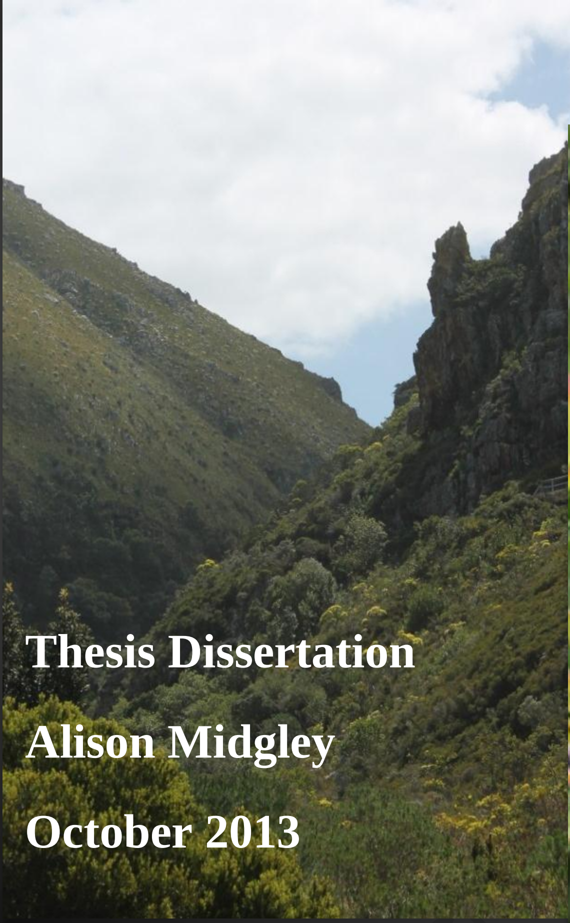
The Many forms of thirst: Investigating Forest Constraints in the Cape Floristic Region



Thesis Dissertation

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Abstract:

Identifying the primary determinants of forest distribution has been a considerable challenge for ecologists. Although focus was traditionally directed towards climatological variables, predictive models showed that suitable forest conditions were far more extensive than the actual forest distribution. This study investigated the primary constraints of forests in the Cape Floristic Region (CFR), in South Africa. Based on a study by Lehmann et al. (2011) on savanna ecosystems, it was hypothesised that seasonal drought and moisture balance were more likely to limit forest distribution than broader rainfall patterns. The biomes of the CFR were mapped using Mucina & Rutherford's (2006) vegetation map. Environmental data was extracted from Schulze (2007) and analysed using various statistical methods and the effective rainfall during the wet and dry seasons was examined in relation to vegetation patterns. As a complementary analysis, high resolution spatial data was extracted from the Worldclim database (www.worldclim.org) and run in the program Maximum Entropy. The presence of forest was shown to be constrained by soil moisture deficits in the driest half of the year. However there was considerable overlap of climactic and edaphic conditions across the different biomes. It was suggested that seasonal drought may play an indirect rather than direct role in shaping vegetation type. As the length of the dry season correlated with the length of the dry season, it was determined that seasonal drought may effect vegetation by promoting landscape-shaping fires. These findings have implications for predicting and understanding historical and future ecosystem shifts and their relationship with global and local climate change.

Introduction

Worldwide, closed forest patches have been documented within fire-dependent, sclerophyllous shrubland. The resulting vegetation mosaics have been recorded in Africa (Lehmann et al. 2011), South America (Hoffman et al. 2009), Australia (Warman & Moles, 2009), India (Puyravaud et al. 2003), California (Cowling et al. 1996) and New Caledonia (Ibanez et al. 2003). Similarly, in the Cape Floristic Region (CFR), South Africa, conspicuous forest communities form sharp boarders with the largely tree-less fynbos (Manders et al. 1992). Despite their widespread distribution, the environmental factors that limit their expansion are, to this day, heavily contested. This study aims to investigate the environmental variables that determine forest distribution in the Cape Floristic Region. Although understanding the multiple interacting variables that govern vegetation change at their boundaries is a challenge, there is much to gain from unravelling these variables. Forests are ecologically and economically valuable (Shackleton et al. 2007), and an understanding of the processes that determine their distribution can provide insight into the causes of past, present and future ecosystem change. This is particularly relevant given the uncertainty of ecosystem trajectory in response to global climate change.

Overview of the contemporary and historical context of the Cape Floristic Region

The Cape Floristic Region covers 90 000 km^2 at the southern tip of Africa. It is dominated by fire-prone, sclerophyllous fynbos shrubland (56%), which is characteristic of the Mediterranean-type climates (warm, dry summers and cold, wet winters). Mean annual precipitation ranges from 60 to 3345 mm, although rainfall is more evenly distributed in the east (Mucina & Rutherford, 2006, Schulze, 2007).

Contemporary forests in the Cape Floristic Region occur in a few highly fragmented patches (often smaller than 0.1 km^2) along the coastal platforms and river valleys within the larger biomes of Fynbos, Grassland, Albany Thicket and Savanna (Mucina & Rutherford, 2006, Moll et al. 1984). They are generally found from 22°40’S in the north, to 27°S in the east and to approximately 34°S in the west (Mucina & Rutherford, 2006). Despite their patchy distribution, the CFR holds the largest single forest patch in South Africa (257 km^2), the Knysna forest (Mucina & Rutherford, 2006). Indigenous forests are defined by closed, multi-layered vegetation that form part of the Afromontane or Southern Coastal Forest belt (Shackleton et al. 1999). Albany thicket, which is a dry, closed shrubland, has been recently redefined as a separate biome from forests (Cowling et al. 2005).

Current forest patches are believed to be ancient remnants of more extensive subtropical forests, which decreased at the onset of global cooling and aridification in the Pliocene (Cowling et al. 1996). This is evident from Paleo-ecological evidence of shared taxa between patches of afrotemperate and coastal forests (Mucina & Rutherford, 2006). Fluctuations between forest cover and dry, sclerophyllous vegetation are hypothesised to be linked to hyperthermal and hypothermal climatic periods. The former was characterised by warm, wet conditions and forest expansion, the latter characterised by drier, cooler climates and forest reduction (Eeley et al. 1999). Sclerophyllous shrubland is believed to have expanded after development of seasonal Mediterranean climates during the Quaternary (Cowling et al. 1996). Fire probably became a more influential in shaping vegetation patterns during this period. Thus, extant vegetation in the CFR is largely comprised of relic forests and recent drought and fire adapted species (Cowling et al. 2005)

Forests, Thicket and Fynbos biomes are described as alternative ecosystem states, which refer to the strikingly different species composition, structure and functions of these biomes, despite occurring within the same landscape and under similar environmental conditions (see: Fig. 4) (Manders, 1991, Warman & Moles, 2009). For example, fynbos species have regenerative biologies that depend on fire for germination or resprouting, and establish from soil or canopy-stored seed banks in the period after a fire (Cowling et al. 1997, Manders, 1990). In contrast, forest species rarely burn, and persist through fire cycles, and resprout from fleshy, vertebrate-dispersed propagules during fire intervals (Manders, 1990; Cowling et al. 1997). Thicket is long-lived and able to resprout after and between disturbances, while propagules are dispersed by local fauna (Cowling et al. 1997). Although the interactions between these stable states have been recognised by several studies (e.g. Warman & Moles, 2009) this study focusses primarily on the abiotic factors that establish forests in the fynbos individually.

The environmental conditions in the Cape Floristic Region are highly variable, and the region is characterised by its phenomenal floristic biodiversity (Forest et al. 2007, Rouget et al. 2003). This presents a unique opportunity from which to analyse the key determinants of vegetation patterns across variable environmental conditions, and determine how fluctuating environmental conditions may alter vegetation type.

Determining the environmental influences of forest distribution

Traditionally, patterns of vegetation were believed to be broadly correlated with climate (particularly temperature and moisture) (Staver et al. 2011), while soil nutrients (particularly phosphorus) were considered influential on a local scale (Bond et al. 2003, Cramer, 2010). Water availability, in particular, is recognised as a common limiting factor for tree and seedling growth (Cowling et al 2004). Mean annual precipitation (MAP) is often measured to estimate an upper limit (or threshold) of the vegetative potential (or biomass production) of a region, in the presence of adequate light, nutrients, topography and temperature (Cowling et al. 2004). Minimum moisture thresholds for forests have been quoted to range from 500 mm in certain winter rainfall areas (Geldenhuys, 1994a), to 700 mm in summer rainfall areas (Mucina & Rutherford, 2006). However, total annual precipitation is not the only important attribute for limiting forests: seasonality and inter-annual variability of rainfall have also been identified as important (Cowling et al. 2004).

In South Africa, indigenous forests only cover 0.1% of the land (Eeley et al. 1999). However, over 7% of South Africa, including most of the fynbos, is estimated to have suitable climate and substrate for colonisation by afrotemperate forests (Mucina & Rutherford, 2006; Manders & Richardson, 1992; Bond et al. 2003). In fact, mesic shrubland or grassland communities, as in the CFR, often dominate areas that are more suitable for forests climatologically, topographically and edaphically (Staver et al. 2011; Bond, 2008). This has been one of the major flaws in attributing forests to climatic factors, as is apparent from the occurrence of distinct forest-fynbos communities in close proximity and on soils of the same geological composition (see: Fig. 1) (Muscina & Rutherford, 2006; Cramer, 2010). Consequently, several alternative hypotheses have attempted to explain the abrupt boundaries between closed, indigenous forests and pyrophytic (fire-dependent) fynbos. Examples include the clearing of forest by man (e.g. Ibanez et al. 2003), the presence of fire (e.g. Bond, 2005), topography (e.g. Geldenhuys, 1994a) and niche construction (e.g. Day, 2003).

The role of soil nutrients (particularly phosphorus) in the creation/maintenance of the forest-fynbos-boundary, has also been intensely debated. Forests have been found to persist on more nutrient-rich soils (particularly in phosphorus) than fynbos if derived from the same substrate (see also: Manders, 1991, Hoffman et al. 2009). One explanation for this is that frequent fynbos fires mobilise nutrients, exporting them from fynbos soils through leaching, volatalisation or ash loss. Forests, which are rarely penetrated by fire, thus trap organic and inorganic matter, collecting resources (nutrients, water) from deep within the soil (Hoffman et al. 2009; Cramer, 2010). This has been labelled “niche differentiation” (see: Day et al. 2003). Soil nutrients have been used to explain distinct boundaries between forest and fynbos communities where neither topographic nor fire-related disturbances are clear (Bond, 2008).

However, not all forest-fynbos boundaries occur across geological boundaries, and studies around the world show that such vegetation boundaries are constantly shifting (Warman & Moles, 2009) and that forests and thicket can colonise nutrient-poor fynbos soils when fire intervals exceed 50 years (Manders et al. 1992). Savannas are also known to occur on both nutrient poor soils and those suitably nutrient-rich for forest persistence (Bond, 2008). In the CFR, the persistence of forests on different geological substrates and soil depths (from deep soils to shallow, rocky soils) has been recorded by several studies (Geldenhuys, 1994a; Manders, 1991; Mucina & Rutherford, 2006). Patterns of effective rooting depth for forest species, such as *Pinus*, have also been shown to vary between patches (Geldenhuys, 1994a).

Also, the active role that vegetation plays in altering soils itself is often overlooked (e.g. through the deposition of nutrient-rich leaf litter) (Warman & Moles, 2009). Thus, soil nutrient differences between forest and fynbos may be the result, rather than the source of forest/fynbos boundaries.

The existence of savannas where forest should be has also been attributed to the clearing and burning of forests by humans (Bond, 2008). While it is true that anthropogenic impacts have severely affected the extent of forests in some savannah regions, the Paleo-record (for example, charcoal evidence from the Tswaing crater and pollen cores) indicates that forests were even more sparsely distributed during the Last Glacial Maximum, before the establishment of pastoralists (Bond et al. 2003). The archaeological record (based on the frequency of hearths) indicates that the domestic use of fire in South Africa commenced at least a hundred thousand years ago, while grasslands began their expansion millions of years prior (Bond & Midgley, 2003).

The potential importance of fire in limiting the distribution of forests in the CFR was addressed by Geldenhuys, (1994a), who postulated that, while climatic and edaphic thresholds determine the potential for forest distribution, disturbance factors such as fire and herbivory delineate actual forest boundaries. Geldenhuys (1994a) studied Afrotemperate forests in the Knysna forest, and found that forests persisted in topographic shadow areas. These areas are sheltered from hot, desiccating Berg winds that are associated with high frequencies of severe fire. It was thus suggested that the shelter provided by the topographic configuration of the plateau, escarpment and coastal plain, and the severity of fire was a more accurate determinant of current forest boundaries than climate or substrate.

Indeed, forest patches within the fynbos are often sheltered from fire within ravines, stream banks, boulders and on patches of rock scree (Manders, 1991, personal observation, see: Fig. 2). These areas serve as microclimates, providing dual protection from fire while reducing the evapotranspiration, and are often situated over landscape drainage lines that provide moisture to forest species (Cramer, 2010; Manders, 1991). Topographic protection from fire is often vital for tree seedlings, as forests are often excluded where fire-return intervals are too frequent, and seedling growth rates are limited by available nutrients (Bond, 2010).

The impacts of fire on the distribution of forests have been well recorded throughout African savannas and fynbos shrublands (e.g. Sankaran et al. 2005; Bond et al. 2008; Manders, 1991; Archibald et al. 2009). Bond et al. (2003) used a Dynamic Global Vegetation Model (DGVM) to simulate vegetation responses to fire as well as climatic and edaphic variables. The simulations suggested that, if climate was the primary determinant of forest distribution, forests should cover over double their current extent. However, on the inclusion of fire in the model, the simulations matched actual forest distribution more accurately.

The length and intensity of seasonal drought as a factor limiting forest distribution has also been investigated in both experimental (Hoffman et al. 2004) and correlative studies (Bowman & Murphy, 2012; Lehmann et al. 2012). Seasonal drought has been shown to severely constrain forest productivity; altering both tree growth and transpiration rates (Breda et al. 2006). Lehmann et al. (2011), for example, examined possible drivers of savannah/non-savanna (forest) including effective rainfall (the difference between monthly evapotranspiration and monthly rainfall), rainfall seasonality, soil fertility and topographic complexity through a series of statistical analyses, including regression tree modelling. They found that forests in mesic savannas were constrained by low effective rainfall and high rainfall seasonality, while soil was only regionally important. Lehmann et al. (2011) showed that dry season duration greater than 5 months was correlated with the distribution of savannas across three continents, in the Southern Hemisphere. They argued that rainfall seasonality indirectly affected forest distribution, by influencing fire frequency and the ability of forest patches to resist fires. Forests accounted for one fifth of all sample sites across the entire climate gradient, which meant that long dry seasons did not directly constrain forest.

Similarly, Murphy & Bowman (2012) used satellite-derived data for tree cover to investigate forest-savanna boundaries in South Africa, Australia and South America. The best predictor of forest cover was found to be an approximation of soil water content (%) during the six driest consecutive months. This was effectively a measure of monthly soil water budget, based on inputs of monthly rainfall and potential evapotranspiration at the assumed soil depth of 2 meters (see: Trabucco et al. 2008). This measure was found to be a superior indicator of seasonal drought than annual rainfall.

Objectives and Aims of the current study

This dissertation aims to identify what limits forest distribution in the fynbos biome in the CFR, considering the multiple possible key determinants suggested in previous literature. The analysis grouped the vegetation of the CFR into Afrotemperate forests, Fynbos shrublands and Albany thickets, and compared them as separate ecological communities. The conclusions drawn from the savannah-based studies of Lehmann et al. (2011) and Murphy & Bowman (2012) were used as a baseline reference for this study. Thus, although forests are often seen as indicators of a climate with high rainfall, it was hypothesised that climate seasonality, or more specifically, the duration and severity of the dry season may be more important than edaphic and climatological factors in limiting forests.

The principal objectives of the study are to:

1. Systematically isolate the most important environmental variables influencing forest distribution and to develop a predictive model of forest distribution in the CFR.

2. Investigate the relationship between different vegetation types and their environmental conditions using different correlative statistical analyses.

Considering the strikingly different life histories and relationships to fire of the plant communities within the Fynbos, Thicket and Forest biome, it is hypothesised that the distribution of forests in the CFR may, like savannas, be only indirectly determined by climate. In areas where weather conditions increase the frequency of fire, such as a long dry season, forests may be excluded from fynbos, due to their sensitivity to disturbance and moisture stress. If this were the case, Mediterranean-type climates would more likely determine the fire regime of an area and, in turn, indirectly affect the distribution of characteristic fynbos shrubland.

Multivariate statistical analyses were used to provide correlative evidence for the importance of environmental variables emphasised in previous studies. Forest species occurrence records, Geographic Information System (GIS) environmental layers (including bioclimatic, edaphic and topographic layers) and the Maximum Entropy distribution modelling approach (Phillips et al. 2006) to predict forest distribution in the CFR. Although humans have undoubtedly altered indigenous forest distribution in the CFR, the focus of this study remains on the natural determinants of forest distribution, and so human impacts are largely excluded.

Materials and Method

Data Collection and Preparation

Data collection for this study commenced in April 2013 at the South African National Biodiversity Institute (SANBI), Western Cape with the aid of Ms. Danni Guo (see: Acknowledgements). The distribution of different biomes within the Cape Floristic region was mapped on Quantum GIS ver. 1.8.0., using the vegetation map from Mucina & Rutherford’s (2006) *Vegetation of South Africa, Lesotho and Swaziland.* The vegetation biomes were grouped into “forest”, “thicket” and “fynbos”. Strandveld, which is a low, closed indigenous forest type, dominated by broad-leaved shrubs or small trees was included in forest samples (see: Fig 4). These vegetation types were treated separately in this analysis, although many of the component species overlap within the greater structural mosaic of the landscape at ground level (Mucina & Rutherford, 2006).

Thereafter, random sample points were selected from within each biome of the vegetation map by Ms. Guo and myself: 598 data points from the fynbos biome, 200 data points from the thicket biome and 339 from the forest biome. The number of sampling points per biome was restricted by the relative scarcity of forests and thicket patches compared to forest. Fig. 4 shows the distribution of sample points over the CFR compared to actual biome distribution.

Environmental data for the Cape Floristic Region was then compiled from the *South African Atlas of Agro-hydrology and Climatology* (Schulze’s 2007) for each sample point in the dataset. Geological data for each biome was provided by the Council of Geoscience, Pretoria. This dataset included variables of importance for biome-type, predominantly identified from other studies: terrain morphology, altitude and relative relief (Geldenhuys, 1994), fire frequency, or fire interval (Staver et al. 2011), soil type (or geology) (Manders, 1991), seasonality of rainfall and effective rainfall (Lehmann et al, 2011), plant available water and seasonal means of solar radiation, temperature ranges, evapotranspiration and median rainfall. Mean annual precipitation (MAP) in the CFR is highly variable, thus yearly averages are easily inflated by few, extreme events (Schulze, 1997), especially in drier areas. Median rainfall is a more representative measure of rainfall, despite having slightly lower absolute values than MAP. The list of chosen variables, their sources and/or method of collection, are included in Table A1.

In this study, seasons were defined as summer (December, January, February), spring (September, October, November), autumn (March, April, Map) and winter (June, July, August). In order to incorporate a measure of moisture balance for the driest half (September to February) and wettest half (March to August) of the year, (following Lehmann et al. 2011), effective rainfall was calculated by subtracting the mean potential evapotranspiration (PET) from the median rainfall (MAP). Potential evapotranspiration, the sum of evaporation and plant transpiration, directly controls water fluxes along the soil-tree-atmosphere continuum and transpiration is the driver behind internal water transfer within the plant (Breda et al. 2006).

The FAO Penman Monteith method was used to derive PET, which is standardised based on the evapotranspiration of a reference crop, in good conditions, more specifically, well watered grass, 12 cm in height, a surface resistance of 70 s/m and an albedo of 0.23 (Allan et al. 2006).

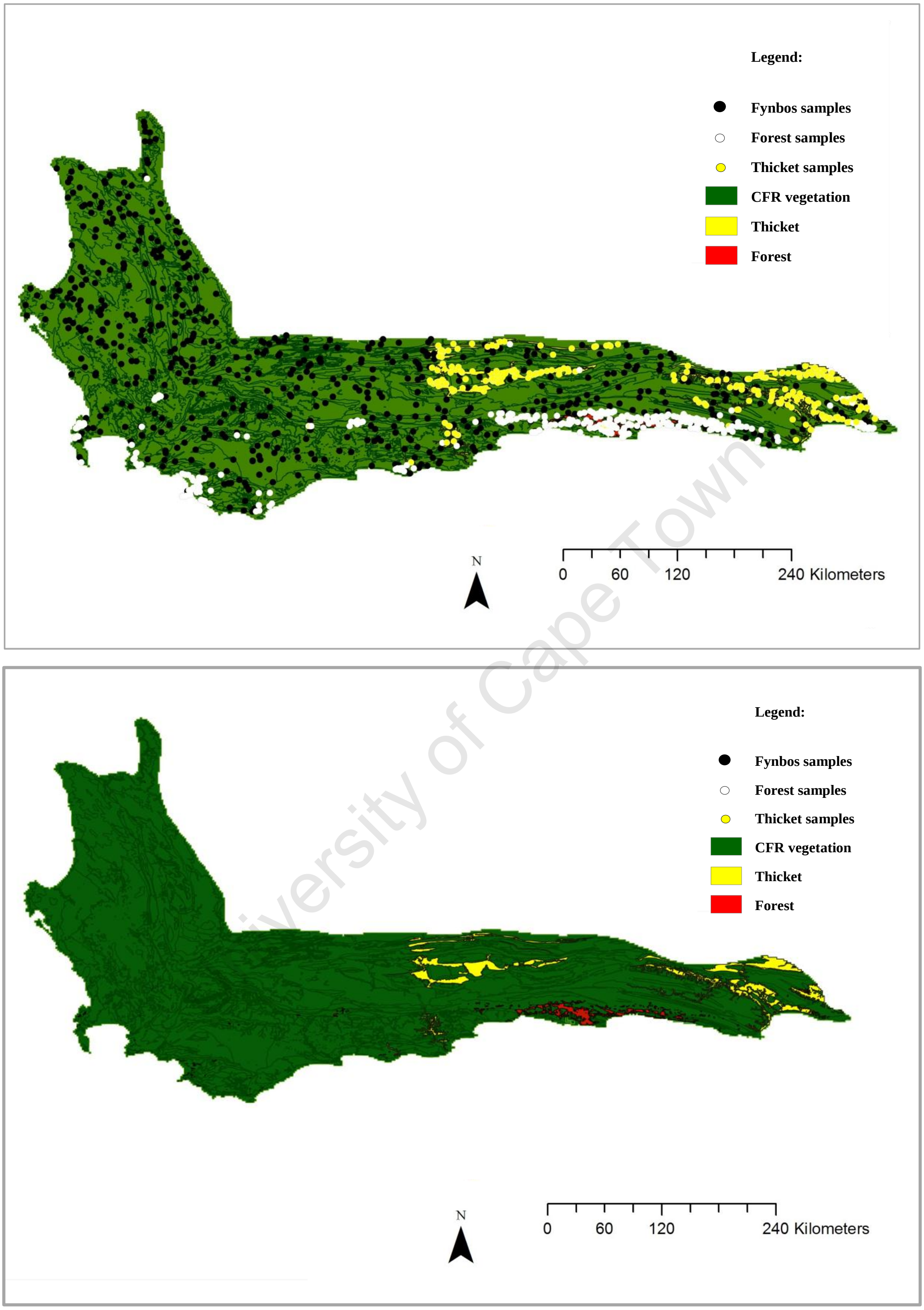

FIGURE 4 (A) Map of the Cape Floristic Region showing the points sampled in the study: 598 data points were chosen from the fynbos biome (black points), 200 data points from the thicket biome (yellow points) and 339 from the forest biome (white points). The yellow areas are dominated by thicket, while the red areas are dominated predominantly by forest [Quantum GIS]. **(B):** Map of actual forest and thicket distribution in the Cape Floristic Region [Data source: Mucina & Rutherford, 2006).

Species Distribution Modelling with Maximum Entropy

Multivariate analyses were used to investigate patterns within the data. A Principal Components Analysis (PCA) was done using the statistical software Statistica ver. 8. The PCA was originally done in R, (see: Acknowledgments) and compared to the PCA in Statistica ver. 8. Although differences were minimal, Statistica results were used in the report.

Principal Components Analysis

The Principal Components Analysis is a correlation analysis that determines linear relationships linear relationships between multiple co-varying environmental variables (Schlens, 2005). Principal Component Analyses summarise all variations for many different sample points in the study area. The two primary principal components derived from the analysis were plotted on a Cartesian plain, allowing for investigation of variable spatial patterns and correlations. Variables that had high factor loadings with the principal components (R>0.9) were kept, while others were excluded. Rainfall was grouped into median rainfall in the driest and wettest halves of the year, as done for effective rainfall, as Mediterranean seasonality can be variable and thus is best analysed over half years instead of monthly periods. The Principal Components Analysis (PCA) was run several times to analyse correlations between various variables. Variables that showed weak correlations to other variables or were consistently uncorrelated were excluded. The final PCA presented in Fig. 5 represents the analysis that accounted for the most variation within samples. The factor scores were used to plot where the vegetation samples clustered along the linear axes of the environmental variables.

Classification tree modelling

A classification tree was modelled in Statistica ver. 8., to explore how environmental data is correlated with forest distribution. The Classification Tree recursively partitions data into sub-sets (or nodes) that are increasingly more similar (Lehmann et al. 2011). It classifies data into categories (forest, thicket and fynbos) by identifying split conditions that decrease the deviations at each sub-set, forming a tree structure. These split conditions are accommodating to non-linear relationships and the model is applicable for both categorical and continuous variables. The Classification Tree was used to isolate particular variables of importance amongst: seasonal rainfall and effective rainfall per driest and wettest halves of the year and values for solar radiation, evaporation and morphology. Geology was excluded from the Classification analysis as significantly more forest samples occurred on “mixed substrates” than other vegetation points. (i.e. fynbos: 6 samples, thicket: 0 samples, forest: 340 samples). The individual permutations of each environmental variable were tabulated, as they provided insight into the importance of different explanatory variables.

Using Maximum Entropy

Given the wide range of studies emphasising the contribution of different variables on forest distribution, another method of analysis was also used to compare results. Thus, a comparative dataset was collected for input into a Maximum Entropy analysis. Maximum Entropy, or Maxent, Ver. 3.3.3k (http://www.cs.princeton.edu/~schapire/maxent/), is a powerful machine-learning based program developed by Phillips et al. (2006) that uses geospatial data to make predictions about the potential distribution of a given species (i.e. where conditions are optimal, even if there is no records of it in the area), based on its current distribution. Maxent has been found to perform best amongst many different modelling methods (Kumar & Stohlgren, 2009; Elith et al. 2011). It has also been shown to remain effective in cases where there are small sample sizes. Maxent uses presence-only data (as opposed to presence-absence data) which is useful in the case of forests, as they are highly fragmented and most patches are too small to be mapped.

Data was prepared for Maxent by following the procedures of Nielsen (2012), using the program ArcGIS in the Geospatial laboratory, University of Cape Town (see: Acknowledgements) Geospatial data at the highest resolution accessible (30 arc seconds or 1km^2) was extracted from the Worldclim database (source: Hijmans et al. 2005, http://www.worldclim.org/bioclim.htm). This included altitude and a set of bioclimatic variables which represented annual trends (e.g. mean annual temperature and precipitation), seasonality (e.g. annual temperature range) and plant limiting factors (e.g. driest and wettest month of the year). Geospatial data for variables not included in the Worldclim database was extracted from Schulze (2007), and fire burn data from the online database Biodiversity GIS (BGIS, http://www.bgis.sanbi.org). This provided a better estimate of the contribution of fire than the previous dataset as it included patch burn size and boundaries, as well average frequency from 1927 to 2008 (although the length of the fire record differed for different reserves). All layers were resampled to a 1km^2 spatial resolution, as an unprojected reference system, WGS 84. The variables included in the analysis are included in Table C1.

Highly correlated data pairs (identified from the PCA), were removed from the dataset (as identified from the PCA), so as to improve the value of the outputs.

Maxent was then run several times to record the most important predictive variables for forest distribution. The random test percentage was set at 20, indicating that 20% of the sample records were for testing. At each rerun, variables that had both low permutation values (<1) and low contributions (<3%) were excluded, to improve the quality of the model.

As suggested by Kumar & Stohlgren (2009), an independent dataset should be used in Maxent to test performance value. However, as one was not available, the Jackknife or "leave-out-one" procedure was used, where the performance of the model is judged by its ability to predict a single locality, which is excluded from the training set. Thus, predictions are made where one of the occurrence records is excluded in each prediction (procedure of Pearson et al. 2007; as cited and followed by Kumar & Stohlgren, 2009). This means that the probability of finding forest can be plotted against individual environmental variables, separating their contribution from the influences of co-varying variables. A final habitat map showing predicted potential distribution was generated (Fig. C3), which was adjusted in Arc GIS to provide a better resolution (see: Acknowledgements).

Assessing Effective Rainfall Distribution

Effective rainfall within the driest and wettest half of the year (six months) was graphed against the probability of forest occurrence over the sample points, following Murphy & Bowman (2012), who followed the methodology of Trabucco et al. (2008). Trabucco et al. (2008) modelled estimates of water balance to land use change on a global and local scale. Moisture balance is a better indicator of the available moisture for vegetation per season, as it considers moisture loss from potential evapotranspiration (PET).

The estimates of effective rainfall (MAP-PET) were a simplified proxy for moisture balance based on the original calculation of soil water balance budget:

$$\Delta Soil\ Water\ Content\ (SWC) = Effective\ Precipitation + Irradiation - Actual\ Evapotranspiratin - runoff\ \ (mm/month)$$

Actual evapotranspiration is the quantity of water removed from the soil by evaporation and transpiration (Trabucco et al. 2008). Its estimation requires multiplication by a vegetation co-efficient (between 0.3 and 1.3) and a reduction factor based on soil moisture content (usually between 0-1).In this study, this was approximated to 1. In this study, I wished to determine climate constraints on vegetation distribution so both the vegetation coefficient and the soil moisture reduction factor were set at constant values of 1. The annual sum of monthly precipitation minus monthly evapotranspiration gives a good indication of effective precipitation (Lehmann et al. 2011) and of moisture inputs from rainfall compared to moisture loss by evapotranspiration

Images Forests within the Cape Floristic Regions

FIGURE1: Boundaries between forests and fynbos in the area around Betty’s Bay, Western Cape. Forest species are distinctly different from fynbos species, and can be distinguished in these photos by plant height. Similarly distinct boundaries between closed forests and low, sclerophyllous shrubland have been recorded worldwide. Photo taken: October 2013. Photo by: Alison Midgley.

FIGURE 3: Forests patches in the Cape Floristic Region, Betty’s Bay, Western Cape, sheltered from fire and moisture loss in: **(A)** ravines, **(B)** mountain valleys, and **(C)** beneath large boulders. Photo taken: October 2013. Photo by: Alison Midgley.

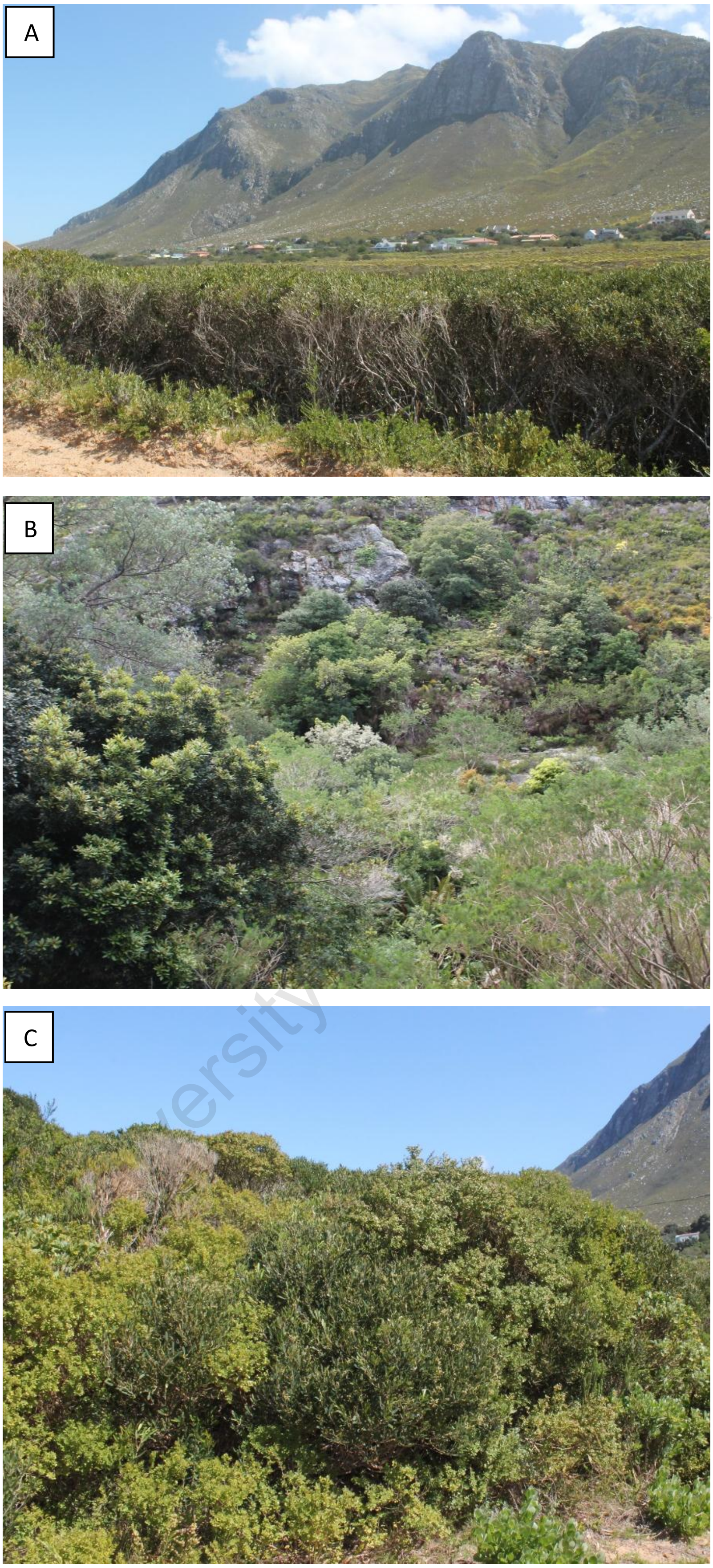

FIGURE 3: Images of **(A)** Strandveld, **(B)** Afrotemperate forest and **(C)** thicket in the vicinity of Betty’s Bay, Western Cape. Photo taken: October 2013. Photo by: Alison Midgley.

Results:

Summary Statistics of initial Dataset (Schulze, 2007)

Table 1 shows the summary statistics of the variables selected for the Principal Components Analysis. The summary statistics show that forested areas have a lower frequency than surrounding vegetation, and seem to be found at far lower altitudes compared to thicket and fynbos (286 m on average, as opposed to thicket and fynbos, which approach 500 m on average).

Table 1: The summary statistics of continuous environmental variables used in the multivariate analyses.

Environmental Variables	Fynbos		Thicket		Forest	
	Mean	St.Dev	Mean	St.Dev	Mean	St.Dev
Fire Frequency (number/yr over CFR)	0.5	1.0	0.4	1.0	0.2	0.6
Rain concentration (%)	25.7	16.9	10.2	6.5	13.0	11.7
Altitude (m)	498.4	391.5	491.3	268.8	286.2	218.2
Autumn solar radiation (MJ.m-2.month-1)	13.5	1.3	14.3	1.0	12.3	1.7
Spring solar radiation (MJ.m-2.month-1)	18.9	1.8	19.4	1.0	16.9	2.6
Summer solar radiation (MJ.m-2.month-1)	23.8	2.5	24.4	1.4	21.2	3.5
Winter solar radiation (MJ.m-2.month-1)	9.7	0.8	10.7	0.6	9.1	1.3
Summer max temp (°C)	26.9	3.0	28.1	1.9	25.1	3.0
Summer min temp (°C)	14.1	1.7	14.7	1.1	14.6	1.7
Winter max temp (°C)	17.3	2.1	19.1	1.5	18.1	2.3
Winter min temp (°C)	5.5	2.3	4.8	1.7	7.3	1.7
Plant available water (mm)	52.7	27.9	44.3	26.3	57.0	28.2
Median spring rainfall (total) (mm)	75.6	49.6	74.6	41.7	177.9	57.2
Median autumn rainfall (total) (mm)	89.0	47.3	78.7	34.3	169.9	49.1
Median summer rainfall (total) (mm)	40.8	40.0	61.7	32.0	137.7	63.3
Median winter rainfall (total) (mm)	130.5	94.4	52.7	30.8	183.5	105.7
Mean autumn PET[1] (mm)	85.6	12.6	92.1	7.7	75.6	11.8
Mean spring PET (mm)	111.4	15.8	119.0	9.8	96.1	16.2
Mean summer PET (mm)	148.9	22.8	156.1	14.4	126.6	23.4
Mean winter PET (mm)	54.3	7.3	63.4	4.7	51.3	8.9
Total med. rainfall, wettest months (mm)	219.5	134.5	131.4	63.7	353.4	143.6
Total med. rainfall, driest months (mm)	116.3	86.4	136.3	72.6	315.6	116.8
Median annual rainfall (mm)	335.9	198.1	267.7	134.8	669.0	213.3
Mean PET (mm)	400.2	56.8	430.5	35.0	349.6	58.0
Effective rainfall[2] wettest months (mm)	79.6	142.2	-24.0	65.5	226.5	150.9
Effective rainfall driest months (mm)	-144.0	109.9	-138.7	83.3	92.9	129.4

Note: These values were sourced from Schulze (2007). [1]PET denotes Potential Evapotranspiration. [2]Effective rainfall is calculated as (median rainfall-PET)

Forested areas also have a lower rainfall concentration (%) and a greater total rainfall during the summer and spring periods (drier months) than thicket and fynbos. Rainfall concentration specifies the evenness of distribution of rainfall (magnitude and month of year), with lower values indicating that rainfall is evenly distributed throughout the year (see: Markham's Technique (Markham, 1970 for a more detailed explanation of methodology).

Solar radiation (MJ.m^{-2}.month^{-1}) seems to be marginally lower for forested regions, which tend towards more temperate environments with higher minimum temperatures in winter and lower maximum temperatures in summer. Forests also seemed to need higher plant available water. As a measure of means, forested areas seem to have both greater seasonal rainfall and median annual rainfall than fynbos and thicket (669 mm, 335 mm and 267 mm respectively). This is also true of effective rainfall (median precipitation – mean potential evapotranspiration) in the wettest months (March to August) and in the driest months (September to February). The importance of water availability and decreased moisture loss from evapotranspiration for forested areas seems to be emphasised strongly in the summary statistics.

Principal Components Analysis

The eigenvalues determined from the PCA grouped the variables into four principal factors (see: Table A2). Factor 1 explained 42% of the variance in the dataset, factor 2 explained 21% of the variance, while factors 3 and 4 explained only 12% and 11% respectively (Table 2). The cumulative variance gives the amount of variance that the first 2 factors explain. It is indicative of the quality of representation of the two principal factors, giving the number of principal components that could ideally represent the whole dataset. Thus, when factors one and two were plotted against one another in the principal components analysis (Fig. 5), 64% of the variance in the dataset was explained by the included variables.

The raw unrotated factor loadings (which are the weights and correlations between each variable and the factor) are given in Appendix 1 (Table A2). Fig. 5a has plotted Principal Components 1 (PC1) and 2 (PC2) on a Cartesian plane, which report linear correlations of variables (R) with each principal component. R values range from -1 to 1, with numbers closer to the absolute value ±1 being highly correlated. Variables with high loadings on the first two components (R>0.7) are marked in blue, and those on the same end of the axes are highly positively correlated, while those at opposite ends are negatively correlated.

Rain concentration was the only significantly correlated value of Principal component 3, (PC3), and was not plotted against PC1 and PC2. The unrotated factor scores are plotted in Fig. 5b, as PC1 against PC2, showing samples clustering around their respective environmental conditions, as mirrored in Fig. 5a.

Table 2: Eigenvalues for the Principal Components Analysis showing the amount of variability accounted for by each factor

Principal Component	Eigenvalue	Total variance (%)	Cumulative Variance
1	6.4	42.4	42.4
2	3.2	21.5	63.9
3	1.9	12.04	76.0
4	1.7	11.3	87.2

Fig. 5b shows substantial vegetation overlap between forest, fynbos and thicket. Fynbos sites were scattered across the entire ordination. However, there was a slight clustering of fynbos sites in the right of the plane, indicating climates with higher solar radiation, higher potential evapotranspiration, and higher summer minimum temperatures. It is likely that the higher solar radiation in fynbos sites is linked to higher latitudes. It is also indicative of drier, warmer climates. Thicket sites were more commonly distributed on the left, bottom half of the ordination plane, in cooler, wetter areas, while forests were well distributed into typically fynbos climates, (defined by warm, dry summers). Both forests and thickets were associated more closely with conditions of higher effective rainfall in summer and winter than fynbos.

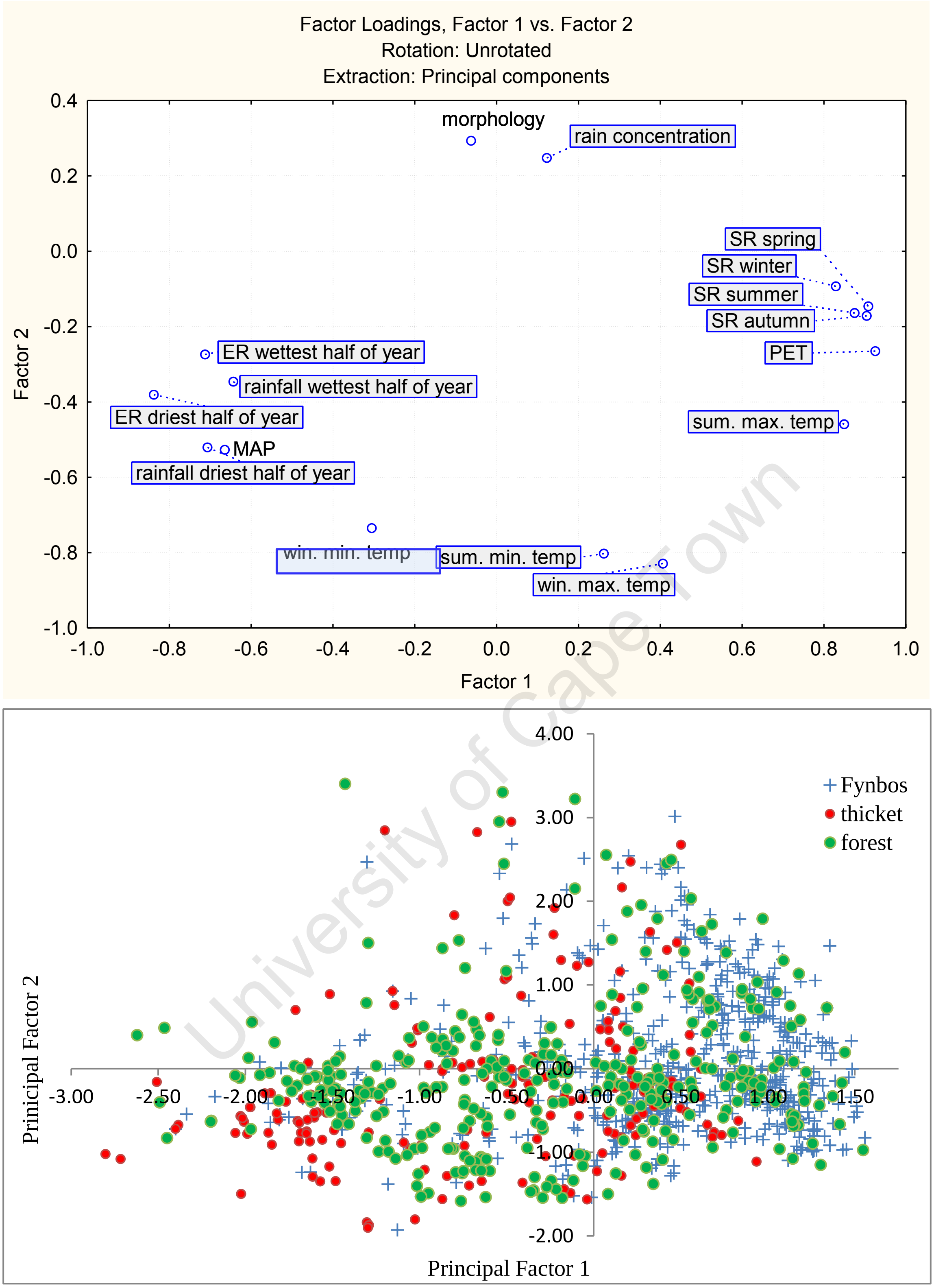

FIGURE 5: Principal components analysis, of the sixteen climactic variables shown to be significantly highly correlated with the 1400 different samples of vegetation, showing: **(A).** The relationship between climactic variables and the primary two principal components. Values in blue are significantly are highly correlated (R>0.7 or <-0.7). “ER” denotes effective rainfall in the driest and wettest months of the year; “SR” is solar radiation per season; “PET” is mean annual potential evapotranspiration. Clustered values are highly correlated. **(B)** Plot of the separated vegetation subtypes: green points represent forest; red points represent thicket, and blue crosses represent fynbos.

Classification and Regression Tree

The Classification and Regression tree (Table 3) showed the primary differentiator between forest distribution and other vegetation to be median rainfall in the driest half of the year (>252 mm was forest, <=253 mm was thicket). Thereafter, PET in the winter differentiated forest from thicket (<=65 mm, forest, >65 mm, thicket). Sites with drier summers were differentiated fynbos from thicket by effective rainfall in the winter (>22.5 mm and <=22.5 mm respectively). Thereafter, PET in the winter differentiated fynbos (<=58.8 mm) from thicket (>58.8 mm). Where effective rainfall in the winter exceeds 22.5 mm, effective rainfall in the driest half of the year is most important, with fynbos distribution being rather ubiquitous. Finally, in areas where effective rainfall in the dry summer drops below -124 mm, morphology becomes important. Forest is generally confined to the lowlands while fynbos extends into the high mountains.

The predictive value of the Classification Tree when compared to the observed values was quite high. Fynbos was predicted correctly in 91% of the cases, as was forest for 96% of the cases. However, thicket was more difficult to differentiate, and was predicted correctly for only 63% of the cases.

Table 3: Results of a Classification Tree presented as a dichotomous key. The number of samples listed in forest, thicket, or fynbos indicates how many samples of each vegetation type fell into the category stipulated by the variables (marked in red). The first split is based on the "lateral displacement" between different quantities of rainfall in the driest half of the year, showing that forests are mostly differentiated from fynbos by their summer/spring rain (>252mm is forests, <=252 mm is fynbos). The second split shows that forests are differentiated from thicket by PET (potential evapotranspiration) in the winter season (forests are found in <65 mm, thickets in <=65 mm). The splits in environmental conditions defining vegetation groups are ordered by number (1-5), and give information about the conditions that differentiate the vegetation group

Environmental categoriser variable:	Total number of observations per in vegetation type		
	Fynbos	Thicket	Forest
1. Med. rain driest half of the year >252 mm	52	20	250
2. PET in the winter season <=65 (mm)	51	2	244
2. PET in the winter season >65 (mm)	1	18	6
1. Med. rain driest half of the year <=252 mm	547	181	87
3. Effective rainfall in the winter <=22.5 mm	160	172	20
4. PET in the winter season <=58.8 (mm)	88	22	8
4. PET in the winter season >58.8 (mm)	72	150	12
3. Effective rainfall in the winter >22.5 mm	387	9	67
5. Effective rainfall driest half of the year <= -124 mm	279	0	2
5. Effective rainfall driest half of the year > -124 mm	108	9	65
6. Morphology (high mountains)	88	9	24
6. Morphology (all lower lands)	20	0	41

The proportional importance of the tested climatic variables is shown in Table 4. Effective and median rainfall in the driest half of the year appeared to be most important (100% and 90% respectively), as was summer rainfall (100%) and winter solar radiation (96%).

Table 4: Proportional Importance of different climatic variables in determining vegetation type (fynbos, forest, thicket) as well as their comparative rating.

Environmental variable:	Variable ranking	Importance
Effective rainfall driest half of year	100	1.00
Summer rainfall (med)	100	1.00
Winter solar radiation	96	0.96
Med. rainfall driest half of year	90	0.90
Effective rainfall summer	85	0.85
Evaporation winter	84	0.84
Effective rainfall spring	83	0.83
Spring rainfall (med.)	82	0.82
Effective rainfall autumn	78	0.78
Morphology	75	0.75
Autumn rainfall	74	0.74
Effective rainfall wettest half of year	71	0.71
Effective rainfall winter	69	0.69
Rain concentration	67	0.67
Med. rainfall wettest half of year	60	0.60
Winter rainfall (med.)	57	0.57
Solar radiation autumn	54	0.54
Evaporation spring	45	0.45

In summary, there is considerable climate overlap for all three major vegetation types in the Cape Floristic Region. Seasonal moisture balance seems to be the most important indicator of vegetation type, although overall rainfall and edaphic factors were still primary indicators on a larger scale. Moisture in the dry season needs to be adequately high for forests to occur, and the amount of moisture lost to evaporation from solar radiation, during the wet season, seems to separate forest from thicket, with thicket withstanding greater moisture loss. Rain concentration does not seem a vital component (67% importance), and effective and median rainfall in the drier seasons outranks rainfall in the wetter seasons (<=71%).

Maximum Entropy results

The predictive performance of the Maxent model for suitable forest habitat was very good, as modelled in Fig. C1, where the omission rates closely matched the predicted omission rate. The high Receiver Operating characteristic (ROC) value (>0.9, St. dev 0.017) (Fig. C2) also showed the fit of the training curves to the test data. Background and presence points were used to determine Maxent distribution (10 202 points), while 243 points were used for training and 60 for testing.

The original map of predicted forest distribution in the CFR is shown in Fig. C3, and is modelled without the training and test points in Fig. 6a. This is compared to Fig. 6b, which shows the actual distribution of forests (and thicket) in the CFR.

Overall, the predicted distribution was greater than the actual distribution, and there was some predictive overlap in the east between predicted forests and actual thicket patches. Forests were predicted in lower altitudes, on the southern and eastern coasts of the CFR, where solar radiation is relatively low all year round due to lower latitudes (Schulze, 2007). There were no areas predicted to be highly suitable for forests (>80% probability), although there was a 61-80% probability of forest being distributed around the Knysna forest area and the South western coastal areas (Cape Peninsula), although the distribution is somewhat fragmented (Fig. 6a). Areas within the CFR predicted as having low “suitability” (<0.1 probability of occurrence), tended to focus around the interior and west coast. Predicted areas were somewhat larger than the observed forest and thicket distribution combined (Fig. 6a and 6b).

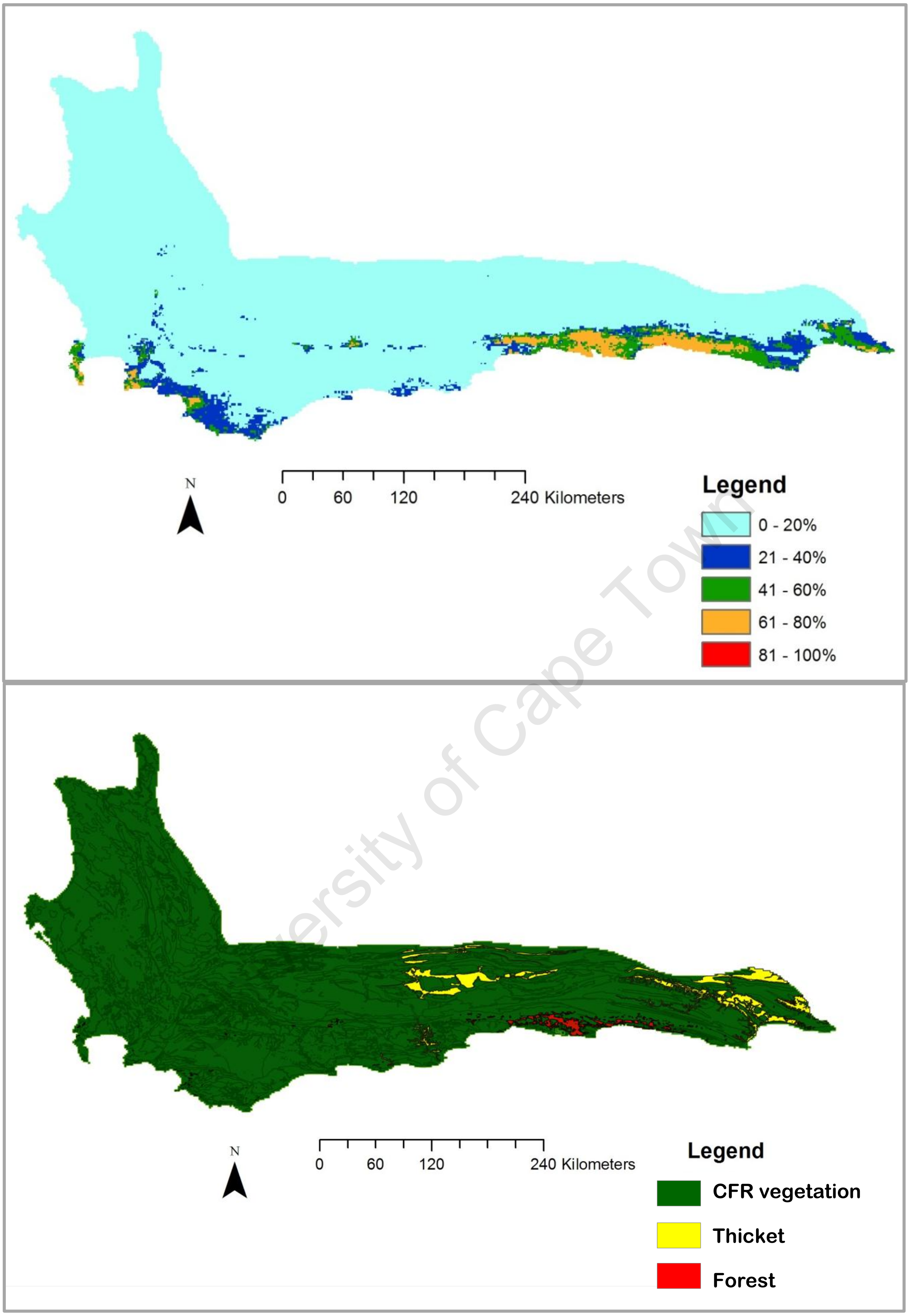

FIGURE 6: (A): Predicted habitat with suitable forest conditions specifically within the Cape Floristic Region, Western Cape, South Africa. The map indicated the probability of finding forests, with warmer colours indicating a higher probability of finding forests, and cooler colours a lower probability. [Arc GIS, data source: Maxent results] (**B):** Actual current range of South African forests (red) and thickets (yellow). CFR vegetation encompasses all non-thicket, non-forest vegetation, and is predominantly fynbos. These are mapped at 1:20 000 scale [Quantum GIS, data source: Mucina & Rutherford, 2006]

cent) so as to compare the effects of rain distribution over the year. In this analysis the percentage of days under soil stress in the dry season (January) contributed 37%, with median rain in October (17%), April (16%), February (9%) and solar radiation in August (8%) contributing substantially.

Table 5: Selected environmental variables and their percentage contribution in Maxent for forest distribution in the CFR, South Africa

Variable	Information	Per cent contribution	Permutation importance	Source/Reference:
Soil water stress in (January)	Days under soil water stress (%)	37.5	1.5	Schulze, 2007
Median rain (October)	mm	17.3	0.9	Worldclim; Hijmans et al. 2005
Median rain (April)	mm	16.1	15.5	Worldclim; Hijmans et al. 2005
Median rain (Feb)	mm	9.4	17.1	Worldclim; Hijmans et al. 2005
Solar radiation (Aug)	MJ.m^{-2}.month^{-1}	7.7	32.1	Worldclim; Hijmans et al. 2005
Median rain (Nov)	mm	4.5	5.4	Worldclim; Hijmans et al. 2005
Median rain (Dec)	mm	1.9	5.1	Worldclim; Hijmans et al. 2005
Median rain (Jan)	mm	1.9	14.5	Worldclim; Hijmans et al. 2005
Median rain (March)	mm	1.3	0.4	Worldclim; Hijmans et al. 2005
Median rain (June)	mm	1.1	2	Worldclim; Hijmans et al. 2005
Median rain (Aug)	mm	0.9	0.6	Worldclim; Hijmans et al. 2005
Median rain (May)	mm	0.2	4.7	Worldclim; Hijmans et al. 2005
Median rain (July)	mm	0.1	0.2	Worldclim; Hijmans et al. 2005

Note: (bio4) refers to the Bioclimatic variables obtained from WorldClim dataset-http:www.worldclim.org, University of Maryland, USA.

The Jackknife test of variable importance for the training samples is shown in Fig. 7 and the Jackknife test for the test samples is shown in Fig. C4. Both show almost identical values, although the gains may be exaggerated in the test samples (especially for winter rain).

Both the test and training samples noted that summer rain (December, January, February), and to a lesser extent spring rain (October, November), are important variables. The variable with the highest gain in isolation is median rain in January, which has the most useful information by itself. The variable that decreases the gain the most when omitted is solar radiation in August, which has the most information not available in other variables.

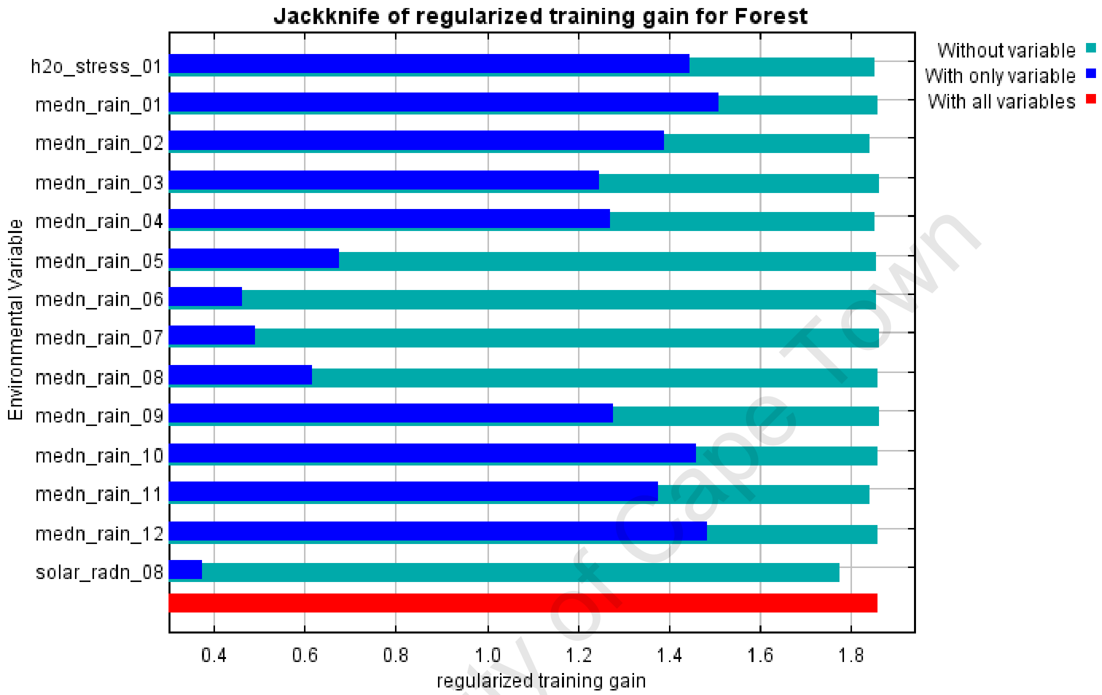

FIGURE 7: Results of Jackknife test of variable importance for the training samples. These show the gain of the variables individually (dark blue) compared to the lighter blue bars which indicate that no variables contain a substantial amount of useful information that is not present in other variables. The variables include percentage days of soil water stress (h20_stress), solar radiation (solar_rad) and median rain (med_rain) for months 1 (February) to 12.

In Fig. 7, median rainfall values for the wettest third of the year (May, June, July and August) seem also seem to increase the gain most when omitted, although they are not considered important contributors to table 5. However, in order to gauge the effects that these variables have on the distribution of forest, the response curves (Figs. C5 and C6) must be closely analysed.

The response curves in Fig. C5 show how each environmental variable affects the Maxent distribution. The curves show how the logarithmic probability of forest occurrence changes as each environmental variable is varied, keeping all other variables at their average sample value. Although an effort was made to reduce strongly correlated or redundant variables incorporated into the analysis, there are strong correlations between seasonal rainfall, which may distort results. Such strongly correlated rainfall variables were also revealed from the PCA (Fig. 5a). The response curves of Fig. C6, on the other hand, use only the corresponding variable. These plots reflect the dependence of predicted suitability both on the selected variable and on dependencies induced by correlations between the selected variable and other variables.

The individual response curves (Fig. C5) indicate that the probability of finding forests as rainfall increases is higher in December, January and February (summer), while in the winter months (June, July, August) and spring, a minimum moisture threshold suffices, after which the probability of finding forests is unaffected or slowly decreases. Solar radiation increases the optimal habitat for forests at lower levels in August. The probability of finding forest under dry season soil water stress remains relatively constant (pr=50%) until about 70% moisture stress.

However, in the presence of highly correlated surrounding variables (Fig. C6) the probability of forest drops dramatically when the percentage days exceed 70%. Similar trends are shown here, although spring trends (October, November) are contrastingly different, with more rainfall in November increasing forest probability, but rainfall in October reaches a peak before plummeting at approximately 100mm rainfall.

Investigation into Effective Rainfall distribution

Results of the previous analyses varied slightly depending on the number of reruns, or on the specific combination of variables (however correlated) incorporated. However, moisture balance in the dry season clearly an important explanatory variable, overall.

Effective rainfall, the moisture deficit remaining after evapotranspiration, for the wet and dry season was investigated further, as shown in Fig. 8a and 8b respectively. Fig. 8a shows the probability of finding forest, thicket and fynbos based on effective rainfall in the wet season (March to August). No clear patterns emerge, although there is evidently a higher probability of finding thicket in drier climates (<100mm). Fynbos is relatively ubiquitous throughout, while forests are shown to be variable in areas of greater effective rainfall.

Fig. 8b, shows the probability of finding fynbos, thicket and forest based on effective moisture in the dry seasons (September to February). A clear pattern emerges, with a higher probability of finding forests in areas above 50 mm, while the probability of finding fynbos increases evenly below 0 mm effective rainfall. Thicket has a low probability of occurrence generally, which peaks at 25% in areas where moisture input roughly equals moisture loss (effective rainfall = 0 mm).

The results of this graph are indicative of potential complementary patterns of forest and fynbos distribution, which are determined by the summer moisture balance. Forests occur where moisture deficits are small, while fynbos dominates where deficits are greater.

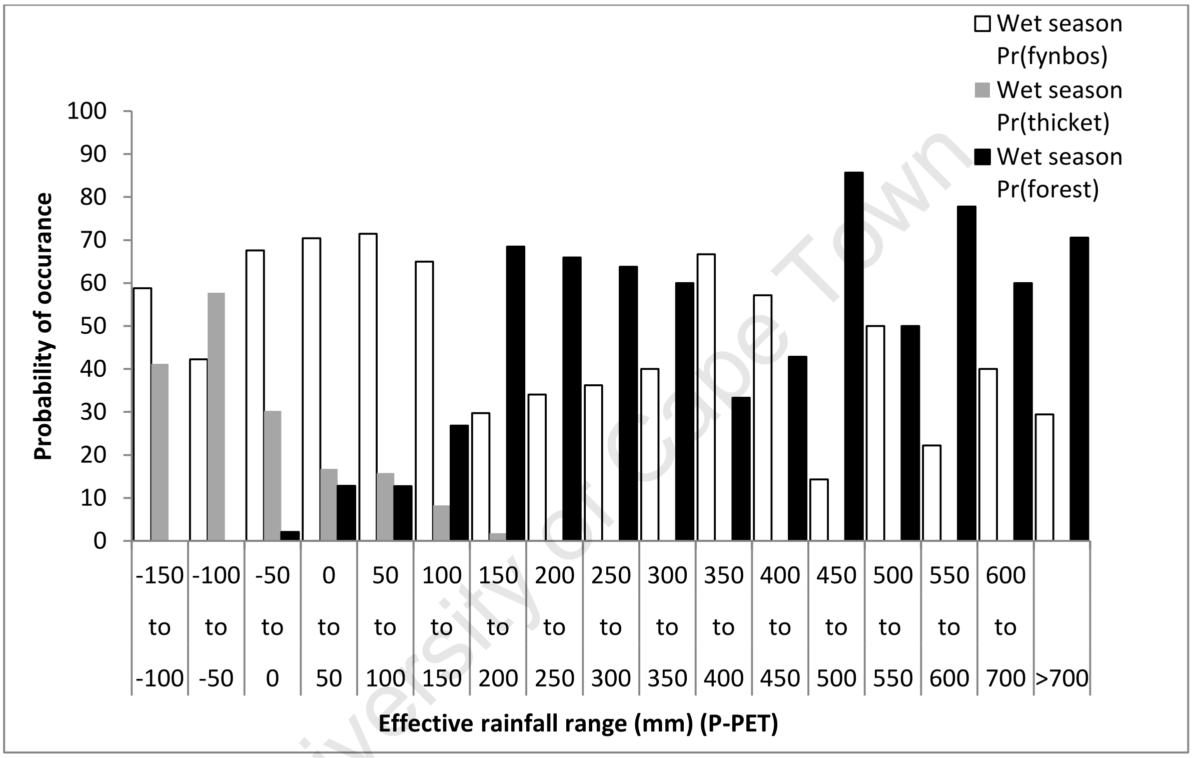

FIGURE 8a: Probability of occurrence of forest, thicket and thicket within the CFR during the wet period (March to August) based on the effective rainfall (median annual precipitation (MAP) minus potential evapotranspiration (PET)).

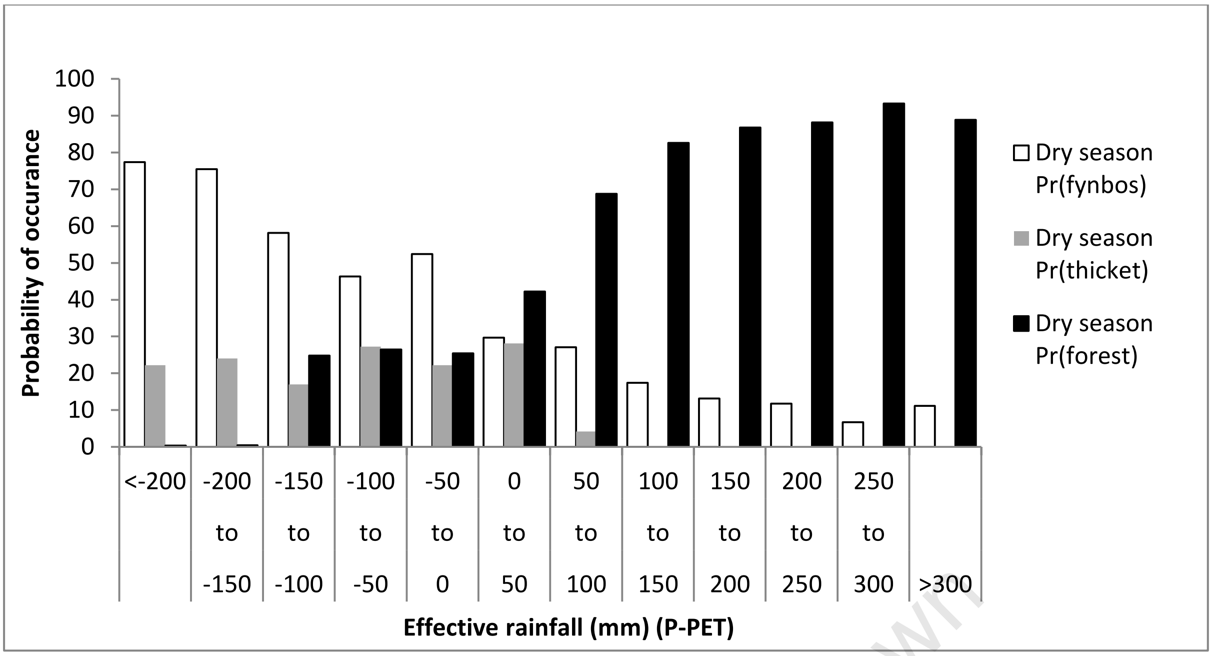

FIGURE 8b: Probability of occurrence of forest, fynbos and thicket within the CFR during the dry period (September to February) based on the effective rainfall (median annual precipitation (MAP) minus potential evapotranspiration (PET)).

Discussion

Differentiating vegetation type from climatic conditions

In this investigation, the effects of climate took precedence over edaphic, morphological and disturbance-based factors, in all analyses. This resulted in great overlap between the environmental conditions associated with forests, fynbos and thicket. Most likely, this is due to the proximity of the sample sites, as well as the mosaic-form vegetation structure typical of the CFR landscape. It is also likely that the extent of climatic overlap was underestimated in this study, as smaller patches of forest and thicket were not mapped by Mucina & Rutherford (2006).

The statistical and Maxent models had considerable predictive power overall, (e.g. Fig. C1, Fig. C2), however, there was some difficulty in distinguishing vegetation types from one another. Thicket, for example, was only correctly predicted 63% of the time in the Classification Tree (Table 3), while Maxent predicted that forest distribution should cover greater parts of the fynbos and thicket, encroaching along the south coast and Cape Peninsula (Fig. 6a). These areas were predicted to be climatically suitable for forest distribution, despite few large forest patches being present. The Principal Components Analysis (Fig. 5b) graphically showed the extent to which forests in particular (although all samples were well integrated) spread into the more typical warm, dry summer climates of the fynbos, and the cooler, wet winters of the thickets.

Edaphic conditions (fertility score, underlying geology) were not identified as key determinants of forest distribution, despite the use of substrate variables in different statistical analyses. Forests were not confined to a particular geological substrate, which may explain why it was not considered in the analyses. This is supported by similar findings by Manders (1991). However, it is possible that the effects of geological substrate on forests can only be appreciated on a local or micro-scale, as opposed to on a meso-scale, as done in this project. The effects of soil type may thus be underestimated, especially given that ecological soil studies often only include biologically controlled nutrients, (such as nitrogen) and that soil nutrients are often only sampled from surface soil layers (Bond, 2010; Cramer, 2010).

Despite the overlap in fynbos, thicket and forest conditions, there were several key variables that were strongly emphasised in the analyses. These will be discussed in the following section.

Moisture Balance and Seasonal drought as an indicator of forest distribution

In this study, moisture balance in the dry season was strongly emphasised as a determinant of forest distribution, regardless of different analytical methods and data sources (Table 3, Table 4, and Table 5). One of the principal constraints on forests was the number of days under soil moisture stress in January (Table 5): as the number of drought days approached 70%, the probability of finding forests decreased (Fig. C6). However, soil moisture stress was not effective on its own. It is fair to conclude that forests are found where moisture deficit is high due to low summer rainfall and high evapotranspiration (Table 4, Fig. 8b).

Solar radiation in the winter was identified as an important factor (Table 4, Table 5). Forests were not predicted where winter solar radiation was too high (Fig. C5 and C6). As high solar radiation is often associated with low latitudes, higher soil moisture loss, higher potential evapotranspiration (PET) and lower stream flows (Cowling et al. 2004), it is assumed that forests occur where there is low water loss in the wet season. However, increasing levels of winter rainfall did not increase the likelihood of forest presence (Fig. C6). Although a minimum rainfall threshold seemed to be required in the winter (Fig. C6), in many cases this was below 200 mm, far below the expected minimum threshold of 525 mm predicted for forests in winter rainfall regions (Mucina & Rutherford, 2006). In fact, forest distribution was even predicted to decrease as winter rainfall volumes increased, where monthly winter rainfall variables were isolated from other variables (Fig. C5).

What can be gauged from these results is that the quantity of winter rainfall plays a relatively insignificant role in the distribution of forests, compared to summer moisture deficits. Forests species are clearly less tolerant of prolonged seasonal drought, and the expected moisture threshold during the wet season is significantly lower than that postulated by previous studies (Geldenhuys, 1994a; Manders & Richardson, 1992; Bond et al. 2003). Forests seem to fare better in areas with evenly distributed (but not necessarily high) rainfall throughout the year.

Seasonal drought in the CFR is associated with high summer temperatures. This may be a contributing factor to indigenous tree leaf-loss in the mid-summer, as leaf-fall peaks from December to January (Mucina & Rutherford, 2006). Thus, physiological drought stress may make forest trees in winter-rainfall regions particularly susceptible to mortality. This is likely to exclude them from Mediterranean-type ecosystems and vegetation.

The relationship between moisture balance in the dry season and the probability of finding forest was shown visually in Fig. 8b, where forests were found in areas with higher effective rainfall in the summer months. The same distribution pattern, however, was not evident in the wet season (Fig. 8a). Effective rainfall is a proxy for moisture balance as it encompasses the loss of moisture through evapotranspiration (i.e. irradiance and vapour pressure deficit) from total precipitation. The importance of effective rainfall in the driest half of the year was emphasised in the correlation analysis (Fig. 5) as well as in the classification analysis (Table 4).

Although the values of effective rainfall are relative as opposed to absolute, they give an indication of the respective seasonal aridity of environments in which forests and fynbos are found. Several studies have also recognised that soil-moisture balance is a better delineator of major vegetation sub-divisions than annual precipitation (Cowling et al. 2004; Tinley, 1982; Murphy & Bowman, 2012). Other studies also rainfall seasonality or, in particular, dry season duration, as a key predictor of forest distribution (Lehmann et al. 2011; Staver et al. 2011).

While it is possible that moisture balance and summer drought directly affects the forest distribution in the CFR, there are a few anomalous patterns that are not explained by seasonal moisture deficits. These include the overestimation of predicted forest distribution based on soil moisture balance (Fig. 4a), the low moisture thresholds in winter for adequate forest persistence (Fig. C5) and the fact that increasing volumes of rainfall in the spring and (to a lesser degree) autumn (October and April, specifically) were associated with decreasing probabilities of forest distribution (Fig. C6) in Maxent. Rainfall variation within October and April were emphasised as the most important contributing factors to the model, after soil moisture (Table 5).

It is possible that moisture balance and seasonality are proximal variables for other underlying constraints to forest distribution. The Maxent analysis highlighted the inter-related nature of environmental variables, and the difficulty in separating their effects (Fig C5 compared to C6). The impacts of secondary factors, which are also derived from seasonal drought, should be considered to create more comprehensive understanding of forest-fynbos ecosystems dynamics.

Correlates of seasonal drought: fire and topography

Fire and topography were not considered pivotal in the statistical analyses of this investigation. However, one of the central weaknesses of the study was that meso-scale climatological variables completely overrode variables that may contribute to vegetation distribution on a local scale.

Morphology, which was a proxy for topography in this study, was identified to have an importance of 75% in separating forest (lowlands) from fynbos (high mountains), in the Classification Tree (Table 3). Its contribution was nonetheless secondary to climate variables. However, morphology effects vegetation in numerous ways: it provides topographic complexity for soil moisture accumulation (Cowling et al. 2004), channels for plants to access groundwater (Cramer, 2010), protection from soil-desiccating fires (Manders, 1990) and is correlated with altitude. Indeed, forest species in the CFR are known to reside in topographically sheltered areas (see: Fig. 2), or in lowlands, where plants are less likely to experience physiological drought from seasonal water stress and low temperatures (Eeley et al. 1999)

Another factor which may play a greater role at a local level and which is often promoted or hindered by topography (see: Geldenhuys, 1994a), is fire. Fire is a difficult variable to measure using correlative studies such as this, as it also co-varies with multiple factors, including climatic variability, weather and changing distributions of fuel (Wilson et al. 2010; Archibald et al. 2009). Fire data derived from Schulze (2007) was limited in that it did not include intensity, size of burn patch, or type of fire. Similarly, the fire burn data derived from Cape Nature were restricted to Cape Nature reserves, of which the time span of records differed somewhat. Fynbos fires occur on average every 10-30 years (Wilson et al. 2010). However, studies in several fire-prone systems have shown that a relatively small number of severe fires, often brought about by extreme weather conditions, are responsible for the majority of the burn area (Dickenson et al. 2006; Archibald et al. 2009). Thus, the time span (1927 to 2008) may not have been an adequate representation of the overall effects of fire on vegetation.

Climatic conditions are essentially the drivers of fire regimes in fire-prone ecosystems (Archibald et al. 2009). High precipitation has been shown to be positively correlated with both fire frequency (Archibald et al. 2009, Higgins et al. 2000), and post-fire tree mortality (Hoffman et al. 2009). Given sufficient rainfall, plant matter can accumulate, cure and be ready to burn after merely a few weeks of dry weather in savannas (Archibald et al. 2009). Thus areas where high rainfall is followed by a long dry season are particularly predisposed to wildfires (Archibald et al. 2009).

Indeed, Thonicke et al. (2001) created a fire model using only leaf litter moisture and fuel loads to determine the probability of fire ignition. The model successfully simulated the fire return intervals of many fire-prone ecosystems worldwide, including CFR. Thonicke et al (2001) argued that the length of the fire season (i.e. the dry season) increased the probability of fires by decreasing the moisture in litter loads. This suggests that in areas with long fire seasons, fire frequency and intensity are likely to increase. This includes the CFR, where the fire season (i.e. the dry season) extends from September in one year to April in the following year (De Klerk et al. 2012).

Since the fire regime is sensitive to the seasonal climates, particularly summer moisture deficits, fire frequency and intensity may directly determine of forest distribution, while long dry seasons determine the high rates of fire frequency that exclude forests from fynbos. High levels of rainfall in the growing season (e.g. October) may lead to accumulation of fuel loads, increasing the risk of severe fires during the extended dry season of the CFR (Table 5).

Study constraints and improvements

The climatological and edaphic values of the Schulze (2007) atlas, from which this dataset is derived, should be viewed in relative rather than absolute terms. This is because the simulations and regressions used to derive the point-values may smooth local effects and supress outliers (Schulze, 2007). The edges of vegetation mapped at a spatial resolution of 1km^2 or more are also likely to have arbitrary cut-offs or simplifications of vegetation boundaries. Furthermore, the effects of variables considered in this paper are equally weighted, despite the fact that most are effective at one or different spatial scales.

The map of forest patches in the CFR (originally by Mucina & Rutherford, 2006) excluded vegetation patches in mosaic-form landscapes. All vegetation becomes somewhat patchy on regional scales and thus small-scale data is absent from the original distribution of forests and thickets. This was confirmed in Betty's Bay, where forests patches were present, but too small to be mapped (personal observation).

During data collection, no minimum distance was enforced between the data points, due to the scarcity of geospatially referenced data for forests and thicket. This could lend itself to pseudo-replication. There is no current method of accounting for spatial-autocorrelation within the Classification Tree analysis, which must be taken into account when assessing the model (Lehmann et al. 2011). Spatial autocorrelation, which refers to site properties that are more or less similar than expected due to their physical proximity (Legendre & Gallagher, 1998), may result from variables that have not been quantified in the study, or from overlapping biophysical processes. This may be improved upon if a greater spatial resolution is used in future studies, or if geographical range is expanded to include more wide-ranging forest patches.

Further investigation into the relationship between fire, moisture and vegetation

The correlation analyses in this study hint at potential direct (e.g. seasonal drought and effective rainfall) and indirect (e.g. resulting fire) determinants of forest distribution and the underlying relationship between them. However, the primary determinant is not clearly identified. It would be interesting to complement the results of this study by experimentally comparing soil moisture variability between and amongst forest and fynbos boundaries. It would also be interesting to factor in the effects of different vegetation types and soil textures on evapotranspiration rates and precipitation absorption in effective rainfall measurements.

The effects that vegetation itself has on local soil and moisture conditions, as well as on encouraging or discouraging wildfires according to the individual life history traits of CFR species, (i.e. “niche construction”), would be an interesting complementary study. It has also been suggested that fire and water form feedback loops, whereby pyrophytic vegetation increases fire frequency thereby excluding forest, while forests promote consistent moisture levels that make vegetation less flammable (Warman & Moles, 2009). The effects of seasonal moisture stress on vegetation and fire distribution in these areas would provide an interesting complementary study.

Study implications

This study provides insights into the effects of soil moisture balance on vegetation type in Mediterranean-type ecosystems, and provides an opportunity to assess the potential for ecosystem shifts in the CFR under different climatic conditions. These findings have implications for studies on historical and future ecosystem shifts, and their relationship with climate change.

If these results are reflective of past climates, then the spread of sclerophyllous vegetation and the reduction of forests in the Quaternary may have been as a result of increasing seasonality. Where long dry summers followed periods of higher rainfall, wildfires would have replaced closed forests with fire-prone fynbos shrublands.

Conclusion

Clearly, forests in the Cape Floristic Region show patterns analogous to those found in tropical savannas that require further investigation. However, although the correlative research of this study hints at possible explanations for forest distribution, the impacts of meso-scale climatic variables have not been separated from local-scale effects. Forest distribution may be directly determined by the availability of soil moisture in the dry season, with trees persisting so long as levels of moisture gain do not drop below levels of moisture loss. However, it is also possible that summer drought indirectly effects forest distribution by predisposing areas to frequent, severe fires. Like Lehmann et al. (2011) found for savannah-forest ecosystems, this study suggests that effective rainfall and seasonality are proximate drivers of vegetation distribution in the CFR.

The paper provided insight into the relationship between vegetation types in the Cape Floristic Region and surrounding climatic influences, emphasising the importance of the moisture balance, as opposed to patterns of precipitation. This paper provides a framework from which to consider the constraints of forest species in light of historical and future climate change. The relationship between vegetation and its environment is dynamic, and often dominated by multiple feedback processes. Further investigation into the relationship between seasonality and fire may shed light on the underlying processes that define forest-fynbos boundaries. Similarly, the patterns revealed in this study serve to guide investigations into the physiological effects of seasonality on tree growth and survivorship. This would aid in evaluating the relative importance of direct and indirect effects of plant available moisture on forest distribution.

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Appendix A:

Table A1: Environmental variables, their units and sources extracted included in the statistical analysis dataset

Contents	Units	Information	Source
Vegetation Type	-	Vegetation zonality	Mucina & Rutherford (2006)
Biome	-	Plant community groups	Mucina & Rutherford (2006)
Group	-	Geology	Council of Geoscience
fire frequency	(number of occurrences: 0-6)	Annual recorded frequency of occurrence	CSIR
Relative Relief	%	Difference in elevation between the top of a slope/hill and the bottom	Council of Geoscience
Altitude	m	Height above sea level	Schulze (2007)
Terrain morphology	-	Relief plains, lowlands, hills and mountains	Schulze (2007)
Solar radiation (summer, winter, spring, autumn)	average $MJ.m^{-2}.month^{-1}$	Based on Clemence's (1992) Equation	Schulze (2007)
Rainfall Concentration	%	Based on Markham's (1970) Technique	Schulze (2007)
Rainfall Seasonality	Season of most rainfall	After Dent, Lynch & Schulze (1989)	Schulze (2007)
Monthly means Of Maximum Temperature (summer, winter, spring, autumn)	^{o}C	-	Schulze (2007)
Monthly means Of Minimum Temperature (summer, winter, spring, autumn)	^{o}C	-	Schulze (2007)
Mean Evapotranspiration (summer, winter, spring, autumn)	mm	FAO Penman - Montheith (1992) Method	Schulze (2007)
Median rainfall (summer, winter, spring, autumn)	mm		Schulze (2007)
Plant Available Water	mm	Autosoils(SIRI)	Schulze (2007)

Table A2: Unrotated factor loadings for Principal Components Analysis showing correlation significance and explaining the total variance (marked loadings are statistically significant (>0.7%)).

Environmental variable	Factor 1	Factor 2	Factor 3	Factor 4
Morphology	-0.062419	0.293500	0.513429	-0.393350
Rain concentration	0.122620	0.247670	-0.894846	-0.001873
Solar radiation (autumn)	0.904363	-0.171593	-0.036453	-0.343725
Solar radiation (spring)	0.908398	-0.146484	-0.143769	-0.321353
Solar radiation (winter)	0.829206	-0.093184	0.317890	-0.303134
Solar radiation (summer)	0.874849	-0.163915	-0.231138	-0.329789
Summer max. temp	0.849569	-0.459209	-0.086855	-0.040635
Summer min, temp.	0.261887	-0.802361	-0.007857	0.415450
Winter max. temp.	0.406390	-0.828899	0.252066	0.185455
Winter min. temp.	-0.305146	-0.734837	-0.244610	0.475169
Rain wettest half of year (median)	-0.643387	-0.346119	-0.477597	-0.445066
Rain driest half of year (median)	-0.706486	-0.520708	0.268906	-0.320207
Median Annual rainfall	-0.664241	-0.526743	0.086390	-0.366013
Mean annual PET	0.925334	-0.265106	-0.035015	-0.130027
Effective Rainfall wettest half of year	-0.712998	-0.274263	-0.462930	-0.408010
Effective Rainfall driest half of year	-0.837795	-0.380843	0.256462	-0.223667
Expl.Var	**7.584347**	**3.274586**	**1.960988**	**1.679209**
Prp.Totl	**0.474022**	**0.204662**	**0.122562**	**0.104951**

Appendix B:

Table B1: Environmental variables and their sources originally incorporated into the Maximum Entropy geospatial analysis

Contents:	**Units:**	**Information:**	**Source:**	**Record time span:**
Terrain morphology	Scale	after Kruger (1983)	Schulze (2007)	1950-2000
Solar Radiation (Jan-Dec)	MJ.m-2.day-1	Based on Clemence's (1992) Equation	Schulze (2007)	1950-2000
Rainfall Concentration	%	Based on Markham's (1970) Technique	Schulze (2007)	1950-2000
Rainfall Seasonality	Seasons	After Dent, Lynch & Schulze (1989)	Schulze (2007)	1950-2000
Median Rainfall (Jan- Dec) (2003)	mm	After Lynch (2003)	Schulze (2007)	1950-2000
Daily Mean Temperature (Jan-Dec)	°C	-	Schulze (2007)	1950-2000
Average Duration of Frost Period	Days	Screen Minimum Temperature < 0oC	Schulze (2007)	1950-2000
Mean Relative Humidity (January to December)	%	-	Schulze (2007)	1950-2000
Potential Evapotranspiration (Jan-Dec)	mm	FAO Penman - Montheith (1992) Method	Schulze (2007)	1950-2000
Plant Available Water - 84 soil zones	mm	Autosoils(SIRI)	Schulze (2007)	1950-2000
Depth top soil horizon - 84 soil zones	mm	Autosoils(SIRI)	Schulze (2007)	1950-2000
Depth sub soil horizon - 84 soil zones	mm	Autosoils(SIRI)	Schulze (2007)	1950-2000
Top soil to sub soil daily drainage fraction	fraction	Autosoils(SIRI)	Schulze (2007)	1950-2000
Sub soil daily drainage fraction	fraction	Autosoils(SIRI)	Schulze (2007)	1950-2000
Soil Fertility	Fertility Score	-	Schulze (2007)	1950-2000
Primary Production	t.ha-1.season-1	-	Schulze (2007)	1950-2000
Soil Water Stress Per Cent Days Under Stress (Jan)	%	-	Schulze (2007)	1950-2000
Soil Water Stress Per Cent Days Under Stress (July)	%	-	Schulze (2007)	1950-2000
Moisture Growing Season Duration of Season	day	Based on FAO (1978) Method	Schulze (2007)	1950-2000
Altitude	m		Worldclim database	1950-2000
Annual Mean Temperature	°C	Bio1	Worldclim database	1950-2000
Mean Diurnal Range (Mean of monthly (max temp - min temp))	°C	Bio2	Worldclim database	1950-2000
Isothermality (Mean Diurnal Range/Temperature Annual Range) (* 100)	%	Bio3	Worldclim database	1950-2000
Temperature Seasonality (standard deviation *100)		Bio4	Worldclim database	1950-2000

Max Temp. of Warmest Month		Bio5	Worldclim database	1950-2000
Min Temp. of Coldest Month		Bio6	Worldclim database	1950-2000
Temperature Annual Range (BIO5-BIO6)		Bio7	Worldclim database	1950-2000
Mean Temperature of Wettest Quarter (3 months)		Bio8	Worldclim database	1950-2000
Mean Temperature of Driest Quarter (3 months)		Bio9	Worldclim database	1950-2000
Mean Temperature of Warmest Quarter (3 months)		Bio10	Worldclim database	1950-2000
Mean Temperature of Coldest Quarter (3 months)		Bio11	Worldclim database	1950-2000
Annual Precipitation		Bio12	Worldclim database	1950-2000
Precipitation of Wettest Month		Bio13	Worldclim database	1950-2000
Precipitation of Driest Month		Bio14	Worldclim database	1950-2000
Precipitation of Wettest Quarter (3 months)		Bio16	Worldclim database	1950-2000
Precipitation of Driest Quarter (3 months)		Bio17	Worldclim database	1950-2000
Precipitation of Warmest Quarter (3 months)		Bio18	Worldclim database	1950-2000
Precipitation of Coldest Quarter (3 months)		Bio19	Worldclim database	1950-2000
Fire burn units		C.A.P.E. Nature fire dtatbase	BGIS	1927-2009

Appendix C:

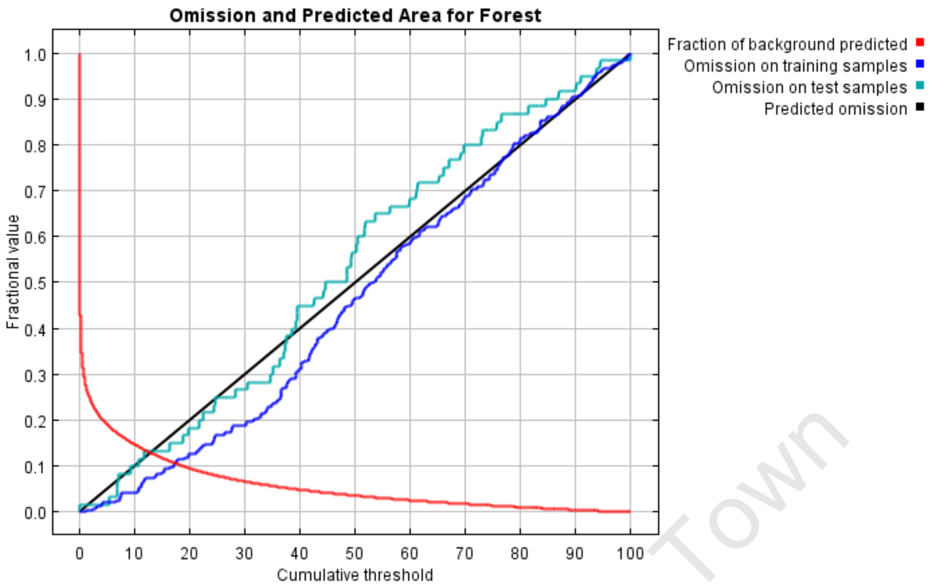

FIGURE C1: The omission rate for the training data drawn from the Maxent distribution. This shows the degree to which the omission rate on test samples matches the predicted omission rate. The predicted omission rate is a straight line (defined as the cumulative output), while the training omission line follows the fit closely. The turquoise line is what would be expected for a random model.

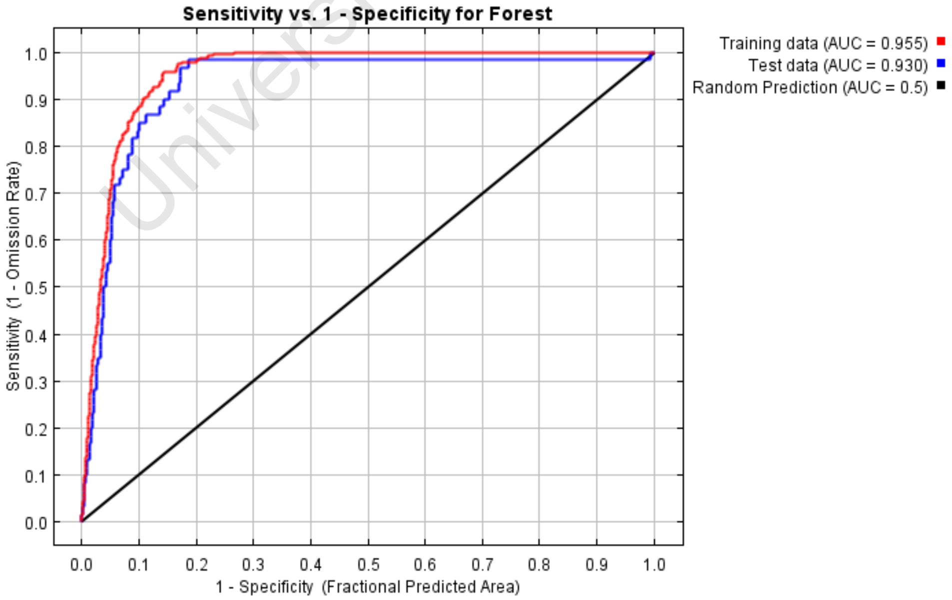

FIGURE C2: This shows the receiver operating curve (ROC) for both training (actual) and test data. The red "training" line shows the fit of the model to the actual data and as the area under the ROC curve (AUC) is 0.9, this indicates an excellent fit.

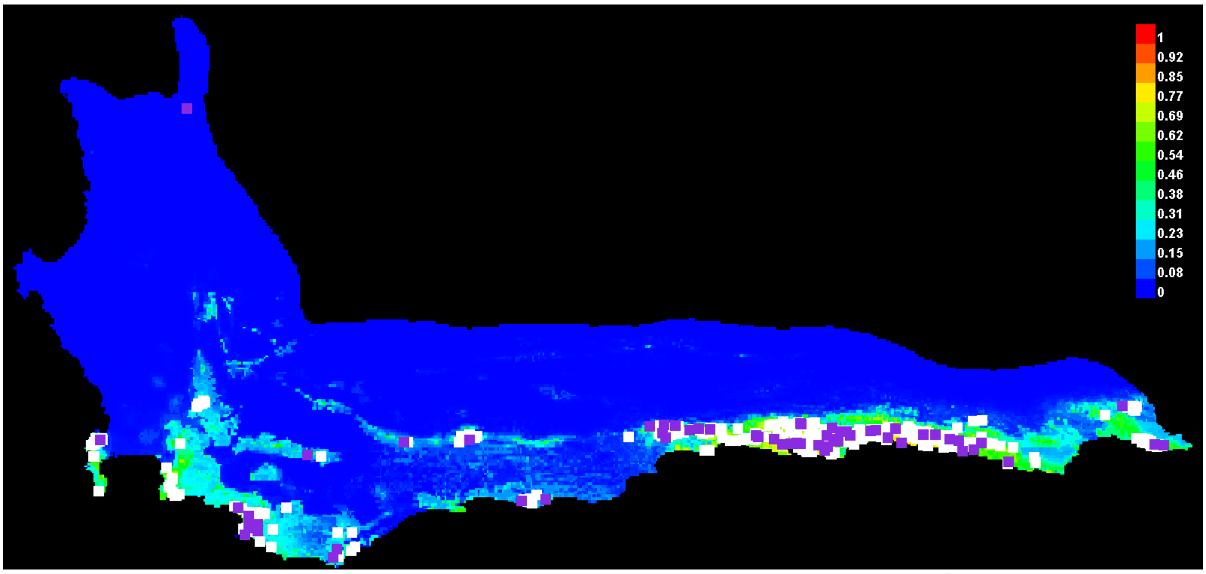

FIGURE C3: Original map generated in Maxent, showing the predicted area of forest distribution. The image uses colour to predict suitable conditions for forest habitat. Red values indicate areas of high probability, green values where the species is generally found, and lighter shades of blue where there is a low probability of species distribution. White points show the “training” (or actual samples) compared to the purple points, which signify the test samples. Test samples are a random sample taken from within a species presence locality (Phillips et al. n.d.)

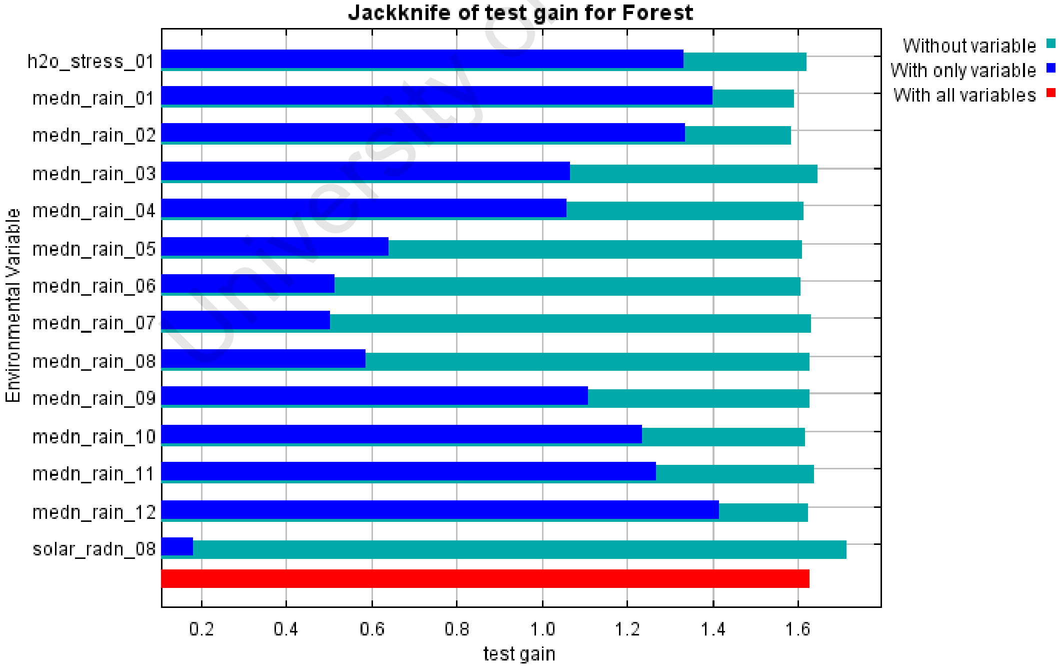

FIGURE C4: Results of the same jackknife test of variable importance, although for the test samples. These show the gain of the variables individually (dark blue) compared to the lighter blue bars which indicate that no variables contain a substantial amount of useful information that is not present in other variables. These values replicate the training samples well. The variables include percentage days of soil water stress (h20_stress), solar radiation (solar_rad) and median rain (med_rain) for months 1 (February) to 12 (December).

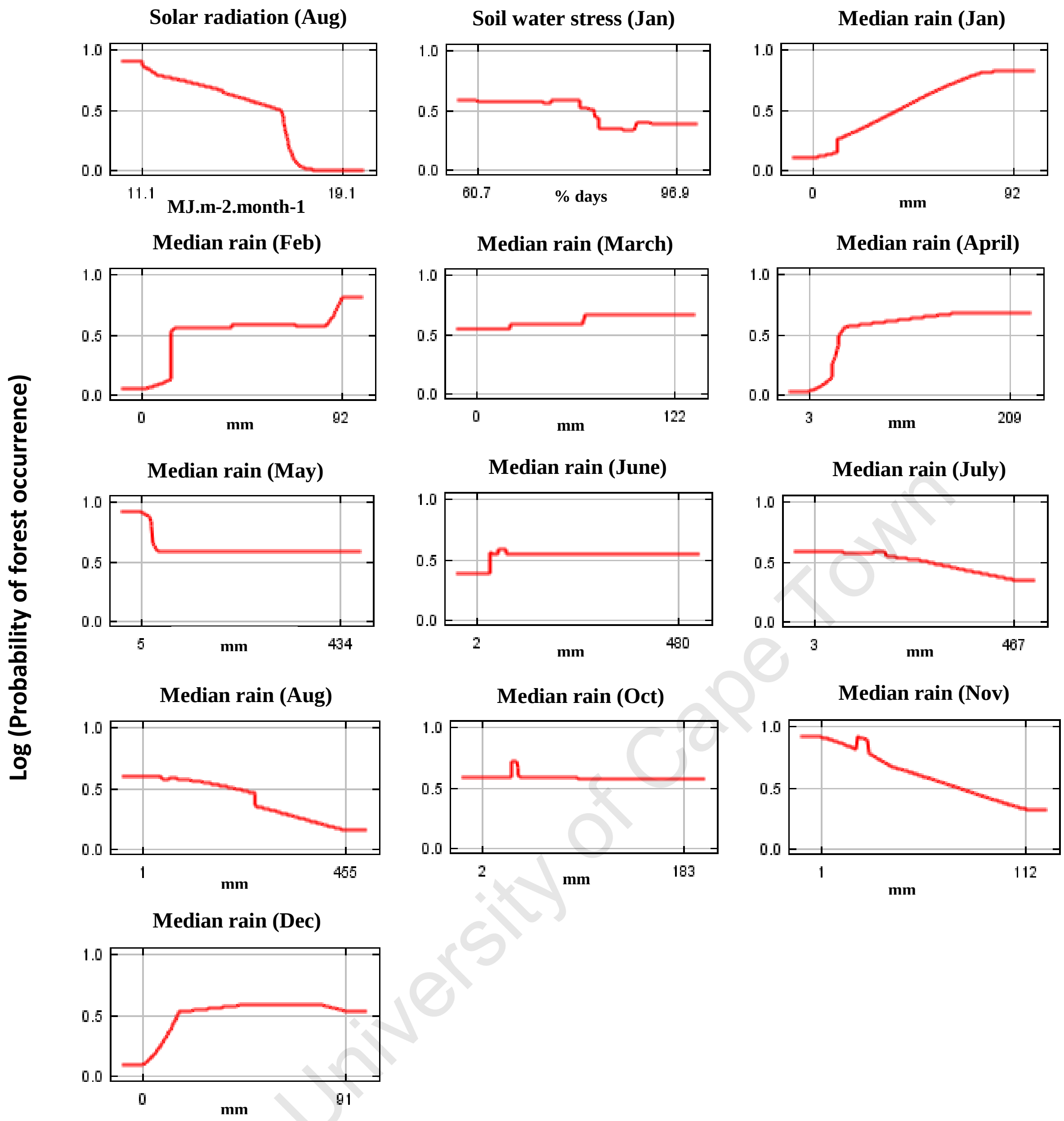

FIGURE C5: Response of forest distribution to each environmental variable excluding other potentially influential environmental variables. The graphs show the probability of forests occurrence depending on the values of the variable. Values are calculated with the formulae stipulated in Worldclim: http://www.worldclim.org/bioclim-aml.

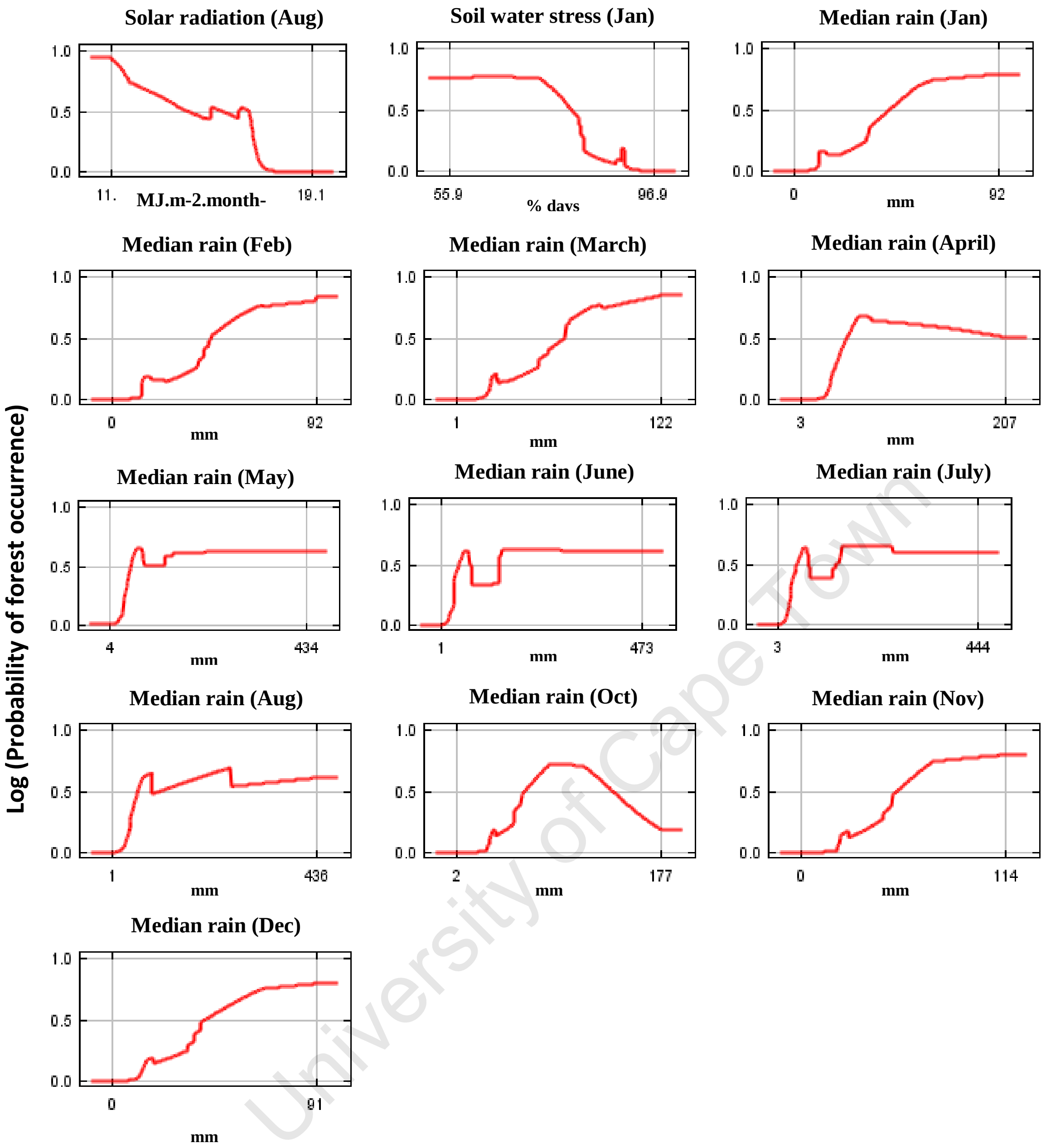

FIGURE C6: Responses of forest distribution to individual environmental variables with the influence of all other environmental variables. In the case of strongly correlated variables, these graphs may be easier to interpret. The graphs show the probability of the forests occurrence depending on the values of the variable. Values are calculated with the formulae stipulated in Worldclim: http://www.worldclim.org/bioclim-aml.