumalanga.

Key words

Bray-Curtis distance, dispersal, distance-based Redundancy Analysis, environmental scale, forest composition, geographic space, ordination, partial ordination, semivariogram.

INTRODUCTION

Observed variation in vegetation patterns may be partly interpreted by means of various ecological and biogeographical theories, ranging from Diamond's (1975) community "assembly rules" to differences in assembly history (Chase 2003) such as historic biogeography (i.e. glaciation), where the resulting flora was formed by environmental and ecological processes that may no longer exist. Current community composition may then be the result of either deterministic niche-based or stochastic neutral processes, where stochastic processes may result in chance colonisation or ecological drift. Neutral theory is an ensemble of different neutral models for community assembly where neutrality is based on the stochasticity in demographic rates (Rosindell et al. 2012). Dispersal limitation is a much debated process that may in fact influence both niche-based and stochastic processes (Chase and Myers 2011).

Stochastic processes such as dispersal, seen as a sequence of random events, are also influenced by the size of available species pools (i.e. metacommunity; McGill et al. 2006) or "dark diversity" (Pärtel et al. 2011). Niche-based processes include both environmental (abiotic) filtering and biotic interactions but may also be structured by morphological characteristics such as plant size, propagule pressure, availability of niches and niche competition, but all of these interact across a range of scales of environmental processes to alter community composition (Chase and Myers 2011).

Ecologists occasionally use ordination and variation partitioning (Legendre 1990; Borcard et al. 1992; Wagner 2004; Legendre et al. 2009) to decompose and disentangle the variation in community composition according to current ecological theory. In particular, variation partitioning has previously been applied to interpret the influences of neutral and niche-based theories (see Laliberté et al. 2009; Legendre et al. 2009), where it has generally been claimed that the portion attributable towards "space" directly represents the relative importance of "neutral processes" (*sensu* Hubbell 2001), while that portion attributable to "environment" represents the relative importance of "niche-based processes" (Legendre et al. 2009). However recent studies (Anderson et al. 2010; Smith and Lundholm 2010; Heino 2011) have shown this approach to be flawed based on (1) the spatial structure in measured environmental variables (leading to overlap in explained variation) precludes any logical inference about whether processes were niche-based or neutral (Anderson et al. 2010); (2) the apparently spatial portions interpreted as "neutral" could simply have been due to unmeasured environmental variables (Anderson et al. 2010); (3) both niche and neutral processes generate similar spatial patterns where dispersal between adjacent sites generates spatial autocorrelation in neutral communities. In niche-structured communities, community similarity declines with increasing environmental distance and environmental conditions are frequently spatially autocorrelated (Legendre 1993). Data from both truly neutral and niche-based communities may thus appear to have environmental structure, since both community data and environmental variables may be spatially autocorrelated (Smith and Lundholm 2010); and (4) if study sites are distributed across a very wide geographical region, then spatially structured variation in community composition increases and niche-structured control decreases. This suggests that dispersal limitation increases with increasing geographical extent and niche-based processes increase with decreasing regional extent (Heino 2011).

As inferred above, the influence of niche-based processes on composition varies with scale (Chase and Myers 2011), where vegetation patterns result from environmental factors operating at different scales and can be ordered in a hierarchical system from small to large (Sieben et al. 2009). Within a study area, as the geographic area considered becomes smaller or the environment becomes more uniform, the importance of these factors decline in favour of others expressed at scales of greater detail (de Miguel et al. 2005). In addition, as community composition is a complex product of many different processes that are difficult to decompose at a single scale, a significant challenge in ecological studies has been defining scales of

observation that match the ecological scales affecting the organisms or processes of interest (Karl and Maurer 2010). In this study we incorporate geostatistics (Legendre 1993; Blanchet et al. 2008) to define scales of observation that are linked to spatial ecological scales, and that inform the identification of multiple-scales of environmental variables that may individually influence forest composition. These multiple-scales form a hierarchy that consist of local, regional and supra-regional environmental variables. By embracing processes across scales, one can build a more integrated framework for understanding how niche and stochastic processes result in species patterns that emerge from a variety of scales (Chase and Myers 2011).

Dispersal is not purely a neutral process (de Casas et al. 2012). In variation portioning models, dispersal would influence both geographic spatial structure as well as environmental control (Smith and Lundholm 2010), and consequently the proportion of variation attributable to spatial and environmental variables may not identify the relative contribution of neutral and niche-based processes in shaping the community under study. Simulations with low migration rates (dispersal) and high mortality resulted in different species becoming dominant in cells with the same environmental values. As migration increases, exchange of individuals between adjacent cells produces a more invariant community associated with each value of the environmental variable. At high migration rates this consistency declines, as migrating individuals increasingly establish in cells with suboptimal habitat conditions, resulting in mass effects (Shmida and Wilson 1985; Smith and Lundholm 2010). The implication of the above is reiterated in that dispersal, or migration, alters both environmental as well as spatial variability and makes it difficult to distinguish between either using variation partitioning.

In most plants, seed dispersal is the only mechanism to reach new localities, and is therefore the primary means of habitat selection (de Casas et al. 2012). But dispersal probabilities say little about the likelihood that species will persist. At the community level, the influence of diaspore arrival (i.e. regional dispersal or immigration) on species patterns may depend on niche-based environmental filters (Chase and Myers 2011). Dispersal rates can also influence similarity of local communities (Chase 2003).

Our knowledge of causal environment-vegetation relationships may be improved by means of constrained ordinations and variation partitioning. We apply this approach to the indigenous forests in Mpumalanga Province, South Africa, to further our understanding of dispersal and the relative significance of environmental variables operating at various spatial scales of influence and geographic space as drivers structuring species composition in naturally fragmented vegetation.

To our knowledge, the current study is the first exploration into the influence of geographic space and local, regional and supra-regional scales of environmental variables on forest composition globally. In addition, our application of semivariogram analysis in determining the spatial scales of environmental variables is novel. The specific key questions central to

understanding the influence of geographic space and scale's of environmental variables on the compositional structure of forests, include:

- What are the main environmental variables driving variation in species composition and do any of these contribute towards species richness?
- What is the influence of local, regional and supra-regional scales of environmental variables on forest composition?
- To what extent can species-compositional gradients be interpreted in environmental and geographic space, and can they further our understanding of the relative effects of environmental control and neutral processes?
- To what extent does the influence of geographic distance and scale of environmental variables differ across the individual forest strata?
- Is dispersal an important driver of species patterns in forests?

The present study is preceded by a regional-scale classification of indigenous forests into forest subtypes *(*Lötter et al. 2014) nested within the National Forest Classification (NFC; von Maltitz et al. 2003), sufficiently circumscribing compositional pattern, but failing to investigate causal factors. The NFC contains seven forest groups, comprising 24 forest types. This paper explorers the influence of space and environmental variables on the new regional forest classification (Table 1).

MATERIALS AND METHODS

Study area

The study was carried out in the forest biome of Mpumalanga Province, situated in the north-eastern part of South Africa; an area of 76,520 km². The Province comprises a diversity of landscapes characteristic of the grassland, savanna and warm-temperate and subtropical forest biomes, the latter two usually occurring in scattered patches. Grasslands are most prevalent, making up 65% of the Province, while forests occupy only 0.51%. The altitude at which the forest patches occur varies between 251 m and 1974 m while mean annual rainfall varies between 500 to 1635 mm and mean annual temperature between 14°C and 22°C (according to modelled data of Schulze 2007). The indigenous forests are largely confined to the north-south running Mpumalanga Escarpment. Phytogeographically this area forms part of the Drakensberg Afromontane Region, with lower altitude parts classified as the Maputaland-Pondoland Region (Van Wyk and Smith 2001; Lötter *et al.* 2002). The forests are naturally very fragmented with a median patch size of 4.6 ha (range: 0.04 — 3790 ha; Chapter 5).

Table 1 Syntaxonomic classification of Mpumalanga forests into subtypes (Lötter et al. 2014), nested within the National Forest Classification (von Maltitz *et al*. 2003) and Eastern Scarp subtype classification (Mucina *et al.* 2007). Names in brackets correspond to legend used in Figure 4 and Appendix S2.

IV Northern Mistbelt Group

IV2 TYPE: Mpumalanga Mistbelt Forest

SUBTYPE: Mariepskop Mistbelt Forest (Marieps Mistb)
SUBTYPE: Blyde Canyon Dry Afromontane Forest (Blyde Dry Afrom)
SUBTYPE: Long Tom Mistbelt Forest (LongTom Mistb)
SUBTYPE: Foothills Mistbelt Forest (Foothills Mistb)
SUBTYPE: Barberton Mistbelt Forest (Barberton Mistb)

II Northern Afrotemperate Group

II2 TYPE: Northern Highveld Forest

SUBTYPE: Eastern Dry Afrotemperate Forest (East Dry Afrotem)
SUBTYPE: Northern Highveld Kloof Forest (NorthHigh Kloof)
SUBTYPE: Lydenburg Kloof Forest (Lydenburg Kloof)
SUBTYPE: Wakkerstroom Midlands Forest (Wakkerstroom Midlands)

V Scarp Forest Group

V1 TYPE: Eastern Scarp Forest

SUBTYPE: Mapulaneng Scarp Forest (Mapulaneng Scarp)
SUBTYPE: Blyde Scarp Forest (Blyde Scarp)
SUBTYPE: Barberton Scarp (Barberton Scarp)
SUBTYPE: Legogote Scarp (Legogote Scarp)

Field sampling

In total, 430 vegetation plots were sampled throughout the South African provinces of Mpumalanga, Gauteng, southern Limpopo and northern KwaZulu-Natal. Sampling involved selecting sites across a range of altitudes, landscapes, and climatic conditions. The sample sites were restricted to those forest patches with little evidence of recent human disturbance or where the floristic composition was natural (we avoided areas where invasive alien plant species were present). At each site several plots were preferentially located throughout the forest as far as accessibility allowed. Plots of 20 m x 20 m (0.04 ha) were used to sample species composition. Cover-abundance values were recorded for each plant species according to the seven-class Braun-Blanquet cover-abundance scale (Mueller-Dombois and Ellenberg 1974). The plots included a list of all vascular plant species recorded according to the particular stratum (tree, shrub, herbaceous) in which the species was present, with tree seedlings included in the shrub layer. Plants were identified to species or infraspecific levels (subspecies or variety) wherever possible. The term 'species' is hereafter used to refer to the lowest recognised taxonomic category. All plots, except for 36 plots from Pedlar's Bush (Morgenthal and Cilliers 1999) are original data. The plot data set were pre-classified into forest subtypes (Lötter et al. 2014) to assist the interpretation of vegetation patterns.

The plot data were stored in a Turboveg 2.8 database (Hennekens and Schaminée 2001) for ease of extraction and information management. For the objectives of this study, four data sets were exported from Turboveg. These included a full species data set for all three layers

(trees, shrubs and herbs) comprising 592 species. Species with less than 3 occurrences were removed, resulting in 442 species in the full data set. The (i) tree canopy, (ii) shrub and (iii) herbaceous plants data sets comprised 142, 211 and 178 species, within 430, 430 and 428 plots respectively (two plots contained no herbaceous species).

Environmental variables

The development of our environmental variable framework was informed by 1) actual field observations of certain local-scale variables, and 2) the development of a comprehensive GIS data set of a range of environmental variables that could be generated for any plot or area (Table 2).

During field observations, for each plot we measured environmental variables such as slope (using a clinometer), rockiness (5 classes from no rocks to plentiful boulders), and water drainage (3 classes from dry through seepage to river bank). Aspect was occasionally missing or difficult to assess in the field, therefore it was GIS derived together with the remainder of the variables.

The GIS data sets were derived from the finest-scale data available. The 30 m Aster GDEM (Tachikaw *et al*. 2011) was the basis for several DEM derived products using ArcView 3, ArcGIS 10 (ESRI 1999–2011) or IDRISI Taiga (Eastman 2009). The GIS data sets covered a variety of substrates, topographic, and climate-related variables. The substrate variables were sampled from the national Land Type Survey maps (Land Type Survey Staff 1972–2006), published at 1:250,000 scale and broad geological formations and geology types (both published at the 1:1,000,000 scale). We also included soil depth and clay content from GIS raster data obtained from the Department of Agriculture in Mpumalanga.

Specifically the 30 m GDEM formed the basis for the development of the following topographic variables: altitude, aspect (measured as a continuous scale of Sine and Cosine of aspect for eastiness and northiness), curvature, hillshade, landform classification (Jenness 2006), two scales of Topographical Positional Index (120 m and 3 km neighbourhoods; Jenness 2006), slope, and solar radiation, processed using ArcGIS 10. The solar radiation tool is provided in the ArcGIS Spatial Analyst extension (ESRI 2011). It analyses the effects of the sun over a geographic area for specific time periods. It accounts for atmospheric effects, site latitude and elevation, steepness (slope), aspect, daily and seasonal shifts of the sun angle, and effects of shadows cast by surrounding topography (i.e. hillshading). We also included Enhanced Vegetation Index (EVI) and Normalized Difference Vegetation Index (NDVI) data for the month of May 2008 from the Moderate Resolution Imaging Spectroradiometer (MODIS) sensor aboard the NASA Terra satellite. The 250 m resolution MODIS derived variables were considered as a proxy for vegetation cover and fine-scaled unmeasured variables influencing local vegetation growth.

The climate data were assembled from three sources. Precipitation, rainfall, temperature and evaporation related variables were obtained from the South African Atlas of Climatology and Agrohydrology (Schulze 2007). Isothermality was sourced from the WorldClim database (Hijmans et al. 2005; http://www.worldclim.org/), which is a set of global climate layers generated through interpolation of climate data from weather stations on a 30" grid (ca. 1 km² resolution). Lastly we included the climatic data sets identified in Rutherford *et al*. (2006), which were effective in modelling the distribution of vegetation biomes across South Africa. The constituent GIS raster's included: mean minimum temperature of the coldest month, heat units above 18°C, annual mean evaporation, and soil moisture days in winter and in summer. In total 29 continuous and 5 nominal variables (expanding to 43 variables) were recorded or developed to cover the range of environmental variables likely to have an influence on species composition.

Determining the scale of environmental variables

The scale of individual environmental variables was established by means of geostatistics and the application of *semivariogram analysis* (plot of variance between pairs of points as a function of distance between points). The form of the semivariogram can provide an indication of the nature of spatial dependence in a data set and the range over which the dependent variable is spatially dependent (Phillips 1986). We used IDRISI Taiga (Eastman 2009) to apply the omnidirectional semivariogram model to each of the environmental variables using the Gstat package (Pebesma 2004). The semivariogram model was characterized by its *nugget* (i.e. variability at distances smaller than the shortest distance between sample points, including measurement error), *sill* (i.e. total observed variation of the variable), and the *range* (i.e. total separation distance from the lowest variance to the sill – the distance at which two observations could be considered independent; Karl and Maurer 2010).

Because our sampling points were very limited and irregularly clustered (owing to the naturally fragmented distribution of forests in Mpumalanga), we needed to generate an additional 2000 random points across the study area to adequately sample the variability of environmental variables. These were primarily outside of forested areas. The comprehensive data set of GIS-derived environmental variables was then used to assign values to each of the new random sampling points (Figure 1).

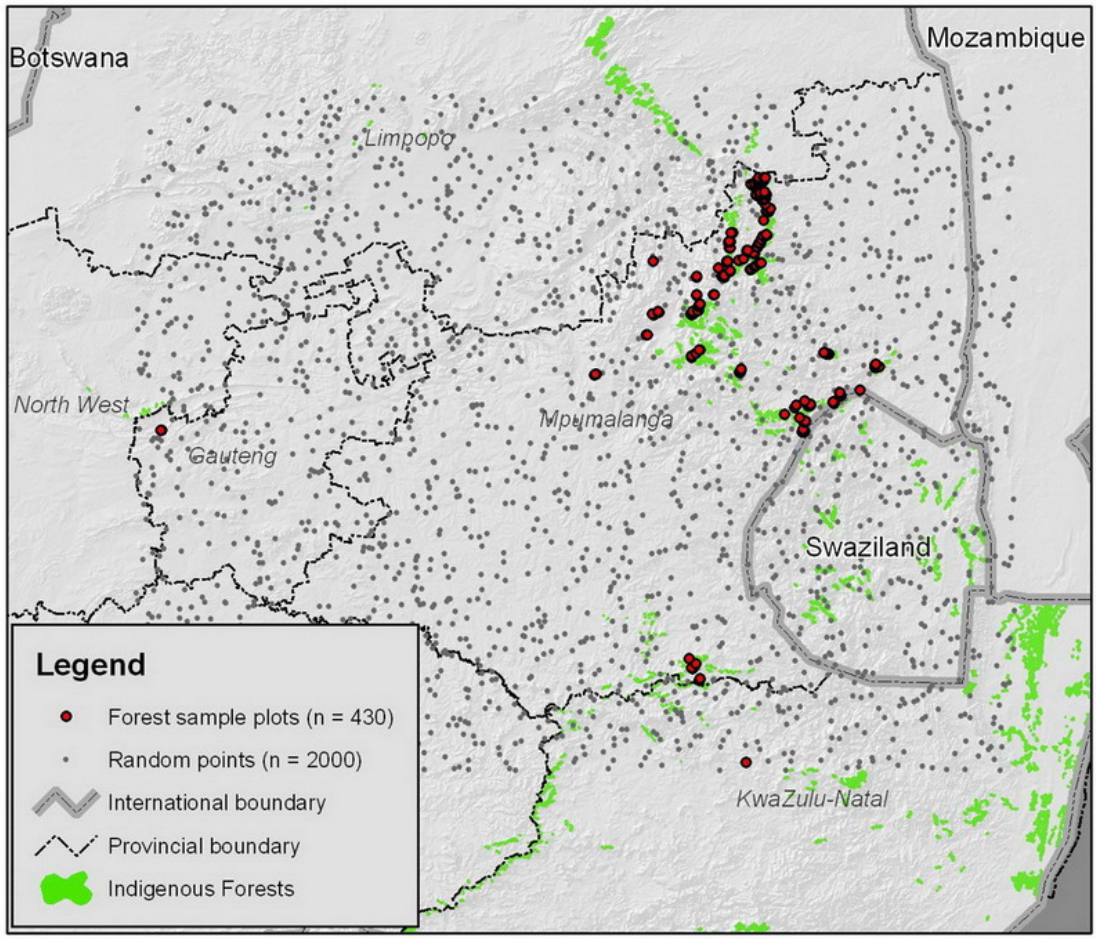


Figure 1 Location of the 430 forest plots and the 2000 randomly generated sample points used to inform the semivariogram analysis, Mpumalanga Province, South Africa.

Based on a visual inspection of the resulting nuggets, sills, and range values, the variables were assessed in terms of variance distance and shape of modelled curve. If the nugget values were large, this represented large local-scale variability; i.e. that did not change much over greater separation distance. If the curve peaked within the range sampled, then the variable was of a regional scale, and finally if the curve did not flatten and the range exceeded the scale of measurements, then it indicated a supra-regional scaled variable. Large nugget values would be independent of range and sill values in our interpretation as the observed variation (with high nugget values) would be as great between plots within a forest than between different forests across the province. Hence range and sill values become irrelevant when nugget values are large. For the purpose of illustrating the application of semivariograms to the classification of spatial scales, Figure 2 shows six semivariograms classified into one of the three scales. Most variables were easy to place into one of the three categories, but altitude and EVI (enhanced Vegetation Index) were almost 'transitional' between categories and were subsequently assigned to both categories.

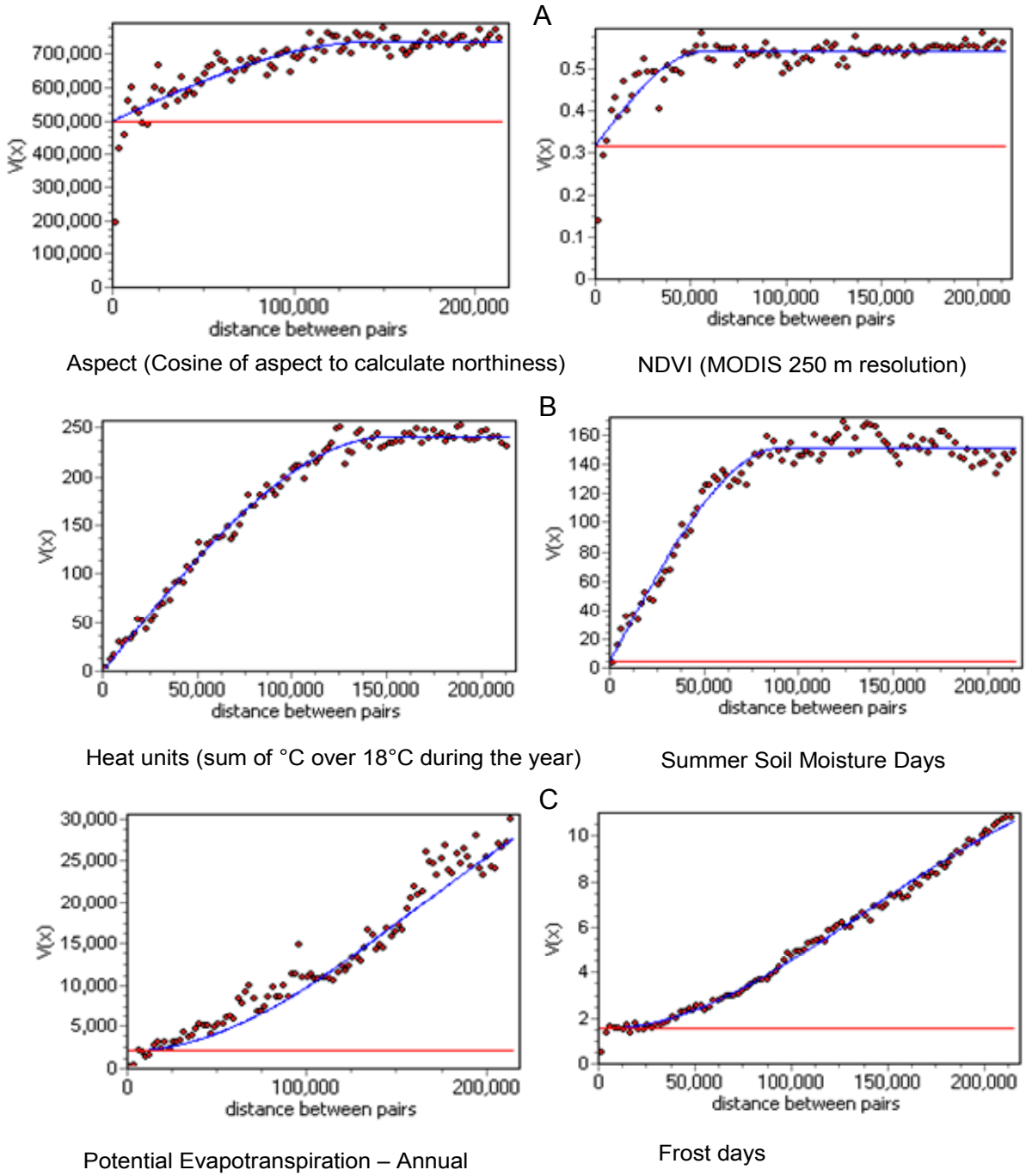


Figure 2 Semivariogram of six of the environmental variables classified into one of three scales of measurement: A) local, B) regional and C) supra-regional scale. The measurement scale of the X-axis is in meters.

Geographic spatial variables

We used a polynomial function of the geographic coordinates of the sampling sites to represent broad-scale spatial relationships in models aimed at explaining variation in species patterns and dispersal. The use of polynomials for analysing the spatial structure of ecological

communities was first proposed by Legendre (1990). The method ensures that not only the linear gradient structures in the species data are extracted, but also the more complex features such as patches or gaps, which require the quadratic and cubic terms of the coordinates for their interactions to be correctly decomposed (Borcard *et al.* 1992). Coordinates were first projected into meters before using SpaceMaker 2 (Borcard and Legendre 2011) to centre the coordinates on their respective means, before computing the monomials. The spatial variable matrix initially contained sixteen terms of a forth-order polynomial regression of geographic coordinates. Fourteen terms were retained for both db-RDA and partial db-RDA following forward selection.

In recent years numerous methodological developments have been proposed to model space more effectively, namely principal coordinates of neighbour matrices (Borcard and Legendre 2002; Borcard *et al.* 2004), Moran's eigenvector maps (Dray *et al*. 2006) and Multi-Scale Pattern Analysis (Jombart *et al*. 2009). We investigated the application of these approaches to our data set but our highly irregular sampling pattern, based on the irregular natural distribution of forests in Mpumalanga, resulted in the unsuccessful application of these techniques. The reason for this is the difficulty of generating a suitable neighbourhood matrix which is necessary to link autocorrelation to the notion of scale/distance. We therefore settled on generating polynomial trend surfaces that are capable of decomposing larger-scale spatial structures.

Numerical data collation and analysis

The purpose of the numerical analysis was to develop a model to compare the interaction effects of locally-, regionally- and supra-regionally-scaled environmental and spatial explanatory variables on forest composition and individual forest strata. Explanatory variables were grouped into seven matrices (local variable matrix, regional, supra-regional, local and regional variable matrix, local and supra-regional, regional and supra-regional and spatial variable matrix). Four response variable matrices were calculated from the log-transformed species cover data of the 430 plots:

(1) all species (full complement);

(2) species recorded in the canopy stratum;

(3) species recorded in the shrub layer (including tree seedlings); and

(4) herbaceous plants (including herbaceous epiphytes).

We applied the Bray-Curtis distance measure in combination with distance-based redundancy analysis (db-RDA). Bray-Curtis is generally acknowledged to be a good measure of ecological resemblance for species abundances (Faith *et al.* 1987; Legendre and Legendre

1998; Legendre and Anderson 1999; Clarke and Gorley 2006) particularly for the forests in Mpumalanga (Lötter *et al*. 2013). We selected db-RDA over canonical correspondence analysis (CCA; Lepš and Šmilauer 2003) since the latter includes chi-square as the resemblance measure, which is not unanimously accepted among ecologists (Kenkel and Orlóci,1986); and Faith *et al.* (1987) concluded that it was one of the worst "distances" for community composition data. In contrast the db-RDA method allows an ecologist to select the distance measure, with emphasis on situations where the chosen measure is semi-metric (such as the Bray-Curtis measure). The db-RDA begins with the calculation of dissimilarities among samples, followed by principal coordinates analysis (PCoA), followed by redundancy analysis (RDA), where the *X* matrix (independent environmental or spatial variables) contains dummy variables in an ANOVA model and the *Y* matrix (species response variables) consists of the principal coordinates. (Legendre and Anderson 1999). All analyses were conducted using Canoco for Windows 4.5 and PrCoord 1.0 (ter Braak and Šmilauer 2002; Lepš and Šmilauer 2003).

We then applied the variation partitioning approach as described by Borcard *et al.* (1992), Borcard and Legendre (1994) and Økland (2003), using (partial) constrained ordinations to give quantitative information on the relative importance of competing sets of explanatory variables as possible primary causes of variation in species composition. We applied the above approach using the full species complement and each of the forest strata separately on (1) geographic space and environmental variables, and (2) three scales of environmental variables. See Figure 3 for graphical example of partitioning out the components of (a) a non-spatially-structured component explained by the environmental variables in the model, (b) a spatially-structured component of environmental variation (i.e. semivariogram analysis established that several environmental variables varied over distance), (c) a fraction of spatially-structured variation which is not explained by the environmental variables and possibly results from community dynamics, and (d) a residual fraction that may be a result of either biological or environmental variables not measured, or historic biogeographic processes.

Individual and combined environmental (local, regional and supra-regional) and spatial matrices were screened using forward selection procedure and associated Monte Carlo tests to facilitate selection of variables with significant conditional effects on species response. Only statistically significant ($P<0.002$) variables were selected (Lepš and Šmilauer 2003). The selection process was then repeated in the context of partial db-RDA. Table 2 provides a list of continuous environmental variables (excluding dummy/nominal variables) classified according to scale and retained following forward selection procedures for inclusion in subsequent db-RDA and partial db-RDA ordinations.

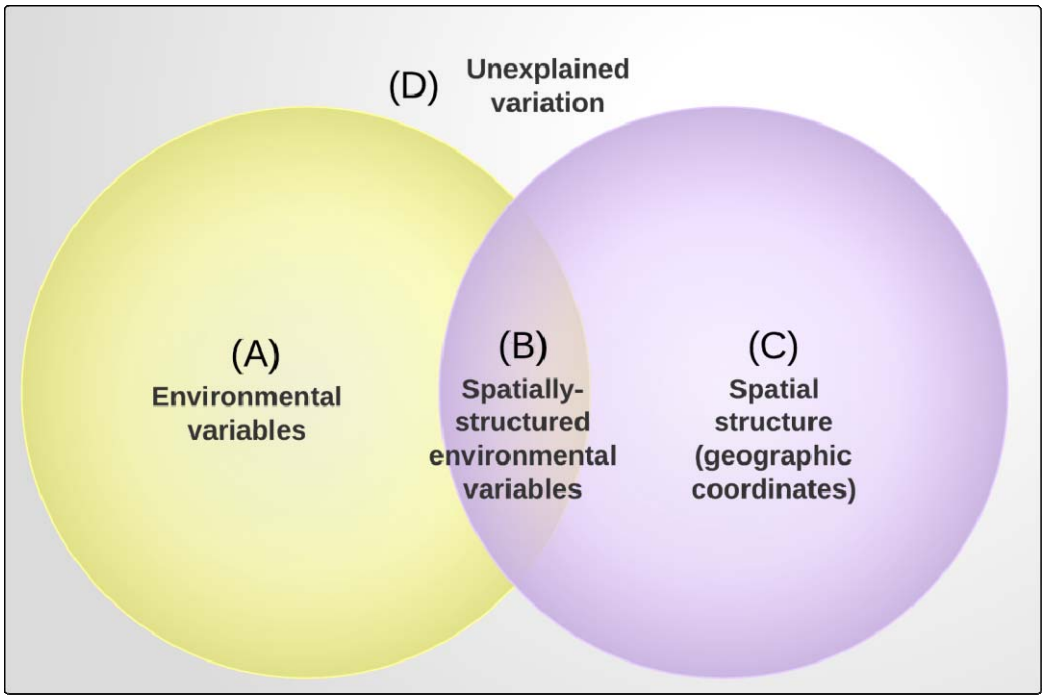


Figure 3 Partition of variation of a species response matrix between environmental and spatial explanatory variables based on geographic coordinates. The grey box, which corresponds to 100% of the variation in the species matrix, is divided into four fractions labelled [a] to [d]. Adapted from Borcard *et al.* (1992).

The null hypothesis tested was that of independence of species-response data from explanatory variable sets. The Monte Carlo test was used to assess the significance of each variable upon inclusion in the regression model. Simple correlations of individual explanatory variables with species data are presented as a vector biplot. Vector angles and lengths correspond to the degree and strength of correlations. Significant correlations between canonical scores and species richness (number of species per 400 m²) are similarly presented. The fraction of the variation explained by a set of explanatory variables was the sum of all canonical eigenvalues. Fractions representing two- and three-way interactions, and the fraction of unexplained variation were calculated indirectly from simple and partial terms and were not statistically testable (Carr *et al*. 2009). Variation partitioning and statistical tests were performed using CANOCO ver. 4.5 (ter Braak and Šmilauer 2002; Lepš and Šmilauer 2003).The total variance explained (TVE) represents the 'total inertia' attributable to explanatory factors in the model (ter Braak and Šmilauer 2002). Following Carr *et al.* (2009), we similarly present explained variance in terms of proportions of TVE only (reported TVE fractions are expressed as a % of TVE, unless otherwise indicated).

Table 2 List of continuous environmental variables following the forward selection procedures. The environmental variables are classified into one of three scales based on semivariogram analysis. Names correspond to labels in Figure 4. Eigenvalues for marginal and conditional effects are presented. Marginal effects occur when only one variable is used in a constrained ordination whereas a conditional effect is the (partial) influence of a particular variable when the rest of the variables are used as covariables.

Names	Group	Variable	Marginal effect	Conditional effect	P	*f*
Local scale environmental variables						
Clay	Substrate	Soil Clay Content	0.01	0	0.002	1.89
EVI	Topographic	Enhanced Vegetation Index May 2008 (based on MODIS)	0.04	0.01	0.002	9.09
Hillshad	Topographic	Hillshading calculated in GIS	0.03	0.01	0.002	3.87
NDVI	Topographic	Normalized Difference Vegetation Index May 2008	0.03	0.01	0.002	1.8
Slope	Topographic	Slope (derived from 30 m ASTER GDEM2 (degrees)	0.01	0	0.002	2.82
TopoPos Index3km	Topographic	Topographical Positional Index – 3 km neighbourhood	0.05	0.02	0.002	9.17
TPI4	Topographic	Topographical Positional Index – 120 m neighbourhood	0.02	0	0.002	1.93
Regional scale environmental variables						
Altitude	Topographic	30 m ASTER GDEM2	0.09	0.09	0.002	42.15
EVI	Topographic	Enhanced Vegetation Index May 2008 (based on MODIS)	0.04	0.01	0.002	9.09
SoilDept	Substrate	Soil Depth	0.01	0.01	0.002	2.53
SolRad AM	Topographic	High resolution Solar Radiation based on 30m GDEM	0.02	0	0.002	2.7
H2Ostres	Climate	Water Stress in July	0.05	0.01	0.002	2.74
Htunit18	Climate	Heat units (sum of °C over 18° C during the year)	0.07	0.01	0.002	6.93
Isotherm	Climate	Isothermality (mean diurnal range/temperature annual range)	0.05	0	0.002	2.62
MaxTemp	Climate	Maximum Average Temperature in January	0.05	0	0.002	3.19
Rainfall	Climate	Mean Annual Precipitation	0.05	0.01	0.002	3.76
Summer Soil Moisture Days	Climate	Summer Soil Moisture Days	0.06	0.06	0.002	29.02
Winter Soil Moisture Days	Climate	Winter Soil Moisture Days	0.06	0	0.002	2.36
Supra-regional scale environmental variables						
Altitude	Topographic	ASTER 30 m GDEM	0.09	0.09	0.002	42.15
Coldest	Climate	Minimum Mean Temp of Coldest Month	0.05	0	0.002	2.06
Frost	Climate	Number of Frost Days in a Year	0.03	0.01	0.002	1.86
MinTemp	Climate	Minimum Average temperature in July	0.05	0.01	0.002	4.28
PotEvap	Climate	Potential Annual Evapotranspiration	0.03	0.02	0.002	13.26
Temp	Climate	Mean Annual Temperature	0.05	0.01	0.002	3.12
PotEva January	Climate	Potential Evapotranspiration in January	0.05	0.01	0.002	8.15

RESULTS

Contribution of environmental variables and species richness

The results of the db-RDA of the environmental variables on forest composition are shown in Figure 4. Axes 1 and 2 explain 18.5% of the variability in species data and 36.1% of the variability is explained by environmental variables (51.2% of total variability is explained by environmental variables across all axes). The forest subtype classification is overlaid to highlight forest compositional differences relating to various environmental variables. The environmental variables were correlated with species response variables. The marginal effects (which only considers the effect of one variable at a time; see Table 2), highlight the significance of altitude (r^2 = -0.76, Axis 1), heat units (sum of °C over 18°C during the year; r^2 = 0.69, Axis 1), summer soil moisture days (r^2 = -0.57, Axis 2), Topographical Positional Index (3 km neighbourhood; r^2 = -0.56, Axis 1), H_2O stress in July (r^2 = 0.62, Axis 2), Minimum Average temperature in July (r^2 = 0.45, Axis 1), Potential Evapotranspiration, January (r^2 = 0.52, Axis 1), Mean annual precipitation (r^2 = -0.49, Axis 2) and Mean annual temperature (r^2 = -0.52, Axis 2). These exclude marginal variables that had zero conditional effects.

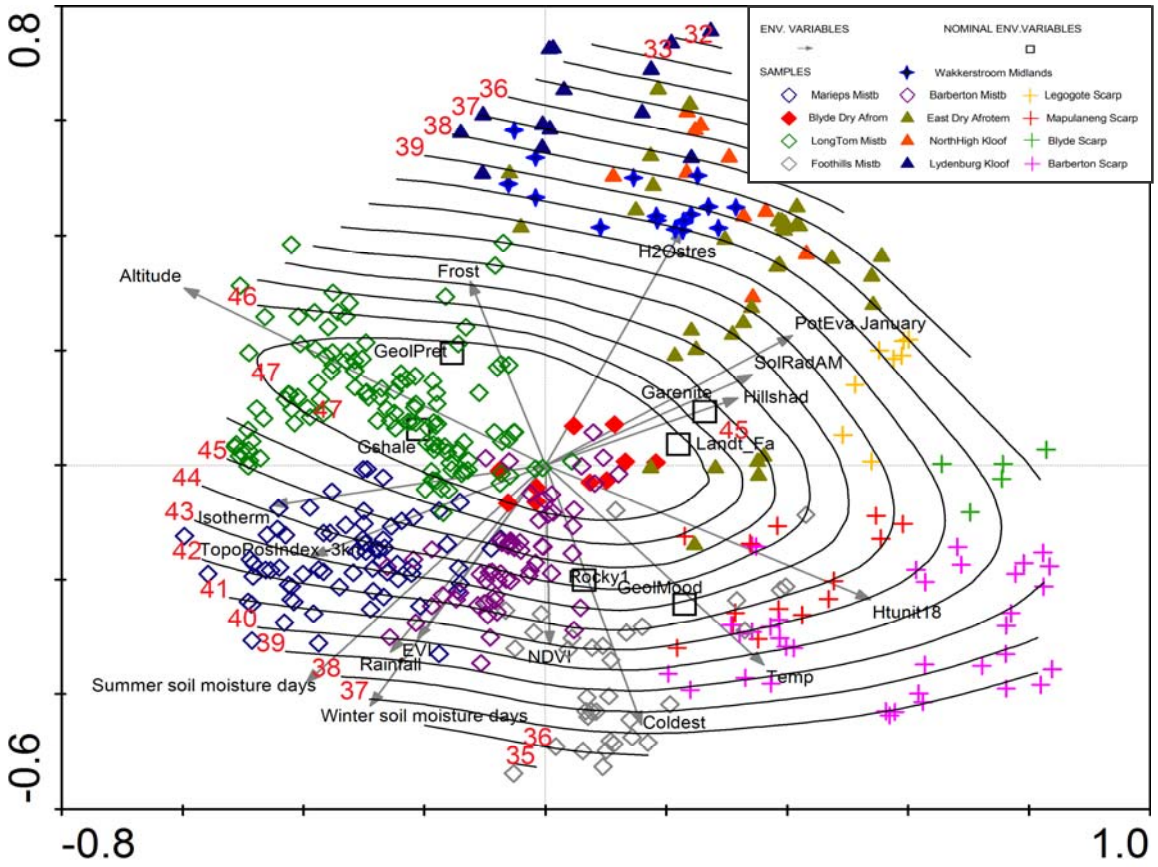


Figure 4 Db-RDA biplot of ordination of species data constrained by all measured environmental variables (430 plots, 442 species). Only environmental variables with a correlation value >0.35, or <-0.35, are displayed. Contours (with labels in red) indicate correlation of species richness with axes (r^2 = 0.18). Visualisation of species richness is calculated using Loess smoothing regression (Lepš and Šmilaur 2003).

Some of the nominal environmental variables had significant effects on species composition. These include shale geology (Gshale; r^2 = -0.47, Axis 1) which predominantly underlies the Long Tom Pass forests and which also forms part of the larger Pretoria Group geological formation (GeolPret; r^2 = 0.43, Axis 2). The arenite geology (Garenite; r^2 = 0.46, Axis 1) with Glenrosa and/or Mispah soil forms (Landtype_fa; r^2 = 0.35, Axis 1) were correlated with the diverse Eastern Dry Afrotemperate forests. The Moodies Group (geological formation) underlies the Barberton Scarp forests in the Barberton area (GeolMood; (r^2 = 0.38, Axis 2).

The measured environmental variables explained 44.3% (tree stratum), 50.2% (shrub stratum), and 39.1% (herbaceous stratum) of total variation. This indicates that the shrub stratum was the most responsive to measured environmental variables.

An analysis of species richness and environmental variables (Figure 4) reveal an interesting pattern. At either end of the environmental gradients species richness tends to be lower. At the centre is the Blyde Dry Afromontane forest in which over 100 species were recorded in a single 400 m² plot. The mean recorded species richness value across all plots is 45. Altitude was strongly correlated with species richness and subsequently the Long Tom Mistbelt forest was more species rich than most other forest subtypes. Extreme cold and dry conditions result in lower species richness.

Partitioning of environmental scales

The influence of the three scales of environmental variables on forest composition is summarised in the combined strata model. The largest fraction of TVE was explained by the regional variable matrix (44.8%) followed by the effects of supra-regional and local variable matrices (21.4% and 18.8%, respectively). Then in terms of the explained variation, proportions of measured variance explained are calculated as a percentage with each adding up to 100% (Figure 5), the main effect of the regional variable matrix comprised single fraction (39%), with the effects of local and supra-regional matrices removed. Three-way interaction with local and supra-regional variable matrices comprised 17%, in contrast to the low shared effect between local and supra-regional explanatory variables (0.04%). Intuitively this is expected and supports the accuracy of semivariogram classification into 3 classes of scale. Local- and supra-regional scales variables should not share any effects.

A similar pattern of fractions of TVE is repeated when analysing individual tree, shrub and herbaceous strata. The combined fractions (or proportions) of TVE explained by the local and regional explanatory matrices were similar amongst the tree, shrub, and herbaceous strata (33–38% for local scale; 81–88% for regional scale). In contrast, supra-regional scale variables only accounted for 28% of observed variance in the herbaceous strata compared to the 40% and 43% for tree and shrub strata, respectively. The higher residual values indicate that either other

processes are influencing species patterns or we failed to include appropriate environmental variables.

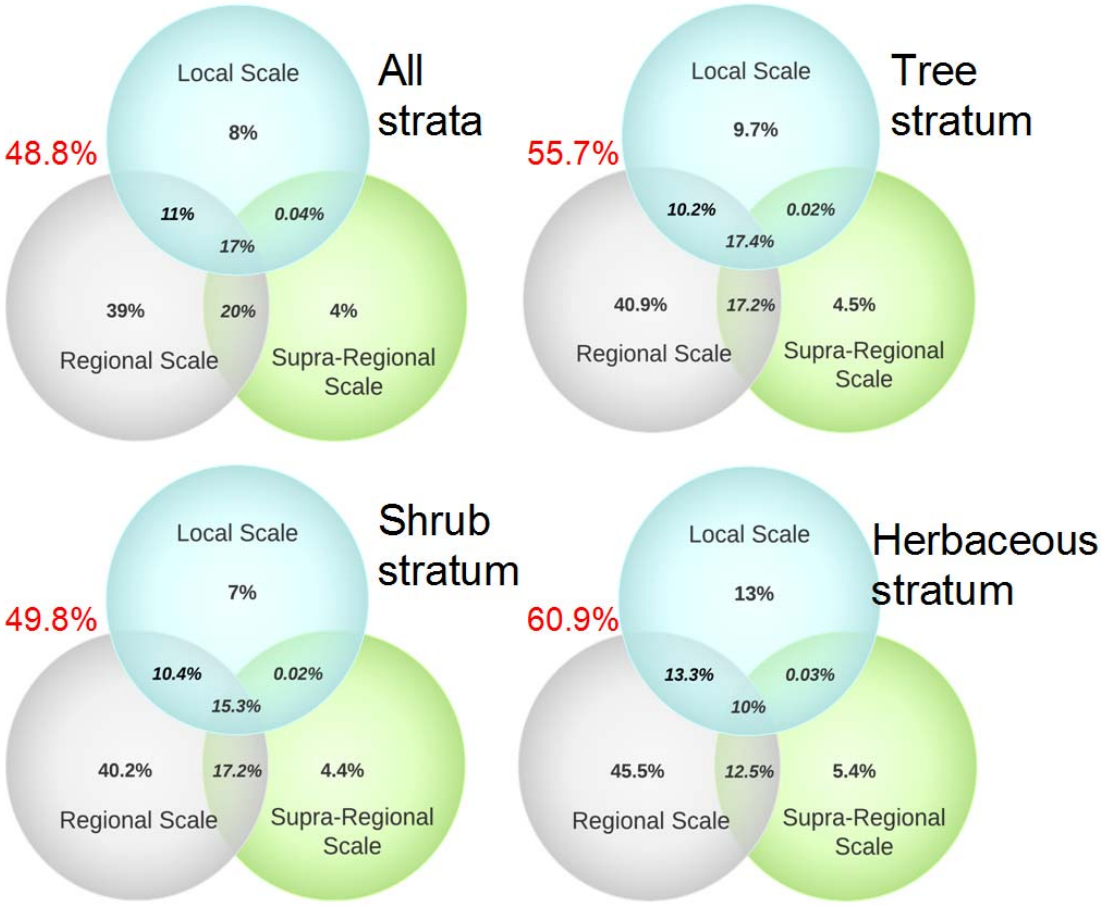


Figure 5 Venn diagrams of the variation partition model, with colours representing variation in species data explained by main and interaction effects of three environmental variable matrices (local, regional, supra-regional) on all strata, tree stratum, shrub stratum and herbaceous stratum. Percentage values within all circles = total variance explained. Variance not explained (and excluded from calculations); all strata = 48.8%; tree stratum = 55.7%; shrub stratum = 49.8%; and herbaceous stratum = 60.9%.

Partitioning of environment and space

The fractions of TVE reported below are based on total inertia, rather than proportions of TVE (as above). The spatial variable matrix accounted for 23.5% of the variation in the full floristic data set, 17.5% in the tree, 25.4% in the shrub, and 14.6% in the herbaceous data sets. Geographic space has a greater influence on shrubs, indicating that perhaps different processes are also in operation in the tree or herbaceous strata.

In the full floristic data set (Figure 6, column 1), both the environmental and spatial variable matrices accounted for 54.8% of the observed variation. In addition, most (19.4%) of the spatial variation (23%) can be explained by spatially structured environmental variables. Only 3.6% of the variation is attributed to pure spatial variables. The pattern described for the full floristic data compliment is similarly repeated for the tree (second column), shrub (third column), and herbaceous strata (fourth column). Yet, in general, the fraction of TVE is higher for the shrub than the other strata. The least amount of variation was explained in the herbaceous stratum that partitions the effect of space (14%) and environmental variables (39%), with a 10.5% overlap.

A detailed analysis of geographic space and three scales of environmental variables across all forest strata is provided in Appendix S1. The above pattern is largely repeated for the analysis of spatial and regionally-scaled environmental variables. In contrast, the analysis of effects of space and local-scale environmental variables for the full floristic complement revealed that only a small fraction (6.8%) of the spatial variation can be explained by the environmental variables and that 16.7% of the variation is attributed to space only. For the full floristic data set, the analysis of supra-regional variables and space revealed that both space and environment account for a small portion of the TVE (33%, similar to local variables) and that only half of the spatial matrix can be explained by the supra-regional scale environmental variables.

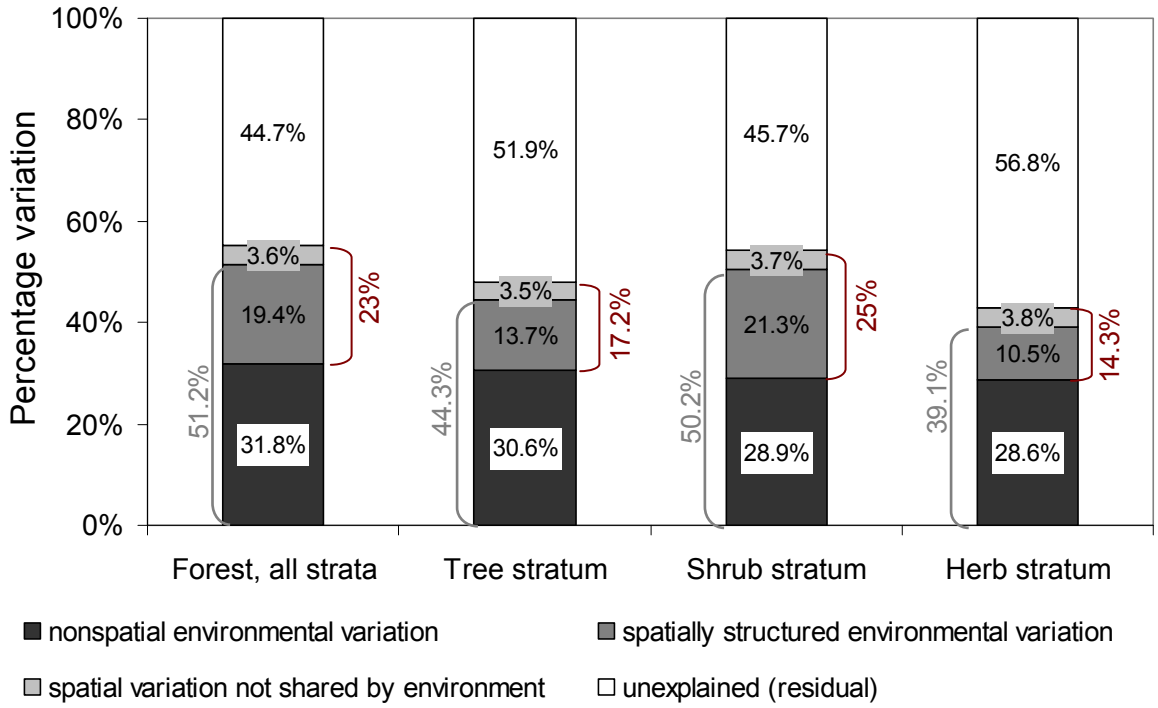


Figure 6 Variation partitioning of geographic distance and environmental variables for the forest flora, and each of the forest strata for Mpumalanga forest data set.

The partial db-RDA (Appendix S2) presents the influence of the spatial (geographic coordinates) variable matrix on the full floristic complement with the effects of the environmental matrix removed. The output is classified according to forest subtypes. The original db-RDA of spatial matrix accounted for between 14.6 and 25.4% of the variation in species data, but once removed, the effects of the environmental variables (many of which are also spatially structured), then only 3.5–3.8% could be attributed to geographic space alone. Certain forest types initially displayed obvious spatial structure (i.e., the spatial coordinates explained differences in species composition; results not shown), but after removing the effect of the environmental variables the differences were then largely intra-specific to forest subtypes, not inter-specific. The identified spatial structure (in Appendix S2) does not distinguish between forest subtypes, i.e. there is no clustering of subtypes in any one area and that the purely spatial variables are influencing composition rather similarly across all subtypes. Perhaps only the Eastern Dry Afrotemperate forest appears to be clustering towards the right, otherwise we infer that perhaps pure spatial processes are happening within specific plots, not consistently to subtypes, as plots appear to be randomly scattered across the biplot in no specific pattern. It is possible that ecological drift or neutral processes may be responsible but it could also be unrecorded environmental variables.

DISCUSSION

Contribution of environmental variables and species richness

Our results confirm that the shrub stratum, with its constituent tree seedlings, is more responsive to the measured environmental variables than the tree or herbaceous strata alone. In a region-wide forest assessment, it may better reflect differences in environmental conditions than the other strata. Their responsiveness highlights the importance of including them in vegetation assessments. Geldenhuys and Mucina (2006) report that several vegetation studies in South Africa only considered large canopy trees (usually stems ≥10 cm or ≥5 cm DBH). But depending on the purpose of these studies, they may have failed to adequately identify associations that reflect differences in the environment.

Although the correlation between environmental variables and species richness was weak, it did highlight that extremes in environmental variables measured were generally associated with lower species richness. It may also reflect some kind of optimal environmental conditions for forest habitat and thus species diversity within Mpumalanga. Other processes may also be responsible for influencing species richness. Biogeography and historic processes are difficult to describe and quantify (Chase and Myers 2011), but our results support Geldenhuys and Mucina (2006) who described the Northern Highveld forests as being the most “biogeographically eroded” forest type, as they contain only a very small portion of the typical Afrotemperate or Afromontane elements. They were probably once linked to the species-rich Afromontane forests found along the Mpumalanga escarpment. From Figure 4, the solid

triangles and blue star represent the subtypes comprising the Northern Highveld forests types, and the contours show lower species richness for the plots of this forest type.

An alternative explanation for observed differences in species richness may be associated with dispersal and connectivity between forest patches. Using multiple regression, Geldenhuys (1992) established that proximity to other forest patches and dispersal corridors provided a significant explanation of observed variation in species richness, while the analysis of patch size and richness was not significant. But using simple linear regression richness did tend to increase slightly with patch size. Furthermore the number of dispersal corridors was the strongest variable explaining richness in woody species. There is also greater similarity in flora between forests which are in closer proximity to one-another, supporting the importance of dispersal events in maintaining forest composition. The smaller similarity between relatively isolated forests is attributed to the abiotic and biotic barriers to dispersal of diaspores between them, and the lack of dispersal corridors.

Partitioning of environmental variables

Although the study of ecosystems has always been highly influenced by the scale at which research is conducted (Sieben et al. 2009), our results still show that regionally scaled environmental variables have a greater influence on forest composition across all forest strata than either local or supra-regional environmental variables. As a proportion of TVE, it accounted for 81 – 87% of the observed variation in species composition. It was highest in the shrub stratum and lowest in the herbaceous stratum. The caveat is that Borcard *et al.* (1992) recommend comparable numbers of variables to be included in each set of explanatory variables. In our study (including nominal classes as individual variables), the number of local variables = 20, regional = 46, and supra-regional = 7). But Økland and Eilersten (1994) report that as long as forward selection of variables is used prior to constrained ordination, the number of variables included in a set is not important. But we suspect that perhaps the greater contribution of the regionally scaled variables may be related to the spatial scale of the measured environmental variables themselves. The reason for this being that environmental variables are primarily derived from coarse-scale GIS data sets and may not necessarily reflect fine-scale variation at the local scale. Many locally-scaled variables that may have an influence on community composition were not recorded or considered for inclusion as these would not be available for all of the random points (i.e. soil moisture, soil nutrient status, pH). Caution is therefore required when interpreting the above results given this deficiency.

Local, regional, and supra-regional scaled variables are deemed to interactively structure forest composition, given the large amount of shared variation (17%). But for the herbaceous stratum the amount of shared variation was lower (10%). Considering that both altitude and EVI were intermediate and both assigned to two categories (altitude to regional and supra-regional

scales, and EVI to local and regional scales), this would certainly influence the amount of shared variation with regionally-scaled variables.

Partitioning of environment and space

As an important ecological process, dispersal rates and distance influence the ability of plants to colonize suitable environments. Dispersal rates can influence all three variation partitions (a-c; Figure 3). Using simulations, Smith and Lundholm (2010) established that increasing dispersal rates resulted in increases in spatial variation as well as environmental variation. This means that increases in dispersal results in an increase in both niche and neutral processes.

Even though variation partitioning approach cannot clearly decompose niche and neutral processes, our results further our understanding of the factors driving forest composition. The results support our hypothesis that spatial and environmental structures act simultaneously across a range of spatial and environmental scales. These factors also have broadly similar observed effects on the three forest strata, although the shrub stratum is more strongly influenced by the environmental and spatial matrices. More than half of the variability in the species data (55.3%) can be explained by the measured environmental and spatial variables. This is considerably higher than typically reported in other studies (Økland and Eilersten 1994; Carr *et al*. 2009). During our initial model development, the application of db-RDA to this floristically complex data set instead of the traditional CCA approach resulted in a significant improvement in the explained variation (51.2% versus 41.6% of TVE, results not shown).

The large effect of environmental variables that lack any spatial structure could possibly be explained by those environmental variables that had large nugget effects in the semivariogram analysis, i.e. the local variables. However this may only in part explain the effect of spatially-independent environment as local variables only explained 19% whereas overall the environment accounts for 32% of the variation. We infer that some of the spatially-independent environmental variables may still have spatial structure; i.e. the polynomial function of the geographic coordinates did not detect this, but the semivariogram analysis did.

We anticipated a higher contribution of geographic distance in forest trees compared to the herbaceous stratum, given that large fleshy propagules primarily occur in the forest canopy (Geldenhuys 1994; Bollen *et al.* 2004). Bollen *et al*. (2004) reported that in tropical forests, dispersal by vertebrates is the most common means of seed dispersal involving 75% of all plant species. Within forests dispersal away from conspecific trees is important as it increases both seed and seedling survival (Chapman and Chapman 1996). Clark and Poulsen (2001) established that the majority of bird dispersal occurred in the middle to upper canopy levels. Therefore we expected that the tree stratum would show a higher correlation with geographic coordinates than the herbaceous stratum. In contrast, we expected that the herbaceous stratum, with several visually dominant ballistically dispersed species, would not be strongly

spatially structured. However we were incorrect on both accounts. The spatial matrix had the greatest influence in the shrub layer, less in the tree canopy, and slightly less in the herbaceous stratum (at 14%).

We can only infer possible explanations without detailed experimental plots, but we suspect that because the shrub stratum also included tree seedlings and saplings, that dispersal was still the primary driver of spatial structure. Finding a suitable niche in which to germinate did not guarantee a species would reach maturity in the canopy, owing to resource competition (Tilman 1982) or niche saturation (Palmer and Maurer 1997). Many, if not most tree seedlings may never reach the canopy if not given a chance to fill a gap in the forest canopy. Norden *et al.* (2009) suggest that examining early life stages of plants, such as seedlings, may better reflect the footprint of dispersal events, stochastic demography (*sensu* Hubbell 2001) and niche differences (Grubb 1977; Poorter 2007).

The unexpected spatial structure (including spatially structured environmental variables and pure spatial structure) in the herbaceous stratum led us to investigate the dispersal distances of constituent species (Chapter 5) as possible causes. Figure 7 shows the potential dispersal distances for each of the tree, shrub, and herbaceous strata.

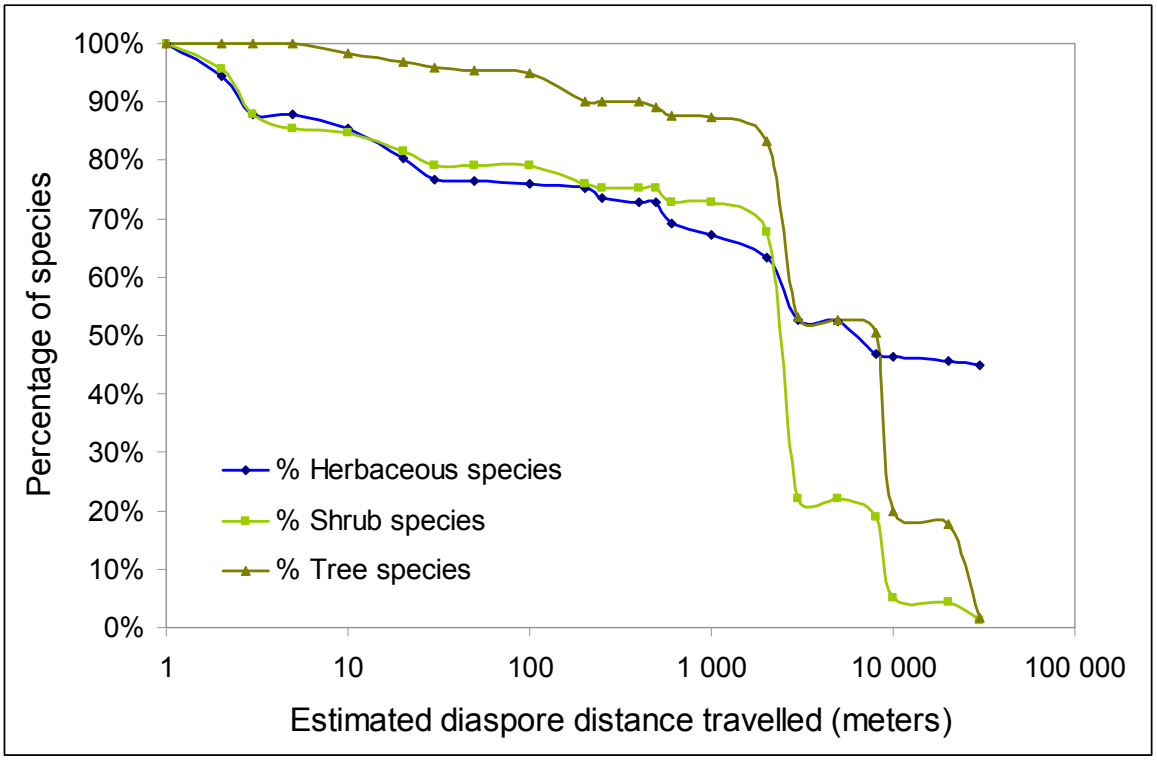


Figure 7 Dispersal distance per stratum as a proportion of forest flora where each diaspore is expected to reach a certain distance (adapted from Chapter 5). The x-axis is $\log_{10}$ scaled. N = 619 species.

It is apparent that initially a higher proportion of tree species are able to disperse greater distances but after 3 km it is the shrub and herbaceous strata that have a higher proportion of species that can disperse further, and after about 7.5km it is the herbaceous stratum that has the highest proportion of species that are long-distance dispersers (>20km dispersal for 46% of herbs, but <20% of trees and <5% of shrubs). For the herbaceous flora, 93 species (or 15%) are Pteridophyta that are able to disperse great distances. In addition 23 species of Orchidaceae were recorded that are similarly able to disperse great distances. Therefore we conclude that dispersal across the three strata is likely to explain a large part of the geographic spatial matrix, which would highlight the importance of dispersal driving forest composition within Mpumalanga.

The results suggest that dispersal distance is an important structuring factor across all forest strata. Species are generally limited by seed dispersal to suitable, but unoccupied, patches. The distribution of species, as well as species richness and composition of forest communities cannot be explained without accounting for dispersal processes occurring at various scales (Ehrlén and Eriksson 2000).

Importance of historic biogeography

Our results provide for the consideration of an additional theory to the observed spatial structure which may not necessarily be attributed to dispersal or (measured) environmental variables, namely historic biogeography. Biogeography is the historic and current interaction of niche-based and neutral theories in a dynamic landscape. Current biogeographic processes correspond to niche-based and some neutral processes while historic biogeography relates to niche-based patterns that no longer exist and well established neutral processes. We suspect that much of the observed community composition in our data set is partly due to historic biogeography where the drivers of historic composition no longer exist. We expect that historic biogeography will result in purely spatial structures (unrelated to current environmental structures), as well as to current yet unexplained processes within our variation partitioning model. We are also cognisant that some of the purely spatial pattern may also result from unmeasured variables.

Our methodological framework is not aligned with the requirements of a biogeographic investigation (see Geldenhuys 1994) as we do not establish generalised distribution ranges for all species that are then correlated with contemporary geographic and environmental variables. Our focus is on the association of species and correlations with environmental variables.

It is difficult to quantify biogeographic influences, other than personal interpretations. Strictly spatial variation may have several origins (Borcard *et al.* 1992; Økland and Eilertsen 1994), including historical biogeography. Phenomena such as historic biogeography in part

explain the similarities in disjunct forest patches throughout much of the Afromontane forest range (the Afromontane archipelago *sensu* White 1983).

We occasionally recorded species that fell outside their regular distribution ranges. This legacy of historical biogeography is still visible and it is believed to have largely structured Mpumalanga's forest composition as there are several species or species assemblages that do not follow any predictable or repeatable patterns (i.e. dispersal or environmental basis). We believe these species are relics from adjacent flora, although they may also possibly be expanding their range into this region and have not yet saturated suitable niches. We suspect that these species are not well established locally and seem to have persisted in our flora. These relics are thought to be either from the Cape region (*Alsophila capensis, Cassine peragua, Ocotea bullata, Rumohra adiantiformis*); the Transkei/KwaZulu-Natal flora but reaching their northern-most limits in Mpumalanga (*Atalaya natalensis, Buddleja dysophylla, Chionanthus peglerae, Olinia radiata, Micrococca capensis, Scolopia oreophila*); from tropical flora (*Allophylus chaunostachys, Aphloia theiformis, Arthropteris monocarpa, Asplenium unilaterale, Cola greenwayi, Ocotea kenyensis, Trichilia dregeana, Shirakiopsis elliptica, Trilepisium madagascariense*), the Lebombo-coastal region (*Atalaya alata, Vitellariopsis marginata*), or species with a very unusual or disjunct distribution (*Buddleja pulchella, Dombeya cymosa, Memecylon natalense, Ptaeroxylon obliquum*). Finally there are 'new' species such as *Syzygium* sp. nov. and *Hippocratea* sp. nov. that are unknown and their biogeographical links would be difficult to trace and their localised occurrence difficult to interpret.

These species occurrences highlight that our spatial and environmental decomposition of explanatory variables is not sufficiently effective to fully understand the drivers behind current forest composition. These are also some of the more noticeable 'relic' species that highlight the importance of historic biogeography, but the same process may similarly have a more nuanced influence on composition in general. We suspect that a large part of the 'unexplained variation' or residual value from the (partial) constrained ordinations can be attributed to historic biogeographic processes.

Validation of proposed forest subtype classification and interpretation

The db-RDA ordination of species and environmental variables (Figure 4) supports and interprets the recent forest subtype classification in a constrained ordination (Lötter et al. 2014). In a constrained ordination, plots that share the same environmental variables would share the location on ordination graphs regardless of their species composition. Therefore Figure 4 has the additional utility of being used as external criteria (e.g. Gauch and Whittaker 1981) to assess classification effectiveness. The NFC forest types (see forest hierarchy in Table 1) are presented by means of different symbol shapes. The subtypes are distinguished by means of symbol colours. The Mpumalanga Mistbelt forest subtypes (diamond symbol) cluster together and do not contain plots from other forest types. Comparatively, the Mpumalanga Mistbelt

Forest type occurred at higher altitudes with significant positive correlations for soil moisture days during summer and winter, similarly there was a correlation for higher rainfall regions with lower evaporation and solar radiation. Within this forest type, Long Tom Mistbelt subtype occurred at highest altitudes with lower temperatures and heat units above 18ºC. Geology was largely derived from shale of the Pretoria geological formation. The Mariepskop Mistbelt subtype favoured the mountain summits or upper slopes in high rainfall regions characterised by lower evaporation and solar radiation. Barberton Mistbelt subtype favoured lower H_2O stress areas, higher rainfall, and areas with high Enhanced Vegetation Index value (EVI; MODIS). Foothills Mistbelt subtype was strongly correlated with lower number of frost days, rockiness, and Normalized Difference Vegetation Index (NDVI; MODIS). The Blyde Canyon Dry Afromontane subtype exhibited intermediate values for measured environmental variables. As its name declares, it is the driest of the Mistbelt forest subtypes.

The Northern Highveld Forest type (solid triangle) was correlated with cold, dry areas that experienced an abundance of frost and water stress. The distinction of individual forest subtypes were not that clearly defined. Lydenburg Kloof occurred in areas with a large number of frost days and a dry climate. Northern Highveld Kloof subtype occurred in H_2O stressed areas, low rainfall and low soil moisture days in both winter and summer. The Eastern Dry Afrotemperate forests were varied in the environmental correlations, but generally favouring lower altitudes and dry conditions. Interestingly, in terms of the NFC, the Wakkerstroom Midlands forest subtype geographically falls within the Low Escarpment Mistbelt Forest type. However, Lötter *et al*. (2014) found them to be embedded within the Northern Highveld Forest type and proposed the shift from Low Escarpment Mistbelt to Northern Highveld. This study supports the transfer to the Northern Highveld Forest type. The Wakkerstroom Midlands forest subtype's plots tend to cluster together and occur in H_2O stressed and low rainfall areas, with low soil moisture days in both winter and summer.

The Eastern Scarp Forest types form a coherent group, generally favouring low altitudes and hot temperatures in both winter and summer. Specifically, the Legogote Scarp subtype is strongly correlated with shaded slopes in valley bottoms, granite geology, high solar radiation, and high potential evaporation. The Blyde Scarp subtype occurs in lower altitudes, valley bottoms or kloofs, with low isothermality (mean diurnal temperature range/temperature annual range). Low isothermality is an expression of a constant temperature range. The Mapulaneng Scarp and Barberton Scarp subtypes both occurred at the lowest altitudes, warmest temperatures (year round), and associated with the Moodies geological formation (Barberton Scarp only).

Application of semivariogram analysis

Lastly, the recent application of geostatistics in the field of ecology (Legendre and Fortin 1989; Blanchet et al. 2008; Bacaro et al. 2011) is extended in our study with the categorisation

of environmental variables according to scale. The semivariogram analysis provides for a robust and defensible categorisation of environmental layers based on the spatial dependence of the dependent variables, and further application, interrogation, and exploration of its applicability in vegetation science is encouraged. It further supports the spatial structure identified for many of the environmental variables.

CONCLUSION

This paper assesses several issues relating to our understanding of causal mechanisms in understanding species patterns in the forest composition of Mpumalanga. It identifies and quantifies the scales of environmental variables influencing composition; it explores the spatial and environmentally structured variables and links them to the importance of dispersal; it highlights the existence and difficulty in assessing historic biogeographic processes that are also contributing towards species patterns; and lastly it validates and identifies main environmental drivers for the recently developed forest subtype classification for Mpumalanga Province. Our results are descriptive and we may infer causal mechanisms but our approach highlights the limitations of the variation partitioning approach in explaining the applicability of current ecological theories.

We recognise that our interpretation of spatial variables is based on the polynomial regression of geographic coordinates and is somewhat rudimentary and a probable underestimation of the importance of geographic space in structuring communities. Similarly the large number of environmental variables analysed using the db-RDA variation partitioning approach may subtly have over-inflated the explanatory power based on the collinearity of some of the variables, but once again we acknowledge that it is the resulting patterns that are of more importance than absolute values.

Lastly, the importance of including the shrub data set in forest floristic surveys is highlighted owing to its significance in explaining the space and environmental variables, more so than the traditionally surveyed tree layer alone. It is notable that the herbaceous layer is also, but to a lesser degree, influenced by geographic distance, supra-regional and regional environmental variables, and not only to anticipated locally-scaled environmental variables.

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LITERATURE CITED

Anderson, M.J., T.O. Crist, J.M. Chase, M. Vellend, B.D. Inouye, A.L. Freestone, N.J. Sanders, H.V. Cornell, L.S. Comita, K.F. Davies, S.P. Harrison, N.J.B. Kraft, J.C. Stegen, and N.G Swenson. 2010. Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist. Ecology Letters 14: 19–28.

Bacaro, G., E. Santi, D. Rocchini, F. Pezzo, L. Puglisi, and A. Chiarucci. 2011. Geostatistical modelling of regional bird species richness: exploring environmental proxies for conservation purpose. *Biodiversity and Conservation* 20: 1677–1694.

Blanchet, F.G., P. Legendre, and D. Borcard. 2008. Modelling directional spatial processes in ecological data. *Ecological Modelling*: 4, 325 – 336.

Bollen, A., L. Elsacker, and J.U. Ganzhorn. 2004. Tree Dispersal Strategies in the Littoral Forest of Sainte Luce (SE-Madagascar). *Oecologia* 139: 604–616.

Borcard, D., and P. Legendre. 1994. Environmental control and spatial structure in ecological communities: an example using Oribatid mites (Acari, Oribatei). *Environmental and Ecological Statistics* 1: 37–61.

Borcard, D., and P. Legendre. 2002. All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. *Ecological Modelling* 153: 51–68.

Borcard, D., and P. Legendre. 2011. SpaceMaker 2. A FORTRAN program compiled versions for Macintosh and DOS. http://www.bio.umontreal.ca/casgrain/en/labo/spacemaker.html; accessed on 12 June 2011.

Borcard, D., P. Legendre, C. Avois-Jacquet, and H. Tuomisto. 2004. Dissecting the spatial structure of ecological data at multiple scales. *Ecology* 85:1826–1832.

Borcard, D., P. Legendre, and P. Drapeau. 1992. Partialling out the spatial component of ecological variation. *Ecology* 73: 1045–1055.

Carr, S.C., K.M. Robertson, W.J. Platt, and R.K. Peet. 2009. A model of geographical, environmental and regional variation in vegetation composition of pyrogenic grasslands of Florida. *Journal of Biogeography* 36: 1600–1612.

Chapman, J.D., and L.J. Chapman. 1996. Frugivory and the fate of dispersed and non-dispersed seeds of six African tree species. *Journal of Tropical Ecology* 12: 491–504.

Chase, J. M. 2003. Community assembly: When should history matter? *Oecologia* 136: 489–498.

Chase, J.M., and J.A. Myers. 2011. Disentangling the importance of ecological niches from stochastic processes across scales. Philosophical transactions of the Royal Society of London, Series B 366: 2351–2363.

Clark, C.J., and J.R. Poulsen. 2001. The role of arboreal seed dispersal groups on the seed rain of a lowland tropical forest. *Biotropica* 33: 606–620.

Clarke, K.R., and R.N. Gorley. 2006. PRIMER v6: User Manual/Tutorial. PRIMER-E, Plymouth.

de Casas, R.R., C.G. Willis, and K. Donohue. 2012. Plant dispersal phenotypes: a seed perspective of maternal habitat selection. Pages 171–184 *in* Clobert, J., M. Baguette, T. Benton and J. Bullock, editors. *Dispersal ecology and evolution*. Oxford University Press, Oxford.

de Miguel, J.M., L. Ramírez-Sanz, I. Castro, M. Costa-Tenorio, M.A. Casado, and F.D. Pineda. 2005. Plant Species Richness and Spatial Organization at Different Small Scales in Western Mediterranean Landscapes. *Plant Ecology* 176: 185–194.

Diamond, J.M. 1975. Assembly of species communities. Pages 342–444 *in* Cody, M.L., J.M. Diamond, editors. *Ecology and evolution of communities*. Harvard University Press, Cambridge, Mass.

Dray, S., P. Legendre, and P.R. Peres-Neto. 2006. Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). *Ecological Modelling* 196: 483–493.

Eastman, J.R. 2009. IDRISI Taiga (Worcester, MA: Clark University)

Ehrlén, J., and O. Eriksson. 2000. Dispersal limitation and patch occupancy in forest herbs. *Ecology* 81: 1667–1674.

ESRI. 1999–2011. ArcView (Version 3.2) and ArcGIS (Version 10.0). Environmental Systems Research Institute, Redlands, CA.

ESRI. 2011. Solar Radiation Tool. Retrieved November 12, 2011, from http://www.esri.com/software/arcgis/extensions/spatialanalyst/solar.html.

Faith, D.P., P.R. Minchin, and R. Belbin. 1987. Compositional dissimilarity as a robust measure of ecological distance. *Vegetatio* 69: 57–68.

Gauch Jr., H.G., and R.H. Whittaker.1981. Hierarchical classification of community data. *Journal of Ecology* 69: 537–557.

Geldenhuys, C.J. 1992. Richness, composition and relationships of the floras of selected forests in southern Africa. *Bothalia* 22: 205–233.

Geldenhuys, C.J. 1994. Phytogeography of the southern Cape forest flora. Pages 969–992 in Seyani, J.H., and A.C. Chikuni, editors. Proceedings of the XIII Plenary Meeting AETFAT, Malawi.

Geldenhuys, C.J., and L. Mucina. 2006. Towards a new national forest classification for South Africa. Pages 111–129. in S.A. Ghazanfar & H.J. Beentje, editors. *Taxonomy and ecology of African plants, their conservation and sustainable use*. Royal Botanic Gardens, Kew.

Grubb, P.J. 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biological Reviews of the Cambridge Philosophical Society* 52: 107–145.

Heino, J. 2011. A macroecological perspective of diversity patterns in the freshwater realm. *Freshwater Biology* 56: 1703–1722.

Hennekens, S., and J. Schaminée. 2001. TURBOVEG, a comprehensive data base management system for vegetation data. *Journal of Vegetation Science* 12: 589–591.

Hijmans, R.J., S.E. Cameron, J.L. Parra, P. Jones, and A. Jarvis. 2005. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* 25: 1965–1978.

Hubbell, S.P. 2001. The Unified Neutral Theory of Biodiversity and Biogeography. Princeton University Press, Princeton.

Jenness, J. 2006. Topographic Position Index (tpi_jen.avx) extension for ArcView 3.x, v. 1.3a. Jenness Enterprises. Available at: http://www.jennessent.com/arcview/tpi.htm.

Jombart, T., S. Dray, and A-B, Dufour. 2009. Finding essential scales of spatial variation in ecological data: a multivariate approach. *Ecography* 32: 161–168.

Karl, J.W., and B.A. Maurer. 2010. Spatial dependence of predictions from image segmentation: A variogram-based method to determine appropriate scales for producing land-management information. *Ecological Infomatics* 5: 194–202.

Kenkel, N.C., and L. Orlóci. 1986. Applying metric and nonmetric multidimensional scaling to ecological studies: some new results. *Ecology* 67: 919–928.

Laliberté, E., A. Paquette, P. Legendre, and A. Bouchard. 2009. Assessing the scale-specific importance of niches and other spatial processes on beta diversity: a case study from a temperate forest. *Oecologia* 159: 377–388.

Land Type Survey Staff. 1972 – 2006. Land Types of South Africa: Digital map (1:250 000 scale) and soil inventory databases. ARC-Institute for Soil, Climate and Water, Pretoria.

Legendre, P. 1990. Quantitative methods and biogeographic analysis. Pages 9–34 in Garbary, D.J., and R.G. South, editors. *Evolutionary Biogeography of the Marine Algae of the North Atlantic*. Springer–Verlag, Berlin.

Legendre, P. 1993. Spatial autocorrelation: trouble or new paradigm? *Ecology* 74: 1659–1673.

Legendre, P., and M.J. Anderson. 1999. Distance-based redundancy analysis: testing multispecies responses in multifactorial ecological experiments. *Ecological Monographs* 69: 1–24.

Legendre, P., and M. Fortin. 1989. Spatial pattern and ecological analysis. *Vegetatio* 80: 107–138.

Legendre, P., and L. Legendre. 1998. Numerical Ecology, 2nd English ed. Elsevier Science BV, Amsterdam.

Legendre, P., M. Xiangcheng, R. Haibao, M. Keping, Y. Mingjian, I-F. Sun, and H. Fangliang. 2009. Partitioning beta diversity in a subtropical broad-leaved forest of China. *Ecology* 90: 663–674.

Lepš, J., and P. Šmilauer. 2003. Multivariate analysis of ecological data using CANOCO. Cambridge, UK: Cambridge University Press.

Lötter, M.C., J.E. Burrows, and A.J. Emery. 2002. Phytochoria, Centres and regions of endemism. Pages 48–59 *in* Emery, A.J., M.C. Lötter and S.D. Williamson, editors. *Determining the conservation value of land in Mpumalanga*, Report, Mpumalanga Parks Board, Nelspruit.

Lötter, M.C., L. Mucina, and E.T.F. Witkowski. 2013. The classification conundrum: species fidelity as leading criterion in search of a rigorous method to classify a complex forest data set. *Community Ecology* 14: 121–132.

Lötter, M.C., L. Mucina, and E.T.F. Witkowski. 2014. Classification of the indigenous forests of Mpumalanga Province, South Africa. *South African Journal of Botany* 90: 37–51.

McGill, B.J., B.A. Maurer, and M.D. Weiser. 2006. Empirical evaluation of neutral theory. *Ecology* 87: 1411–1423.

Morgenthal, T.L, and S.S. Cilliers. 1999. Vegetation analysis of Pedlar's Bush, Mpumalanga, and its conservation. *South African Journal of Botany* 65: 270–280.

Mucina, L., E. Pienaar, A. van Niekerk, M.C. Lötter, C.R. Scott-Shaw, M. Meets, L. Seoke, T. Sekome, S.J. Siebert, L. Loffler, S.G. Cawe, A.P. Dold, A. Abbott, J. Kalwij, and L. Tichý. 2007. Habitat-level Classification of the Albany Coastal, Pondoland Scarp and Eastern Scarp Forests. Unpublished Report for DWAF, Stellenbosch University, Matieland.

Mueller-Dombois, D., and H. Ellenberg. 1974. Aims and Methods of Vegetation Ecology. Wiley, New York.

Norden, N., R.L. Chazdon, A. Chao, Y.-H. Jiang, and B. Vilchez Alvarado. 2009. Resilience of tropical rain forests: tree community reassembly in secondary forests. *Ecology Letters* 12: 384–394.

Økland, R.H. 2003. Partitioning the variation in a plot-by- species data matrix that is related to n sets of explanatory variables. *Journal of Vegetation Science* 14: 693–700.

Økland, R.H., and O. Eilertsen. 1994. Canonical correspondence analysis with variation partitioning: some comments and an application. *Journal of Vegetation Science* 5: 117–26.

Palmer, M.W., and T.A. Maurer. 1997. Does diversity beget diversity? A case study of crops and weeds. *Journal of Vegetation Science* 8: 235–240.

Pärtel, M., R. Szava-Kovats, and M. Zobel. 2011. Dark diversity: shedding light on absent species. *Trends in ecology and evolution* 26: 124–128.

Pebesma, E.J. 2004. *Gstat, a program for geostatistical modelling, prediction and simulation*. Interface, Eastman, J.R., 2009, IDRISI Taiga (Worcester, MA: Clark University).

Phillips, J. 1986. Measuring complexity of environmental gradients. *Vegetatio* 64: 95–102.

Poorter, L. 2007. Are species adapted to their regeneration niche, adult niche, or both? *The American naturalist* 169: 433–442.

Rosindell, J., S.P. Hubbell, F. He, L.J. Harmon, and R.S. Etienne. 2012. The case for ecological neutral theory. *Trends in Ecology & Evolution* 27: 203 – 208.

Rutherford, M.C., L. Mucina, and L.W. Powrie. 2006. Biomes and bioregions of South Africa. Pages 31–50 *in* Mucina, L., and M.C. Rutherford, editors. The vegetation of South Africa, Lesotho and Swaziland. South African National Biodiversity Institute, Pretoria.

Schulze, R.E. 2007. South African Atlas of Climatology and Agrohydrology. Water Research Commission, Pretoria, RSA, WRC Report 1489/1/06.

Sieben, E.J.J., L. Mucina, and C. Boucher. 2009. Scaling hierarchy of factors controlling riparian vegetation patterns of the Fynbos Biome at the Western Cape, South Africa. *Journal of Vegetation Science* 20: 17–26.

Shmida, A., and M.V. Wilson. 1985. Biological determinants of species diversity. *Journal of Biogeography* 12: 1–20.

Smith, T.W., and J.T. Lundholm. 2010. Variation partitioning as a tool to distinguish between niche and neutral processes. *Ecography* 33: 648–655.

Tachikawa, T., M. Kaku, and A. Iwasaki. 2011. ASTER GDEM Version 2 Validation Report. Report to the ASTER GDEM Version 2 Validation Team.

ter Braak, C.J.F., and P. Šmilauer. 2002. CANOCO Reference Manual and CanoDraw for Windows User's Guide: Software for Canonical Community Ordination (Version 4.5). Ithaca, New York, USA: Microcomputer Power.

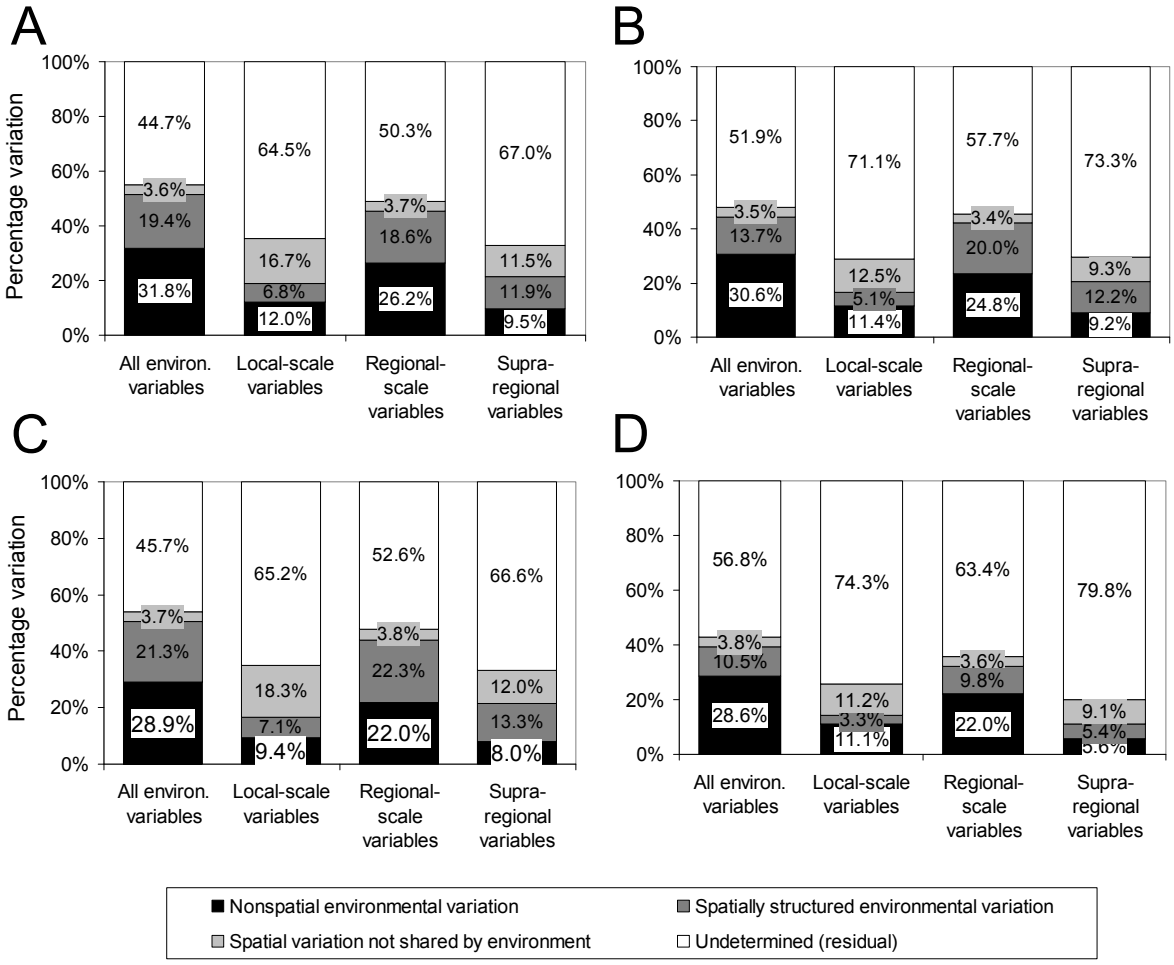
Tilman, D. 1982. *Resource competition and community structure*. Princeton University Press, Princeton, NJ.

Van Wyk, A.E., and G.F. Smith. 2001. *Regions of Floristic Endemism in Southern Africa*. Hatfield, SA, Umdaus Press.

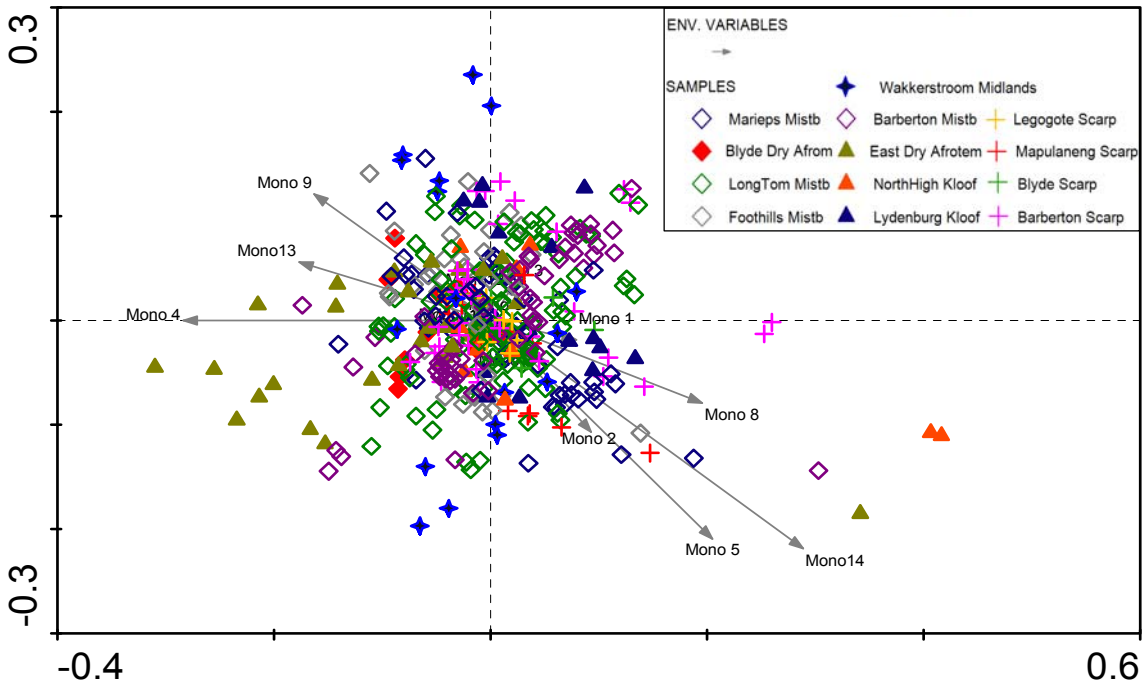
Von Maltitz, G., L. Mucina C.J. Geldenhuys, M.J. Lawes, H. Eeley, H. Aidie, D. Vink, G. Fleming, and C. Bailey. 2003. Classification system for South African Indigenous Forests. An objective classification for the Department of Water Affairs and Forestry. Unpublished Report No ENV-P-C 2003-017. Environmentek, CSIR, Pretoria.

Wagner, H. 2004. Direct multi-scale ordination with canonical correspondence analysis. *Ecology* 85: 342–351.

White, F. 1983. The vegetation map of Africa. UNESCO, Paris.



Appendix S1 Variation partitioning of spatial and four combinations of environmental variable matrices (all environmental variables, local scale variables, regional scale variables, and supra-regional scale variables) for Mpumalanga forest data set using A) full floristic component, and species recorded in B) tree stratum, C) shrub stratum, and D) herbaceous stratum.



Appendix S2 Partial db-RDA biplot of the 13 zonal forest subtypes and the spatial variable matrix (geographic coordinates with the effect of the environmental variable matrix removed). Monomials correspond to the 4th order polynomial function of the geographic coordinates. TVE = 3.6%

CHAPTER FIVE:

Staying the distance: dispersal, connectivity and persistence in systematic conservation planning

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ABSTRACT

Incorporating ecological processes into systematic conservation planning (SCP) to ensure species persistence is challenging. Globally SCP is rapidly informing conservation priorities yet much of its methodology is in its infancy, particularly the inclusion of ecological processes in light of climate change. We offer an applied example where minimum patch distance for a forest community parameterizes a connectivity index to identify individual forest patches important in maintaining this connectivity, within the context of fragmented forests of Mpumalanga Province, South Africa. We propose a new method built on graph theory that incorporates dispersal connectivity for a community of species (i.e. forest subtypes). Minimum patch distance is determined by dispersal range ensuring 75% of the flora can disperse between patches, yielding minimum patch distances of 0.6 km, 1 km and 2 km for the Northern Escarpment, Barberton and Wakkerstroom Regions, respectively. Persistence within a landscape depends on more than just connectivity, but also on patch quality and the nature of the intervening landscape matrix. In the absence of available data on patch quality, we propose using the proportion of the surrounding matrix that is still natural as a surrogate for forest patch condition thereby ensuring that forest patches were prioritised within largely natural landscapes. The prioritisation of each forest patch for maintaining overall landscape connectivity is determined by the *dPC* index and its three fractions. Connectivity analyses have great potential for improving the manner in which functional connectivity can be applied to support resilience and persistence in SCP scenarios.

Keywords

Connectivity, dispersal, ecological processes, forest, graph theory, habitat quality, persistence, systematic conservation planning.

Definitions

Diaspore: a plant dispersal unit consisting of a seed, fruit, infructescence or spore and any associated tissues that might assist dispersal.

dPC: Index calculated from the attributes of the patches and the weighted distances between them. It takes into account the connected area existing within the patches, the estimated dispersal flux between different patches, and their contribution as stepping stones or connecting elements that uphold the connectivity between other patches (Saura & Rubio 2010).

dPCconnect: The fraction of dPC measuring the contribution of the analysed patch to the connectivity between other patches, as a connecting element or stepping stone between them (Saura & Rubio 2010).

dPCflux: The fraction of dPC estimating the amount of dispersal fluxes between a particular patch (as the origin or destination of those fluxes) and the rest of the patches in the landscape (Saura & Rubio 2010).

dPCintra: The fraction of dPC that measures intrapatch connectivity and which is independent of other patches. It is equivalent to the variation in a family of fragmentation indices that take the squared patch area as the basis for their computation (Saura & Rubio 2010).

INTRODUCTION

Planning for pattern and processes in systematic conservation planning (SCP; Margules & Pressey 2000; Margules & Sarkar 2007) are two of the key principles that distinguish it from many other planning approaches. If biodiversity is to persist in conservation area networks, then a variety of ecological and evolutionary processes need to be incorporated (Sarkar *et al.* 2006). Representation is easier to define spatially than delineating ecological processes that may vary both spatially and temporally. Ecological processes are more difficult to include into SCP and attempts to do so may detract from the scientific rigour of a conservation plan. Pressey *et al*. (2007) warned that planning only for biodiversity pattern (representivity) is likely to jeopardize the persistence of many processes that require conservation management, yet there has been little progress towards implementing ecological processes into SCP (Groves *et al.* 2012). Studies that target both biodiversity pattern and processes in one plan are rare (Klein *et al*. 2009). More effective conservation planning depends partly on science catching up with our ability to include both pattern and ecological processes (Pressey *et al*. 2007).

As comparatively few of the SCP generated worldwide for implementation get published in peer-reviewed journals, it is difficult to judge progress over time. To our knowledge the application of forest specific ecological processes as input features have been limited to either forest edge disturbance and decomposition (Lawes *et al*. 2007), clusters of forest patches embedded within a largely natural vegetation matrix (Ferrar & Lötter 2007), priority forest

patches and priority forest clusters (Berliner 2009), connected forest habitats for individual species and successional forest types (Mikusiński *et al*. 2007); multi-feature and reserve connectivity (Lehtomäki et al. 2009); riverine corridors (Cowling *et al*. 2003), and disturbance events (Drechsler *et al*. 2009).

Systematic conservation plans have been developed by many government and non-government organisations but numerous species and ecosystems in these plans are being affected by climate change. Groves *et al*. (2012) identified a critical need to incorporate new and complimentary approaches that would aid these plans in adjusting to potential climate change impacts. It is anticipated that climate change will alter the geographic location of suitable climatic niches, resulting in shifts in species distributions. In extreme cases, the entire future climatically suitable niche may lie outside the present species' range, necessitating dispersal to colonise novel habitats for the species to persist (Le Galliard *et al.* 2012). In a review of 112 scholarly articles on biodiversity management and climate change, improving connectivity was ranked as the most recommended response for climate change adaptation strategies (Heller & Zavaleta 2009). Maintaining landscape connectivity will play an increasingly important role in the persistence of many plant and animal populations in the face of the expected shifts in species distributions (Taylor *et al.* 2006). In fragmented landscapes, the survival of plant populations may depend on sufficient rates of migration between fragments to counteract local extinctions and maintain species diversity (Hewitt & Kellman 2002; Saura *et al*. 2011). When vertebrates are capable of migrating between fragments, the effects of small population size may be greatly mitigated (Estrada *et al.* 1993). Dispersal, even infrequent, of a great number of plant species can be disproportionately important in survival and recruitment, genetic structure, and range expansion rates of populations (Clark *et al*. 2001; Merwin *et al*. 2012).

Dispersal and the associated colonisation of forest patches was identified as an important process in the Drakensberg montane forests of South Africa (Lawes *et al.* 2007). Small patch size and isolation can contribute directly to local extinction and a species' dispersal ability will determine its likelihood of re-colonising a habitat patch and persisting within the landscape as part of a dynamic metapopulation (Lawes *et al.* 2007). Stochastic population theory predicts that if there is no movement between patches, extinction is the inevitable fate of the population. Without dispersal, populations with low density would not be 'rescued' by immigration (Benton & Bowler 2012). In this sense dispersal is the key ecological process that maintains species and population diversity within fragmented forest ecosystems. Dispersal by animals is particularly important in the tropics where up to 90% of tropical tree species have fleshy, vertebrate-dispersed fruit (Jordano 1992), and up to 75% of all species may be vertebrate dispersed (Bollen *et al*. 2004).

Landscape connectivity is defined as 'the degree to which the landscape facilitates or impedes movement among resource patches' (Taylor *et al.* 2006), whereby it determines what proportion of the total habitat area can be reached and is available for an organism located at a particular point in the landscape (Saura *et al*. 2011). Accounting for the effects of habitat

connectivity and the elevated importance of certain patches in maintaining connectivity, and contributing to habitat availability, is important for numerous reasons (Taylor *et al*. 2006; Awade *et al*. 2012). There is consensus that connectivity is species-specific and hard to implement across multiple species or communities (Nicholson *et al.* 2006). Connectivity should be measured from a functional perspective, whereby not only is the spatial arrangement of the habitat considered (structural connectivity), but also dispersal distances and/or behavioural responses of focal species to the physical structure of the landscape (functional connectivity; Taylor *et al*. 2006; Saura & Torné 2009).

Loss in connectivity contributes towards a decrease in habitat availability in fragmented landscapes (Awade *et al.* 2012). For a habitat to be easily available for an animal population, it should be both abundant and well connected (Saura & Torné 2009). Habitat availability across fragmented landscapes is governed by the availability of reachable natural vegetation of suitable cover (Pascual-Hortal & Saura 2006; Saura *et al.* 2011).

Driven by a desire for a more functional quantitative approach, landscape ecologists are increasingly using graph theory to examine patterns of connectivity, identify potential dispersal pathways, and prioritize habitat patches for conservation (Kupfer 2012). Graph theory offers a very efficient method to assess connectivity by representing the landscape as a set of nodes (patches) and links (representing the potential ability of an organism to directly disperse between two habitat nodes) (Cook *et al*. 2009). However this approach requires knowledge of species inter-patch movement - information that is difficult to obtain (Taylor *et al*. 2006). Besides, detailed dispersal information is scarce for most species (Saura *et al*. 2011; Awade *et al.* 2012).

Although all processes are important in the persistence of forest species, we focus on dispersal as the key process, but acknowledge the importance of other processes, such as pollination (supporting genetic diversity) and resprouting (persistence of individuals).

The application of graph theory within SCP is still largely new, with few examples of its potential utility available. Applications to date have centred on reserve design or the evaluation of proposed protected area network connectivity (Rothley & Rae 2005 and references therein; Fuller *et al*. 2006; Wang & Önal 2011). In this paper we present a novel method for applying connectivity metrics to a community of species, where previously connectivity metrics have only been applied to individual species. We aim to identify priority forest patches as an input layer into a SCP that ensures a functionally connected forest network (i.e. dispersal abilities maintained), which supports the persistence of forest processes that maintains species diversity across a largely natural landscape. To do so, we assess seed/diaspore dispersal distances in temperate forests of Mpumalanga Province, South Africa, to inform the minimum distance between forest patches that allows 75% of species to be functionally connected. The South African National Biodiversity Institute (SANBI) has adopted the principle target of securing the area required to represent a single occurrence of at least 75% of plant species in a given

vegetation unit (Desmet 2004; Rouget *et al*. 2004; Reyers *et al*. 2007). This principle is now firmly embedded in national government's policies and strategies such as the National Biodiversity Strategy and Action Plan (DEAT 2005), and the gazetted National List of Ecosystems that are Threatened and in need of Protection (DEAT 2011). These targets have also subsequently been adopted in all local, regional and national scale SCP initiatives.
We ask the following questions:

(a) What are the dispersal modes characterising forests in Mpumalanga?

(b) Are there any differences in dispersal modes at either provincial or regional scales?

(c) What dispersal distance allows for at least 75% of species to disperse between patches?

Further we shall use the minimum patch distances to parameterise forest patch connectivity indices in order

(d) to assess the relative contribution of various connectivity fractions to the importance of forest patches in maintaining connectivity;

(e) to identify priority forest patches within a largely natural landscape matrix, and

(f) to identify the critically important forest patches that play a significant role in maintaining a functionally connected forest network for inclusion within a SCP.

MATERIAL AND METHODS

Study area

A data set of 434 vegetation plots (20 x 20 m; 0.04 ha; all plant species recorded) of the indigenous warm-temperate forests of Mpumalanga Province, South Africa was compiled (Lötter et al. 2014). In this region the forests are naturally fragmented and make up only 0.51% of the Province's vegetation cover, and generally occur in small clustered fragments ($P<0.01$). The forest boundary in natural landscapes is usually clear-cut creating a strong contrast between forest patches and the surrounding matrix which is often comprised of grassland, afforested plantations, urban or rural settlements, or agricultural lands. The mean distance between nearest forest patches is 837 m (SD: 1660 m). The median patch size is 4.6 ha (range: 0.04 ha to 3790 ha; 1914 forest patches considered).

Altitude of the forest patches varies between 251 m and 1974 m above sea level. The climate is largely (warm) temperate with mean annual temperature varying between 14°C and 22°C and the mean annual rainfall spans 500 mm to 1635 mm (modelled GIS data based on Schulze, 2007). Three geographically distinct forested regions were distinguished in Mpumalanga. The Northern Escarpment, Barberton and Wakkerstroom Regions comprise 1170, 520 and 224 forest patches, respectively. Forest patches are regionally clustered, crossing a variety of environmental gradients but regionally coherent.

Dispersal modes

Each forest plant species encountered in the plot data set was categorised into one of seven dispersal modes (wind, vertebrate, ant, ballistic, adhesive, water, and unassisted). The dispersal mode adopted by a plant species is frequently associated with other attributes of the plant and its habitat (Hughes *et al.* 1994). We scored the values of plant traits using literature sources, field data, and expert opinion. The relevant literature sources include (Pooley 2006; Boon 2010) for plants, (Hockey *et al.* 2005) for avifauna, and (Skinner & Chimimba 2005; Monadjem *et al.* 2010) mammals. The expert opinion input was based on focused workshops with botanical experts or email to initially categorise and propose likely dispersal mechanisms. A knowledgeable bird guide with strong botanical knowledge was finally consulted for input and refinement of dispersal vectors and estimated dispersal ranges for bird dispersed species. Dispersal ranges/distances were estimated and proposed for each species based on a conservative and probable dispersal distance, in the absence of species-specific data. Furthermore, scientific papers were scrutinised for empirical data on dispersal distances of similar species. The species categorisation and dispersal estimates are provided in Table S1 (see Supporting Material). Our estimates are probably conservative as diplochory (>one vector contributes to diaspore dispersal) is reported to occur rather frequently (de Casas *et al*. 2012).

We assessed the occurrence of regional variation in dispersal by categorising the flora into dispersal modes in each of the geographically distinct regions from the plot data, and then compared proportions of plant species in different dispersal modes across the regions using a χ^2 contingency table. Variation in dispersal modes would indicate probable variation in dispersal distances between regional forest communities.

Interpatch distance

The minimum dispersal distance that functionally connects two forest patches was calculated from the plot data for each region. In order to ensure that at least 75% of the regional species composition would be able to disperse between forest patches, the proportion of species (y axis) and the expected diaspore distance that each species could travel (x axis) was displayed on a line-graph and the 75% proportional cut-off value used to determine minimum patch distance thresholds for each region, and the whole Province.

Patch quality

Based on the objectives of this paper, dispersal processes would be interrupted across environments that are transformed or no longer natural. The likelihood of persistence is dependent on local population size which in turn is influenced by patch quality and size (Benton

& Bowler 2012). We expect that vertebrate diversity and population size would be greater in natural areas devoid of noise, pollution, unnatural disturbances, harvesting or hunting. A decrease in abundance of vertebrate dispersers will inevitably lead to reduced diaspore dispersal rates and lower net average dispersal distance as a higher proportion of seeds is predicted to land under parent trees (see Lehouck *et al*. 2012). Similarly dispersal between patches across a 'hostile' matrix would be undesirable when conservation priorities should consider a more permeable matrix to support dispersal, acknowledging that avifauna and bats may be less influenced by the intervening landscape matrix than non-volant vertebrates. As no province-wide information exists on forest patch quality, we used the proportion of vegetation that is still in a natural state within a 1 km buffer around each forest patch as a surrogate for vertebrate and forest patch health. We use the term *naturalness* to refer to the proportion of buffer that is still in a natural state. The 1 km buffer was the average provincial cross-regional distance that would allow for 75% of the species to disperse.

Connectivity metrics

For the analysis of forest connectivity we used the probability of connectivity (*dPC*) habitat availability index (Saura & Pascual-Hortal 2007; Saura & Rubio 2010) in the Conefor Sensinode 2.6 software (Saura & Torné 2009; www.conefor.org, accessed 5 June 2012) to identify priority forest patches for conservation. Habitat availability indices integrate, in a single measure, the area existing within the habitat patches (intra-patch connectivity) with the area made available (reachable) through the connections with other habitat patches in the landscape (inter-patch connectivity) (Pascual-Hortal & Saura 2006; Saura *et al.* 2011). The *dPC* is defined as the probability that two points randomly placed within the landscape fall into habitat areas that are reachable from each other (interconnected) given a set of *n* habitat patches and the links (direct connections) among them (Saura & Pascual-Hortal 2007; Saura & Rubio 2010; *Saura et al.* 2011). The application of probability of connectivity index is strongly supported in recent literature (see Visconti & Elkin 2009; Baranyi *et al.* 2011; Pereira *et al.* 2011; Kupfer 2012). Habitat patch area, quality and inter-patch distances for calculation of the indices were measured using ESRI ArcMap 10.1 software (ESRI 1999–2011) and the Conefor Inputs Tool extension for ArcGIS (www.jennessent.com/arcgis/conefor_inputs; accessed 5 June 2012) to generate input files based on Euclidean distances between edges of all forest patches.

The *dPC* provides results for individual patches which include values of the three fractions that make up the *dPC* metric (*dPCintra, dPCflux, dPCconnect*). The *connect fraction* evaluates a patch's contribution to connectivity between other patches by acting as an intermediate stepping stone patch (Saura & Rubio 2010). The *flux fraction* measures how much a specific node sits between all other pairs of nodes in a network, i.e. it captures how many pairs of nodes are connected through that specific node, while the *intra fraction* measures intra-patch connectivity that is independent of other patches (Bodin & Saura 2010).These three

fractions are also measured in the same units and allow for prioritizing the landscape elements and their different roles within an integrated analytical framework (Saura & Rubio 2010). They provide for unpacking and interpreting the different ways in which habitat patches can contribute to habitat connectivity and availability in the landscape.

In this study, a probability of direct dispersal value of P=0.5 was set for the reference dispersal distances, a value frequently used in similar studies (Saura & Rubio 2010; Baranyi *et al*. 2011; Awade *et al.* 2012). Other input data require the identification of (1) a minimum patch distance (defined in our study as the minimum area that would still allow 75% of the species composition to disperse); (2) a node or patch value (which could represent some relevant patch attribute such as habitat quality, although we use the proportion of the surrounding matrix which is still natural); and (3) a spatial layer representing the landscape configuration of forest patches. The distance thresholds required to define regional minimum patch distances for the habitat availability index (*dPC*) were obtained from analysing the estimated dispersal distances (Table S1) where two nodes are linked if 75% of the species can disperse between them.

We created a table to summarise our choice of using *naturalness* as a node value in the connectivity metrics over *size* as an alternative input value, while being cognisant that size is also an important attribute. This table allowed us to assess the effect of using either option. As a benchmark, mean patch size and naturalness were calculated for all forest patches, and for comparison, we compared these to selected values (top 5th quantile) for *dPC* index and its fractions.

We used PRIMER v6 (Clarke & Gorley 2006) to visually assess the similarity of *dPC* and the various connectivity fractions by means of non-metric multidimensional scaling (nMDS) ordination, using the Bray-Curtis similarity measure standardized by sample unit totals with no transformation. Ordination graphs were created for the four data sets, namely a collated data set for the Province and each of the three forest regions. In each ordination graph, the actual values for the *dPC* index and the three fractions for each forest patch were used as *variables* while the index and fractions were used as *samples*.

Finally, to select prioritised forest patches for inclusion in a SCP, we used histograms and scatter plots of the various connectivity fractions and their performance to identify disjunctions and those patches that contribute significantly towards connectivity across each region.

RESULTS

Dispersal

Forest plant dispersal modes (Fig. 1) and dispersal distances (Fig. 2) are presented, for both the Province and the forest regions. Regional variation was observed in both the analyses of dispersal modes (although observations were not statistically significant; results not shown) and dispersal distance. Applying a 75% species dispersal requirement, yielded minimum patch

distances of 0.6 km, 1 km and 2 km for the Northern Escarpment, Barberton and Wakkerstroom Regions, respectively. These distances were used to parameterise the connectivity indices that require a minimum distance between any two patches that still enable them to be functionally connected.

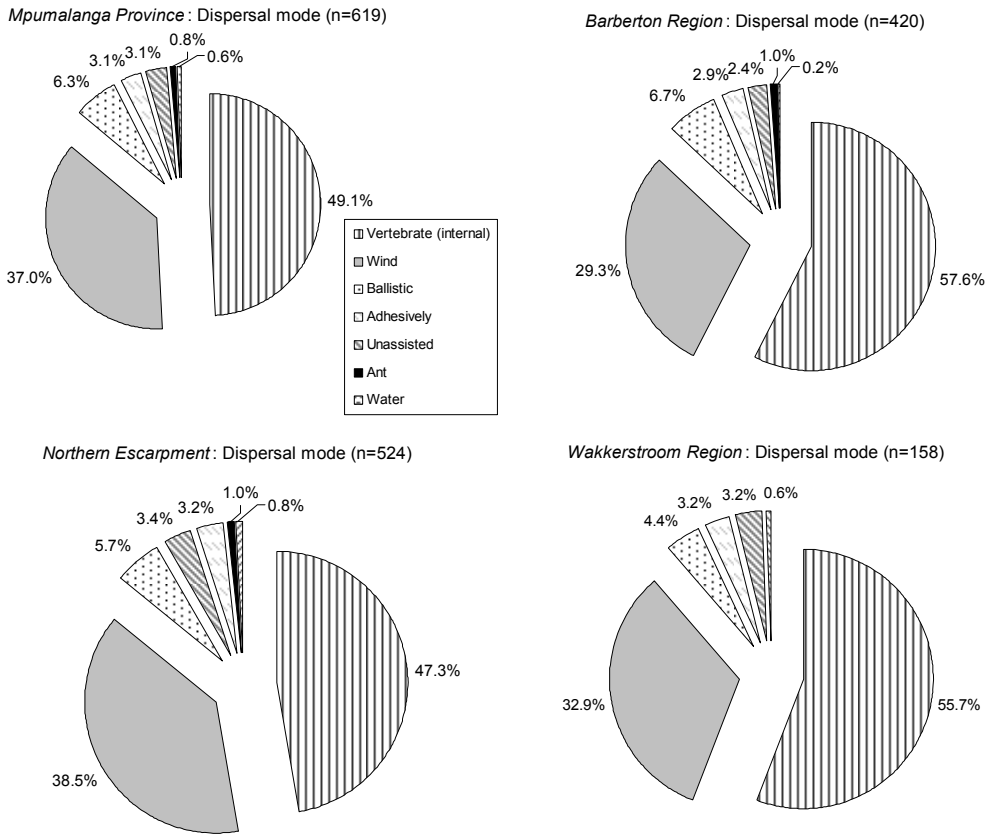


Figure 1 Proportional variation in dispersal modes for temperate forests in A) Mpumalanga Province, South Africa, B) Barberton Region, C) Northern Escarpment Region, and D) Wakkerstroom Region.

Connectivity

The main result of the connectivity analysis is the importance of each individual forest patch for maintaining overall landscape connectivity according to the *dPC* index and its three fractions. This allows for patch prioritisation and ranking of forest patches by their contribution to landscape connectivity, which provides objective criteria for the selection of the most critical forest patches for conservation planning purposes.

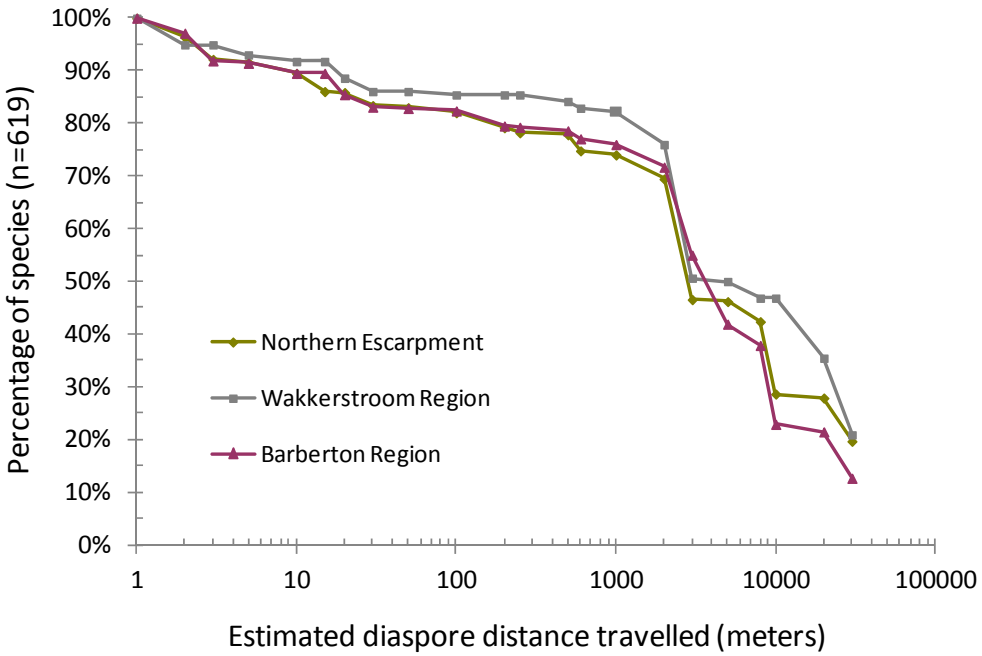


Figure 2 Minimum patch distance as a measure of expected diaspore dispersal distance that would allow for 75% of the forest flora to reach a new patch. Dispersal distance curves are presented for each of the three forest regions in Mpumalanga. The x-axis is $\log_{10}$ scaled.

The *dPC* index and fractions were partitioned to highlight individual patch characteristics according to their contribution to landscape connectivity. The *dPCintra* fraction measured the intrinsic patch attributes and therefore prioritised patch value; *dPCflux* measured the amount of flux a patch is estimated to receive and prioritised patches that were well connected to other patches (it extended its available habitat to these patches); and *dPCconnect* measured the importance of patches as connecting elements (stepping stones). An example of individual patch values for the various metrics, presented in Fig. 3, highlights an area in the Wakkerstroom Region. Patch values appear to differ significantly between fractions and utility of the individual fractions is highlighted. The two more similar outputs appear to be the *dPCflux* and *dPC* index.

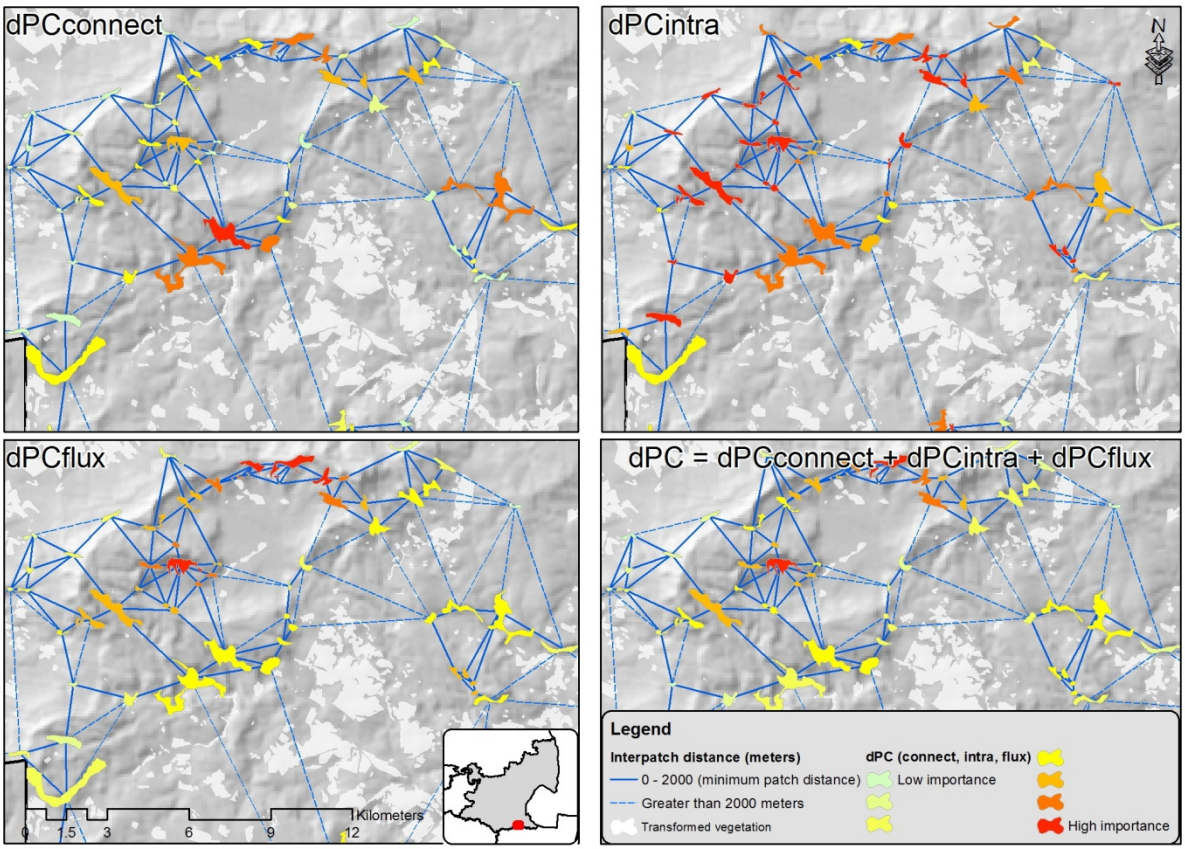


Figure 3 Conservation priority values for individual forest patches based on the three fractions of *dPC* and the combined result. A subset of patches is presented for a Wakkerstroom area, based on an expected dispersal distance of 2 km (the range where at least 75% of the diaspores are able to disperse). Solid blue lines are less than 2 km while dotted blue lines are greater than 2 km. White on the map represent areas where the natural habitat has been transformed.

Comparison of connectivity index and fractions

A comparison of the similarity of the various fractions against the *dPC* index and across all three regions and the whole province shows that for each region, the *dPC* and *dPCflux* are consistently the most similar (Fig. 4). The *dPCconnect* fraction is consistently more dissimilar to the other fractions. These results suggest that at least two indices should be considered for inclusion in a SCP, which would provide more useful information by characterizing the different aspects of positional importance of patches



Figure 4 Similarity of the *dPC* connectivity metric and its three fractions (*dPCintra, dPCflux, and dPCconnect*) for (A) Mpumalanga Province (results summarised), and each of its three regions (B) Barberton, (C) Northern Escarpment, and (D) Wakkerstroom. nMDS ordination plots (axes 1 and 2) are shown.

Ensuring connected network of forest patches in natural landscape matrix

Recalling that both patch size and quality influence persistence, our stated objectives include the prioritisation of patches within largely natural landscapes. The degree to which the various fractions were able to meet this requirement is summarised in Table 1. The mean baseline values for all forest patches (across all regions) are presented in Column A. Columns B and C show the effect of conducting the analysis using either size or naturalness as input values for patch quality on mean patch size and naturalness values. The purpose was to assess to what extent we are failing to incorporate patch size by selecting patch quality over patch size. Although mean patch size is higher when basing analysis on size rather than quality (68 ha vs. 38 ha), basing the value on naturalness still identified priority patches that are much higher than the mean value across all regions (38 ha vs. 19 ha). The loss of size is offset by large gains in naturalness of surrounding matrix (influencing patch quality). There was little difference between Columns A and B (71% vs. 69%), yet large gains when using naturalness as node value when comparing Columns B and C (69% vs. 88%).

In addition Table 1 assesses the various patch size and naturalness differences between the *dPC* index and its fractions in Column C. Prioritised patches based on *dPCintra* reflected patch quality (i.e. naturalness), and patch size was lower than mean patch size values. Once more *dPC* and *dPCflux* produced similar outputs, a result supported in Figures 3 and 4. *dPCconnect* generally identified larger forest patches as important stepping stones (55 ha vs. 38 ha for *dPC*), yet the naturalness of the surrounding matrix was slightly lower than the mean value (76% vs. 88% for *dPC*).

Table 1 Descriptive statistics comparing the mean values for the proportion of a 1 km buffer around each forest patch still natural (naturalness) and mean patch size values for: (A) all forest patches in Mpumalanga; (B) only forest patches from the top 5th quantile selected on the basis of their *dPC* index values where the index applied patch size as node value; in contrast to (C) applying naturalness as node value in *dPC* index and related fractions. This enables us to assess the extent to which the *dPC* index and the choice of either patch size or naturalness as node values, can influence the selection of forest patches from an untransformed landscape matrix and favour the selection of large patch sizes (*natural* = *naturalness* in columns B and C).

			(B) PC index node value based on patch size		(C) PC index node value based on naturalness of 1km buffer							
Region	*Naturalness (1km buffer)*	*Mean patch size (ha)*	*dPC (patch size)*		*dPC*		*dPCintra*		*dPCflux*		*dPCconnect*	
			Natural	*Size (ha)*	*Natural*	*Size (ha)*	*Natural*	*Size (ha)*	*Natural*	*Size (ha)*	*Natural*	*Size (ha)*
Barberton	66.2%	17.9	65.8%	64.6	82.6%	34.5	99.9%	15.4	86.5%	31.6	69.6%	40.0
Northern Escarpment	53.3%	23.9	47.4%	96.2	84.8%	63.5	99.8%	7.5	84.6%	56.9	62.4%	98.6
Wakkerstroom	92.4%	13.8	93.5%	44.0	95.4%	15.0	99.9%	8.4	94.5%	11.4	96.5%	26.9
Mean value	*71%*	*19 ha*	*69%*	*68 ha*	*88%*	*38 ha*	*99.8%*	*10 ha*	*89%*	*33 ha*	*76%*	*55 ha*

Forests were selected for inclusion in a SCP based on the performance of the *dPC* and *dPCconnect* fractions (see Figures 3 and 4, Table 1). The selected patches were required to have significantly higher values for either *dPC* or *dPCconnect* indices in each of the regions. Scatter plots were generated for each region assisting in the identification of graph disjunctions and those patches significantly contributing towards connectivity (Fig. 5).

DISCUSSION

Designing effective SCPs requires the inclusion and prioritising of the relative importance of patches in maintaining connectivity and supporting persistence. We applied the probability of connectivity (*dPC*) index with its three fractions to prioritise the connectivity importance of individual patches for conservation.

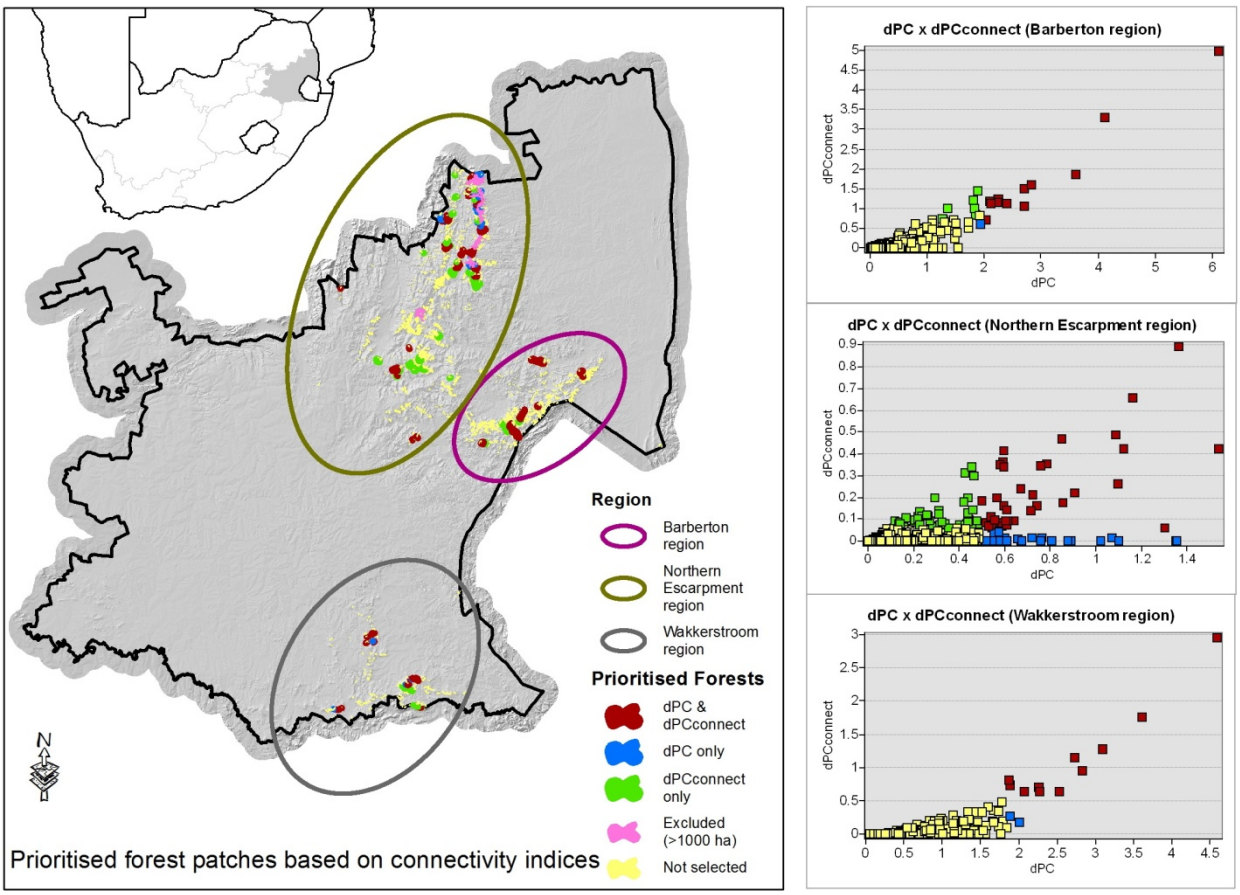


Figure 5 Forest patches selected for inclusion in a systematic conservation plan based on performance of *dPC* and *dPCconnect* indices for each of the three forest regions of the Mpumalanga Province, South Africa. The majority of selected patches are important for both *dPC* and *dPCconnect* indices (red colour). Scatter plots were generated for each region assisting in the identification of disjunctions and those patches significantly contributing towards connectivity.

This study furthers the recent body of connectivity theory in community ecology by applying the graph theoretical framework to a community of organisms, not just individual species. Our approach can help ecologists and conservation planners identify priority forest patches that contribute towards upholding dispersal across a landscape. Diaspore dispersal is a critical forest process that can mediate the effect of small populations or patches by means of colonisation. As climate change starts to influence community composition and range expansion (Le Galliard *et al.* 2012), species will need to respond by means of emigration and immigration of diaspores better suited to the new climate. Our application of ecosystem wide dispersal and connectivity conforms with two of Groves *et al*.'s (2012) five explicit climate change adaptation approaches that can be incorporated into regional-scale SCP, namely (1) enhancing regional connectivity, and (2) sustaining ecosystem processes and function.

Imperfect knowledge on species-specific dispersal attributes can be partly circumvented by means of expert consultation. But in predicting dispersal ranges (Table S1), there is more uncertainty when diaspores are able to disperse greater distances. The rather abrupt decline

after 2 000 meters (Fig. 2) may be less severe if we were able to more accurately predict dispersal ranges over greater distances. Our regional analysis of dispersal characteristics demonstrated the dominant function of frugivores in dispersing diaspores between forests, with roughly half of all plant species being vertebrate dispersed. One of the implications of this is that the hostility of the surrounding landscape matrix to vertebrates would influence the success and distance of diaspore dispersal. After frugivore dispersal, wind dispersal was the second largest dispersal mode which we expect is largely uninfluenced by matrix permeability, but dependent on suitable habitat in which to establish. With 51% of all the forest plant species being obligate forest species (Lötter *et al.* 2014), we anticipate that several facultative species may occur within the intervening matrix between forest patches. These species would not be as dispersal limited as obligate species and therefore the results we present are perhaps more conservative or precautionary than what is expected to occur naturally.

The application of the principle target of ensuring that at least 75% of all diaspores could disperse to the nearest forest patch provided a minimum patch distance that allowed for functional connectivity and the identification of the distinctive contributions of individual forest patches to connectivity. Nonetheless population persistence at the landscape scale depends on more than just connectivity, but also on the amount and quality of habitats available across the landscape which influences the balance between reproduction and mortality (Taylor *et al.* 2006). Although results were not statistically significant, the observed differences between the regional dispersal modes was also corroborated in the analysis of dispersal distance (meeting the 75% dispersal requirement), which varied between the three regions, namely 600 m along the Northern-Escarpment, 1 km in the Barberton Region, and 2 km in the Wakkerstroom Region. Interestingly mean forest patch size appears to decline with increased dispersal distances (24, 18 and 14 ha, respectively).

In comparing the effects of the various *dPC* indices, our results affirm the observations of Baranyi *et al.* (2011) where the *dPCflux* fraction largely dominated the total *dPC* value for species with medium to large dispersal ranges. In our study the *dPC* and *dPCflux* indices were consistently similar across our limited range of dispersal distances (0.6 to 2 km; Fig. 4). Saura & Rubio (2010) corroborate this observation and add that at intermediate dispersal distances, the loss of an individual patch or corridor can be more critical and can cause a significant drop in the ability of a species to reach other high quality patches, which would be highlighted by large *dPCconnect* values. The *dPCconnect* fraction evaluates how irreplaceable a forest patch is as a connectivity provider and that no other patches exist that are able to compensate for its loss (Bodin & Saura 2010). Baranyi *et al.* (2011) further note that very few patches can a) be well connected stepping stones that sit in the usual movement pathways between other patches and (b) be irreplaceable as a connectivity provider because the alternative movement pathways that would be available after their loss are much weaker than those that were facilitated by their presence in the intact network. We therefore decided to incorporate both the patch importance

values from the *dPC* and *dPCconnect* indices for each of the three regions as input layers in our SCP as no single connectivity index is able to account for all aspects of connectivity.

Visconti & Elkin (2009) state that an estimate of patch quality significantly increased the ability of a given connectivity metric to correctly rank habitat patches according to their contribution to metapopulation viability, and hence persistence. Failing to have accurate measurements of habitat quality for each of our forest patches in our study area, our approach of assessing the proportion of the surrounding matrix that is still natural as a surrogate for forest condition (and an increase in the number of potential dispersers as a function of patch quality) is an improvement on basing the analysis on patch size alone.

Forests were selected based on high *dPC* and *dPCconnect* values. The surface area of these patches comprised 19% for the Barberton Region, 14.7% for the Northern Escarpment Region, and 16.6% for the Wakkerstroom Region. Five patches larger than 1000 ha were excluded as they rapidly increased the total size of selected patches to be included in the SCP. In addition we expect that larger patches would be less likely transformed and that intra-patch dispersal would occur within these forests. We further propose that a buffer, equal to the minimum patch distance, for each of the selected patches be included as a separate feature with a 60% pre-transformation target. A target of 60% is a threshold value below which larger habitat fragments generally break apart (Baguette *et al.* 2012) and compromise ecological processes.

The ultimate goal in SCP is to ensure the persistence of regional biodiversity through the inclusion of appropriate ecological process data. We recognise that a focus on landscape connectivity to the exclusion of habitat amount and quality will not guarantee population persistence or maintenance of biodiversity (highlighted by Taylor *et al*. 2006). However, we anticipate that the inclusion of landscape connectivity and the prioritization of important forest patches based on both *dPC* and *dPCconnect* metrics, into a SCP approach with its associated pattern, process, boundary costs, planning unit costs, etc. as input data or parameters (see Margules & Sarkar 2007), will contribute towards the persistence of forest species diversity within the Mpumalanga planning region. What we propose is a method to identify important spatial ecological process features for inclusion into a SCP. Ultimately planning needs to move into the realm of implementation (Knight *et al*. 2006) before persistence can be effected.

An alternative approach for incorporating connectivity within SCP is to use a spatial prioritisation technique such as Zonation (Moilanen *et al*. 2012), with its embedded optimization algorithms, that include several different approaches for incorporating connectivity (distribution smoothing, connectivity interaction, and matrix connectivity) within a SCP (Lehtomäki & Moilanen 2013).

CONCLUSION

Can the variability in dispersal ecology across a forest ecosystem be spatially translated to support the adaptation and maintenance of communities in a changing environment? We offer an applied example where minimum patch distance for an entire community parameterizes a connectivity index to identify individual forest patch importance values.

Our study contributes to the recent body of connectivity theory in community ecology by applying the graph theoretical framework to a community of organisms, not just individual species. Connectivity analyses have great potential for improving the manner in which functional connectivity (i.e. dispersal) can be incorporated and applied to ensure persistence within SCP. But persistence across a landscape depends on more than just connectivity, it is also reliant on patch quality as well as the intervening landscape matrix. In the absence of available data on patch quality, our approach of assessing the proportion of the surrounding matrix that is still natural as a surrogate for forest patch quality also ensured that priority patches were identified within largely natural landscapes.

Uncertainties are inherent in our analysis (i.e. what are the actual dispersal agents for all forest taxa), but in light of a paucity of literature available on species-specific dispersal within our region, the documentation, even as a first approximation, of expected and estimated dispersal modes and distances contributes towards the growing body of dispersal science. Under these circumstances our approach translates to a rapid cost- and time-efficient method that can be practically applied to identify conservation priorities.

This study may also stimulate further developments incorporating dispersal, connectivity and graph theory in SCP. To what extent could our approach to dispersal as an ecological process be adapted for other regions? We realise that some areas may not necessarily have the required species dispersal information nor the expertise to categorise the dispersal distances, but in general this approach could easily be replicated in other regions with vegetation units comprising ‘hard’ boundaries (such as abrupt structural changes from forest to grassland), the availability of species lists, and the appropriate involvement of experts.

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REFERENCES

Awade, M., Boscolo, D. & Metzger, J.P. (2012). Using binary and probabilistic habitat availability indices derived from graph theory to model bird occurrence in fragmented forests. *Landsc. Ecol.*, 27, 185–198.

Baguette, M., Legrand, D., Fréville, H., Van Dyck, H. & Ducatez, S. (2012). Evolutionary ecology of dispersal in fragmented landscapes. In: *Dispersal ecology and evolution* (eds Clobert, J., Baguette, M., Benton, T. & Bullock, J.). Oxford University Press, Oxford, pp. 251–265.

Baranyi, G., Saura, S., Podani, J. & Jordán, F. (2011). Contribution of habitat patches to network connectivity: Redundancy and uniqueness of topological indices. *Ecol. Indic.*, 11, 1301–1310.

Benton, T.G. & Bowler, D.E. (2012). Linking dispersal to spatial dynamics. In: *Dispersal ecology and evolution* (eds Clobert, J., Baguette, M., Benton, T. & Bullock, J.). Oxford University Press, Oxford, pp. 251–265.

Berliner, D. (2009). *Systematic conservation planning for South Africa's forest biome: An assessment of the conservation status of South Africa's forests and recommendations for their conservation*. PhD Thesis, University of Cape Town, Cape Town, ZA.

Bodin, O. & Saura, S. (2010). Ranking individual habitat patches as connectivity providers: Integrating network analysis and patch removal experiments. *Ecol. Model.*, 221, 2393–2405.

Bollen, A., Van Elsacker, L. & Ganzhorn, J.U. (2004). Tree dispersal strategies in the littoral forest of Sainte Luce (SE-Madagascar). *Oecologia*, 139, 604–616.

Boon, R. (2010). *Pooley's trees of eastern South Africa: A complete guide*. Flora and Fauna Publication Trust, Durban, ZA.

Clark, C.J., Poulsen, J.R. & Parker, V.T. (2001). The role of arboreal seed dispersal groups on the seed rain of a lowland tropical forest. *Biotropica*, 33, 606–620.

Clarke, K.R. & Gorley, R.N. (2006) *PRIMER v6: User Manual/Tutorial.* PRIMER-E, Plymouth.

Cook, B., Puotinen, M.L. & Borah, R. (2009). Ranking habitat patches by contribution to network connectivity: tradeoffs between processing time and spatial realization. In: *18th world IMACS/MODSIM Congress, Cairns, 13–17 July 2009*, pp. 1922–1928.

Cowling, R.M., Pressey, R.L., Rouget, M. & Lombard, A.T. (2003). A conservation plan for a global biodiversity hotspot: the Cape Floristic Region, South Africa. *Biol. Conserv.,* 112, 191–216.

de Casas, R.R., Willis, C.G. & Donohue, K. (2012). Plant dispersal phenotypes: a seed perspective of maternal habitat selection. In: *Dispersal ecology and evolution* (eds Clobert, J., Baguette, M., Benton, T. & Bullock, J.). Oxford University Press, Oxford, pp. 171–184.

DEAT (2005). *South Africa's National Biodiversity Strategy and Action Plan*. Department of Environmental Affairs and Tourism, Pretoria, ZA.

DEAT (2011). *Gazette Notice 1002. National list of ecosystems that are threatened and in need of protection. National Environmental Management: Biodiversity Act, 2004.* Department of Environmental Affairs and Tourism, Pretoria, ZA.

Desmet, P. (2004). Appendix B: Developing Species Representation Targets for South African Vegetation Types. In: *SANBI National Spatial Biodiversity Assessment. Technical Report. Vol. 1 Terrestrial Component*. (eds Rouget, M., Reyers, B., Jonas, Z., Desmet, P., Driver, A., Maze, K., Egoh, B. & Cowling, R.M.) pp. 94–107. South African National Biodiversity Institute, Pretoria, ZA.

Drechsler, M., Lourival, R. & Possingham, H.P. (2009). Conservation planning for successional landscapes. *Ecol. Model*., 220, 438–450.

ESRI (1999–2013) ArcView (Version 3.2) and ArcGIS (Version 10.1). Environmental Systems Research Institute, Redlands, CA.

Estrada, A., Coates-Estrada, R., Meritt, D., Montiel, S. & Curiel, D. (1993). Patterns of frugivore species richness and abundance in forest islands and in agricultural habitats at Los Tuxtlas, Mexico. *Vegetatio,* 107-108, 245–257.

Ferrar, A.A. & Lötter, M.C. 2007. *Mpumalanga Biodiversity Conservation Plan Handbook*. Mpumalanga Tourism & Parks Agency, Nelspruit, ZA. http://bgis.sanbi.org/MBCP/MBCPHandbook.pdf

Fuller, T., Munguia, M., Mayfield, M., Sánchez-Cordero, V. & Sarkar, S. (2006). Incorporating connectivity into conservation planning: A multi-criteria case study from central Mexico. *Biol. Conserv.*, 133, 131–142.

Groves, C. R., Game, E. T., Anderson, M. G., Cross, M., Enquist, C., Ferdaña, Z., Girvetz, E., Gondor, A., Hall, K.R., Higgins, J., Marshall, R., Popper, K., Schill, S. & Shafer, S. (2012). Incorporating climate change into systematic conservation planning, *Biodivers. Conserv.*, 21, 1651–1671.

Heller, N.E. & Zavaleta, E.S. (2009). Biodiversity management in the face of climate change: A review of 22 years of recommendations. *Biol. Conserv.*, 142, 14–32.

Hewitt, N. & Kellman, M. (2002). Tree seed dispersal among forest fragments: I. Conifer plantations as seed traps. *J. Biogeogr.*, 29, 337–349.

Hockey, P.A.R., Dean, W.R.J. & Ryan, P.G. (eds) (2005). *Roberts' Birds of Southern Africa.* 7th edn. John Voelcker Bird Book Fund, Cape Town, ZA.

Hughes, L., Dunlop, M., French, K., Leishman, M., Rice, B., Rodgerson, L. & Westoby, M. (1994). Predicting dispersal spectra: a minimal set of hypotheses based on plant attributes. *J. Ecol.*, 82, 933–950.

Jordano, P. (1992). Fruits and frugivory. In: *Seeds: the ecology of regeneration in plant communities*. (ed. Fenner, M.). CABI, Wallingford, United Kingdom, pp. 105–156.

Klein, C.J., Wilson, K.A., Watts, M., Stein, J., Berry, S., Carwardine, J., Smith, M.S., Mackey, B.G. & Possingham, H.P. (2009). Incorporating ecological and evolutionary processes into large–scale conservation planning. *Ecol. Appl.*, 19, 206–217.

Knight, A.T., Cowling, R.M. & Campbell, B.M. (2006). Planning for implementation: an operational model for implementing conservation action. *Conserv. Biol.*, 20, 549–561.

Kupfer, J.A. (2012). Landscape ecology and biogeography: Rethinking landscape metrics in a post-FRAGSTATS landscape. *Progr. Phys. Geog.,* 36, 400–420.

Lawes, M.J., Adie, H., Eeley, H.A.C., Kotze, D.J. & Wethered, R. (2007). *An assessment of the forests of the Maloti-Drakensberg Transfrontier Bioregion, with reference to important ecosystem processes*. Forest Biodiversity Research Unit, School of Biological and Conservation Sciences, University of KwaZulu-Natal, Pietermaritzburg, ZA.

Le Galliard, J.F., Massot, M. & Clobert, J. (2012). Dispersal and range dynamics in changing climates: a review. In: *Dispersal ecology and evolution* (eds Clobert, J., Baguette, M., Benton, T. & Bullock, J.). Oxford University Press, Oxford, pp. 317–336.

Lehouck, V., Bonte, D., Spanhove, T. & Lens, L. (2012). Integrating context- and stage-dependent effects in studies of frugivorous seed dispersal: an example from south-east Kenya. In: *Dispersal ecology and evolution* (eds Clobert, J., Baguette, M., Benton, T. & Bullock, J.). Oxford University Press, Oxford, pp. 50–62.

Lehtomäki, J. & Moilanen, A. (2013). Methods and workflow for spatial conservation prioritization using Zonation. *Environ. Modell. Softw*., 47, 128–137.

Lehtomäki, J., Tomppo, E., Kuokkanen, P., Hanski, I & Moilanen, A. (2009) Applying spatial conservation prioritization software and high-resolution GIS data to a national-scale study in forest conservation. *Forest Ecol. Manag.*, 258, 2439–2449.

Lötter, M.C., Mucina, L. & Witkowski, E.T.F. (2014). Classification of the indigenous forests of Mpumalanga Province, South Africa. *S. Afr. J. Bot*., 90, 37–51.

Margules, C.R. & Pressey, R.L. (2000). Systematic conservation planning. *Nature*, 405, 243–253.

Margules, C.R. & Sarkar, S. (2007). *Systematic conservation planning*. Cambridge University Press, New York.

Merwin, L., He, T., Lamont, B.B., Enright, N.J. & Krauss, S.L. (2012). Low rate of between-population seed dispersal restricts genetic connectivity and metapopulation dynamics in a clonal shrub. *PLoS ONE*, 7(11): e50974. doi:10.1371/journal.pone.0050974

Mikusiński, G., Pressey, R.L., Edenius, L., Kujala, H., Moilanen, A., Niemelä, J. & Ranius, T. (2007). Conservation planning in forest landscapes of Fennoscandia and an approach to the challenge of Countdown 2010. *Conserv. Biol.*, 21, 1445–1454.

Monadjem, A., Taylor, P.J., Cotterill, F.D.P. & Schoeman, M.C. (2010). *Bats of Southern and Central Africa. A Biogeographic and taxonomic synthesis*. Wits University Press, Johannesburg, ZA.

Moilanen, A., Meller, L., Leppänen, J., Pouzols, F.M., Kujala, H., Arponen, A. (2012). *Zonation Spatial Conservation Planning Framework and Software V3.1, User Manual*. http://cbig.it.helsinki.fi/files/zonation/ZONATION_v3.1_Manual_120416.pdf

Nicholson, E., Westphal, M.I., Frank, K., Rochester, W.A., Pressey, R.L., Lindenmayer, D.B. & Possingham, H.P. (2006). A new method for conservation planning for the persistence of multiple species. *Ecol. Lett.*, 9, 1049–1060.

Pascual-Hortal, L. & Saura, S. (2006) Comparison and development of new graph-based landscape connectivity indices: towards the priorization of habitat patches and corridors for conservation. *Landsc. Ecol.*, 21, 959–967.

Pereira, M., Segurado, P. & Neves, N. (2011). Using spatial network structure in landscape management and planning: a case study with pond turtles. *Landsc. Urb. Plan.*, 100, 67–76.

Pooley, E. (2006). *Forest plants in the forest and in the garden: Popular guides to the biomes of South Africa Book 1*. The Flora Publications Trust, Durban, ZA.

Pressey, R.L., Cabeza, M., Watts, M.E., Cowling, R.M. & Wilson, K.A. (2007). Conservation planning in a changing world. *Trends Ecol. Evol.*, 22, 582–592.

Pressey, R.L., Cowling, R.M. & Rouget, M. (2003). Formulating conservation targets for biodiversity pattern and process in the Cape Floristic Region, South Africa. *Biol. Conserv.*, 112, 99–127.

Reyers, B., Rouget, M., Zonas, Z., Cowling, R.M., Driver, A. Maze, K. & Desmet, P. (2007). Developing products for conservation decision-making: lessons from a spatial biodiversity assessment for South Africa. *Diversity Distrib*., 13, 608–619.

Rothley, K.D. & Rae, C. (2005). Working backwards to move forwards: Graph-based connectivity metrics for reserve network selection. *Environ. Model. Assess.*, 10, 107–113.

Rouget, M., Reyers, B., Jonas, Z., Desmet, P., Driver, A., Maze, K., Egoh, B. & Cowling, R.M. (eds) (2004). *SANBI National Spatial Biodiversity Assessment. Technical Report. Vol. 1. Terrestrial Component.* South African National Biodiversity Institute, Pretoria, ZA.

Sarkar, S., Pressey, R.L., Faith, D.P., Margules, C.R., Fuller, T., Stoms, D.M., Moffett, A., Wilson, K.A., Williams, K.J., Williams, P.H. & Andelman, S. (2006). Biodiversity conservation planning tools: present status and challenges for the future. *Annu. Rev. Environ. Resour.*, 31, 123–159.

Saura, S., Estreguil, C., Mouton, C. & Rodríguez-Freire, M. (2011). Network analysis to assess landscape connectivity trends: application to European forests (1990–2000). *Ecol. Indic.*, 11, 857–860.

Saura S. & Pascual-Hortal, L. (2007). A new habitat availability index to integrate connectivity in landscape conservation planning: comparison with existing indices and application to a case study. *Landsc. Urb. Plan.*, 83, 91–103.

Saura, S. & Rubio, L. (2010). A common currency for the different ways in which patches and links can contribute to habitat availability and connectivity in the landscape. *Ecography*, 33, 523–537.

Saura, S. & Torné, J. (2009). Conefor Sensinode 2.2: a software package for quantifying the importance of habitat patches for landscape connectivity. *Environ. Modell. Softw.*, 24, 135–139. www.conefor.org, accessed June 2012.

Schulze, R.E. (2007). *South African Atlas of Climatology and Agrohydrology.* WRC Report 1489/1/06. Water Research Commission, Pretoria, ZA,

Skinner, J.D. & Chimimba, C.T. (eds) (2005). *The mammals of the Southern African Subregion.* 3rd edn. Cambridge University Press, New York.

Taylor, P.D., Fahrig, L. & With, K.A. (2006). Landscape connectivity: a return to the basics. In: *Connectivity conservation* (eds Crooks, K.R. & Sanjayan, M.). Cambridge University Press, Cambridge, pp. 29–43.

Visconti, P. & Elkin, C. (2009). Using connectivity metrics in conservation planning: when does habitat quality matter? *Divers. Distrib.*, 15, 602–612.

Wang, Y. & Önal, H. (2011). Designing connected nature reserve networks using a graph theory approach. *Acta Ecol. Sin.*, 31, 235–240.

SUPPLEMENTARY INFORMATION

Table S1 The classification of forest species (n=619) according to dispersal modes and expected dispersal distances

Family	Species	Mode	Distance	Notes on disperser	Key Forest Bird Species	Forest Bird Species	Forest Margin Birds
Acanthaceae	*Barleria rotundifolia*	Ballistic	<2m				
Acanthaceae	*Dicliptera clinopodia*	Ballistic	<2m				
Acanthaceae	*Duvernoia aconitiflora*	Ballistic	<2m				
Acanthaceae	*Duvernoia adhatodioides*	Ballistic	<2m				
Acanthaceae	*Hypoestes aristata*	Ballistic	<2m				
Acanthaceae	*Hypoestes triflora*	Ballistic	<1m				
Acanthaceae	*Isoglossa cooperi*	Ballistic	<2m				
Acanthaceae	*Justicia campylostemon*	Ballistic	<2m				
Acanthaceae	*Mackaya bella*	Ballistic	<3m				
Acanthaceae	*Pseuderanthemum subviscosum*	Ballistic	<2m				
Acanthaceae	*Ruttya ovata*	Ballistic	<2m				
Acanthaceae	*Sclerochiton harveyanus*	Ballistic	<2m				
Acanthaceae	*Thunbergia alata*	Ballistic	<2m				
Acanthaceae	*Thunbergia natalensis*	Ballistic	<2m				
Amaranthaceae	*Achyranthes aspera var. aspera*	Vertebrate - int.	<10km	Very adhesive			
Amaranthaceae	*Cyathula cylindrica var. cylindrica*	Vertebrate - int.	<20km	Very adhesive			
Amaranthaceae	*Cyathula uncinulata*	Vertebrate - int.	<20km	Very adhesive			
Amaranthaceae	*Pupalia lappacea*	Vertebrate - int.	<10km	Very adhesive			
Amaryllidaceae	*Clivia caulescens*	Vertebrate - int.	<600m	Primate and possibly other mammals			
Amaryllidaceae	*Clivia miniata*	Vertebrate - int.	<600m	Primate and possibly other mammals			
Amaryllidaceae	*Haemanthus humilis* subsp. *hirsutus*	Vertebrate - int.	<600m	Bird & primate			
Amaryllidaceae	*Scadoxus multiflorus*	Vertebrate - int.	<600m	Bird & primate		Red-capped Robin-Chat; Brown Scrub-Robin	
Amaryllidaceae	*Scadoxus puniceus*	Vertebrate - int.	<600m	Bird & primate		Red-capped Robin-Chat; Brown Scrub-Robin	
Anacardiaceae	*Harpephyllum caffrum*	Vertebrate - int.	<8km	Bird & mammal (incl. bat)	Purple-crested Turaco; Black-bellied Starling		
Anacardiaceae	*Protorhus longifolia*	Vertebrate - int.	<8km	Bird & mammal (incl. bat)	Knysna Turaco; Purple-crested Turaco		
Anacardiaceae	*Searsia chirindensis*	Vertebrate - int.	<8km	Bird & primate	Knysna Turaco; Purple-crested Turaco; Sombre Greenbul	Black-collared Barbet; Cape Robin-Chat; Chorister Robin-Chat	Golden Weaver
Anacardiaceae	*Searsia dentata*	Vertebrate - int.	<8km	Bird & primate	Knysna Turaco; Purple-crested Turaco; Sombre Greenbul	Black-collared Barbet; Cape Robin-Chat; Chorister Robin-Chat	Golden Weaver
Anacardiaceae	*Searsia gerrardii*	Vertebrate - int.	<8km	Bird & primate	Knysna Turaco; Purple-crested Turaco; Sombre Greenbul	Black-collared Barbet; Cape Robin-Chat; Chorister Robin-Chat	Golden Weaver
Anacardiaceae	*Searsia leptodictya*	Vertebrate - int.	<8km	Bird & primate	Knysna Turaco; Purple-crested Turaco; Sombre Greenbul	Black-collared Barbet; Cape Robin-Chat; Chorister Robin-Chat	Golden Weaver
Anacardiaceae	*Searsia lucida*	Vertebrate - int.	<8km	Bird & primate	Knysna Turaco; Purple-crested Turaco; Sombre Greenbul	Black-collared Barbet; Cape Robin-Chat; Chorister Robin-Chat	Golden Weaver
Anacardiaceae	*Searsia pallens*	Vertebrate - int.	<8km	Bird & primate	Knysna Turaco; Purple-crested Turaco; Sombre Greenbul	Black-collared Barbet; Cape Robin-Chat; Chorister Robin-Chat	Golden Weaver
Anacardiaceae	*Searsia pentheri*	Vertebrate - int.	<8km	Bird & primate	Knysna Turaco; Purple-crested Turaco; Sombre Greenbul	Black-collared Barbet; Cape Robin-Chat; Chorister Robin-Chat	Golden Weaver
Anacardiaceae	*Searsia pyroides* var. *gracilis*	Vertebrate - int.	<8km	Bird & primate	Knysna Turaco; Purple-crested Turaco; Sombre Greenbul	Black-collared Barbet; Cape Robin-Chat; Chorister Robin-Chat	Golden Weaver
Anacardiaceae	*Searsia pyroides* var. *pyroides*	Vertebrate - int.	<8km	Bird & primate	Knysna Turaco; Purple-crested Turaco; Sombre Greenbul	Black-collared Barbet; Cape Robin-Chat; Chorister Robin-Chat	Golden Weaver
Anacardiaceae	*Searsia taxon C*	Vertebrate - int.	<8km	Bird & primate	Knysna Turaco; Purple-crested Turaco; Sombre Greenbul	Black-collared Barbet; Cape Robin-Chat; Chorister Robin-Chat	Golden Weaver
Anacardiaceae	*Searsia tumulicola* var. *tumulicola*	Vertebrate - int.	<8km	Bird & primate	Knysna Turaco; Purple-crested Turaco; Sombre Greenbul	Black-collared Barbet; Cape Robin-Chat; Chorister Robin-Chat	Golden Weaver
Anacardiaceae	*Sclerocarya birrea* subsp. *caffra*	Vertebrate - int.	<10km	Bird & mammal (incl. bat)			
Anemiaceae	*Anemia dregeana*	Wind	>20 km	Probably our furthest disperser			
Annonaceae	*Annona senegalensis* subsp. *senegalensis*	Vertebrate - int.	<8km	Bird & mammal (incl. bat)			
Annonaceae	*Monanthotaxis caffra*	Vertebrate - int.	<2km	Bird & primate		Trumpeter Hornbill	
Anthericaceae	*Chlorophytum comosum*	Wind	<5m	Also unassisted			
Anthericaceae	*Chlorophytum krookianum*	Wind	<5m	Also unassisted			
Apiaceae	*Heteromorpha arborescens* var. *abyssinica*	Vertebrate - int.	<1km	Granivore, seeds edible; possibly unassisted			
Apiaceae	*Hydrocotyle verticillata*	Unassisted	<1m	Also water dispersed			
Apiaceae	*Sanicula elata*	Water	<30m	Unassisted and mud			
Apocynaceae	*Acokanthera oppositifolia*	Vertebrate - int.	<8km	Bird & bats	Knysna Turaco; Black-bellied Starling		
Apocynaceae	*Carissa bispinosa* subsp. *zambesiensis*	Vertebrate - int.	<2km	Bird & primate	Knysna Turaco	Sombre Greenbul	
Apocynaceae	*Carissa edulis*	Vertebrate - int.	<2km	Bird & primate		Sombre Greenbul	
Apocynaceae	*Ceropegia linearis* subsp. *woodii*	Wind	<2km				
Apocynaceae	*Cryptolepis capensis*	Wind	<2km				
Apocynaceae	*Gomphocarpus physocarpus*	Wind	<2km				
Apocynaceae	*Gonioma kamassi*	Wind	<2km				

Apocynaceae	*Marsdenia sylvestris*	Wind	<2km				
Apocynaceae	*Oncinotis tenuiloba*	Wind	<2km				
Apocynaceae	*Rauvolfia caffra*	Vertebrate - int.	<10km	Bird, primate & bat	Trumpeter Hornbill		
Apocynaceae	*Riocreuxia picta*	Wind	<2km				
Apocynaceae	*Secamone alpini*	Wind	<2km				
Apocynaceae	*Secamone filiformis*	Wind	<2km				
Apocynaceae	*Secamone parvifolia*	Wind	<2km				
Apocynaceae	*Strophanthus speciosus*	Wind	<2km				
Apocynaceae	*Tabernaemontana elegans*	Vertebrate - int.	<5km	Primate & mammal			
Apocynaceae	*Tabernaemontana ventricosa*	Vertebrate - int.	<8km	Primate & mammal (incl. bats)			
Apocynaceae	*Tacazzea apiculata*	Wind	<2km				
Apocynaceae	*Telosma africana*	Wind	<2km				
Apocynaceae	*Tylophora flanaganii*	Wind	<2km				
Aquifoliaceae	*Ilex mitis* var. *mitis*	Vertebrate - int.	<20km		African Olive-Pigeon; Knysna Turaco	White-starred Robin; Cape Robin-Chat	
Araceae	*Stylochiton natalensis*	Vertebrate - int.	<20m	Probably rodent			
Araceae	*Zantedeschia albomaculata* subsp. *albomaculata*	Vertebrate - int.	<2km	Bushpig, porcupine, rodent (confirmed)			
Araliaceae	*Cussonia paniculata* subsp. *sinuata*	Vertebrate - int.	<2km	Bird and probably primate	Sombre Greenbul		
Araliaceae	*Cussonia sphaerocephala*	Vertebrate - int.	<2km	Bird and probably primate	Sombre Greenbul		
Araliaceae	*Cussonia spicata*	Vertebrate - int.	<2km	Bird and probably primate	Sombre Greenbul		
Araliaceae	*Schefflera umbellifera*	Vertebrate - int.	<20km	Bird	African Olive-Pigeon; Sombre Greenbul		
Arecaceae	*Phoenix reclinata*	Vertebrate - int.	<8km	Bird & mammal (and water assisted)	Black-bellied Starling	Cape Robin-Chat	
Asparagaceae	*Asparagus aethiopicus*	Vertebrate - int.	<5km	Small birds, like Bulbul		Red-capped Robin-Chat; Chorister Robin-Chat	
Asparagaceae	*Asparagus angusticladus*	Vertebrate - int.	<5km	Small birds, like Bulbul		Red-capped Robin-Chat; Chorister Robin-Chat	
Asparagaceae	*Asparagus falcatus*	Vertebrate - int.	<5km	Small birds, like Bulbul		Cape Robin-Chat; Red-capped Robin-Chat; Chorister Robin-Chat	
Asparagaceae	*Asparagus ramosissimus*	Vertebrate - int.	<5km	Small birds, like Bulbul		Red-capped Robin-Chat; Chorister Robin-Chat	
Asparagaceae	*Asparagus setaceus*	Vertebrate - int.	<5km	Small birds, like Bulbul		Red-capped Robin-Chat; Chorister Robin-Chat	
Asparagaceae	*Asparagus setaceus* (Lebombo form)	Vertebrate - int.	<5km	Small birds, like Bulbul		Red-capped Robin-Chat; Chorister Robin-Chat	
Asparagaceae	*Asparagus sp. nov (A. robustus, sp. nov.)*	Vertebrate - int.	<5km	Small birds, like Bulbul		Red-capped Robin-Chat; Chorister Robin-Chat	
Asparagaceae	*Asparagus virgatus*	Vertebrate - int.	<5km	Small birds, like Bulbul		Red-capped Robin-Chat; Chorister Robin-Chat	
Asphodelaceae	*Aloe arborescens*	Wind	<10m	Short distance, & water-wash			
Asphodelaceae	*Aloe barberiae*	Wind	<10m	Short distance, & water-wash			
Asphodelaceae	*Aloe dyeri*	Wind	<10m	Short distance, & water-wash			
Aspleniaceae	*Asplenium adiantum-nigrum* var. *adiantum-nigrum*	Wind	>20 km	Probably our furthest disperser			
Aspleniaceae	*Asplenium aethiopicum*	Wind	>20 km	Probably our furthest disperser			
Aspleniaceae	*Asplenium anisophyllum*	Wind	>20 km	Probably our furthest disperser			
Aspleniaceae	*Asplenium boltonii*	Wind	>20 km	Vegetative dispersal and wind			
Aspleniaceae	*Asplenium cordatum*	Wind	>20 km	Probably our furthest disperser			
Aspleniaceae	*Asplenium erectum* var. *erectum*	Wind	>20 km	Probably our furthest disperser			
Aspleniaceae	*Asplenium erectum* var. *usambarense*	Wind	>20 km	Probably our furthest disperser			
Aspleniaceae	*Asplenium friesiorum*	Wind	>20 km	Probably our furthest disperser			
Aspleniaceae	*Asplenium gemmiferum*	Wind	>20 km	Vegetative dispersal and wind			
Aspleniaceae	*Asplenium inaequilaterale*	Wind	>20 km	Probably our furthest disperser			
Aspleniaceae	*Asplenium lividum*	Wind	>20 km	Probably our furthest disperser			
Aspleniaceae	*Asplenium lobatum*	Wind	>20 km	Probably our furthest disperser			
Aspleniaceae	*Asplenium lunulatum*	Wind	>20 km	Vegetative dispersal and wind			
Aspleniaceae	*Asplenium monanthes*	Wind	>20 km	Vegetative dispersal and wind			
Aspleniaceae	*Asplenium preussii*	Wind	>20 km	Vegetative dispersal and wind			
Aspleniaceae	*Asplenium protensum*	Wind	>20 km	Vegetative dispersal and wind			
Aspleniaceae	*Asplenium rutifolium*	Wind	>20 km	Vegetative dispersal and wind			
Aspleniaceae	*Asplenium sandersonii*	Wind	>20 km	Vegetative dispersal and wind			
Aspleniaceae	*Asplenium splendens*	Wind	>20 km	Probably our furthest disperser			
Aspleniaceae	*Asplenium theciferum*	Wind	>20 km	Probably our furthest disperser			
Aspleniaceae	*Asplenium varians*	Wind	>20 km	Probably our furthest disperser			
Asteraceae	*Brachylaena huillensis*	Wind	<1km				
Asteraceae	*Brachylaena transvaalensis*	Wind	<1km				
Asteraceae	*Gerbera jamesonii*	Wind	<500m				
Asteraceae	*Helichrysum splendidum*	Wind	<500m				
Asteraceae	*Melanthera scandens*	Wind	<500m				

Asteraceae	*Mikania capensis*	Wind	<500m				
Asteraceae	*Pluchea dioscoridis*	Wind	<500m				
Asteraceae	*Schistostephium heptalobum*	Wind	<500m				
Asteraceae	*Senecio deltoideus*	Wind	<500m		Forest Canary		
Asteraceae	*Senecio panduriformis*	Wind	<500m				
Asteraceae	*Senecio pleistocephalus*	Wind	<500m				
Asteraceae	*Senecio tamoides*	Wind	<500m		Forest Canary		
Asteraceae	*Senecio venosus*	Wind	<500m				
Asteraceae	*Seriphium sp* (escarpment form)	Wind	<500m				
Asteraceae	*Tarchonanthus trilobus* var. *galpinii*	Wind	<1km				
Asteraceae	*Vernonia mespilifolia*	Wind	<1km				
Asteraceae	*Vernonia myriantha*	Wind	<1km				
Asteraceae	*Vernonia wollastonii*	Wind	<500m				
Balsaminaceae	*Impatiens hochstetteri* subsp. *hochstetteri*	Ballistic	<2m				
Balsaminaceae	*Impatiens sylvicola*	Ballistic	<2m				
Begoniaceae	*Begonia sonderiana*	Wind	<250m				
Begoniaceae	*Begonia sutherlandii*	Wind	<250m	Possibly water assisted			
Behniaceae	*Behnia reticulata*	Vertebrate - int.	<8km	Uncertain, Bushpig or bat (white fruit)			
Bignoniaceae	*Tecomaria capensis*	Wind	<20m				
Blechnaceae	*Blechnum attenuatum* var. *giganteum*	Wind	>20 km	Probably our furthest disperser			
Blechnaceae	*Blechnum australe*	Wind	>20 km	Probably our furthest disperser			
Blechnaceae	*Blechnum capense*	Wind	>20 km	Probably our furthest disperser			
Blechnaceae	*Blechnum punctulatum* var. *atherstonei*	Wind	>20 km	Probably our furthest disperser			
Boraginaceae	*Cordia caffra*	Vertebrate - int.	<2km	Bird & primate			
Boraginaceae	*Ehretia obtusifolia*	Vertebrate - int.	<2km	Bird			
Brassicaceae	*Cardamine africana*	Ballistic	<1m				
Buddlejaceae	*Buddleja auriculata*	Wind	<1km				
Buddlejaceae	*Buddleja dysophylla*	Wind	<1km				
Buddlejaceae	*Buddleja pulchella*	Wind	<1km				
Buddlejaceae	*Buddleja saligna*	Wind	<1km				
Buddlejaceae	*Buddleja salviifolia*	Wind	<1km				
Buddlejaceae	*Nuxia congesta*	Wind	<1km				
Buddlejaceae	*Nuxia floribunda*	Wind	<1km				
Burseraceae	*Commiphora harveyi*	Vertebrate - int.	<2km	Bird			
Burseraceae	*Commiphora mollis*	Vertebrate - int.	<2km	Bird			
Capparaceae	*Boscia albitrunca*	Vertebrate - int.	<2km	Bird & mammal		Black-collared Barbet; Violet-backed Starling	
Capparaceae	*Capparis fascicularis* var. *fascicular*	Vertebrate - int.	<8km	Bird	Purple-crested Turaco		
Capparaceae	*Capparis tomentosa*	Vertebrate - int.	<8km	Bird & mammal	Purple-crested Turaco		
Capparaceae	*Maerua cafra*	Vertebrate - int.	<2km	Bird, primate			
Capparaceae	*Maerua rosmarinoides*	Vertebrate - int.	<2km	Bird (probable)			
Celastraceae	*Cassine peragua*	Vertebrate - int.	<20km	Bird	African Olive-Pigeon; Knysna Turaco		
Celastraceae	*Catha edulis*	Wind	<50m	Bird			
Celastraceae	*Elaeodendron croceum*	Vertebrate - int.	<8km	Bird, primate & bat	Purple-crested Turaco; African Green Pigeon		
Celastraceae	*Elaeodendron zeyheri*	Vertebrate - int.	<8km	Bird	Purple-crested Turaco; African Green Pigeon		
Celastraceae	*Gymnosporia buxifolia*	Vertebrate - int.	<8km	Bird	Knysna Turaco	Cape Robin-Chat	
Celastraceae	*Gymnosporia glaucophylla*	Vertebrate - int.	<8km	Bird		Cape Robin-Chat	
Celastraceae	*Gymnosporia grandifolia*	Vertebrate - int.	<8km	Bird	Knysna Turaco	Cape Robin-Chat	
Celastraceae	*Gymnosporia harveyana*	Vertebrate - int.	<8km	Bird	Knysna Turaco	Cape Robin-Chat	
Celastraceae	*Gymnosporia rubra*	Vertebrate - int.	<2km	Bird		Cape Robin-Chat	
Celastraceae	*Gymnosporia sp. nov . (D graniticola)*	Vertebrate - int.	<2km	Bird		Cape Robin-Chat	
Celastraceae	*Hippocratea africana*	Wind	<50m				
Celastraceae	*Hippocratea longipetiolata* (forest form)	Wind	<50m				
Celastraceae	*Lauridia tetragona*	Vertebrate - int.	<2km	Bird & primate			
Celastraceae	*Maytenus acuminata* var. *acuminata*	Vertebrate - int.	<8km	Bird	Red-eyed Dove		
Celastraceae	*Maytenus albata*	Vertebrate - int.	<8km	Bird	Red-eyed Dove		
Celastraceae	*Maytenus deflexa*	Vertebrate - int.	<8km	Bird	Red-eyed Dove		
Celastraceae	*Maytenus peduncularis*	Vertebrate - int.	<8km	Bird	Red-eyed Dove	Red-capped Robin-Chat	
Celastraceae	*Maytenus sp nov (G. filiformis)*	Vertebrate - int.	<8km	Bird	Red-eyed Dove		
Celastraceae	*Maytenus species A*	Vertebrate - int.	<8km	Bird	Red-eyed Dove		
Celastraceae	*Maytenus undata* (woodland form)	Vertebrate - int.	<8km	Bird	Red-eyed Dove		
Celastraceae	*Mystroxylon aethiopicum* subsp. *aethiopicum*	Vertebrate - int.	<8km	Bird	African Green Pigeon	Brown-headed Parrot	
Celastraceae	*Pleurostylia capensis*	Vertebrate - int.	<8km	Bird			
Celastraceae	*Pterocelastrus rostratus*	Vertebrate - int.	<8km	Bird	Knysna Turaco	Cape Robin-Chat	
Celastraceae	*Robsonodendron eucleiforme*	Vertebrate - int.	<20km	Bird	African Olive-Pigeon; Knysna Turaco		
Celastraceae	*Salacia gerrardii*	Vertebrate - int.	<8km	Bird & primate			

Celtidaceae	*Celtis africana*	Vertebrate - int.	<20km	Bird & primate	African Olive-Pigeon; Knysna Turaco; Purple-crested Turaco; Tambourine Dove; Thick-billed Weaver	Cape Robin-Chat; Chorister Robin-Chat; Violet-backed Starling	
Celtidaceae	*Chaetachme aristata*	Vertebrate - int.	<8km	Bird, primate & bat	Purple-crested Turaco; Thick-billed Weaver		
Celtidaceae	*Trema orientalis*	Vertebrate - int.	<8km	Bird, primate & bat	Red-eyed Dove; Yellow-rumped Tinkerbird; Tambourine Dove; Black-bellied Starling	Red-capped Robin-Chat; Brown Scrub-Robin	
Chrysobalanaceae	*Parinari curatellifolia*	Vertebrate - int.	<8km	Primate & mammal (incl. bats)	Purple-crested Turaco		
Clusiaceae	*Garcinia gerrardii*	Vertebrate - int.	<8km	Bird & mammal (including bats)			
Clusiaceae	*Garcinia livingstonei*	Vertebrate - int.	<8km	Mammal (incl. primate & bat)			
Colchicaceae	*Littonia modesta*	Vertebrate - int.	<2km	Bird dispersed			
Combretaceae	*Combretum edwardsii*	Wind	<100m	Probably rodent assisted			
Combretaceae	*Combretum erythrophyllum*	Wind	<100m	Probably rodent assisted			
Combretaceae	*Combretum kraussii*	Wind	<100m	Probably rodent assisted			
Combretaceae	*Combretum molle*	Wind	<100m	Probably rodent assisted			
Combretaceae	*Combretum sp* (aff. *C. woodii*)	Wind	<100m	Probably rodent assisted			
Combretaceae	*Combretum woodii*	Wind	<100m	Probably rodent assisted			
Combretaceae	*Terminalia phanerophlebia*	Wind	<100m	Probably rodent assisted			
Commelinaceae	*Aneilema aequinoctiale*	Vertebrate - int.	<10m	Sticky, not hooks. Small mammal suspected.			
Commelinaceae	*Commelina africana* var. *africana*	Vertebrate - int.	<10m				
Commelinaceae	*Commelina benghalensis*	Vertebrate - int.	<10m				
Commelinaceae	*Cyanotis lapidosa*	Unassisted	<2m	Unassisted			
Connaraceae	*Cnestis polyphylla*	Vertebrate - int.	<2km	Bird			
Cornaceae	*Curtisia dentata*	Vertebrate - int.	<2km	Bird & primate & Bushpig			
Crassulaceae	*Crassula pellucida* subsp. *alsinoides*	Wind	<200m	Possibly also unassisted.			
Crassulaceae	*Kalanchoe rotundifolia*	Wind	<200m				
Cucurbitaceae	*Coccinia palmata*	Vertebrate - int.	<2km	Bird, primate & rodent			
Cucurbitaceae	*Cocculus hirsutus*	Vertebrate - int.	<2km	Bird, primate & rodent			
Cucurbitaceae	*Momordica foetida*	Vertebrate - int.	<2km	Bird, primate & rodent			
Cucurbitaceae	*Zehneria scabra*	Vertebrate - int.	<2km	Bird, rodent			
Cyatheaceae	*Cyathea capensis*	Wind	>20 km	Probably our furthest disperser			
Cyatheaceae	*Cyathea dregei*	Wind	>20 km	Probably our furthest disperser			
Cyperaceae	*Carex mossii*	Unassisted	<1m				
Cyperaceae	*Carex spicato-paniculata*	Ant	<5m				
Cyperaceae	*Carex zuluensis*	Ant	<5m				
Cyperaceae	*Costularia natalensis*	Vertebrate - int.	<50m	Barbed bristles			
Cyperaceae	*Cyperus albostriatus*	Unassisted	<1m				
Cyperaceae	*Cyperus keniensis*	Unassisted	<1m				
Cyperaceae	*Cyperus pseudoleptocladus*	Unassisted	<1m				
Cyperaceae	*Cyperus sexangularis*	Unassisted	<1km	Rivers			
Cyperaceae	*Kyllinga odorata*	Unassisted	<1m				
Cyperaceae	*Schoenoxiphium lehmannii*	Unassisted	<1m				
Cyperaceae	*Scleria transvaalensis*	Unassisted	<1m				
Dennstaedtiaceae	*Blotiella natalensis*	Wind	>20 km	Probably our furthest disperser			
Dennstaedtiaceae	*Histiopteris incisa*	Wind	>20 km	Probably our furthest disperser			
Dennstaedtiaceae	*Hypolepis sparsisora*	Wind	>20 km	Probably our furthest disperser			
Dennstaedtiaceae	*Microlepia speluncae*	Wind	>20 km	Probably our furthest disperser			
Dennstaedtiaceae	*Pteridium aquilinum*	Wind	>20 km	Probably our furthest disperser			
Dioscoreaceae	*Dioscorea cotinifolia*	Wind	<10m				
Dioscoreaceae	*Dioscorea dregeana*	Wind	<10m				
Dioscoreaceae	*Dioscorea retusa*	Wind	<10m				
Dracaenaceae	*Dracaena aletriformis*	Vertebrate - int.	<2km	Probably bird & primate		Red-capped Robin-Chat; Brown Scrub-Robin	
Dracaenaceae	*Dracaena transvaalensis*	Vertebrate - int.	<2km	Probably bird & primate		Red-capped Robin-Chat; Brown Scrub-Robin	
Dracaenaceae	*Sansevieria hyacinthoides*	Vertebrate - int.	<2km	Bird - source Andrew Hankey			
Dryopteridaceae	*Arachniodes webbiana* subsp. *foliosa*	Wind	>20 km	Probably our furthest disperser			
Dryopteridaceae	*Cyrtomium micropterum*	Wind	>20 km	Probably our furthest disperser			
Dryopteridaceae	*Dryopteris inaequalis*	Wind	>20 km	Probably our furthest disperser			
Dryopteridaceae	*Nothoperanema squamiseta*	Wind	>20 km	Probably our furthest disperser			
Dryopteridaceae	*Polystichum luctuosum*	Wind	>20 km	Probably our furthest disperser			
Dryopteridaceae	*Polystichum macleae*	Wind	>20 km	Probably our furthest disperser			
Dryopteridaceae	*Polystichum pungens*	Wind	>20 km	Probably our furthest disperser			
Dryopteridaceae	*Polystichum transkeiense*	Wind	>20 km	Probably our furthest disperser			
Dryopteridaceae	*Polystichum transvaalense*	Wind	>20 km	Probably our furthest disperser			
Dryopteridaceae	*Rumohra adiantiformis*	Wind	>20 km	Probably our furthest disperser			
Ebenaceae	*Diospyros galpinii*	Vertebrate - int.	<5km	Primate & mammal			

Ebenaceae	*Diospyros lycioides* subsp. *guerkei*	Vertebrate - int.	<8km	Bird, primate & mammal (incl. bats)	Purple-crested Turaco	Black-collared Barbet	
Ebenaceae	*Diospyros lycioides* subsp. *sericea*	Vertebrate - int.	<8km	Bird, primate & mammal	Purple-crested Turaco	Black-collared Barbet	
Ebenaceae	*Diospyros mespiliformis*	Vertebrate - int.	<10km	Bird, primate & mammal	Trumpeter Hornbill; Purple-crested Turaco; African Green Pigeon	Black-collared Barbet; Brown-headed Parrot	
Ebenaceae	*Diospyros natalensis* subsp. *nummularia*	Vertebrate - int.	<8km	Bird, primate & mammal	Knysna Turaco; Purple-crested Turaco; African Green Pigeon	Black-collared Barbet	
Ebenaceae	*Diospyros whyteana*	Vertebrate - int.	<8km	Bird, primate & mammal	Knysna Turaco; Purple-crested Turaco	Black-collared Barbet	
Ebenaceae	*Euclea crispa* subsp. *crispa*	Vertebrate - int.	<20km	Bird, primate & mammal	African Olive-Pigeon; Knysna Turaco; Black-bellied Starling	Black-collared Barbet	
Ebenaceae	*Euclea natalensis*	Vertebrate - int.	<20km	Bird, primate & mammal (incl. bats)	African Olive-Pigeon; Knysna Turaco; Black-bellied Starling	Black-collared Barbet	
Ebenaceae	*Euclea schimperi*	Vertebrate - int.	<8km	Bird, primate & mammal	Black-bellied Starling	Black-collared Barbet	
Equisetaceae	*Equisetum ramosissimum*	Wind	>20 km	Also water dispersed			
Ericaceae	*Vaccinium exul*	Vertebrate - int.	<8km	Bird, primate & mammal (incl. bats)			
Erythroxylaceae	*Erythroxylum delagoense*	Vertebrate - int.	<5km	Bird, primate & mammal		Red-capped Robin-Chat	
Erythroxylaceae	*Erythroxylum emarginatum*	Vertebrate - int.	<5km	Bird, primate & mammal		Red-capped Robin-Chat	
Escalloniaceae	*Choristylis rhamnoides*	Wind	<10m				
Euphorbiaceae	*Acalypha glabrata*	Ballistic	<10m	Hairy capsule; and surface wash			
Euphorbiaceae	*Adenocline acuta*	Ballistic	<10m	Capsule; wash			
Euphorbiaceae	*Andrachne ovalis*	Ballistic	<10m	Capsule; wash			
Euphorbiaceae	*Antidesma venosum*	Vertebrate - int.	<8km	Bird, primate & mammal	Yellow-rumped Tinkerbird; Purple-crested Turaco	Trumpeter Hornbill; Red-capped Robin-Chat	
Euphorbiaceae	*Bridelia cathartica* subsp. *melanthioides*	Vertebrate - int.	<8km	Bird, primate & mammal			
Euphorbiaceae	*Bridelia micrantha*	Vertebrate - int.	<8km	Bird, primate & mammal (incl. bats)	Yellow-rumped Tinkerbird; Black-bellied Starling	Red-capped Robin-Chat	
Euphorbiaceae	*Clutia affinis*	Unassisted	<1m	Capsule, possibly frugivore but too uncertain			
Euphorbiaceae	*Clutia pulchella* var. *pulchella*	Unassisted	<1m	Capsule, possibly frugivore but too uncertain			
Euphorbiaceae	*Croton gratissimus* var. *gratissimus*	Vertebrate - int.	<8km	Bird	Red-eyed Dove; Tambourine Dove		
Euphorbiaceae	*Croton sylvaticus*	Vertebrate - int.	<8km	Bird, primate & mammal	Red-eyed Dove; Tambourine Dove		
Euphorbiaceae	*Drypetes gerrardii*	Vertebrate - int.	<10km	Bird & primate	Lemon Dove; Trumpeter Hornbill		
Euphorbiaceae	*Euphorbia ingens*	Vertebrate - int.	<2km	Bird & primate			
Euphorbiaceae	*Flueggea virosa*	Vertebrate - int.	<2km	Bird & primate			
Euphorbiaceae	*Margaritaria discoidea* var. *fagifolia*	Vertebrate - int.	<2km	Bird			
Euphorbiaceae	*Micrococca capensis*	Ballistic	<10m				
Euphorbiaceae	*Phyllanthus nummulariifolius*	Vertebrate - int.	<2km	Bird			
Euphorbiaceae	*Phyllanthus reticulatus*	Vertebrate - int.	<2km	Bird & mammal			
Euphorbiaceae	*Sclerocroton integerrimum*	Vertebrate - int.	<2km	Fallen fruit eaten by bird & mammal			
Euphorbiaceae	*Shirakiopsis elliptica*	Vertebrate - int.	<2km	Fallen fruit eaten by bird & mammal			
Euphorbiaceae	*Spirostachys africana*	Vertebrate - int.	<2km	Bird			
Euphorbiaceae	*Suregada africana*	Vertebrate - int.	<2km	Bird and/ or mammal			
Euphorbiaceae	*Tragiella natalensis*	Vertebrate - int.	<1km				
Fabaceae	*Abrus laevigatus*	Vertebrate - int.	<2km	Large mammal			
Fabaceae	*Abrus precatorius*	Vertebrate - int.	<2km	Large mammal			
Fabaceae	*Acacia ataxacantha*	Vertebrate - int.	<2km	Mammal			
Fabaceae	*Acacia caffra*	Vertebrate - int.	<2km	Mammal			
Fabaceae	*Acacia karroo*	Vertebrate - int.	<2km	Mammal			
Fabaceae	*Acacia robusta* subsp. *clavigera*	Vertebrate - int.	<2km	Mammal	Thick-billed Weaver		
Fabaceae	*Acacia schweinfurthii*	Vertebrate - int.	<2km	Mammal			
Fabaceae	*Adenopodia spicata*	Wind	<10m	Partly unassisted			
Fabaceae	*Albizia versicolor*	Vertebrate - int.	<2km	Mammal	Tambourine Dove; Thick-billed Weaver		
Fabaceae	*Argyrolobium tomentosum*	Ballistic	<1m				
Fabaceae	*Bauhinia galpinii*	Ballistic	<10m				
Fabaceae	*Calpurnia aurea*	Unassisted	<1m				
Fabaceae	*Crotalaria capensis*	Ballistic	<2m				
Fabaceae	*Dalbergia armata*	Wind	<50m				
Fabaceae	*Desmodium repandum*	Vertebrate - int.	<2km				
Fabaceae	*Dichrostachys cinerea* subsp. *nyassana*	Vertebrate - int.	<2km				
Fabaceae	*Dumasia villosa* var. *villosa*	Ballistic	<1m				
Fabaceae	*Erythrina lysistemon*	Vertebrate - int.	<2km	Large mammal			
Fabaceae	*Indigofera macrantha*	Ballistic	<1m				
Fabaceae	*Indigofera swaziensis* var. *perplexa*	Ballistic	<1m				
Fabaceae	*Peltophorum africanum*	Wind	<10m				
Fabaceae	*Psoralea pinnata*	Ballistic	<3m				
Fabaceae	*Pterolobium stellatum*	Wind	<15m				
Fabaceae	*Sesbania macrantha*	Unassisted	<1m	Possibly water assisted			
Fabaceae	*Smithia erubescens*	Water	<200m	Also dehiscent			
Fabaceae	*Tephrosia subulata*	Ballistic	<1m				

Flacourtiaceae	*Aphloia theiformis*	Vertebrate - int.	<2km	Bird & primate			
Flacourtiaceae	*Dovyalis lucida*	Vertebrate - int.	<20km	Bird & primate	African Olive-Pigeon; Knysna Turaco; Black-bellied Starling	Black-collared Barbet	
Flacourtiaceae	*Dovyalis rhamnoides*	Vertebrate - int.	<20km	Bird & primate	African Olive-Pigeon; Knysna Turaco; Black-bellied Starling	Black-collared Barbet	
Flacourtiaceae	*Dovyalis zeyheri*	Vertebrate - int.	<20km	Bird & primate	African Olive-Pigeon; Knysna Turaco; Black-bellied Starling	Black-collared Barbet	
Flacourtiaceae	*Homalium dentatum*	Wind	<100m				
Flacourtiaceae	*Kiggelaria africana*	Vertebrate - int.	<20km	Bird & primate	African Olive-Pigeon; Knysna Turaco; Lemon Dove; Cape White-eye; Thick-billed Weaver	White-starred Robin; Cape Robin-Chat; Chorister Robin-Chat	
Flacourtiaceae	*Rawsonia lucida*	Vertebrate - int.	<1km	Primate & Bushpig			
Flacourtiaceae	*Scolopia mundii*	Vertebrate - int.	<20km	Bird, primate & Bushpig	African Olive-Pigeon; Knysna Turaco	Chorister Robin-Chat	
Flacourtiaceae	*Scolopia oreophila*	Vertebrate - int.	<20km	Bird & primate	African Olive-Pigeon; Knysna Turaco	Chorister Robin-Chat	
Flacourtiaceae	*Scolopia zeyheri*	Vertebrate - int.	<20km	Bird	African Olive-Pigeon; Knysna Turaco	Chorister Robin-Chat	
Flacourtiaceae	*Trimeria grandifolia*	Vertebrate - int.	<8km	Bird & primate	Knysna Turaco		
Gentianaceae	*Anthocleista grandiflora*	Vertebrate - int.	<2km	Bird			
Gesneriaceae	*Streptocarpus confusus* subsp. *confusus*	Ballistic	<2m	Possibly also wind & wash from rain			
Gesneriaceae	*Streptocarpus cyaneus* subsp. *cyaneus*	Ballistic	<2m	Possibly also wind & wash from rain			
Gesneriaceae	*Streptocarpus fenestra-dei*	Ballistic	<5m	Possibly also wind & wash from rain			
Gesneriaceae	*Streptocarpus micranthus*	Ballistic	<5m	Possibly also wind & wash from rain			
Gesneriaceae	*Streptocarpus pentherianus*	Ballistic	<2m	Possibly also wind & wash from rain			
Gesneriaceae	*Streptocarpus polyanthus* subsp. *comptonii*	Ballistic	<2m	Possibly also wind & wash from rain			
Gesneriaceae	*Streptocarpus wilmsii*	Ballistic	<2m	Possibly also wind & wash from rain			
Gleicheniaceae	*Gleichenia umbraculifera*	Wind	>20 km	Probably our furthest disperser			
Greyiaceae	*Greyia radlkoferi*	Ballistic	<500m				
Hamamelidaceae	*Trichocladus grandiflorus*	Wind	<500m				
Heteropyxidaceae	*Heteropyxis canescens*	Wind	<500m	Also water dispersed			
Heteropyxidaceae	*Heteropyxis natalensis*	Wind	<1km				
Hyacinthaceae	*Drimia delagoensis*	Wind	<10m				
Hyacinthaceae	*Drimia robusta*	Wind	<10m				
Hymenophyllaceae	*Cephalomanes rigidum*	Wind	>20 km	Also water dispersed			
Hymenophyllaceae	*Crepidomanes borbonicum*	Wind	>20 km	Also water dispersed			
Hymenophyllaceae	*Crepidomanes melanotrichum*	Wind	>20 km	Also water dispersed			
Hymenophyllaceae	*Hymenophyllum capense*	Wind	>20 km	Also water dispersed			
Hymenophyllaceae	*Hymenophyllum tunbrigense*	Wind	>20 km	Also water dispersed			
Hymenophyllaceae	*Sphaerocionium capillare*	Wind	>20 km	Also water dispersed			
Icacinaceae	*Apodytes dimidiata*	Vertebrate - int.	<20km		African Olive-Pigeon; Yellow-rumped Tinkerbird; Black-bellied Starling	Cape Robin-Chat	
Icacinaceae	*Cassinopsis ilicifolia*	Vertebrate - int.	<2km	Bird			
Icacinaceae	*Cassinopsis tinifolia*	Vertebrate - int.	<2km	Bird			
Icacinaceae	*Pyrenacantha grandiflora*	Vertebrate - int.	<1km				
Iridaceae	*Aristea ecklonii*	Wind	<10m				
Iridaceae	*Crocosmia aurea* var. *aurea*	Vertebrate - int.	<1km	Granivore suspected, also unassisted			
Iridaceae	*Dietes iridioides*	Unassisted	<1m	Primarily vegetative			
Kirkiaceae	*Kirkia wilmsii*	Wind	<100m				
Lamiaceae	*Aeollanthus buchnerianus*	Wind	<20m				
Lamiaceae	*Clerodendrum glabrum* var. *glabrum*	Vertebrate - int.	<2km	Bird			
Lamiaceae	*Karomia speciosa*	Wind	<30m	Wind			
Lamiaceae	*Lantana rugosa*	Vertebrate - int.	<2km	Bird	Sombre Greenbul; Cape White-eye		
Lamiaceae	*Leonotis ocymifolia*	Unassisted	<3m				
Lamiaceae	*Plectranthus ciliatus*	Wind	<20m	Andrew Hankey believes wind disp. as inflorescence may be wind dispersed	Forest Canary (possible)		
Lamiaceae	*Plectranthus fruticosus*	Wind	<20m	Andrew Hankey believes wind disp. as inflorescence may be wind dispersed	Forest Canary (possible)		
Lamiaceae	*Plectranthus grallatus*	Wind	<20m	Andrew Hankey believes wind disp. as inflorescence may be wind dispersed	Forest Canary (possible)		
Lamiaceae	*Plectranthus hereroensis*	Wind	<20m	Andrew Hankey believes wind disp. as inflorescence may be wind dispersed	Forest Canary (possible)		
Lamiaceae	*Plectranthus laxiflorus*	Wind	<20m	Andrew Hankey believes wind disp. as inflorescence may be wind dispersed	Forest Canary (possible)		
Lamiaceae	*Plectranthus rubropunctatus*	Wind	<20m	Andrew Hankey believes wind disp. as inflorescence may be wind dispersed	Forest Canary (possible)		
Lamiaceae	*Plectranthus verticillatus*	Wind	<20m	Andrew Hankey believes wind disp. as inflorescence may be wind dispersed	Forest Canary (possible)		
Lamiaceae	*Rotheca myricoides*	Vertebrate - int.	<8km	Bird & primate	Black-bellied Starling	Violet-backed Starling	
Lamiaceae	*Solenostemon latifolius*	Wind	<20m				

Lamiaceae	*Stachys natalensis*	Wind	<10m				
Lamiaceae	*Tetradenia riparia*	Wind	<5m	Nutlet			
Lamiaceae	*Vitex obovata* subsp. *wilmsii*	Vertebrate - int.	<2km	Bird	Purple-crested Turaco		
Lauraceae	*Cryptocarya transvaalensis*	Vertebrate - int.	<2km	Bird & primate			
Lauraceae	*Cryptocarya woodii*	Vertebrate - int.	<2km	Bird & primate			
Lauraceae	*Ocotea bullata*	Vertebrate - int.	<20km	Bird, primate & bat	African Olive-Pigeon; Knysna Turaco		
Lauraceae	*Ocotea kenyensis*	Vertebrate - int.	<20km	Bird, primate & bat	African Olive-Pigeon; Knysna Turaco		
Lomariopsidaceae	*Elaphoglossum acrostichoides*	Wind	>20 km	Probably our furthest disperser			
Lomariopsidaceae	*Elaphoglossum aubertii*	Wind	>20 km	Probably our furthest disperser			
Lomariopsidaceae	*Elaphoglossum macropodium*	Wind	>20 km	Probably our furthest disperser			
Lycopodiaceae	*Huperzia dacrydioides*	Wind	>20 km	Probably our furthest disperser			
Lycopodiaceae	*Huperzia verticillatum*	Wind	>20 km	Probably our furthest disperser			
Lycopodiaceae	*Lycopodium clavatum*	Wind	>20 km	Probably our furthest disperser			
Maesaceae	*Maesa lanceolata*	Vertebrate - int.	<8km	Bird	Purple-crested Turaco		
Malpighiaceae	*Acridocarpus natalitius* var. *natalitius*	Wind	<20m				
Malvaceae	*Hibiscus calyphyllus*	Wind	<2m				
Malvaceae	*Hibiscus pedunculatus*	Wind	<2m				
Malvaceae	*Hibiscus vitifolius*	Wind	<2m				
Malvaceae	*Pavonia burchellii*	Wind	<2m				
Malvaceae	*Pavonia columella*	Wind	<2m				
Malvaceae	*Sida serratifolia*	Wind	<2m				
Marattiaceae	*Marattia fraxinea*	Wind	>20 km	Also water dispersed			
Melastomataceae	*Memecylon natalense*	Vertebrate - int.	<2km	Bird			
Meliaceae	*Ekebergia capensis*	Vertebrate - int.	<20km	Bird & primate & bat	African Olive-Pigeon; Knysna Turaco; Purple-crested Turaco; Black-bellied Starling	Trumpeter Hornbill	
Meliaceae	*Ekebergia pterophylla*	Vertebrate - int.	<20km	Bird & primate	African Olive-Pigeon; Purple-crested Turaco; Black-bellied Starling		
Meliaceae	*Trichilia dregeana*	Vertebrate - int.	<8km	Bird, primate & bat	Black-bellied Starling	Trumpeter Hornbill	
Meliaceae	*Trichilia emetica*	Vertebrate - int.	<8km	Bird, primate & bat	Black-bellied Starling	Trumpeter Hornbill; Brown-headed Parrot	
Melianthaceae	*Bersama lucens*	Vertebrate - int.	<5km	Bird & primate (and possibly bat)			
Melianthaceae	*Bersama tysoniana*	Vertebrate - int.	<5km	Bird & primate (and possibly bat)			
Menispermaceae	*Cissampelos torulosa*	Vertebrate - int.	<2km	Bird			
Menispermaceae	*Stephania abyssinica*	Vertebrate - int.	<2km	Bird			
Menispermaceae	*Tiliacora funifera*	Vertebrate - int.	<8km	Bird & primate & bat			
Monimiaceae	*Xymalos monospora*	Vertebrate - int.	<2km	Bird & primate		White-starred Robin; Cape Robin-Chat	
Moraceae	*Ficus burkei*	Vertebrate - int.	<20km	Bird and most mammal groups	African Olive-Pigeon; Yellow-rumped Tinkerbird; Knysna Turaco; Purple-crested Turaco; Sombre Greenbul; Cape White-eye	Scaly-throated Honeyguide; Black-collared Barbet; Crowned Hornbill; Black-headed Oriole	Golden Weaver
Moraceae	*Ficus craterostoma*	Vertebrate - int.	<20km	Bird and most mammal groups	African Olive-Pigeon; Yellow-rumped Tinkerbird; Knysna Turaco; Purple-crested Turaco; Sombre Greenbul; Cape White-eye	Scaly-throated Honeyguide; Black-collared Barbet; Crowned Hornbill; Black-headed Oriole	Golden Weaver
Moraceae	*Ficus ingens*	Vertebrate - int.	<20km	Bird and most mammal groups	African Olive-Pigeon; Yellow-rumped Tinkerbird; Knysna Turaco; Purple-crested Turaco; Sombre Greenbul; Cape White-eye	Scaly-throated Honeyguide; Black-collared Barbet; Crowned Hornbill; Trumpeter Hornbill; Black-headed Oriole	Golden Weaver
Moraceae	*Ficus sur*	Vertebrate - int.	<20km	Bird and most mammal groups	African Olive-Pigeon; Yellow-rumped Tinkerbird; Knysna Turaco; Purple-crested Turaco; African Green Pigeon; Sombre Greenbul; Cape White-eye	Scaly-throated Honeyguide; Black-collared Barbet; Crowned Hornbill; Trumpeter Hornbill; Black-headed Oriole	Golden Weaver
Moraceae	*Ficus sycomorus*	Vertebrate - int.	<20km	Bird and most mammal groups	African Olive-Pigeon; Yellow-rumped Tinkerbird; Knysna Turaco; Purple-crested Turaco; African Green Pigeon; Sombre Greenbul	Scaly-throated Honeyguide; Black-collared Barbet; Crowned Hornbill; Trumpeter Hornbill; Brown-headed Parrot; Black-headed Oriole	Golden Weaver
Moraceae	*Trilepisium madagascariense*	Vertebrate - int.	<8km	Bird and most mammal groups			
Myricaceae	*Morella pilulifera*	Vertebrate - int.	<20km	Bird	African Olive-Pigeon; African Green Pigeon		
Myrsinaceae	*Myrsine africana*	Vertebrate - int.	<2km	Bird			
Myrsinaceae	*Rapanea melanophloeos*	Vertebrate - int.	<20km	Bird & mammal (& probably bats)	African Olive-Pigeon; Knysna Turaco; Black-bellied Starling		
Myrtaceae	*Eugenia mossambicensis*	Vertebrate - int.	<8km	Bird & primate (probably bat)	Purple-crested Turaco		
Myrtaceae	*Eugenia natalitia*	Vertebrate - int.	<8km	Bird & primate (& bat probable); water dispersed probable	Purple-crested Turaco		
Myrtaceae	*Eugenia natalitia* (river form)	Vertebrate - int.	<8km	Bird & primate (probably bat)	Purple-crested Turaco		
Myrtaceae	*Eugenia woodii*	Vertebrate - int.	<8km	Bird & primate (probably bat)	Purple-crested Turaco		
Myrtaceae	*Syzygium cordatum*	Vertebrate - int.	<8km	Bird & primate (& bat)	Knysna Turaco; Purple-crested Turaco; African Green Pigeon; Tambourine Dove; Thick-billed Weaver	Black-collared Barbet	
Myrtaceae	*Syzygium gerrardii*	Vertebrate - int.	<8km	Bird & primate (probably bat)	Knysna Turaco; Purple-crested Turaco; Tambourine Dove; Thick-billed Weaver	Black-collared Barbet	

Myrtaceae	*Syzygium guineense*	Vertebrate - int.	<8km	Bird & primate (probably bat)	Knysna Turaco; Purple-crested Turaco; African Green Pigeon; Tambourine Dove; Thick-billed Weaver	Black-collared Barbet	
Myrtaceae	*Syzygium species A*	Vertebrate - int.	<8km	Bird & primate (probably bat)	Knysna Turaco; Purple-crested Turaco; Tambourine Dove; Thick-billed Weaver	Black-collared Barbet	
Ochnaceae	*Ochna arborea var. arborea*	Vertebrate - int.	<2km	Bird & primate		Knysna Turaco	
Ochnaceae	*Ochna arborea var. oconnorii*	Vertebrate - int.	<2km	Bird & primate		Knysna Turaco	
Ochnaceae	*Ochna gamostigmata*	Vertebrate - int.	<2km	Bird & primate		Knysna Turaco	
Ochnaceae	*Ochna holstii*	Vertebrate - int.	<2km	Bird & primate		Knysna Turaco	
Ochnaceae	*Ochna natalitia*	Vertebrate - int.	<2km	Bird & primate		Knysna Turaco	
Olacaceae	*Olax dissitiflora*	Vertebrate - int.	<2km	Bird & primate			
Oleaceae	*Chionanthus foveolatus* subsp. *foveolatus*	Vertebrate - int.	<20km	Bird & primate	African Olive-Pigeon; Knysna Turaco		
Oleaceae	*Chionanthus foveolatus* subsp. *major*	Vertebrate - int.	<20km	Bird & primate	African Olive-Pigeon; Knysna Turaco		
Oleaceae	*Chionanthus peglerae*	Vertebrate - int.	<20km	Bird & primate	African Olive-Pigeon; Knysna Turaco		
Oleaceae	*Jasminum abyssinicum*	Vertebrate - int.	<20km	Bird	African Olive-Pigeon		
Oleaceae	*Jasminum fluminense*	Vertebrate - int.	<2km	Bird			
Oleaceae	*Jasminum streptopus*	Vertebrate - int.	<2km	Bird			
Oleaceae	*Olea capensis* subsp. *enervis*	Vertebrate - int.	<20km	Bird & primate	African Olive-Pigeon; Purple-crested Turaco; Cape White-eye; Black-bellied Starling		
Oleaceae	*Olea capensis* subsp. *macrocarpa*	Vertebrate - int.	<20km	Bird & primate	African Olive-Pigeon; Knysna Turaco; Purple-crested Turaco; Black-bellied Starling		
Oleaceae	*Olea europaea* subsp. *africana*	Vertebrate - int.	<8km	Bird & primate	Purple-crested Turaco; Cape White-eye; Black-bellied Starling	Black-headed Oriole	
Oleaceae	*Schrebera alata*	Wind	<100m				
Oleandraceae	*Arthropteris monocarpa*	Wind	>20 km	Probably our furthest disperser			
Oleandraceae	*Oleandra distenta*	Wind	>20 km	Probably our furthest disperser			
Oliniaceae	*Olinia emarginata*	Vertebrate - int.	<8km	Bird	Knysna Turaco		
Oliniaceae	*Olinia radiata*	Vertebrate - int.	<8km	Bird	Knysna Turaco		
Oliniaceae	*Olinia rochetiana*	Vertebrate - int.	<8km	Bird	Knysna Turaco		
Orchidaceae	*Acampe pachyglossa*	Wind	>20 km	Confirmed with D. McMurtry			
Orchidaceae	*Ansellia africana*	Wind	>20 km	Confirmed with D. McMurtry			
Orchidaceae	*Brownleea coerulea*	Wind	>20 km	Confirmed with D. McMurtry			
Orchidaceae	*Bulbophyllum sandersonii*	Wind	>20 km	Confirmed with D. McMurtry			
Orchidaceae	*Cynorkis kassneriana*	Wind	>20 km	Confirmed with D. McMurtry			
Orchidaceae	*Cyrtorchis arcuata* subsp. *arcuata*	Wind	>20 km	Confirmed with D. McMurtry			
Orchidaceae	*Diaphananthe caffra*	Wind	>20 km	Confirmed with D. McMurtry			
Orchidaceae	*Disperis fanniniae*	Wind	>20 km	Confirmed with D. McMurtry			
Orchidaceae	*Disperis lindleyana*	Wind	>20 km	Confirmed with D. McMurtry			
Orchidaceae	*Disperis micrantha*	Wind	>20 km	Confirmed with D. McMurtry			
Orchidaceae	*Eulophia horsfallii*	Wind	>20 km	Confirmed with D. McMurtry			
Orchidaceae	*Huttonaea fimbriata*	Wind	>20 km	Confirmed with D. McMurtry			
Orchidaceae	*Liparis bowkeri*	Wind	>20 km	Confirmed with D. McMurtry			
Orchidaceae	*Mystacidium capense*	Wind	>20 km	Confirmed with D. McMurtry			
Orchidaceae	*Mystacidium flanaganii*	Wind	>20 km	Confirmed with D. McMurtry			
Orchidaceae	*Mystacidium venosum*	Wind	>20 km	Confirmed with D. McMurtry			
Orchidaceae	*Nervilia crociformis*	Wind	>20 km	Confirmed with D. McMurtry			
Orchidaceae	*Polystachya fusiformis*	Wind	>20 km	Confirmed with D. McMurtry			
Orchidaceae	*Polystachya ottoniana*	Wind	>20 km	Confirmed with D. McMurtry			
Orchidaceae	*Polystachya pubescens*	Wind	>20 km	Confirmed with D. McMurtry			
Orchidaceae	*Polystachya transvaalensis*	Wind	>20 km	Confirmed with D. McMurtry			
Orchidaceae	*Stenoglottis fimbriata*	Wind	>20 km	Confirmed with D. McMurtry			
Orchidaceae	*Tridactyle tricuspis*	Wind	>20 km	Confirmed with D. McMurtry			
Orobanchaceae	*Harveya silvatica*	Unassisted	<1m	Capsule; mode uncertain			
Osmundaceae	*Osmunda regalis*	Wind	>20 km	Also water dispersed			
Osmundaceae	*Todea barbara*	Wind	>20 km	Also water dispersed			
Passifloraceae	*Adenia digitata*	Vertebrate - int.	<2km	Primate			
Passifloraceae	*Adenia gummifera*	Vertebrate - int.	<2km	Primate			
Piperaceae	*Peperomia blanda*	Vertebrate - int.	<1km				
Piperaceae	*Peperomia retusa*	Vertebrate - int.	<1km				
Piperaceae	*Peperomia tetraphylla*	Vertebrate - int.	<1km				
Piperaceae	*Piper capense*	Vertebrate - int.	<2km	Bird & primate			
Pittosporaceae	*Pittosporum viridiflorum*	Vertebrate - int.	<2km	Bird (and adhesive)			
Poaceae	*Brachypodium flexum*	Vertebrate - int.	<5km	Granivore			Natal Spurfowl; Red-necked Spurfowl; Green Twinspot; African Firefinch, Red-backed Mannikin

Poaceae	*Ehrharta erecta* var. *natalensis*	Vertebrate - int.	<5km	Granivore			Natal Spurfowl; Red-necked Spurfowl; Green Twinspot; African Firefinch, Red-backed Mannikin
Poaceae	*Melinis repens*	Wind	<200m		Forest Canary		Natal Spurfowl; Red-necked Spurfowl; Green Twinspot; African Firefinch, Red-backed Mannikin
Poaceae	*Oplismenus hirtellus*	Vertebrate - int.	<5km	Granivore	Forest Canary; Swee Waxbill		Natal Spurfowl; Red-necked Spurfowl; Green Twinspot; African Firefinch, Red-backed Mannikin
Poaceae	*Panicum maximum*	Vertebrate - int.	<5km	Granivore	Forest Canary; Thick-billed Weaver; Swee Waxbill		Natal Spurfowl; Red-necked Spurfowl; Green Twinspot; African Firefinch, Red-backed Mannikin; Golden Weaver
Poaceae	*Panicum monticola*	Vertebrate - int.	<5km	Granivore	Forest Canary; Thick-billed Weaver; Swee Waxbill		Natal Spurfowl; Red-necked Spurfowl; Green Twinspot; African Firefinch, Red-backed Mannikin; Golden Weaver
Poaceae	*Phragmites mauritianus*	Wind	<3km	Also water dispersed			
Poaceae	*Prosphytochloa prehensilis*	Vertebrate - int.	<5km		Forest Canary		Natal Spurfowl; Red-necked Spurfowl; Green Twinspot; African Firefinch, Red-backed Mannikin
Poaceae	*Setaria megaphylla*	Vertebrate - int.	<5km	Granivore	Forest Canary; Thick-billed Weaver; Swee Waxbill		Natal Spurfowl; Red-necked Spurfowl; Green Twinspot; African Firefinch, Red-backed Mannikin
Poaceae	*Setaria sphacelata* var. *sphacelata*	Vertebrate - int.	<5km	Granivore	Forest Canary; Thick-billed Weaver; Swee Waxbill		Natal Spurfowl; Red-necked Spurfowl; Green Twinspot; African Firefinch, Red-backed Mannikin
Podocarpaceae	*Podocarpus falcatus*	Vertebrate - int.	<20km	Bird & mammal (incl. bat)	African Olive-Pigeon; Knysna Turaco; Lemon Dove; African Green Pigeon		
Podocarpaceae	*Podocarpus latifolius*	Vertebrate - int.	<20km	Bird & mammal (incl. bat)	African Olive-Pigeon; Knysna Turaco; Lemon Dove		
Polygalaceae	*Polygala virgata* var. *decora*	Wind	<3m				
Polygonaceae	*Persicaria decipiens*	Vertebrate - int.	<2km	Seeds thought to be ingested			
Polypodiaceae	*Lepisorus excavatus*	Wind	>20 km	Probably our furthest disperser			
Polypodiaceae	*Lepisorus schraderi*	Wind	>20 km	Probably our furthest disperser			
Polypodiaceae	*Loxogramme lanceolata*	Wind	>20 km	Probably our furthest disperser			
Polypodiaceae	*Pleopeltis macrocarpa*	Wind	>20 km	Probably our furthest disperser			
Polypodiaceae	*Polypodium polypodioides*	Wind	>20 km	Probably our furthest disperser			
Proteaceae	*Faurea galpinii*	Ant	<5m				
Proteaceae	*Faurea macnaughtonii*	Ant	<5m				
Proteaceae	*Faurea saligna*	Ant	<5m				
Ptaeroxylaceae	*Ptaeroxylon obliquum*	Wind	<100m				
Pteridaceae	*Adiantum incisum*	Wind	>20 km	Probably our furthest disperser			
Pteridaceae	*Adiantum poiretii*	Wind	>20 km	Probably our furthest disperser			
Pteridaceae	*Cheilanthes bergiana*	Wind	>20 km	Probably our furthest disperser			
Pteridaceae	*Cheilanthes hirta* var. *hirta*	Wind	>20 km	Probably our furthest disperser			
Pteridaceae	*Cheilanthes hirta* var. *nemorosa*	Wind	>20 km	Probably our furthest disperser			
Pteridaceae	*Cheilanthes multifida*	Wind	>20 km	Probably our furthest disperser			
Pteridaceae	*Cheilanthes pentagona*	Wind	>20 km	Probably our furthest disperser			
Pteridaceae	*Cheilanthes viridis* var. *glauca*	Wind	>20 km	Probably our furthest disperser			
Pteridaceae	*Cheilanthes viridis* var. *viridis*	Wind	>20 km	Probably our furthest disperser			
Pteridaceae	*Doryopteris concolor*	Wind	>20 km	Probably our furthest disperser			
Pteridaceae	*Pteris catoptera*	Wind	>20 km	Probably our furthest disperser			
Pteridaceae	*Pteris cretica*	Wind	>20 km	Probably our furthest disperser			
Pteridaceae	*Pteris dentata*	Wind	>20 km	Probably our furthest disperser			
Pteridaceae	*Pteris friesii*	Wind	>20 km	Probably our furthest disperser			
Ranunculaceae	*Clematis brachiata*	Wind	<20m				
Ranunculaceae	*Ranunculus meyeri*	Water	<1km	Probably also via mud			
Ranunculaceae	*Thalictrum rhynchocarpum*	Vertebrate - int.	<2km				
Rhamnaceae	*Berchemia zeyheri*	Vertebrate - int.	<10km	Bird & primate (probably bat)	Trumpeter Hornbill; Purple-crested Turaco		
Rhamnaceae	*Helinus integrifolius*	Vertebrate - int.	<2km	Bird & primate			
Rhamnaceae	*Rhamnus prinoides*	Vertebrate - int.	<2km	Bird & primate	Cape White-eye	Cape Robin-Chat	
Rhamnaceae	*Scutia myrtina*	Vertebrate - int.	<8km	Bird & primate	Yellow-rumped Tinkerbird; Knysna Turaco; Sombre Greenbul	Black-collared Barbet; Southern Boubou; Cape Robin-Chat; Red-capped Robin-Chat; Chorister Robin-Chat	
Rhamnaceae	*Ziziphus mucronata*	Vertebrate - int.	<8km	Bird & primate & larger mammal	Purple-crested Turaco; Thick-billed Weaver		

Rhizophoraceae	*Cassipourea malosana*	Vertebrate - int.	<2km	Bird		White-starred Robin; Cape Robin-Chat; Chorister Robin-Chat	
Rosaceae	*Agrimonia procera*	Vertebrate - int.	<1km				
Rosaceae	*Leucosidea sericea*	Wind	<3km				
Rosaceae	*Prunus africana*	Vertebrate - int.	<20km	Bird & primate & bat	African Olive-Pigeon; Knysna Turaco		
Rosaceae	*Rubus apetalus*	Vertebrate - int.	<8km	Bird & primate	Knysna Turaco	Chorister Robin-Chat	
Rosaceae	*Rubus pinnatus*	Vertebrate - int.	<8km	Bird & primate	Knysna Turaco	Chorister Robin-Chat	
Rosaceae	*Rubus rigidus*	Vertebrate - int.	<8km	Bird & primate	Knysna Turaco	Chorister Robin-Chat	
Rubiaceae	*Breonadia salicina*	Vertebrate - int.	<2km	Bird & primate			
Rubiaceae	*Burchellia bubalina*	Vertebrate - int.	<2km	Bird		Chorister Robin-Chat	
Rubiaceae	*Canthium ciliatum*	Vertebrate - int.	<2km	Bird			
Rubiaceae	*Canthium inerme*	Vertebrate - int.	<2km	Bird & primate		White-starred Robin; Red-capped Robin-Chat	
Rubiaceae	*Canthium kuntzeanum*	Vertebrate - int.	<2km	Bird			
Rubiaceae	*Canthium mundianum*	Vertebrate - int.	<2km	Bird & primate			
Rubiaceae	*Cephalanthus natalensis*	Vertebrate - int.	<2km	Bird & primate			
Rubiaceae	*Coddia rudis*	Vertebrate - int.	<2km	Bird & primate & rodent		Black-headed Oriole; Cape Robin-Chat	
Rubiaceae	*Conostomium natalense*	Wind	<2m				
Rubiaceae	*Coptospermum supra-axillaris* subsp. *barbertonensis*	Vertebrate - int.	<2km	Bird			
Rubiaceae	*Galopina circaeoides*	Vertebrate - int.	<10m				
Rubiaceae	*Hyperacanthus amoenus*	Vertebrate - int.	<2km	Bird & primate			
Rubiaceae	*Keetia gueinzii*	Vertebrate - int.	<2km	Bird & primate			
Rubiaceae	*Kraussia floribunda*	Vertebrate - int.	<2km	Bird & primate			
Rubiaceae	*Oxyanthus pyriformis*	Vertebrate - int.	<2km	Bird & primate			
Rubiaceae	*Oxyanthus speciosus* subsp. *gerrardii*	Vertebrate - int.	<2km	Bird & primate			
Rubiaceae	*Pachystigma bowkeri*	Vertebrate - int.	<2km	Bird & primate			
Rubiaceae	*Pachystigma macrocalyx*	Vertebrate - int.	<2km	Bird & primate			
Rubiaceae	*Pavetta barbertonensis*	Vertebrate - int.	<2km	Bird			
Rubiaceae	*Pavetta cooperi*	Vertebrate - int.	<2km	Bird			
Rubiaceae	*Pavetta galpinii*	Vertebrate - int.	<2km	Bird			
Rubiaceae	*Pavetta gardeniifolia*	Vertebrate - int.	<2km	Bird & primate			
Rubiaceae	*Pavetta inandensis*	Vertebrate - int.	<2km	Bird			
Rubiaceae	*Pavetta kotzei*	Vertebrate - int.	<2km	Bird			
Rubiaceae	*Pentas micrantha* subsp. *wyliei*	Vertebrate - int.	<1km	Bird & rodent dispersed			
Rubiaceae	*Psychotria capensis* (forest form)	Vertebrate - int.	<2km	Bird & primate			
Rubiaceae	*Psychotria zombamontana*	Vertebrate - int.	<2km	Bird & primate			
Rubiaceae	*Psydrax obovata* subsp. *elliptica*	Vertebrate - int.	<2km	Bird			
Rubiaceae	*Rothmannia capensis*	Vertebrate - int.	<2km	Primate & Bushpig			
Rubiaceae	*Rothmannia globosa*	Vertebrate - int.	<2km	Primate			
Rubiaceae	*Tricalysia capensis* var. *transvaalensis*	Vertebrate - int.	<2km	Bird			
Rubiaceae	*Tricalysia lanceolata*	Vertebrate - int.	<2km	Bird & primate			
Rubiaceae	*Vangueria infausta*	Vertebrate - int.	<8km	Bird & mammal (& probably bats)			
Rutaceae	*Calodendrum capense*	Vertebrate - int.	<20km	Bird & primate	African Olive-Pigeon; Lemon Dove		
Rutaceae	*Clausena anisata*	Vertebrate - int.	<2km	Bird			
Rutaceae	*Oricia bachmannii*	Vertebrate - int.	<2km	Bird			
Rutaceae	*Teclea natalensis*	Vertebrate - int.	<2km	Bird			
Rutaceae	*Toddalia asiatica*	Vertebrate - int.	<2km	Bird & primate			
Rutaceae	*Vepris lanceolata*	Vertebrate - int.	<8km	Bird	Red-eyed Dove	Chorister Robin-Chat	
Rutaceae	*Vepris reflexa*	Vertebrate - int.	<8km	Bird	Red-eyed Dove	Chorister Robin-Chat	
Rutaceae	*Zanthoxylum capense*	Vertebrate - int.	<2km	Bird	Thick-billed Weaver		
Rutaceae	*Zanthoxylum davyi*	Vertebrate - int.	<2km	Bird	Thick-billed Weaver		
Rutaceae	*Zanthoxylum thorncroftii*	Vertebrate - int.	<2km	Bird	Thick-billed Weaver		
Santalaceae	*Osyridicarpos schimperianus*	Vertebrate - int.	<2km	Bird			
Sapindaceae	*Allophylus africanus* var. *africanus*	Vertebrate - int.	<2km	Bird			
Sapindaceae	*Allophylus chaunostachys*	Vertebrate - int.	<2km	Bird			
Sapindaceae	*Atalaya alata*	Wind	<400m				
Sapindaceae	*Atalaya natalensis*	Wind	<400m				
Sapindaceae	*Hippobromus pauciflorus*	Vertebrate - int.	<2km	Bird	Sombre Greenbul		
Sapotaceae	*Englerophytum magalismontanum*	Vertebrate - int.	<8km	Bird & mammal (& probably bats)			
Sapotaceae	*Englerophytum natalense*	Vertebrate - int.	<8km	Bird & mammal (& probably bats)			
Sapotaceae	*Manilkara discolor*	Vertebrate - int.	<8km	Bird & mammal	African Green Pigeon		
Sapotaceae	*Mimusops obovata*	Vertebrate - int.	<8km	Bird & mammal (including bats)	Knysna Turaco; Purple-crested Turaco; African Green Pigeon; Black-bellied Starling		
Sapotaceae	*Mimusops zeyheri*	Vertebrate - int.	<8km	Bird & mammal (including bats)	Knysna Turaco; Purple-crested Turaco; African Green Pigeon; Black-bellied Starling		

Sapotaceae	*Vitellariopsis marginata*	Vertebrate - int.	<2km	Bird & mammal			
Scrophulariaceae	*Bowkeria cymosa*	Wind	<1km	Capsule			
Scrophulariaceae	*Halleria lucida*	Vertebrate - int.	<20km	Bird & mammal (including bats)	African Olive-Pigeon; Knysna Turaco; African Green Pigeon; Black-bellied Starling	White-starred Robin; Cape Robin-Chat; Red-capped Robin-Chat	
Selaginellaceae	*Selaginella kraussiana*	Wind	>20 km	Probably our furthest disperser			
Selaginellaceae	*Selaginella mittenii*	Wind	>20 km	Probably our furthest disperser			
Smilacaeae	*Smilax anceps*	Vertebrate - int.	<2km	Bird			
Solanaceae	*Solanum americanum*	Vertebrate - int.	<2km				
Solanaceae	*Solanum anguivi*	Vertebrate - int.	<2km	Bird & mammal	Tambourine Dove		
Solanaceae	*Solanum giganteum*	Vertebrate - int.	<2km	Bird	Tambourine Dove		
Solanaceae	*Solanum lichtensteinii*	Vertebrate - int.	<2km				
Solanaceae	*Solanum pseudocapsicum*	Vertebrate - int.	<2km	Bird	Tambourine Dove		
Solanaceae	*Solanum retroflexum*	Vertebrate - int.	<2km	Bird	Tambourine Dove		
Solanaceae	*Solanum terminale* subsp. *terminale*	Vertebrate - int.	<2km	Bird	Tambourine Dove		
Sterculiaceae	*Cola greenwayi*	Vertebrate - int.	<2km	Bird, mammal and rodent			
Sterculiaceae	*Dombeya cymosa*	Wind	<20m				
Sterculiaceae	*Dombeya pulchra*	Wind	<20m				
Sterculiaceae	*Dombeya rotundifolia*	Wind	<20m				
Sterculiaceae	*Sterculia murex*	Vertebrate - int.	<2km	Bird (and possibly primate)			
Strelitziaceae	*Strelitzia caudata*	Vertebrate - int.	<5km	Bird & monkeys eat aril			
Strychnaceae	*Strychnos henningsii*	Vertebrate - int.	<8km	Bird & primate	Purple-crested Turaco	Trumpeter Hornbill	
Strychnaceae	*Strychnos madagascariensis*	Vertebrate - int.	<2km	Primate			
Strychnaceae	*Strychnos mitis*	Vertebrate - int.	<8km	Bird & primate	Purple-crested Turaco	Trumpeter Hornbill	
Tectariaceae	*Tectaria gemmifera*	Wind	>20 km	Vegetative dispersal and wind			
Thelypteridaceae	*Amauropelta bergiana*	Wind	>20 km	Also water dispersed			
Thelypteridaceae	*Christella dentata*	Wind	>20 km	Also water dispersed			
Thelypteridaceae	*Christella gueinziana*	Wind	>20 km	Also water dispersed			
Thelypteridaceae	*Cyclosorus interruptus*	Wind	>20 km	Also water dispersed			
Thelypteridaceae	*Pneumatopteris unita*	Wind	>20 km	Vegetative dispersal & water			
Thelypteridaceae	*Stegnogramma pozoi*	Wind	>20 km	Also water dispersed			
Thelypteridaceae	*Thelypteris confluens*	Wind	>20 km	Also water dispersed			
Thymelaeaceae	*Dais cotinifolia*	Unassisted	<5m	Suspect ants or rodents disperse seed			
Thymelaeaceae	*Englerodaphne pilosa*	Unassisted	<2m	Suspect ants or rodents disperse seed			
Thymelaeaceae	*Passerina montana*	Wind	<100m		Forest Canary		
Thymelaeaceae	*Peddiea africana*	Vertebrate - int.	<2km	Bird & primate			
Thymelaeaceae	*Synaptolepis kirkii*	Vertebrate - int.	<2km	Bird			
Tiliaceae	*Grewia flavescens* var. *flavescens*	Vertebrate - int.	<2km	Bird	Yellow-rumped Tinkerbird; Thick-billed Weaver		
Tiliaceae	*Grewia occidentalis*	Vertebrate - int.	<8km	Bird & mammal	Knysna Turaco; Thick-billed Weaver		
Tiliaceae	*Sparrmannia ricinocarpa*	Vertebrate - int.	<200m				
Tiliaceae	*Triumfetta pilosa*	Vertebrate - int.	<1km				
Urticaceae	*Laportea alatipes*	Ballistic	<100m				
Urticaceae	*Laportea peduncularis*	Ballistic	<100m				
Urticaceae	*Obetia tenax*	Wind	<100m	Probably wind (10-100m)			
Urticaceae	*Pilea rivularis*	Wind	<100m	Probably wind (10-100m)			Honey bees and distance?
Urticaceae	*Pouzolzia mixta*	Wind	<100m	Probably wind (10-100m)			
Urticaceae	*Urtica species*	Wind	<100m	Probably wind (10-100m)			
Velloziaceae	*Talbotia elegans*	Water	<2km				
Violaceae	*Rinorea angustifolia*	Vertebrate - int.	<2km	Bird			
Vitaceae	*Rhoicissus digitata*	Vertebrate - int.	<20km	Bird & mammal	African Olive-Pigeon; Knysna Turaco; Purple-crested Turaco		
Vitaceae	*Rhoicissus rhomboidea*	Vertebrate - int.	<20km	Bird & mammal	African Olive-Pigeon; Knysna Turaco; Purple-crested Turaco		
Vitaceae	*Rhoicissus* sp. nov.	Vertebrate - int.	<20km	Bird & mammal	African Olive-Pigeon; Knysna Turaco; Purple-crested Turaco		
Vitaceae	*Rhoicissus tomentosa*	Vertebrate - int.	<20km	Bird & mammal	African Olive-Pigeon; Knysna Turaco; Purple-crested Turaco		
Vitaceae	*Rhoicissus tridentata* subsp. *cuneifolia*	Vertebrate - int.	<20km	Bird & mammal	African Olive-Pigeon; Purple-crested Turaco		
Vitaceae	*Cyphostemma anatomicum*	Vertebrate - int.	<2km	Bird			
Vitaceae	*Cyphostemma cirrhosum* subsp. *transvaalense*	Vertebrate - int.	<2km	Bird			
Vitaceae	*Cyphostemma woodii*	Vertebrate - int.	<2km	Bird			
Vittariaceae	*Vittaria isoetifolia*	Wind	>20 km	Probably our furthest disperser			
Woodsiaceae	*Athyrium scandicinum*	Wind	>20 km	Probably our furthest disperser			
Zamiaceae	*Encephalartos paucidentatus*	Vertebrate - int.	<600m				

CHAPTER SIX:

How much is enough: developing representation and persistence targets for indigenous forests in Mpumalanga, South Africa

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ABSTRACT

Systematic conservation plans require the inclusion and setting of quantitative representation targets for both pattern and process features. In this paper we present both for the indigenous forests occurring in Mpumalanga Province. With an overarching goal of ensuring that at least 75% of species are represented by at least one individual within each forest subtype in a conservation network, we apply the Species Area Relationship (SAR) approach to our sample data where the log–transformation of the power form of the SAR is a straight line. It is therefore possible to determine the slope of the curve, or *z*–value, from the average number of species recorded per sample and an estimate of the true number of species in each forest subtype. We used EstimateS to determine species richness. The *z*–value is then used to estimate the proportion of area required to represent a given proportion of species present in a forest subtype, i.e. 75% representation of all species. As the number of plots in our data set was low for certain subtypes, this necessitated utilising the highest values from estimators of species richness and integrating forest subtype targets with those for forest types (of a higher level in the NFC) comprising a larger plot data set. We also propose forest process targets for including important forest patches supporting dispersal connectivity. We subsequently integrate forest connectivity into pattern targets as a precautionary approach, given the landscape's dependency on a network of connected forest patches, as well as the risk of biasing pattern target achievement in overlapping areas that serve a different and specific purpose because of higher quantitative process targets. The resulting forest pattern targets ranged between 24.9% and 49.7% for forest subtypes, with a mean of 34.8%. Targets for spatially fixed forest processes, such as important forest patches acting as important stepping stones between other forest patches, were set at 100%. For spatially flexible forest processes, such as the supporting landscape matrix around important forest patches, the targets were set at 60% of original extent. Finally consideration needs to be given to analytical design criteria which can assist in

developing a framework for prioritising conservation actions for forest planning units based on vulnerability and irreplaceability.

Keywords

Biodiversity, connectivity, pattern, process, representivity, species area relationships, systematic conservation planning, targets.

INTRODUCTION

Systematic conservation planning (SCP) has several distinctive characteristics, one of which is the translation of explicit conservation goals into quantitative, operational targets (Margules & Pressey 2000; Margules & Sarkar 2007). The realisation of these goals require that targets be quantified, measured and progress assessed. Explicitly stated targets provide a clear purpose for conservation decisions, lending them accountability and defensibility (Pressey et al. 2003). Targets are generally required for both pattern (representativeness) and process (persistence) to allow for the effective contribution that a selection of areas can make towards conservation goals. For biodiversity pattern, the historically popular target of 10% of area for countries or vegetation types has been criticized because it is too small to prevent the extinction of many species (Margules & Pressey 2000). Such uniform targets are not based on information about representivity nor the requirements for persistence of species or natural processes (Pressey et al. 2003). In fact protection of only 10% of Earth's ecosystems could make at least half of all terrestrial species vulnerable to extinction (Lawes et al. 2007). But then targets of less than 100% are likely to miss some biodiversity, and even 100% targets cannot guarantee biodiversity persistence because of extinction debt (Pressey et al. 2003). Targets are generally calculated in ways that differentiate between features according to their relative importance or urgency for protection (Carwardine et al. 2009). Besides uniform targets, which may even be based on political discourse or economic concerns (Wilhere 2008), more rigorous approaches for a community of species that differentiates between features include: 1) normalising the spatial data using a square root transformation and then scaling representation targets in proportion to the square-root of the representative features' area (Ardron et al. 2010); or 2) the application of a target setting approach based on the Species Area Relationship (SAR) of Desmet & Cowling (2004). The latter approach identified area targets of between 16% and 36% for vegetation types in South Africa (Rouget et al. 2004).

The proposed forest subtype classification for Mpumalanga Province, South Africa (Lötter et al. 2014) is the finest scale categorisation of biodiversity pattern available, however it still requires the calculation of explicit area representation targets for each subtype so that they can be incorporated within a SCP, such as the revised Mpumalanga Biodiversity Sector Plan (Lötter 2013). The required provincial target setting approach should be nested within that of the South African national vegetation type targets and based on a similar approach whereby area

representation targets are proposed that would include at least one individual of 75% of the species composition occurring within that vegetation unit (Desmet 2004; Rouget et al. 2004). That is to say that within any vegetation community, enough area needs to be set aside so that 75% of the vegetation units' species composition can be protected. This representation target is expressed as a proportion of the original extent of a vegetation unit that is required to protect 75% of its species composition.

Setting conservation targets for ecological processes is more problematic (Margules & Pressey 2000). Because conservation planning is spatially explicit, protection of ecological processes is only really possible if based on their spatial surrogates rather than the processes themselves (Margules & Pressey 2000; Margules & Sarkar 2007). For example, dispersal cannot be directly incorporated in most SCP optimization algorithms but the spatial network of forest patches supporting dispersal across the landscape may be mapped and incorporated. Zonation is one of the few SCP programs that is able to include dispersal functions via dispersal kernels (Moilanen et al. 2012).

Margules & Pressey (2000) warn that setting process targets can be difficult in practice because the environment is heterogeneous in space and time and different species function at different spatial and temporal scales, further complicating the incorporation of process features and targets into SCP. This contributes to the absence or weak integration of ecological processes in the planning process (Groves et al. 2012). Studies that target both biodiversity pattern and processes in one plan are rare (Klein et al. 2009).

One of the most studied relationships in ecology is that between species richness and area sampled, or the species area curve (Palmer & White 1994). Measuring rates at which species accumulate with increased sampling is important for various applied issues in conservation. One of these is where the SAR has been used to estimate the number of species at larger spatial scales than that sampled (Chapman & Underwood 2009).

There are different forms of the SAR, although the two most widely used are the Exponential (Gleason 1922) and Power functions (Arrhenius 1921; Tjørve 2003; Chapman & Underwood 2009). Neither of the curves for the exponential and power functions have an upper asymptote (Tjørve 2003) as theoretically new species are always being added with increasing area. The above functions can be described using either the semi–log (exponential) or log–log (power) models (see equations 1 and 2; Williamson et al. 2001).

1. Semi–log model: $S = k_0 + k_1 (\log (A))$

2. Log–log model: $\log(S) = c + z(\log(A))$ or $S = CA^z$

where *S* = mean number of species in area *A, C* and *z* are fitted constants. *C* is a scaling factor related to the sample size and can be ignored when comparing proportions or percentages of area and species (Desmet & Cowling 2004).

A modification of the SAR approach enables it to be useful in the identification of quantitative targets in SCP (Desmet & Cowling 2004; Rouget et al 2004). This approach requires an estimate of true species richness (Desmet & Cowling 2004). As exhaustive biodiversity surveys are nearly always impractical or impossible, we frequently need to rely on extrapolation of sample data to estimate species richness (Colwell et al. 2012). Sampling limitations create challenges for making accurate estimates of alpha diversity, or the number of species within approximately homogeneous assemblages, particularly for assemblages with high species richness and a large fraction of rare species (Colwell & Coddington 1994; Chao et al. 2005). Several methods have been developed to estimate species richness, including non-parametric methods that involve the estimation of unseen species. Unseen species are those likely to be present in a larger homogenous sample of the assemblage but are missing from actual sample data (Chao et al. 2005). Magurran (2004) credits the non-parametric estimators of Anne Chao and colleagues as probably the most significant advance in diversity measurement in more than a decade. Their accessibility has been increased by means of the EstimateS program (Colwell 2004). For more information on species richness estimators used, see Colwell & Coddington (1994), Chazdon et al. (1998), and Magurran (2004).

This paper describes the process of formulating biodiversity targets for forest pattern and processes as a basis for inclusion into the revised Mpumalanga Biodiversity Sector Plan (Lötter 2013). We use the term biodiversity targets to refer to quantitative estimates of how much area of each feature (e.g. forest subtype) should be included in the provincial plan, presented as a percentage.

Our aim is to quantify the representation targets for the indigenous forests of Mpumalanga for the inclusion into a SCP to ensure that forest biodiversity persists.

Our specific objectives include:

1. To develop quantitative pattern targets for the new Mpumalanga forest subtypes based on species area relationships;
2. To develop quantitative process targets for including critical forest patches supporting dispersal into systematic conservation planning;
3. Where appropriate, to integrate pattern and process targets for inclusion into SCP.

STUDY AREA

The context for target setting is Mpumalanga Province, South Africa, where the recent development of a regional forest subtype classification (Lötter et al. 2014) and the identification

of important forest patches that support dispersal between forest patches (Chapter 5) needs to be translated into quantitative targets. In this region indigenous forests are naturally fragmented, unlike the continuous forests of Eurasia and North America, and make up only 0.51% of the province's vegetation cover, and generally occur in small clustered fragments (ArcGIS Average Nearest Neighbor analysis = forest patches clustered, P<0.01). The forest boundary in natural landscapes is usually clear-cut, creating a strong contrast between forest patches and the surrounding matrix which is often comprised of grassland, afforested plantations, urban or rural settlements, or agricultural lands. The mean distance between nearest forest patches is 837 m (SD: 1660 m). The median patch size is 4.6 ha (range: 0.04 — 3790 ha).

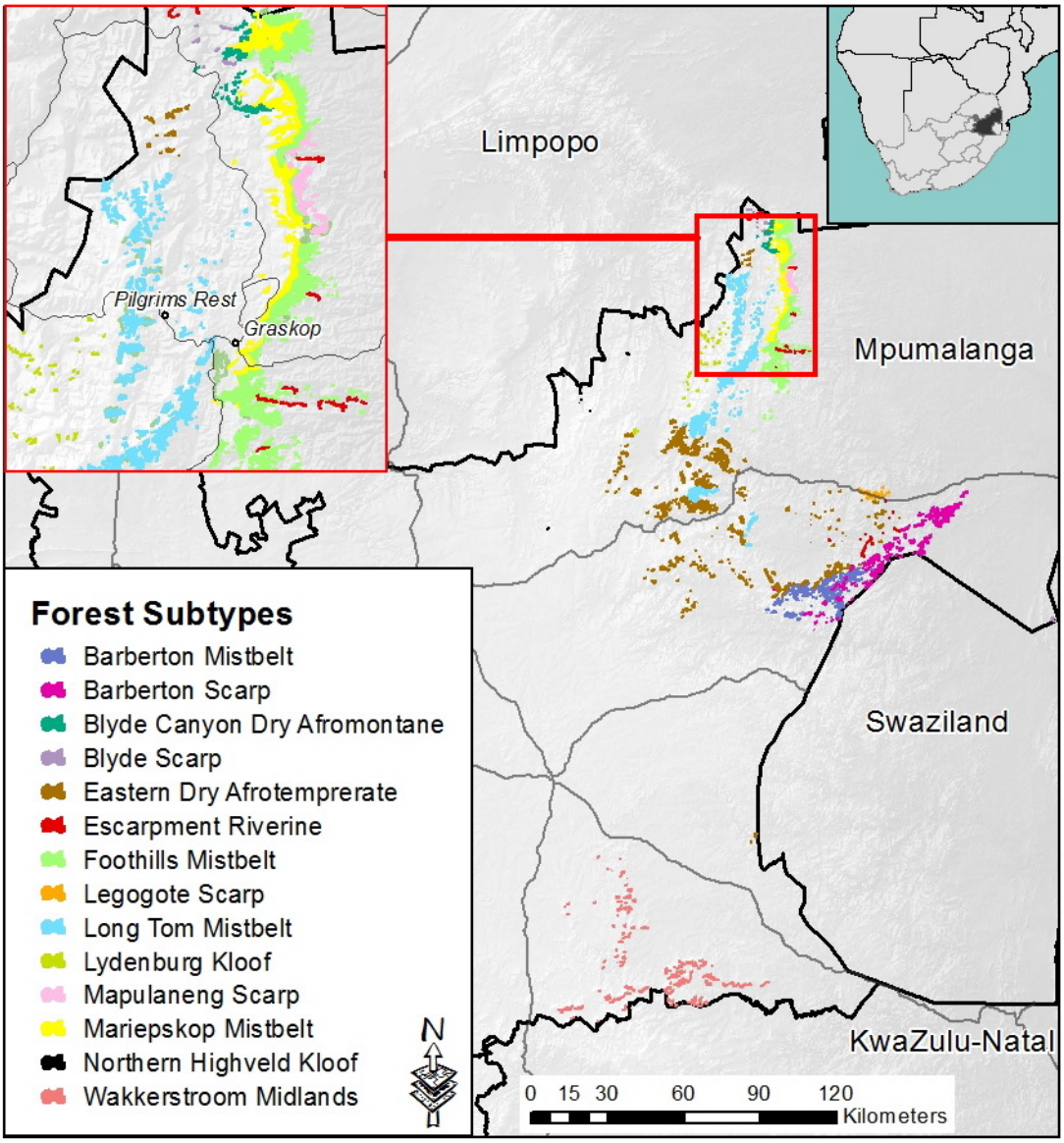


Fig. 1. Location and classification of indigenous forests into fourteen subtypes for Mpumalanga Province, South Africa.

A data set of 438 vegetation plots (20 m x 20 m; 0.04 ha each) were used to sample species composition. Each sample included a list of all vascular plant species recorded. This

data set included four additional plots previously not included in this thesis which sampled Escarpment Riverine forest from the Wolkberg to increase the low sample size from four to eight plots for this vegetation unit. The authors believe the species composition of the canopy trees to be similar and possibly of the same subtype. Sampling generally involved selecting sites across a range of altitudes, landscapes, and climatic conditions. The sample sites were restricted to those forest patches with little evidence of recent human disturbance or where the floristic composition was natural (we avoided areas where invasive alien plant species were present).

Altitude of forest patches varies between 251 m and 1974 m above sea level. The climate is largely temperate with mean annual temperature varying between 14°C and 22°C and the mean annual rainfall spans 500 to 1635 mm (modelled GIS data, based on Schulze 2007). Three geographically distinct forested regions were distinguished in Mpumalanga (see Chapter 5). The Northern Escarpment, Barberton and Wakkerstroom Regions comprise 1170, 520 and 224 forest patches, respectively. Forest patches are regionally clustered, crossing a variety of environmental gradients but regionally coherent.

A total of 1914 forest patches have been digitised and classified into one of fourteen forest subtypes (Lötter et al. 2014), embedded within the National Forest Classification (NFC: von Maltitz et al. 2003). Figure 1 presents the results of the forest subtype classification and the distribution of the various subtypes within Mpumalanga.

METHODS

SAR and quantitative baseline representation targets

We used the reordered equation of Desmet & Cowling (2004) to calculate representation targets for each forest subtype based on the proportion of area required to represent a given percentage of species (Equation 3). Therefore S' and A' denote the proportion of species and area rather than absolute values. S' = mean number of species in area A', z is a fitted constant (Desmet & Cowling 2004).

$$A' = z\sqrt{S'} \quad \text{or} \quad \text{Log}A' = \text{Log}S'/z \tag{3}$$

The calculation of the representation targets required the use of sample data to estimate the parameters of the power form of Eq. 3. To calculate the *z*–value, it is necessary to generate a SAR curve based on inventory data. Because the curve of the power model is a straight line in log–log space and the slope is the *z*–value, it is possible to calculate the *z*–value without generating the actual curve by using species–area data that sample larger and larger proportions of vegetation units. There is also no need to demonstrate the relationship by fitting the power curve, because the suitability of the model is assumed *a priori*. For the log

transformation of the power model, the slope of the curve (hence, the *z*–value) can be determined using the formula for calculating the slope of a straight line (Desmet & Cowling 2004):

$$4. \qquad z = (y_2 - y_1)/(x_2 - x_1)$$

Here z is the slope of the straight line, y_2 = log(total number of species in a vegetation unit); y_1 = log(average number of species per survey sample); x_2 = log(total area of vegetation unit); and, x_1 = log(average area of samples). When using inventory data, the total number of species is usually not known (Desmet & Cowling 2004). Several non-parametric estimator functions are available for estimating the total number of species in an area based on a set of random samples (Colwell & Coddington 1994). We applied eight estimators of species richness to each forest type and subtype. The resulting species richness values were then incorporated into eq. 4 (above) and used to calculate the proportion of land in which 75% of the plant species would occur and be represented by at least one individual.

Adequacy of sample data to assess richness

Two data requirements that can influence estimates of richness values include, (1) homogeneity of vegetation units (where we are advised that it is inappropriate to attempt to estimate richness across sites where there are large compositional differences such as ecological gradients; Magurran 2004), and (2) inadequate sample size (Colwell & Coddington 1994), where all estimators will underestimate richness if the samples are too sparse. Gotelli & Colwell (2011) further suggest that more than 20 samples would be a minimum and 50 ideal (Colwell & Coddington 1994) and point out that the Chao 2 and Jacknife 2 provide the better estimates at low sample sizes. Yet it also makes intuitive sense that samples sizes that do not capture the spread diversity within the targeted vegetation unit will not be able to predict their richness contribution.

The application of species estimators across ecological gradients has highlighted the need for estimators that incorporate compositional turnover. Jobe (2008) describes how estimators that separate sampling processes from ecological ones offer the greatest potential for advances in estimating species richness, since estimators that do not include ecological processes tended to underestimate species richness. The adequacy of our data set to represent the vegetation units from which they were sampled was assessed by means of the SAR, or species accumulation curves. This approach helps assess the extent to which a vegetation unit has been adequately sampled, with the slope of the curve reaching an asymptote as few new species are recorded with increased sampling. As number of sample plots surveyed varied

considerably between the forest subtypes, we relativised the sample area data by displaying the x-axis as a proportion of area sampled (a percentage value). The SAR can also provide an indication of the rate of species turnover between communities if the x-axis is log transformed (Lennon et al. 2001).

Quantitative forest patch process targets

The inclusion of forest processes that support the existing forest species composition is achieved by means of identifying forest patches important in supporting dispersal between patches (see Chapter 5). The Probability of connectivity index (*dPC*) was applied using Conefor Sensinode (Saura & Torné 2009) to the Mpumalanga forest data set. This index comprises three fractions (*dPCintra, dPCflux, dPCconnect*), each quantifying different ways in which a habitat patch can contribute to habitat connectivity and availability in the landscape. Forest patches with significantly higher values for the *dPC* metric and the *dPCconnect* fraction were selected to identify priority forest patches (see Chapter 5). The *dPCconnect* fraction evaluates a patch's contribution to connectivity between other patches by acting as an intermediate stepping stone patch (Saura & Rubio 2010).

The prioritisation of spatially fixed forest patches as process features within a SCP will require the setting of a representation target (i.e. the proportion of the process feature that would be required within the identified conservation portfolio). Pressey *et al*. (2003) applied a 100% target for spatially fixed process features. Within the Northern Escarpment region, the four largest forest patches (each over 1000 ha) were also identified as priority patches but they were not included as not only are they large enough for dispersal to occur within these forests, but their selection would preclude the inclusion of any other smaller and more vulnerable forest patches important in maintaining connectivity. A maximum patch size limit for selection was set to 1000 ha for Northern Escarpment forests.

Quantitative forest matrix process targets

Chapter 5 established the minimum dispersal distance that would ensure that 75% of forest species are able to disperse to the nearest forest patch, for each of the three regions. The dispersal distance for Barberton was 1000 m, Northern Escarpment 600 m, and Wakkerstroom Region 2000 m. This minimum distance in turn informed the buffer width around each forest patch, which represents the surrounding matrix around each patch across which the diaspores would disperse. We only buffered selected priority patches for each of the three regions, after which we erased transformed areas (based on 2010 landcover; Lötter 2013).

Adjustment of pattern targets to take into account dispersal connectivity

The extent to which forest patches are functionally connected to other forest patches (not subtypes) is calculated in terms of connectivity metrics and the Probability of Connectivity index (*dPC*). The Probability of Connectivity index determines patch importance values by means of supporting emigration and colonization of forest diaspores (in terms of intra-patch dispersal, the amount of habitat being made available to other patches, and the importance of patches as 'stepping stones'). This index is informed by a minimum patch distance which was established for each of the three broad forest regions across Mpumalanga Province (discussed above).

To determine the extent to which forest patches within one subtype may be connected to one-another, we used the mean connectivity value for each forest subtype. This enabled us to interpret the extent to which each subtype may be vulnerable to dispersal disruption, in comparison to other subtypes. See equation 5.

$$5. \quad \text{Subtype connectivity importance} = \frac{\sum dPC \text{ values per subtype}}{\#\text{ of patches per subtype}}$$

We felt it necessary to integrate dispersal connectivity into pattern targets. Primarily because areas selected to achieve process targets, may not necessarily be the best areas for achieving pattern targets. One needs to be cautious of including pattern and process targets for spatially similar areas where high targets for one feature could bias the selection of the other feature and in so doing fail to achieve the desired objective for one of them. For example, if the spatial extent for both forest pattern and process layers overlapped, a 100% target for dispersal process features would force Marxan's optimisation algorithm (used in SCP) to meet all pattern targets in the same areas as for process targets. But there are also other important factors to consider and implement for pattern features via the SCP process, such as cost surfaces (meeting targets in areas with lower cost – financial or ecological costs or avoiding areas of land-use conflict), adjacency to existing reserves, climate change refugia, or areas where species of conservation concern occur. The inclusion of point records for species of conservation concern is considered as a "fine filter" in which to focus the priorities of the "coarse filter" forest pattern data set (sensu Noss 1987). Pressey et al. (2003) similarly proposed adjustments in pattern targets for the CAPE conservation plan where they overlapped with process targets. By including spatially fixed process features with a 100% target, a significant amount of the pattern targets were also being met in the same areas as the ecological processes. By increasing the pattern targets they were able to avoid over-representation in process areas such as edaphic and upland–lowland interfaces.

Secondly, forest pattern targets are based on the current configuration of forest patches across the landscape. Intuitively any loss or disruption in connectivity between these forest patches would negatively influence emigration and immigration rates and result in a loss of

species. Forest subtypes that are less connected may be more vulnerable to changes in forest patch configuration and surrounding matrix. Therefore we propose that dispersal distances and the degree to which forest subtypes are connected, be incorporated into the representivity (pattern) targets.

To avoid the risk of biasing pattern target achievement to specific areas serving a specific purpose, it is possible to either add pattern and process targets so that the target is large enough to be met in areas that are not necessarily specific process areas, or pattern and process targets can be combined in a more ecologically substantiated manner. We propose the application of ranking the subtypes according to their mean connectivity values (based on *dPC* metric), then assigning the least connected subtype an additional connectivity value based on the average percentage process target across the three regions (which is 15.3%). (i.e. Lydenburg Kloof Forest pattern target of 18.76% (pattern) + 15.3% (process) = 34.06%). The least connected subtype would receive the highest values while the most connected subtype would not gain any additional area. However to avoid this process forcing that entire pattern target to be met in areas important for process targets, we propose the inclusion of a baseline target which is the difference between the maximum process target (19%) and the average process target (15.3%), and should be added to the pattern target for each forest subtype. This process is explained in Figure 2.

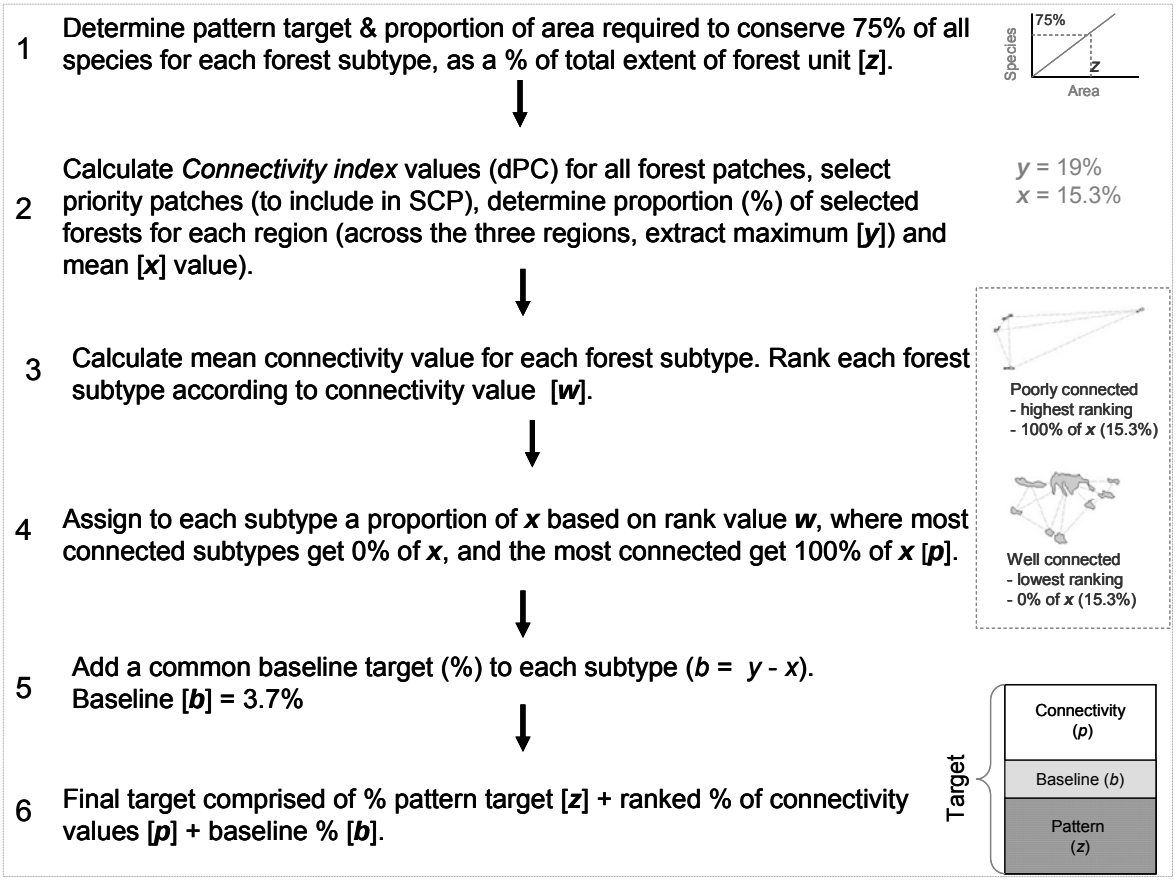


Fig. 2. Flow diagram of the process of determining integrated targets for each forest subtype.

RESULTS

SAR and representation targets

EstimateS estimated true species richness using eight non-parametric predictors. The results for each forest subtype (Table 1) are summarised according to the predicted value for each estimator per subtype. All estimators generated results that were greater than observed richness (mean of 173) but also that were broadly similar (with values: ACE = 188, ICE = 223, Chao = 189, Chao 2 = 223, Jacknife 1 = 217, Jacknife 2 = 238, Bootstrap = 196 , Michaelis–Menten = 223). The average and maximum values across the range of eight species richness estimators are also provided. Seventy one percent of the maximum values were predicted by the Jacknife 2 estimator, which is reported to provide stable and accurate values (Colwell & Coddington 1994). Chao 2, Bootstrap and Michaelis–Menten runs also identified highest predicted values for at least one subtype.

Table 1: Summary of the estimator values predicting total species richness for each forest subtype. Values in bold indicate the maximum estimated richness value across all eight predictors. Mean values are averaged across all eight predictors and maximum values provided are from summarised results. Boot = Bootstrap estimator, Jack = Jacknife estimator, M–M run = Michaelis–Menten estimator.

Forest subtype	Plots	Recorded species	*Mean*	*Highest*	ACE	ICE	Chao1	Chao2	Jack1	Jack 2	Boot	M–m run
Barberton Mistbelt	59	191	*212*	*238*	201	213	201	220	222	**238**	206	193
Barberton Scarp	36	229	*271*	*312*	250	278	249	278	286	**312**	256	256
Blyde Canyon Dry Afromontane	11	183	*227*	*260*	209	233	208	246	233	**260**	206	222
Blyde Scarp	5	117	*202*	*442*	125	224	121	198	169	196	140	**442**
Eastern Dry Afrotemperate	36	240	*278*	*314*	260	285	258	280	294	**314**	267	265
Escarpment Riverine	8	167	*257*	*310*	215	304	212	**310**	244	293	200	277
Foothills Mistbelt	35	175	*197*	*220*	184	202	184	198	209	**220**	192	189
Legogote Scarp	8	113	*143*	*165*	126	152	126	153	148	**165**	129	141
Long Tom Mistbelt	118	241	*261*	*292*	241	253	273	250	268	279	**292**	233
Lydenburg Kloof	14	112	*126*	*137*	117	130	117	121	133	133	124	**137**
Mapulaneng Scarp	13	167	*218*	*263*	183	242	177	260	226	**263**	193	201
Mariepskop Mistbelt	68	216	*239*	*268*	224	233	230	253	249	**268**	231	223
Northern Highveld Kloof	10	117	*145*	*164*	125	158	121	145	153	**164**	135	162
Wakkerstroom Midlands	17	158	*195*	*231*	169	211	165	210	207	**231**	180	186
Average values	***31***	***173***	***212***	***258***	***188***	***223***	***189***	***223***	***217***	***238***	***196***	***223***

Figure 3 (A) presents a species accumulation curve for the samples collected in each forest subtype. The extent to which the curve starts to flatten, or reach an asymptote, is used as an indicator that few additional species will be added with additional sampling effort. The x-axis scores are relativised so as to display multiple accumulation curves of differing sample sizes on the same axis for comparison. Figure S1 (Supplementary material) plots individual species area curves for each subtype to visually validate individual curve shapes.

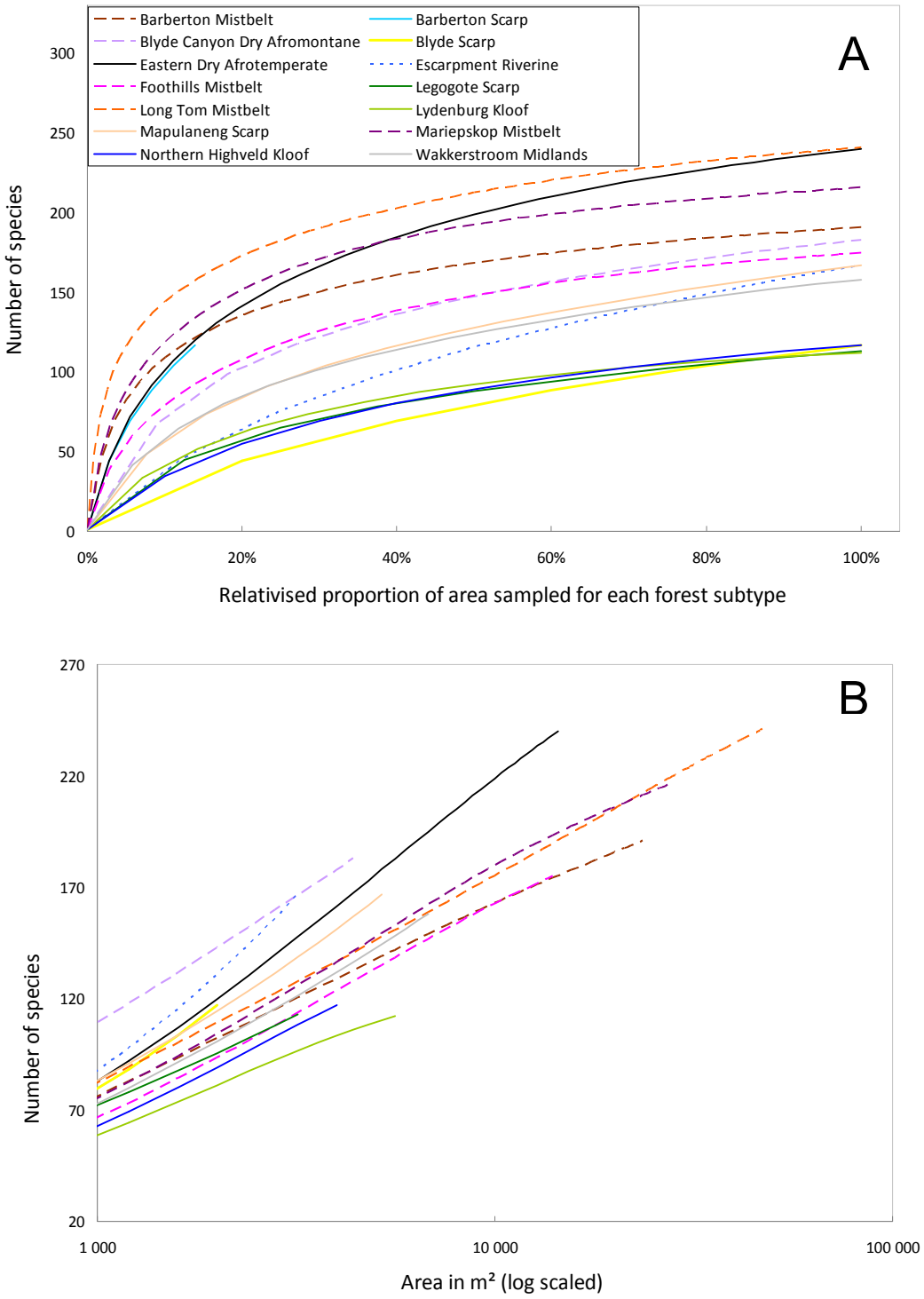


Fig. 3. Species accumulation curves for the forest sample data collected for each of the 14 forest subtypes. Plots are based on species recorded per 400 m² sample (with different sampling intensities per subtype). Average species richness (based on 50 randomizations; see Colwell 2004) is shown. In graph A, the x–axis is relativised as a percentage value of area sampled to account for different sampling sizes. In graph B (a semi–log SAR), the x–axis is $\log_{10}$ scaled highlighting the relationship between the number of species and area. The log of the x-axis was one of the earliest predictors of species richness which tended to overestimate species richness (Palmer 1990).

As can be seen from Figure 3 (A) all of the curves are not yet showing signs of flattening. Some forest subtypes are showing a tendency to flatten more so than other types, such as Barberton Mistbelt, Mariepskop Mistbelt, Foothills Mistbelt forests, and the Kloof forests.

Those forest subtypes with less tendency to flatten, include: Escarpment Riverine, Eastern Dry Afrotemperate, Blyde Canyon Dry Afromontane and Blyde Scarp forests. The results from Figure 3 (A) suggest that perhaps an insufficient number of samples were used to calculate species richness for several of the forest subtypes. Figure 3 (B) is a semi–log SAR where the slope and steepness of the near-straight lines are good indicators for rates of species accumulation within a unit. Historically this approach was used to estimate species richness although it is now realised that it tends to overestimate species richness (Palmer 1990). The semi–log SAR indicate rates of species accumulation, where the steeper (more vertical) lines indicate greater species accumulation than those forest subtypes with more horizontal lines.

The graph shows that most of the forest subtypes exhibit similar rates of species accumulation (with parallel lines), however the exceptions are the Escarpment Riverine, Eastern Dry Afrotemperate, and Mapulaneng Scarp forests, with higher than average rates of accumulation. The Lydenburg Kloof forest exhibited lower than average rates of species accumulation. But overall, the observation that there is a near-linear relationship between species richness and log area reiterates the fact that species area curves can never truly reach an asymptote.

Table 2: Forest subtypes and the values that informed the % area required for each subtype to meet 75% species representation target. Plot size is 400 m^2 throughout.

Forest subtype	Plots	Size (m²)	Total species	Average species per plot	z–value	**% Area incl. 75% of species**	% of forest subtype sampled
Barberton Mistbelt	59	24 006 282	*238*	43	0.156	**15.8%**	0.098%
Barberton Scarp	36	45 146 947	*312*	42	0.172	**18.8%**	0.032%
Blyde Canyon Dry Afromontane	11	4 872 729	*260*	68	0.143	**13.4%**	0.090%
Blyde Scarp	5	1 315 140	*442*	45	0.282	**36.1%**	0.152%
Eastern Dry Afrotemperate	36	83 968 204	*314*	45	0.159	**16.4%**	0.017%
Escarpment Riverine	8	3 926 544	*310*	43	0.215	**26.2%**	0.081%
Foothills Mistbelt	35	76 672 123	*220*	39	0.142	**13.2%**	0.018%
Legogote Scarp	8	7 375 610	*165*	32	0.165	**11.3%**	0.043%
Long Tom Mistbelt	118	70 842 717	*292*	49	0.148	**14.3%**	0.067%
Lydenburg Kloof	14	2 721 388	*137*	33	0.162	**16.9%**	0.206%
Mapulaneng Scarp	13	9 843 141	*263*	49	0.166	**17.7%**	0.053%
Mariepskop Mistbelt	68	41 874 277	*268*	43	0.158	**16.2%**	0.065%
Northern Highveld Kloof	10	466 166	*164*	34	0.223	**27.5%**	0.858%
Wakkerstroom Midlands	17	30 502 784	*231*	41	0.154	**15.4%**	0.022%
Average values	31	28 823 861	258.5	43.3	0.175	**18.5%**	0.129%

Given the criticism of sample size on predicting species richness and the shortcomings of number of samples recorded per subtype, we selected to use the maximum estimated values as a measure of species richness. Less than 50% of the subtypes had more than the recommended minimum of 20 samples. In addition to the results from Figure 3 (A), in terms of the actual area sampled per forest subtype (see Table 2), our sample data covered only between 0.017% (for Eastern Dry Afrotemperate Forests) and 0.206% (for Lydenburg Kloof Forest) which is low for estimating total species richness. The proportional target area required to represent at least one example of 75% of the species composition is highlighted in bold in Table 2.

Forest patch process targets

Chapter 5 identified the important forest patches that support dispersal between forest patches. These patches are mapped and are spatially fixed. Forest patch quality values were determined by the intactness of a 1 km buffer around each forest patch. This resulted in forest patches within largely natural areas being identified as important patches requiring inclusion within SCP. Important forest patches were identified in each of three regions (Barberton, Northern Escarpment, Wakkerstroom) and comprised 19, 14.7 and 16.6% of the regions forests, respectively. These accounted for 155 forest patches out of a total of 1914 patches, which amounts to 15.3% of all forests being identified to support dispersal connectivity. Entire forest patches are required to provide for dispersal and connectivity, and only conserving a proportion of a forest patch would not ensure that the forest patch could still fulfil its functional purpose. Therefore it is proposed that a 100% target be set for these patches (see Chapter 5).

Forest matrix process targets

The extent of transformation of the selected forest patch buffer ranged from 7.1% for the Wakkerstroom region, 26.1% for Barberton region, and 34.7% for the Northern Escarpment region. Each region will be treated as a separate biodiversity feature layer to avoid targets for more transformed regions being met in the largely untransformed regions. A target of 60% of original matrix extent will be set for each region (see Table 3).

Table 3: Summary of three buffer regions identified around important forest patches (n=155) that support dispersal connectivity. A target of 60% of original buffer extent is set and the proportion of remaining natural vegetation within the buffer that is required for target achievement is presented indicating flexibility in target achievement.

Biodiversity Feature	Buffer distance	Buffer total (ha)	Buffer natural (ha)	Target (ha)	% Buffer natural	% of Natural buffer required to meet target
Forest Matrix, Barberton Region	1000 m	14578.8	10773.2	8747.3	73.9	81.2
Forest Matrix, NE Region	600 m	26324.4	17188.6	15794.6	65.3	91.9
Forest Matrix, Wakkerstroom Region	2000 m	21122.0	19612.6	12673.2	92.9	64.6

Integrated pattern and process targets

To accommodate the probable underestimation of species richness at the subtype level, species richness was also calculated for the higher-level forest types, with only three forest types recorded within Mpumalanga (Lötter et al. 2014). The subtypes are nested within the National Forest Classification (von Maltitz et al. 2003). For each of these types, more than 65 samples were used to estimate species richness. Table 4 summarises the output from estimating true species richness using EstimateS and eight non-parametric estimators for forest types. The Jacknife 2 estimator again consistently predicted the highest estimated values.

The proportion of each forest type that would include at least 75% of all species within a forest type was determined following the same method as for forest subtypes (results not shown). Then for each forest subtype, target values from both the assessment of forest types and subtypes were added and then averaged to provide a better indication of total species richness although we suspect that this may still be an underestimation given our small sample size relative to the entire extent of forests throughout Mpumalanga.

Table 4: Summary of the estimator values predicting total species richness for each forest type. Values in bold indicate the maximum estimated richness value across all eight predictors. Mean values are averaged across all eight predictors and maximum values provided are summarised from results.
Boot = Bootstrap estimator, Jack = Jacknife estimator, M–M run = Michaelis–Menten estimator.

Forest Type	Plots	Observed	*Mean*	*Highest*	ACE	ICE	Chao1	Chao2	Jack1	Jack 2	Boot	M–m run
Eastern Scarp	66	408	*492*	*588*	440	514	430	534	524	**588**	461	450
Mpumalanga Mistbelt	291	368	*405*	*458*	384	411	382	435	424	**458**	393	353
Northern Highveld	77	326	*362*	*397*	342	368	340	361	384	**397**	356	346
Average values	***145***	***367***	***420***	***481***	***389***	***431***	***384***	***443***	***444***	***481***	***403***	***383***

Table 5 and Figure 2 summarise the integration of the forest type and subtype targets (B) with that of the connectivity target (A) into a proposed integrated pattern target that is cognisant of connectivity capacity (C). Therefore the most connected forest subtype is the Mapulaneng Scarp Forest which has an averaged pattern target (B) of 22%. Being the most connected subtype, we add 0% as connectivity extent and a 3.7% connectivity baseline target (the difference between provincial average of 15.3% and maximum connectivity extent of 19%, which was for Barberton Region). The Mapulaneng Scarp Forest occurs in the Northern Escarpment region, for which 14% of its forest patches have been identified as important for supporting connectivity (an overlapping process target). Therefore there is now an 11.7% margin for identifying pattern features that are an addition to the overlapping process features. For the least connected forest subtype, Lydenburg Kloof Forest, the averaged pattern target (B)

is 18.8% to which we add 14.9% for connectivity value, plus 3.7% (baseline). Therefore the revised pattern target is 37.3%.

It is recommended that the values in column C of Table 5 provide the target to be used in a SCP as the proportion of original extent of each forest subtype. Marxan will consider these targets in conjunction with the process targets when finding the most optimal portfolio of planning units required to meet targets.

Table 5: Summary of *dPC* connectivity index values averaged per subtype. Connectivity values are ranked from 0.15 to 5.18 (best connected) and assigned a ranked value between 0 and 100 for each forest subtype. They are then assigned a % connectivity value as a proportion of average dispersal extent (proportion of 15.3%) plus a baseline connectivity value of 3.7%.

Forest subtype	Connectivity index (*dPC*) averaged per subtype	Ranked (0–100) based on *dPC* index	**(A)** % Area connectivity value (proportional to average dispersal extent – proportion of 15.3% + 3.7% baseline)	Forest subtype target	Forest type target	**(B)** Average richness target	**(C) = A+B** Revised pattern target (incl. connectivity target)
Barberton Mistbelt	1.35	26	15%	15.8%	19.5%	17.7%	**32.7%**
Barberton Scarp	0.76	15	16.8%	18.8%	26.2%	22.5%	**39.3%**
Blyde Canyon Dry Afromontane	3.56	69	8.5%	13.4%	19.5%	16.4%	**24.9%**
Blyde Scarp	0.16	3	18.5%	36.1%	26.2%	31.1%	**49.7%**
Eastern Dry Afrotemperate	0.19	4	18.4%	16.4%	20.6%	18.5%	**36.9%**
Escarpment Riverine	0.63	12	17.1%	26.2%	26.2%	26.2%	**43.4%**
Foothills Mistbelt	2.91	56	10.4%	13.2%	19.5%	16.3%	**26.8%**
Legogote Scarp	1.82	35	13.6%	11.3%	26.2%	18.8%	**32.4%**
Long Tom Mistbelt	0.21	4	18.4%	14.3%	19.5%	16.9%	**35.3%**
Lydenburg Kloof	0.15	3	18.6%	16.9%	20.6%	18.8%	**37.3%**
Mapulaneng Scarp	5.18	100	3.7%	17.7%	26.2%	22%	**25.7%**
Mariepskop Mistbelt	3.65	70	8.2%	16.2%	19.5%	17.8%	**26.1%**
Northern Highveld Kloof	0.24	5	18.3%	27.5%	20.6%	24.1%	**42.3%**
Wakkerstroom Midlands	0.79	15	16.7%	15.4%	20.6%	18.%	**34.7%**
Average values	*1.54*	*30*	*14.4%*	*18.5%*	*22.2%*	*20.4%*	***34.8%***

DISCUSSION

Quantitative targets for forest pattern

We applied the power form of the Species-Area-Relationship (SAR) to determine the proportion of each forest subtype that needs to be 'conserved' within the Mpumalanga Biodiversity Sector Plan (MBSP). It is well established that plans based on arbitrary targets of 10–12% are inadequate to ensure the effective conservation of a region's biodiversity (Margules & Pressey 2000; Pressey et al. 2003; Margules & Sarkar 2007). Our initial target setting approach based on the SAR to conserve 75% of all species within a forest subtype suggested a pattern target range of between 11.3% and 36.1%. However most of the lower values appear to be for the subtypes with steeper species accumulation curves with lower tendency to reach an asymptote. The outlier is the Blyde Scarp forest which had the lowest number of plots (n=5),

highest estimated species richness, high species accumulation rates, and this target was 36% where the next highest target was 8.5% lower (for Northern Highveld Kloof forest).

Berliner et al. (2008) calculated area representation targets, also based on the 75% species representation requirement, for forests groups, Forest groups are the higher hierarchical level than forest types in the NFC. They determined targets at the forest group level to overcome the deficiency in the number of sample plots. Their representation targets, based on maximum values, ranged between 13.5% (for Southern Afrotemperate group) to 22.4% for the Scarp group of forests. In our study, an analysis of the three forest types produced similar though slightly higher targets than for forest groups (range of 19.5% to 26.2%) which could be attributed to a complete floristic assessment for each plot rather than sample plot data from various sources with a focus on trees (Geldenhuys & Mucina 2006).

From Figure 3 (B) the slope of most curves show a similar parallel pattern, except for three forest subtypes, with steeper curves indicating greater species accumulation. These were the Escarpment Riverine, Eastern Dry Afrotemperate, and Mapulaneng Scarp forests. For the Escarpment Riverine forests, the higher species accumulation can possibly be attributed to the fact that an insufficient number of plots (n=8) had been used to calculate targets and that four of these were from Limpopo Province (to boost the number of plots) and may in fact represent a different forest subtype and hence add to the rate of species turnover between plot data. Secondly, for Eastern Dry Afrotemperate forests are geographically widespread and their circumscription was not clear and obvious (Lötter et al. 2014). The results from Figure 3 (B) suggest that the higher rate of species accumulation may in fact represent a need for more sample plot data and the further distinction of forest communities/subtypes within this subtype. In particular, the sample plot membership of this forest subtype varied greatly depending on the resemblance measure chosen (data not shown), and eventually the current classification was accepted after detailed interrogation of the data set. Interestingly this is also the forest subtype with the lowest proportion of forest extent sampled when compared to the other forest subtypes (see Table 2, right-hand column), which may be a contributing factor. Lastly, the Mapulaneng Scarp forest also exhibited high species turnover but this subtype was only represented by 13 plots and perhaps this low number, together with a higher average species richness per plot (2nd highest, Table 3, Chapter 4), may contribute to the higher rate of species turnover.

The successful application of the SAR is dependent on incorporating values for true species richness for each forest subtype, a requirement which is usually nearly impossible to determine (Colwell et al. 2012). The investigation and application of various estimators of species richness were explored in combination with the suitability of our data set to this approach. Estimators of species richness are not without criticism (Jobe 2008), but they still provide a valuable ‘best guess’ which is defendable and possible to explain to stakeholders who would use the results of a SCP (Margules & Pressey 2000; Reyers et al. 2007). The application of a transparent and scientific approach is better than an approach with no scientific foundation.

Given the shortcomings of estimating species richness, we chose to integrate forest subtype targets with those for forest types of a higher level in the National Forest Classification (von Maltitz et al. 2003), which increased the mean target values from 18.5% to 22.2% (range of 16.3% to 31.1%), and to add to these targets a variable baseline target based on forest connectivity values where more fragmented (naturally) forest subtypes would require higher pattern targets to maintain species composition through immigration and emigration of forest diaspores between forest patches. The range in baseline connectivity targets varied between 3.7% and 18.6% and the final pattern target to be implemented in the MBSP ranged between 24.9% for Blyde Canyon Dry Afromontane forest to 43.4% for Escarpment Riverine forest.

Shortcoming of applying estimators of species richness to our data set

Our results generally corroborate the criticism of species areas curves, where estimators of species richness are generally correlated to sample size (Magurran 2004; Chapman & Underwood 2009), or provide lower estimates of richness across environments with a higher species turnover, where high turnover is responsible for greater richness in larger areas than would be suggested by extrapolation from small areas (Jobe 2008). Unfortunately closer inspection of our data set revealed its shortcomings in terms of sample size (only 3 subtypes with more than the recommended 50 samples; and the extent of sampling across all subtypes varied between 0.017 and 0.206%). Desmet and Cowling (2004) set a minimum sample size limit of 30 samples for the Succulent Karoo biome, determined by means of exploratory analyses for the smallest average number of samples for which the standard deviation of the final estimate was less than 5% of the estimate. Only 6 of our 14 subtypes meet this limit. Berliner et al. (2008) set a higher limit of 100 samples when determining forest group targets based on the SAR, but this was for a higher level in the forest hierarchy utilising a national vegetation data set (von Maltitz et al., 2003). Lawes et al. (2007) used 80 or more plots for the northern and southern Drakensberg montane forest subtypes, based on determining the proportional area target to conserve 75% of all species within a forest subtype.

These shortcomings in our study are further confirmed by the failure of our species accumulation curves to approach an asymptote and the high rates of species accumulation in some units with lower number of samples highlighting the inadequacy of our data set to comfortably predict true species richness. In addition, integrating forest subtype targets with that determined for forest types (which had a greater number of aggregated plot data to work with), raised the targets by an average of 3.7% (see Table 5).

Owing to our low sample size and the tendency of estimators to under predict true richness, we opted to use the maximum richness values in our calculation of targets. Our results showed that the Jacknife 2 estimator most consistently predicted the highest species richness values. Chapman & Underwood (2009) conclude that Jacknife 2 was the only non-parametric estimator that did not on average underestimate species richness in their test of 12 estimators

and was assessed to be the best estimator of species richness across a range of tests and sample sizes. Therefore we do not feel that the use of the maximum richness values in any way inflated or misrepresented the targets, and if anything, we suspect they are still lower than true species richness values.

Quantitative targets for forest processes

Forest processes may be either spatially fixed or spatially flexible (*sensu* Rouget et al. 2006). Spatially fixed processes would require the full extent of the process feature mapped with a 100% target, while spatially flexible processes would require only a portion of the current or original extent of the mapped feature surrogate to fulfil its functional role. For spatially fixed processes, such as a forest patch important in maintaining connectivity between other forest patches (Chapter 5), there is no flexibility in meeting targets other than securing the entire forest patch with a 100% target. Even the partial loss of a portion of this patch may detract from its ecological functioning, such as an unwanted human settlement in part of the forest where there may be both direct and indirect impacts from noise, trapping of fauna for food, or harvesting of plants.

But connectivity not only depends on the characteristics of the habitat patches and the distance between patches, but also on the suitability and permeability of the surrounding matrix (Berliner 2009; Mimet et al. 2013). Intuitively, the composition of the forest matrix, i.e. the landscape surrounding the indigenous forests, can have an impact on the success of diaspore dispersal across this matrix. Species with relatively limited mobility are those potentially more sensitive to the changes and permeability losses in the landscape matrix, especially those that occur within their limited dispersal range (Saura et al. 2011). Specifically, in our study the dispersal matrix is defined as the surrounding landscape across which 75% of forest diaspores need to disperse. This was determined for each forest region and distance values varied between 600 m to 2 km. With 52.2% of all forest diaspores being vertebrate dispersed, the permeability or resistance of the surrounding forest matrix will likely have an impact on dispersal success (Leimu et al. 2010; Herrera et al. 2011), and the possible failure of achieving dispersal of 75% of forest diaspores to nearest forest patches. Furthermore, fragmentation disrupts landscape level ecosystem processes and increases the vulnerability of forests to biodiversity loss (Berliner 2009). The proportion of the surrounding forest matrix which is still natural (based on region-specific dispersal distances) varied from 65.3% to 92.8% for the three regions. We therefore propose that a buffer equal to the minimum patch distance for each region, for each of the selected patches, be included as a separate process feature with a 60% pre-transformation (or original extent) target. A target of 60% is a threshold value below which larger habitat fragments generally breaks apart (Baguette et al. 2012) and processes are compromised.

Vulnerability and conservation urgency

Including spatially explicit forest features (such as the forest subtypes, important forest patches, etc.) and their quantitative pattern or process targets, is an optimization requirement to prioritise areas for conservation. Depending on how a particular SCP is structured and the choice of cost layer to incorporate, reducing vulnerability may also be factored into the Marxan optimisation algorithm that uses a mathematical objective function to select planning units based on various costs and the penalties for not meeting conservation targets. A cost layer that includes development pressures or competing land-use information may avoid the meeting of targets in areas of greater vulnerability (if the targets are not near 100%). In its simplest form, the Marxan objective function is a combination of the total cost of the reserve system and a penalty for any of the pattern or process targets that are not met. The objective function is designed so that the lower the value the better. Marxan also allows a measure of reserve system fragmentation to be taken into account, by means of limiting boundary length (see Game & Grantham (2008) for more details relating specifics of Marxan's objective function).

The objective function takes the form of:

$$\sum Cost + BLM \sum Boundary + \sum Species\ Penalty\ Factor \times Penalty$$

BLM stands for Boundary Length Modifier value which is user defined and influences clustering of planning units to avoid high boundary costs. What is not explicitly mentioned, but is implicit in the SCP approach adopted in the revised MBSP 2013, is the vulnerability and conservation urgency for some forests and parts of the forest matrix. This is addressed in the analytical stage of SCP when running the Marxan algorithm, and in the implementation stage by expressing each planning unit's irreplaceability value (or frequency of selection value) against its threat/vulnerability value and then targeting implementation in the higher threat/higher irreplaceable areas (see Margules & Pressey 2000). Figure 4 applies this methodology to the forest planning units within the MBSP, highlighting frequency of selection or irreplaceability on the y–axis and vulnerability in terms of conflict with other land-uses on the x–axis (methodology adapted from Margules & Pressey (2000) and applied to Mpumalanga's forest data set). This framework of four quadrants and actions can be used to prioritise conservation actions.

The development of representivity or pattern targets for forest subtypes differs somewhat from the target setting process developed for largely contiguous vegetation types that are only based on SAR approach and derived z–values (Desmet & Cowling 2004). Our inclusion and integration of connectivity process targets into the pattern target is perhaps a precautionary approach given the landscape dependency of forest patches that require the emigration and immigration of plant diaspores. The shortcomings of non-parametric estimators of species richness further urged us to consider integrated target approaches. It is also appropriate to

review these targets at 5–year intervals so that they reflect advances in knowledge about the region's biodiversity and its requirements for persistence.

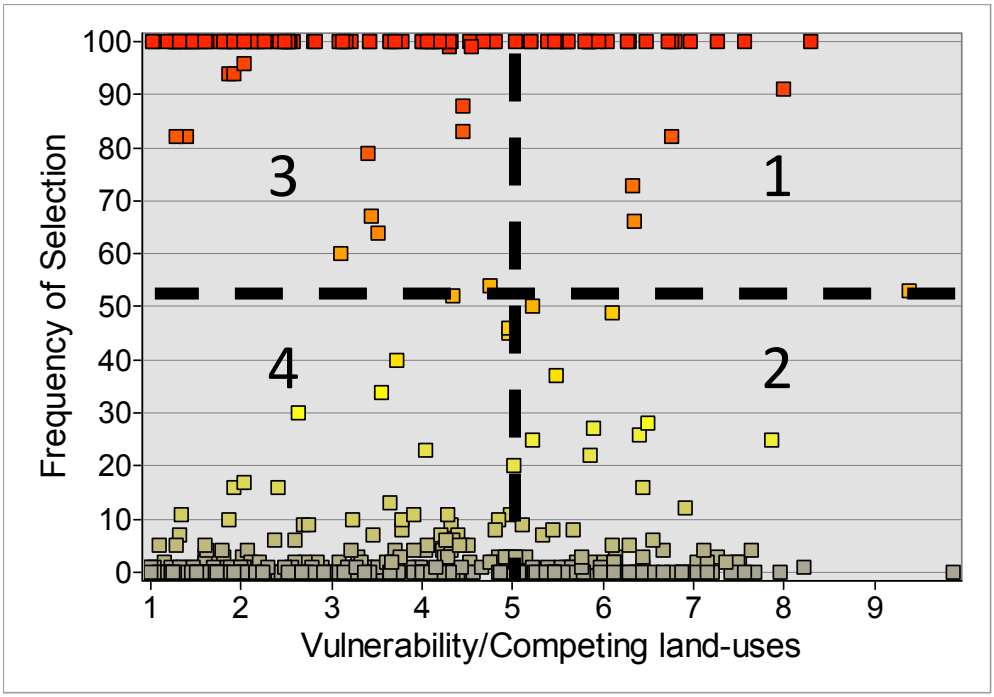


Fig. 4. A framework for prioritising conservation action specifically for forest planning units, measured against vulnerability as determined by likely conflict with other land uses. Brighter (more red) colours have higher irreplaceability values. Appropriate response from conservation planners may be linked to quadrants. Quadrant 1: forests most likely to be lost but with fewer replacements. Protection is urgent to avoid compromising forest targets. Quadrant 2: forests vulnerable to loss but with more replacements, either because features are relatively common and extensive relative to targets or because targets have been met in existing reserves. Conservation measures are necessary to avoid loss of some areas causing others to move into quadrant 1. Quadrant 3: Areas with lower risk but high irreplaceability. Protection is less urgent and possibly more feasible than quadrant 1. Quadrant 4: these forests are likely to be more stable and of lower conservation value (adapted from Margules & Pressey 2000).

CONCLUSION

Establishing appropriate quantitative pattern and process targets for biodiversity features enables them to be used within a SCP framework. Process features and their targets are designed to support persistence, but so too can the quantitative pattern targets that are translated from the conservation objectives. Pattern targets are also called representation targets whereby the target is quantified to represent at least 75% of all species within a proportion of a vegetation unit, but a measure of persistence may be introduced into particularly vulnerable ecosystems. We recognise that although the addition of a connectivity value (as a percentage value) to the pattern targets is not very elegant and rather cumbersome, it is very necessary as conservation cannot always wait for detailed sampling, field work and analysis. Realising the potential implication of insufficient sample data, and the vulnerability of naturally disconnected forest patches to disruption of dispersal events, what we propose is an interim

step for including connectivity into naturally fragmented vegetation units that rely on dispersal to maintain their composition. To quote Pressey et al. (2003), “Like any other conservation targets, they are estimates of the requirements for persistence of a region’s biodiversity made within the constraints of limited information. We expect them to be improved in future reviews of appropriate targets ....”.

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REFERENCES

Arrhenius, O. 1921. Species and area. *Journal of Ecology* **9**: 95–99.

Baguette, M., D. Legrand, H. Fréville, H. Van Dyck, H., and S. Ducatez. 2012. Evolutionary ecology of dispersal in fragmented landscapes. Pages 251–265 in Clobert, J., M. Baguette, T. Benton, and J. Bullock, editors. Dispersal ecology and evolution. Oxford University Press, Oxford.

Berliner, D. 2009. *Systematic conservation planning for South Africa’s forest biome: An assessment of the conservation status of South Africa’s forests and recommendations for their conservation*. PhD Thesis, University of Cape Town, Cape Town.

Berliner, D., P. Desmet, and L. Mucina. 2008. Revision of forest conservation targets and data preparation for the refinement of SANBI criteria for the listing of threatened forest ecosystems under the Biodiversity Act: Phase 1 and 2. Department of Water Affairs and Forestry, Project no. WP 6763.

Chao, A., R.L. Chazdon, R.K. Colwell, and T.J. Shen. 2005. A new statistical approach for assessing similarity of species composition with incidence and abundance data. *Ecology Letters* **8**: 148–159.

Chapman, M.G., and A.J. Underwood. 2009. Evaluating accuracy and precision of species–area relationships for multiple estimators and different marine assemblages. *Ecology* **90**: 754–766.

Chazdon, R., R.K. Colwell, J.S. Denslow, and M. Guariguata. 1998. Statistical methods for estimating species richness of woody regeneration in primary and secondary rain forests of NE Costa Rica. Pages 285–309 in Dallmeier, F., and J.A. Comiskey, editors. Forest biodiversity research, monitoring and modelling: conceptual background and Old World case studies. Parthenon Publishing Group, Paris.

Colwell, R.K. 2004. *EstimateS: statistical estimation of species richness and shared species from samples. v. 8.0.* Available from http://purl.oclc.org/estimates (accessed July 2012).

Colwell, R.K., and J.A. Coddington. 1994. Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society of London B* **345**: 101–118.

Colwell, R., A. Chao, N. Gotelli, S-Y. Lin, C.X. Mao, R.L. Chazdon, and J.T. Longino. 2012. Models and estimators linking individual-based and sample-based rarefaction, extrapolation and comparison of assemblages. *Journal of Plant Ecology* **5**: 3–21.

Carwardine, J., C.J. Klein, K.A. Wilson, R.L. Pressey, and H.P. Possingham. 2009. Hitting the target and missing the point: target-based conservation planning in context. *Conservation Letters* **2**: 3–10.

Desmet, P. 2004. Appendix B: Developing Species Representation Targets for South African Vegetation Types. Pages 94–107 in Rouget, M., B. Reyers, Z. Jonas, P. Desmet, A. Driver, K. Maze, B. Egoh, and R.M. Cowling, editors. *SANBI National Spatial Biodiversity Assessment. Technical Report Vol. 1 Terrestrial Component*. South African National Biodiversity Institute, Pretoria.

Desmet, P., and R. Cowling. 2004. Using the species–area relationship to set baseline targets for conservation. *Ecology and Society* **9**: 11. [online] URL: http://www.ecologyandsociety.org/vol9/iss2/art11

Game, E.T., and H.S. Grantham. 2008. Marxan User Manual: For Marxan version 1.8.10. University of Queensland, St. Lucia, Queensland, Australia, and Pacific Marine Analysis and Research Association, Vancouver, British Columbia, Canada.

Geldenhuys, C.J., and L. Mucina. 2006. Towards a new national forest classification for South Africa. Pages 111–129 in Ghazanfar, S.A., and H.J. Beentje, editors. Taxonomy and ecology of African plants, their conservation and sustainable use. Royal Botanic Gardens, Kew.

Gleason, H.A. 1922. On the relation between species and area. *Ecology* **3**: 158–162.

Gotelli, N.J., and R.K. Colwell. 2011. Estimating species richness. Pages 39–54 in Magurran, A.E., and B.J. Mcgill, editors. *Biological diversity: frontiers in measuring biodiversity*. Oxford University Press, New York.

Groves, C.R., et al. 2012. Incorporating climate change into systematic conservation planning. *Biodiversity and Conservation* **21**: 1651–1671.

Herrera, J.M., J.M. Morales, and D. Garcia. 2011. Differential effects of fruit availability and habitat cover for frugivore–mediated seed dispersal in a heterogeneous landscape. *Journal of Ecology* **99**: 1100–1107.

Jobe, R. 2008. Estimating landscape–scale species richness: reconciling frequency–and turnover–based approaches. *Ecology* **89**: 174–182.

Klein, C.J., K.A. Wilson, M. Watts, J. Stein, S. Berry, J. Carwardine, M.S. Smith, B.G. Mackey, and H.P. Possingham. 2009. Incorporating ecological and evolutionary processes into large–scale conservation planning. *Ecological Applications* **19**: 206–217.

Lawes, M.J., H. Adie, H.A.C. Eeley, D.J. Kotze, and R. Wethered. 2007. *An assessment of the forests of the Maloti–Drakensberg Transfrontier Bioregion, with reference to important ecosystem processes*. Forest Biodiversity Research Unit, School of Biological and Conservation Sciences, University of KwaZulu–Natal, Pietermaritzburg.

Leimu, R., P. Vergeer, F. Angeloni, and N.J. Ouborg. 2010. Habitat fragmentation, climate change, and inbreeding in plants. *Annals of the New York Academy of Sciences* **1195**: 84–98.

Lennon, J.J., P. Koleff, J.J.D. Greenwood, and K.J. Gaston. 2001. The geographical structure of British bird distributions: diversity, spatial turnover and scale. *Journal of Animal Ecology* **70**: 966–979.

Lieberknecht, L, J.A. Ardron, R. Wells, N.C. Ban, M.C. Lötter, J.L. Gerhartz, and D.J. Nicolson. 2010. Addressing ecological objectives through the setting of targets. Pages 24–38 in Ardron, J.A., H.P. Possingham, and C.J. Klein, editors. *Marxan Good Practices Handbook, Version 2*. Pacific Marine Analysis and Research Association, Victoria, BC, Canada. www.pacmara.org.

Lötter, M.C. 2013. Technical Report for the Mpumalanga Biodiversity Sector Plan – MBSP 2013. Mpumalanga Tourism & Parks Agency, Nelspruit.

Lötter, M.C., L. Mucina, and E.T.F. Witkowski. 2014. Classification of the indigenous forests of Mpumalanga Province, South Africa. *South African Journal of Botany* **90**: 37–51.

Margules, C.R., and R.L. Pressey. 2000. Systematic Conservation Planning. *Nature* **405**: 243–253.

Margules, C.R., and S. Sarkar. 2007. *Systematic Conservation Planning*. Cambridge University Press, New York.

Magurran, A.E. 2004. *Measuring biological diversity*. Blackwell Publishing, United Kingdom.

Moilanen, A., L. Meller, J. Leppänen, F.M. Pouzols, H. Kujala, and A. Arponen. 2012. *Zonation Spatial Conservation Planning Framework and Software V3.1, User Manual*. http://cbig.it.helsinki.fi/files/zonation/ZONATION_v3.1_Manual_120416.pdf

Mimet, A., T. Houet, R. Julliard, and L. Simon. 2013. Assessing functional connectivity: a landscape approach for handling multiple ecological requirements. *Methods in Ecology and Evolution* **4**: 453–463.

Noss, R.F. 1987. From plant communities to landscape in conservation inventories: a look at The Nature Conservancy (USA). *Biological Conservation* **41**: 11–37.

Palmer, M.W. 1990. The estimation of species richness by extrapolation. *Ecology* **3**: 1195–1198.

Palmer, M.W., and P.S. White. 1994. Scale dependence and the species–area relationship. *The American Naturalist* **144**: 717–740.

Pressey, R.L., R.M. Cowling, and M. Rouget. 2003. Formulating conservation targets for biodiversity pattern and process in the Cape Floristic Region, South Africa. *Biological Conservation* **112**: 99–127.

Rouget, M., B. Reyers, Z. Jonas, P. Desmet, A. Driver, K. Maze, B. Egoh, R.M. Cowling, L. Mucina, and M. Rutherford. 2004. *South African National Spatial Biodiversity Assessment Technical Report. Volume 1: Terrestrial Component.* South African National Biodiversity Institute, Pretoria.

Rouget, M., R.M. Cowling, A.T. Lombard, A.T. Knight, and G.I.H. Kerley. 2006. Designing large–scale conservation corridors for pattern and process. *Conservation Biology* **20**: 549–561.

Reyers, B., M. Rouget, Z. Jonas, R.M. Cowling, A. Driver, K. Maze, and P. Desmet. 2007. Developing products for conservation decision–making: lessons from a spatial biodiversity assessment for South Africa. *Diversity and Distributions* **13**: 608–619.

Saura, S., and L. Rubio. 2010. A common currency for the different ways in which patches and links can contribute to habitat availability and connectivity in the landscape. *Ecography* **33**: 523–537.

Saura, S., and J. Torné. 2009. Conefor Sensinode 2.2: a software package for quantifying the importance of habitat patches for landscape connectivity. *Environmental Modelling & Software* **24**: 135–139. www.conefor.org (accessed June 2012).

Saura, S., C. Estreguil, C. Mouton, and M. Rodriguez–Freire. 2011. Network analysis to assess landscape connectivity trends: application to European forests (1990–2000). *Ecological Indicators* **11**: 857–860.

Schulze, R.E. 2007. South African Atlas of Climatology and Agrohydrology. Water Research Commission, Pretoria, RSA, WRC Report 1489/1/06.

Tjørve, E. 2003. Shapes and functions of species–area curves: a review of possible models. *Journal of Biogeography* **30**: 827–835.

Von Maltitz, G., L. Mucina, C.J. Geldenhuys, M. Lawes, H. Eeley, H. Aidie, D. Vink, G. Fleming, and C. Bailey. 2003. Classification system for South African indigenous forests. An objective classification for the Department of Water Affairs and Forestry. Report ENV-P-C 2003–017. Environmentek, CSIR, Pretoria.

Wilhere, G.F. 2008. The how−much-is-enough myth. *Conservation Biology* **22**: 514–517.

Williamson, M., K.J. Gaston, and W.M. Lonsdale. 2001. The species–area relationship does not have an asymptote! *Journal of Biogeography* **28**: 827–830.

SUPPLEMENTARY MATERIAL

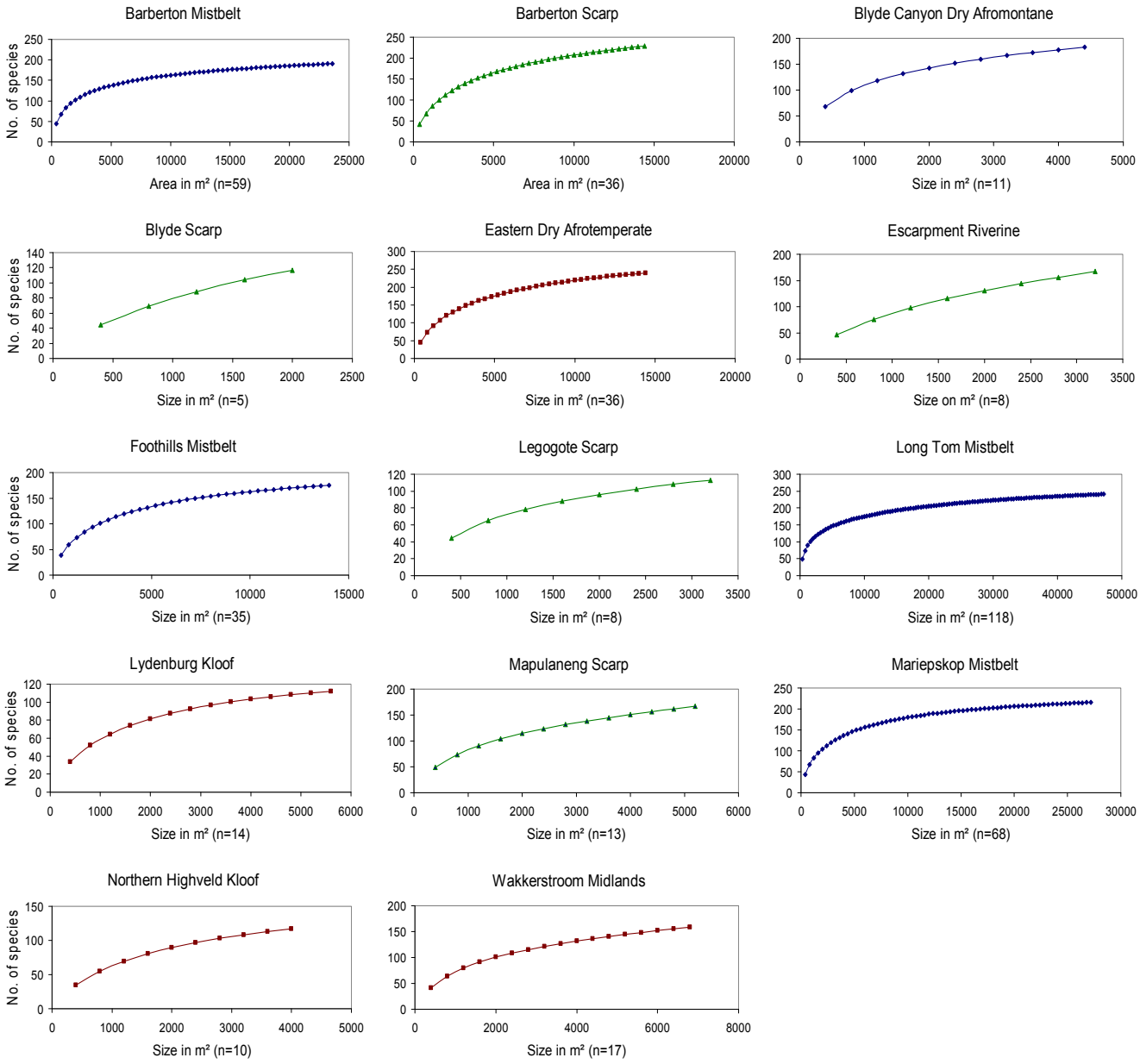


Figure S1 Individual species accumulation curves for each forest subtype showing the averaged species richness on an x-axis based on accumulated plot sizes (each plot 400m²). Colours of lines are based on forest types: blue = Mpumalanga Mistbelt forests; green = Eastern Scarp forests; and Brick red = Northern Highveld forests

CHAPTER SEVEN:

Synopsis and Conclusion

7.1. SYNOPSIS

Systematic conservation planning (SCP) relies fundamentally on spatial information about the distribution of biodiversity (Margules and Pressey, 2000; Rodrigues and Brooks, 2007), which is still very limited. My thesis focuses on the development of appropriate data sets for indigenous forests to ensure their adequate inclusion within a regional SCP so as to contribute towards their conservation. The purpose of my thesis was not to finalise a SCP of the provinces' forests, but to prepare and create the necessary input files and develop explicit quantitative targets for their inclusion within a SCP. Indigenous forests may only form one part of the entire SCP data set, which would typically also include other important data sets and layers from other biomes, such as wetlands or grasslands (Ferrar and Lötter, 2007). Furthermore, for Mpumalanga, indigenous forests only comprise about 0.51% of the land area. Finally, SCP develop over time and require the input of various stakeholders.

To summarise my thesis, in the absence of an appropriate regional-scale forest classification to represent forest biodiversity (forest pattern) in Mpumalanga Province, I first needed to develop a forest classification that could serve as a surrogate for forest biodiversity pattern, based on the identification of forest communities (or subtypes as called in this thesis). A multitude of numerical classification techniques are available to classify plot data and the selection of the most appropriate and rigorous technique required detailed testing and analysis, prior to selection and application to my data set (Chapter 2). Various methods exist to evaluate the relative performance of different numerical classification techniques, such as OptimClass (Tichý et al., 2009) which in my study proved to be particularly efficient in simultaneously assessing 322 different data analytical techniques. The evaluation of appropriate methodology prior to the running of classification algorithms is seldom reported in the literature, yet its usefulness cannot be over emphasised, particularly when the research is applied and the resulting classifications influence conservation actions and policy development.

Since the 1990s, there have been increased demands from the field of nature conservation for comprehensive systems of vegetation classifications as a product to use in conservation planning (Chytrý et al., 2011). In Chapter 3 I applied the most appropriate classification technique to my data set and the resulting classification is presented within the nested hierarchy of the National Forest Classification (von Maltitz et al., 2003). The recognition and circumscription of subtypes is the first necessary step to allow for the conservation of this biome in Mpumalanga Province. The forest subtypes are described in terms of various floristic, growth forms, forest dependency, and leaf retention characteristics.

It is anticipated that these new forest communities also represent communities of other taxonomic groups not yet surveyed. In this sense, forest communities serve as surrogates for other taxonomic groups and that by conserving particular forest communities identified on the basis of their floristic composition, they also conserve a host of other taxonomic groups not yet sampled, such as invertebrates, fungi, rodents and shrews. Biodiversity is too complex to measure directly so conservation planning needs to rely on surrogates for the representation of biodiversity pattern (Lewandowski et al., 2010; Lombard et al., 2003; Rouget et al., 2004). Arponen et al. (2008) conclude in their analysis of various environmental and community-level surrogate approaches that community-level surrogates hold great promise for conservation planning.

The forest subtype classification employed (Chapters 2 and 3) is based on the Bray-Curtis resemblance measure, standardized by sample unit totals. This coefficient can be used to compare the similarity of two samples (see McCune and Grace, 2002), but it can simultaneously be used as a measure of beta diversity, where β diversity is the variation in community structure among a set of sample points (Anderson et al., 2010). The application of Bray-Curtis resemblance and Flexible beta clustering is expected to partition the floristic diversity into homogenous communities which share a similar level of resemblance and diversity. This partitioned floristic biodiversity is a basic requirement for its use in SCP, where the objective is to conserve a representative sample of the biodiversity pattern by means of setting explicit targets.

But biodiversity pattern is easier to define and identify spatially than delineating ecological processes that may vary both spatially and temporally. Ecological processes are exponentially more difficult to include in a SCP. Pressey et al. (2007) warned that planning only for biodiversity pattern is likely to jeopardize the persistence of many processes that require conservation management, yet there has been little progress towards implementing ecological processes into SCP (Groves et al., 2012). More effective conservation planning depends partly on science catching up with our ability to include both pattern and ecological processes (Pressey et al., 2007). Therefore in my thesis I needed to assess and identify the important ecological processes that could be spatially delineated.

In Chapter 4 I first assessed the main ecological and environmental drivers informing the observed variation in forest composition using variation partitioning and ordination. I explored the influence of geographic space and three scales of environmental variables (local, regional, supra-regional) on forest composition, also across all strata (herbaceous, shrub, tree). Semivariogram analyses were used to categorise environmental variables into three scales based on sill, nugget, and range values. Regional scaled variables explained the largest fraction of variation (45%), followed by supra-regional (21%) and local-scaled variables. Geographic space and dispersal were important across all forest strata. This chapter provided insight into the relative contribution of environmental variables and the scale of their influence, and

highlighted the importance of dispersal in explaining forest vegetation patterns in Mpumalanga Province.

In Chapter 5 I assessed dispersal modes and distances, to inform a graph theoretic approach that quantified the connectivity value for each forest patch. Minimum patch distance is informed through a dispersal range ensuring 75% of diaspores can disperse between forest patches. The connectivity analysis and prioritisation of forest patches supports resilience in SCP scenarios.

Finally, in Chapter 6 I needed to set quantitative targets for forest pattern and process features for their inclusion within a SCP. With an overarching goal of ensuring that at least 75% of all species are represented by at least one individual within each forest subtype in a SCP, I utilised the Species Area Relationship (SAR) to determine the slope of the relationship and to estimate the proportion of area required to represent 75% of species. I integrated forest connectivity into pattern targets as a precautionary approach given the vulnerability of naturally disconnected forest patches and the importance of emigration and immigration of plant diaspores in maintaining forest composition across a network of small forest patches. The resulting forest pattern targets ranged between 24.9% and 49.7% for forest subtypes, with a mean value of 34.8%. I also proposed forest process targets for spatially fixed processes, such as the important forest patches supporting connectivity, as well as the spatially flexible buffers around each priority forest patch. Spatially fixed forest process targets are set at 100% and for spatially flexible forest processes the targets are set at 60% of original extent. Finally I highlight the need for design criteria that can assist in developing a framework for prioritising conservation actions based on vulnerability and irreplaceability.

7.2. FUTURE AREAS OF RESEARCH

From this study several further areas of research have been identified.

7.2.1. Validating ability of forest subtypes to serve as surrogates for forest biodiversity

In SCP surrogates can be used as proxies for a broader set of taxonomic groups when the number of species of concern is too great to allow for each to be considered individually (Wiens et al., 2008), or when information on the other taxonomic groups is lacking. The use of surrogate approaches may be correlated with other taxonomic groups, but this is not always the case (Arponen et al., 2010; Rodrigues and Brooks, 2007; Wiens et al., 2008).

Planners assume that conservation efforts made to protect the biodiversity features explicitly incorporated in a SCP exercise are also effective for the conservation of unmapped biodiversity, where they hope that the known biodiversity is a good surrogate for the unknown (Rodrigues and Brooks, 2007). Critics argue that the assumption that management of surrogates will adequately address the factors that enhance or threaten the persistence of individual species is unfounded, or that the effectiveness of the approaches has not been

rigorously tested (Wiens et al., 2008). Further research that looks at the ability of the subtype classification to serve as a surrogate for other taxonomic groups is encouraged.

7.2.2. Ecological processes

Ensuring the persistence of forest biodiversity by means of identifying important ecological processes within SCP ultimately relies on the inclusion of additional ecological processes other than dispersal and connectivity. Dispersal was identified in my thesis as a very important regional ecological driver supporting and maintaining forest species composition, particularly among the smaller forest patches, but there are several other ecological processes that can also be incorporated into SCP in addition to dispersal. Few studies have explored incorporating large-scale ecological processes into SCP (Klein et al., 2009) or studied the viability or effect of various ecological processes on forests. For example, the study undertaken by Kotze and Lawes (2007) who studied the viability of various processes in small forest patches, such as seed and egg predation as well as regeneration in small forest patches. From studies like these spatially explicit processes can be identified for inclusion into SCPs. Some of the ecological processes particular pertinent to forests in SCPs include: forest edge disturbance; litter and dung decomposition for the quick release of nutrients (Lawes et al., 2007); clusters of forest patches embedded within a largely natural vegetation matrix (Ferrar and Lötter, 2007); riverine corridors (Cowling et al., 2003); and disturbance events (Drechsler et al., 2009). Ecological processes also occur at a variety of scales, such as decomposition and disturbance at fine/local scales while others occur at larger scales, such as seasonal altitudinal migration of birds. I recommend that additional forest processes and their surrogates occurring in Mpumalanga be investigated and assessed for possible incorporation into future SCP processes, such as forest edge to core ratios, fragment size and richness, altitudinal migration, etc..

7.2.3. Mapping forest types

Determining the main environmental drivers influencing species composition (Chapter 4) also enables the identification of key environmental variables that could be used in statistical species distribution models (SDMs) to predict the potential distribution of vegetation units (Guisan and Zimmermann, 2000). SDMs statistically relate the geographical distribution of species or communities to their present environment. The quantification of such species–environment relationships represents the core of predictive geographical modelling in ecology. Several models exist that are generally based on various hypotheses as to how environmental factors control the distribution of species and communities (Guisan and Zimmermann, 2000). The MaxEnt model (Phillips et al., 2006) appears to be widely supported in the literature as a consistently competitive model and performs well in comparative tests (Elith et al., 2006).

Guisan and Zimmermann (2000) report that from a mechanistic point of view, it is desirable to predict the distribution of biotic entities on the basis of ecological parameters that are believed to be the causal, driving forces for their distribution and abundance. The assessment of drivers contributing towards species variation determined by means of CANOCO analysis (ter Braak and Šmilauer, 2002; Chapter 4) would be useful to inform the selection of environmental variables to be used in SDMs. The usefulness of SDMs would enable the identification and classification of forest patches previously not sampled according to the new forest subtype classification, as only 4% of the forest patches occurring within Mpumalanga were surveyed. The use of SDMs would be a more rigorous approach to classify all forest patches, estimated at around 1914 patches in Mpumalanga (Lötter, 2013), using MaxEnt or similar SDM methodology.

7.3. CONCLUDING REMARKS

7.3.1. Contribution towards science

In Chapter 2, the application of a framework for assessing the most robust classification technique to a particular data set highlights the historic single-minded application of the TWINSPAN approach to vegetation classification (Hill, 1979), particularly in South Africa. TWINSPAN remains globally popular (Roleček et al., 2009) despite the numerous criticisms this technique has rightly received (Belbin and McDonald, 1993; McCune and Grace, 2002; van Groenewoud, 1992). The framework that I propose is new, it highlights the misapplications of many techniques, it builds on existing techniques for assessing classification output, and it will hopefully be used to inform the selection of appropriate numerical classification techniques into the future. The results of this chapter have both national and international application.

In Chapter 3, the presentation of the new detailed subtype classification is new for South Africa. The combination of a thorough taxonomic and physiognomic description for forest subtypes is new, but the application is primarily of national and provincial interest. The proposed forest subtype classification will be submitted to the National Vegetation Map Committee, a committee established to review and accept changes to the National Vegetation Types, for review and incorporation of proposed subtypes into the national hierarchy. It will simultaneously be incorporated into the vegetation classification for Mpumalanga Province (coordinated by the Mpumalanga Tourism & Parks Agency) for use in the revision of their systematic conservation plan, locally known as the Mpumalanga Biodiversity Sector Plan (MBSP). The benefit of the proposed classification can be summarised as providing a complete forest classification accurate at a regional scale which categorises forest biodiversity into floristic forest subtypes that are spatially discrete. Prior to this study forest classifications were either very localised for a particular forest or group of forests in an area, or at a much broader national scale where 82% of all forests in Mpumalanga are classified as Mpumalanga Mistbelt Forest (von Maltitz et al., 2003: Mucina et al., 2006).

In Chapter 4, the application of semivariogram analyses to categorising the scale of environmental variables is new to vegetation science. Geostatistics has occasionally been used but my application of semivariogram analysis furthers its utility and provides a more robust method of assessing the scale of variability in environmental variables. Furthermore, the analysis of three scales (local, regional, and supra-regional) and geographic space within the process of variation partitioning is a new approach in vegetation science to interpret vegetation pattern.

In Chapter 5, my particular application of graph theory to directly inform ecological processes for use in a SCP is new. However, the major advance in science has been the application of connectivity metrics to a community of species (forest communities), instead of the traditional approach of applying connectivity metrics to single species. Minimum patch distance was informed by the ability for 75% of the diaspores to disperse to the next nearest forest patch.

In Chapter 6, the application of species area relationships to determine quantitative conservation targets is not new. However I present visual methods for assessing quality of input data and a method for circumventing small sample sizes. I also integrate forest connectivity into pattern targets as a precautionary approach given the vulnerability of naturally disconnected forest patches and the importance of emigration and immigration of plant diaspores in maintaining forest composition across a network of small forest patches.

7.3.2. Conclusion

The complex and occasionally nuanced variation in Mpumalanga's indigenous forests has been successfully deciphered and circumscribed in this thesis to represent forest pattern. The importance of dispersal as a forest process, critical amongst small forest patches, is highlighted and used to support persistence of biodiversity pattern. Persistence is also ensured through the development of explicit quantitative pattern and process targets.

The identification of appropriate forest pattern and certain process features now allows for their incorporation within SCPs, as well as in other conservation management processes. Their inclusion within the Mpumalanga SCP, known now as the Mpumalanga Biodiversity Sector Plan (Lötter, 2013), will contribute towards their conservation by means of appropriate governance and land-use planning tools and processes.

REFERENCES

Anderson, M.J., Crist, T.O., Chase, J.M., Vellend, M., Inouye, B.D., Freestone, A.L., Sanders, N.J., Cornell, H.V., Comita, L.S., Davies, K.F., Harrison, S.P., Kraft, N.J.B., Stegen, J.C., Swenson, N.G., 2010. Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist. *Ecology Letters* 14, 19–28.

Arponen, A., Moilanen, A., Ferrier, S., 2008. A successful community-level strategy for conservation prioritisation. *Journal of Applied Ecology* 45, 1436–1445.

Belbin, L., McDonald, C., 1993. Comparing three classification strategies for use in ecology. *Journal of Vegetation Science* 4, 341–348.

Chytrý, M., Schaminée, J.H.J., Schwabe, A., 2011. Vegetation survey: a new focus for Applied Vegetation Science. *Applied Vegetation Science* 14, 435–439.

Cowling, R.M., Pressey, R.L., Rouget, M., Lombard, A.T., 2003. A conservation plan for a global biodiversity hotspot: the Cape Floristic Region, South Africa. *Biological Conservation* 112, 191–216.

Drechsler, M., Lourival, R., Possingham, H.P., 2009. Conservation planning for successional landscapes. *Ecological Modelling* 220, 438–450.

Elith, J., Graham, C.H., Anderson, R.P., Dudík, M., Ferrier, S., Guisan, A., Hijmans, R.J., Huettmann, F., Leathwick, J.R., Lehmann, A., Li, J., Lohmann, L.G., Loiselle, B.A., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., Overton, J. McC. Peterson, A.T., Phillips, S.J., Richardson, K.S., Scachetti-Pereira, R., Schapire, R.E., Soberón, J.,Williams, S., Wisz, M.S., Zimmermann, N.E., 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29, 129–151.

Ferrar, A.A., Lötter, M.C., 2007. *Mpumalanga Biodiversity Conservation Plan Handbook*. Mpumalanga Tourism & Parks Agency, Nelspruit.

Groves, C.R., Game, E.T., Anderson, M.G., Cross, M., Enquist, C., Ferdaña, Z., Girvetz, E., Gondor, A., Hall, K.R., Higgins, J., Marshall, R., Popper, K., Schill, S., Shafer, S., 2012. Incorporating climate change into systematic conservation planning. *Biodiversity and Conservation* 21, 1651–1671.

Guisan, A., Zimmermann, N.E., 2000. Predictive habitat distribution models in ecology. *Ecological Modelling* 135, 147– 186.

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

Klein, C.J., Wilson, K.A., Watts, M., Stein, J., Berry, S., Carwardine, J., Smith, M.S., Mackey, B.G., Possingham, H.P., 2009. Incorporating ecological and evolutionary processes into large–scale conservation planning. *Ecological Applications* 19, 206–217.

Kotze, D.J., Lawes, M.J., 2007. Viability of ecological processes in small Afromontane forest patches in South Africa. *Austral Ecology* 32, 294–304.

Lawes, M.J., Adie, H., Eeley, H.A.C., Kotze, D.J., Wethered, R., 2007. An assessment of the forests of the Maloti-Drakensberg transfrontier bioregion, with reference to important ecosystem processes. Forest Biodiversity Research Unit, School of Biological and Conservation Sciences, University of KwaZulu-Natal. URL: http://www.ukzn.ac.za/Biology/1156.aspx.

Lewandowski, A.S, Noss, R.F., Parsons, D.R., 2010. The effectiveness of surrogate taxa for the representation of biodiversity. *Conservation Biology* 24, 1367–1377.

Lombard, A.T., Cowling, R.M., Pressey, R.L., Rebelo, A.G., 2003. Effectiveness of land classes as surrogates for species in conservation planning for the Cape Floristic Region. *Biological Conservation* 112, 45–62.

Lötter, M.C., 2013. *Technical Report for the Mpumalanga Biodiversity Sector Plan* – MBSP 2013. Mpumalanga Tourism & Parks Agency, Nelspruit.

Margules, C.R., Pressey, R.L., 2000. Systematic conservation planning. *Nature* 405, 243–253.

McCune, B., Grace, J.B., 2002. *Analysis of Ecological Communities*. MjM Software, Gleneden Beach, OR.

Mucina, L., Geldenhuys, C.J., Rutherford, M.C., Powrie, L.W., Lötter, M.C., von Maltitz, G.P., Euston-Brown, D.I.W., Matthews, W.S., Dobson, L., McKenzie, B., 2006. Afrotemperate, subtropical and azonal forests, in: Mucina, L., Rutherford, M.C. (Eds.), *The vegetation of South Africa, Lesotho and Swaziland*. pp. 584–615. South African National Biodiversity Institute, Pretoria.

Phillips, S.J., Anderson, R.P., Schapire, R.E., 2006. Maximum entropy modelling of species geographic distributions. *Ecological Modelling* 190, 231–259.

Pressey, R.L., Cabeza, M., Watts, M.E., Cowling, R.M., Wilson, K.A., 2007. Conservation planning in a changing world. *Trends in Ecology and Evolution* 22, 582–592.

Rodrigues, A., Brooks, T., 2007. Shortcuts for biodiversity conservation planning: the effectiveness of surrogates. *Annual Review of Ecology, Evolution, and Systematics* 38, 713–737.

Roleček, J., Tichý, L. Zelený, D., Chytrý, M., 2009. Modified TWINSPAN classification in which the hierarchy respects cluster heterogeneity. *Journal of Vegetation Science* 20, 596–602.

Rouget, M., Reyers, B., Jonas, Z., Desmet, P., Driver, A., Maze, K., Egoh, B., Cowling, R.M., Mucina, L., Rutherford, M.C., 2004. South African National Spatial Biodiversity Assessment 2004: *Technical Report. Volume 1: Terrestrial Component*. South African National Biodiversity Institute, Pretoria.

ter Braak, C.J.F., Šmilauer, P., 2002. *CANOCO Reference manual and CanoDraw for Windows User's guide: Software for Canonical Community Ordination (version 4.5).* Microcomputer Power, Ithaca, NY, US.

Tichý, L., Chytrý, M., Hájek, M., Talbot, S., Botta-Dukát, Z., 2009. OptimClass: Using species-to-cluster fidelity to determine the optimal partition in classification of ecological communities. *Journal of Vegetation Science* 21, 287–299.

van Groenewoud, H., 1992. The robustness of Correspondence, Detrended Correspondence, and TWINSPAN Analysis. *Journal of Vegetation Science* 3, 239–246.

von Maltitz, G., Mucina, L., Geldenhuys, C.J., Lawes, M., Eeley, H., Aidie, H., Vink, D., Fleming, G., Bailey, C., 2003. Classification system for South African indigenous forests. An objective classification for the Department of Water Affairs and Forestry. Report ENV-P-C 2003-017. Environmentek, CSIR, Pretoria.

Wiens, J.A., Hayward, G.D., Holthausen, R.S., Wisdom, M.J., 2008. Using Surrogate Species and Groups for Conservation Planning and Management. *BioScience* 58, 241–252..