Water regime requirements and possible climate change effects on Fynbos Biome Restionaceae

by

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DEDICATION

I dedicate this thesis to my parents, **Pa Paul Egbe Ayuk** and **Ma Magdalene Ebangha Ayuk**, who are both of blessed memory.

DECLARATION

I declare that **Water regime requirements and possible climate change effects on Fynbos Biome Restionaceae** is my own work, and has not been submitted for any degree or examination in any other University and that all the sources I have used or quoted have been indicated and acknowledged by complete references.

Signed: ______________________ Date: 2018

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ABSTRACT

The Cape Floristic Region (CFR) of southern Africa is one of the world's most unique biodiversity hotspots. However, this biodiversity continues to be threatened by habitat loss due to rapid urbanisation, agriculture and alien vegetation encroachment, and now, by future groundwater extraction and climate change. Previous work had shown that soil moisture is important in structuring wetland plant communities at fine-scale. What is not fully known, however, is how the spatial distribution of species at a local scale is related to soil hydrology and what the response in the future of species distributions will be to perturbations arising from changes in climate or subsurface moisture in the future. The current research investigated the water regime of the Restionaceae which is a key family in the Fynbos biome and the implications of possible changes in soil hydrology caused by climate change in communities within this region. The Restionaceae were particularly appropriate because they are shallow rooted perennials with the ability to tolerate a wide range of water regimes which allows them to successfully co-habit within mixed plant communities as segregated clusters along fine-scale hydrologic gradients. Vegetation survey counts for the presence of these species along with measurements of soil water table depth and moisture content data generated from eight small-scale plots (50 x 50 m) were used to investigate the possible hydrological niches and to envision the potential impacts of a substantial reduction in rainfall and an increase in temperature as projected by Global Climate Models (GCMs) on the structure of Restionaceae communities in seasonal wetlands by 2100. A comparative analysis of the effects of two extreme Representative Concentration emission Pathways (RCP2.6 and RCP8.5) on significant hydrological variables to plant water regimes was carried out. The IPCC AR5 report describes the RCP8.5 emissions scenario as the likely 'business as usual' scenario where emissions continue to rise through the 21st century while the RCP2.6 scenario assumes that emissions peak between 2010 and 2020 and substantially subside thereafter.

An analysis of variance (ANOVA) tested if soils, where the Restionaceae species were present, were significantly different from those where these species were absent; and if Restionaceae species occupied significantly different hydrological niches at each site of study. It showed that at most sites, the soils that were occupied by Restionaceae species were significantly hydrologically different from the soils where the species were absent with just a few exceptions of where some species occurred irrespective of hydrological conditions (ubiquitous species). Meanwhile, Canonical Discriminant Analysis differentiated species into groups based on the influences of environmental variables. This confirms the primary role played by hydrological variables in determining the distribution patterns of the Restionaceae. Additionally, canonical discriminant analysis indicated each hydrological variable contributed differently to this dynamic between the different sites resulting in slight differences in species-specific water relations which enable them to co-exist. On the whole, statistical analysis demonstrated that species segregation in wetland communities in the south-western CFR is significantly explained by the soil hydrology. The findings show that hydrological gradients play a major role in the maintenance of species of the Restionaceae in Fynbos wetland communities. This relationship between species distribution and hydrological gradients makes it possible to predict the impacts of potential hydrological changes on species distributions.

The Jensen-Haise and Makkink methods were used to quantify evapotranspiration (ET) using weather data from plot locations to provide some comparative insight into the rate of moisture loss in the present and in the future. ET rates were shown to be statistically significantly different at the different stations that were studied. Potential reference evapotranspiration rates are expected to significantly increase in the near to far future as precipitation rates decrease while both radiation and temperature expected generally to rise in the south-western CFR. ET rates will be higher under the more extreme RCP8.5 scenario conditions relative to the RCP2.6 scenario. An increase in the ecological significance of ET rates was particularly noted.

The effects of variations in ET were investigated at microscale using hydrological modelling. Bi-weekly aggregates of rainfall and evapotranspiration (ET) estimates were the only model inputs while soil water measurements calibrated the model simulations. Soil moisture levels peaked during the winter months of June, July and August. The impacts of future climate scenarios on soil water levels were assessed and the possible changes were spatially mapped. These revealed significant changes between the current and future levels in climatic variables. Local microclimatic layers were generated for each site and the associated impacts on the distribution of Restionaceae species in wetland ecosystems were inferred.

The Maximum Entropy (MaxEnt) species distribution model used the novel microclimatic grids to generate hydrological niches at very fine spatial scale. The predictive quality of the models as indicated by the AUC values varied for the same species between the experimental sites. Visual assessment confirmed the proximity of actual (observed) sampled occurrences to the predicted (modelled) locations on spatial maps, which made the outputs valid for the interpretation of community structure and deemed fit for predicting the potential future species distributions based on novel environmental conditions introduced by climate change. The MaxEnt algorithm indicated that mean water table depth (MWTD) and to a lesser extent dryness or drought conditions (SEVd) appeared to be the main drivers of the potential present distribution of most of these species. Based on the robust species hydrological niche models, the potential future distributional changes of the selected Restionaceae species were predicted. Three possibilities of change were exhibited – stable or no change, reduction, expansion. Projected species change results revealed that the majority of Restionaceae species would experience some form of change and differ from their current distribution. The greatest impact was projected for extreme future climate scenarios with increasing emission levels. The prospect of species disappearing was the most prominent outcome based on the reduction in suitable microclimatic space for a number of species. Future species models predicted instances of resilience (by either remaining unchanged or by expanding their ranges) and of catastrophe (disappearance) at certain sites. The maintenance of diversity or possible expansion is most probable for the RCP2.6 GCM scenario. The severity of catastrophe on species occurrence is expected to be high if the RCP8.5 GCM scenarios persist into the future. Generally, the response of most species whether positively or negatively to climate change cannot be predicted with certainty due to the variedness in the nature of the expected distributional changes. For instance *Staberoha distachyos* (Rottb.) Kunth might remain stable at altitudinal conditions but is mostly predicted to disappear at most places where they presently occur. Additionally, the species is seen to expand in population under RCP2.6 scenario conditions but on the other hand shrink under RCP8.5 scenario conditions. A similar trend is expected for *Elegia filacea* Mast.,*Hypodiscus aristatus* (Thunb.) C. Krauss and *Staberoha cernua* (L.f.) T.Durand & Schinz.

Based on their contributions to defining species niches, hydrological factors are considered ecologically important to account for the expected differences in the response of individual species and for species diversity in these Fynbos wetland communities. Because of the very fine scale and localized nature of this study, distribution trends could not be aligned with numerous established outcomes at large scales which have reported the pole ward and upslope migration of species in response to climate change. Species distribution has mainly been underpinned by a moisture gradient rather than by the overarching climatic variations seen in larger settings. Finally, the results derived from different possible climatic scenarios may guide future decisions on conservation. While the direction to which species

change would definitely take remains uncertain in the future, these results are a firm pointer towards the most likely occurrences and a guide to maintain the survival of these species into the distant future.

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GLOSSARY OF TERMS

ANN	Artificial Neural Network
ANOVA	Analysis of variance
AR5	Fifth Assessment Report
ASCII	American Standard Code for Information Interchange
AUC	Area Under the Curve
BHU	Broad Habitat Unit
BRT	Boosted Regression Trees
CAPE	Cape Action Plan for People and the Environment
CART	Classification and Regression Trees algorithm
CCAFS	Climate Change Agriculture and Food Security
CFR	Cape Floristic Region
CGIAR	Consultative Group for International Agricultural Research
CMIP(5)	Climate Intercomparison Project (Phase 5)
COLA	Centre for Ocean Land Atmosphere
ECHAM	European Centre Hamburg Model (MPI model)
Elev	Elevation relative to a reference point
ESM	Earth Systems Models
ESRI	Environmental Systems Research Institute
ET	Evapotranspiration
FAO	Food and Agriculture Organization of the United Nations
GAM	Generalised Additive Model
GARP	Genetic Algorithms for Rule Production
GCM	General Circulation Model.
GIS	Geographic Information System.
GLM	Generalized Linear Model.
GPS	Global Positioning System.
HAMOCC	Hamburg Model of the Ocean Carbon Cycle
IDW	Inverse Distance Weighted.
IPCC	Intergovernmental Panel on Climate Change.
IUCN	International Union for Conservation of Nature.
MaxEnt	Maximum entropy model
MERRA	Modern Era Restrospective Analysis for Research and Applications
MPI	Max Planck Institute for Meteorology
MPIOM	Max Planck Institute ocean model
MONARCH	Modelling Natural Resource Responses to Climate Change.

MWTD	Mean water table depth
NMDS	Non-Metric Multidimensional Scaling
RCM	Regional Climate Model
RCP	Representative Concentration Pathway
ROC	Receiver Operating Characteristic
SANParks	South African National Parks
SDM	Species distribution modelling
SDM	Species distribution modelling
SEVa	Sum exceedance value for aeration stress
SEVd	Sum exceedance value for drought stress
SPSS	Statistical Package for the Social Sciences
UTM	Universal Transverse Mercator
WGS	World Geodetic System

CHAPTER 1 INTRODUCTION AND BACKROUND

1.1 The Fynbos biomes of Southern Africa- the Cape Floristic Region (CFR)

This section focuses on the variability and typification of the Fynbos biome in relation to geographical conditions, and comparative ecological and evolutionary driving forces that shaped this unique and rich flora.

The Fynbos biome is located in the characteristically Mediterranean belt of south-western Africa lying between latitude 31° and $34^{o}30^{'}$ south of the equator and extends to approximately 87 892 km^2 in surface area (Goldblatt and Manning, 2002). It is one of six floral kingdoms in the world and called the Cape floral kingdom (Takhtajan, 1986). Though the smallest, comprising less than 0.5% of the area of Africa, it is home to nearly 20% of the continent's flora giving it the highest concentration of plant species in an area (Goldblatt and Manning, 2002, Rebelo et al., 2006). This makes it a regional centre of endemism based on the exceptional species richness and high endemicity (Taylor, 1978, White, 1983) as well as a biodiversity hotspot (Myers et al., 2000). For these reasons, it is an internationally recognised biodiversity biosphere heritage since 2004 (UNESCO, 2009). It has been referred to as the Cape Floristic Region (CFR) by Goldblatt and Manning (2002) and will here forth be referred to as such in this thesis. Due to its floristic, evolutionary and ecological perculiarities, it has experienced intensive botanical research over the years (Mucina and Rutherford, 2006).

The geographical extent of the CFR and its Broad Habitat Units (BHUs) has been defined (Cowling and Heijnis, 2001). South-western CFR includes the Bolands, the West Coast and the Greater Cape Metropolitan Authority administrative areas of the Republic of South Africa (Mucina and Rutherford, 2006). Generally, the physiography of the Cape region can be summarised as having highly heterogeneous relief (uneven topography), with very diverse soil types and wide variation in the local climate (Goldblatt and Manning, 2002).

1.1.1 Climate, topography and soils

There is climatic diversity within the CFR. There is both a South-North gradient of increasing aridity and a West-East seasonality gradient, moving from predominantly winter to year-round rainfall (Cowling et al., 1996, Midgley et al., 2005). The pattern of climate is dominated by the positioning of Southern Africa within the mid-latitudes where it encounters prevailing eastbound cold fronts and low-pressure systems. The presence of these low-pressure systems causes seasonal rainfall and the Cape Fold mountain ranges contribute to the uneven distribution of orographic rains with the leeward interiors receiving very little rain (Tyson and Preston-Whyte, 2000, Chase and Meadows, 2007). The regional mean annual rainfall ranges from 60 to >3300 mm and the mean annual temperature is 16.5ºC (Schulze et al., 2007). Warm to extreme conditions are associated with hot-dry ‘Berg winds’ that flow into the prevailing low-pressure systems from the interior landmasses.

However, significant changes in the frequency of daily atmospheric circulation patterns in the recent past led to significant changes in local rainfall patterns (Midgley et al., 2005). These findings were based on data collated from 12 strategically localised weather stations that together best reflected the local climatic dynamics in the south-western CFR (Table 1.1). The data revealed slight rainfall increase in mountainous regions and the opposite in lowlands. Seasonal patterns have become even more complex (Midgley et al., 2005).

Table 1.1. List of meteorological stations used for the historical climate trends analysis in the south-western Cape, South Africa (Midgley et al., 2005).

Station name	*District*	*Latitude*	*Longitude*	*Altitude (m)*	*Period*
De Keur	Ceres (Koue Bokkeveld)	32° 58’S	19° 18’E	945	1966-2000
La Plaisante	Wolseley	33° 27’S	19° 12’E	260	1963-2000
De Doorns Exp. Farm	De Doorns	33° 28’S	19° 40’E	457	1963-2000
Veldreserve	Worcester	33° 39’S	19° 27’E	275	1962-2000
Robertson Exp. Farm	Robertson	33° 50’S	19° 54’E	156	1962-2000
Bien Donne Exp. Farm	Groot-Drakenstein	33° 50’S	18° 59’E	138	1942-2000
Nietvoorbij	Stellenbosch	33° 54’S	18° 52’E	146	1967-2000
Elgin Exp. Farm	Elgin	34° 08’S	19° 02’E	305	1963-2000
Tygerhoek Exp. Farm	Riviersonderend	34° 08’S	19° 54’E	168	1966-2000
Weltevrede	Barrydale	33° 56’S	20° 37’E	405	1965-2000
Outeniqua Exp. Farm	George	33° 55’S	22° 25’E	204	1967-2000
Langkloof Exp. Farm	Joubertina	33° 47’S	23° 35’E	722	1966-2000

Furthermore, atmospheric perturbations resulted in significant warming trends in both minimum and maximum temperature in the south-western CFR (Midgley et al., 2005). This is evident in the increased minimum temperature observed during December to March and July to September, and increased maximums observed in January, May and August (Figure 1.1). This basically shows that minimum temperature trends increased almost through the year while maximum temperature trends occurred mostly in spring and autumn. On the whole, extreme temperature events seemed to have increased in frequency in recent times.

Topographically, this region is diverse consisting of plains, and undulating mountains with deep ravines (Midgley et al., 2005). The elevations range from sea level to over 2000 m and this is reflected in the elevation of sampled sites. Certainly, this diverse topography and climate seasonality played a key role in the derivation of contrasting nutrient-poor, highly leached sandstone derived soils to heavier shale soils which support the immensely diverse flora in the ecoregion.

Similarly, it was difficult to use the existing network weather stations in the south Western Cape region due to the variability in the landscape. Additionally, the study sites were considerably distant from the existing weather station network which posed a risk in the accuracy of climatic estimates if extrapolated from these stations. For this reason, climatic characterisation of the study (experimental) sites was done based on data point data extracted from the FAO weather database using the New_LocClim software (Grieser et al., 2006). Table 1.2 shows the geographical locations, elevation and annual estimates of maximum and minimum temperature, and mean annual precipitation as indicators of the moisture regimes. The sites ranged from semi-arid dry-stressed to super humid moist-stressed local environments (Schulze, 1997, Schulze and Mararaj, 2007). Bastiaanskloof and New Years Peak are the driest sites and received a mean annual precipitation (MAP) of <500 mm while Silvermine is the wettest site with a MAP of 1127 mm. The records in Table 1.2 reveal a rainfall gradient from the more arid north to the wetter coastal sites in the south. Temperature variation between sites is less apparent although there is an altitudinal adiabatic influence shown particularly at NYP which is the highest site and with the lowest average minimum temperature.

The most appropriate form of climatic data that suited the objectives of this study was insitu weather collected at experimental sites. Due to logistical constrains such was collated from only four of the eight study sites through the use of automatic weather stations. These stations could not adequately represent weather conditions for the full study region because they were geographically distant from each other. This made it inappropriate to relate such data with the other sites.

Climate change projections for the CFR show a drying trend with the gradient weakening eastwards due to weakening winter rainfall, and possibly slightly more irregular but intense summer rainfall (mainly in the east of the region), and generally rising temperatures (Midgley et al., 2005). In essence, there is complex microclimate in the south western CFR which potentially presents difficulty in discussing broad scale species diversities. Notwithstanding, the area is expected to be warmer and drier in the future. This knowledge informs the strategic planning in biodiversity management in the ecoregion.

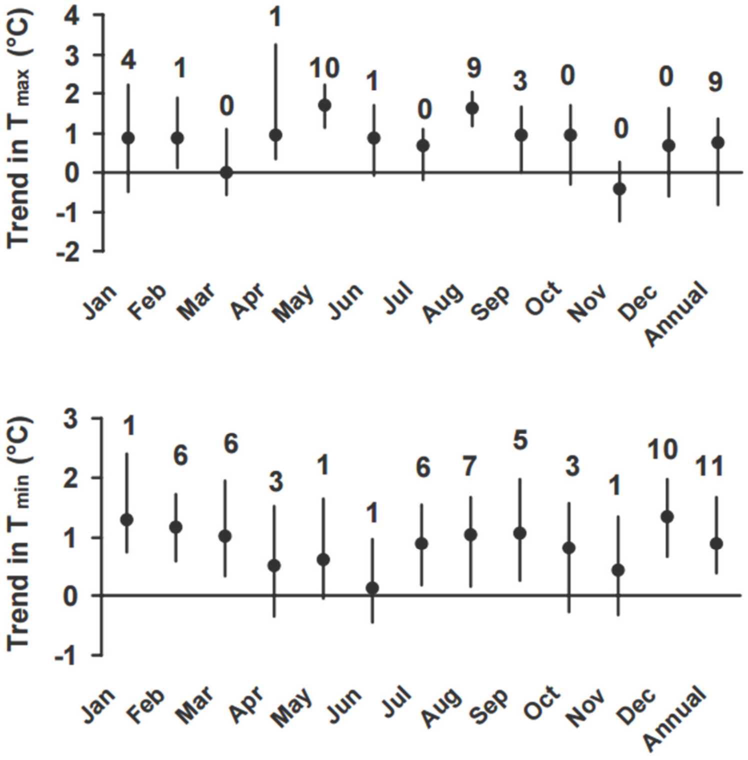


Figure 1.1 Trends in minimum (bottom) and maximum (top) monthly temperatures for 12 stations between 1958 and 2001 (Midgley et al., 2005). Solid dots represent mean change. Bars represent the range between lowest and highest trend value. The number of stations which showed statistically significant linear trends is printed on each data point.

Table 1.2. Locational, climatic and elevation attributes of study sites. Climate data include, maximum temperature (T_{max}), minimum temperature (T_{min}) and mean annual precipitation (MAP) acquired from the FAO Agromet database

Source population	**Acronym**	**Latitude (DD)**	**Longitude (DD)**	**Elevation (m)**	**Tmax (°C)**	**Tmin (°C)**	**MAP (mm)**
Bastiaanskloof	BKF	33.540600S	19.152253E	281	22.5	10.8	468
Cape Point	CP	34.294750S	18.438528E	120	19.5	10.7	541
Jonkershoek	JNK	33.993333S	18.952900E	350	22.4	10.3	933
Kogelberg	KGB	34.279083S	19.008467E	131	21.0	11.5	633
New Years Peak	NYP	33.688806S	19.100806E	1080	23.8	6.8	429
Riverlands	RL	33.486889S	18.595361E	120	21.9	11.5	504
Silvermine	SLM	34.109250S	18.448350E	390	19.5	9.2	1127
Theewaterskloof	TKF	33.981767S	19.131450E	347	22.8	10.3	791

1.1.2 Vegetation

Moll & Bossi (1984) described four distinctive vegetation types in the Fynbos biome, namely Renosterveld, western Strandveld, mesic mountain Fynbos and Sandplain Fynbos, though later on Fynbos has been reclassified into more detailed vegetation units based on their floristic composition and underlying geology (Mucina and Rutherford, 2006). The predominant vegetation in the Cape Floristic Region is fine-leaved Fynbos, a shrubland that occurs mainly on well-leached, infertile soils (Cowling and Holmes, 1992, Richards et al., 1997, Rebelo et al., 2006). Towards the north, this vegetation becomes mixed with and then replaced by grass-like Renosterveld which is in turn replaced by arid Succulent Karoo vegetation (Moll and Bossi, 1984, Rebelo et al., 2006). To the west, are the low growing sclerophyllous broad-leaved Strandveld shrublands which do prograde into taller scrub forest vegetation towards the West Coast (Bossi et al., 1984). Also, embedded within the Fynbos are edaphically specialised vegetation units that occur in randomly located freshwater wetlands, alluvial or salt pan vegetation (Mucina and Rutherford, 2006). The bioregions that make up the Fynbos biome are classified according to the geology (origin) of their substrates while also considering climate and centres of endemism.

Fynbos is the key vegetation type of the CFR and consists of ericoid, proteoid, geophytes and restioid life forms (Cowling et al., 1997). Within Fynbos, water availability seems to be a key element in structuring the community into its components across the landscape (Mucina and Rutherford, 2006). E.g. in the arid extreme, asteraceous Fynbos are established; in moist extremes, restioids, gramminoids, proteoids, ericoids and waboomveld are common; in deep soils with widely fluctuating water tables are dominated by restioids and occasionally ericoids. Additionally, the composition of the plant biota appears to be determined by success of post-fire establishments because shrub seedlings fail to keep up in root contact with the dropping water table) (Kruger, 1983, Moll and Bossi, 1984). In the absence of fire, Fynbos becomes senescent and forest and thicket elements begin invading (Cowling and Bond, 1991, Bond and Keeley, 2005).

Embedded within the Fynbos units are vegetation units that are edaphically characterised as wetlands of varying permanency and origins (Sieben et al., 2004, Mucina and Rutherford, 2006). CFR wetlands are mostly mountain seeps in sandstone located on the side-slopes of valleys and dominated by colluvial (i.e. gravity-driven), unidirectional movement of water down-slope. Water inputs are primarily via subsurface in flows from the upper slope direction and direct falls from precipitation. Water movement through the wetland is mainly in the form of interflow, with diffuse overland flow (known as sheet wash) especially with significant downpours. The frequency and duration of inundation and saturation of the wetland determines its soil morphology and chemistry (e.g. level of oxygenation, build-up of carbon and nutrient cycling), and is thus one of the key determinants for the types of vegetation inhabiting the wetland. Within Fynbos wetlands, species may occur in zones where often a single species may dominate, or different species may occupy apparently identical ecological niches in different geographical areas. These communities are best mapped at scales finer than 1:25 000 (Boucher, 1978). Structurally, Fynbos wetlands are mostly restioid and ericoid but may also be dominated by Poaceae.

The Fynbos Biome and the Fynbos vegetation in particular are immensely threatened by both urban and alien vegetation incursions. Among the critically endangered are those in the low-lying and flat areas whereas the sandstone mountain Fynbos are the least threatened. As such, a network of nature reserves managed by both the national government and regionally e.g. South African National Biodiversity Institute (SANBI), South African National Parks (SANParks), Cape Nature, etc. have been established in the biome to help curb external threats. Other initiatives enhance the reestablishment of Fynbos in the area like the Cape Action Plan for People and the Environment (CAPE) and Working for Fire, etc.

1.2 Plant - soil moisture relationships

The water requirement of any plant species includes the quantity, quality and timing of the water needed to complete its life cycle. This collectively includes the depth, duration, frequency and timing of moisture availability, all of which define the water regime in the habitat. It has been observed that water is not evenly distributed in the soil environment (Rodriquez-Iturbe et al., 1995, Qiu et al., 2001). In some cases, water availability is observed to change along a gradient. Plants, too, have been observed to segregate along such water gradients in nature (Silvertown et al., 1999, Araya et al., 2011). This is because specific plant species have unique optima for available environmental resources forming niches that tend to be geographically structured based on the variations of such optima along any existing environmental gradients. Although, niche overlap may also occur between optima of different species, the overall structuring of the community might be influenced by interspecific competition (Ellenberg, 1953, Bartelheimer and Poschlod, 2016). Such competition may cause species to shift from the fundamental to the realised niche in a process termed niche differentiation. As a result of niche differentiation, interacting species get arranged in zones along the hydrological gradient, the result of which is the existence of groups of species that coexist in interactive assemblages and species that occupy distinct microhabitats.

The hydrology of the soil in wetlands is defined by the positioning of the water table and the duration of inundation as such described to range between frequently to constantly waterlogged soils (Araya et al., 2011). Groundwater levels in the soil can have important implications for plants performance. Low water levels during drought conditions lead to drought stress in plants while high water levels induce waterlogging that causes hypoxic stress (low oxygen concentrations) conditions in soils or even results in accumulation of toxic compounds if sustained over a long time span (Barber et al., 2004, Silvertown et al., 2015). Wetland plants respond in a number of ways to wet and waterlogged conditions. These plants exhibit certain adaptation, such as, formation of aerenchyma and adventitious roots causing them to be tolerant to water logging stress (Keddy, 2010).

For Fynbos wetland species are sustained by moisture from direct rainfall or from shallow seeps associated shallow groundwater levels. This thesis focuses on a Fynbos family, the Restionaceae, in eight wetland communities in the Cape Floristic Region (CFR) in South Africa. Although often comprising a majority, Restionaceae are not the only species inhabiting wetlands in the region. However, an understanding of how a key plant group like Restionaceae survive in typical wetland regimes would provide a further understanding of the requirements and supply of water for the rest of the species in these communities taking into consideration that most species rely on this important shared resource though to varying degrees. Because niche differentiation in Fynbos is not fully understood, it is important to investigate some of the dynamics that characterise the hydrology of the habitat. The current study investigates the water regime requirements of Restionaceae in mountain wetlands, in the CFR and the impact of variations in the hydrological gradient at a local scale.

1.3 Niche segregation

The uneven distribution of plant species on both global and local scales is attributed to their adaptation to environmental disparities. At the localized scale, various niche hypotheses have been proposed to explain the simultaneous occurrence of many different plant species in any one habitat (Hutchinson, 1957). Grinnell (1917) just defined the species niche as the sum of all physical, chemical and biological conditions required by a species for survival, growth and reproduction. The Hutchinsonian niche hypothesis considers the niche as a multidimensional hypervolume in which the physiological adaptability of species to existing available resource is an added dimension to the previously defined environmental conditions. Hence, the niche of any species is defined by the environmental dimension within the hypervolume in which that species can survive interspecific competition (Hutchinson, 1957, Warren, 2012). Based on this, the niche of any species is the space where it is considered to out-compete other members of the local ecological community.

The distribution of plant communities is limited by both dispersal and physical factors. Physical influences may vary at different ecological scales. At a regional level, the distribution of plant communities is often related to precipitation differences associated with topographic features such as elevation. At the local scale, e.g. within small plots, plant species distribution is also affected by the seasonal variation in the availability and behaviour of water. This has been demonstrated in wetlands where observed changes in plant species diversity reflect their combined response to changes in water levels, temperature, nutrient cycling, physiological acclimatization and community reorganisation (Raulings et al., 2010).

Niche segregation occurs among different plant species in a community where some species experience higher levels of tolerance to prevailing local environmental conditions than their competing rivals (Whittaker, 1965, Silvertown, 2004). For example, forest species are partitioned by light gradients through a trade-off between growth rate in better light conditions and survival in shade (Kobe, 1999, Holste et al., 2011, Way and Pearcy, 2012). Herb species in temperate grasslands (Denslow et al., 1998) and shrub and herb species in arid ecosystems are segregated according to rooting depth (Briones et al., 1996). Tundra species which utilize different nitrogen sources also show some partitioning based on the temporal availability of nitrogen resources (McKane et al., 2002). These experiments point also to the importance of nutrients and hydrology in niche segregation (Reynolds et al., 2003). Meadow plants segregate along hydrological gradients (Silvertown et al., 1999). Segregation along the hydrological gradient, in particular, has been attributed to root competition between congeneric species as shown in mesocosm experiments (Bartelheimer et al., 2010).

Sometimes, however, internal topographical variations generate mosaics of water regimes at local spatial scales thereby allowing plants species with different water regime requirements and or moisture tolerances to segregate over small distances (Raulings et al., 2010). Fine-scale differences in water regime result in a gradient of water stress where different plants tolerate varying levels of stress in different ways and therefore their competitive ability changes along these hydrological gradients (Araya and Garcia-Baquero, 2007). This results in niche segregation (Silvertown, 2004) which may be explained as a trade-off between tolerance of both excess wetness and dryness also referred to as ‘aeration stress’ and ‘drying stress’ (Silvertown et al., 1999).

By definition, hydrological niche segregation is the partitioning of species on a soil moisture gradient (Araya et al., 2011). Hydrological niche segregation occurs in many different vegetation biomes whether in wet, mesic or arid environments. Species in riparian meadows in the USA, for example, appear just as differentially sensitive to water table depth as plants in European wet meadows (Castelli et al., 2000, Dwire et al., 2006). In tallgrass prairie in Kansas, coexisting C3 grasses are partitioned according to soil water availability (Nippert and Knapp, 2007) and there is also indirect evidence of this occurring in European experimental grasslands (Verheyen et al., 2008). Partitioning of competing species due to soil moisture availability has been repeatedly found amongst desert plants (Nobel, 1997, Reynolds et al., 1999, Schwinning and Ehleringer, 2001, Wilcox et al., 2004), in Mediterranean shrublands (Filella and Penuelas, 2003, Parolin, 2001) in woodlands (Groom, 2004), in savannah (Weltzin and McPherson, 1997, Jackson et al., 1999, Kulmatiski and Beard, 2013) and in temperate (Dawson, 1996, February et al., 2013) and tropical forests (Meinzer et al., 1999, Stratton et al., 2000, Estrada-Medina et al., 2013, Mendivelso et al., 2013). Likewise, littoral (Grace and Wetzel, 1982) and fen (Kotowski et al., 2006) species segregate under interspecific competition into distinct zones along hydrological gradients. Similarly, investigations on the patterns of water use among coexisting plant species in Mediterranean-climate ecosystems of southern Spain have shown that the existence of species-specific isotopic niches reflects eco-physiological niche segregation (Moreno-Gutiérrez et al., 2012).

Both phylogenetic and physiological mechanisms have been examined in hydrological niche segregation. Molecular phylogenetic analysis of traits that determine within-habitat diversity in two mesotrophic grassland communities in which species segregate along hydrological gradients has shown practically no evidence of a correlation between the ecological and evolutionary distances separating species (Silvertown et al., 2006). These findings indicate that hydrological niches are evolutionarily labile and that species must occupy different niches in order to coexist. In species-rich plant communities, highly significant trade-offs between species tolerance of soil aeration stress and soil drying stresses have been demonstrated in niche separation (Silvertown et al., 1999).

The above soil stress factors (Bartholomeus, 2009) are quantified by sum exceedance values (SEVs). These define the duration of physiologically extreme conditions of aeration stress in soil (caused by waterlogging) and soil drying stress which occurs during dry spells (Stroh et al., 2013). A sum exceedance value for soil drying - denoted by SEVd - is the cumulative period in which the soil moisture tension exceeds 50 kPa, a level that potentially induces stomatal closure (Henson et al., 1989). Alternatively, a sum exceedance value for soil for aeration, - denoted by SEVa - is the cumulative period in which the soil air-filled porosity falls below 10% of the soil volume level which precludes free diffusion of oxygen in the topsoil (Wesseling and Van Wijk, 1957, Stroh et al., 2013). Sum exceedance values are expressed in units of pressure over time and have the advantage that they incorporate a measure of temporal variation in soil moisture at a scale relevant to the physiological tolerances of plants (Araya and Garcia-Baquero, 2007). In summary, high values of SEVa indicate waterlogging and high values of SEVd indicate drought.

Two underlying physiological mechanisms have been proposed that may explain differential plant species tolerance of either dry or waterlogged conditions along a soil moisture gradient. The first is species differences in water use efficiency (WUE), namely the ratio of CO_2 assimilated to water transpired (Araya et al., 2011). The second is species differences in nutrient acquisition (Araya, 2005), especially nitrogen whose mineralization is limited by anoxia in waterlogged soils and by lack of water in dry soils (Bartelheimer et al., 2010).

1.4 Climate change impacts

It has been proposed that climate change is likely to have a major influence on biodiversity worldwide after 2050 (Strengers et al., 2004, Assessment, 2005, Solomon et al., 2007). While the predicted ultimate percentage loss of species due to climate change varies widely from study to study (Thomas et al., 2004b, Malcolm et al., 2006, Thomas et al., 2006, Chen et al., 2011) the IPCC reports that 20–30% of animal and plant species are likely to be at high risk of extinction with a global mean annual temperature rise of 2–3 ^{o}C (Solomon et al., 2007). A study of 1350 European species under seven climate change scenarios showed that more than half of them were vulnerable to future scenarios, with the most impacted species being those in the Mediterranean climate regions (Thuiller et al., 2005). Current trends in the seasonal distribution of available moisture in the southern African region indicate that the region is semi-arid and highly vulnerable to climate change (Williams et al., 2010). Indeed, global climate change models predict significant drifts in climatic trends by the year 2100 (IPCC, 2007). As such, plant available moisture may become much more seasonal in the region and result in likely shifts in plant community structures (Zedler, 2009). Research has shown that, despite the numerous possible explanations for changes in biological patterns and communities, climate change effects are already affecting biodiversity through range shifts and alteration of phenology (Fahrig, 2003, Parry, 2007, De Chazal and Rounsevell, 2009).

One of the major pathways through which climate change may impact biodiversity patterns is through altered hydrologic patterns and processes (Weltzin et al., 2003, Konar et al., 2013, Reyer et al., 2013). It is well known that climate change will impact global precipitation patterns (Solomon et al., 2007, Arnell et al., 2011), resulting in increased variability in rainfall regimes both temporally and spatially (O'Gorman and Schneider, 2009, Chou et al., 2012), which, in turn, will affect the hydrologic conditions that regulate ecological processes (Currie, 1991, Rosenzweig, 1995, McGill et al., 2010, Poff and Zimmerman, 2010). The hydrologic control of niches occurs across both terrestrial and aquatic environments and is best reflected in the biodiversity within ecosystems.

The number of niches that a given ecosystem contains has long been thought to be a major driver of species diversity (Hutchinson, 1959, Rosenzweig, 1995). This is best displayed within wetlands which have been a principal location for studying the relationship between hydrology and the structuring of vegetation communities (Mitsch and Gosselink, 2007). Due to their dynamic hydrology, climate change impacts in wetland communities are likely to be particularly severe, since slight changes in water availability may profoundly influence their biodiversity.

1.4.1 Wetland ecosystems and climate change impacts

The hydrology of a wetland environment is often described by its hydro-pattern or hydroperiod (Ollis et al., 2015). This is the combination of the frequency of inundation events along with the duration and depth of inundation. However, the role of hydrology in structuring vegetation communities in wetlands is difficult to determine due to a suite of interacting variables (Busch et al., 1998, Ross et al., 2003, Zweig and Kitchens, 2008). Despite this, multiple studies have shown a strong relationship between hydrologic patterns and wetland vegetation communities in the Everglades National Park (Davis and Ogden, 1994, Gunderson, 1994, Zweig and Kitchens, 2009). An examination of hydrological niches across temporal and spatial scales in this wetland environment found that mean water table depth and percentage time inundated best describe the vegetation niches. For example, muhly grass (*Muhlenbergia* sp.) occurred most often at shallower water table depths and at locations that were not inundated for long periods of time whereas the converse applied to bay scrub (*Laurus* sp.) plants. However, results for sawgrass (genus: *Cladium*, a large sedge plant), the most common vegetation community across the Everglades National Park, supported the conclusion of earlier studies that hydrology is not the only factor structuring sawgrass niches (Hofstetter and Parsons, 1979, Gunderson, 1994). Todd et al. (2012) concluded that, while multiple factors can influence the landscape distribution of vegetation communities, hydrology often plays a principal role.

The Earth's climate is changing more rapidly than in the past because of anthropogenically increased emissions and atmospheric concentrations of greenhouse gases and impact both human livelihoods and natural ecosystems at the local scale

(Acreman et al., 2009). Wetlands are one example of local ecosystems and their spatial nature is controlled by prevailing environmental variables like precipitation, temperature and the associated evapotranspiration levels (Mitsch and Gosselink, 2007). Hence, wetland ecosystems are likely to be altered because of the direct influence of climate changes on precipitation and its indirect impacts on evapotranspiration through changes to temperature, radiation and wind speed (Acreman et al., 2009). This means that wetland ecosystems that are solely dependent on precipitation are the most vulnerable to climate change because of the direct influence of precipitation to available soil moisture (Winter, 2000). Indeed, the nature of the responses by a variety of wetland ecosystems assessed for climate change impacts has been attributed to the balance between changes in water table and other physical elements (Erwin, 2009).

In an effort to gauge the impacts of projected changes in precipitation on plant diversity in the Everglades National Park, relationships developed between vegetation communities and hydrologic variables (Todd et al., 2012) were utilized to model future hydroperiod characteristics for the region (Todd et al., 2010). Projected changes in mean water table depth and percentage time inundated under various climate change scenarios were used to determine potential impacts on vegetation communities (Todd et al., 2012). The findings showed that under a high atmospheric carbon dioxide emission scenario, precipitation would decrease across the Everglades National Park by as much as 8%, leading to an associated decrease in mean water table depth and percentage time inundated. Under this climate scenario, vegetation communities such as muhly grass, which favour xeric conditions, would increase by 15% whereas that of bay-hardwood scrub, which favours wetter environments, would decrease by 66% (Todd et al., 2012).

Another wetland region that has undergone intense research regarding the influence of changing climate on vegetation community structure and biodiversity is the Prairie Pothole Region of North America. This region has numerous wetlands covering a suite of inundation regimes, ranging from temporarily (one to two months) to semi-permanently (mostly throughout the year) inundated areas each associated with different vegetation types. For this region, several models have been developed that simulate changes in vegetation across a range of hydrologic parameters including precipitation, runoff, potential evapotranspiration, snowpack and subsurface in-flow (Poiani and Johnson, 1993, Poiani et al., 1996, Johnson et al., 2004, Johnson et al., 2005). When climate change scenarios of increased temperature were incorporated into these models, these wetlands showed increased rainfall, earlier snow melting, decreased soil water depths and volume, diminished hydroperiods, and reduced runoff from snowmelt and rainfall, and less-dynamic vegetation cycles (Werner et al., 2013), especially in vegetation with low productivity and biodiversity (Johnson et al., 2010).

Similarly, climate change features prominently as a real threat to meadows of the Sierra Nevada mountain ecosystems. Here, snowpack melts earlier than estimated in response to increased temperature coupled with the fact that, most of the rain falls in winter leading to very long and increasingly drier growing seasons. As a consequence, more xerophytic species would proliferate as opposed to wet meadow types (Lowry et al., 2011). In temperate Europe, summer temperature increases of 2°C would cause increased groundwater levels swelled by moisture from a 6% increase in winter precipitation, resulting in decreased seepage fluxes and reduced supply of nutrient-poor groundwater favourable to semi-terrestrial vegetation (Van der Knaap et al., 2015).

Furthermore, the vulnerability of wetland ecosystems to climate change has been demonstrated in tropical mangroves and floodplains in the Brazilian Amazon (Barros and Albernaz, 2014). Here, different climate change scenarios have demonstrated modifications of hydrological regimes leading to severe droughts or inundations, a cause for concern for Amazonian communities that depend on these assets as an economic resource. For example, a reduction in rainfall would lower water levels thereby reducing the extent of mangroves and floodplains and their species diversity. Conversely, an increase in rainfall would lead to a substitution of species less adapted to extended inundation. Similarly, studies of the Macquarie Marshes, the largest semi-permanent wetlands in south-east Australia that sustain a wide range of floodplain woodlands species, have revealed the likely disappearance of many species that are intolerant of projected dry spells. Although prolonged wet spells would be detrimental to river red gum and black box woodlands at the same sites (Fu et al., 2015). This implies that whichever way the turn of climate extremities, there will be dire consequences for less resilient species to such adversities resulting in devastating results on biodiversity.

In line with global trends, climate change will also significantly impact the distribution of many species in the Cape Floristic Region (Yates et al., 2010) where the climate is predicted to become warmer and drier with a shift from a winter to summer precipitation (Hewitson and Crane, 2006) and a likely alteration in niche segregation amongst Restionaceae species in this region (Araya et al., 2011). Species in the CFR tend to be locally abundant but also commonly patchy and limited in distribution ranges (Cowling et al., 1992, Myers et al., 2000, Latimer et al., 2005). These factors suggest that the region's biodiversity may be sensitive to shifts in the precipitation regime predicted under future climate change (Christensen et al., 2007, Wilson and Silander, 2014).

In conclusion, change in the environment is continuous and is the consequence of diverse factors and to some extent plants of all habitat types have developed the ability to readjust to the constantly changing environment on which they depend for survival. Change in global climate is primarily natural but also significantly influenced in recent times by anthropogenic activities (drivers). Each species has particular water regime requirements. Under future climates, these water regimes are likely to change in wetlands. Changes on the hydrological system have direct impact on the availability of soil moisture which is a major component in terrestrial habitats and by extension a control on the community composition and species richness. In response real-time shifts in species distribution are observed which then highlights the need to understand existing and future patterns to better manage future impacts in potentially vulnerable communities. So far most assessments of wetlands for possible impacts of climate change including Acreman et al. (2009) have been at a regional scale. The focus of this thesis is on how hydrological alterations caused by climate change will impact the fine scaled wetland ecosystems in the Fynbos Biomes of the CFR.

1.4.2 Species distribution modelling as a tool for biodiversity impact assessment

To address the ever-increasing need for understanding processes that underlie the distribution of plant species and communities as well as predicting the impacts of climate change, the most traditional method in use has been the modelling of species distributions and assessing the distributional change possibilities (Guisan and Thuiller, 2005). Species modelling also referred to as habitat distribution modelling or niche habitat modelling, has proven to be an excellent tool for assessing the impacts of changes in environmental variables in the ecosystem (Araújo et al. 2005, Hijmans and Graham 2006). A number of such studies assessed the impact of climate change on the vegetation biomes and were paired against hydrological conditions (both dry and/or wet) (Midgley et al., 2003, Hayhoe et al., 2007, Bellard et al., 2012, Flint and Flint, 2012, Guo et al., 2016a). Similarly, hydrological variation along a gradient have been considered in attempts to study the possible impacts of climate change in the CFR using hydrological variables (Miller and Bever, 1999, Bendix and Hupp, 2000, Silvertown et al., 1999, Araya et al., 2011). Hence, the resulting niches can correctly be referred to as hydrological niches (Silvertown et al., 2015).

1.4.3 The Restionaceae in the CFR

Fynbos is the key vegetation type of the CFR and consists of ericoid, proteoid, geophytes and restioid life forms (Cowling et al., 1997). The restioids are comprised of Restionaceae which based on evidence from fossil pollens originated more than 65 million years ago (Bremer, 2002). They are a family of perennial, evergreen, grass-like plants that range in height between 10 and 300 cm (Rebelo et al., 2006) and do dominate large areas of the Cape Floristic Region (Goldblatt and Manning, 2002). The Restionaceae include about 480 species globally with 330 species occurring in Africa, 150 species in Australia, four species in New Zealand, one species found in South East Asia and one in South America (Cowling et al., 1996). The Restionaceae, along with other plants in the CFR, are threatened by urbanization, agricultural expansion, alien plant invasion and groundwater abstraction from sandstone aquifers which underlie the Fynbos communities (Rouget et al., 2003).

The ability of the Restionaceae to tolerate a wide range of water regimes allows them to successfully co-habit within mixed plant communities (Linder et al., 1998, Hardy et al., 2008). The species is capable of niche segregation along fine-scale hydrologic gradients (Silvertown, 2004) as is already observed in seasonally saturated wetland habitats (Aston, 2007, Araya et al., 2011). This is attributed to their differential tolerance of excess soil wetness or dryness (Silvertown et al., 1999).

What is not known, however, is how the spatial distribution of Restionaceae species at a local scale is related to soil hydrology and what the response in the future of species distributions will be due to perturbations arising from changes in climate or subsurface moisture in the future. Similar studies of the ecohydrology of diverse grassland communities in English meadows have successfully informed managers what their water regime requirements and their response to hydrological change are (Gowing et al., 2002, Johnson et al., 2010). Consequently, knowledge of the impacts of climatic and anthropogenically induced hydrological changes on the Restionaceae could inform managers and other decision-making bodies about the most effective future planning strategies for conserving its biodiversity. Effective management requires an understanding of the nature of current and future climate changes in terms of changes in evapotranspiration and the impact on local soil hydrology. Furthermore, hydro-ecological models can be used to quantify the impact of climatic changes subsequent to an understanding of water regime requirements in Restionaceae communities. So far, it has been established that, the distribution of the Restionaceae is mostly influenced by the depth to the water table relative to other hydrological parameters at a Silvermine in the CFR (Guo et al., 2015). This kind of knowledge adds to the understanding of important environmental variables through adequate monitoring (Huntley et al., 2006). Such control may aid in maintaining the species natural abundance trends and the species variability of habitats (Ferreira et al., 2011, Ehrlén and Morris, 2015).

The primary goal of this research was to develop multipliable analytical methods and procedures to quantitatively assess how climate controls current subsurface hydrological and ecological systems in the Fynbos region of South Africa. The collected ecological data was expected to appropriately address some principal research questions, including: what are the water regimes of key Cape Restionaceae species, how do these underpin their spatial distribution at fine spatial scale and how might changes in water availability (either through abstraction from underlying aquifers or future changes in climate) affect Restionaceae community composition? In addressing the above key questions, the following concerns get resolved:

1. Do Restionaceae species occupy distinct hydrological niches?

2. Which hydrological variables best explain this spatial distribution?

3. What are the relationships between the spatial distribution of Restionaceae species and hydrologic variables at plot scale?

4. To what extent would changes in climatic variables affect soil moisture contents?

5. How would changes in future climate scenarios affect the future distribution of Restionaceae?

6. What are the implications of changes in soil moisture for the potential distribution, management and conservation of Restionaceae?

The content of this thesis will to a great extent provide answers to the above key questions.

1.5 Objectives

The main aim of this thesis is to envision the potential impact of a change in local shallow hydrological systems on the diversity of seasonal wetland communities in the south-western Cape Floristic Region through ecohydrological modelling at fine spatial scale (within micro-scale plots). The specific objectives addressed are the following:

Objective (i): To assess the distribution and ecology of Restionaceae species in selected Fynbos wetlands in order to decipher the underlying factors that underpin their distribution. Chapter 3

Objective (ii): To quantify the nature of evapotranspiration (ET) as the main driver of soil hydrology in this semi-arid region now and in the future. Chapter 4

Objective (iii): To derive soil parameters and test for predictability of a workable soil moisture model which simulates variations in soil moisture contents with the aim of replicating the hydrological framework at other study sites. Chapter 5

Objective (iv): To establish models of the potential distributions of Restionaceae species under current microclimatic (hydrological) conditions using the Maximum Entropy (MaxEnt) species distribution modelling algorithms. Chapter 6

Objective (v): Establish potential future distribution ranges of the Restionaceae species by forecasting the hydrological space by 2100; and assess the impact of climate change and possible distributional changes at a fine scale. Chapter 7

1.6 Approach

This thesis integrates the application of ecohydrology, Geographic Information System (GIS), ecological multivariate analyses and spatial ecology at plot scale using primarily species distribution modelling (SDM) techniques that have, thus far, been applied mainly within regional settings. Research results would add to the pre-existing ecological perspective of the African Restionaceae within the area, and further ecologically assess the Restionaceae across wetland sites in the CFR. The initial chapters are devoted to the experimental setup and assessment of spatial as well as the ecological status of Cape restioids within these sites. These assessments were then used to support and contribute to the interpretation of the SDM analyses (Chapters 6 and 7).

Most of the data that was used for this thesis was collected from fine-scale experimental plots. The microclimate data were specifically generated for use within the scope of the study. The SDM techniques used were adapted from international literature and applied locally at fine scale.

1.7 Thesis Structure

This thesis is presented as chapters which between them address the aims and objectives as well the key research questions of this study. The order of discussion of the chapters is as follows:

Chapter One introduces key concepts in the study as the Restionaceae in the CFR. The rationale and the general objectives of the study are explained. These are framed into key questions are addressed in later chapters, and form the basis of the chapter structuring.

Chapter Two is a descriptive account of the study area, sample sites and an overview of ecological data.

Chapter Three presents an assessment of the distribution and ecology of Restionaceae species in selected Fynbos wetlands order to decipher the underlying factors that underpin their distribution. A link between the ecological diversity and the environmental variability is examined.

Chapter Four presents the quantification of evapotranspiration using daily climatic data collated from synoptic (automatic) weather stations in parts of the south western CFR. The outlook of ET under two possible emission scenarios by 2100 was also analysed using downscaled daily temperature and solar radiation derived from Global Circulation Models (GCM).

Chapter Five presents a soil water balance model which was developed specifically to simulate soil moisture variation in fine-scale field plots. The focus of the chapter is on the application rather than on the development of the hydrological model. It includes a detailed description of the modelling approach that is used to analyse for both current and future variations of soil water contents using climatic records (rainfall and evapotranspiration) which were derived in Chapter Four as inputs. Model results were compared with observed field measurements while sensitivity analysis and calibration were implemented to improve the fits of the model.

Chapter Six presents the modelling of Restionaceae niches in wetland communities in the CFR at fine spatial scale. Spatial interpolation is used to establish continuous hydrological surfaces from the in situ field measurements which then served as spatial inputs for ecological niche modelling. The species hydrological niche models also explained the importance of individual hydrological (physical) variables; species preferred ranges and afforded a comparison of the niches of frequently occurring species.

Chapter Seven is an account of the potential future distributional ranges of the Restionaceae species by forecasting the hydrological space by 2100 including possible distributional changes as an impact of climate change.

Chapter Eight is a synthesis of the major findings, their implications for managing the biodiversity of Restionaceae and recommendations for future when moisture regimes change.

CHAPTER 2 DESCRIPTION OF STUDY AREA, SITES AND ECOLOGICAL DATA

2.1 Introduction

The aim of this chapter is to provide a description of the experimental (study) sites by discussing the locations, sampling distributions, species compositions, data capture and an exploratory data analysis. For a number of decades, the Cape Floristic Region has undergone intensive botanical research since it was established to have perculiar floristic, evolutionary and ecological characteristics. This chapter is an attempt at describing the ecology of study sites.

2.2 Study area

The study area is limited to the southwest part of the Cape Floristic Region (CFR) which makes up part of the Fynbos biome of Southern Africa. The Southwest Fynbos Bioregion (F02) forms the floristic heartland of the Fynbos biome and is flanked by the West Coast (F07) and East Coast (F08) Renostervelds(Mucina and Rutherford, 2006). It makes up about 12 500 sq. km of the approximately 90 000 sq. km total area covered by the CFR. The substrate geology is sandstone (occasionally granite) and sand-defined units. It includes mountains of the Kogelberg, Du Toits Kloof, Riviersonderend, Cape Peninsula, Bredasdorp highlands and Sandveld on the flats such as in the Hopefield District.

2.3 Sites

Eight sites representing much of the vegetation diversity in the CFR were established in the area (Figure 2.1). The ecological considerations and the experimental outlay of these sites have been detailly described by Araya et al. (2011). The setup methodology of Araya et al. (2011) was replicated in two additional sites at Bastiaanskloof and Silvermine which were laid out afterwards with the assistance of the student. The sampled sites ranged from lowland (120 m) to montane (1080 m) points and their distribution represented much of the Fynbos diversity the bioregion.

Sites are labelled A to H in a north-south orientation in Figure 2.1 which is the current local climatic gradient described by Midgley et al. (2003) and referred to in Section 1.1.1 above. These sites as shown in Figure 2.1 included: A. Riverlands (33º 29'S 18º 35'E) located on Atlantis Sand Fynbos, B. Bastiaanskloof (33º 32’S 19º 09’E) located on Hawequas Sandstone Fynbos, C. New Years Peak (33º 41’S 19º 06’E) located on Boland Granite Fynbos, D. Theewaterskloof (33º 58’S 19º 07’E) located on Western Ruens Shale Renosterveld, E. Jonkershoek (33º 59’S 18º 57’E) located on Boland Granite Fynbos, F. Kogelberg 34º 16’S 19º 00’E located on Ruens Silcrete Renosterveld, G. Silvermine 34º 06’S 18 26’E located on Peninsula Sandstone Fynbos and H. Cape Point 34º17’S 18º 26’E located on Hangklip Sand Fynbos (Mucina and Rutherford, 2006).

2.4 Data

The total of 1763 quadrats was examined at eight sites labelled A to H in a north-south orientation in Figure 2.1. Fifty-five species of Restionaceae representing 12 genera were examined at these sites. Figure 2.2 shows the phylogenic relationships between these genera. A listing of these species including authorities and references is found in Table 2.1. The relative frequency of occurrence of species as a percentage of the total number of species that are present at each site and the frequency of occurrence of each species is shown in Table 2.2. The values in this table clearly show the unevenness in both species diversity and density among the sites.

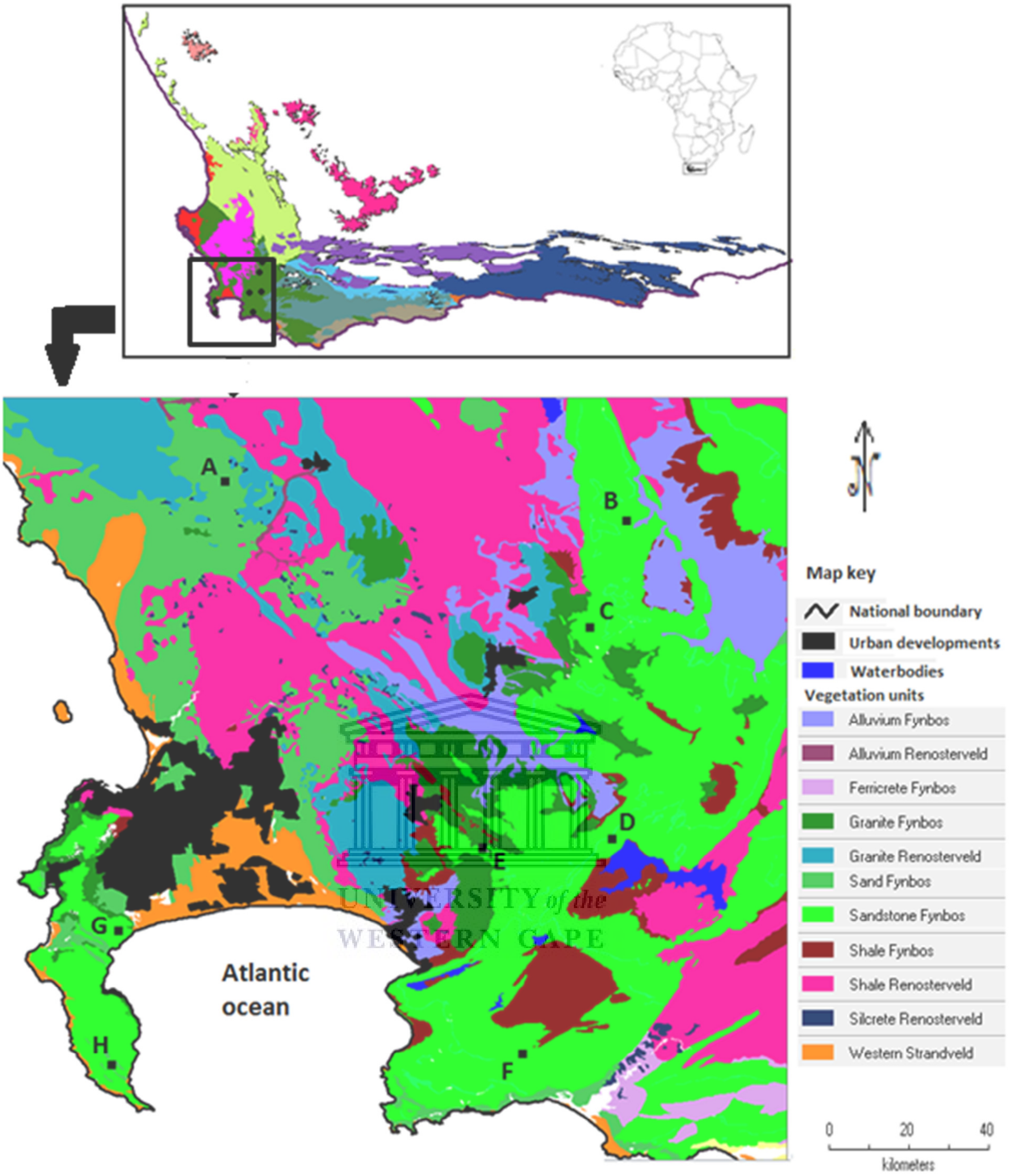


Figure 2.1 Map showing vegetation units of the south-westernFynbos biome. Points A to H represent study sites. A = Riverlands (RL), B = New Years Peak (NP), C = Bastiaanskloof (BK), D = Theewaterskloof (TK), E = Jonkershoek (JH), F = Kogelberg (KB), G = Silvermine (SM), H = Cape Point (CP). Map generated by author using Diva-GIS®. Data sourced from Mucina and Rutherford (2006).

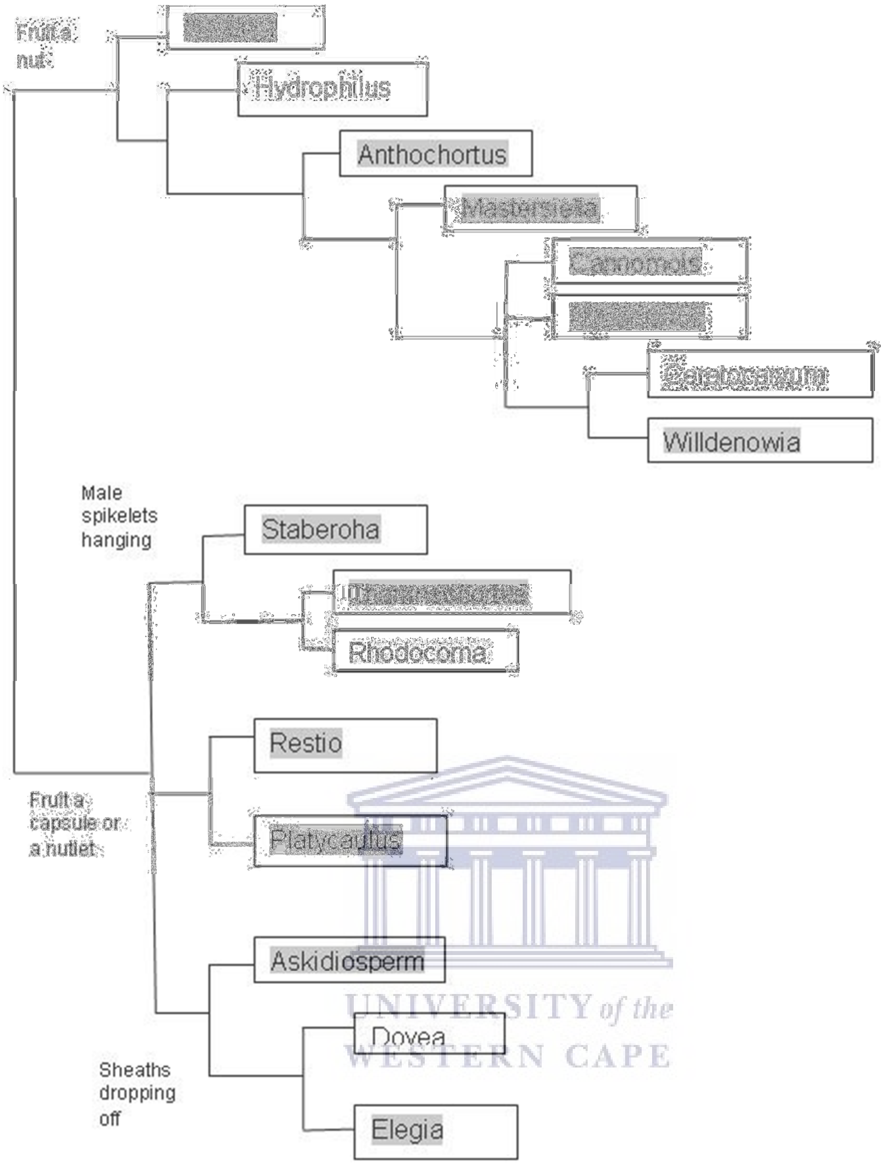


Figure 2.2 Phylogenic relationships between Restionaceae genera. The shaded boxes are genera that are represented in study samples. Source: Haaksma and Linder (2000).

Table 2.1. Names and authors of Restionaceae from all sampled sites.

Restionaceae species	**References**
Anthochortus crinalis (Mast.) H.P.Linder	Bothalia 15: 486 (1985)
Askidiosperma nitidum (Mast.) H.Linder	Bothalia 15: 432 (1985)
Cannomois parviflora (Thunb.) Pillans	Trans. Roy. Soc. South Africa 16: 415 (1928)
Elegia asperiflora (Nees) Kunth	Enum. Pl. 3: 474 (1841)
Elegia caespitosa Esterh.	Bothalia 15: 421 (1985)
Elegia capensis (Burm.f.) Schelpe	J. S. African Bot. 33: 156 (1967)
Elegia coleura Nees ex Mast.	Monogr. Phan. 1: 358 (1878)
Elegia cuspidata Mast.	J. Linn. Soc., Bot. 10: 240 (1869)
Elegia deusta (Rottb.) Kunth	Enum. Pl. 3: 460 (1841)
Elegia filacea Mast.	J. Linn. Soc., Bot. 21: 589 (1885)
Elegia hookeriana (Mast.) Moline & H.P.Linder	Syst. Bot. 30: 772 (2005)
Elegia juncea L.	Mant. Pl. 2: 297 (1771)
Elegia neesii Mast.	J. Linn. Soc., Bot. 10: 246 (1869)
Elegia nuda (Rottb.) Kunth	Enum. Pl. 3: 462 (1841)
Elegia thyrsifera (Rottb.) Pers.	Syn. Pl. 2: 607 (1807)
Elegia vaginulata Mast.	J. Linn. Soc., Bot. 21: 586 (1885)
Hypodiscus alboaristatus (Nees) Mast.	J. Linn. Soc., Bot. 8: 255 (1865)
Hypodiscus aristatus (Thunb.) C.Krauss	Flora 28: 338 (1845)
Hypodiscus willdenowia (Nees) Mast.	J. Linn. Soc., Bot. 10: 259 (1869)
Mastersiella digitata (Thunb.) Gilg-Ben.	Nat. Pflanzenfam. ed. 2, 15a: 25 (1930)
Nevillea obtusissimus (Steud.) H.P.Linder	Bothalia 15: 66 (1984)
Platycaulos callistachyus (Kunth) H.P.Linder	Bothalia 15: 436 (1985)
Restio bifidus Thunb.	Phytogr. Blätt. 1: 7 (1803)
Restio bifurcus Nees ex Mast.	J. Linn. Soc., Bot. 8: 247 (1865)
Restio bolusii Pillans	Trans. Roy. Soc. South Africa 16: 247 (1928)
Restio capensis (L.) H.P.Linder & C.R.Hardy	Bothalia 40: 30 (2010)
Restio cincinnatus Mast.	J. Linn. Soc., Bot. 8: 240 (1865)
Restio curviramis Kunth	Enum. Pl. 3: 395 (1841)
Restio dispar Mast.	J. Linn. Soc., Bot. 8: 246 (1865)
Restio distichus Rottb.	Descr. Pl. Rar.: 6 (1772)
Restio dodii Pillans	Ann. Bolus Herb. 3: 85 (1921)
Restio hyalinus (Mast.) H.P.Linder & C.R.Hardy	Bothalia 40: 21 (2010)
Restio macer Kunth	Enum. Pl. 3: 390 (1841)
Restio miser Kunth	Enum. Pl. 3: 392 (1841)
Restio monanthos Mast.	J. Linn. Soc., Bot. 8: 238 (1865)
Restio multiflorus Spreng.	Syst. Veg. 1: 187 (1824)
Restio nudiflorus (Pillans) H.P.Linder & C.R.Hardy	Bothalia 40: 22 (2010)
Restio obscurus Pillans	Trans. Roy. Soc. South Africa 29: 341 (1942)
Restio pedicellatus Mast.	J. Linn. Soc., Bot. 8: 252 (1865)
Restio quinquefarius Nees	Linnaea 5: 639 (1830)
Restio sporadicus (Esterh.) H.P.Linder & C.R.Hardy	Bothalia 40: 26 (2010)
Restio tenuissimus Kunth	Enum. Pl. 3: 394 (1841)
Restio triticeus Rottb.	Descr. Pl. Rar.: 7 (1772)
Restio vimineus Rottb.	Descr. Icon. Rar. Pl.: 4 (1773)
Staberoha cernua (L.f.) T.Durand & Schinz	Consp. Fl. Afric. 5: 520 (1894)
Staberoha distachyos (Rottb.) Kunth	Enum. Pl. 3: 444 (1841)
Thamnochortus arenarius Esterh.	Bothalia 15: 472 (1985)
Thamnochortus fruticosus P.J.Bergius	Descr. Pl. Cap.: 353 (1767)
Thamnochortus gracilis Mast.	Monogr. Phan. 1: 327
Thamnochortus punctatus Pillans	Trans. Roy. Soc. South Africa 16: 376 (1928)
Thamnochortus sporadicus Pillans	J. S. African Bot. 18: 116 (1952)
Willdenowia arescens Kunth	Enum. Pl. 3: 454 (1841)
Willdenowia glomerata (Thunb.) H.P.Linder	Bothalia 15: 494 (1985)
Willdenowia sulcata Mast.	J. Linn. Soc., Bot. 10: 270 (1869)

Table 2.2 The percentage abundance and frequency of occurrence of Restionaceae per site.

Species (no. of 1-m-square plots)	**BK (200)**	**CP (225)**	**JH (200)**	**KB (200)**	**NP (233)**	**RL (305)**	**SM (200)**	**TK (200)**	**Occurrence frequency**
Anthochortus crinalis					35.6			10	2
Askidiosperma nitidum					1.3				1
Cannomois parviflora						1.3			1
Elegia asperiflora			20.5					3	2
Elegia caespitosa				45.5					1
Elegiacapensis								2	1
Elegiacoleura	35				13.3				2
Elegia cuspidata		44		49					2
Elegiadeusta		1.3							1
Elegia filacea		88.4		51.5	24	28.2	15.5		5
Elegiahookeriana				91.5			2		2
Elegia juncea			43.5						1
Elegia neesii					50.6			42.5	2
Elegia nuda		4				21			2
Elegia thyrsifera								6.5	1
Elegia vaginulata								2	1
Hypodiscus alboaristatus			6						1
Hypodiscus aristatus		3.1	6.5	1	3		23		5
Hypodiscus willdenowia						13.1	3.5		2
Mastersiella digitata				16					1
Nevilleaobtusissimus				3				0.5	2
Platycaulos callistachyus								10	1
Restio bifidus				34.5					1
Restio bifurcus		94.2							1
Restio bolusii					24				1
Restiocapensis	10					10.5	11		3
Restio cincinnatus							83.5		1
Restio curviramis	21.5				27			60.5	3
Restio dispar				4.5					1
Restio distichus			4	55					2
Restio dodii		19.6							1
Restiohyalinus				12.5					1
Restio macer						9.2			1
Restio miser					14.6				1
Restio monanthos						12.5			1
Restio multiflorus			1						1
Restionudiflorus				22					1
Restio obscurus					3				1
Restio pedicellatus					10.7			3.5	2
Restio quinquefarius		90.2				1.3			2
Restio sporadicus	11.5					2.3			2
Restio tenuissimus		26.7							1
Restio triticeus			69.5			0.3			2
Restio vimineus						10.2			1
Staberoha cernua			20		4.3		6.5	41.5	4
Staberoha distachyos	43	34.2		24.5		24.9		9.5	5
Thamnochortus arenarius							3	1.5	2
Thamnochortus fruticosus			1.5					5.5	2
Thamnochortus gracilis		1.3					2.5		2
Thamnochortus punctatus						38.4			1
Thamnochortus sporadicus	14								1
Willdenowia arescens						17			1
Willdenowia glomerata							1		1
Willdenowia sulcata	30		0.5			5.2			3

2.5 Exploratory analysis ecological data

Graphical representations were used to spatially examine each site. Each bubble in the bubble map (or cartogram) represents the geographic location of quadrats. The size of the bubble represents the value of the variables within a quadrat. Bubble maps revealed the spatial variability of each quantity – a precursor to developing hypotheses about underlying influences or processes acting behind the scene. Shapiro-Wilk statistical test *W* analysed if the environmental variables are samples of a normally distributed population or not (Shapiro and Wilk, 1965).

There were 200 quadrats at the Bastiaanskloof site (Figure 2.3a). The site is gently sloping showing a slope gradient 2.8^{O}. Figure 2.3b shows the spatial distribution of water table depths was uneven across this slope gradient. The Shapiro-Wilk analysis confirms a non-uniform distribution of moisture levels in the soil amongst all quadrats ($W = 0.8624$; $p < 0.001$). There is a wet-dry gradient as shown in Figure 2.3b. This gradient corresponds with the local relief in the experimental plot. Water table depths varied between 0.6 and 0.9 m with an average annual depth of 0.73 m which gives the impression that this site is relatively dry.

Seven Restionaceae species coexist in the plot (Table 2.3 above). Figure 2.3c shows that there is an uneven distribution of Cape Restio species in the plot. However, none of these species was dominantly spread in the plot. Only *Staberoha distachyos* (43%) showed a spread beyond 40% of the plot area followed by *Elegia coleura* (35%), *Willdenowia sulcata* (30%), *Restio curvirami*s (21.1%) were mostly localised (in niches) (Table 2.3). Three other species, *Thamnochortus sporadicus* (14%), *Restio sporadicus* (11.5%) and *Restio capensis* (10%) were relatively rare in abundance.

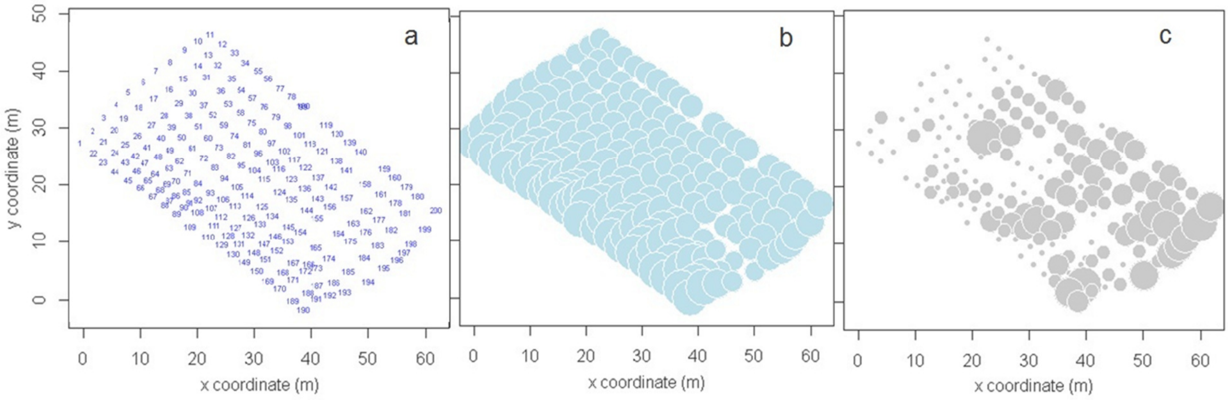


Figure 2.3 Maps showing the spatial distribution of a. quadrats, b. moisture levels, c. species densities at Bastiaanskloof site.

There were 255 quadrats at the Cape Point site (Figure 2.4a). The site is close to flat having a slope gradient of about 1.1^{O}. Shapiro-Wilk's W showed insignificant results for water table depth meaning that mean water table depth measurements at the Cape Point site were normally distributed (Shapiro-Wilk, W = 0.9906; p = 0.1538) with most values ranging between 0.54 and 0.63 m in depth (Figure 2.4b).

Twelve Restionaceae species coexisted though unevenly distributed among the quadrats. Figure 2.4c shows the variation in abundance of these species across the plot surface. Indeed *Elegia filacea* (88.4%), *Restio quinquefarius* (90.2%) and *Restio bifurcus* (94.2%) were the most common species (≥80% occupancy in the plot). Six other species (*Restio dodii* (19.6%), *Restio tenuissimus* (26.7%), *Staberoha distachyos* (34.2) and Elegia cuspidata (44%)) had very narrow occurrence (≤20% space in the plot). Meanwhile, the remaining 6 species, *Restio capensis* (0%), *Thamnochortus gracilis* (1.3%), *Elegia deusta* (1.3%), *Hypodiscus aristatus* (3.1%), *Elegia nuda* (4%) were the rare species at Cape Point.

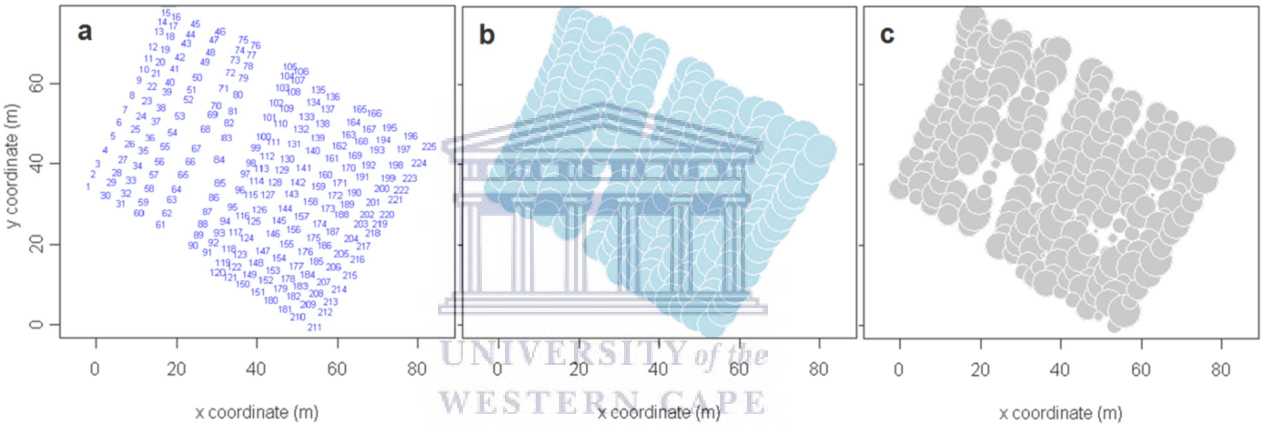


Figure 2.4 Maps showing the spatial distribution of, a. quadrats, b. moisture levels c. species densities at Cape Point site.

The Jonkershoek site is strongly sloping having has a slope gradient of about 10.1^{O}. It is situated on slopes of a mountain. The boundaries of this plot were limited by a footpath and a flowing stream on opposite sides thereby reducing it to a triangular geometry (Figure 2.5). It had 200 quadrats which were habited by 11 Restio species. Figure 2.5a shows the distribution of quadrats in this plot.

The water table depth measurements were not normally distributed based on normality tests (Shapiro-Wilk, W = 0.919; p< 001). Figure 2.5b below shows a clear water table gradient within the plot. The average water table depth was 0.6 m with most values ranging between 0.5 and 0.7 m depths.

Figure 2.5c shows that plants are unevenly distributed at this site. *Restio triticeus* (69.5%) and *Elegia juncea* (43.5%) were the most abundant species followed by *Elegia* *asperiflora* (20.5%), *Staberoha cernua* (20%), *and Restio filacea* (14.5%) with fairly widespread occurrences. Finally, *Hypodiscus aristatus* (6.5%), *Hypodiscus alboaristatus* (6%), *Restio distichus* (4%), *Thamnochortus fruticus* (1.5%), *Restio multiflorus* (1%) and *Willdenowia sulcata* (0.5%) were the rare species.

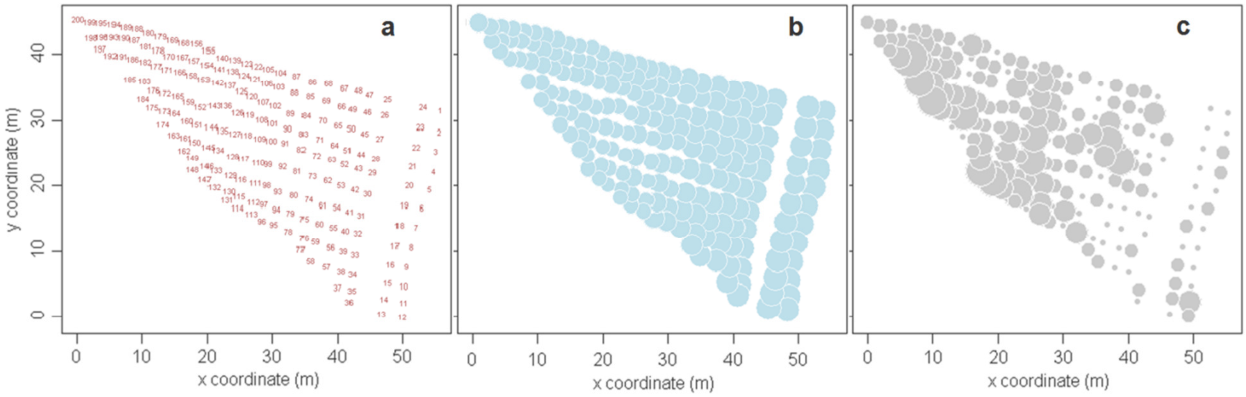


Figure 2.5 Maps showing the spatial distribution of a. quadrats, b. moisture levels, c. species richness at Jonkershoek site.

The Kogelberg site had 200 quadrats and is gently sloping with a slope gradient of 3.4^{O} confirming the presence of a physical gradient. Figure 2.6a shows the spatial outlay of quadrats. Statistical tests also confirm non-uniformity in the distribution of these records (Shapiro-Wilk, $W = 0.9704$, and p-value < 0.001). Figure 2.6b shows there are variations in water table depth measurements across the plot and along this site gradient (Figure 2.6c). The average water table depth is 0.7 m with most values ranging between 0.65 and 0.79 m.

Fourteen Restionaceae species coexisted at the site. Figure 2.6c shows an uneven distribution of species among quadrats. The most abundant species were *Elegia hookeriana* (91.5%), *Restio fest* (55.0%), *Elegia filacea* (51.5%), *Elegia cuspidata* (49.0%), *and Elegia caespitosa* (45.5%). *Restio bifidus* (34.5%), *Staberoha distachyos* (24.5%), *Elegia nuda* (22.0%), *Mastersiella digitata* (16.0%), *Elegia hyalinus* (12.5%) is moderately distributed and *Restio dispar* (4.5%), *Nevillea obtusissimus* (3.0%), *Hypodiscus aristatus* (1.0%) is relatively rare in the plot.

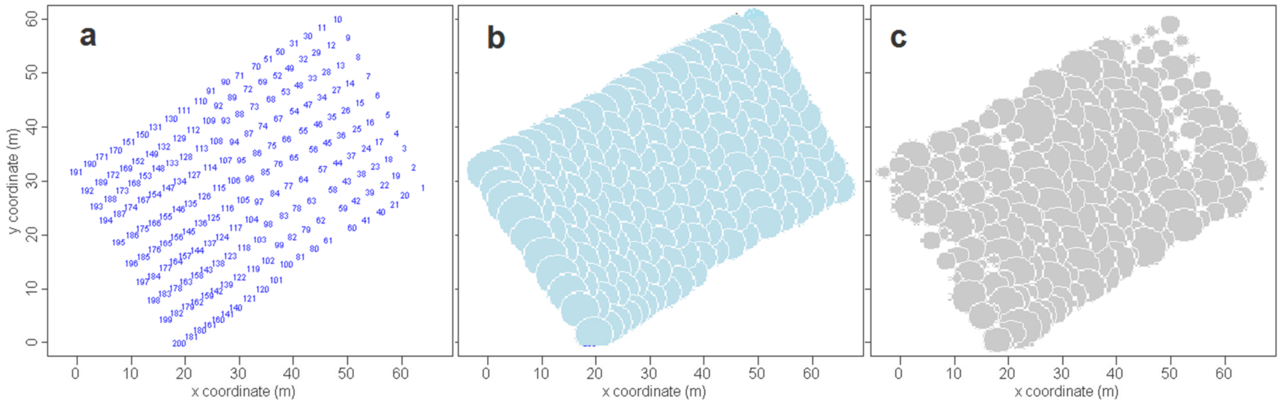


Figure 2.6 Maps showing the spatial distribution of a. quadrats, b. moisture levels, c. species richness at Kogelberg site.

At New Years Peak the plot had 235 quadrats and 12 coexisting Restionaceae species (Figure 2.7a). The site is gently sloping and there is a water table gradient which is analogous to the existing 2.1^{O} slope of the site (Figure 2.7b). Water table data are not normally distributed (Shapiro-Wilk, W = 0.9296, p-value < 0.001) and values vary between 0.16 m and 0.69 m below the surface.

Figure 2.7c shows how the plants are unevenly distributed in the plot. *Elegia neesii* 50.6% is the most widespread followed by *Anthochortus crinalis* (35.7%), *Restio curviramis* (26.8%), *Restio boluscii* (23.8%), *Elegia filacea* (23.8%) and which have relative frequency beyond 20%. The rest of the species occupy less than 15% of the plot (*Askiodesperma nitidum* 1.3%, *Restio obscurus* 3.0%, *Hypodiscus aristatus* 3.0%, *Staberoha cernua* 4.3%, *Restio pedicellatus* 10.6%, *Elegia coleura* 13.2%, *Restio miser* 14.5%). Most species are rare in occurrence or localised, with just one species (*E. neesii*) showing a dominant presence.

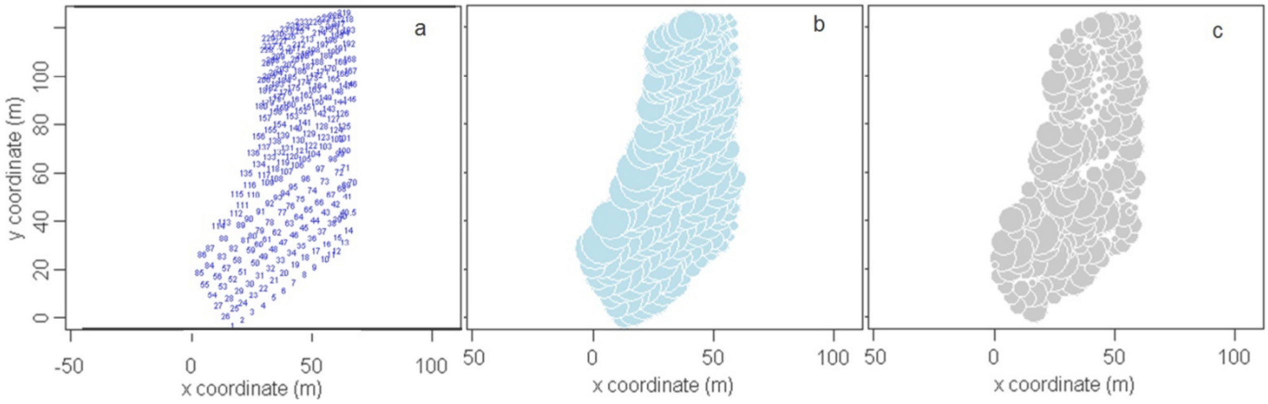


Figure 2.7 Maps showing the spatial distribution of a. quadrats, b. moisture levels, c. species densities at New Years Peak site.

At the Riverlands there are 305 quadrats (Figure 2.8a). Mean water table depth measurements revealed a steep hydrological gradient which accompanies a very gently sloping 1.7^{O} slope gradient across the plot (Figure 2.8b). The accumulated data showed a non-normal distribution (Shapiro-Wilk, W = 0.9363, p-value < 001) with a range between 0.58 m and 0.9 m. A significant proportion of plot shows mainly dry conditions.

There were 15 coexisting Restionaceae species which occupied merely 12% of this site. As seen in Figure 2.8c species densities vary across the plot. The percentage abundances in Table 2.5 above show that none of the species is dominant in occurrence in the plot. *Thamnochortus punctatus* is the most widespread with occupancy of 38.4% of the plot space. Respective percentage frequencies were *Elegia filacea* 28.2%, *Staberoha distachyos* 24.9%, *Elegia nuda* 21.0%, *Willdenowia arescens* 17.0%, *Hypodiscus willdenowia* 13.1%, *Restio monanthos* 12.5%, *Restio capensis* 10.5%, *Restio vimiceus* 10.2 %, *Restio macer* 9.2%, *Willdenowia sulcata* 5.2%, *Restio sporadicus* 2.3%, *Cannomois parviflora* 1.3%, *Restio quinquefarius* 1.3%, *Restio triticeus* 0.3%.

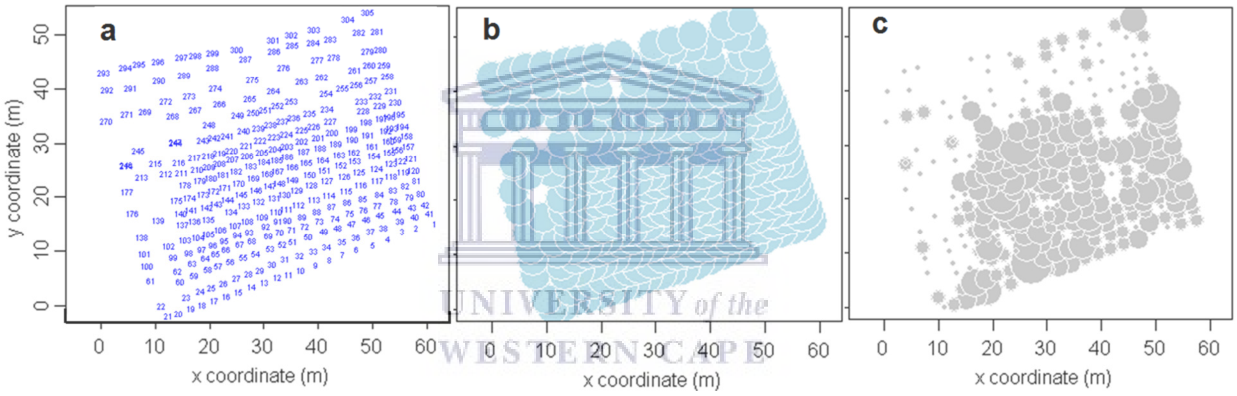


Figure 2.8 Maps showing the spatial distribution of a. quadrats, b. moisture levels, c. species densities at Riverlands site.

Silvermine site consisted of 200 quadrats (Figure 2.9a). Water table depth measurements from this site show a non-normal distribution (Shapiro-Wilk, W = 0.9058, p-value < 001). Figure 2.9b shows the variation in water table depth forms a moisture gradient underlain by a 5.1^{O} moderately sloping field gradient across the site. Mean water table depth ranged from 0.65 to 0.89 m averaging 0.79 m per annum.

Ten coexisting Restionaceae species were counted. Figure 2.9c shows that the species are unevenly distributed across the plot. Species data show that the most dominant species was *Restio cincinnatus* which occupied 83.5% of the plot area followed by *Hypodiscus aristatus* (23.0%), *Elegia filacea* (15.5%) and *Restio capensis* (11%). The rest of the species were very rare in occurrence (S*taberoha cernua* 6.5%, *Hypodiscus* *willdenowia*3.5%, *Thamnochortus arencens* 3.0%, *Thamnochortus gracilis* 2.5%, *Elegia hookeriana* 2.0% and *Willdenowia glomerata* 1.0%.

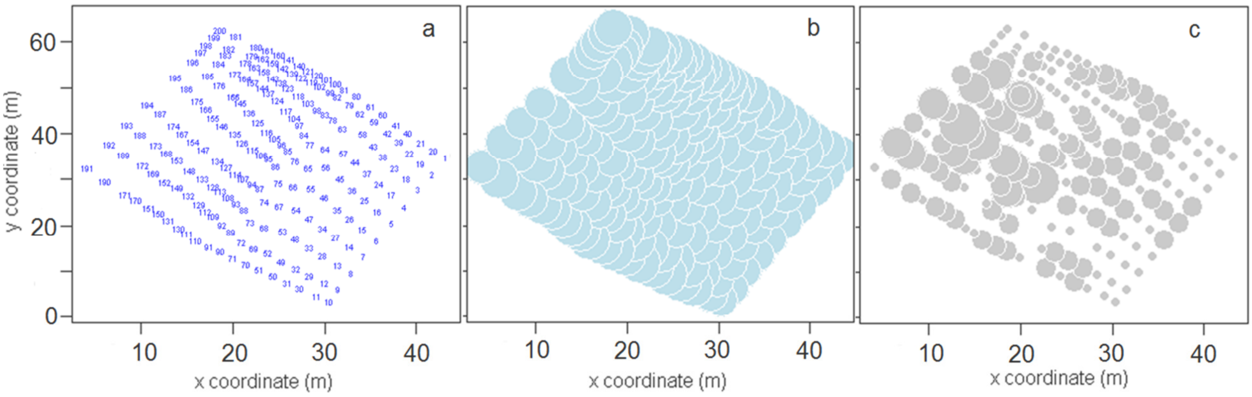


Figure 2.9 Maps showing the spatial distribution of a. quadrats, b. moisture levels, c. species densities at Silvermine site.

Theewaterskloof site consists of 201 quadrats (Figure 2.10a). The plot has a slope gradient of 1.0^{O}. Water table values showed a non-normal distribution (Shapiro-Wilk, W = 0.9614, p-value < 0.001). Values ranged between 0.47 and 0.65 m with an annual average of 0.57 m.

Fourteen Restionaceae were counted at this site. Of these, *Restio curviramis* (60.7%) was the most abundant followed by *Elegia neesii* (42.3%) and *Staberoha cernua* (41.3%). The rest of the species were rare species occupying less than 10% of the available.

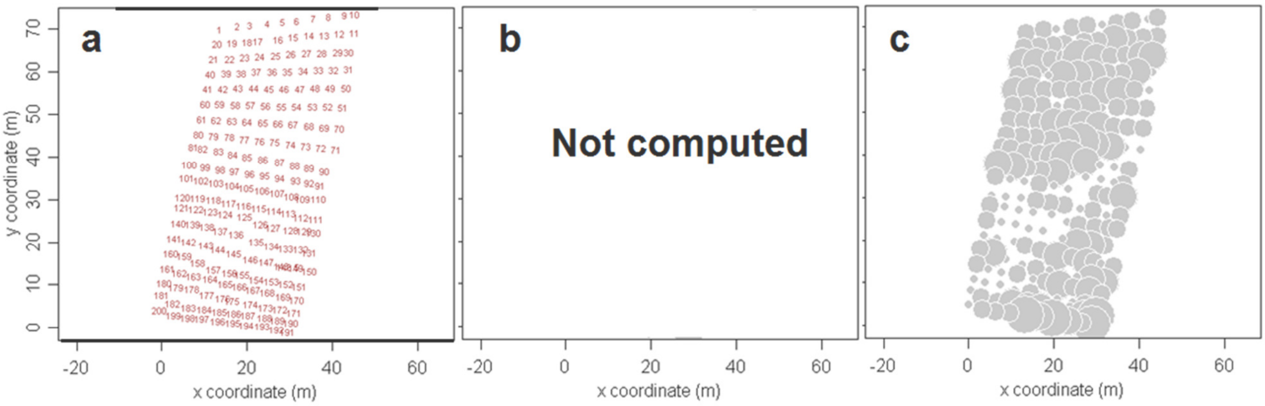


Figure 2.10 Maps showing the spatial distribution of a. quadrats, b. moisture levels (could not be computed), c. species densities at Theewaterskloof site.

The use of data exploration tools has given a general impression of the fine-scale ecological data of this study. Graphical representations like bubble maps revealed how the variables are spatially organised which is a precursor to developing hypotheses about underlying influences or processes that underpin this distribution pattern by species. There is sufficient evidence that all sites are highly rich in Restionaceae species relative to the very minute spatial scales. In addition, the distribution of species is hardly uniform across the plots at all sites. This diversity is accompanied by both a field altitude gradient and a hydrological gradient. Beyond this exploration phase is the identification, verification and investigation of the patterns and relationships between the ecological variables. Does the existence of hydrological gradients play any role in this observed species trend?

2.6 Conclusion

Eight Restionaceae communities in seasonal wetlands in parts of the south western Cape have been studied. The distribution of sites represented a subregional climatic gradient that ranged from moister coastal to more arid interiors. Accordingly, the plots exhibited varying levels of soil moisture conditions. The driest sites (Bastiaanskloof and Riverlands) were the most interior sites while the coastal sites were generally showed wetter sandy clayey soils. Each site is a fine scale plot that consisted of a number of quadrats or sampling sites. In a total of 1763 quadrats observed, 55 Restionaceae species were identified. The most common species *Staberoha distachyos* (Rottb.) Kunth, *Hypodiscus aristatus* (Thunb.) C.Krauss and *Elegia filacea* Mast. were seen in five of the eight sites. Also, common in four sites was *Staberoha cernua* (L.f.) T.Durand & Schinz. Lastly, *Restio capensis* (L.) H.P.Linder & C.R.Hardy, *Restio curviramis* Kunth and *Willdenowia sulcata* Mast. occurred in three sites each. The above common species would provide opportunity for comparative analysis across multiple ecological settings. The species composition observed in the fine-scale plots that were sampled in the south western CFR show relatively high richness and diversity. There is unevenness in diversity among sites. Most observed species are endemic to the region and reflect local abundance even at such very small topographic scales hence warranting conservation concerns. There are high levels of species cohabitation on all (small scale) plots attributed to the high diversity within. The shared existing space should warrant interspecific competitions which can be the possible reason for existing species segregation. All 8 sites were observed to show moisture gradient along which segregation was observed. Species segregation can also be attributed to tolerance of excess soil wetness or dryness in the shared space. A few species were shown to have niches that extended across a number of sites. It is necessary to account for the factors that have contributed to this dynamic community structure. Mapping the species and relating their distribution to prevailing local environmental factors is a key step towards resolving the above issue. Equally important is an assessment of the impact of any possible changes in environmental variables particularly as a result of climate change on this biodiversity.

CHAPTER 3 AN ANALYSIS OF ECOHYDROLOGICAL NICHE SEGREGATION AMONG RESTIONACEAE

3.1 Introduction

According to niche theory, the habitat of any plant species within a community is the space where it outcompetes all other counterparts within that community (Whittaker, 1965, Silvertown, 2004). For example, forest species may be partitioned by light gradients through a trade-off between growth rate in better light conditions and survival in shade (Kobe, 1999). Meanwhile, among temperate grassland herbs, niche segregation occurs by rooting depth (Denslow et al., 1998) and in arid environments between shrubs and herbs (Briones et al., 1996, Nobel, 1997). Meadow plants segregate along hydrological gradients (Silvertown et al., 1999), whereas tundra communities utilize different nitrogen sources and also show some temporal partitioning of these resources (McKane et al., 2002).

At a regional level, plant communities are determined by precipitation differences associated with topographic features such as elevation. At a more local scale, e.g. within small plots, plant species distribution is often determined by the seasonal variation in the availability and behaviour of water. Internal topographical variations generate mosaics of water regimes at fine spatial scales thereby allowing plants species with different water regime requirements and or moisture tolerances to segregate over small distances (Raulings et al., 2010). Hydrological niche segregation occurs in a great variety of vegetation types across an entire spectrum of environments from wet to mesic to arid. For example, littoral (Grace and Wetzel, 1981) and fen (Kotowski et al., 2006) species segregate under inter-specific competition into distinct zones along hydrological gradients. Species in riparian meadows in the USA appear to be just as differentially sensitive to water-table depth as plants in European wet meadows (Castelli et al., 2000, Dwire et al., 2006). In tallgrass prairie in Kansas, soil water resources are partitioned among coexisting C3 grasses (Nippert and Knapp, 2007) and there is also indirect evidence of this occurring in European experimental grasslands (Verheyen et al., 2008). Partitioning of soil moisture among competing species has been found repeatedly among desert plants (Manning and Barbour, 1988, Nobel, 1997), in Mediterranean shrublands (Filella and Penuelas, 2003) and woodlands (Groom, 2004), in savannah (Weltzin and McPherson, 1997, Jackson et al., 1999) and in temperate (Dawson, 1996) and tropical forest (Meinzer et al., 1999, Stratton et al., 2000). Tropical trees also differ significantly in their drought tolerance, with consequences for their distribution (Engelbrecht et al., 2007, Baltzer et al., 2008). Also, investigations on the patterns of water use among coexisting plant species in Mediterranean-climate ecosystems of South Eastern Spain have shown that the existence of species–specific isotopic niches reflects eco-physiological niche segregation (Moreno-Gutiérrez et al., 2012).

In South Africa, the Restionaceae, a family of perennial, evergreen, grass-like plants (Rebelo et al., 2006) dominate over large areas of the Cape Floristic Region (Goldblatt and Manning, 2002). This is attributed to the tolerance of the Restionaceae of a wide range of water regimes that allows them to successfully co-habit within mixed plant communities (Linder et al., 1998, Hardy et al., 2008). An explanation for such success is niche segregation along fine-scale hydrologic gradients (Silvertown, 2004) since Restionaceae species in seasonally saturated habitats have been observed to segregate along hydrological gradients (Aston, 2007, Araya et al., 2011). This is attributed to their differential tolerance of excess soil wetness or dryness (Silvertown et al., 1999). However, the relationship between Restionaceae species and moisture variables in distinct hydrological niches has not been quantified. Equally, knowledge is scarce about which hydrologic variables can be best used to discriminate between the spatial distributions of the Restionaceae species.

Typical Fynbos wetland communities were selected in the south-western corner of the Cape Floristic Region (CFR) of South Africa which is managed by South African National Parks and Cape Nature as experimental sites. The sites are inundated during the wet months of winter and begin to dry up towards summer in most sites. Previous studies have established that water table depth and soil moisture are the most important factors that determine vegetation distribution because these two factors directly influence the extent of root zone saturation and moisture or drought stress levels. As such, the moisture condition in the soil may indirectly account for the soil physicochemical properties as these conditions control soil chemical reactions and nutrient variations (DeBusk and Reddy, 2003, Bai et al., 2012).

The aim of the study is to quantify the influence of water table depth and soil moisture stress and topographical elevation on the species abundance. The specific objectives are to 1) characterize and compare the spatial dynamics of water table depth and soil moisture stress among the experimental wetlands, 2) compare the species composition and diversity among communities, and 3) relate the hydrological variables to the spatial distribution patterns of vegetation communities and species abundance. The study findings should improve knowledge on the dynamics between vegetation and hydrological conditions in Cape wetlands. This is vital information for proper biodiversity management.

3.2 Methods

Permanent plots of variable sizes, the precise dimensions differing with site topography, were established at each of eight sites between 2005 and 2008 as reported by Araya et al. (2011). In 2010, two other sites were established at Silvermine (18°25'54"E, 34°06'33"S, 390 m a.s.l.) and Bastiaanskloof (19°09'08"E, 33°32'26"S, 281 m a.s.l.) in 2010. Collectively, the distribution of these sites considerably represented the vegetation diversity in the Cape Floristic Region ranging from lowland (120 m) to montane (1080 m) Fynbos as well as a north-south rainfall gradient. Sampling sites were chosen based on the fact that they were species-rich wetlands and were occupied by Fynbos species which are endemic in the region. The experimental set up and sampling procedures for the first eight sites have been explicitly reported by Araya et al. (2011). These same procedures were replicated in the latter two sites (not reported in Araya et al. 2011). Hence, the following sections details the experimental set and sampling design at both Silvermine and Bastiaanskloof.

Respectively, each site gridded with 200 one-square-metre quadrats (subplots) placed 1 metre apart of each other were surveyed for the presence or absence of Restionaceae species whose identity was verified against voucher specimens lodged at Compton Herbarium, South African National Biodiversity Institute, Kirstenbosch.

The topography at all quadrats and tube well locations was surveyed using a total station device (Leica Geosystems TPS300, Heerbrugg, Switzerland). The water table depth was monitored through an array of nine tube wells read manually every two weeks. The soil water regime within the quadrats was quantified using hydrological models (Gowing and Young, 1997). Water table depths for each subplot location were obtained from spatial hydrological model of each site (Araya et al., 2011). The moisture regime at each quadrat was measured using sum exceedance values (SEVs) metrics which defined both the degree aeration (SEVa) and soil dryness (SEVd) water stress (Gowing and Spoor, 1998). These models were built from onsite inputs of water table depth behaviour in the field, topographic variation and soil characteristics. Both SEVs are in metre-weeks units and have the advantage that they integrate temporal variation in soil moisture at a scale relevant to the physiological tolerances of plants.

The procedures for deriving SEVs have been described by (Araya et al., 2011). The waterlogging threshold was calculated from the soil moisture release curve as the depth that gives 10% air-filled porosity. The soil drying threshold was calculated using Richard's equation (Gowing and Spoor, 1998) as the depth that gives 5 kPa tension at the shallow depths, that is, where plants start to show effects of water stress (Henson et al., 1989). For each threshold, the SEV represented the degree to which water tables exceed it, that is, SEVa for aeration stress and SEVd for soil drying. The extent of the exceedance and its duration throughout the growing season was cumulated over a 12-month season to obtain the respective SEVs measured in metre-weeks (m. wk).

Ecological data for eight wetland communities (excluding Cape Point 2 and Steenbras) strategically selected to represent the wetland Fynbos vegetation diversity in the study area were used to test for ecological hypotheses that explain the relationship between vegetation communities and their environments when the latter is spatially structured, and to analyse for spatial structures in the living communities. The data set comprises abundance (presence/absence) records of Restionaceae species, environmental parameters and the x-y Cartesian coordinates of the quadrats (subplots) at each hydrological niche site. Table 3.1 shows the four environmental variables with the units of measurement as well as the codes which were used to represent these variables during analyses.

Table 3.1. Environmental variable of the hydrological niche data set and their units

Variable	Code	Units
Sum exceedance values for aeration stress	SEVa	m.week
Sum exceedance values for dryness stress	SEVd	m.week
Topographical elevation based on a reference point	Elev	m
Cartesian (x-y) coordinates	x & y	No units
Mean water table depth	MWTD	m

3.3 Statistical Analysis

Infrequent species, namely those with a frequency of occurrence below 10% at each site, were excluded from the statistical analyses. An analysis of variance (generalized linear model) was applied to test: 1) whether hydrological niches in terms of water table depth, soil dryness and soil aeration stress occupied by each Restionaceae species where present at each site were significantly different from those where the species was absent; 2) whether different Restionaceae species occupied significantly different hydrological niches in terms of water table depth, soil dryness and soil aeration stress at each site. Significantly different ($P \leq 0.05$) species niches were separated with a Duncan's multiple range tests as it detects true differences and maintains a low overall type I error (Carmer and Swanson, 1973).

Also, canonical discriminant analysis, a dimension-reduction technique related to principal component analysis and canonical correlation was also applied to construct linear combinations of water table depth, soil drying and soil aeration stress variables that best discriminated between the spatial distributions of the Restionaceae species at each site i.e. that had the highest possible (maximal) multiple correlations with the species. The coefficients of the linear combination are the canonical coefficients and the variable defined by the linear combination is the first canonical component. The second canonical component was obtained by finding the linear combination uncorrelated with the first canonical component that had the highest possible multiple correlations with the species. The process of extracting canonical components was repeated until the number of canonical components equalled the number of original variables. For each canonical correlation, canonical discriminant analysis tested the hypothesis that it and all smaller canonical correlations were zero in the population. Wilks' lambda was used to test the significance of all the canonical components.

Three dimensional scatter plots of mean water table depths (MWTD), soil dryness (SEVd) and soil aeration (SEVa) stress derived from the ANOVA and average canonical discriminant scores derived from the canonical discriminant analysis for each Restionaceae species indicated the species proximity in terms of the hydrological niches they occupied at each site.

3.4 Results

The analysis of intra specific and inter specific variances (ANOVA) for mean annual water table depth (MWTD), soil dryness stress (SEVd) and soil aeration stress (SEVa) as well asthe discriminant analysis (canonical discriminant analysis) which tested for the variable that best discriminated the species into their respective spatial aggregates, are shown in Tables 3.2 to 3.9. Letters have been used to show the significance of the difference in occurrence of species both where they are present and where they are absent. Different lowercase letters show a significant difference between species within the present and absent columns. Different uppercase letters show significant differences within each species across present and absent columns. Values with dissimilar letters are significantly different at *P ≤ 0.05, **P ≤ 0.01, ***P ≤ 0.001. NS = not significant (P ≥ 0.05).

3.4.1 Bastiaanskloof

The seven Restionaceae species (>10% abundance) mostly occupied soils with significantly (P ≤ 0.05) different water table depths, dryness and aeration thresholds at locations where they were present compared with those locations where they were absent. The exceptions were *Restio capensis* and *R. sporadicus* which occupied soils with non-significantly (P ≥ 0.05) different water table depths at locations where they were present compared with those locations where they were absent. Another exception was *R. capensis* which occupied soils with non-significantly (P ≥ 0.05) different dryness thresholds at locations where they were present compared with those locations where they were absent. Likewise, *R. curviramis*, *R. capensis*, *R. sporadicus* and *Staberoha distachyos* occupied soils with non-significantly (P ≥ 0.05) different aeration thresholds at locations where they were present compared with those locations where they were absent (Table 3.2). Also, at locations where the Restionaceae species were present, the different species occupied soils with significantly (P ≤ 0.001) different water table depths, dryness and aeration. Four groups of Restionaceae species occupying soils with significantly (P ≤ 0.05) different water table depths, dryness and aeration thresholds were distinguished (Table 3.2; Figure 3.1). The first group comprised *Elegia coleura* and *R. curviramis*, the second group comprised *R. capensis* and R*. sporadicus* which overlapped with both the first group and the third group which comprised *S. distachyos* and a fourth distinct group which comprised *Thamnochortus sporadicus* and *Willdenowia sulcata* (Table 3.2; Figure 3.1). Canonical discriminant analysis indicated that the spatial segregation of the Restionaceae species was due primarily to soil dryness and to a lesser extent to water table depth. The significant first (P ≤ 0.001) and third (P ≤ 0.05) canonical components, which collectively comprised 92.2% of the total variance, both had soil dryness as the largest standardised coefficients. In contrast, the significant (P ≤ 0.01) second canonical component which comprised 7.8% of the total variance had water table depth as the largest standardised coefficient of (Table 3.2).

Table 3.2. Analysis of variance which tested for intra species (row) and inter species (column) differences in mean annual water table depth (MWTD), soil dryness stress (SEVd) and soil aeration stress (SEVa) and canonical discriminant analysis which tested linear combinations of MWTD, SEVd and SEVa that best discriminated between species spatial distributions at the Bastiaanskloof site. Different lowercase letters show significant difference between Restionaceae species within the present and absent columns. Different uppercase letters show significant differences within each species across present and absent columns. Values with dissimilar letters are significantly different at *P ≤ 0.05, **P ≤ 0.01, ***P ≤ 0.001. NS = not significant (P ≥ 0.05).

	MWTD (m)		**ANOVA**		**SEVd (m wk)**		**ANOVA**
Species	**Present**	**Absent**	**F-ratio**	**Species**	**Present**	**Absent**	**F-ratio**
Elegia coleura	0.6416a	0.7849d	$F_{1,198}$ = 65.9***	*Elegia coleura*	15.67a	19.54d	$F_{1,198}$ = 68.8***
Restio curviramis	0.6496a	0.7581d	$F_{1,198}$ = 23.5***	*Restio curviramis*	15.96a	18.79d	$F_{1,198}$ = 22.5***
Restio capensis	0.6827abd	0.7405d	$F_{1,198}$ =3.2 (NS)	*Restio capensis*	16.73abd	18.34d	$F_{1,198}$ = 3.6 (NS)
Restio sporadicus	0.6847abd	0.7412d	$F_{1,198}$ =3.5 (NS)	*Restio sporadicus*	16.23ab	18.44d	$F_{1,198}$ = 7.7**
Staberoha distachyos	0.6925b	0.7666d	$F_{1,198}$ = 15.3***	*Staberoha distachyos*	17.06b	19.03d	$F_{1,198}$ = 15.4***
Thamnochortus sporadicus	0.8372c	0.7181d	$F_{1,198}$ = 19.9***	*Thamnochortus sporadicus*	20.99c	17.73d	$F_{1,198}$ = 21.3***
Willdenowia sulcata	0.8580c	0.6819d	$F_{1,198}$= 105.6***	*Willdenowia sulcata*	21.65c	16.69d	$F_{1,198}$ = 126.2***
ANOVA (F-ratio)	$F_{6,323}$ = 37.3***	NS		**ANOVA (F-ratio)**	$F_{6,323}$ = 42.1***	NS	
	SEVa (m wk)		**ANOVA**	**Canonical Discriminant**	**Component (% total variance)**		
Species	**Present**	**Absent**	**F-ratio**	**Analysis**	**1 (88.5%)**	**2 (7.8%)**	**3 (3.7%)**
Elegia coleura	0.2303a	0.0611c	$F_{1,198}$ = 15.6***	**Canonical statistics**			
Restio curviramis	0.1282abc	0.1181c	$F_{1,198}$= 0.1 (NS)	Wilks Lambda	0.5026	0.9094	0.9673
Restio capensis	0.1032abc	0.1222c	$F_{1,198}$= 0.1 (NS)	Chi Square	222.9	32.7	10.8
Restio sporadicus	0.0519bc	0.1292c	$F_{1,198}$= 1.4 (NS)	DoF	18	10	4
Staberoha distachyos	0.1067abc	0.1305c	$F_{1,198}$= 0.3 (NS)	Probability	0.0000	0.0003	0.0295
Thamnochortus sporadicus	0.0000b	0.1399c	$F_{1,198}$ = 5.4*	**Standardised coefficients**			
Willdenowia sulcata	0.0078b	0.1685c	$F_{1,198}$ = 12.8***	SEVd	1.7102	-4.5915	1.1929
				SEVa	-0.2201	1.4379	0.7922
				MWTD	-0.8190	5.3800	-1.0071
ANOVA (F-ratio)	$F_{6,323}$ = 5.8***	NS					

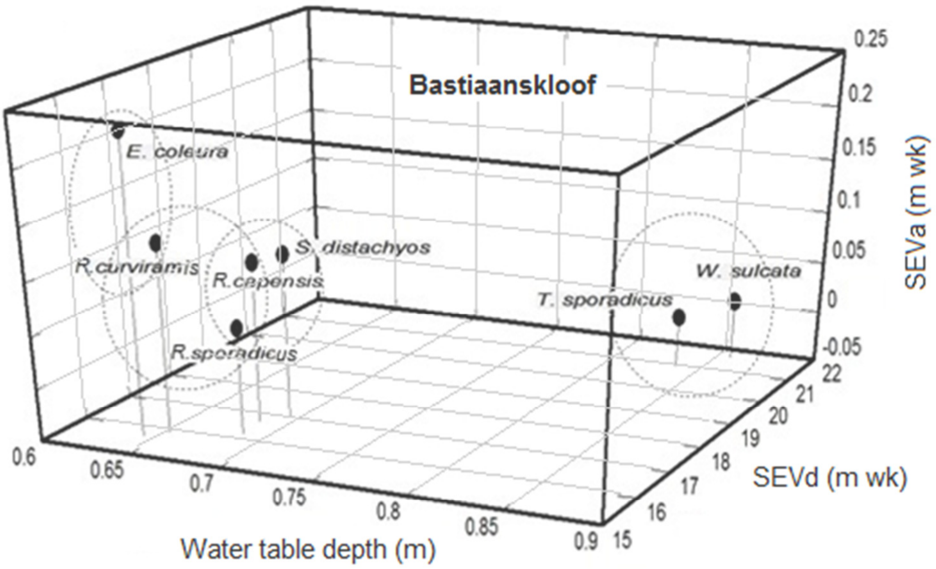


Figure 3.1 Three dimensional scatter plots water table depth, soil dryness (SEVd) and soil aeration (SEVa) stress for Restionaceae species at the Bastiaanskloof site. Non-overlapping encircled species occupying different hydrological niches. Hydrological niches occupied by grey shaded species where present are significantly different from those where absent.

3.4.2 Cape Point

The seven Restionaceae species that were examined mostly occupied soils with significantly ($P \leq 0.05$) different water table depths, dryness and aeration at locations where they were present compared with those locations where they were absent. The exceptions were *Elegia filacea* and *Restio bifurcus* which occupied soils with non-significantly ($P \geq 0.05$) different water table depths and dryness at locations where they were present compared with those locations where they were absent and *E. cuspidata*, *E. filacea*, *R. bifurcus* and *R. tenuissimus* which occupied soils with non-significantly ($P \geq 0.05$) different aeration at locations where they were present compared with those locations where they were absent (Table 3.3). Also, at locations where the Restionaceae species were present, the different species occupied soils with significantly ($P \leq 0.001$) different water table depths, dryness and aeration. Three groups of Restionaceae species occupying soils with significantly ($P \leq 0.05$) different water table depths, dryness and aeration were distinguished (Table 3.3; Figure 3.2). The first distinct group comprised *R. dodii* and *E. cuspidata*, the second group comprised *E. filacea*, *R. bifurcus* and *R. quinquefarius* which overlapped partially with the third group which comprised *T. sporadicus* and *W. sulcata* (Table 3.3; Figure 3.2). Canonical discriminant analysis indicated that the spatial segregation of the Restionaceae species was due primarily to water table depth. The significant ($P \leq 0.001$) first canonical component, which comprised 92.1% of the total variance, had water table depth as the largest standardised coefficient (Table 3.3).

Table 3.3. Analysis of variance which tested for intraspecies (row) and interspecies (column) differences in mean annual water table depth (MWTD), soil dryness stress (SEVd) and soil aeration stress (SEVa) and canonical discriminant analysis which tested linear combinations of MWTD, SEVd and SEVa that best discriminated between species spatial distributions at the Cape Point site. Different lowercase letters show a significant difference between Restionaceae species within the present and absent columns. Different uppercase letters show significant differences within each species across present and absent columns. Values with dissimilar letters are significantly different at *P ≤ 0.05, **P ≤ 0.01, ***P ≤ 0.001. NS = not significant (P ≥ 0.05).

	MWTD (m)		**ANOVA**	**Species**	**SEVd (m wk)**		**ANOVA**
Species	**Present**	**Absent**	**F-ratio**		**Present**	**Absent**	**F-ratio**
Restio dodii	0.5577a	0.5889d	$F_{1,223} = 11.4$***	*Restio dodii*	11.96a	12.44d	$F_{1,223} = 12.7$***
Elegia cuspidata	0.5650a	0.5968d	$F_{1,223} = 18.9$***	*Elegia cuspidata*	12.04a	12.58d	$F_{1,223} = 26.5$***
Elegia filacea	0.5824bd	0.5859d	$F_{1,223} = 0.1$ (NS)	*Elegia filacea*	12.33bd	12.43d	$F_{1,223} = 0.3$ (NS)
Restio bifurcus	0.5845bd	0.5543d	$F_{1,223} = 3.6$ (NS)	*Restio bifurcus*	12.37bd	11.98d	$F_{1,223} = 2.7$ (NS)
Restio quinquefarius	0.5862b	0.5514d	$F_{1,223} = 7.8$**	*Restio quinquefarius*	12.38b	11.98d	$F_{1,223} = 4.3$*
Restio tenuissimus	0.5979bc	0.5773d	$F_{1,223} = 6.0$*	*Restio tenuissimus*	12.57bc	12.26d	$F_{1,223} = 6.5$*
Staberoha distachyos	0.6031c	0.5722d	$F_{1,223} = 16.2$***	*Staberoha distachyos*	12.61c	12.21d	$F_{1,223} = 13.1$***
ANOVA (F-ratio)	$F_{6,887} = 6.3$***	NS		**ANOVA (F-ratio)**	$F_{6,887} = 6.7$***	NS	

	SEVa (m wk)		**ANOVA**	**Canonical Discriminant**	**Component (% total variance)**		
Species	**Present**	**Absent**	**F-ratio**	**Analysis**	**1 (92.1%)**	**2 (6.6%)**	**3 (1.3%)**
Restio dodii	0.3175c	0.2052d	$F_{1,223} = 3.9$*	**Canonical statistics**			
Elegia cuspidata	0.2615bcd	0.2002d	$F_{1,223} = 1.8$ (NS)	Wilks Lambda	0.9470	0.9956	0.9993
Elegia filacea	0.2272bcd	0.2268d	$F_{1,223} = 0.0$ (NS)	Chi Square	48.4	3.9	0.7
Restio bifurcus	0.2175bcd	0.3846d	$F_{1,223} = 2.9$ (NS)	DoF	18	10	4
Restio quinquefarius	0.2035abc	0.4454d	$F_{1,223} = 10.4$**	Probability	0.0001	0.9524	0.9563
Restio tenuissimus	0.1656abd	0.2496d	$F_{1,223} = 2.7$ (NS)	**Standardised coefficients**			
Staberoha distachyos	0.1187a	0.2836d	$F_{1,223} = 12.5$***	SEVd	-1.8816	-0.2046	-8.5789
				SEVa	1.5309	1.7632	3.6354
				MWTD	3.9903	1.2763	11.1085
ANOVA (F-ratio)	$F_{6,887} = 2.6$*	NS					

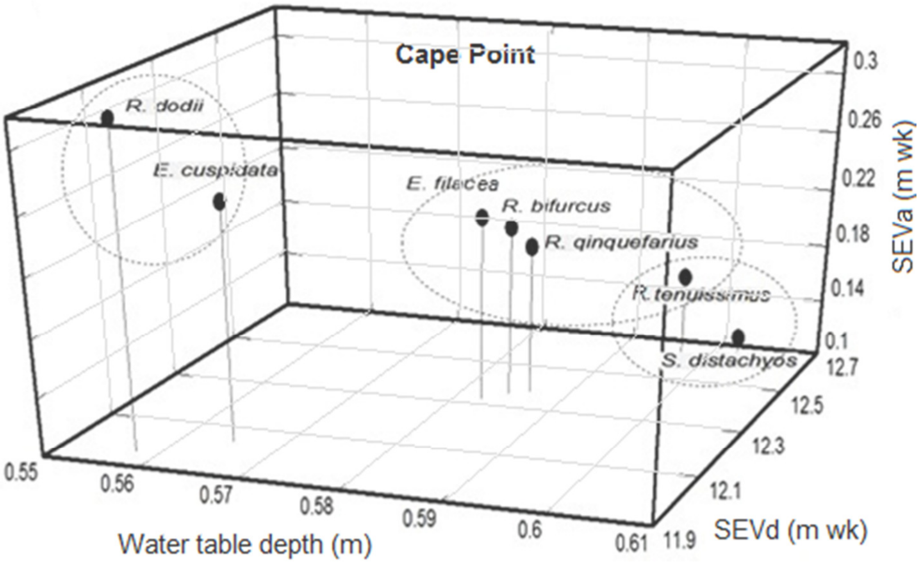


Figure 3.2 Three dimensional scatter plots water table depth, soil dryness (SEVd) and soil aeration (SEVa) stress for Restionaceae species at the Cape Point site. Non-overlapping encircled species occupying different hydrological niches. Hydrological niches occupied by grey shaded species where present are significantly different from those where absent.

3.4.3 Jonkershoek

The five recorded Restionaceae species mostly occupied soils with significantly ($P \leq 0.05$) different water table depths, dryness and aeration at locations where they were present compared with those locations where they were absent. The exceptions were *Restio triticeus* and *Elegia asperiflora* which occupied soils with non-significantly ($P \geq 0.05$) different water table depths and dryness at locations where they were present compared with those locations where they were absent and *R. triticeus* which occupied soils with non-significantly ($P \geq 0.05$) different aeration at locations where it was present compared with those locations where it was absent (Table 3.4). Also, at locations where the Restionaceae species were present the different species occupied soils with significantly ($P \leq 0.001$) different water table depths, dryness and aeration. Two distinct groups of Restionaceae species occupying soils with significantly ($P \leq 0.05$) different water table depths, dryness and aeration were distinguished (Table 3.4; Figure 3.3). The first distinct group comprised *R. filiformis*, *S. cernua* and *E. juncea* and the second distinct group comprised *R. triticeus* and *E. asperiflora* (Table 3.4; Figure 3.3). Canonical discriminant analysis indicated that the spatial segregation of the Restionaceae species was due primarily to water table depth. The significant ($P \leq 0.001$) first canonical component, which comprised 87.1% of the total variance, had water table depth as the largest standardised coefficient (Table 3.4).

Table 3.4. Analysis of variance which tested for intraspecies (row) and interspecies (column) differences in mean annual water table depth (MWTD), soil dryness stress (SEVd) and soil aeration stress (SEVa) and canonical discriminant analysis which tested linear combinations of MWTD, SEVd and SEVa that best discriminated between species spatial distributions at the Jonkershoek site. Different lowercase letters show a significant difference between Restionaceae species within the present and absent columns. Different uppercase letters show significant differences within each species across present and absent columns. Values with dissimilar letters are significantly different at $^{*}P \leq 0.05$, $^{**}P \leq 0.01$, $^{***}P \leq 0.001$. NS = not significant ($P \geq 0.05$).

	MWTD (m)		**ANOVA**		**SEVd (m wk)**		**ANOVA**
Species	**Present**	**Absent**	**F-ratio**	**Species**	**Present**	**Absent**	**F-ratio**
Restio filiformis	0.5246a	0.5990d	$F_{1,198}$ = 18.5***	*Restio filiformis*	12.88a	13.69d	$F_{1,198}$ = 13.4***
Staberoha cernua	0.5375a	0.6009d	$F_{1,198}$ = 17.2***	*Staberoha cernua*	12.96a	13.73d	$F_{1,198}$ = 15.9***
Elegia juncea	0.5407a	0.6249d	$F_{1,198}$ = 54.9***	*Elegia juncea*	13.09a	13.95d	$F_{1,198}$ = 32.7***
Restio triticeus	0.5866bd	0.5921d	$F_{1,198}$ = 0.2 (NS)	*Restio triticeus*	13.53bd	13.67d	$F_{1,198}$ = 0.7 (NS)
Elegia asperiflora	0.6109bd	0.5824d	$F_{1,198}$ = 3.4 (NS)	*Elegia asperiflora*	13.64bd	13.56d	$F_{1,198}$ = 0.2 (NS)
ANOVA (F-ratio)	$F_{4,331}$ = 10.5***	NS	-	**ANOVA (F-ratio)**	$F_{4,331}$ = 6.3***	NS	-
	SEVa (m wk)		**ANOVA**	**Canonical Discriminant**	**Component (% total variance)**		
Species	**Present**	**Absent**	**F-ratio**	**Analysis**	**1 (87.1%)**	**2 (12.0%)**	**3 (0.9%)**
Restio filiformis	1.7070a	0.7749d	$F_{1,198}$ = 22.2***	**Canonical statistics**			
Staberoha cernua	1.4614a	0.7722d	$F_{1,198}$ = 15.2***	Wilks Lambda	0.8169	0.9762	0.9980
Elegia juncea	1.4996a	0.4562d	$F_{1,198}$ = 66.3***	Chi Square	66.9	9.2	0.7
Restio triticeus	0.8772bd	0.9851d	$F_{1,198}$ = 0.5 (NS)	DoF	12	6	2
Elegia asperiflora	0.5298b	1.0081d	$F_{1,198}$ = 7.2**	Probability	0.0000	0.1622	0.7169
				Standardised coefficients			
				SEVd	-2.3350	4.0753	-0.9519
ANOVA (F-ratio)	$F_{4,331}$ = 10.5***	NS	-				

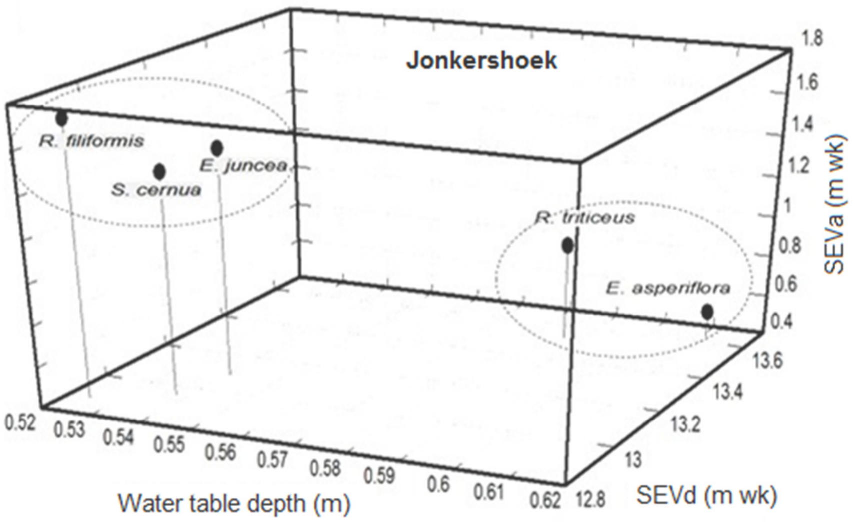


Figure 3.3 Three dimensional scatter plots water table depth, soil dryness (SEVd) and soil aeration (SEVa) stress for Restionaceae species at the Jonkershoek site. Non-overlapping encircled species occupying different hydrological niches. Hydrological niches occupied by grey shaded species where present are significantly different from those where absent.

3.4.4 Kogelberg

The ten recorded Restionaceae species mostly occupied soils with significantly (P ≤ 0.05) different water table depths, dryness and aeration at locations where they were present compared with those locations where they were absent. The exceptions were *Elegia filacea* and *E. hookeriana* which occupied soils with non-significantly (P ≥ 0.05) different water table depths. *E. filacea*, *E. hookeriana* and *Staberoha distachyos* which occupied soils with non-significantly (P ≥ 0.05) different dryness at locations where they were present compared with those locations where they were absent and *Restio bifidus*, *R. distichus*, *E. filacea*, *E. hookeriana*, *R. nudiflorus* and *Mastersiella digitata* which occupied soils with non-significantly (P ≥ 0.05) different aeration at locations where they were present compared with those locations where they were absent (Table 3.5). Also, at locations where the Restionaceae species were present, the different species occupied soils with significantly (P ≤ 0.001) different water table depths, dryness and aeration. At Kogelberg, the first canonical function discriminates between five groups of Restionaceae species occupying soils with significantly (P ≤ 0.05) different water table depths, dryness and aeration were distinguished (Table 3.5; Figure 3.4). The first distinct group comprised *E. caespitosa*, *E. cuspidata* and *R. bifidus*, the second distinct group comprised *R. distichus*, the third group comprised *E. filacea*, *E. hookeriana* and *S. distachyos* which overlapped partially with the fourth group comprising *R. nudiflorus* and a fifth distinct group comprising *M. digitata* and *R. hyalinus* (Table 3.5; Figure 3.4). Canonical discriminant analysis indicated that the spatial segregation of the Restionaceae species was due primarily to water table depth. The significant ($P \leq 0.001$) first canonical component, which comprised 90.3% of the total variance, had water table depth as the largest standardised coefficient (Table 3.5).

Table 3.5. Analysis of variance which tested for intraspecies (row) and interspecies (column) differences in MWTD, SEVd and SEVa and canonical discriminant analysis which tested linear combinations of MWTD, SEVd and SEVa that best discriminated between species spatial distributions at the Kogelberg site. Values with dissimilar letters significantly different at *P ≤ 0.05, **P ≤ 0.01, ***P ≤ 0.001. NS = not significant (P ≥ 0.05).

	MWTD (m)		**ANOVA**		**SEVd (m wk)**		**ANOVA**
Species	**Present**	**Absent**	**F-ratio**	**Species**	**Present**	**Absent**	**F-ratio**
Elegia caespitosa	0.6594aA	0.7366aB	$F_{1,198}$ = 187.0***	*Elegia caespitosa*	15.41aA	16.65aB	$F_{1,198}$ = 70.7***
Elegia cuspidata	0.6648aA	0.7367aB	$F_{1,198}$ = 145.9***	*Elegia cuspidata*	15.46aA	16.67aBe	$F_{1,198}$ = 67.3***
Restio bifidus	0.6696aA	0.7183aB	$F_{1,198}$ = 42.3***	*Restio bifidus*	15.54aA	16.37aB	$F_{1,198}$ = 23.6***
Restio distichus	0.6842bA	0.7227aB	$F_{1,198}$ = 27.1***	*Restio distichus*	15.57aA	16.58aB	$F_{1,198}$ = 33.2***
Elegia filacea	0.6999cA	0.7031aA	$F_{1,198}$ = 0.2 (NS)	*Elegia filacea*	16.15bcA	16.01aA	$F_{1,198}$ = 0.6 (NS)
Elegia hookeriana	0.7017cA	0.6993aA	$F_{1,198}$ = 0.1 (NS)	*Elegia hookeriana*	16.09bA	16.03aA	$F_{1,198}$ = 0.0 (NS)
Staberoha distachyos	0.7154cdB	0.6970aA	$F_{1,198}$ = 4.2*	*Staberoha distachyos*	16.19bcdA	16.05aA	$F_{1,198}$ = 0.5 (NS)
Restio nudiflorus	0.7182dB	0.6968aA	$F_{1,198}$ = 5.2*	*Restio nudiflorus*	16.43cdB	15.98aA	$F_{1,198}$ = 4.8*
Mastersiella digitata	0.7411eB	0.6939aA	$F_{1,198}$ = 21.5***	*Mastersiella digitata*	16.63dB	15.98aA	$F_{1,198}$ = 8.1**
Restio hyalinus	0.7435eB	0.6955aA	$F_{1,198}$ = 17.9***	*Restio hyalinus*	16.63dB	16.00aA	$F_{1,198}$ = 6.0*
ANOVA (F-ratio)	$F_{9,794}$ = 22.6***	NS		**ANOVA (F-ratio)**	$F_{9,794}$ = 14.2***	NS	

	SEVa (m wk)		**ANOVA**	**Canonical Discriminant**	**Component (% total variance)**		
Species	**Present**	**Absent**	**F-ratio**	**Analysis**	**1 (90.3%)**	**2 (7.8%)**	**3 (1.8%)**
Elegia caespitosa	0.2810aB	0.0067aA	$F_{1,198}$ = 43.9***	**Canonical statistics**			
Elegia cuspidata	0.2609abB	0.0071aA	$F_{1,198}$ = 36.8***	Wilks Lambda	0.7481	0.9692	0.9940
Restio bifidus	0.1822abcA	0.1048aA	$F_{1,198}$ = 2.6 (NS)	Chi Square	231.1	24.9	4.8
Restio distichus	0.1679cdA	0.0870aA	$F_{1,198}$ = 3.1 (NS)	DoF	27	16	7
Elegia filacea	0.1499cdA	0.1119aA	$F_{1,198}$ = 0.7 (NS)	Probability	0.0000	0.0716	0.6878
Elegia hookeriana	0.1432cdA	0.0055aA	$F_{1,198}$ = 2.9 (NS)	**Standardised coefficients**			
Staberoha distachyos	0.0391dA	0.1615aB	$F_{1,198}$ = 5.5*	SEVd	-0.8468	2.2737	-0.4096
Restio nudiflorus	0.0719cdA	0.1483aB	$F_{1,198}$ = 1.9 (NS)	SEVa	0.4754	-0.4907	1.3128
Mastersiella digitata	0.0091dA	0.1548aB	$F_{1,198}$ = 0.0 (NS)	MWTD	1.9362	-1.9557	0.8891
Restio hyalinus	0.0000dA	0.1503aB	$F_{1,198}$ = 4.9*				
ANOVA (F-ratio)	$F_{9,794}$ = 4.7***	NS					

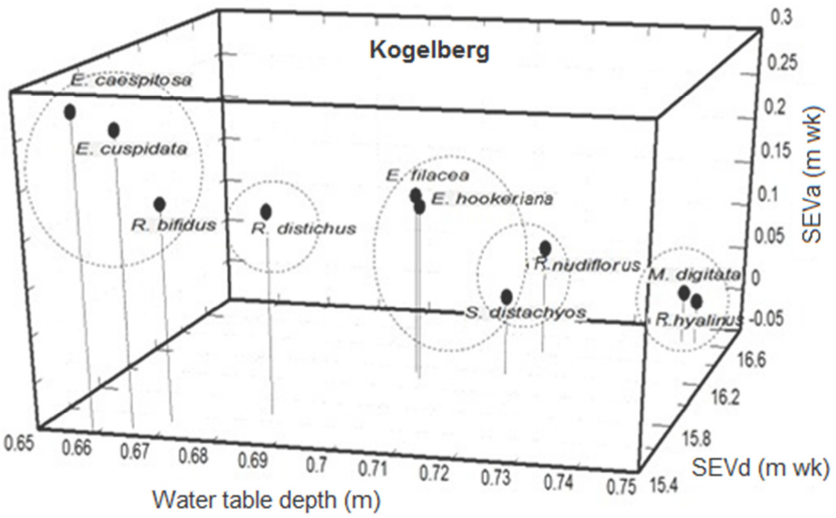


Figure 3.4 Three dimensional scatter plots water table depth, soil dryness (SEVd) and soil aeration (SEVa) stress for Restionaceae species at the Kogelberg site. Non-overlapping encircled species occupying different hydrological niches. Hydrological niches occupied by grey shaded species where present are significantly different from those where absent.

3.4.5 New Years Peak

The eight recorded Restionaceae species of more than 10% occurrence mostly occupied soils with significantly ($P \leq 0.05$) different water table depths, dryness and aeration at locations where they were present compared with those locations where they were absent. The exceptions were *Elegia coleura* which occupied soils with non-significantly ($P \geq 0.05$) different water table depths and aeration at locations where it was present compared with those locations where it was absent and *Restio pedicellatus* which occupied soils with non-significantly ($P \geq 0.05$) different dryness at locations where it was present compared with those locations where it was absent (Table 3.6). Also, at locations where the Restionaceae species were present the different species occupied soils with significantly ($P \leq 0.001$) different water table depths, dryness and aeration. Four distinct groups of Restionaceae species occupying soils with significantly ($P \leq 0.05$) different water table depths, dryness and aeration were distinguished (Table 3.6; Figure 3.5). The first distinct group comprised *R. miser*, the second distinct group comprised *Anthochortus crinalis*, the third distinct group comprised *E. coleura* and the fourth distinct group comprised *E. neesii*, *R. boluscii*, *R. curviramis*, *R. pedicellatus* and *E. filacea* (Table 3.6; Figure 3.5). Canonical discriminant analysis indicated that the spatial segregation of the Restionaceae species was due primarily to water table depth. The significant ($P \leq 0.001$) first canonical component, which comprised 95.4% of the total variance, had water table depth as the largest standardised coefficient (Table 3.6).

Table 3.6. Analysis of variance which tested for intraspecies (row) and interspecies (column) differences in mean annual water table depth (MWTD), soil dryness stress (SEVd) and soil aeration stress (SEVa) and canonical discriminant analysis which tested linear combinations of MWTD, SEVd and SEVa that best discriminated between species spatial distributions at the New Years Peak site. Values with dissimilar letters significantly different at *P ≤ 0.05, **P ≤ 0.01, ***P ≤ 0.001. NS = not significant (P ≥ 0.05).

	MWTD (m)		**ANOVA**		**SEVd (m wk)**		**ANOVA**
Species	**Present**	**Absent**	**F-ratio**	**Species**	**Present**	**Absent**	**F-ratio**
Restio miser	0.2515aA	0.4945aB	$F_{1,231} = 163.5$***	*Restio miser*	8.98aA	10.25aB	$F_{1,231} = 37.1$***
Anthochortus crinalis	0.3570bA	0.5155aB	$F_{1,231} = 111.1$***	*Anthochortus crinalis*	9.35abA	10.46aB	$F_{1,231} = 56.4$***
Elegia coleura	0.4196cA	0.4651aA	$F_{1,231} = 3.1$ (NS)	*Elegia coleura*	9.55bA	10.15aB	$F_{1,231} = 6.6$*
Elegia neesii	0.5012dB	0.4158aA	$F_{1,231} = 26.5$***	*Elegia neesii*	10.28cB	9.85aA	$F_{1,231} = 7.7$**
Restio bolusii	0.5114dB	0.4425aA	$F_{1,231} = 11.9$***	*Restio bolusii*	10.49cB	9.93aA	$F_{1,231} = 9.5$**
Restio curviramis	0.5143dB	0.4386aA	$F_{1,231} = 15.7$***	*Restio curviramis*	10.38cA	9.9511aA	$F_{1,231} = 5.9$*
Restio pedicellatus	0.5164dB	0.4522aA	$F_{1,231} = 5.3$*	*Restio pedicellatus*	10.38cA	10.03aA	$F_{1,231} = 1.9$ (NS)
Elegia filacea	0.5288dB	0.4370aA	$F_{1,231} = 21.9$***	*Elegia filacea*	10.54cB	9.92aA	$F_{1,231} = 11.9$***
ANOVA (F-ratio)	$F_{7,458} = 41.7$***	NS	-	**ANOVA (F-ratio)**	$F_{7,458} = 15.5$***	NS	-
	SEVa (m wk)		**ANOVA**	**Canonical Discriminant**	**Component (% total variance)**		
Species	**Present**	**Absent**	**F-ratio**	**Analysis**	**1 (95.4%)**	**2 (3.0%)**	**3 (1.6%)**
Restio miser	2.8309aB	0.5796aA	$F_{1,231} = 141.9$***	**Canonical statistics**			
Anthochortus crinalis	1.8202bB	0.4035aA	$F_{1,231} = 88.6$***	Wilks Lambda	0.5722	0.9675	0.9884
Elegia coleura	1.1137cA	0.8766aA	$F_{1,231} = 0.9$ (NS)	Chi Square	256.5	15.2	5.4
Elegia neesii	0.4781dA	1.3494aB	$F_{1,231} = 29.8$***	DoF	21	12	5
Restio bolusii	0.5726dA	1.0143aB	$F_{1,231} = 5.1$*	Probability	0.0000	0.2316	0.3743
Restio curviramis	0.3391dA	1.1190aB	$F_{1,231} = 18.0$***	**Standardised coefficients**			
Restio pedicellatus	0.3376dA	0.9767aB	$F_{1,231} = 5.6$*	SEVd	-0.5510	1.6807	-1.4033
Elegia filacea	0.3447dA	1.0864aB	$F_{1,231} = 14.9$***	SEVa	0.1975	-0.2855	2.4931
				MWTD	1.5462	-1.2516	3.0825
ANOVA (F-ratio)	$F_{7,458} = 34.2$***	NS	-				

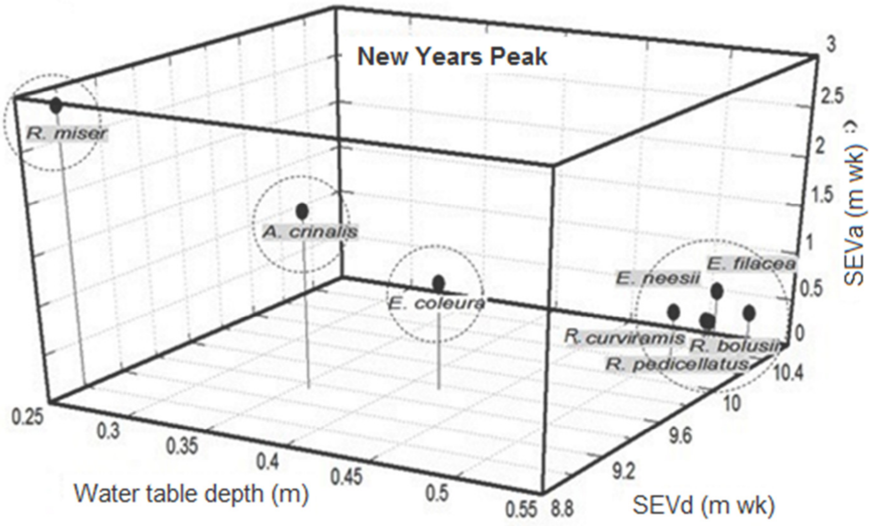


Figure 3.5 Three dimensional scatter plots water table depth, soil dryness (SEVd) and soil aeration (SEVa) stress for Restionaceae species at the New Years Peak site. Non-overlapping encircled species occupying different hydrological niches. Hydrological niches occupied by grey shaded species where present are significantly different from those where absent.

3.4.6 Riverlands

The eleven recorded Restionaceae species mostly occupied soils with significantly (P ≤ 0.05) different water table depths, dryness and aeration at locations where they were present compared with those locations where they were absent. The exceptions were *Restio capensis*, *Hypodiscus willdenowia* and *Elegia nuda* which occupied soils with non-significantly (P ≥ 0.05) different water table depths at locations where they were present compared with those locations where they were absent and *R. capensis*, *E. nuda* and *Staberoha distachyos* which occupied soils with non-significantly (P ≥ 0.05) different aeration dryness at locations where they were present compared with those locations where they were absent and *R. macer* and *R. capensis* which occupied soils with non-significantly (P ≥ 0.05) different aeration at locations where they were present compared with those locations where they were absent (Table 3.7). Also, at locations where the Restionaceae species were present the different species occupied soils with significantly (P ≤ 0.001) different water table depths, dryness and aeration. Five groups of Restionaceae species occupying soils with significantly (P ≤ 0.05) different water table depths, dryness and aeration were distinguished (Table 3.7; Figure 3.6). The first distinct group comprised *E. filacea*, the second group comprising *R. vimineus* and *R. macer* which overlapped with the third group comprising *R.*

capensis and *H. willdenowia* which in turn overlapped with the fourth group comprising *E. nuda* and *S. distachyos* and a fifth distinct group comprising *Willdenowia arescens*, *Cannomois acuminata*, *R. monanthos* and *Thamnochortus punctatus* (Table 3.7; Figure 3.6). Canonical discriminant analysis indicated that the spatial segregation of the Restionaceae species was due primarily to water table depth and to a lesser extent to soil dryness. The significant ($P \leq 0.001$) first canonical component, which comprised 88.6% of the total variance, had water table depth as the largest standardised coefficient with the second significant ($P \leq 0.001$) canonical component, which comprised 9.9% of the total variance, having soil dryness as the largest standardised coefficient of (Table 3.7).

Table 3.7. Analysis of variance which tested for intraspecies (row) and interspecies (column) differences in MWTD, SEVd and SEVa and canonical discriminant analysis which tested linear combinations of MWTD, SEVd and SEVa that best discriminated between species spatial distributions at the Riverlands site. Values with dissimilar letters significantly different at *P ≤ 0.05, **P ≤ 0.01, ***P ≤ 0.001. NS = not significant (P ≥ 0.05).

	MWTD (m)		**ANOVA**
Species	**Present**	**Absent**	**F-ratio**
Elegia filacea	0.6619a	0.7829aB	$F_{1,303} = 170.4$***
Restio vimineus	0.7082b	0.7534aB	$F_{1,303} = 7.0$**
Restio macer	0.7145b	0.7522aB	$F_{1,303} = 4.4$*
Restio capensis	0.7291bcA	0.7511aA	$F_{1,303} = 1.7$ (NS)
Hypodiscus willdenowia	0.7385bcA	0.7503aA	$F_{1,303} = 0.6$ (NS)
Elegia nuda	0.7538cdA	0.7474aA	$F_{1,303} = 0.3$ (NS)
Staberoha distachyos	0.7734dB	0.7406aA	$F_{1,303} = 7.6$**
Willdenowia arescens	0.8067eB	0.7369aA	$F_{1,303} = 27.7$***
Cannomois parviflora	0.8230eB	0.7434aA	$F_{1,608} = 30.8$***
Restio monanthos	0.8267eB	0.7377aA	$F_{1,303} = 35.5$***
Thamnochortus punctatus	0.8273eB	0.6999aA	$F_{1,303} = 265.0$***
ANOVA (F-ratio)	$F_{10,594} = 52.2$***	NS	

	SEVd (m wk)		**ANOVA**
Species	**Present**	**Absent**	**F-ratio**
Elegia filacea	15.28aA	18.68aB	$F_{1,303} = 121.1$***
Restio vimineus	16.37bA	17.88aB	$F_{1,303} = 7.8$**
Restio macer	16.52bcA	17.85aB	$F_{1,303} = 5.5$*
Restio capensis	16.95bcA	17.82aA	$F_{1,303} = 2.6$ (NS)
Hypodiscus willdenowia	16.79bcA	17.87aB	$F_{1,303} = 4.9$*
Elegia nuda	17.45cdA	17.79aA	$F_{1,303} = 0.8$ (NS)
Staberoha distachyos	18.13dA	17.59aA	$F_{1,303} = 2.0$ (NS)
Willdenowia arescens	19.28eB	17.41aA	$F_{1,303} = 19.6$***
Cannomois parviflora	20.34fB	17.54aA	$F_{1,608} = 38.9$***
Restio monanthos	20.01efB	17.40aA	$F_{1,303} = 30.1$***
Thamnochortus punctatus	20.09fB	16.25aA	$F_{1,303} = 226.1$***
ANOVA (F-ratio)	$F_{10,594} = -40.8$***	NS	

	SEVa (m wk)		**ANOVA**
Species	**Present**	**Absent**	**F-ratio**
Elegia filacea	0.2600aB	0.0524aA	$F_{1,303} = 59.4$***
Restio vimineus	0.2049abB	0.1003aA	$F_{1,303} = 5.8$*
Restio macer	0.1282bcA	0.1092aA	$F_{1,303} = 0.2$ (NS)
Restio capensis	0.1048cdA	0.1117aA	$F_{1,303} = 0.0$ (NS)
Hypodiscus willdenowia	0.0107eA	0.1261aB	$F_{1,303} = 8.9$**
Elegia nuda	0.0406deA	0.1297aB	$F_{1,303} = 7.7$**
Staberoha distachyos	0.0165eA	0.1423aB	$F_{1,303} = 17.8$***
Willdenowia arescens	0.0113eA	0.1314aB	$F_{1,303} = 12.1$***
Cannomois parviflora	0.0273deA	0.1170aB	$F_{1,608} = 5.8$*
Restio monanthos	0.0000eA	0.1268aB	$F_{1,303} = 10.3$**
Thamnochortus punctatus	0.0009eA	0.1795aB	$F_{1,303} = 50.0$***
ANOVA (F-ratio)	$F_{10,594} = 18.7$***	NS	

Canonical Discriminant	**Component (% total variance)**		
Analysis	**1 (88.6%)**	**2 (9.9%)**	**3 (1.4%)**
Canonical statistics			
Wilks Lambda	0.4299	0.8801	0.9803
Chi Square	469.7	71.1	9.3
DoF	27	16	7
Probability	0.0000	0.0000	0.2307
Standardised coefficients			
SEVd	-1.2679	2.8274	-3.0336
SEVa	0.1880	0.1039	1.5113
MWTD	2.2369	-2.3579	3.4046

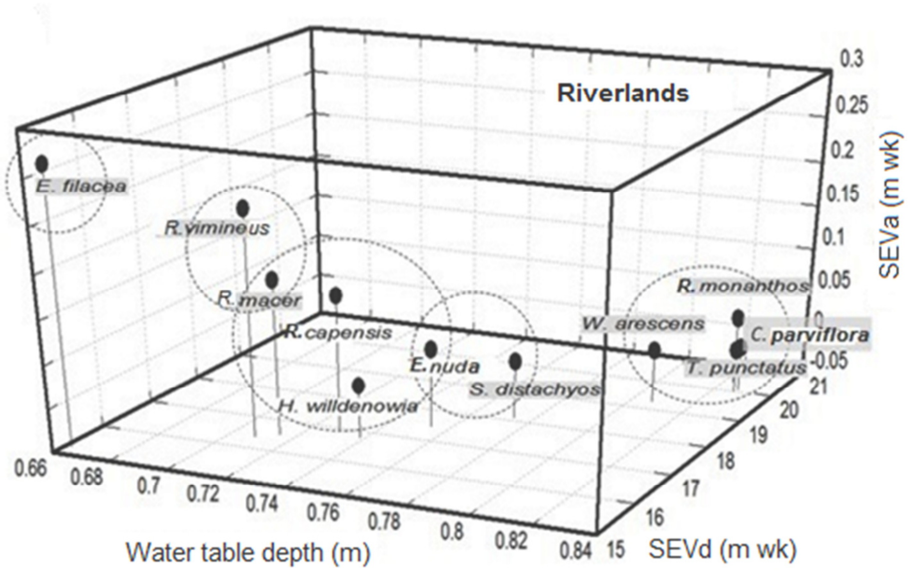


Figure 3.6 Three dimensional scatter plots water table depth, soil dryness (SEVd) and soil aeration (SEVa) stress for Restionaceae species at the Riverlands site. Non-overlapping encircled species occupying different hydrological niches. Hydrological niches occupied by grey shaded species where present are significantly different from those where absent.

3.4.7 Silvermine

Of the four recorded Restionaceae species, only *Elegia filacea* occupied soils with significantly ($P \leq 0.05$) different water table depths, dryness and aeration at locations where it was present compared with those locations where it was absent (Table 3.8). Also, at locations where the Restionaceae species were present the different species occupied soils with significantly ($P \leq 0.001$) different water table depths, dryness and aeration. Two distinct groups of Restionaceae species occupying soils with significantly ($P \leq 0.05$) different water table depths, dryness and aeration were distinguished (Table 3.8; Figure 3.7). The first distinct group comprised *E. filacea* and the second distinct group comprised *R. cincinnatus*, *R. capensis* and *H. aristatus* (Table 3.8; Figure 3.7). Canonical discriminant analysis indicated that the spatial segregation of the Restionaceae species was due primarily to soil dryness. The significant ($P \leq 0.001$) first canonical component, which comprised 97.7% of the total variance, had soil dryness as the largest standardised coefficient (Table 3.8).

Table 3.8. Analysis of variance which tested for intraspecies (row) and interspecies (column) differences in mean annual water table depth (MWTD), soil dryness stress (SEVd) and soil aeration stress (SEVa) and canonical discriminant analysis which tested linear combinations of MWTD, SEVd and SEVa that best discriminated between species spatial distributions at the Silvermine site. Values with dissimilar letters significantly different at *P ≤ 0.05, **P ≤ 0.01, ***P ≤ 0.001. NS = not significant (P ≥ 0.05)

	MWTD (m)				SEVd (m wk)		
Species	Present	Absent	ANOVA F-ratio	Species	Present	Absent	ANOVA F-ratio
Elegia filacea	0.7366aA	0.8064aB	$F_{1,198}$ = 42.0***	*Elegia filacea*	17.01aA	19.47aB	$F_{1,198}$ = 42.9***
Restio cincinnatus	0.7988bA	0.7792aA	$F_{1,198}$ = 2.9 (NS)	*Restio cincinnatus*	19.22bA	18.45aA	$F_{1,198}$ = 3.7 (NS)
Restio capensis	0.8078bA	0.7941aA	$F_{1,198}$ = 1.0 (NS)	*Restio capensis*	19.44bA	19.05aA	$F_{1,198}$ = 0.7 (NS)
Hypodiscus aristatus	0.8104bA	0.7912aA	$F_{1,198}$ = 3.6 (NS)	*Hypodiscus aristatus*	19.60bA	18.94aA	$F_{1,198}$ = 3.6 (NS)
ANOVA (F-ratio)	$F_{3,262}$ = 12.5***	NS		ANOVA (F-ratio)	$F_{3,262}$ = 12.8***	NS	
	SEVa (m wk)			Canonical Discriminant Analysis	Component (% total variance)		
Species	Present	Absent	ANOVA F-ratio		1 (97.7%)	2 (2.3%)	3 (0.0%)
Elegia filacea	0.3010aA	0.0812aB	$F_{1,198}$ = 31.3***	Canonical statistics			
Restio cincinnatus	0.1062bA	0.1608aA	$F_{1,198}$ = 1.8 (NS)	Wilks Lambda	0.8490	0.9960	1.0000
Restio capensis	0.0797bA	0.1196aA	$F_{1,198}$ = 0.7 (NS)	Chi Square	42.8	1.1	0.0
Hypodiscus aristatus	0.0706bA	0.1285aA	$F_{1,198}$ = 2.6 (NS)	DoF	9	4	1
				Probability	0.0000	0.9008	0.9931
				Standardised coefficients			
				SEVd	2.2522	-5.2175	0.2324
				SEVa	-0.8158	1.3390	1.4065
				MWTD	-1.8783	6.4400	0.9616
ANOVA (F-ratio)	$F_{3, 262}$ = 9.0***	NS					

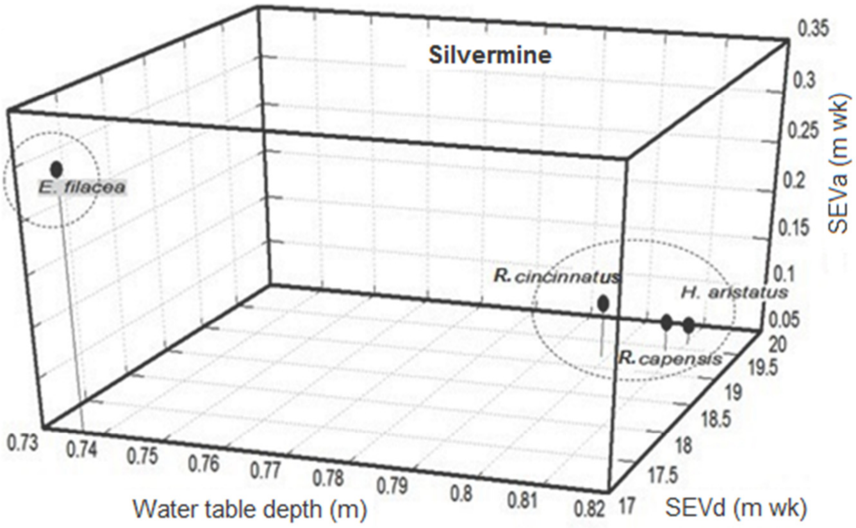


Figure 3.7 Three dimensional scatter plots water table depth, soil dryness (SEVd) and soil aeration (SEVa) stress for Restionaceae species at the Silvermine site. Non-overlapping encircled species occupying different hydrological niches. Hydrological niches occupied by grey shaded species where present are significantly different from those where absent.

3.4.8 Theewaterskloof

Of the five recorded Restionaceae species, all species except *Elegia neesii* occupied soils with significantly (P ≤ 0.05) different water table depths, dryness and aeration at locations where they were present compared with those locations where they were absent (Table 3.9). Also, at locations where the Restionaceae species were present the different species occupied soils with significantly (P ≤ 0.001) different water table depths, dryness and aeration. Four distinct groups of Restionaceae species occupying soils with significantly (P ≤ 0.05) different water table depths, dryness and aeration were distinguished (Table 3.9; Figure 3.8). The first distinct group comprised *Anthochotus crinalis* and *Platycaulos callistachyus*, the second distinct group comprised *E. neesii*, the third distinct group comprised *Restio curviramis* and the fourth distinct group comprised *Staberoha cernua* (Table 3.9; Figure 3.8). Canonical discriminant analysis indicated that the spatial segregation of the Restionaceae species was due primarily to soil aeration. The significant first (P ≤ 0.001) and second (P ≤ 0.05) canonical components, which collectively comprised 98.7% of the total variance, both had soil aeration as the largest standardised coefficients (Table 3.9).

Table 3.9. Analysis of variance which tested for intraspecies (row) and interspecies (column) differences in mean annual water table depth (MWTD), soil dryness stress (SEVd) and soil aeration stress (SEVa) and canonical discriminant analysis which tested linear combinations of MWTD, SEVd and SEVa that best discriminated between species spatial distributions at the Theewaterskloof site. Values with dissimilar letters significantly different at *P ≤ 0.05, **P ≤ 0.01, ***P ≤ 0.001. NS = not significant (P ≥ 0.05).

	MWTD (m)		
Species	Present	Absent	ANOVA F-ratio
Anthochortus crinalis	0.4456aA	0.5834aB	$F_{1,198}$ = 38.4***
Platycaulos callistachyus	0.4683aA	0.5825aB	$F_{1,198}$ = 27.7***
Elegia neesii	0.5559bA	0.5822aA	$F_{1,198}$ = 3.6 (NS)
Restio curviramis	0.6063cB	0.5170aA	$F_{1,198}$ = 49.1***
Staberoha cernua	0.6618dB	0.5067aA	$F_{1,198}$ = 309.5***
ANOVA (F-ratio)	$F_{4,322}$ = 52.4***	NS	

	SEVd (m wk)		
Species	Present	Absent	ANOVA F-ratio
Anthochortus crinalis	10.97aA	12.71aB	$F_{1,198}$ = 26.7***
Platycaulos callistachyus	11.17aA	12.71aB	$F_{1,198}$ = 22.4***
Elegia neesii	12.29bA	12.75aB	$F_{1,198}$ = 4.9*
Restio curviramis	13.00cB	11.86aA	$F_{1,198}$ = 34.6***
Staberoha cernua	13.90dB	11.59aA	$F_{1,198}$ = 321.6***
ANOVA (F-ratio)	$F_{4,322}$ = 42.4***	NS	

	SEVa (m wk)		ANOVA
Species	Present	Absent	F-ratio
Anthochortus crinalis	2.5038aB	0.7677aA	$F_{1,198}$ = 56.4***
Platycaulos callistachyus	2.0361aB	0.8004aA	$F_{1,198}$ = 27.9***
Elegia neesii	1.1073bA	0.7884aB	$F_{1,198}$ = 4.5*
Restio curviramis	0.5082cA	1.5607aB	$F_{1,198}$ = 61.7***
Staberoha cernua	0.0706dA	1.5293aB	$F_{1,198}$ = 171.3***
ANOVA (F-ratio)	$F_{4,322}$ = 60.1***	NS	

Canonical Discriminant	Component (% total variance)		
Analysis	1 (94.0%)	2 (4.7%)	3 (1.3%)
Canonical statistics			
Wilks Lambda	0.5356	0.9521	0.9892
Chi Square	201.1	15.8	3.5
DoF	12	6	2
Probability	0.0000	0.0148	0.1740
Standardised coefficients			
SEVd	0.7174	0.8719	-4.0846
SEVa	-1.1236	1.4814	2.2347
MWTD	-0.7497	0.8148	6.0439

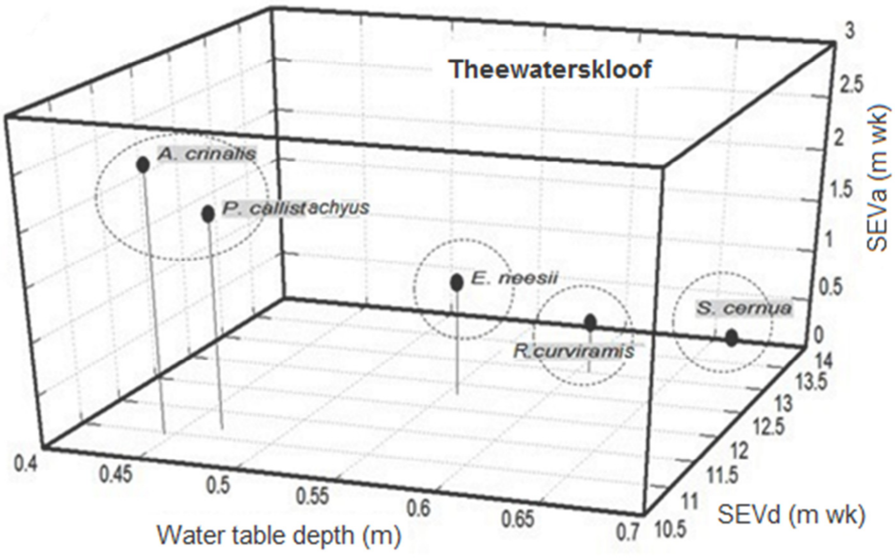


Figure 3.8 Three dimensional scatter plots water table depth, soil dryness (SEVd) and soil aeration (SEVa) stress for Restionaceae species at the Theewaterskloof site. Non-overlapping encircled species occupying different hydrological niches. Hydrological niches occupied by grey shaded species where present are significantly different from those where absent.

From the above results, there are four species that occur in more than one site, here referred to as common speciesin the current data set. Table 3.10 is a synthesis of some attributes of these four common species. *Elegia filacea* is the most common species occurring in five sites, followed by *Staberoha distachyos* found in four sites. The other two species, *Restio capensis* and *Restio curviramis*, each occur in three sites. All the species exhibit at different hydrological attributes at the different sites. *E. filacea*has SEVa values ranging between 0.1499 and 0.3447 m.wk, SEVdvalues from 10.54 to 17.01m.wk and MWTD between 0.5288 and 0.7366 m. *R. capensis* shows SEVa between 0.0797 and 0.1048 m.wk, SEVd between 16.73 and 19.44m.wk and MWTD between 0.6827 and 0.8078 m. *R. curviramis* shows SEVa between 0.1282 and 0.5082 m.wk, SEVd between 10.38 and 15.96m.wk and MWTD between 0.5143and 0.6496 m. Lastly, *S. distachyos* shows SEVa between 0.0165 and 0.1187 m.wk, SEVd between 12.61 and 18.13 m.wk and MWTD between 0.6031 and 0.7734 m.

Table 3.10. Hydrological niches exhibited by species common to more than two sites.

Species	Frequency (%)	SEVa (m.wk)	SEVd (m.wk)	MWTD (m)	Site/occurrence
E. filacea	88.4	0.2272	12.3	0.5824	Cape Point
	51.5	0.1499	16.15	0.6999	Kogelberg
	24	0.3447	10.54	0.5288	NYP
	28.2	0.26	15.28	0.6619	Riverlands
	15.5	0.301	17.01	0.7366	Silvermine
	Hydrological range	0.1499–0.3447	10.54-17.01	0.5288-0.7366	
R. capensis	10	0.1032	16.73	0.6827	Bastiaanskloof
	10.5	0.1048	16.95	0.7291	Riverlands
	11	0.0797	19.44	0.8078	Silvermine
	Hydrological range	0.0797-0.1048	16.73-19.44	0.6827-0.8078	
R. curviramis	21.5	0.1282	15.96	0.6496	Bastiaanskloof
	27	0.3391	10.38	0.5143	NYP
	60.5	0.5082	13	0.6063	Theewaterskloof
	Hydrological range	0.1282-0.5082	10.38-15.96	0.5143-0.6496	
S. distachyos	43	0.1067	17.06	0.6925	Bastiaanskloof
	34.2	0.1187	12.61	0.6031	Cape Point
	24.5	0.0391	16.19	0.7154	Kogelberg
	24.9	0.0165	18.13	0.7734	Riverlands
	Hydrological range	0.0165-0.1187	12.61-18.13	0.6031-0.7734	

3.5 Discussion

Hydrological niche segregation occurs in a great variety of vegetation types across all environments from wet to mesic to arid environments. Evidence from species occurrence analysis in this study reveals that restioids in Fynbos communities in the south-western CFR segregate along fine hydrological gradients at a localised scale. This is not different from the findings of Araya et al. (2011) that analysed hydrological niches in Fynbos communities and found that Restionaceae species of Fynbos communities segregate along local soil moisture gradients, just like plant species in English meadows (Silvertown et al., 1999). Plants distribution at this local scale is often determined by the seasonal variation in the available moisture and fluctuations in the water table. The existence of mosaics of water regimes can be attributed to internal topographical variations within the small size plot. This mosaic allows plant species with different water regime requirements to segregate over small distances (Raulings et al., 2010).

Individual Restionaceae species survive in suitable hydrological habitats as shown in the current study which according to niche theory is the space where they out-compete other species within that community (Whittaker, 1965). Whereas some species are distinct in their preference for either wetter or drier conditions, some do coexist with other species within the same broad hydrological niche, where there is competition for the common ecological resource. Furthermore, Restionaceae species seem to occupy significantly different hydrological niches in terms of the preferred water table depth, soil dryness and aeration stress across and within the sites. The influence of hydrological variables is best demonstrated where species presence and absence locations are examined together. Results from analysing the variance within the plots show significant inherent hydrological differences between species presence from absence locations which confirms the non-suitability of certain hydrological thresholds for species growth. Also, there is cohabitation amongst some species at most sites wherein these individuals compete for or share the same physical resources although the species constituents in these groupings varied between the sites. On the other hand, there is evidence of adaptation or exclusion where some species assemblages are spatially isolated or seem to have evolved to adapt to specific hydrological conditions better than the others. It is expected that these dynamics would change due to changes in the supply of water resources caused by climate change and human water abstractions. Expectations are that the competition for resources would initiate reorganisation of species assemblages and as a result changes in the community structures.

A trade-off could have resulted in the establishment of these niches according to hydrological traits of the substrate. However, information is scarce on what physiological factors inform the perceived associations amongst species in hydrological niche space. So far, (Silvertown et al., 2012) showed that hydrological niche segregation could potentially originate from seedling stage. Evidence from observation of seedling growth in the field seems to confirm that the patterns observed later originated through selective propagation where seed germination is affected by soil moisture status and by root competition (Silvertown et al., 2012), implying that hydrological niche segregation could potentially originate in the seedling stage. However, the results of this pilot study might lead us to answer fundamentals questions which are key to understanding the factors that underpin species niche segregation and their spatial patterns.

In this study, water table depth and soil moisture conditions (aeration and saturation) are considered as the key factors influencing the distribution patterns of vegetation communities along fine gradients in the CFR. Results here showed that the distribution of Restionaceae species is greatly influenced by all hydrological variables although the different variables do not equally affect the various species distribution at most sites.

Findings from this study show that water table depth explains on average above 80% of the species variations in wetland communities. Four of the eight wetland communities that were examined to diagnose which factor best influenced the species distribution, revealed MWTD as the principal factor affecting the spatial segregation of the Restionaceae species. The exceptions were Bastiaanskloof and Theewaterskloof where SEVs thresholds seem to be of better influence (SEVs were identified as an alternative to the predominantly influential MWTD). Similar findings in riparian meadows in the USA show that species appear to be just as differentially sensitive to water table depth (Castelli et al., 2000, Dwire et al., 2006). Other works showed summarily that water table levels describe hydrological conditions better than other measures of soil moisture (Hájek et al., 2013). However, it should be noted that species segregation might have been influenced to some degree by other factors. E.g. a light gradient might cause the trade-off between growth rate in better light conditions and survival in shady conditions (Kobe, 1999). Niche segregation might be caused by root depth (Nobel, 1997, Denslow et al., 1998) or by nutrient (nitrogen) availability (McKane et al., 2002). In the quest for survival in light challenging situations, resilient species would adopt coping mechanisms that enable them to adapt and survive in darkness whereas others perish at the spot or continue to thrive where there is sufficient light. Also, the availability of soil nutrients and oxygen around the roots is impeded in anoxic conditions which perturb the oxidation-reduction environment thereby impeding plants ability to respire or absorb nutrients

Of the total of 55 species that were examined, only four of these, namely, *Restio curviramis*, *Restio capensis*, *Staberoha distachyos* and *Elegia filacea* showed occurrences in three or more of the eight sites under study. According to Table 3.10, the hydrological niche of each of these species varied across sites. This shows that for these species, we can start approximating the fundamental niche and not just a realised niche. Clearly, the ecological niche exceeds the realised niche. For example, the MWTD range of *E. filacea* varies from approximately 0.53 m - 0.74 m. With such a relatively wide interval, there is more likelihood of an overlap with other species niches.

3.6 Conclusion

Statistical analysis has demonstrated species segregation in wetland communities in the south-west of the CFR. The study demonstrated the high species diversity that is characteristic of the Fynbos biome as a whole. Evidence from the results obtained here revealed species realised niches which have not previously been established for most of the species. Although the results have demonstrated that some pairs of species do share the same niche, this has not been a general trend for most of the Fynbos restioids as the results demonstrated. The determination of a fundamental niche of the more widespread species suggests that the species occurring in several sites have a wider tolerance and are best adapted to environmental changes.

Canonical discriminant analysis was successfully used to discriminate between Restionaceae species in terms of their hydrological affiliations by using three canonical components that are linear combinations of physical measurements. Attempts at discriminating among species using only two canonical components led to classification errors, because the projection onto the span of the first two canonical components does not separate some Restionaceae groupings from the others.

So far, the above findings have shown that hydrological gradients play a role in the maintenance of species richness in Fynbos wetland communities. The current relationships demonstrated between species distribution and hydrological gradients make it possible to predict the result of potential hydrological changes and the expected alterations that they may cause to restioids distributions and Fynbos biodiversity as a whole.

CHAPTER 4 QUANTIFYING EVAPOTRANSPIRATION IN THREE WETLAND COMMUNITIES IN THE SOUTH WEST OF THE CAPE FLORISTIC REGION

4.1 Introduction

South Africa is a semi-arid country, with evaporation rates exceeding the rates of precipitation, (DWAF, 2006) which is the cause of the moisture deficits that characterise such environments. Generally, plants in this region are prone to water stress and are characteristically adapted to prolonged dry or insufficient soil moisture conditions (Maliva and Missimer, 2012). Located in the south-western fringes of Southern Africa, is the Cape Floristic Region (CFR) which is habitat to primarily Fynbos vegetation. The CFR is both a UNESCO heritage site and a biodiversity hotspot (Myers et al., 2000). The climate is characteristically Mediterranean in this region, although being situated in an arid region setting which means that the region is prone to adversities caused by changing soil moisture conditions.

Within the FynbosBiome of the southwestern Cape is found a number of wetland communities which are incidentally islands of high biodiversity (Myers et al., 2000). An understanding of how plants in these mostly ephemeral wetland natural ecosystems are affected by the arid – semi-arid conditions is important considering that they are not exposed to engineered restorative solutions like irrigation. Rainfall is the main moisture input source while evapotranspiration (ET) is the main output from the system – the balance which forms the soil storage becomes moisture available for plant use. Hence, with prevailing arid or semi-arid conditions, ET is a crucial component of the water budget being the main outlet for whatever amounts of precipitation that entered the system. Therefore, ET must be quantified for proper understanding and management of available water resource in these wetland ecosystems.

Evapotranspiration (ET) is the transfer of vaporised water to the atmosphere from open water bodies or non-vegetated soil surfaces unimpeded by hydrostatic forces in the soil (evaporation); and vegetated surfaces through transpiration by plants (Allen et al., 1998, Dingman, 2015). Based on the above definition, the potential rate of ET is affected by the state of atmospheric variables like temperature, humidity, wind speed and solar radiation, as well as by the availability of soil moisture which determines the actual amounts to lose. In arid and semi-arid regions like South Africa, evapotranspiration (ET) is a difficult component to measure because the magnitude of the ET flux is relatively smaller as compared to that of wetter regions (Ramoelo et al., 2014). An additional difficulty in the CFR is the presence of highly variable ET over space and time, due to variability in the landscape, topography, climate, vegetation type, soil properties (Allen et al., 1998, Mu et al., 2007). Generally, accurate spatially explicit information on ET is rare mainly due to lack of appropriate tools (Ramoelo et al., 2014). Remote sensing ET products are favoured in satisfying both large-scale and plots (fine-) scale studies of ET because of their capability to estimate the spatial and temporal variation of ET (Jovanovic et al., 2012, Ramoelo et al., 2014). However, remote sensing methods do not take rainfall (which is the main input component) into account. This limitation makes remote sensing products impractical when accounting for the role of ET in the water budget as the quantification of ET cannot be complete without an account on rainfall and the storage in the soil water budget systems (Dingman, 2015).

Direct quantification or measurement of ET through instrumentation is sophisticated, expensive and sometimes impractical, and a challenge in places with a limited budget to carry on the process prompting the use of less costly empirical means to estimate it. An evaporation pan is used to directly measure actual evapotranspiration (AET) from open water surfaces (Maidment, 1992, Viessman et al., 2003). However, directly measuring potential evapotranspiration (PET) (Penman, 1948) or reference evapotranspiration (ETo) (Allen et al., 1994, Allen et al., 1998) from a vegetated surface under non-limiting conditions is less apparent because both forms of ET are affected by the nature of the plants and the prevailing environmental conditions. Furthermore, some forms of ET like PET are conceptual and cannot be measured directly but can only be quantified through models. Techniques which capture in situ ET have been successful in a number of the agricultural and natural environmental studies within South Africa e.g. natural vegetation (Clulow et al., 2012), wetlands (Everson et al., 2009) and crops (Oelofse and Van Averbeke, 2012). These studies used direct measurements with porometers and lysimeters (Allen et al., 1991), energy balance and micrometeorological techniques which use atmospheric measurements (Bowen, 1926), and so on. The above practices proved expensive both based on affordability of equipment in South Africa and the prevalent culture of vandalism faced by this fragile equipment thereby rendering data discontinuous and even distorted (Jovanovic et al., 2012).

Numerous ET estimation models of varying complexity occur in the literature (McMahon et al., 2013). These models vary in complexity based on their data demands, process representation and assumptions. Complexity ranges from simple models which require mainly temperature and/or net solar radiation e.g. Hargreaves and Samani (1985), Jensen and Haise (1963), and Makkink (1957), to complex data intensive methods which require additional variables, such as relative humidity and wind speed e.g. Penman (1948), Priestley and Taylor (1972) and Thom and Oliver (1977). The United Nation's Food and Agricultural Organisation (FAO) recommended the FAO-56 Penman-Monteith method as the standard method to calculate reference evapotranspiration (ETo) anywhere in the world as long as the required input data are available (Allen et al., 1998). The applicability of the FAO56-PM model is demonstrated around the world (Hess, 1998, Xu et al., 2006, Fooladmand and Haghighat, 2007, Sumner and Jacobs, 2005).

The choice of what form of ET to use depends on the data availability and the purpose of the ET estimates. Pan ET estimates differ considerably from estimates obtained from a vegetated crop surface (Allen et al., 1998), but these estimates are still relevant in that they can be related to ETo after incorporation with an empirical coefficient (Xu et al., 2006). However, actual evapotranspiration (AET) is a preferred input for hydrological modelling (Liu et al., 2005) or for assessing hydrological impacts due to climate change (Donohue et al., 2010). Hence, in practice, potential evapotranspiration (PET) and reference evapotranspiration (ETo) is first calculated for vegetated crop surfaces before applying an appropriate crop coefficient (Kc) to estimate AET (Allen et al., 1998).

All ET estimation methods incorporate observable weather parameters in their formulations even though they are uniquely calibrated to specific environmental conditions wherein they function optimally. Fortunately, most of these models are adaptable to use in other regions simply by customising parameters to existing local conditions. This makes data availability a major determinant of the choice of model in use although sometimes, this choice is influenced by the intended use of the estimated ET e.g. Mintz and Walker (1993).

To quantify ET (in different ecosystems) at a local scale warrants the detailed examination of water flux processes at minute scales. So far, numerical simulation of atmospheric circulation has now advanced to the point where the effects of changing microclimate and ET can be modelled (Small, 2003). Conventional point-based ET estimation methods are most desirable to capture fine-scale variability which becomes suitable inputs for micro-scale soil moisture budgeting although they are difficult to obtain due to time and cost constraints.

Climate change affects Mediterranean regions mostly due to changes in temperature and rainfall patterns. The IPCC global models have generally projected increases in temperature for whole southern Africa and the CFR is particularly vulnerable to climate extremes (Midgley et al., 2005). Such conditions make the region predisposed to any tangible environmental changes. So far, future climate projections predict increased temperature and generally reduced but spontaneous and mostly irregular rainfall in the region (Midgley et al., 2005). What would be the impact of climate change on vegetation diversity in wetlands in the CFR? Already, historical meteorological records indicate a decline in mean annual rainfall in the CFR with a concomitant increase in temperature over the last few decades (Kruger and Shongwe, 2004, New et al., 2006). These conditions are likely to be the cause of increased levels of potential evapotranspiration (PET) (Roderick et al., 2009) and by implication, cause possible changes in soil moisture balance in the area. This makes PET a vital component of the hydrological budget as it is the key flux which regulates soil moisture conditions and returns of moisture to the atmosphere where it forms rain again (Guo et al., 2015).

By definition, potential evapotranspiration (PET) is the estimated total moisture that would possibly be lost to the atmosphere through evapotranspiration by plants at unlimited moisture supply in the soil. As stated above, it is commonly used in conceptual hydrological modelling in the calculation of different components including soil storage levels (indicated by saturation or water table levels) (Prudhomme and Williamson, 2013). PET losses are quite significant to the water budget in semi-arid climates like in SA. Future changes of PET are likely to be as important as changes in precipitation patterns in determining changes in soil moisture storage (Prudhomme and Williamson, 2013). However, PET is not directly calculated by climate models. So PET must be derived independently in order to assess its impact on the future soil moisture storage.

The objectives of this study were to: (1) use suitable empirical formulae to estimate in-situ ET (microclimatic ET) at some wetland communities which should later serve as one input in a simple soil-water budget model in these same wetland communities; (2) compute evapotranspiration rates from GCM-derived scenarios of climate change for the same locations in the CFR.

4.2 Methods

4.2.1 Dataset

Daily records of rainfall (mm), air temperature (°C), humidity (%), solar radiation (W/m^2), wind speed (km/h), wind gust (km/h) and wind direction (deg.) were collated from three automatic weather stations located at Riverlands (33°29’12.8”S, 18°35’43.3”E, alt. 120m, dry interior), Steenbras (34°41’20.0’’S, 18°52’14.0’’E, alt. 350m, coastal) and New Years Peak (33°41’20.0’’S, 19°06’03’’E, alt. 1080m, mountain). Each station is located on an experimental plot on which hydro-physical and ecological surveys were being conducted. They recorded contrasting environmental conditions – Steenbras on the coastal line, Riverlands at a dry interior area and New Years Peak at an altitude close to 2000m above sea level. Due to the localised nature of this study, the existing network of weather stations in the region could not be used. These are much spaced out and good for a regional study but not for a local scale study. In addition, none of the existing stations was located less than 10km from any of the experimental sites. The data records were from 2007 to 2009. Though short, this period was appropriate in the context of the current study as it conformed to the period for which hydrological measurements were measured at these same sites. These represented recent weather and were used to determine current ET at the three experimental sites.

Downscaled Global Climatic Model (GCM) point data were used for estimating ET under two emission scenarios in the future. Unlike synoptic climatic data that have a full complement of weather elements, the GCM data contained only rainfall, temperature, and solar radiation. These were sufficient for use by simple ET algorithms like the Jensen–Haise and Makkink ET models to estimate ET (Jensen and Haise, 1963). Future climate simulation data were obtained from the MPI-ESM-MR model (Max Planck Institute for Meteorology, Earth Systems Models) which is part of the Coupled Model Intercomparison Project Phase 5 (CMIP5). The MPI-ESM model was chosen because it is well suited for predictions of Southern Africa climate, including other significant advantages, it has over the other models (Santer et al., 1989, Connolley and Bracegirdle, 2007). The GCM daily records (data) are calibrated using observations (Reanalysis) and bias correction approaches (Gudmundsson et al., 2012b, Hawkins et al., 2013). GCM data from 2020 – 2100 was provided by the CGIAR Research Program on Climate Change, Agriculture and Food Security (CCAFS). The data are bias-corrected based on the Modern-Era Retrospective Analysis for Research and Applications (MERRA) AgCFSR observational dataset and readily available for use. From this data set, daily data from 2097 – 2100 were extracted to analyse for evapotranspiration rates in the distant future. This was an attempt to synergize the time range of the current and the GCM estimates. Two representative concentration pathways (RCPs), which are the RCP2.6 and RCP8.5, were used as comparative future scenarios to reasonably reflect the lower and upper extremes of modelled changes in solar irradiations (Rogelj et al., 2012). RCPs simulate a possible range of radiative forcing values in the future relative to pre-industrial values, +2.6 and +8.5 W/m^2, respectively. RCP2.6 assumes that global annual emissions measured in CO$_2$-equivalents peak between 2010 - 2020 with emissions declining after, and RCP 8.5 assumes emissions continue to rise throughout the 21st century (Lamarque et al., 2011, Van Vuuren et al., 2011). The RCP2.6 scenario is good but an unlikely future scenario, while the RCP8.5 is a more realistic future scenario based on the present human activity. Interestingly, GCM data records contain a limited number of climatic variables. These include precipitation in mm, maximum temperature (^{o}C), minimum temperature (^{o}C), mean temperature (^{o}C) and solar radiation (W/m^2).

Both contemporary and future daily records were aggregated to provide monthly (long-term) totals. Simple linear plots were created using Microsoft Excel to show seasonal variations for temperature, wind speed, relative humidity and solar radiation for the present using. While only the seasonal variations in temperature and radiation could be shown for the future.

4.2.2 Evapotranspiration modelling

Evapotranspiration was calculated by an *Evapotranspiration* package (Guo et al., 2016c) which was implemented in R statistical software (R Development Core Team, 2015) to estimate both potential and crop reference ET in daily time steps. This tool uses predefined constants and site-specific variables along with the available climate data. It estimates ET in a two-phase process. Phase 1 or the pre-processing phase does data input, quality assessment and calculation of basic statistics, and Phase 2 does the ET estimation proper. More details on the data processing requirements, calculation and model outputs visualisation plots have been explained in the package manual (Guo et al., 2016c).

Temperature and solar radiation were the only two elements found in both contemporary and future climatic data. This influenced the choice of using the Jensen and Haise (Jensen et al., 1990, Jensen and Haise, 1963) and the Makkink equations (Makkink, 1957) which are best suited in instances with data limitations (Xu and Singh, 2000, Prudhomme and Williamson, 2013) and are also recommended when only temperature or radiation data are available (Doorenbos and Pruitt, 1977).

The Jensen-Haise ET model (Equation 4.1) estimates potential evapotranspiration rates as it assumes an evaporative surface within an adequately watered arid/semi-arid area (Jensen and Haise, 1963). Its calibration was based on arid/semi-arid conditions in the western USA and it computes potential evapotranspiration in daily time steps. It uses only average daily temperature (T_a) in ^{o}C (Equation 4.2) and incoming short solar radiation (R_s)

as the principal data inputs. Furthermore, the Jensen-Haise model requires that R_s units are converted from W/m^2 to MJ/m^2 units prior to usage.

$$ET = \frac{0.025}{\lambda}\left(R_s \times (T_a + 3)\right) \qquad \text{Equation 4.1}$$

$$T_a = {(T_{max} + T_{min})}/{2} \qquad \text{Equation 4.2}$$

Where, T_a = average daily temperature (°C); R_s = shortwave radiation (MJ/m^2); Lambda (λ) = latent heat of vaporisation (MJ/kg). The default value of λ is 2.45 at 20°C. In addition to λ, the Jensen-Haise model required the use of additional site-specific constants which is latitude coordinates of the site given in radians.

Similarly, the Makkink model (Equation 4.3) estimated reference crop evapotranspiration in daily time steps. This ET model calculates reference crop ET as it assumes an evaporative surface that is covered by a reference crop (De Bruin, 1981). It is calibrated only to cool climate conditions in the Netherlands and it incorporates both site-specific and predefined variables. It performs quite closely with the modified Priestley and Taylor equations when evaluated with pan evaporation measured at a station in Switzerland (Xu and Singh, 2000). The slope of vapour pressure curve (Δ) was computed from the daily mean temperature (T_a) using Equation 4.4, the psychrometric constant (γ) was computed from elevation (P) in metres above sea level and the latent heat of vaporisation deduced by Equation 4.5.

$$ET = C_1\left(\frac{\Delta}{\Delta+\gamma}\frac{R_s}{2.45}\right) - C_2 \qquad \text{Equation 4.3}$$

Where delta (Δ) is the slope of vapour pressure curve in kPa/°C calculated using Equation 4 as follows:

$$\Delta = \frac{4098\left[0.6108\exp\left(\frac{17.27 * T_a}{T_a+237.3}\right)\right]}{\left(T_a+237.3\right)^2} \qquad \text{Equation 4.4}$$

Where T_a is the average daily temperature calculated as $(T_{max}+T_{min})/2$ in °C; γ is the psychrometric constant in kPa/°C, calculated from Equation 4.5.

$\gamma = 0.00163\frac{\mathrm{P}}{\lambda}$ Equation 4.5

Where P is the elevation z in metres; C_1 = 0.61 (dimensionless), C_2 = 0.12 mm/day.

4.2.3 Statistical analysis and forecasting

The statistical package for the social sciences (SPSS v.22) was used to test the data for normality after which a Kruskal-Wallis test for differences analysis tested if there is no significant change in the daily ET estimates from the most recent times to the future during a selected time range of N=1950 days. The stationarity of ET at each site over time was tested using linear regression between the time of observation (independent) and the ET correspondents (dependents). A trend was assumed if the slope of the least squares regression line was significantly different from zero. Finally, predictive analysis models of ET using Excel's multiple linear regression tools were used to forecast or complete the ET cycle in 2009.

4.3 Results and discussion

This section includes a descriptive analysis of the data pre-screening outputs and some basic statistics as processed by the *Evapotranspiration* modelling package. It also contains a comparative view of the long-term seasonal trends shown by the common weather elements in both in situ current data captured by automatic weather stations and GCM data estimates at three observation sites.

4.3.1 Descriptive analysis and basic statistics

Preliminary analysis of long-term averages illustrated strong seasonal trends in key climate variables in both present and future weather data as shown in Figure 4.1. This figure shows that temperature and solar radiation show a strongest seasonal variation, both in the current and future, with highest values in the summer months (Dec.-Jan.-Feb.) and the lowest values in the winter period (Jun.-Jul.-Aug.). The predicted temperature scenarios (Figure 4.1c), however, show a considerable increase when compared with current levels. NYP station which is located at the highest altitude showed the lowest temperature ranges of all three stations compared to others. A combined view of temperature variation reveals not much difference between the sites. On the other hand, there is minimal difference in levels solar radiation that is absorbed in all the sites.

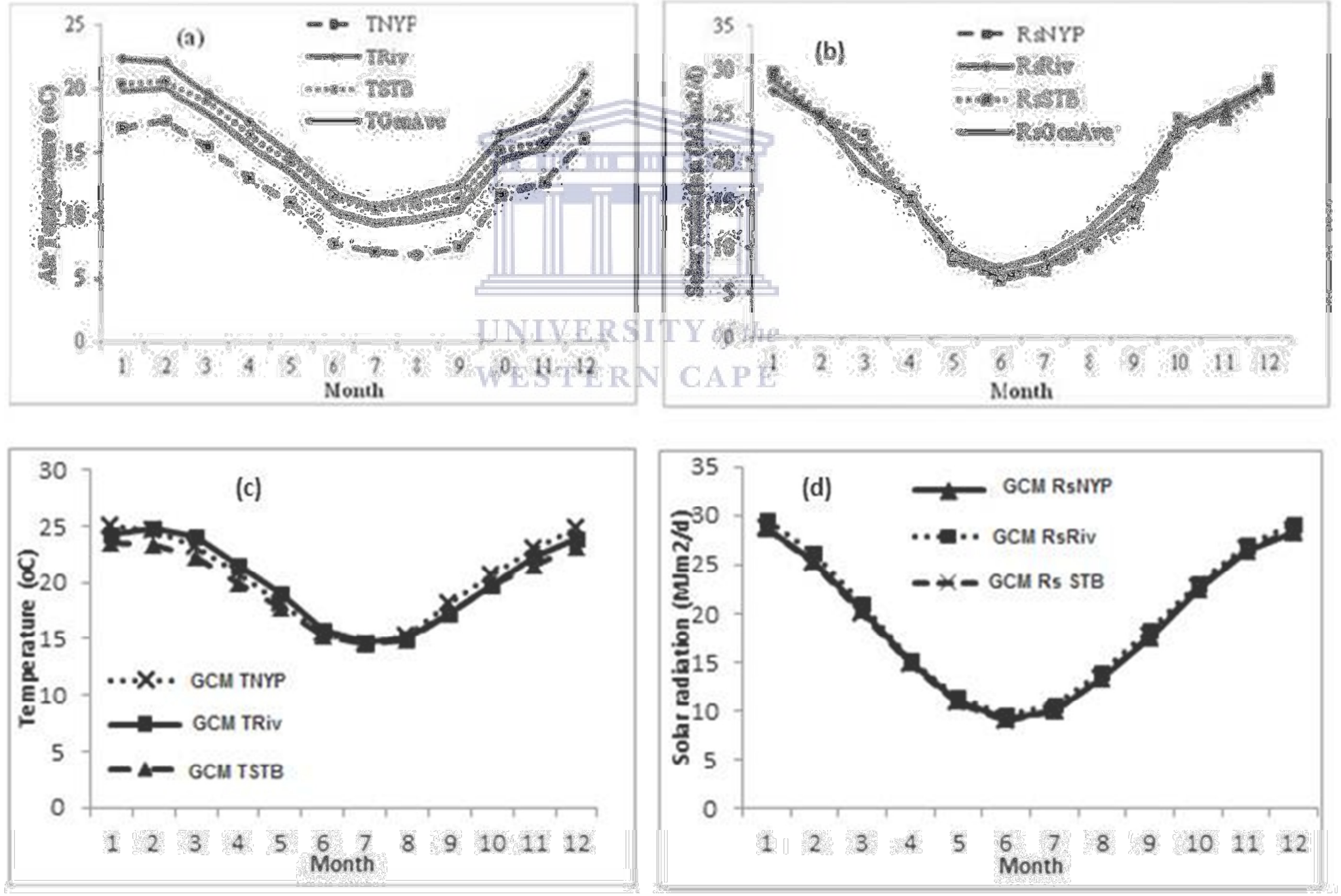


Figure 4.1. Seasonal variation of current: (a) temperature, (b) solar radiation and GCM: (c) temperature, (d) solar radiation at New Years Peak (NYP), Riverlands (Riv) and Steenbras (STB) sites. GenAve is the regional outlook for all stations. Month 1 is January to 12 is December.

The functions from the *Evapotranspiration* R library successfully validated model inputs and estimated both potential and reference crop evapotranspiration for New Years Peak, Riverlands and Steenbras sites. The data pre-screening showed that no corrections were warranted in the data series since the thresholds for missing data and abnormal values were not exceeded. Solar radiation was the main input that was used by both Jensen-Haise (JH) and Makkink (MK) algorithms to estimate daily ET in mm units. Model outputs are shown in Appendix 1 and 2. Appendix 1 shows that 701 ET estimates were obtained for Riverlands (located at -33.486889 S, E, and altitude 120 m). The PET by JH ranged between 0.15 – 12.27 mm with a mean of 3.89 mm while ETo estimated by MK ranged between 0 and 8.6 mm with a mean of 2.87 mm from January of 2007 to December of 2008. Similar results for all other study sites are given in Table 4.1.

Table 4.1 shows a disparity in the length of the current historical ($N_{Current}$=650 days) and the future GCM scenarios ($N_{RCP2.6}$=29585; $N_{RCP8.5}$= 29858). There is a noticeable marked increase in ET from the present into the future with relatively higher rates for RCP85 scenarios compared with the RCP2.6 scenarios at all sites. Among the sites, NYP will have the highest increase in ET (Approximately 2 mm up) in the future compared with projected increases at Riverlands and Steenbras where predicted increases are just slightly above 1 mm from the current to future times.

Table 4.1 Descriptive summary of the analysed current historical and GCM climatic data.

Climate scenario	**Time duration**	**N**	**Jensen-Haise potential ET**			**Makkink reference ET**		
			Mean	**Max**	**Min**	**Mean**	**Max**	**Min**
NYP current	2007/2/28 - 2008/12/08	650	2.81	10.19	0.01	2.37	6.48	-0.1
NYP GCM RCP2.6	2020/01/01-2100/12/31	29585	4.35	13.31	0.07	3.18	6.81	0.02
NYP GCM RCP8.5	2020/01/01-2100/12/31	29858	4.8	14.7	0.16	3.29	6.97	0.03
RVL current	2007/2/28 - 2008/12/08	650	3.89	12.27	0.15	2.87	8.6	-0.03
RVL GCM RCP2.6	2020/01/01-2100/12/31	29585	4.64	12.22	0.13	3.22	6.27	-0.02
RVL GCM RCP8.5	2020/01/01-2100/12/31	29858	4.91	12.47	0.11	3.29	6.38	-0.02
STB current	2007/2/28 - 2008/12/08	650	3.38	13.56	0.01	2.6	10.34	-0.11
STB GCM RCP2.6	2020/01/01-2100/12/31	29585	4.24	11.88	0.14	3.07	6.52	0.02
STB GCM RCP8.5	2020/01/01-2100/12/31	29858	4.58	12.93	0.16	3.16	6.68	0.02

Key: NYP = New Years Peak site; RVL=Riverlands site; STB=Steenbras site.

4.3.2 Comparative analysis between models and different input data sets

4.3.2.1 Potential versus crop reference evapotranspiration

Figures 4.2(a) and 4.2(b) indicate that the Makkink models produce consistently lower estimates than the Jensen-Haise giving the impression that Makkink underestimates ET. However, these results are an artefact of the structural differences between the two model algorithms which, respectively, estimate a potential and the actual evapotranspiration amounts.

Aggregated monthly averages from the highly fluctuating daily estimates revealed a very strong seasonal pattern as shown in Figure 4.2. The peak in ET amounts during the summer months can be attributed to the high temperature and optimal insolation energy during this time of the year in the region. Additionally, seasonal patterns show that the inter-model differences are most significant for the peak estimates during the summer period and these differed between localities. Riverlands showed the highest intermodal difference followed by Steenbras and New Years Peak the least. This can be attributed to the occurrence of a higher mass transfer of ET in the arid or drier interior (Riverlands) compared with similar measurements at the coastal (Steenbras) and altitudinal (NYP) sites (Xu and Singh, 2000).

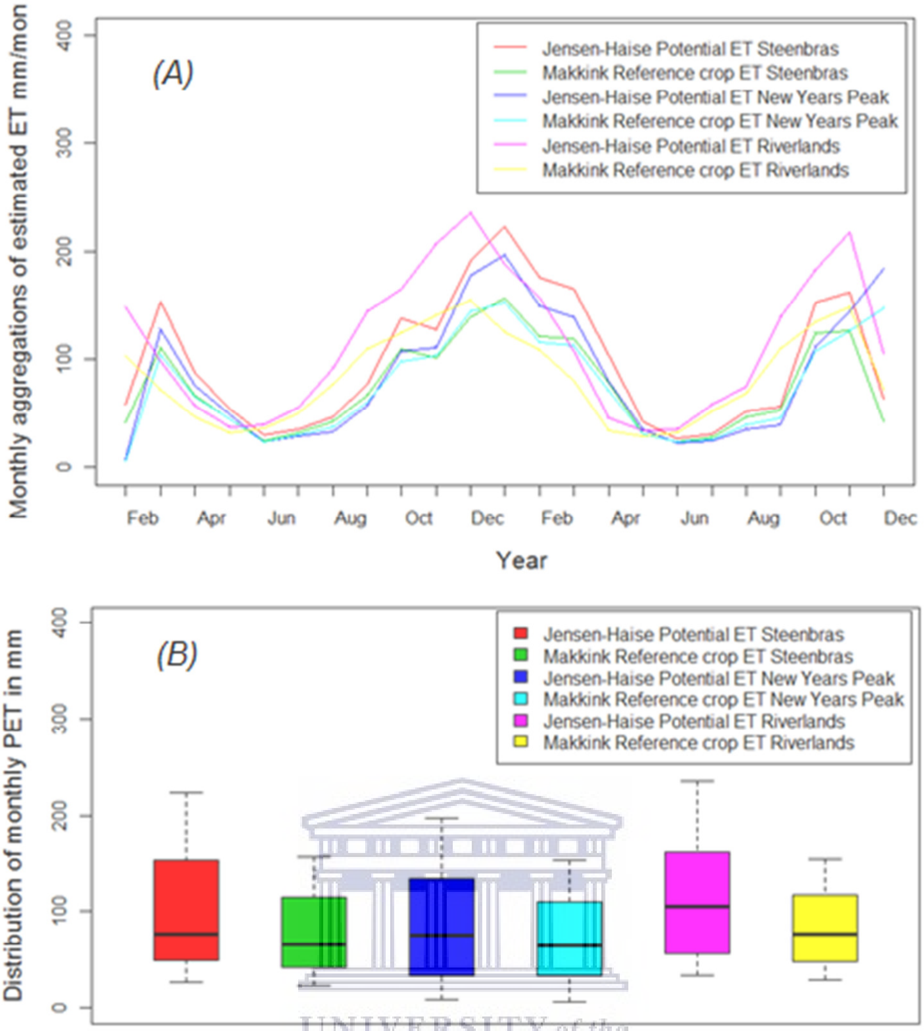


Figure 4.2. Comparison of monthly ET estimates from Jensen-Haise and Makkink models at Steenbras, New Years Peak and Riverlands: (A) time-series (B) distribution

4.3.2.2 Variability in evapotranspiration estimates

A Shapiro-Wilk test ($P<0.05$) (Shapiro and Wilk, 1965, Razali and Wah, 2011) and a visual inspection of their histograms, normal Q-Q plots and boxplots further showed that evapotranspiration estimates were not normally distributed for all stations, with a skewness of 0.72 (S.E. 0.096) and kurtosis of -0.466 (SE 0.191) for NYP, a skewness of 0.561 (SE 0.096) and kurtosis of -0.881 (SE 0.191) for Riverlands and a skewness of 0.63 (SE 0.96) and kurtosis of -0.386 (SE 0.191) for Steenbras.

Kruskal-Wallis test for differences analysis tested if there is no significant change in the daily evapotranspiration estimates from the most recent times to the future during a selected time range (N=1950). According to the Kruskal-Wallis (H) test, there is a statistically significant difference between ET from independently collected onsite data and the GCM climatic scenarios, Kruskal-Wallis test: $H_{(2,\ 59859)}=597.55$, $p<0.001$ for NYP, $H_{(2,\ 59871)}=233.96$, $p<0.001$ for Riverlands and $H_{(2,\ 59328)}=341.03$, $p<0.001$ for Steenbras. Thus, there is sufficient evidence to reject the null hypothesis and to assume a time effect on the variation of ET. Equally, follow up comparisons between climatic scenarios indicated that each pairwise difference was significant, $P<0.05$ (Table 4.2). There was a significant increase in the estimates of ET over time based on the projections of future climate scenarios as shown in Figure 4.3.

Table 4.2. Comparison of sample pairs from Current, RCP2.6 and RCP8.5 climate scenarios.

Site	Current-RCP2.6	Current-RCP8.5	RCP2.6-RCP8.5
New Years Peak			
H statistic (SE)	-9187.75 (665.94)	-11829.27 (665.94)	-2641.52 (142.08)
Adjusted P- value	< 0.05	< 0.05	< 0.05
Riverlands			
H statistic (SE)	-5051.97 (660.48)	-6806.40 (660.47)	-1754.44 (142.11)
Adjusted P- value	< 0.05	< 0.05	< 0.05
Steenbras			
H statistic (SE)	-5924.45 (680.74)	-8095.82 (680.74)	-2171.37 (142.00)
Adjusted P- value	< 0.05	< 0.05	< 0.05

H-statistic tests the null hypothesis that each climate pair distribution is the same
Asymptotic significance P shows significance
The significance level is 0.05

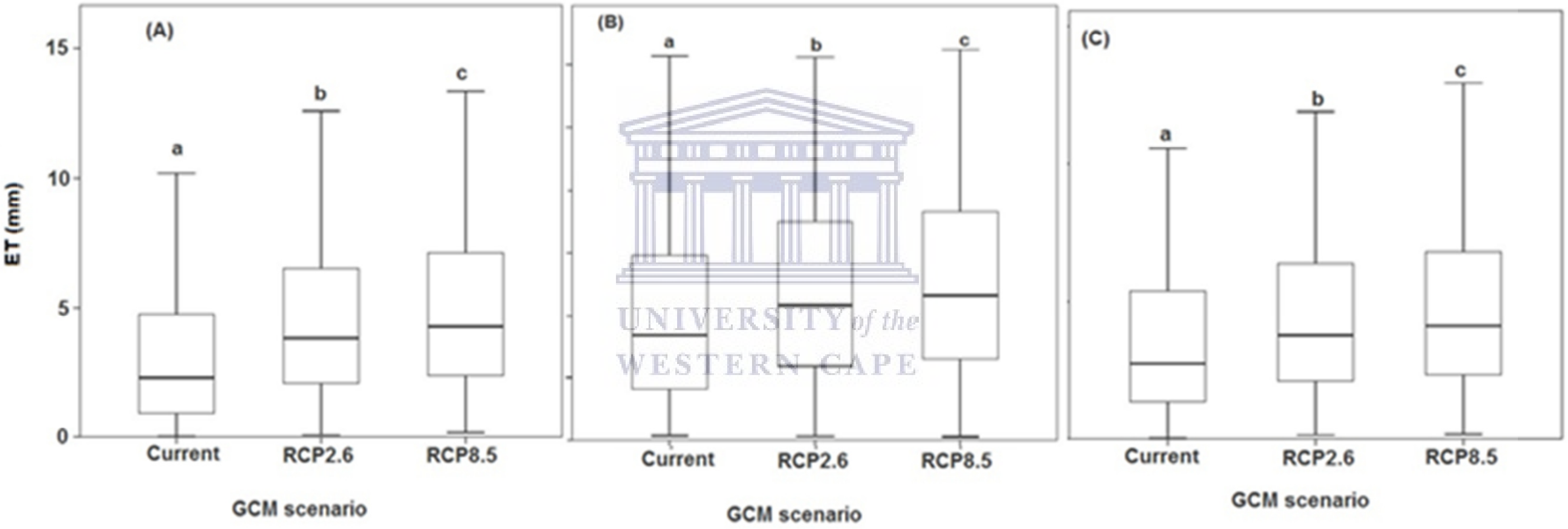


Figure 4.3. Variation in the distribution of ET estimates at three study sites: (A) New Years Peak, (B) Riverlands, (C) Steenbras. The labels a, b and c, represent statistical significantly different ET distributions at Current, RCP2.6 and RCP8.5 scenarios.

4.3.2.3 Trend of mean monthly evapotranspiration

The general trends are summarised in Table 4.3 and Figure 4.4. During the period 2007 – 2009, there is positive (upward) but a not significant trend in the potential evapotranspiration at all three stations which could be attributed to the relatively short observation period range. Under RCP8.5 scenarios, a significant upward trend in potential evapotranspiration is expected at all stations by 2100. Similarly, under RCP2.6 scenarios, most stations show positive but not statistically significant trends except for Riverlands where a non-significant negative trend is expected by 2100.

Trends in seasonal evapotranspiration over the present and the future climate scenarios

Table 4.3 Changes in seasonal evapotranspiration

Scenario	New Years Peak			Riverlands			Steenbras		
	Slope mm/month	Signif.		Slope mm/month	Signif.		Slope mm/month	Signif.	
Current	0.301	0.721		1.459	0.448		1.634	0.516	
RCP2.6	0.001	0.853		-0.00006	0.795		0.00004	0.864	
RCP8.5	0.001	0.000	**	0.0008	0.001	**	0.001	0.000	**

4.4 Conclusion

The future scenario revealed possible significant increases in potential evapotranspiration levels of up to 2 mm (up to 71% increase) (Table 4.1) in places between now and the future if the current projected climatic trends persist. This means that there will be increased evapotranspiration rates in the long-term irrespective of the mitigation steps applied. Rates would, however, be slightly lower if CO_2 emissions were to subside (RCP8.5) beyond 2020. Solar radiation directly influences evapotranspiration rates to a greater extent than other variables like temperature on the surface. Incidentally, and according to global climate model projections, current estimates reveal increased solar radiation in the future which, in turn, should be directly responsible for the increased evapotranspiration rates.

Results from the current analysis clearly indicated that there were statistically significant differences in evapotranspiration rates at the different stations. Average relative humidity from all sites in this study revealed extremely high levels of atmospheric moisture in the region but a strong wind presence at high altitudes (like NYP 1080 m) should favour optimal levels of soil moisture escape through evapotranspiration. Furthermore, the strong seasonal patterns in prevailing winds are an important climatic influence in the region.

Analysis of evapotranspiration consistently showed potential estimates higher than reference crop estimates. Such differences are attributed to computation procedures which differ in their inclusion or consideration of aerodynamic influences. However, most practices have utilised potential evapotranspiration rate in water budget ‘bucket’ systems studies. Hence, in order to explore the possible influence of changes in evapotranspiration in the water budget between the present and the future, future climate scenarios have been compared with current conditions. The RCP8.5 scenario revealed the most influential in escalating evapotranspiration rates in the future compared to the RCP2.6 scenario. Incidentally, it is the more likely of these two scenarios wherein CO_2 emissions are expected to rise unperturbed in the future. The consequence of this would be dire to the soil moisture balance system which has an integral influence on terrestrial ecosystems.

The effect of perturbations in each main climate element on the rate of ET at all sites was examined. Solar radiation showed the most effect on the changes in evapotranspiration in the region followed by temperature and wind speed rates. Further research can attempt the inclusion of an extensive pool of stations whose distribution would best represent the heterogeneity in physical conditions peculiar in the region. The use of other ET estimation techniques like remote sensing techniques as well as increased lysimeter networks for calibration purposes will compliment FAO-PM results. Similar efforts can be made in analysing seasonal and annual spatial distribution patterns of ET which might be valuable for thorough water resources management and biodiversity planning.

CHAPTER 5 A MICROCLIMATIC WATER BALANCE MODEL FOR SOIL WATER LEVEL FLUCTUATION ANALYSIS IN MICRO-WETLAND COMMUNITY

This chapter discusses the procedures used to develop a soil moisture balance model and its parameters for the sandy soils in the south-western CFR. It focused on the modelling of water table fluctuations from measurements in the field. The model set up was made simple but representative of the water distribution flux between different compartments of the ecosystem by using simple linear pool and flux empirical models. Model estimates were validated with field data which made them crucial for current and future conservation efforts.

5.1 Introduction

The impact of soil moisture changes can be studied from the vegetation responses to hydrological gradients specifically in groundwater dependent wetland communities (Gowing et al., 1998, Bartelheimer et al., 2010). One way of doing this is by monitoring and modelling of the water table fluctuation to visualise its variability in the root zone for both wet and dry spells through the year (Barber et al., 2004). This aids an understanding of the moisture dynamics and its potential effects.

The moisture in the soil is contained in the pore matrix and its volume is shown by the height of the saturation column which is the water table level. In wetlands, the water table depth is mostly shallow (<1m) and forms the lower boundary of the vadose zone (Barber et al., 2004). The water column in the topsoil is a combined flux and hydraulic potential boundary. The position of the water table directly influences the water status (soil matrix potential and the water content combined) of the vadose zone (Barber et al., 2004). While the moisture column in the soil top layer is fed from the surface by infiltrating precipitation water, from below it is fed by capillary moisture arriving from the lower groundwater storage. Hence the moisture characteristics of this root zone are controlled by the availability of rain which is a function of climate and also of the availability of subsurface replenishments which are a function of the initial groundwater storage.

The water table depth or moisture status of the soil is not important unless it exerts some form of moisture stress in the soil. This has prompted the derivation of stress indices which aim to quantify both the moisture status and the water table status. Stress indices quantify the two distinct forms of stress that are caused by dryness (drought conditions) and anoxia (saturation conditions) of the soil. These soil moisture indices are the sum exceedance values (SEV) (Gowing and Young, 1997, Gowing et al., 1998, Silvertown et al., 1999). This is a cumulative stress index that uses the position of the water table to account indirectly for the aeration or dryness stress that the plant experiences under threshold water table levels. Equation 5.1 shows SEV being calculated as integral of the difference between the water table and a reference water table depth above or below which the plants are expected to be aeration or drought stressed.

$$\mathrm{SEV} = \int_1^N (\mathrm{D_{ref}} - \mathrm{D_W})\mathrm{dt} \qquad \text{Equation 5.1}$$

Where N is the number of weeks in the period over which the integration is calculated, D_w the average depth to the water table and D_{ref} is the reference water table depth above or below which the plants are expected to be aeration or drought stressed. Only positive difference values are included in the integration. The integral is solved numerically for time increments of 1-week. When D_w and D_{ref} are measured in metres, the units of SEV are metre weeks. The higher the value of SEVs, the greater the supposed aeration stresses.

Subsurface losses through drainage and water extraction through evapotranspiration processes also affect the variations in water levels in the soil. Thus, these hydraulic processes control the prevailing moisture status in the soil (Wesseling and Van Wijk, 1975). For instance, terrestrial plants will experience aeration stress when air-filled porosity controlled by water table position is reduced below 0.1 (Wesseling and Van Wijk, 1975). Furthermore, Gowing et al. (1998) have demonstrated the effectiveness of stress indices from water table positions in explaining spatial variability in plant species. A similar emphasis is required on the implications of water levels on plant performance (Silvertown et al., 1999). Water table depth remains the preferred measure of water status in ecological studies because it can function as a surrogate for aeration stress in order to easily relate aeration stress to plant community structure.

Recent studies have directly attributed the segregation of plant species to their relative position above groundwater levels (Bartelheimer et al., 2010). In a recent investigation Guo et al. (2015) used the maximum entropy species modelling approach to test the hydrological controls on species distributions in part of the current study area. They found that water table depths explained the variance in vegetation composition better than several other hydrological variables. These findings informed the need to develop a model which relates water table depths to the likelihood of the presence of fynbos species in the south-west of the CFR. It gave the best logical basis to investigate or develop an understanding of the dynamics of groundwater levels in the soil water balance budget particularly of wetland ecosystems prior to linking this dynamic to the observed species distribution in the same area.

Wetland plants adapt to changing conditions in their environment in several ways (Barber et al., 2004). These plants respond show distinct responses to different moisture conditions (stimuli) in their environments and the related aeration status in the soil (Silvertown et al., 1999) which implies that the aeration status is one of the traits which determine the diversity in such environments (Barber et al., 2004). Thus, the likelihood that biodiversity in wetland communities is established based on the response of wetland plants to soil water regimes.

Fynbos vegetation of the Cape Floristic Region (CFR) is endemic in this bioregion and it is in danger of being adversely affected by changing environmental conditions that result from climate change and groundwater abstraction (Cowling et al., 1996, Midgley et al., 2003). The changes in moisture supply in the soil caused by changing conditions are frequently quantified using hydrological variables. This brings to focus the role of hydrological variables in changing the richness and diversity within fynbos over time because these variables define the moisture supply to the plants through the soil.

The objectives of this chapter are the following:

1. To design and assign parameters of the components of a soil moisture balance model using field observations
2. To determine the quality of the simulation framework by validation of the model simulations with observed field measurements
3. To attempt a sensitivity analysis of key empirical parameters on model outputs

5.2 Materials and methods

5.2.1 Study site characterisation

New Years Peak (NYP) is a wetland community located at 33º 41'S and 19º 06'E and at a height of 1080 m in the Cape Fold mountain ranges of Southern Africa. The climatic conditions at NYP can be classified as mountainous. Table 5.1 contains the long-term mean data for temperature, rainfall, evapotranspiration and the mean water table depths on site.

The day count shows that there is data bias as the data records from the automatic weather station varied between the months. This indicated the existence of missing data. The long-term mean temperature during the period was approximately 12°C with a maximum of value of 15°C and a minimum of 7°C. Corresponding records of rainfall and ET as recorded on site have been given Table 5.1. Reference evapotranspiration (ET) were obtained from estimates made through the Penman-Monteith ET estimation method and water table records were read from dip wells in the plot.

Table 5.1 Long-term record of temperature, rainfall, evapotranspiration and mean water table depths measured at the NYP site.

	N	Temperature (°C)	Rainfall (mm)	Evapotranspiration (mm)	Water Table Depths (cm)
Jan	107	14.43	1.25	41.00	-73.23
Feb	113	14.65	0.00	40.85	-73.03
Mar	125	15.10	8.23	24.60	-75.24
Apr	108	12.62	36.25	13.70	-71.40
May	122	10.60	10.60	5.80	-6.28
Jun	90	7.76	52.0	4.76	-15.82
Jul	97	7.99	41.5	4.15	-9.35
Aug	124	9.52	57.00	5.95	-13.03
Sep	99	11.81	24.0	14.66	-25.34
Oct	81	12.66	28.48	21.22	-39.96
Nov	90	13.98	29.89	21.53	-39.58
Dec	93	14.72	28.4	22.11	-40.49
Mean		**12.15**	**34.7**	**18.36**	**-40.22**

The study site was a plot of natural Fynbos vegetation occupied predominantly by the family Restionaceae. A total of 768 individual plants were counted. These were made up of 22 species. Twelve of them were Restionaceae which made up close to 60% of the species diversity. Restioids are reed-like evergreen scrubby stems that sometimes grow up to 2 metres. The visible plant architecture is mostly the culms which grow from subterranean rhizoid stems that also bear shallow root systems. This root architecture deprives the plants of vital deeper groundwater sources and hence these depend solely on the moisture at the near-surface shallow reaches of the soil profile. In effect, shallow roots access shallow depth soil water in wetlands although accessibility may be affected by seasonal variations in soil water depths.

Figure 5.1 shows the general plot setting and other attributes of the study site at NYP. The plot showed an elevation gradient which ensured a hydrological gradient at the site (Dingman, 2015). The experimental design and data collection process have been fully described by Araya et al., (2011). Briefly, the NYP site had 9 observation dip wells installed to a depth 1 m in a plot of 238 1-sq.m quadrats. Dip wells were lined with plastic tubing of 5 cm diameter. Groundwater levels (depth) were measured using a calibrated beeping stick at a bi-weekly interval. These observed data were used to validate the modelled water table depths in the hydrological framework.

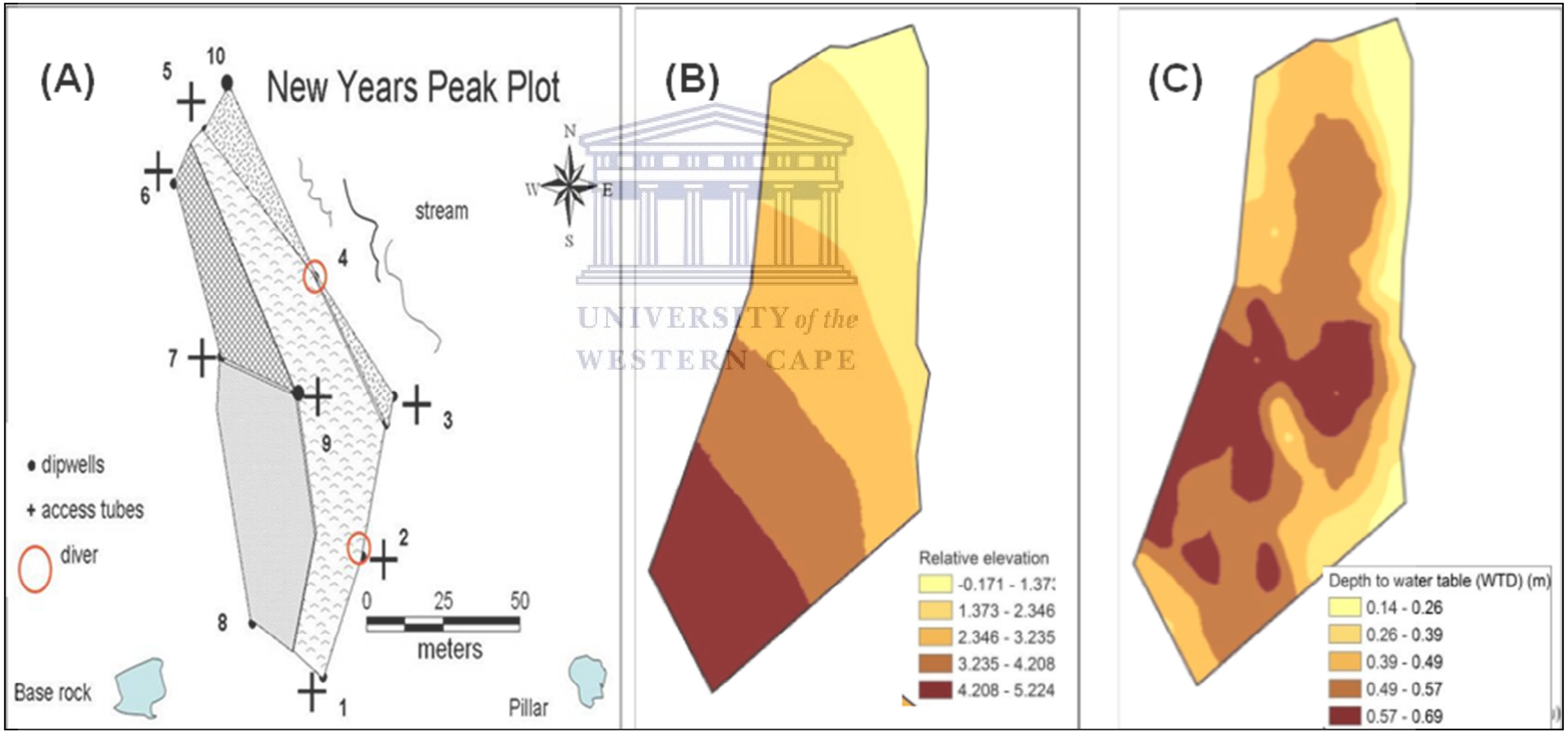


Figure 5.1 Plot setting and attributes of New Years Peak site. (A) The relative position of sampling points (B) Elevation gradients (C) Moisture distribution.

Generally, soil moisture regimes are defined based on the water table level and the presence or absence of available water for plant use. The Mediterranean climate locally provides alternate periods of moist cool winters and hot dry summers exceeding 3 to 4 months each (Verheyen and De la Rosa, 2005). These seasonal patterns in weather directly explain the temporal variation in the moisture conditions of the soil in the NYP. However, being a wetland community, the water table is sustained for longer periods keeping the soil saturated or in mostly saturation conditions. The soil column was shallow (below 1m) and underlain by impervious sandstone.

5.2.2 The soil moisture distribution modelling concept

This section explains the simple water balance budget model. It discusses the basics of the water balance model illustrating moisture storage and key flux processes in the soil - atmosphere continuum. Figure 5.2 illustrates moisture redistribution paths in the subsoil.

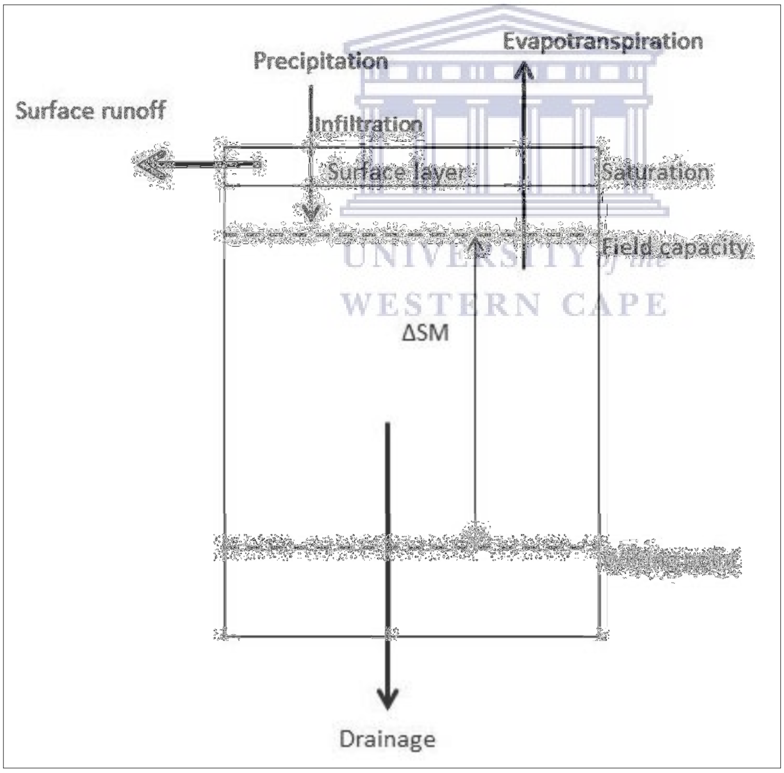


Figure 5.2 Demonstration of the main principles of water balance model in the soil atmosphere system.

The model is a two-dimensional accounting procedure for near-surface soil moisture dynamics. It is created based on the standard water balance equation (Equation 5.2).

$$P - E = D \pm \Delta SM \quad \text{Equation 5.2}$$

Precipitation (P) is only input source in the system. It is the net input of water into the soil minus interception losses at plant canopies and surface runoff (overflow). Surface runoff is the part that does not enter the soil but directly moves over the land surface. Meanwhile, the interflow components of runoff are not taken into account in this model because of the very permeable soil boundary zone which rapidly transmits vertically draining water once inside the soil medium. Moisture that percolates into the sub-layers is the drainage flow (D). D formed a major outflow from the system just like evapotranspiration (E) which is vaporised moisture from the soil and plants entering the atmosphere. The moisture which is available to plants is the net surplus from drainage, evapotranspiration and storage in the soil (∆SM).

5.2.3 Model set up

The model was designed to be simple using few parameters, requiring limited soil physical data. Rainfall and reference evapotranspiration were the only climate input variables. Seepage and percolation coefficients were the only soil parameters used. The key output was soil water table values. Meanwhile, groundwater storage and outflows were two intermittent outputs from the process. Figure 5.3 is a schematic representation that describes the model set up. This model diagram is used to show the various compartments, the flow paths linking them and the influences in the system.

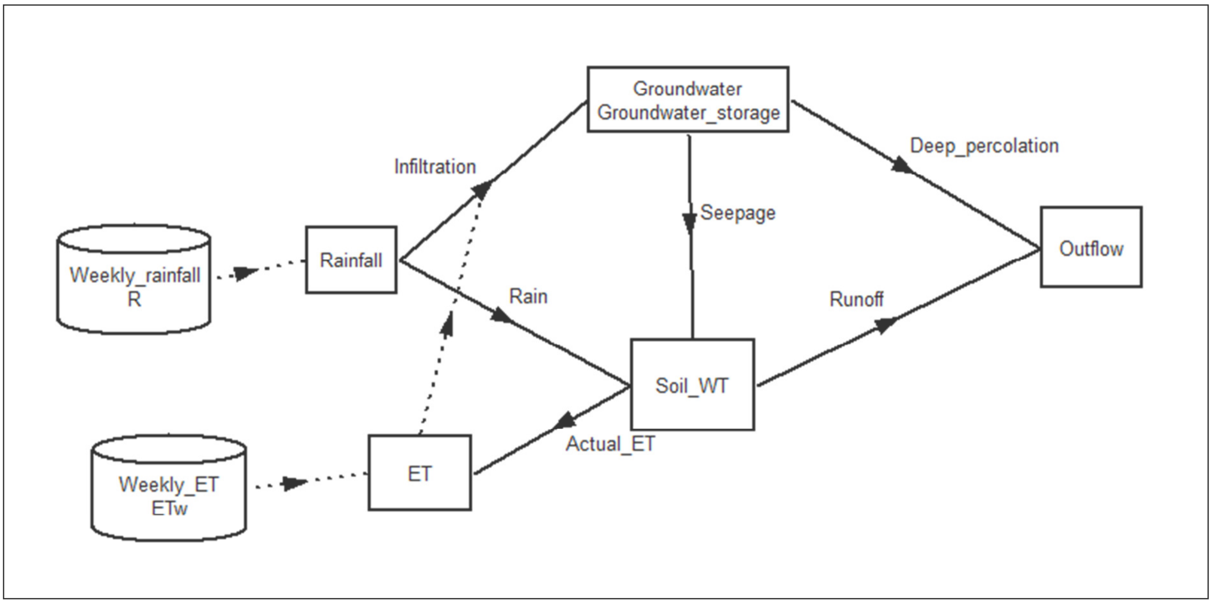


Figure 5.3. Model diagram with the flows between compartments as solid arrows and the model influences are represented by the broken arrows.

5.2.4 Model application

A good modelling tool incorporates mathematical expressions (models) which can predict systems response due to changes in inputs (models based on trigger-response principle). In this study, the model was expected to describe the physical relationships between moisture in the soil and the atmosphere and the storage flow in the hydrological system. This was implemented in *ModelMaker Run-time Version 3.0.3*©.

The model required rainfall and evapotranspiration as the only data inputs. The key output was soil water table level. This made it possible for a prospective response of soils to future changes in rainfall and evapotranspiration (climate) to be predicted. Such results are necessary from both an ecological biodiversity planning and management objectives. These predictions provide the basis for the formation and quantification of hydrological changes.

The change in moisture content in soil water system was modelled as water table fluctuations. Field measurements that were obtained through monitoring provided the required data to validate the modelling effort. Further to this, attempts were made to replicate the model applications to other sites in order that sensible comparisons could be made.

5.2.5 Evaluation of model fit (analysis of goodness of fit - GoF)

The statistical values like the coefficient of determination (R^2), mean absolute error (MAE), mean absolute percentage error (MAPE) and the root mean squared error (RMSE) (Equations 5.3 - 5.6) were used to analyse the model fit for the modelling period (i.e. the calibration period). R^2 quantified the GoF by indicating the proportion of the variance in the dependent variable that is predictable from the independent variable. R^2 is computed as in Equation 5.2 and has values ranging from 0.0 -1.0. High values indicated close model fit with experimental data and zero means that the model data is far from the regression line that defines the observed data. High R^2 values may imply proximity of model with observed data but do not necessarily indicate the level of fit. Considering the limitations of R^2 to give a picture of the fit, other statistics are implemented to complement the R^2. For Equations 5.3 – 5.6, the model fit was considered good when the value remains low. MAPE has a value from zero to +∞. Where zero implies a perfect fit and anything above one showed a 100% deviation from the original model value. The overall model accuracy was calculated by finding the overall average percentage error (PE) which indicates the percentage deviation of the modelled from the observed values (Equation 5.7). Previous literature has stated the following to be acceptable values for each of the error indices: - R^2>0.6; MAPE<0.1; MAE (generally low)<5; PE<10%; RMSE (is generally low)<10.

$$R^2 = 1 - \frac{\sum_{i=1}^{n}(y_i - \hat{y}_i)^2}{\sum_{i=1}^{n}(y_i - \bar{y})^2}$$

Equation 5.3

$$MAE = \frac{1}{n} \cdot \sum_{i=1}^{n} |(y_i - \hat{y}_i)|$$

Equation 5.4

$$MAPE = \frac{1}{n} \cdot \sum_{i=1}^{n} \left| \frac{y_i - \hat{y}_i}{y_i} \right|$$

Equation 5.5

$$RMSE = \sqrt{\frac{1}{n} \cdot \sum_{i=1}^{n} (y_i - \hat{y}_i)^2}$$

Equation 5.6

$$PE = \frac{|y_i - \hat{y}_i|}{y_i} \cdot 100\%$$

Equation 5.7

Where, *i is the* control variable, *n* is the sample size, R^2 is the R square value, y_i represents the observed or experimental values, $\hat{y}$ represents the predicted or modelled values, $\bar{y}$ is the mean of observed values, $(y_i - \hat{y}_i)$ represents the residual..

5.3 Result and discussion

5.3.1 Model outcomes

5.3.1.1 Simple compartment model

The moisture flux between compartments of the soil water system was modelled. Bi-weekly aggregates of rainfall and evapotranspiration (ET) amounts were the only data inputs in the model while measured water levels were used for calibrating the model. Looking again at Figure 6.3 rainfall and evapotranspiration made up two of the five compartments. The other three were the groundwater storage, the depth to water table and outflows/drainage compartments, linked to the input variables. This relatively simple empirical model design was used to calculate the kinetic transfer rates that gave rise to the observed water measurements.

5.3.1.2 Simulated water table depths

Soil water levels simulations were obtained for the NYP site and the model results were validated with observational data that were collected at the NYP site. The results indicated a direct relationship between the climate parameters (rainfall and evapotranspiration) and soil water depths (Figure 5.4(a), 5.4(b) and 5.4(c)).

All three variables follow seasonal patterns in the region relatively well. During the dry summer months (‘Nov’ – ‘Apr’) precipitation is at its lowest, and the warm weather that accompanies such periods due to high-temperature influences high rates of evapotranspiration. As a consequence of the little rain and moisture escape by evapotranspiration, water levels in the soil tend to reduce to their minimum levels. During the winter months (’May’ – ’August’) which are characterised by heavy rains and cold temperatures (consequently less evapotranspiration), soil water content rises to maximum. Interestingly, the experimental records reveal prolonged rainfall throughout spring (i.e. Oct – Nov). Although evaporation rates rose during these periods, soil water contents decreased slowly.

The coherence achieved in Figure 5.4(c) and Figure 5.4(d) show that the soil water model algorithms successfully approximated natural hydrological processes as shown in the plots of predicted water table depths. This implies that not only have they correlated with the experimental water table depth, they have shown direct relationships with the climatic parameters. In addition, the modelled results show water level predictions to go beyond the surface limits of the soil which imply overflow runoff conditions during those times. It is also noted that climatic parameters do not have an exclusive influence on the soil moisture dynamics. Soil characteristics like grain size, porosity and soil type, texture) have influence. This would be demonstrated in subsequent sensitivity analysis of the soil parameters to the modelled results.

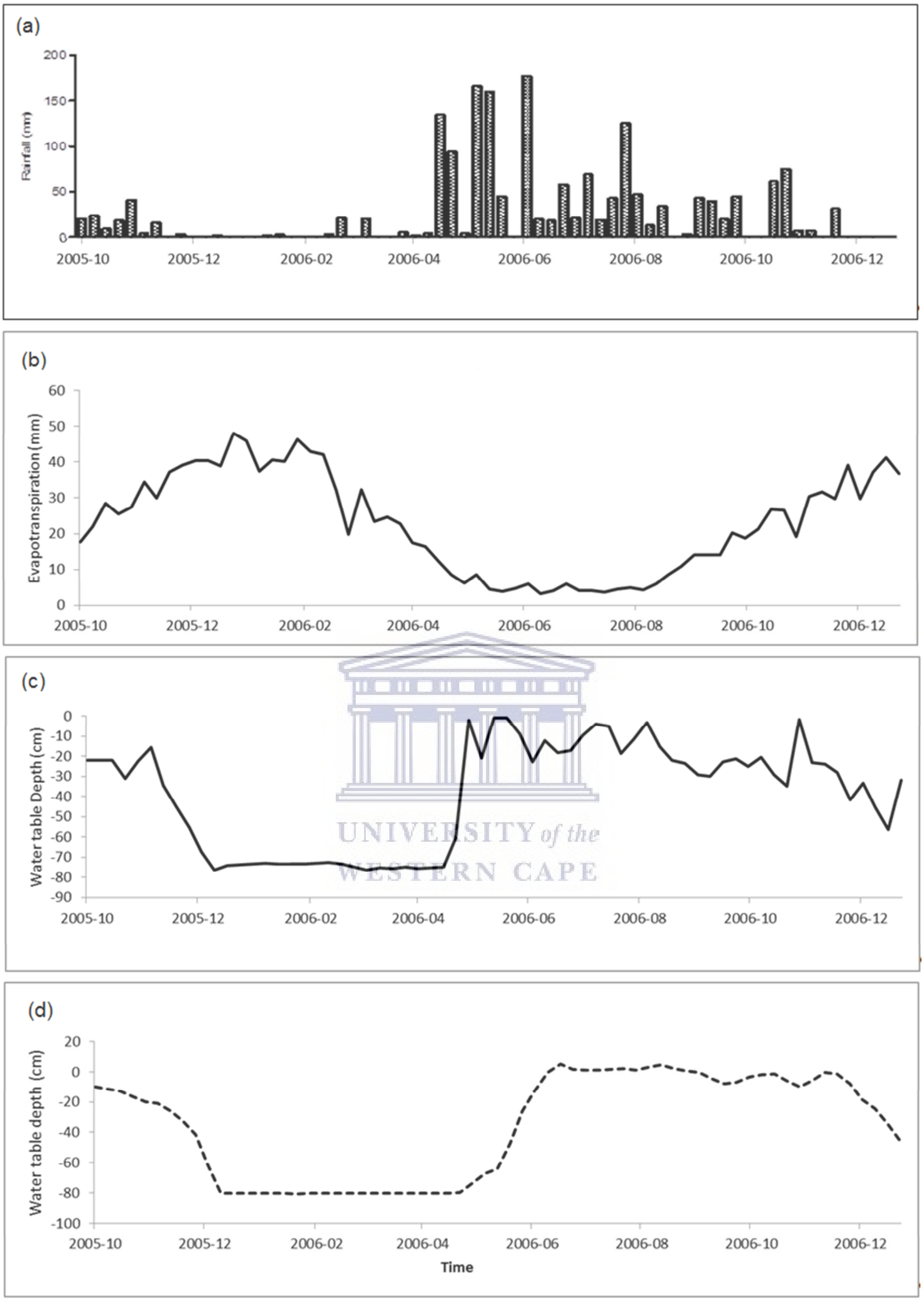


Figure 5.4. Weekly records (a) rainfall, (b) evapotranspiration, (c) measured depth to water table, (d) modelled depth to water table.

5.3.1.3 Model validation and optimisation of model parameters

The data generated by the modelling process are referred to as 'model data' whereas the data measured in the field are referred to as 'experimental data'. Once experimental data were associated with a model, the model fit was improved through optimisation in order to fit the experimental data more accurately. During optimisation, selected model parameters were systematically adjusted from their initial value to reduce the deviation between the model and experimental data. The choice could be made between the Marquardt or the Simplex iterative numerical methods of optimisation with the goal of seeking the best agreement between model and experimental data by adjusting selected parameters. In particular, the Marquardt method uses ordinary least squares to calculate the scaling of the differences between the model values and the experimental data.

The parameters percolation coefficient (with an initial value of 0.50) and seepage coefficient (with an initial value of -0.15) were optimised using the default optimisation settings of Marquardt optimisation and Ordinary least squares weighting. The optimisation eventually converged on the new parameter values for *percolation_coefficient* and *seepage_coefficient* which were 0.47 and -0.16, respectively. These two values were the optimal inputs which assisted in modelling the best possible fit in the process. Both model parameters were later updated to these new parameter values after the optimisation process.

Table 5.2 shows the estimated standard error associated with each optimised parameter value and the statistical breakdown in the computations of R^2. The statistics summary includes the degree of freedom (DF), Weighted sum of squares (WSS) i.e. the variation attributed to each component, Mean square (MS) i.e. the variation per degree of freedom where MS = WSS/DF, Total uncorrected sum of squares (Total WSS), R^2 value i.e. R^2 = WSS/Total WSS, F-value i.e. the variance ratio, where F= model MS/Residual MS, p-value i.e. probability that the difference between the model and data have occurred by chance (Marquardt only).

Optimisation processes revealed a coefficient of determination of 0.9 (Table 5.2). Though not an absolute indicator, such a result indicated that a high proportion of the total variance in the model values can be explained from the experimental values which are an indication of an excellent fit between the model and the experimental data.

Table 5.2. Optimisation statistics from model optimisation processes

Simplex optimisation: Ordinary Least Squares.

	Model	**Residual**	**Total**
Degrees of freedom	1	63	64
Weighted sum of squares	53.758	$8.813e^{-05}$	53.758
Mean Square	53.758	$1.399e^{-06}$	N/A
Total uncorrected sum of squares			65
R^2			0.999
F			3.843+07

5.3.2 Sensitivity analysis

The effects of altering some components and parameters of the model were investigated. Seepage coefficient (seep_coef) and percolation coefficient (perc_coef) are soil parameters that define the soil hydraulic properties of the matrix medium. The model was tested for its sensitivity to both seepage coefficient and percolation coefficient of the soil at NYP. In this process, the model was repeatedly run while parameters and components were systematically adjusted during each run and the results compared thereafter. The aim of this is to investigate the importance of the respective soil factors in the soil moisture hydraulics measured by the amount of deviation from the model line plot.

Figure 5.5 and Figure 5.6 show the results from multiple models runs as seepage and percolation values are adjusted. There are shifts in the models as the soil hydraulic parameters changed. This implies that the soil moisture dynamics are strongly related to the soil properties. We observe that the fit in the model progressively improved towards the mean as the parameter ranges increased. This is a true reflection of soil substrate which is highly permeable well fractured silty sand. However, none of the above parameter alterations amounted to a perfect fit in the model. This implied that there are other parameters which have not been considered in the current processes but are important contributors to the general flow dynamics at the site.

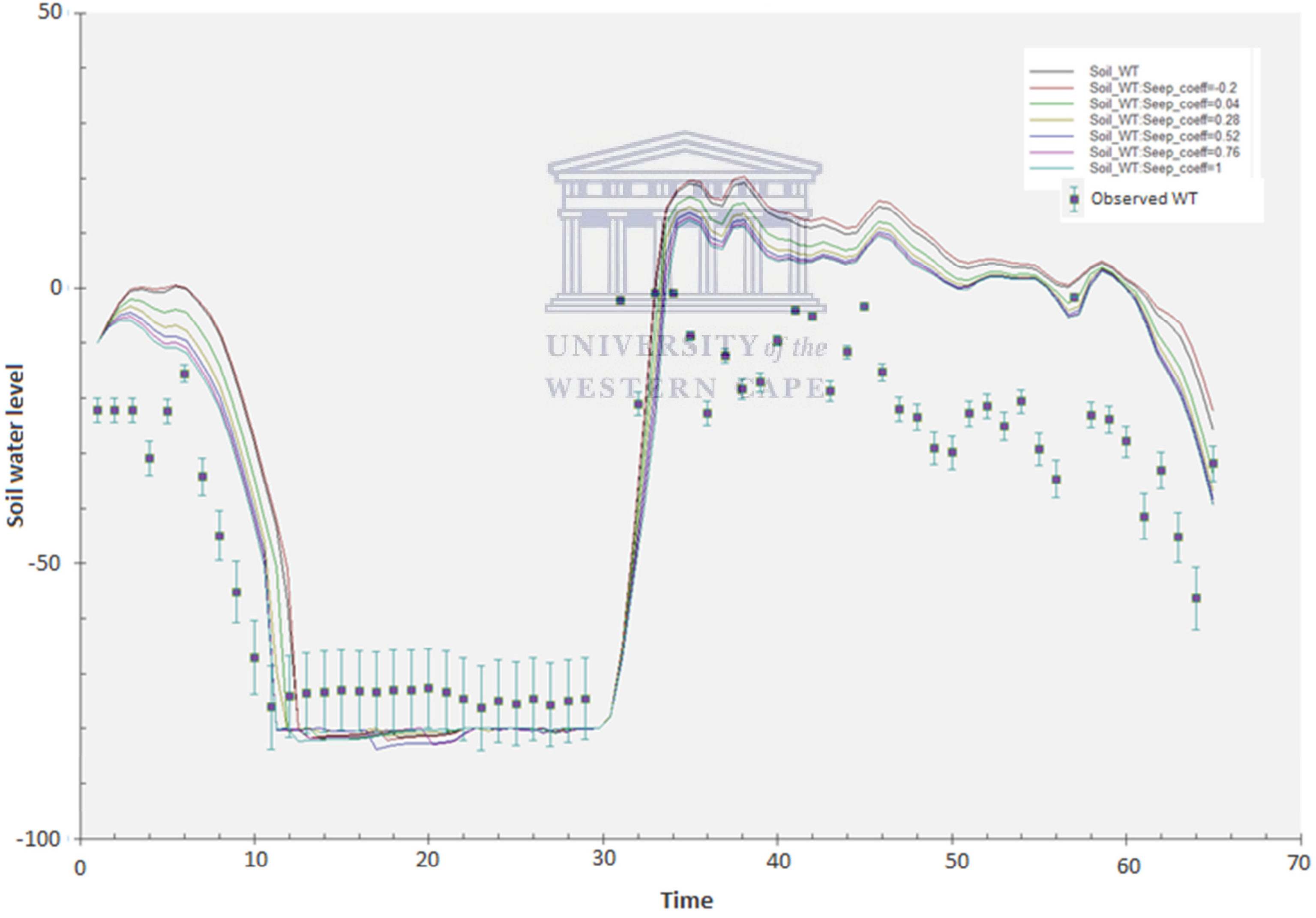


Figure 5.5 Sensitivity analysis: Model response to adjusted seepage parameters

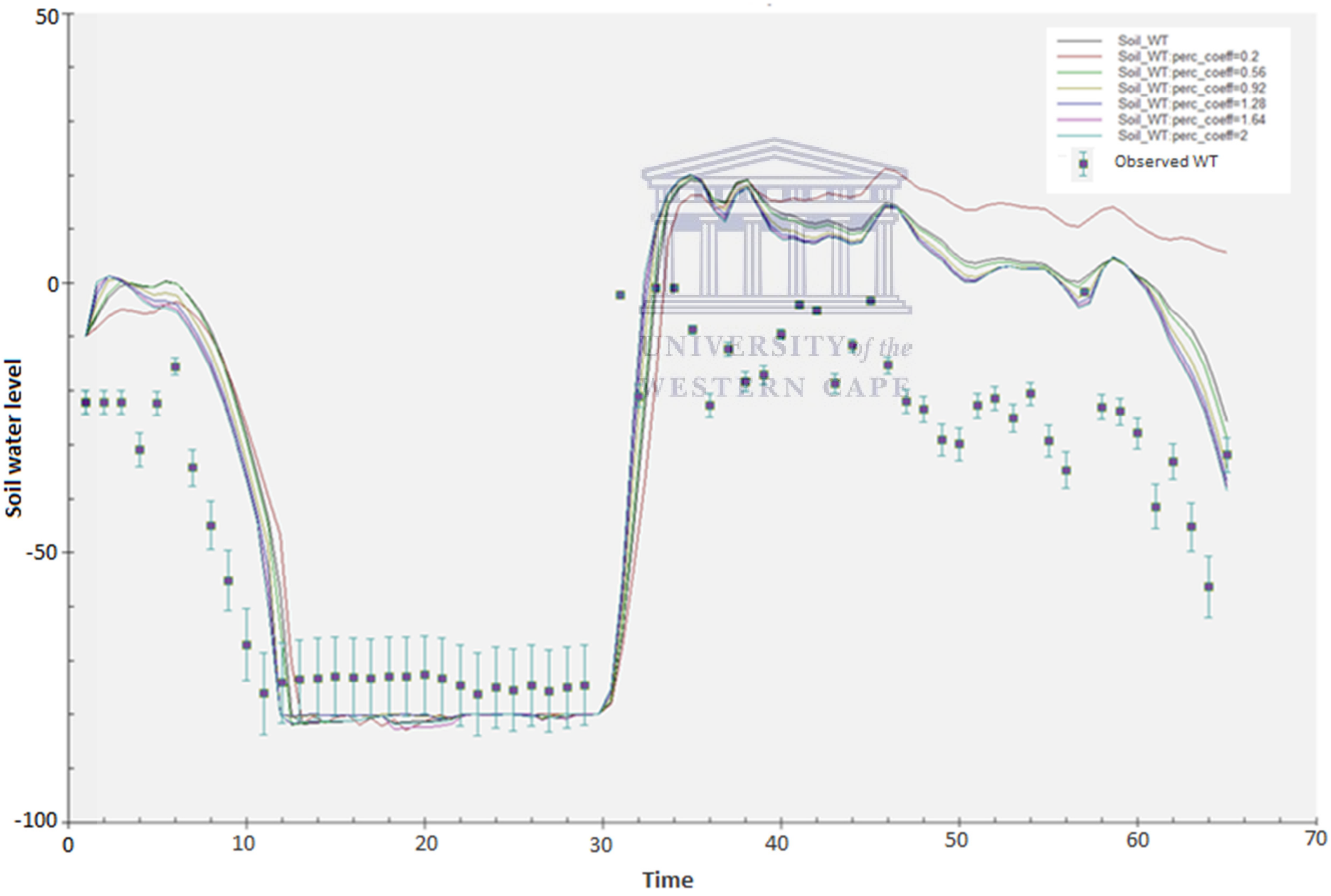


Figure 5.6 Sensitivity analysis: Model response to changing percolation coefficients.

5.3.3 Model fit and accuracy

The best model configuration from numerous attempts is shown in Figure 5.7 where accuracy checks are computed from the R^2, MAPE, RMSE and MAE indices revealed an average model fit. The best values at NYP for the respective indicators were as follows: R^2 = 0.773, MAPE = 0.137, RMSE = 16.592 and MAE = 13.348. The above results are not optimal figures for these indices meaning that the model fit can be improved through further enquiry and adjustments of model parameters.

5.4 Conclusion

Model simulations have always been effective in describing the hydrological system in terrestrial ecosystems. The objectives of this chapter were to derive soil parameters and test the predictability of a workable soil moisture model for the NYP wetland. The aim was to provide a framework which could be applicable to the other sites.

Through optimisation procedures provided by the ModelMaker© platform, the best parameter values for the NYP site were deduced and were successfully implemented in a number of model runs.

The model outcome of the soil moisture model was good. Using the available rainfall and evapotranspiration, the water table fluctuation within a 65 week period was simulated. In general, the simulations of water table trends showed similar patterns with the observed water table depths that were collected by physical means. The model results are deemed satisfactory owing to some of the statistics that showed a measure of good fit.

From the above results, the above model structure is recommended for future simulations of soil moisture and hydrological fluxes under changing climatic conditions in the NYP site. Since there is a slight variation, not a perfect fit, of the simulation curve from the site data curve, further testing and model validation with additional measurements on site is necessary to improve the model precision.

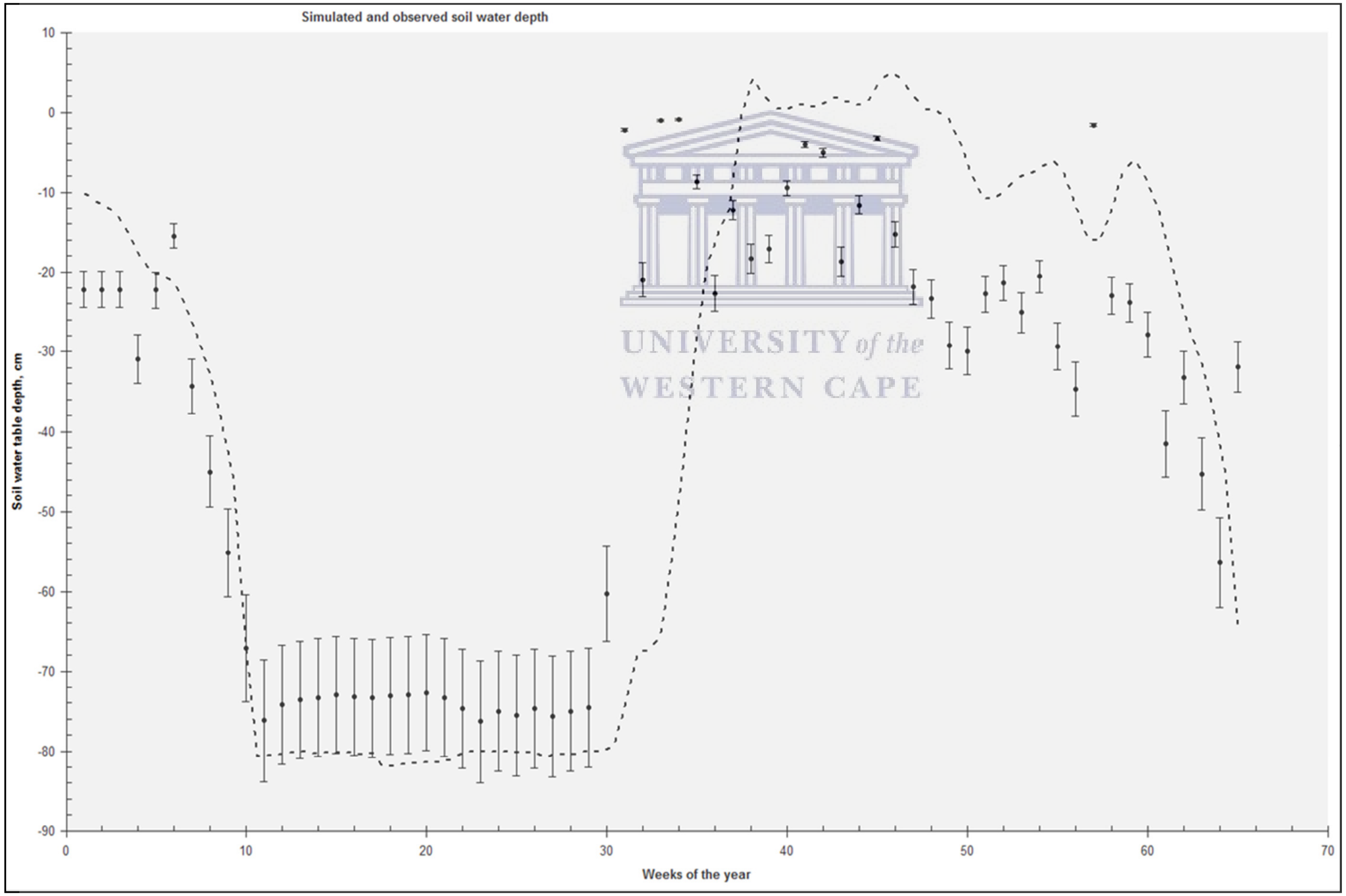


Figure 5.7. Output graph of model (simulated) data and experimental data (observed water table depth) at NYP. The dotted line represents model data. The points with error bars represent experimental (field) data.

CHAPTER 6 MODELLING THE HYDROLOGICAL NICHE OF RESTIONACEAE SPECIES

6.1 Introduction

This chapter discusses the application of the maximum entropy modelling or MaxEnt model (Phillips et al., 2006) for predicting the distribution of Cape Restionaceae, a Fynbos indigenous reed-like plant family. It first discusses several key principles in species distribution modelling and then the modelling procedures. Data preparation is an important component of the modelling process based on the fine scale of the sample areas. The data preparation procedure required the understanding of several other software and file formats including Microsoft Excel©, ESRI ArcGIS©, and Notepad©. It elaborates on how data is acquired and then formatted using the different software before running the MaxEnt model. For instructions on how MaxEnt operates, interpreting results, and advanced modelling options, refer to http://biodiversityinformatics.amnh.org/open_source/maxent. This chapter is the first of a two-part investigation into the use of SDMs as tools for conservation planning and management. The second part discussed in Chapter 7 will dwell on the use of this tool in the face of changing climate in the distant future.

The next sections attempt to build a comprehensive theoretical basis for the suitability of species distribution modelling and geographical information systems (GIS) as the means to assess and model the effectiveness of hydrological variables as determinants of of species hydrological niches in a hydrological gradient. It is the theoretical background of the ecological principles and modelling procedures which are relevant to species distribution modelling at a microscale level and in a context where bioclimatic (environmental) variables are not readily available (downloadable). Aspects like biodiversity degradation, the importance of bioclimatic or environmental variables, the need to employ GIS, species distribution modelling - both mechanistic and correlative approaches and their merits, maximum entropy modelling for habitat suitability predictions, will be discussed.

6.1.1 Biodiversity degradation

Nearly 25% of the estimated 250,000 species of vascular plants in the world may become extinct within the next fifty years partly due to natural phenomena and the activities of humans (Schemske et al., 1994). These two factors have contributed to altering nature through their impacts on the atmosphere, ecosystems and on geological processes (Dirzo and Raven, 2003). As a result, the earth is now faced with a number of adversities including frequent extreme climate effects like prolonged droughts, extreme rainfall, frequent fires, land transformations and deforestation. Many species have already been reduced to one or two populations with few individuals, causing plant conservation to become of vital importance in ecosystems management and planning (Dirzo and Raven, 2003).The concern today is how to arrest this deteriorating trajectory through improved conservation and management of biodiversity. In semi-arid environments like South Africa, hydrological factors contribute significantly to the determination of species niches. Based on its geographical location on the globe, the vegetation biomes in South Africa are predisposed to experience the impacts of extreme climatic changes and encroaching urbanisation (Midgley et al., 2005). One such area in the extreme south of South Africa is the Fynbos vegetation of the Cape Floral Kingdom, threatened by urbanisation, agricultural expansion and groundwater extraction (Rouget et al., 2003). Fynbos is the key vegetation-type and composed of ericoid, proteoid, geophytes and restioid life forms (Goldblatt and Manning, 2002). Although its Mediterranean climate sets it apart from the rest of South Africa in terms of the seasonal patterns (i.e. cold-wet-winters and hot-dry-summers), climatic conditions remain largely semi-arid. Hence, the overall semi arid climate character still causes variability in the main hydrological factors which makes them crucial determinants of species niches in the biome. Goldblatt and Manning (2002) already estimated about 36 plant species to be extinct in this internationally recognised floral kingdom.

Global climate change models predict drastic drifts in climatic trends that will cause more seasonality in moisture in the southern African region and result in likely shifts in plant community structure and composition by the year 2100 (Midgley et al., 2003). Also, being a semi-arid environment, hydrological factors are key in alteration of species niches. The niche defines the way in which a species fits into its ecological community, and this is determined or controlled by existing environmental factors around it (Whittaker et al., 1973). This study examines and explains the hydrological niche of many Restionaceae in their habitat, under the impact of climate change and the resulting predicted hydrological changes at a microscale level.

6.1.2 Bioclimatic (environmental) variables

According to niche theory, species habitats are defined by external environmental factors that are both climatic and non-climatic. Changes in these external predictors may cause physiological constraints on species and therefore can affect species distributions to varying degrees. The relationship between climate and the distribution of a species throughout a landscape varies due to local adaptation and other factors, such as dispersion constraints related to habitat availability. Bioclimatic predictors were derived from two climate data sources to better represent the types of seasonal trends pertinent to the physiological constraints of different species.

Species predictive modelling involves the use of both proximal and distal environmental variables. Proximal variables directly affect the distribution of the species, while distal variables are correlated in varying degrees with underlying influences (Austin, 2002). Biophysical variables such as air temperature, soil water content and solar radiation directly influence plant niches (Dymond and Johnson, 2002). Whereas, variables like elevation, slope angle and slope aspect complement the biophysical variables, rendering an indirect influence on the niche (Gómez-Plaza et al., 2001, Brocca et al., 2007). For instance, (i) elevation is highly correlated with temperature and humidity, (ii) slope angle regulates soil wetness, soil hydraulics and wind impacts, (iii) slope aspect influences solar input and snow persistence. Soil wetness and incoming solar radiation are regarded as substantial proximal variables in niche structuring (Dymond and Johnson, 2002). However, observations have shown that at local to micro scale, climatic factors are overridden by local factors such as the geomorphology and land-cover which exert more control on the species' niche (Pearson et al., 2004). Geomorphology encompasses physical aspects like local relief and gradient which directly impacts water movements and nutrient availability for plant growth (Ellis and Mellor, 2002).

According to Grinnell (1917), the fundamental niche of a species is defined by a set of ecological conditions that are favourable for their optimal growth and survival. The conditions that influence niche establishment range from natural conditions (e.g. climate and soil character) to anthropogenic activities (like groundwater abstraction and the introduction of alien vegetation). These form the primary source of ecological data during habitat modelling studies. Hence, much emphasis is always given to the source and quality of the data. Most habitat suitability models use readily available data from global or regional databases such as the WorldClim dataset (http://www.worldclim.org/bioclim, Hijmans et al., 2005) to predict optimal species ranges. However, such global or regional scale data layers are not suitable in fine-scale studies whose primary objective is focussed at local scale observations. The spatial resolution of the climatic surfaces used in a particular study depends on the needs of the application process. Data at fine (≤ 1km^2) spatial resolution is necessary to capture environmental variability that is sometimes lost at lower resolutions and where there are steep environmental gradients.

Even recently many studies have focused on the regional bioclimatic species modelling rather than on the more detailed local microclimatic alternative when studying the impact of climate change on species niches (McLaughlin et al., 2011, Early and Sax, 2014, Varner and Dearing, 2014, Ehrlén et al., 2015, Guo et al., 2016a, Wang et al., 2016). Key, therefore, is the need to establish microclimatic environmental data for the purpose of modelling micro scale species niches under the influence of hydrological changes. The depth of the water table in the subsurface is a key hydrological variable which defines the soil water regime in addition to the duration of stay at these depths. Shallow water table depths depict saturated soils while deeper water table levels depict high aeration or dry conditions in the soil. Hence, the implementation of these unique microclimate environmental surface or predictors for modelling species niches is innovative in species modelling methodology and formed one of the key objectives of this study which will be discussed later in greater detail.

6.1.3 Geographic Information Systems (GIS)

The use of GIS in ecological modelling is merely complementary as they provide the flexible spatial analytic components which respond to the spatial character of ecological problems (Goodchild, 1993). Advancements in GIS have revolutionised species predictive modelling by significantly improving the abilities to capture, manage, analyse and visualise now increasingly digitally-captured biodiversity resource data (Vogiatzakis, 2003). GIS affords natural resource managers and biological conservationists improved techniques to integrate data from different formats and to generate increasingly required spatial continuous data of environmental variables (Li and Heap, 2014). New techniques with improved data analytical capabilities have afforded researchers the opportunity to quantitatively map and test species distributions based on their association with the environment (Brotons et al., 2004). Predictive maps of species distributions now built, based upon the association between species and their environment, have become reliable tools for conservation and management (Austin, 2007). In addition, the integration of statistical algorithms and spatial analysis in a GIS provides a means to rapidly review the distribution and the status of a species even when information is poor or non-existent and even to predict potential habitat from limited field data (Phillips et al., 2006). In the current study, GIS tools have been used extensively first for pre-processing (e.g. coordinate transformation, projection change) and in post-processing of modelled outputs (e.g. cartographic and visual display, simple spatial analysis) of ecological data.

6.1.4 Species distribution modelling

This section would dwell on the answer to the questions asking ‘What is a species’ distribution model?’ and why? It would also attempt an explanation of some of the ecological principles behind the scheme, its application and an introduction of some of the commonly used statistical algorithms used in aid of the SDM processes.

The following illustration best demonstrates the essence of species distribution modelling. To estimate the distribution of a Restionaceae plant e.g. that is known to thrive in wet sandy soils, the fundamental strategy is to simply identify locations with clay soils and high precipitation to generate an estimate of the Restionaceae species’ distribution. Species distribution models (SDM) otherwise called habitat suitability models or ecological niche models or bioclimatic envelope models predict the relationship between species assemblages and their environments (Pearson, 2007). These are basically statistical algorithms which spatially examine the relationships between species and their habitats and then map the geographic distribution of species (Zaniewski et al., 2002). Use of the term ‘species distribution modelling’ is widespread but somewhat misleading in that it is actually the distribution of suitable environments that is being modelled, rather than the species’ distribution per se (Pearson, 2007). These models are developed based on the suitable habitat conditions of sites where the species are known to occur in geographic space. In other words, these models indirectly model habitats or the distribution of a target species by first modelling the distribution of environmental conditions believed to be suitable for occupation and then assume these to reflect the actual distribution of the species (Pearson, 2007). SDMs may extrapolate beyond the observed known range in space and time and provide ecological insight into the predicted species distributions at such dimensions (Franklin, 2010). Equally, there are a number of reasons why the species may not actually occupy all suitable sites (e.g. geographic barriers that limit dispersal or competition from other species) (Pearson, 2007).

The concept behind these models is the basic ecological principle that there are biotic and abiotic factors that constrain the location of species (Pulliam, 2000). SDMs utilise the principles of biogeography, geographical information systems and ecological gradient analysis (Franklin, 2010). Predictive habitat models seek to describe the limits of these constraints by correlating known species occurrences with environmental factors that define these limits. Additionally, this concept drew attention to the individualistic behaviour of species in their environments and strongly argues in favour of the modelling of individual species rather than communities (Elith and Leathwick, 2009). One family of predictive models are the Climate Envelop Models whose primary objective is predicting species distributions under current, past and future climates (Hijmans and Graham, 2006).

The main applications of SDMs vary. In ecological studies, SDMs solve a range of issues from predicting the suitable habitats (niches) (e.g. Fourcade et al., 2014) to predicting the potential impact of environmental and climate changes on species (the potential distributional changes of species niches) through time and space (Ehrlén et al., 2015, Pacifici et al., 2015).

The usefulness of any SDM analysis is firmly dependent on the quality of the data being used and the proper execution of the appropriate algorithms for each purpose (Guisan and Thuiller, 2005). Robust species distribution models are more likely to make good ecological inferences and are more reliable to inform decision-making by biodiversity management practitioners. However, there are a number of conceptual uncertainties associated with the applicability of these models. E.g. there is high uncertainty associated with predicting species distributions in novel conditions. Novel conditions are new values of predictor variables which fall outside of the original range of the training or species presence conditions. Other uncertainties include the influence of factors such as phenotypic plasticity and genetic variability which cannot be explained through SDM. Such uncertainty makes the output of these models difficult to assess. This impacts the transferability of these models which is their ability to predict the possible presence of species in places (Duque-Lazo et al., 2016, Petitpierre et al., 2017).

6.1.5 Mechanistic versus correlative approaches in species distribution modelling

Mechanistic models in ecological studies aim to incorporate physiologically limiting mechanisms in a species tolerance like injury, phenology, and reproductive success, to environmental conditions. Acquiring the required detailed understanding of the physiological response of species to environmental phenomena is daunting and so such information is hardly available for most species (Pearson, 2007). Correlative models aim to estimate the environmental conditions that are suitable for a species by associating known species' occurrence records with suites of environmental variables that can reasonably be expected to affect the physiology and probability of persistence of species (Pearson, 2007). The hypothesis behind this approach is that the observed distribution of a species provides useful information as to the environmental requirements of that species.

Since spatially explicit occurrence records are available for a large number of species, the vast majority of species distribution models are correlative. The correlative approach to distribution modelling is the choice of modelling approach that has been implemented in this thesis. Figure 6.1 summarises the required steps for building and validating a correlative species distribution model (Pearson, 2007).

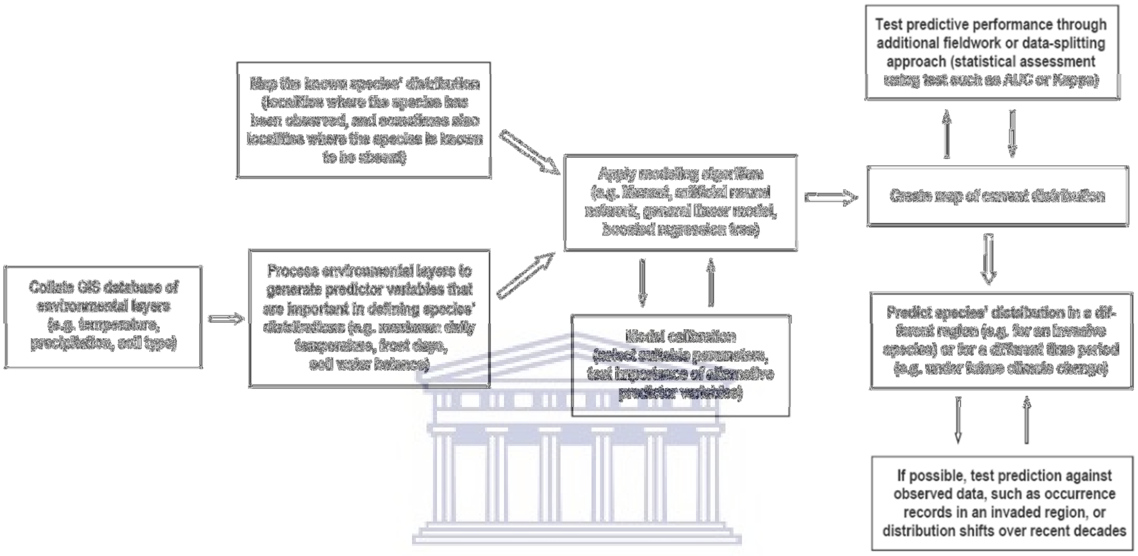


Figure 6.1. Flow diagram detailing the main steps required for building and validating a correlative species distribution model (extracted from Pearson, 2007).

Different types of SDM algorithms or methods have been developed. The algorithms utilized in developing predictive habitat models have been classified into profile regression and machines learning methods based on whether they use presence-only or presence and absence biological data. Whereas profile methods (e.g. BIOCLIM, Domain and Mahalanobis) only use presence data, regression (e.g. Generalised Linear Models - GLM, Generalised Additive Models - GAM) and machine learning techniques use both presence and absence data. These methods are assessed based on their relative performances in habitat prediction (Elith et al., 2006) and in modelling climate change effects (Hijmans and Graham, 2006). Some of these algorithms are briefly described below.

BIOCLIM is bioclimatic envelope models that are used extensively to identify locations that have environmental that fall within this envelop (Nix, 1986). The envelope is a set of predefined multidimensional environmental “box” of conditions of known sites and assumes all sites with environmental conditions within these boundaries are potential sites of species occupancy. Though extensively used, the BIOCLIM climate envelope model does not perform well in the context of climate change when compared with other SDMs (Elith et al., 2006, Hijmans and Graham, 2006, Booth et al., 2014).

The Domain algorithm computes the Gower distance between environmental variables at a location of interest and those at any of the known locations of occurrence (’training sites’) (Carpenter et al., 1993). The Mahalanobis distance technique (Mahalanobis, 1936) uses a Mahalanobis distance to account for the correlations of the variables in the dataset.

Most often, the relationships between biological and environmental variables are neither linear nor straightforward but rather complex in nature (Austin, 2002). Hence, nonlinear models are best suited to define them. However, most often these relationships are complex and represented as complex models. Complex relationships are fitted as linear combinations of basis functions in methods (Guisan et al., 2002). A GLM uses some combination of linear, quadratic and/or cubic terms, to fit non-linear functions (Elith et al., 2006). Generalized additive models (GAMs) (Hastie and Tibshirani, 1990, Wood, 2006) are an extension to GLMs. GAMs use non-parametric, data-defined smoothers to fit non-linear functions. Both GLMs and GAMs use presence and absence to realistically model ecological relationships using their strong statistical foundation to model the distribution of species (Austin, 2002).

Examples of machine learning (data mining) methods include Maximum Entropy (MaxEnt), Genetic Algorithms for Rule Production (GARP), Artificial Neural Networks (ANN) and Classification and Regression Trees (CART), Random Forests, Boosted Regression Trees (BRT), and Support Vector Machines. Hastie et al., (2009) provided an extensive overview of these methods. The Boosted Regression Trees (BRT) (Friedman, 2001, Elith et al., 2008) is extensively used in species distribution modelling (Elith and Leathwick, 2009). Also used is the Classification And Regression Trees (CART) (Breiman, 2017) and its derivatives viz. Random Forest (Breiman, 2001, Peters et al., 2007) and the multivariate regression tree (De'ath and Fabricius, 2000), varieties. The genetic algorithm for rule-set prediction (GARP) modelling technique makes use of presence and absence to predict the species distribution by implementing a set of genetic rules (Stockwell, 1999). Each rule type implements a different method for building species prediction models. GARP searches iteratively for non-random correlations between species presence and absence and environmental parameter values using any of four types of rules, including atomic, logistic regression, bioclimatic envelope, and negated bioclimatic envelope rules.

Further, the choice of which model algorithm to use might depend on the scale, the distribution and even the life history of the species being studied (Franklin, 2010). Since in reality, a species is likely to respond to multiple factors algorithms that can incorporate interactions among variables might be preferable (Elith et al., 2006). However, the choice of algorithm to use might not be determined by a rigid set of rules as described above but by the choice of the user based on their expertise and an appreciation of the kind of data at hand (Merow et al., 2014).

Maximum Entropy (MaxEnt) (Phillips et al., 2006) is the most widely used SDM algorithm. Elith et al. (2010) provide an explanation of the algorithm (and software) for ecological use. MaxEnt outperforms all its predecessors in the climate envelop family (like BIOCLIM, GARP), GAM and GLM in its ability to fit nonlinear response surfaces which are frequently observed in biological data (Elith et al., 2006). MaxEnt uses just the species locational and absences or background data and even categorical predictors to model a complete picture of the species habitat (Barry and Elith, 2006). MaxEnt is particularly popular for modelling habitat change especially as concern over climate change grows (Phillips and Dudík, 2008).Its prediction accuracy is reasonably stable and it produces maximal accuracy levels irrespective of how small the sample size is (Cobben et al., 2015, Ray et al., 2017). Recently, Zaniewski et al. (2002) added to current arguments about the merits and demerits between presence-and-absence and presence-only methods and showed that presence-only methods are efficient for modelling rare species for which limited data are available). Additionally, MaxEnt is best suited for predicting areas that may be suitable for a species outside of its current habitat as well as in determining the density of species within the habitat.

MaxEnt modelling technique was chosen for this study based on its suitability for fine scale, the ability to use limited occurrence data (Elith et al., 2006), the cost-free availability of software for public use, the ability of the software to use categorical data, and the ease by which output can be integrated into a GIS.

6.1.6 Maximum entropy (MaxEnt) Modelling

MaxEnt is a machine learning algorithm that uses the principle of maximum entropy to define the best approximation of the geographic distribution of species (Phillips et al., 2006). This principle states that the best approximation of an unknown species' location id the one with maximum entropy (i.e. best spread out and uniform) subject to known constraints (Phillips and Dudik, 2008). Constraints exclude all conditions and assumptions which are not defined in the occurrence environments.

Statistically, the MaxEnt algorithms estimate the maximum entropy probability distribution function that is used to predict the probability of species occurrences based on environmental constraints at species (presence) locations (Elith et al., 2006). Its algorithm is generative in nature which makes it different from most other SDM algorithms which are discriminative in nature. For a given prediction where X represents the inputs and Y represents the response or probability of occurrence: the discriminative approach models the probability of occurrence given the inputs, Pr(Y/X) whereas, the generative approach used by MaxEnt instead models the probability of occurrence of inputs given the response, Pr(X/Y). Bayes' rule is then used to get from Pr(X/Y) to Pr(Y/X) (Phillips and Dudik, 2008).

The software is designed to suit any sample size and spatial scale. It is also nonlinear, nonparametric and insensitive to multicollinearity of environmental variables. It is freely downloadable upon request from www.cs.princeton.edu/~schapire/maxent along with the necessary java runtime environment and associated literature (Phillips et al., 2009). MaxEnt estimates potential species habitats by the finding probability distribution of maximum entropy subject in such a way that the expected value of each environmental variable should match its average oversampling locations from environmental layers (Phillips et al., 2006). Literally, MaxEnt figures out the relationship between an organism and the environment in which it is known to occur, and uses this relationship to predict other times or places which may be suitable for the organism.

The MaxEnt software is designed to use both species presence and absence data. The latter data type is introduced as background information or pseudo-absence points in the model. The model functions by examining the environmental conditions in the total area of study where the species is present and analyses for a suitability of occurrence relative to where they are absent. In this analysis, the locations where species are not found to occur are not interpreted as absences but as pseudo-absences (i.e. possible presence or absence) and implemented as the background environment. Background points (conditions) have literally been available in the study area but were never occupied by the species. They extend beyond the occurrence range of the species, i.e., include environments with conditions different from those at occurrence locations. The inclusion of pseudo-absences or background points enhances the discriminative ability of MaxEnt. It is a useful inclusion when the objective of the study also includes predictions under novel conditions (Chefaoui and Lobo, 2008).

The environment is usually represented by a selection of environmental variables in the form of raster layers which could be continuous and categorical in format. Furthermore, MaxEnt investigates the relative contribution (or importance) of every explanatory variable through a Jack-knife procedure and has the capability to perform replicate runs to allow cross-validation, bootstrapping and repeated subsampling in order to test model robustness (Pearson, 2007). The mplementation of the model is discussed in more detail in Section 6.2.2 and Section 6.2.3.

This study examines how hydrological variables contribute to defining plant hydrological niches at a micro scale. The primary objective was to assess and model the effectiveness of hydrological variables as determinants of species hydrological niches in a hydrological gradient environment. The outcomes would serve as clues to conservation strategies and future climate change impact analysis.

6.2 Methods

A number of aspects were essential in modelling the probability of occurrence of Restionaceae species. These included: the data requirements, the nature and source of the data, the choice and scale of environmental variables to use.

6.2.1 Data inputs

The data used to model the potential hydrological niches of Restionaceae species included: (i) the locational coordinates of quadrats (latitudes/longitudes); (ii) the vegetation distribution (counts of species presence and absence) in quadrats; (ii) water table depths and moisture content measurements in quadrats; (iii) topographical measurements quadrats, at Fynbos wetland communities in the south-western part of the Fynbos Biome in the Western Cape Province of South Africa in the CFR (Araya et al., 2011). In the experimental design, each vegetation plot contained a number of equally-spaced 1-square-metre quadrats (subplots) placed 1 metre apart. Data collected from eight experimental sites (shown in

Figure 3.1) were used for analysis. The precise size and shape of each plot varied with the local physical constraints like topography and access. Plots were carefully located so that the distribution was broadly representative of the Fynbos vegetation diversity and were suitable for data sampling (Araya et al., 2011).

6.2.1.1 Species occurrences data

In a systematic ecological survey, the quadrats of each plot were sampled for the count of Cape Restionaceae present in them. The species records represented the total known distribution of Restionaceae species in geographically referenced quadrats. Biological data was added to three Excel columns. The first row of the datasheet was made the header line and had the titles of the three columns: Species, Longitude, and Latitude, respectively. Geographical coordinate values were in decimal degrees (DD). Alternatively, Longitude and Latitude could be substituted with Easting/Northing, X/Y, etc. The completed Excel tables were saved as comma-separated delimited values (*.csv) files in readiness for input in MaxEnt model. A list of species and the geographic locational information for each site can be found in the Appendix section.

6.2.1.2 Environmental variables

Site records of the four environmental variables were collected from 2007 to 2009. These variables constituted the current hydrological scenario at the study sites and were included in modelling species distributions for each site.

Both palaeoecological and recent studies have shown that climate is of major importance in influencing the distribution of species (Woodward and Williams, 1987, Harrison and Prentice, 2003, Kelly and Goulden, 2008). This is physical information that expresses the role played by soil hydrology in the distribution of species has been referred to as microclimatic variables in this microscale study. Precipitation (a major climatic element) is the main contributor of moisture to the soil from which plants absorb their needs. Hence a measure of the available moisture levels in the soil was important as an indirect reflection of precipitation.

The depths to the water table were monitored through a number of dip wells in each experimental plot. Hydrological records from the wells were accumulated for a period of at least 12 months and the mean water table depth (MWTD) was computed as the average depth to water over the sampling period measured in metres.

Two other hydrological measures which are the sum exceedance values for dryness and saturation in the soil were computed from the water table depth and duration of dying or flooding. These two moisture coefficients quantified dryness (drought stress) and wetness (aeration stress) in the soil. The sum exceedance value is a scale that quantifies the exposure of plants to either drought stress when the water table falls below a critical threshold level (causing drought), or rises above average causing soil saturation (aeration stress) (Silvertown, 2004). The extent of exceedance is then cumulated to obtain the Sum exceedance value (SEV) measured in m. wk. Poor soil aeration is caused by waterlogging, and drought stress is caused by soil dryness (Silvertown et al., 1999). The soil drying threshold (SEVd) is calculated according to the water-table depth which provides 50 cm (5 kPa) of tension at the soil surface, where the plants show the effects of water stress (Henson et al., 1989). The SEVa threshold is calculated as the water table depth at which the densest rooting, located at a depth of 0-100 mm, becomes waterlogged, or when the air-filled pore space is less than 10% of the total soil volume (Higgins et al., 1987, Araya et al., 2011). For soil, the drying threshold is between 45-48 cm, and the aeration stress threshold is 15-20 cm (Araya et al., 2011, Silvertown et al., 2012).

Elevation has a direct influence on the moisture hydraulics in the soil by providing the gradient that moisture pursues downslope thereby enabling a hydrological gradient along that elevation gradient. On-site topographical elevation/heights above sea level (in metres) were read from the centre of each quadrat by means of survey equipment (Araya et al., 2011).

6.2.1.3 Preparation of microclimatic layers

An important step of the MaxEnt modelling is the preparation of environmental layers which requires the use of other software including Microsoft Excel©, ESRI ArcGIS© and even Notepad©. The environmental variables accumulated in Section 6.2.1.2 were the current observed microclimatic data (2009 – 2011) that were collected at the sites. The data preparation process included importing **.csv* files, ordinary kriging interpolation, and modification of kriged layers to the same extent (geographic bounds and cell size) in ArcGIS 10.3. MaxEnt required that the spatial extent, cell size and coordinate system must be uniform for every data layer that will be used during the processing of species models.

Like for the species data, the environmental layers were entered into four columns in an Excel table with column names: Longitude, Latitude, Quadrat number and ‘name of the environmental variable being considered'. Separate tables were created for SEVa, SEVd, elevation and MWTD values and were saved in **.csv* files in readiness for conversion into continuous raster grid layers useable by MaxEnt.

The conversion into continuous surfaces involves a number of steps: first, the *Add X-Y Data* tool was used to add environmental data in *.csv* files as spatial x-y coordinates point layers in ESRI ArcMap window and then saved as shapefiles. Then, kriging interpolation was used in generating continuous microclimatic raster surfaces from observed environmental data.

The use of different statistical approaches to generate interpolated climate surfaces has been documented. Thornton et al., (1997) used a truncated Gaussian weighting filter to interpolate both temperature and precipitation surfaces using elevation, longitude and latitude as independent variables. Daly et al., (2002) used the PRISM method to generate climate surfaces for, particularly sparsely orientated data. More recently Hijmans et al., (2005) used the thin-plate smoothing spline algorithm to interpolate elevation information. Meanwhile, Li and Heap, (2014) have provided a comprehensive review of interpolation methods that are applicable in spatial surface estimations.

The procedures for implementing kriging generally incorporate measures of error and uncertainty when determining estimations (Ahmadi and Sedghamiz, 2008). Semivariogram models were used to fit surface prediction models from the spatial relationships between sampled points. Conceptually, semivariogram models explore the assumption that points that are closer in distance are more alike than points which are farther apart when determining prediction surface fits (Goovaerts, 1997, Isaaks and Srivastava, 1989, Webster and Oliver, 2007). Hence, the effectiveness of any prediction was predefined by the nature of the semivariogram or the covariance model fitted much earlier in the analysis (Isaaks and Srivastava, 1989). Predictions were validated with observed field values and a standard error value indicating the level of uncertainty associated with the prediction for each point (Webster and Oliver, 2007). This approach is, therefore, a location-dependent weighted average of the observational values from the point locations, where the weights depend upon the spatial correlation structure of the data (Guo et al., 2007, Guo et al., 2011). A detailed description kriging technique is discussed by Goovaerts (1997).

Ordinary kriging was chosen to generate raster surfaces in this study. This statistical method basically produces continuous surfaces from point observations collected in the field to estimate the values on non-sampled locations. Its estimates are weighted linear combinations of the available data. It has an advantage over other kriging options in that it is unbiased (works towards zero mean residual or error) and best at minimising the variance of the errors. The distinguishing feature of ordinary kriging, therefore, is its aim of minimising the error variance (Isaaks and Srivastava, 1989). The formulation of ordinary kriging in the form of a linear predictor is shown in Equation 6.2.

$$\hat{Z}(x_p) = \sum_{i=1}^{N} \lambda_i Z(x_i)$$

Equation 6.1

Unbiased estimates during kriging are obtained by simultaneously solving the following expressions in a linear equation system.

$$\begin{cases} \sum_{i=1}^{N} \lambda_i \gamma(x_i, x_j) - \mu = \gamma(x_i, x) \\ \sum_{i=1}^{N} \lambda_i = 1 \end{cases}$$

Equation 6.2

Where $Z(x_p)$is the kriged value at location x_p, $Z(x_i)$ is the known value at location x_i, λ_i is the weight associated with the data, μ is the Lagrange multiplier, and $\gamma(x_i,x_j)$ is the value of variogram corresponding to a vector with origin in xi and extremity in x_j.

A kriged surface based on the ordinary kriging algorithm was calculated from the event layers using the Spatial Analyst Tools of ArcGIS10.3 (ESRI, 2015). Thereafter, the interpolated surface is exported (using the Export Data command) and saved as raster grid (*.grd). These kriged surfaces were generated at below 1m grid scales. This made them unique and different from frequently utilised mainly regional or global scale bioclimatic surfaces for species habitat modelling (e.g. Hijmans et al. 2005). MaxEnt requires that all spatial environmental layers in raster (ASCII) format of the same cell size, extent and coordinate system (geographic or UTM) in order for modelling to be smoothly executed.

ArcGIS© Spatial Analyst tools were used to modify the environmental layers to be the same extent (geographic bounds and cell size). The ‘Extract by Mask’ tool of Spatial Analyst was used to set clip the environmental layers to the boundary outlines of each plot, assign an output coordinate system and processing the extent of the layers. The WGS84 datum and Universal Transverse Mercator (UTM) projection (zone 34S) systems were used. The rest of the environmental layers were made to have the same coordinates and extent in the *Environment Settings* command. In this command window, the output coordinates, the processing extent, the raster snapping, assigning the cell size and the outline mask, were set to be the same as those of the layer that was first processed. All environmental layers are required to be in ASCII format to run MaxEnt.

The 'Raster to ASCII' conversion tool from ArcGIS' ArcToolbox menu was used to convert environmental layers into ASCII format (*.asc). ASCII grid layers for each site were saved in separate '*ASCII_Environmental_layers*' folders created in *Windows Explorer* from where they were accessed during the MaxEnt run.

6.2.1.4 Defining bias selection or background layer

This section describes the processes of the definition of a bias selection or background sample (also called pseudo-absences) file. The background is literally the total extent of the sampled area covering both the where species were spotted and where they were not counted. The background samples used when developing a distribution model can have significant impacts on the model results (Elith et al., 2011). A number of methods exist for choosing background samples. The choice of method depends on the data available, the geographic characteristics of the area and the size of the surveyed area. If the surveyed area is extensive, a minimum convex polygon is recommended to define a boundary around the sampled points. In a micro or local scale study, the boundary limits of the surveyed area are easily used for this purpose. In this study, the boundary outlines of sampled plots were used. This provides MaxEnt with a background file with the same bias as the presence locations. The Polygon to Raster tool from ArcGIS 10.3's ArcToolbox was used to convert all boundary polygons into raster layers. Then the Map Algebra tool from ArcToolbox Spatial Analyst Tools was used to convert the "NoData" empty polygon into a new raster polygon with all cells assigned the value 1. Thereafter, the resulting polygon was converted into ASCII grid files with the same extent, cell size, snap raster and mask as the other ASCII files for entry into MaxEnt. The following conditional (Con) statement was entered into the Raster calculator window:

Con ("bias_file">=0, 1,"bias_file")

Explanation of con statement: Convert all pixels with values 0 to values 1 and pixels with other values (mostly the no data cells) should remain as is.

6.2.2 Hydrological niche modelling procedure

The MaxEnt (Maximum Entropy) software version 3.3.3K (Phillips et al. 2004, 2006) sourced from biodiversityinformatics.amnh.org/open_source/maxentwas used to create hydrological niche models for Restionaceae species. Details of MaxEnt are included in Section 6.3.5. Hydrological niches represented the relationship between species and the hydrological (environmental) conditions at eight ecologically sampled wetland communities (sites). The following section describes the procedures that were used to determine the suitable Restionaceae hydrological niches.

The Restionaceae presence data were entered in the “Samples” file, and the location of the microclimatic layers folder was linked to “Environmental Layers”. If projections for the future are required, the future files are entered in the “Projection layers directory/file”. An Output directory created using Windows Explorer was assigned to contain the model results. In order to avoid overfitting of the test data, the regularization multiplier was set at the value 1 (Phillips et al., 2004). All the available suite of model features (linear, quadratic, hinge, etc. features) was used in the model runs.

During each model run, 75% of the species occurrences were used for model training while 25% was used for testing the model performance. Four replicate model runs were executed for each species model (Flory et al., 2012) using a threshold rule of 10 percentile training presence. During each replicate run, subsamples with samples that showed sample bias were removed from the process (Hijmans, 2012, Phillips et al., 2009).

Because species were not randomly collected, spatial sampling biases were treated by using a Gaussian kernel density of sampling localities tool to generate a surface of 10,000 random background points in MaxEnt (Elith et al., 2010). This method produces a bias grid that up-weights presence-only data points with fewer neighbours in the geographic landscape (Brown and Yoder, 2015). Other parameters were set to default as the program was already calibrated on a wide range of species datasets (Phillips and Dudík, 2008).

A series of results, including averages, minimums, maximums, medians and standard deviations were generated from the replicate runs. The results were displayed in an HTML file, with the additional capability to edit results. Several charts were produced, including the Area Under the Receiver Operating Characteristic (ROC) Curve, or the AUC. The AUC value gives an indication of the performance of the model with values ranging from 0 to 1. AUC values less than 0.5 indicate the results close to random while confidence increases as AUC increase towards 1.0. In this light, AUC has been categorised as follows: AUC<0.8 as poor, 0.8 - 0.9 as fair, 0.9 - 0.95 as good, 0.95 – 1.0 as very good (Thuiller et al., 2005). However, this study considered AUC of 0.6 and above to indicate a useful model (Fielding and Bell, 1997). Random models (below 0.6 Test AUC) will not be discussed any further.

The results also included a continuous raster layer that displayed the probability of occurrence or the estimates of habitat suitability for species varying from 0 (lowest suitability) to 1 (highest suitability). However, these were regrouped into binary suitable and unsuitable habitats based a '10 percentile training presence' probability threshold (the largest threshold that leaves out 10% of occurrence records) (Pearson et al., 2004). A fade-by-clamping' tool was used to remove heavily clamped pixels that could cause erroneous predictions of suitable habitats under future climate scenarios in the final predictions (Phillips et al., 2006). The MaxEnt modelling process generates response curves which aid in examining the relationships between the habitat suitability for a species and the environmental variables. Finally, a Jack-knife test was used to evaluate the contribution of each environmental variable in defining each model. This test compares the performance of each variable in isolation with its performance when together with other variables during a model run. All graphics results were exported into ArcGIS where the ASCII to Raster tool was used to convert all *.asc result outputs into a *.tiff format. These were edited and displayed as comparable suitable and unsuitable hydrological niche maps.

6.2.3 Post-modelling analyses

The model results are the potential presence distribution of each species modelled expressed as a continuous surface with pixel values ranging from 0 to 1. Each pixel value represented a probability of presence of the species within that pixel. Post-analytical procedures included choosing of a logistic threshold probability of occurrence to discriminate species likely presence from absence pixels, determine the preferred range of hydrological variables, making hydrological niche maps using GIS, and calculating species richness to show spatial biodiversity patterns.

6.2.3.1 Logistic threshold of occurrence

By default, MaxEnt produces a continuous raster surface with values ranging from 0 to 1 representing habitat suitability (Phillips et al. 2006). In discerning the suitable from the unsuitable niches within this range, a threshold of occurrence (i.e. the minimum probability value for suitable habitat) had to be chosen. Several methods for determining this threshold exist (Liu et al., 2005, Pearson et al., 2004, Pearson et al., 2006, Phillips et al., 2006). With no set rule to set these thresholds, a threshold can be decided depending on the data used or on the objective of the map and may vary from species to species. MaxEnt provides thresholds in the *maxentResults.csv* included in the results. These are based on a variety of statistical measures. Examples of logistic thresholds include the minimum training, 10 percentile training presence, and equal training sensitivity and specificity logistic threshold. In this study, a 5% minimum presence threshold was used to define the minimum probability of suitable habitat. This choice assumes up to 95% accuracy in the data or allows for just a 5% chance of error in this systematically collected data. This threshold of occurrence value may vary from species to species depending on the distribution of the logistic probability presence across the number of observed localities.

6.2.3.2 Preferred environmental range of species

Each species has a preferred environmental range within which it can tolerate in the ecosystem. The microclimatic variable values for all species occurrences were extracted using the *Extract Multipoint Values* tool in ArcGIS 10.3 software followed by a descriptive statistic on the deduced tabular data.

6.2.3.3 Species richness

Species richness was defined based on the sum of unique species in a unit area being sampled and was calculated as the total number of species in each grid cell in the resultant binary SDMs. This is the biodiversity metrics were calculated in ArcGIS 10.3 using the *Estimate Species Richness* tool in SDMtoolbox v1.0 (Brown 2014). The tool summed up threshold binary layers and the resultant output layer depicted the spatial richness of species at different climatic scenarios (both current and future scenarios).

6.3 Results

6.3.1 Environmental Surfaces

The map processing tools of ArcGIS® software successfully generated microclimatic surfaces for all environmental variables. Figure 6.2 to 6.9 show the spatial variation in each variable across each sample plot. Elevation values were measured relative to a reference point which was either inside or very close to the plot. Where the reference point is located at an elevation higher than the plot, the resulting values relative to it are negative and vice versa. The distribution of records is shown across a colour scale where the darkest shades indicate the highest values and lighter colours representing the least values. High MWTD values imply that water table levels are low which signify dry conditions and vice versa. Sum exceedance value (SEVd) for soil drying is a value cumulated during periods in which the moisture tension of the surface soil exceeds 5 kPa, which could potentially induce stomatal closure on the plant (Silvertown et al., 1999). High SEVd indicates dry soil conditions. The soil aeration stress value or waterlogging threshold (SEVa) is the cumulative periods in which the soil air-filled porosity fell below 10% by volume, which is assumed to preclude the free diffusion of oxygen in the topsoil (Silvertown et al., 1999). High SEVa indicates wet conditions in the soil.

Figure 6.2 to 6.9 show interpolated microclimate surfaces for the relative elevation derived from a reference point which was outside or inside the plot, and for SEVa, SEVd and MWTD which are moisture indicators.

Figure 6.2 shows the maps of relative elevation, aeration stress, dryness stress and water table depths at the Bastiaanskloof plot. Figure 6.2(a) indicates the presence of a ~3^{o} slope decreasing southwards across the plot. The distribution of moisture varies across the elevation gradient as shown in Figure 6.2(b), Figure 6.2(c) and Figure 6.2(d). The pattern of moisture distribution correlates with the elevation slope where dry sites correspond with the upper slope end while the lower slope end is mostly wetter. The aeration stress threshold ranged between 0 and 1.6 m.wk while drought index ranged between 13.3 and 23.6 m.wk. The depth to the water table ranged between 0.5 and 0.9 m. Generally, when compared with all other plots in this study, this plot is considered drier than average.

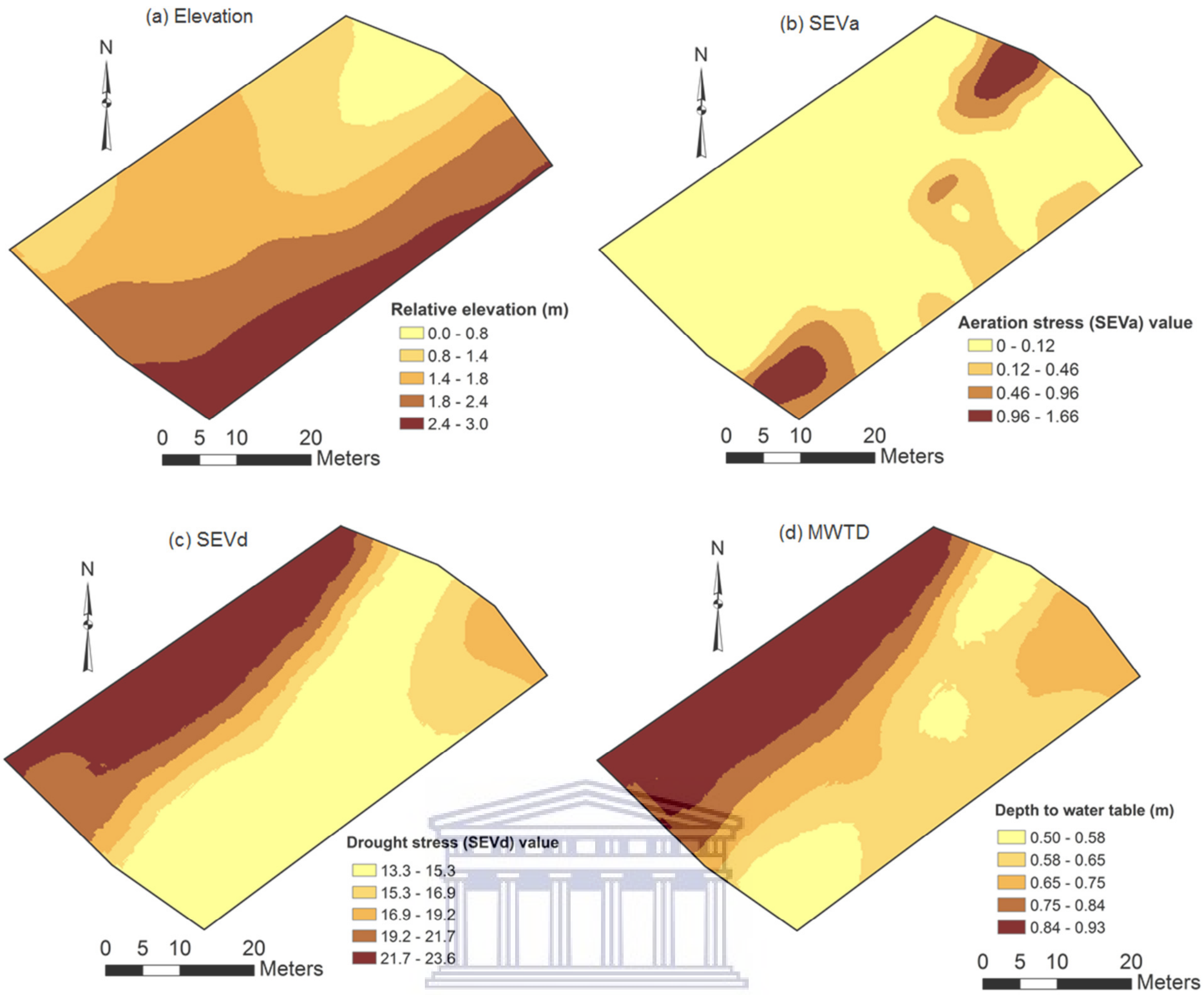


Figure 6.2. Continuous surfaces of four environmental variables measured at the Bastiaanskloof plot.

Figure 6.3 shows the maps of relative elevation, aeration stress, dryness stress and water table depths at Cape Point plot. Figure 6.3(a) shows a very gentle gradient (approx. 1.10°) across the length of the plot. The pattern of saturation in Figure 6.3(b) is random compared with the regular change patterns shown by both dryness indices in Figure 6.3(c) and the mean water table depth in Figure 6.3(d). The distribution of moisture in this plot is uneven but largely corresponds with the elevation gradient with each showing gradation across the length of the plot. There is a positive correlation between the MWTD and dryness stress both of which are inversely correlated with the aeration stress patterns. Comparatively, this plot could be considered as a dry site.

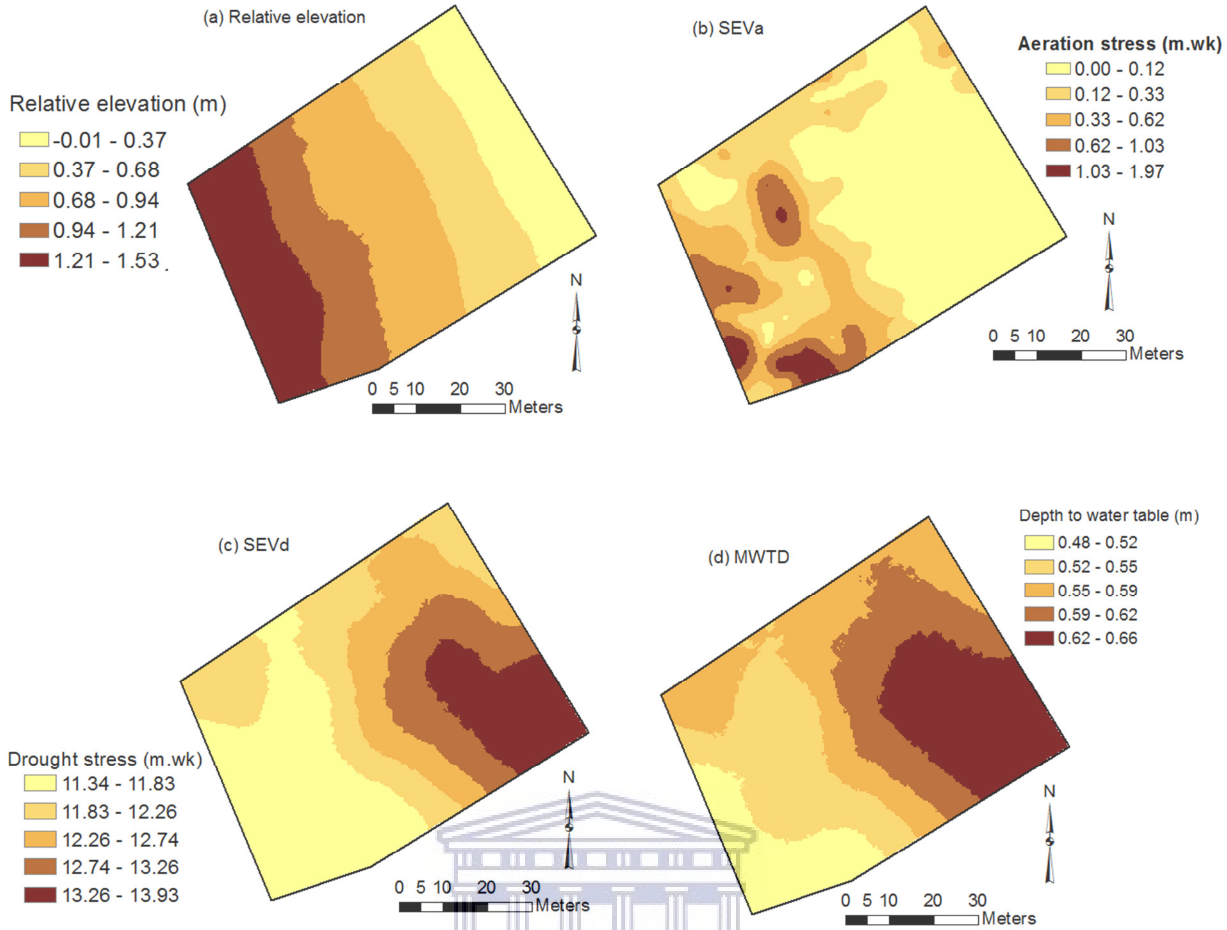


Figure 6.3. Continuous surfaces of four environmental variables measured at Cape Point plot.

In Figure 6.4, maps of relative elevation, aeration stress, dryness stress and water table depths of Jonkershoek plot are shown. At this plot, elevation was recorded relative to that of a reference point located outside the upper slope boundary of the plot. As such, all point measures appear negative as shown in Figure 6.4(a) with the darker colour shades representing the higher elevation in the plot. This is a 10° slope increasing eastwards (left-right) across the length of the plot. The distribution of moisture in Figure 6.4(b), Figure 6.4(c) and Figure 6.4(d) correlates with elevation gradient. The upper slopes of the plots are drier and wet sections of the plot are found at the lower slopes.

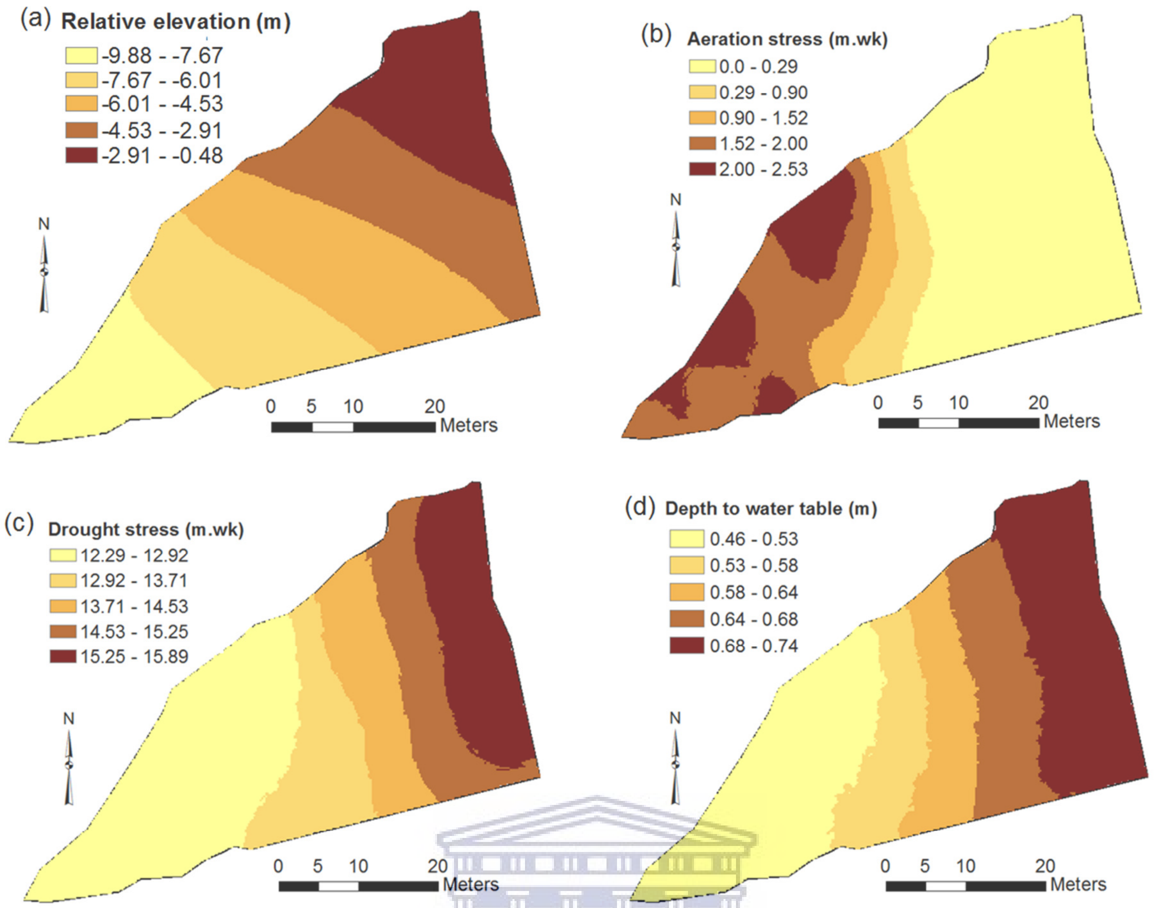


Figure 6.4. Continuous surfaces of four environmental variables measured at Jonkershoek plot.

Figure 6.5 shows the maps of relative elevation, aeration stress, dryness stress and water table depths at the Kogelberg plot. Some elevation points are measured at a height that is lower than the reference height which was within the plot, hence they read as negative. Darker shades indicate higher values in all maps. Figure 6.5(a) displays a continuous elevation gradient across the plot sloping from the left towards the right side. This plot is predominantly wet towards the centre. However, the distribution of moisture shown in Figure 6.5(b), Figure 6.5(c) and Figure 6.5(d) perfectly correlates with the elevation gradient in Figure 6.5(a). The upper slope face corresponds with the dryer of the moisture gradient and vice versa.

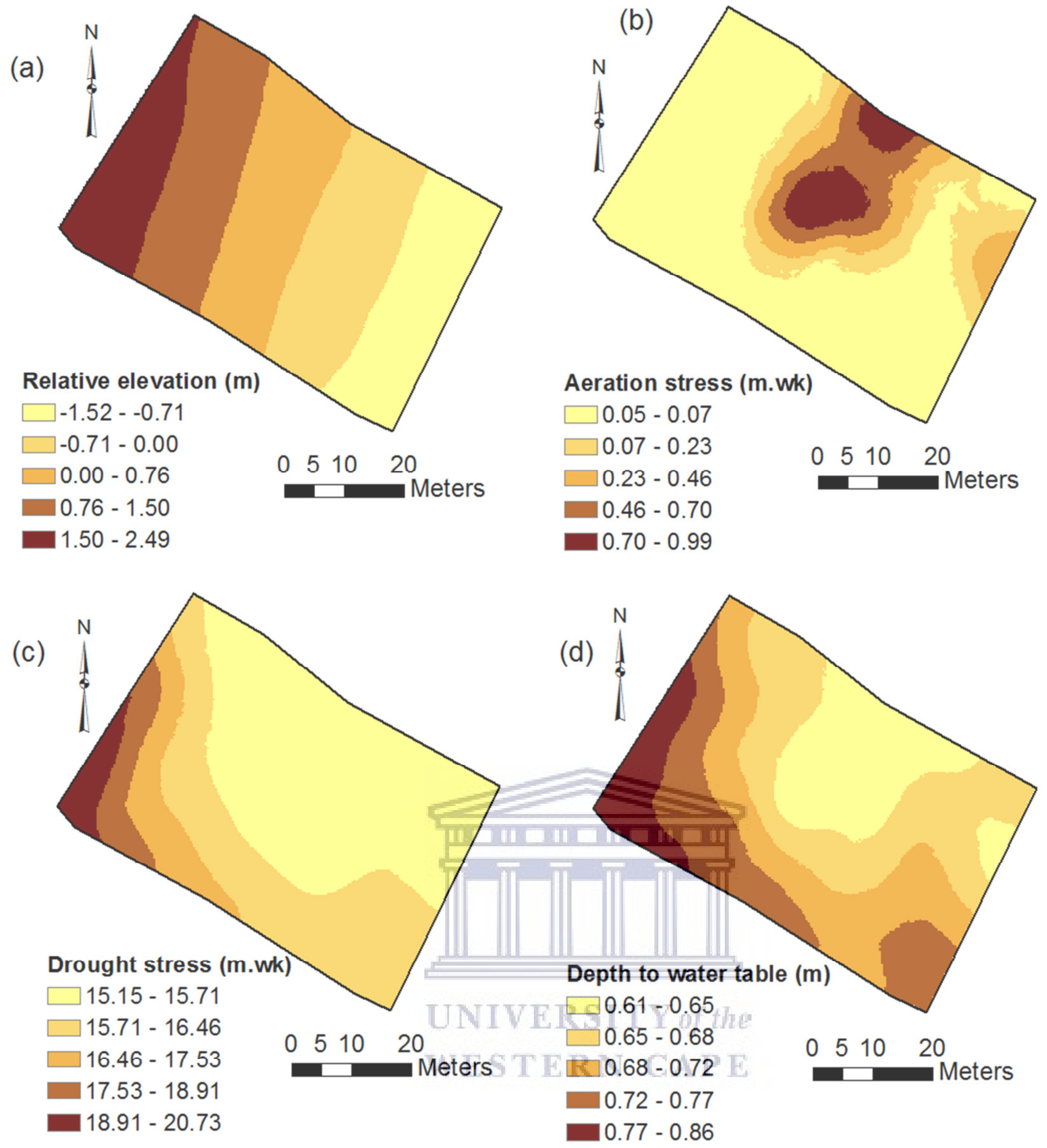


Figure 6.5 Continuous surfaces of (a) relative elevation, (b) aeration stress (SEVa), (c) dryness stress (SEVd) and (d) water table depth (MWTD) measured at Kogelberg plot.

Figure 6.6 shows the maps of relative elevation, soil saturation values, drying stress and water table variations at New Years Peak plot. Map Figure 6.6(a) shows elevation gradient and Figure 6.6(b), Figure 6.6(c), and Figure 6.6(d) show the change in moisture indicators across the plot. The distribution of moisture in Figure 6.6(b), Figure 6.6(c), and Figure 6.6(d), is uneven and correlates with the elevation gradient in Figure 6.6(a). The eastern border of this plot is a seasonal stream; hence this side of the plot remains moist even at higher elevation. Comparatively, this plot could be considered as a wet site.

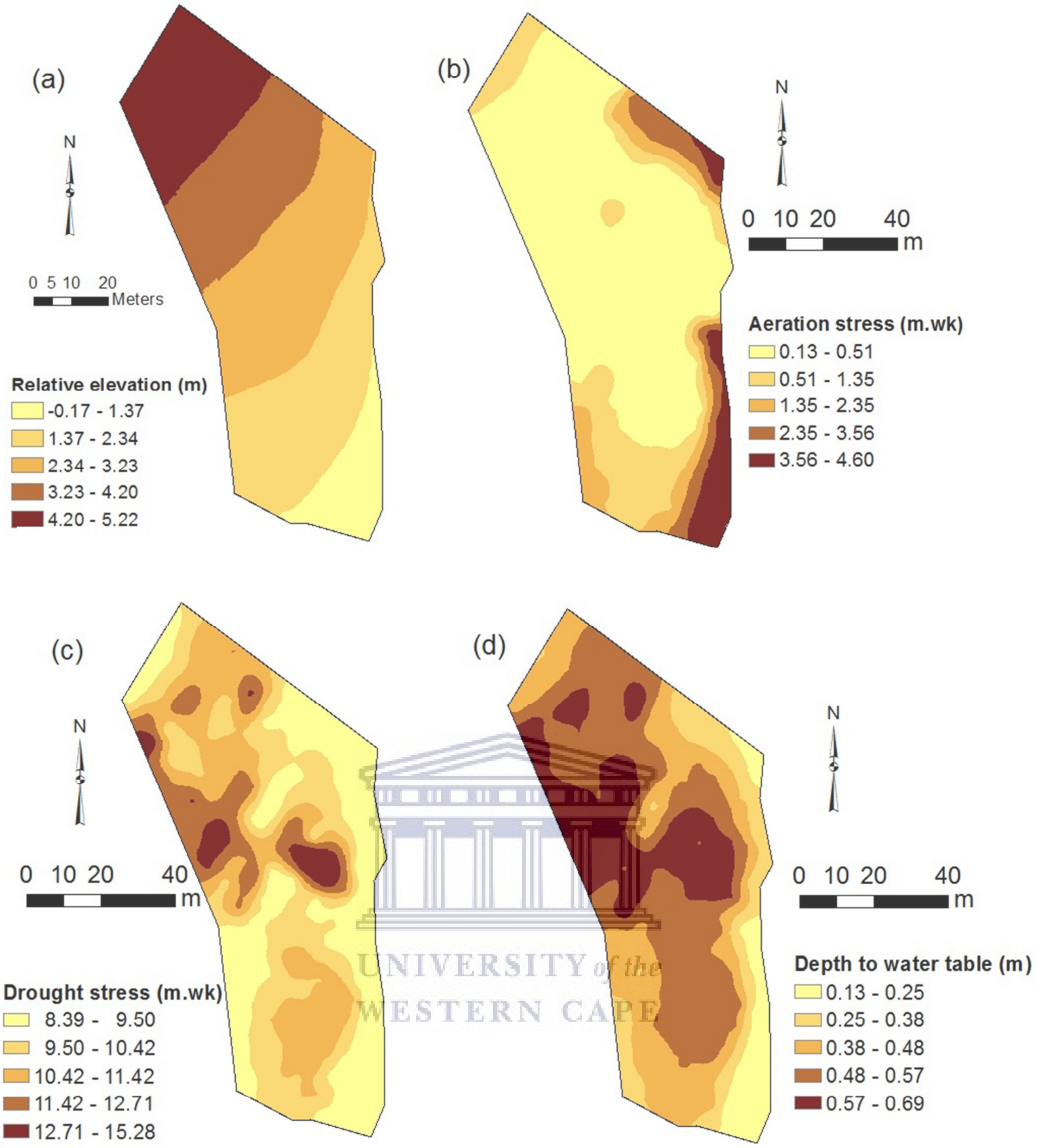


Figure 6.6 Continuous surfaces of (a) relative elevation, (b) aeration stress (SEVa), (c) dryness stress (SEVd) and (d) water table depth (MWTD) measured at New Years Peak plot.

Figure 6.7 shows continuous surfaces of elevation, aeration stress, dryness stress and water table depths at Riverlands plot. Figure 6.7(a) shows an elevation gradient of 1.46 degree sloping southwards across the plot. Similarly, there is a moisture gradient shown in Figure 6.7(b), Figure 6.7(c) and Figure 6.7(d) which correlates with the existing elevation gradient. Moisture levels reduce towards the lower ends of this gradient. The water table depth ranged between 0.6 and 0.9 m with an average of 0.75m which defines a relatively dry plot.

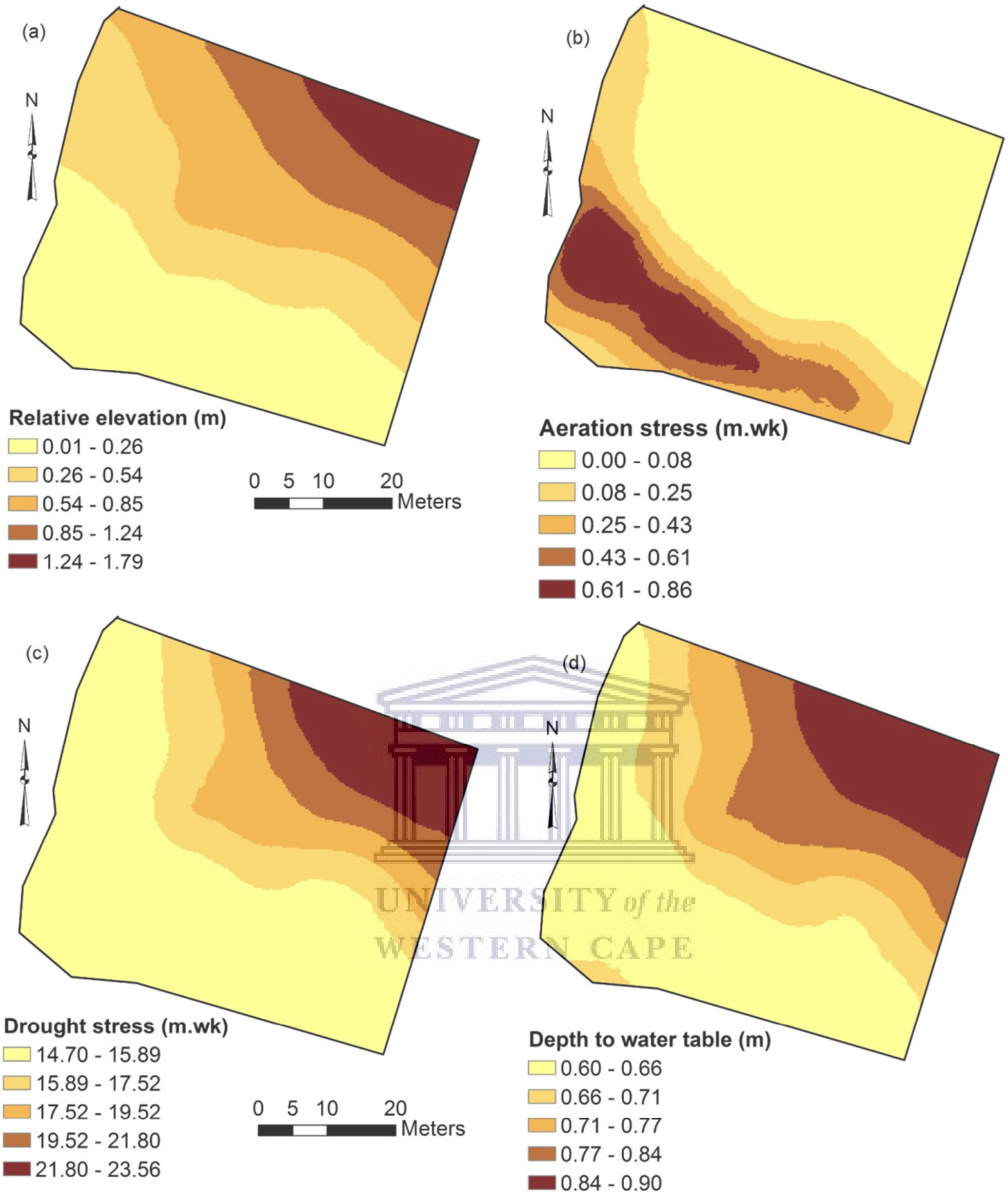


Figure 6.7. Continuous surfaces of (a) relative elevation, (b) aeration stress (SEVa), (c) dryness stress (SEVd) and (d) water table depth (MWTD) measured at Riverlands.

In Figure 6.8, the variation in relative elevation, MWTD, SEVa and SEVd in Silvermine plot are shown. There is a good spatial correlation between moisture gradients in Figure 6.8(b), Figure 6.8(c) and Figure 6.8(d) and the elevation in Figure 6.8(a) at Silvermine plot. There is a moisture (fracture zone) band that is parallel to the slope of the plot both sides of which are drier.

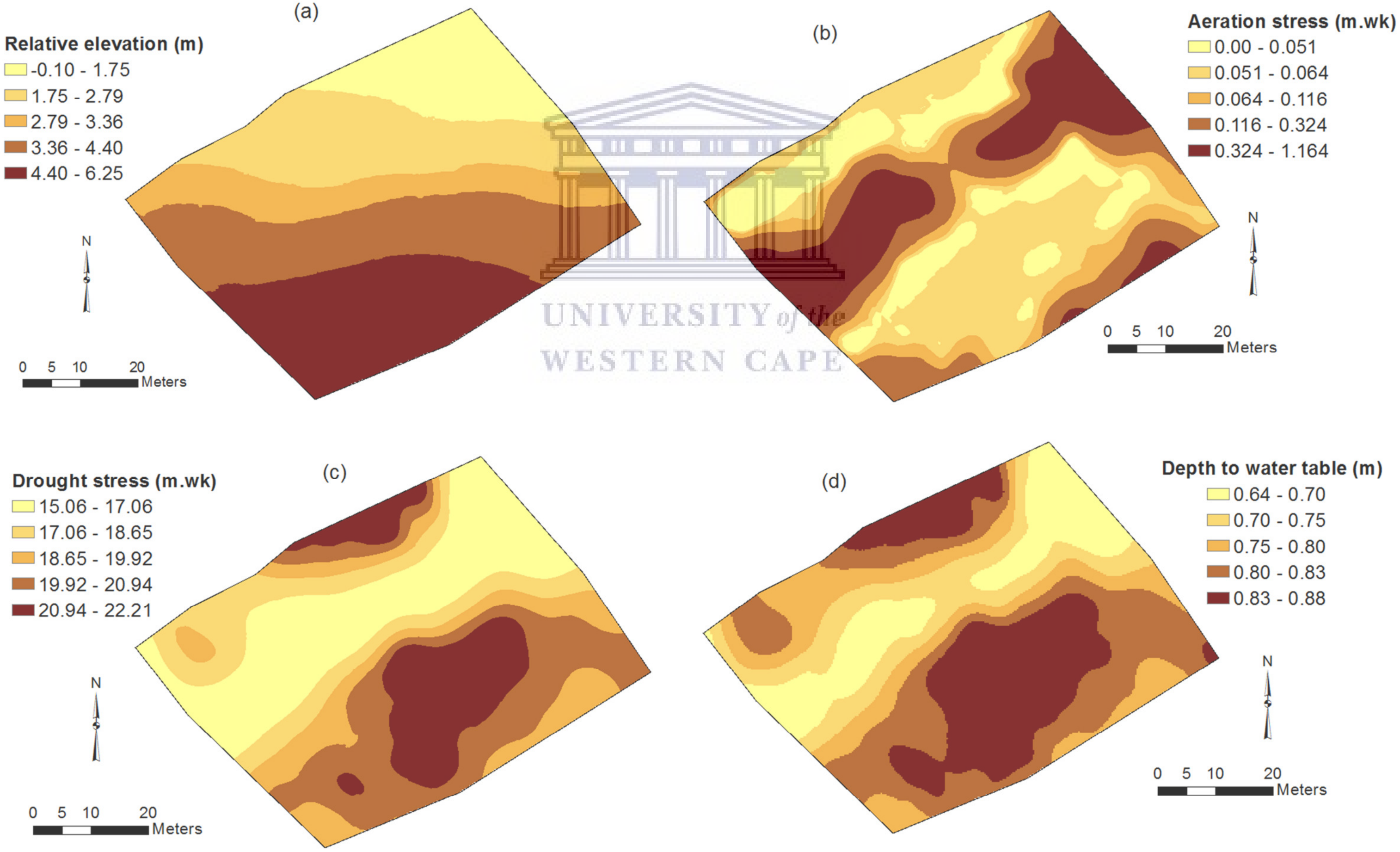


Figure 6.8. Continuous surfaces of (a) relative elevation, (b) aeration stress (SEVa), (c) dryness stress (SEVd) and (d) water table depth (MWTD) measured at Silvermine plot.

Figure 6.9 shows the maps of kriged continuous surfaces for relative elevation, aeration stress, dryness stress and water table depths measured at Theewaterskloof plot. Figure 6.9 (a) clearly shows an elevation gradient sloping northwards with a slope value of ~ degrees. The gradient decreased southwards. There is a strong correlation between the relief change and the moisture variable where it gets wetter at the lower slope ends and drier at the upper slopes. Aeration stress ranged between 0.15 and 2.82 m.wk (Figure 6.9(b)), dryness stress ranged from 10.69 – 15.75 m.wk (Figure 6.9(c)) and the depth to the water table was between 0.42 and 0.73 m (Figure 6.9 (c)).

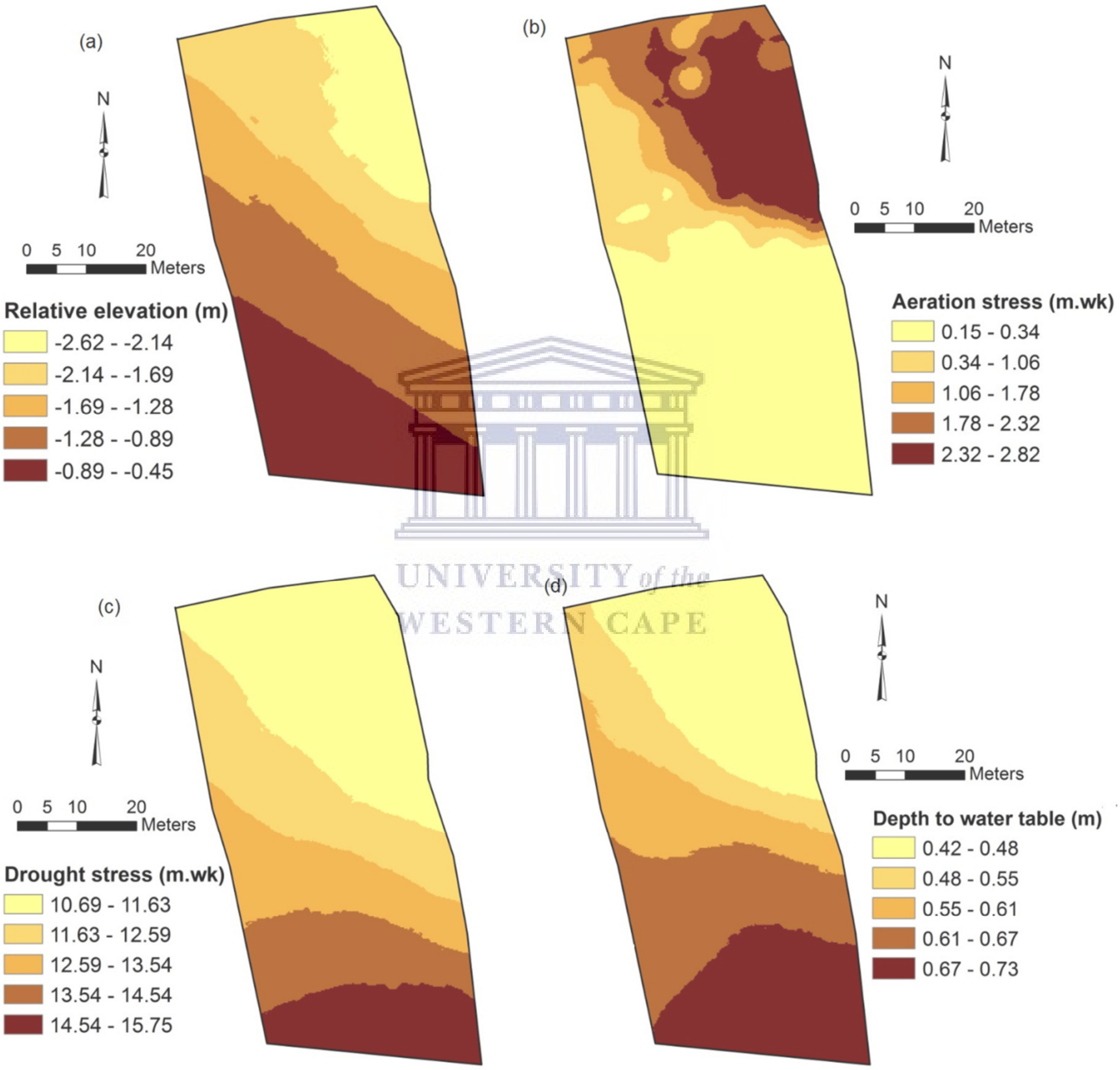


Figure 6.9. Variations in environmental surfaces of (a) relative elevation (b) saturation stress (c) dryness stress (d) depth to the water table at Theewaterskloof plot.

6.3.2 Species distribution mapping

Habitat distribution modelling was performed with 75% training and 25% testing presence records in sub-sampling runs that alternated four random test sample sets from occurrence points. Binary species models distinguished between suitable and unsuitable habitats based on 10 percentile training presence logistic threshold as the minimum probability of suitable habitats. The predictability or strength of each model is indicated on an area under the receiver curve (AUC) scale of 0 – 1 where AUC values below 0.6 define models from a random sampling, while AUC score of 0.6 to 1 prograde towards the perfect models.

In general, there are marked contrasts between the ranges of fundamental and realised niches of individual species. The fundamental niches which are the potential distribution are mostly larger in extent and occupy space beyond the observed (realised) species niches. There are extensive overlaps between the predicted fundamental niches of most species which indicate the likelihood of competition for space. Current distributions of species suggest segregation occurred probably as a consequence of competition or adaptation. The next subsections describe and discuss the predicted potential distribution models of the Restionaceae at all the sites under study.

6.3.2.1 Bastiaanskloof

Overall, the MaxEnt SDMs were successful at discriminating between suitable and unsuitable hydrological niches at the Bastiaanskloof site for all analysed Restionaceae species. Table 6.1 shows the prediction accuracy of species fundamental niche models and the importance of contributing environmental variables at Bastiaanskloof site. Test AUCs for *Elegia coleura*, *Restio capensis*, *Restio curviramis, Restio sporadicus*, *Staberoha distachyos*, *Thamnochortus sporadicus* and *Willdenowia sulcata*, revealed more than randomly predicted niche models for these species. Microclimatic variables contributed variably to configuring the models. MWTD contributed the most in defining suitability habitats for three species viz. *R. capensis* (46.49%), *R. curviramis* (64.78%) and *S. distachyos* (49.37%). SEVd contributed the most in modelling *E. coleura* (61.15%), *R. capensis* (46.48%), *T. sporadicus* (63.88%), *W. sulcata* (88.55%) habitat models (Table 6.1). Both MWTD and SEVd contributed equally in defining hydrological niche of *R. capensis*. The preferred hydrological range of each species with regards to its current occurrence is shown in Table 6.2. Most restioids thrive at a MWTD range of between 0.5 and 0.9 m. Similarly, dryness indices (SEVd), on-site show values of 14 m.wk and beyond which signify significantly dry conditions at this site.

Figure 6.10 shows the hydrological niches of restioids at the Bastiaanskloof plot modelled using four microclimatic variables. At this site, the current occurrence of most of the restioids has been restricted to within the predicted niche space which in general, occupies only a fraction of the modelled potential niche space. This could be attributed to a number of constraints. Furthermore, none of the species seems to be adaptable to conditions all over this plot. *E. coleura*, *R. curviramis* and *W. sulcata* seem to show dominance in their niche space amidst competition with other cohabiting species. *R. sporadicus* (Figure 6.10d) and *S. distachyos* (Figure 6.10e) as well as *T. sporadicus* (Figure 6.10f) and *W. sulcata* (Figure 6.10g) have a common hydrological niche and are competitors. Most competing species show resilience in their modelled niche space based on the current relative abundance in the shared niche space. *T. sporadicus* shows the least presence in its estimated hydrological niche space which indicates is adversely affected by environmental pressures.

Table 6.1 Prediction performance of species models (AUC) and importance of contributing environmental variables at the Bastiaanskloof site. Highest contributors are shown in bold font.

Species	Test AUC±SD	Percentage variable contribution			
		Elevation	SEVa	SEVd	MWTD
Elegia coleura	0.71 ± 0.05	11.39	23.86	**61.15**	3.59
Restio capensis	0.63 ± 0.15	4.17	2.84	**46.48**	**46.49**
Restio curviramis	0.79 ± 0.08	15.60	10.13	9.49	**64.78**
Restio sporadicus	0.77 ± 0.09	**47.02**	24.17	19.56	9.25
Staberoha distachyos	0.64 ± 0.05	5.37	36.30	8.96	**49.37**
Thamnochortus sporadicus	0.74 ± 0.06	2.03	8.09	**63.89**	25.98
Willdenowia sulcata	0.79 ± 0.01	1.52	0.71	**88.55**	9.21

SEVa = aeration stress SEVd = drought stress MWTD = mean water table depth

Table 6.2 The (current observed) preferred hydrological range of occurrence of species at Bastiaanskloof site. Range values in bold correspond with the most important environmental contributor.

Species	Elevation	SEVa	SEVd	MWTD
Elegia coleura	0.0 – 3.0	0.0 – 1.7	**14.1 – 21.9**	0.5 - 0.9
Restio capensis	0.3 – 2.5	0.0 - 1.3	**14.4 - 23.1**	**0.5 – 0.9**
Restio curviramis	0.3 – 2.5	0.0 - 1.3	14.3 - 23.4	**0.5 – 0.9**
Restio sporadicus	**0.0 – 3.0**	0.0 – 1.6	14.0 – 23.4	0.5 – 0.9
Staberoha distachyos	0.3 - 2.5	0.0 - 1.2	14.3 - 23.4	**0.5 – 0.9**
Thamnochortus sporadicus	0.7 - 2.3	0.0 - 0.0	**15.1 - 23.4**	0.6 – 0.9
Willdenowia sulcata	0.6 - 2.4	0.0 - 0.2	**15.4 - 23.4**	0.6 – 0.9

SEVa = aeration stress SEVd = drought stress MWTD = mean water table depth

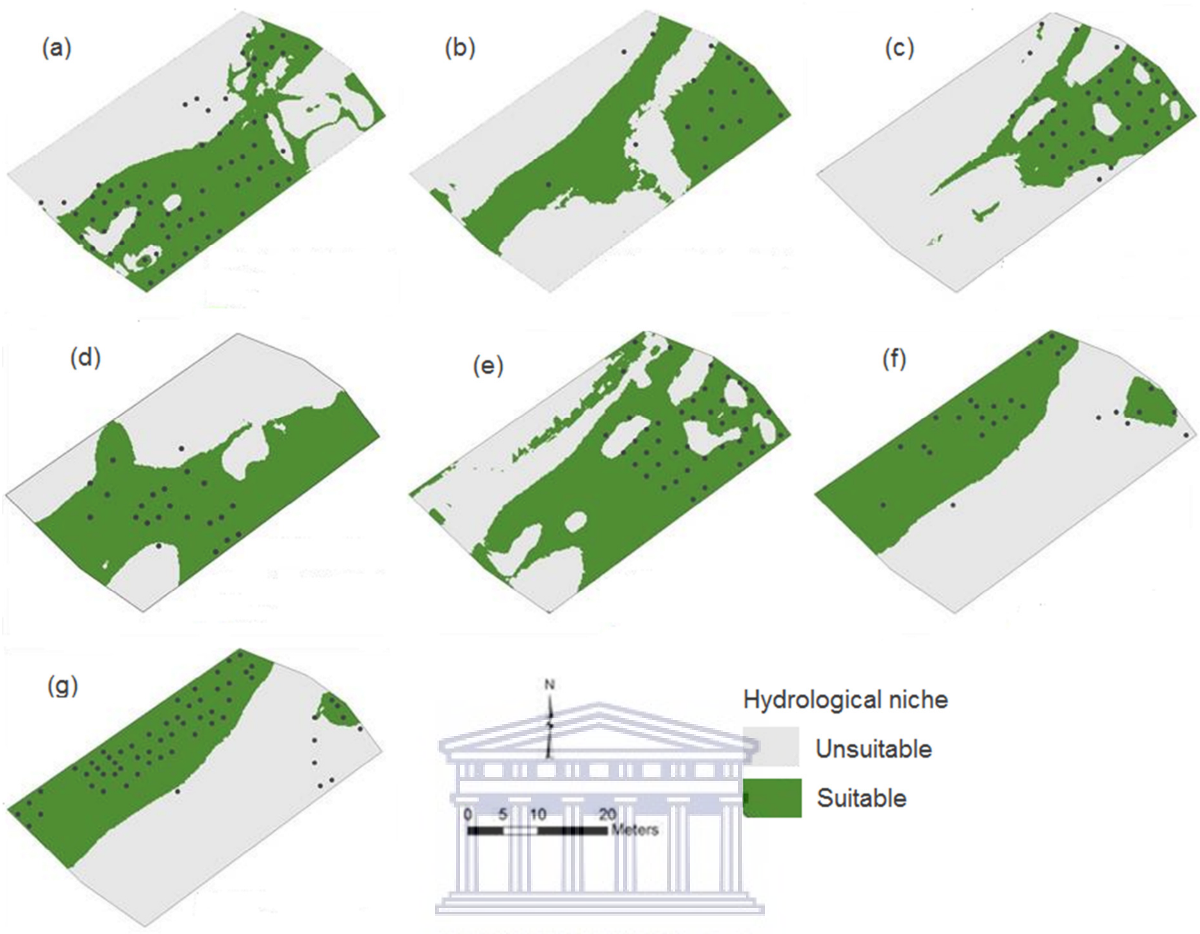


Figure 6.10. Hydrological niches of seven Restionaceae species at the Bastiaanskloof site: (a) *E. coleura*, (b) *R. capensis* (c) *R. curviramis,* (d) *R. sporadicus,* (e) *S. distachyos,* (f) *T. sporadicus,* (g) *W. sulcata*

6.3.2.2 Cape Point

On the whole, MaxEnt SDMs were successful at discriminating between suitable and unsuitable hydrological niches at the Cape Point site for 78% Restionaceae species analysed. Table 6.3 shows the prediction accuracy of Restionaceae species hydrological niches and importance of contributing environmental variables at Cape Point site. The AUC values in Table 6.3 indicate that MaxEnt models for *E. cuspidata*, *E. filacea*, *E. nuda*, *R. bifurcus*, *R. dodii*, *R. tenuissisimus* and *S. distachyos* yielded satisfactory results (i.e. more than random models with AUC≥0.6). Waterlogging (SEVa) thresholds contributed the most in modelling suitability habitats of most species in Table 6.3. The only exceptions are *E. cuspidata* and *R. dodii* which were best influenced by the variations in MWTD; and *E. nuda,* where drought stress (SEVd) made the most contribution to model gains of 88.04% average contribution. The preferred ranges of hydrological variables by species are shown in Table 6.4. Most species seem to thrive within a MWTD range between 0.5 and 0.7 m.

Figure 6.11 shows six predicted species habitats modelled based on four microclimatic variables. The current species presences are restricted within the modelled niches spaces. *Restio bifurcus* (Figure 6.11b), *Elegia cuspidata* (Figure 6.11d) and *Elegia filacea* (Figure 6.11f) are ubiquitous and probably the most resilient species as their spread across the plot area is not restricted by prevailing hydrological conditions. *Elegia nuda* (Figure 6.11e) seem to be the least adaptable species mostly restricted to a specialised zone. *R. dodii* (Figure 5.11a) and *E. cuspidata* (Figure 6.11d) seem to be competitors within the same hydrological niche space.

Table 6.3. Prediction performance of species models (AUC) and importance of contributing environmental variables at Cape Point. Highest contributors are shown in bold font.

Species	Test AUC±SD	Percentage variable contribution			
		Elevation	SEVa	SEVd	MWTD
Elegia cuspidata	0.69 ± 0.05	**37.90**	10.20	3.19	**48.70**
Elegia filacea	0.60 ± 0.04	19.40	**60.34**	11.81	8.45
Elegia nuda	0.86 ± 0.04	11.96	0	**88.04**	0
Hypodiscus aristatus	0.46 ± 1.00	0	**82.93**	17.07	0
Restio bifurcus	0.63 ± 0.04	13.22	**66.38**	12.19	8.20
Restio dodii	0.69 ± 0.08	**35.31**	11.35	5.32	**48.01**
Restio quinquefarius	0.58 ± 0.05	10.64	**66.94**	15.70	6.72
Restio tenuissimus	0.72 ± 0.06	26.74	**47.44**	9.34	16.48
Staberoha distachyos	0.64 ± 0.06	25.89	**65.08**	5.23	3.79

SEVa = aeration stress SEVd = drought stress MWTD = mean water table depth

Table 6.4. The preferred hydrological range of occurrence of species at Cape Point site. Bold values belong to the most important environmental contributor.

Species	Elevation	SEVa	SEVd	MWTD
Elegia cuspidata	**0.0 – 1.4**	0.0 - 2.0	11.4 - 13.5	**0.5 - 0.6**
Elegia filacea	0.0 – 1.5	**0.0 - 2.0**	11.4 - 13.9	0.5 - 0.7
Elegia nuda	1.0 – 1.4	0.1 - 0.8	**11.5 - 11.8**	0.5 - 0.6
Hypodiscus aristatus	0.2 – 1.5	**0.0 - 0.5**	11.4 - 13.8	0.5 - 0.7
Restio bifurcus	0.0 – 1.5	**0.0 - 2.0**	11.4 - 13.9	0.5 - 0.7
Restio dodii	**0.0 – 1.5**	0.0 - 1.2	11.4 - 13.0	**0.5 - 0.6**
Restio quinquefarius	0.0 – 1.5	**0.0 - 1.8**	11.4 - 13.9	0.5 - 0.7
Restio tenuissimus	0.1 – 1.5	**0.0 - 1.2**	11.4 - 13.9	0.5 - 0.7
Staberoha distachyos	0.1 – 1.5	**0.0 - 1.0**	11.4 - 13.9	0.5 - 0.7

SEVa = aeration stress SEVd = drought stress MWTD = mean water table depth

Figure 6.11 Hydrological niches of seven Restionaceae species at the Cape Point site: (a) *Restio dodii*, (b) *Restio bifurcus,* (c) *Restio tenuissimus,* (d) *Elegia cuspidata,* (e) *Elegia nuda* (f) *Elegia filacea.*

6.3.2.3 Jonkershoek

MaxEnt SDMs successfully discriminated between suitable and unsuitable hydrological niches for seven species at the Jonkershoek site. AUC values in Table 6.5 shows the modelled hydrological niches for *E. juncea*, *R. filiformis*, *E. asperiflora*, *H. aristatus*, *H. alboaristatus* and *S. cernua* yielded satisfactory AUC results which range from 0.60 to 0.82. The models were influenced differently by the available environmental variables. SEVd contributed the most in defining four species viz. *E. asperiflora (*83.5%*), H. alboaristatus (*99.99%*), H. aristatus (*79.31%*), S. cernua (*42.09%) followed by SEVa which contributed the most to define 3 species viz. *E. juncea (*78.18%*), R. filiformis (*79.79%*), S. cernua (*41.02%). Both SEVd and SEVa contributed equally in defining the hydroniche of *S. cernua*. MWTD contributed the highest in defining one species i.e. *R. triticeus* (62.02%). Meanwhile, the preferred hydrological ranges for these species with regards to their current occurrences at Jonkershoek site are shown in Table 6.6. These records show that most species currently occur within the 0.5 m to 0.7 m MWTD range. *E. asperiflora*, *H. alboaristatus*, *H. aristatus* and *S. cernua* thrive better under dry conditions as they occur in the drier end of the moisture spectrum based on their high SEVd values. *E. juncea*, *R. filiformis* and *S. cernua* tend to inhabit moistened soils based on their tolerance of relatively high SEVa at this site.

Figure 6.12 shows the hydrological niches of restioids at the Jonkershoek plot modelled using four microclimatic variables. At this site, most of the restioids show current occurrence within the predicted niche space. In general, most species occupy only a fraction of the expected niche space which could be the result of a number of constraints. *Restio triticeus* (Figure 6.12f) is the most adaptable species as it spread over most of its modelled niche space amidst competitions from cohabiting species. A similar trend in resilience is shown also by *Elegia juncea* (Figure 6.12b), *Elegia asperiflora* (Figure 6.12a) and *Staberoha cernua* (Figure 6.12g). *E. juncea* (Figure 6.12b), *H. alboaristatus* (Figure 6.12c), *H. aristatus* (Figure 6.12d) and *R. triticeus* (Figure 6.12f) have a common hydrological niche. Again, *R. triticeus* shows dominance as the best competitor followed by *E. juncea and S. cernua,* as these species have a better relative abundance in this common niche space. On the other hand, *H. alboaristatus* and *H. aristatus* seem to have been adversely affected by environmental pressures as these have sparsely populated their estimated hydrological niche space.

Table 6.5. MaxEnt model performance and percentage contribution of environmental variables at Jonkershoek site. Random models (AUC below 0.6) are excluded.

		Percentage variable contribution			
Species	Test AUC±SD	Elevation	SEVa	SEVd	MWTD
Elegia asperiflora	0.64 ± 0.09	13.35	2.42	**83.50**	0.72
Elegia juncea	0.74 ± 0.04	11.05	**78.18**	9.40	1.37
Hypodiscus alboaristatus	0.82 ± 0.08	0.00	0.00	**99.99**	0.00
Hypodiscus aristatus	0.69 ± 0.08	1.82	10.12	**79.31**	8.75
Restio filiformis	0.79 ± 0.05	15.70	**79.79**	0.39	4.11
Restio triticeus	0.60 ± 0.05	24.44	2.78	10.75	**62.03**
Staberoha cernua	0.79 ± 0.06	13.74	**41.02**	**42.09**	3.14

SEVa = aeration stress SEVd = drought stress MWTD = mean water table depth

Table 6.6. Preferred range of occurrence of species for each hydrological variable at Jonkershoek site

Species	Elevation	SEVa	SEVd	MWTD
Elegia asperiflora	-9.0 - -1.9	0.0 – 2.2	**12.5 - 15.7**	0.5 – 0.7
Elegia juncea	-9.8 - -0.9	**0.0 – 2.5**	12.3 – 15.8	0.5 – 0.7
Hypodiscus albo-aristatus	-9.1 – 3.6	0.1 – 2.4	**12.3 – 13.7**	0.5 – 0.6
Hypodiscus aristatus	-9.1 - -4.8	0.0 – 2.5	**12.3 – 14.3**	0.5 – 0.7
Restio filiformis	-9.3 - -0.9	**0.0 – 2.4**	12.3 – 15.7	0.5 – 0.7
Restio triticeus	-9.8 - -1.3	0.0 – 2.5	12.3 – 15.8	**0.5 – 0.7**
Staberoha cernua	-8.7 - -0.7	**0.0 – 2.5**	**12.3 – 15.7**	0.5 – 0.7

SEVa = aeration stress SEVd = drought stress MWTD = mean water table depth

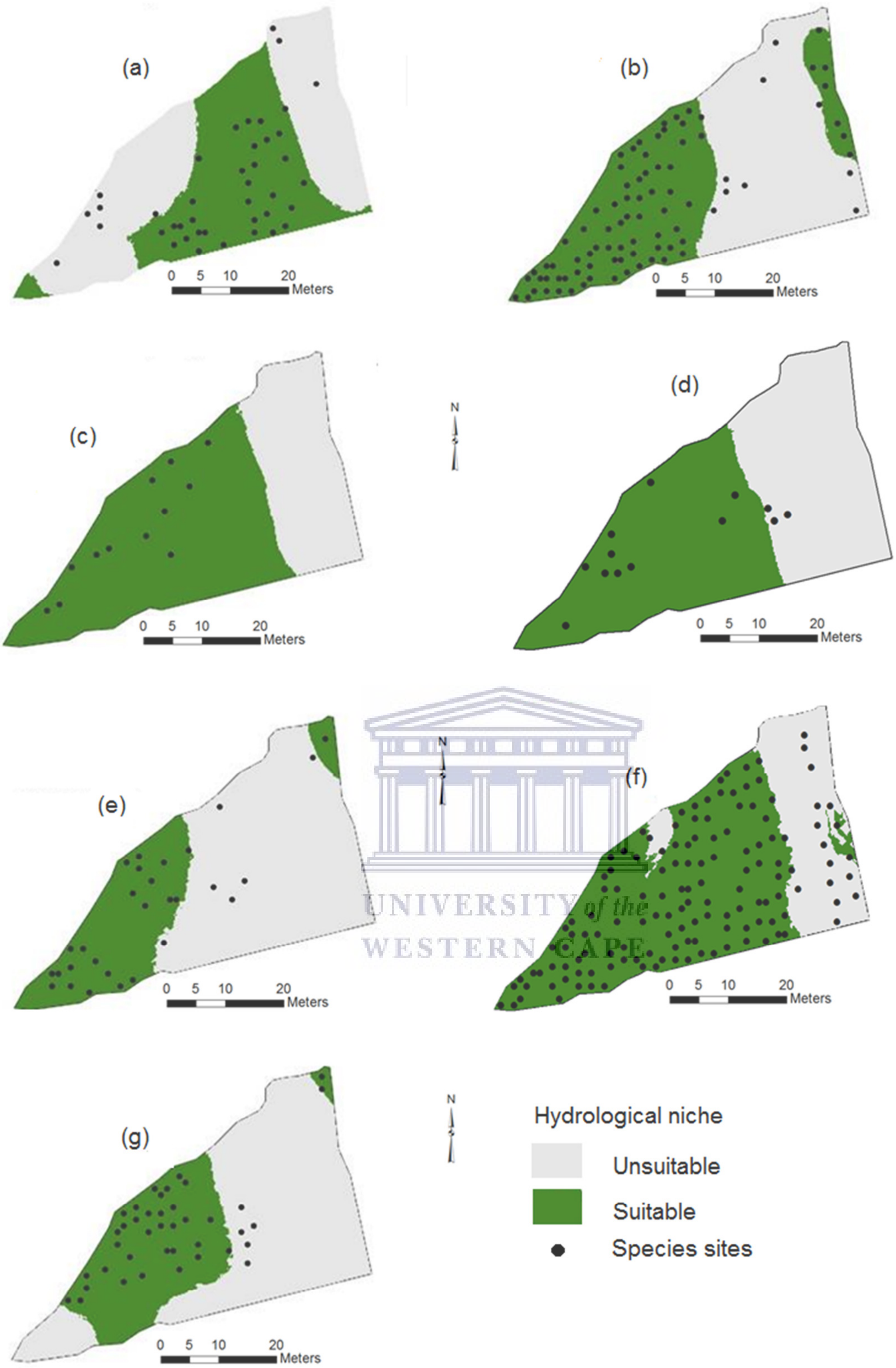


Figure 6.12 Hydrological niches of seven Restionaceae species at the Jonkershoek plot site: (a) *Elegia asperiflora*, (b) *Elegia juncea*, (c) *Hypodiscus alboaristatus*, (d) *Hypodiscus aristatus*, (e) *Restio filiformis*, (f) *Restio triticeus*, (g) *Staberoha cernua.*

6.3.2.4 Kogelberg site

Table 6.7 shows the results of model performance and the importance of hydrological variables in defining hydrological niches at Kogelberg site. AUC values for *Elegia caespitosa, Elegia cuspidata, Mastersiella digitata, Nevillea obtusissima, Restio bifidus, Restio dispar, Restio distichus, Restio hyalinus, Restio nudiflorus and Staberoha distachyos* revealed the hydrological niche models for these species are more than random models. Drought index (SEVd) contributed the most in defining nine out of the twelve modelled hydrological niches. Of the other three models, *E. hookeriana* and *R. dispar* are best influenced by waterlogging conditions (SEVa) (48.19% and 86.60%, respectively). Table 6.8 shows that the preferred MWTD for most restioids at this site ranged between 0.6 and 0.9 m. Similarly, the dryness thresholds were above 15 m.wk which indicates that these species thrive in drier conditions. Predicted distributions in Figure 6.13 show *Elegia caespitosa*, *Elegia cuspidate* and *Restio bifidus* as well as *R. hyalinus*, *R. nudiflorus*, *M. digitata* and *S. distachyos* as competitors in the same niche space. *R. distichus* is the most adaptable or resilient species at the site as it spreads significantly across most of the plot area. *E. caespitosa*, *E cuspidata* and *R. hyalinus* show dominance. *M. digitata* seems to be most affected by environmental conditions and have shifted its habitat and displaced *R. nudiflorus* and *S. distachyos* in the eventual competition.

Table 6.7. Percentage contribution of environmental variables, model performance and the habitat suitability thresholds for each species model.

Species	Test AUC	Percentage variable contribution			
		Elevation	SEVa	SEVd	MWTD
Elegia caespitosa	0.71 ± 0.03	8.28	1.47	**64.61**	25.64
Elegia cuspidata	0.71 ± 0.04	7.97	1.28	**85.99**	4.75
Elegia filacea	0.54 ± 0.05	**88.00**	6.33	1.52	4.16
Elegia hookeriana	0.42 ± 0.04	21.57	**48.19**	5.16	25.08
Mastersiella digitata	0.85 ± 0.04	24.99	1.46	**70.71**	2.84
Nevillea obtusissima	0.92 ± 0.01	0.00	17.13	**82.87**	0.00
Restio bifidus	0.72 ± 0.05	25.43	9.46	**59.91**	5.19
Restio dispar	0.67 ± 0.10	0.00	**86.60**	0.43	12.97
Restio distichus	0.58 ± 0.05	32.52	5.91	**57.71**	3.86
Restio hyalinus	0.79 ± 0.08	39.35	1.28	**58.07**	1.30
Restio nudiflorus	0.69 ± 0.06	34.38	6.18	**59.43**	0.01
Staberoha distachyos	0.73 ± 0.04	33.80	2.67	**60.77**	2.76

SEVa = aeration stress SEVd = drought stress MWTD = mean water table depth

Table 6.8. Preferred range of occurrence of species for each hydrological variable.

Species	Elevation	SEVa	SEVd	MWTD
Elegia caespitosa	-1.5 – 1.7	0.0 - 0.9	**15.1 - 16.4**	0.6 - 0.
Elegia cuspidata	-1.5 - 1.7	0.0 - 0.9	**15.2 - 16.4**	0.6 - 0.7
Elegia filacea	*	*	*	*
Elegia hookeriana	*	*	*	*
Mastersiella digitata	-1.3- 2.3	0.0 - 0.2	**15.6 - 20.2**	0.7 – 0.8
Nevillea obtusissima	*	*	*	*
Restio bifidus	-1.5 -1.8	0.0 - 0.9	**15.2 - 17.5**	0.6 – 0.8
Restio dispar	*	*	*	*
Restio distichus	*	*	*	*
Restio hyalinus	-1.2 – 1.8	0.0 - 0.9	**15.6 - 20.3**	0.6 - 0.8
Restio nudiflorus	-0.8 - 2.4	0.0 - 0.9	**15.2 - 20.5**	0.6 - 0.9
Staberoha distachyos	-1.0 - 2.1	0.0 - 0.9	**15.3 - 19.2**	0.6 - 0.8

SEVa = aeration stress SEVd = drought stress MWTD = mean water table depth

* = blanks indicate no values could be computed

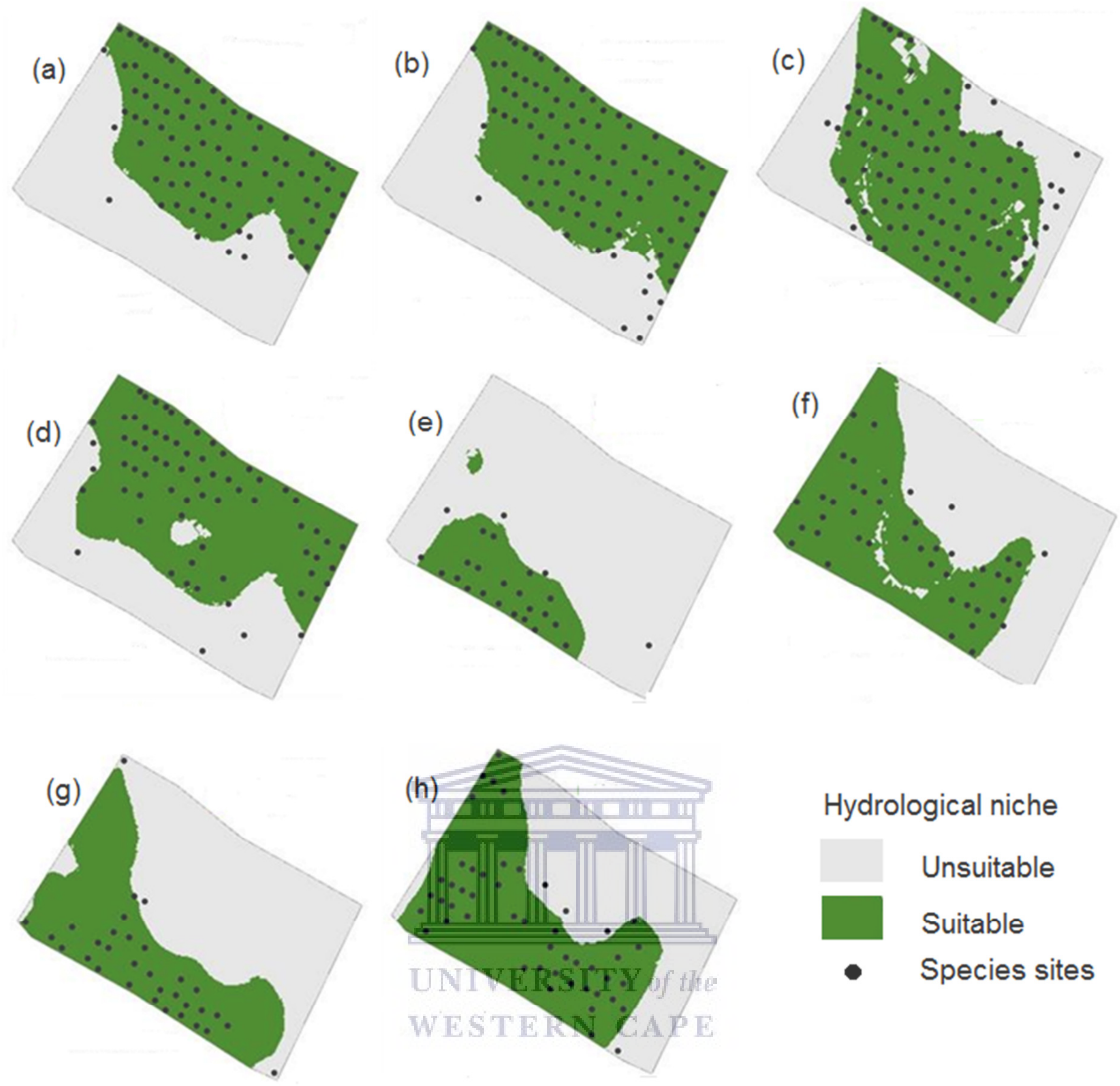


Figure 6.13 Hydrological niches of eight Restionaceae species at the Kogelberg plot site: (a) *E. caespitose,* (b) *E. cuspidate* (c) *R. distichus,* (d) *R. bifidus,* (e) *R. hyalinus,* (f) *R. nudiflorus* (g) *M. digitata* (h) *S. distachyos.*

6.3.2.5 New Years Peak (NYP) site

Table 6.9 shows the prediction accuracy of the hydrological niches and the importance of contributing environmental variables of 11 Restionaceae species at the NYP site. Model calibration (AUC) test values for *A. crinalis, E. coleura, E. filacea, E. neesii, R. curviramis, R. boluscii, R. miser, R. obscurus and S. cernua* yielded more than random (satisfactory) results with test AUC ranges from 0.61 to 0.98. Two species, *H. aristatus* and *R. pedicellatus,* may be depicted as random models as AUCs are below 0.6. Table 6.9 also reveals variability on the influence of hydrological variables to the nature of species niches. SEVd and MWTD contributed the most in modelling suitable hydrological niches for *E. coleura* (36.69% and 32.24%, respectively). MWTD contributed the most in defining niches for *R. micer* (52.89%). The majority of the species models (six species) were best influenced by SEVa. It shows that *A. crinalis*, *E. coleura* and *R. miser* are sensitive to drier conditions and the rest of the species present here responded more to wetter conditions. The preferred hydrological ranges for each species based on the current locations of species are shown in Table 6.10.

Figure 6.14 shows the hydrological niche of species as defined by a 10 percentile training ratio. The predicted distributions (fundamental niche) coincide quite significantly with the observed field records (realised niche) for all species although at some instances some individuals are located outside the estimated hydrological niche space. *Elegia neesii* (Figure 6.14a seems to be the most adaptable species as it thrives outside its expected hydrological niche space. *Restio macer* (Figure 6.14d) and *Anthochortus crinalis* (Figure 6.14i) are competitors sharing the same niche space. Meanwhile, *Hypodiscus aristatus* (Figure 6.14h) which shares the same hydrological niche as *Elegia filacea* (Figure 6.14b), *Restio curviramis* (Figure 6.14e) and *Restio boluscii* (Figure 6.14f), seems a poor competitor and thrives in exclusion (segregated).

Table 6.9. Percentage contribution of hydrological variables, model performance and the habitat thresholds for each species model at New Years Peak site.

Species	Test AUC ± SD	Percentage variable contribution			
		Elevation	SEVa	SEVd	MWTD
Anthochortus crinalis	0.79 ± 0.05	19.99	21.29	**48.53**	10.19
Elegia coleura	0.68 ± 0.08	24.97	6.10	**36.69**	**32.24**
Elegia filacea	0.78 ± 0.05	**46.59**	31.29	8.57	13.55
Elegia neesii	0.72 ± 0.04	20.49	**40.63**	18.33	20.54
Hypodiscus aristatus	0.58 ± 0.01	21.04	**77.87**	0.00	1.09
Restio bolusii	0.67 ± 0.05	**51.24**	21.69	1.95	25.11
Restio curviramis	0.77 ± 0.05	**44.57**	**45.51**	8.97	0.95
Restio miser	0.92 ± 0.02	30.31	11.04	5.76	**52.89**
Restio obscurus	0.61 ± 0.01	3.71	**60.39**	0.00	35.89
Restio pedicellatus	0.54 ± 0.12	12.78	**62.93**	7.59	16.71
Staberoha cernua	0.75 ± 0.03	29.19	**68.69**	0.00	2.11

SEVa = aeration stress SEVd = drought stress MWTD = mean water table depth

Table 6.10. Preferred range of occurrence of species for each hydrological variable at New Years Peak site.

Species	Elevation	SEVa	SEVd	MWTD
Anthochortus crinalis	0.1 – 4.6	0.0 - 4.5	**8.5 - 14.9**	0.1 - 0.7
Elegia coleura	1.0 - 4.6	0.0 - 4.3	**8.5 - 13.1**	**0.2-0.6**
Elegia filacea	**1.8 - 5.2**	0.0 - 1.9	9.1 - 13.9	0.3 - 0.7
Elegia neesii	1.3 - 5.1	**0.0 - 3.0**	8.9 - 15.3	0.3 - 0.7
Hypodiscus aristatus	3.1 - 4.7	**0.0 - 0.4**	9.0 - 12.8	0.4 - 0.7
Restio bolusii	**1.9 - 4.9**	0.0 - 4.2	8.6 - 13.9	0.2 - 0.7
Restio curviramis	**1.6 - 5.1**	**0.0 - 1.7**	9.0 - 13.4	0.4 - 0.7
Restio miser	0.1 - 2.6	0.0 - 4.5	8.5 - 13.1	**0.1 - 0.6**
Restio obscurus	2.7 - 4.8	**0.0 - 0.4**	9.3 - 13.4	0.5 - 0 7
Restio pedicellatus	1.4 - 4.9	**0.0 - 2.5**	8.5 - 12.7	0.3 - 0.7
Staberoha cernua	3.3 - 4.4	**0.0 - 0.3**	9.2 - 12.3	0.5 - 0.7

SEVa = aeration stress   SEVd = drought stress   MWTD = mean water table depth

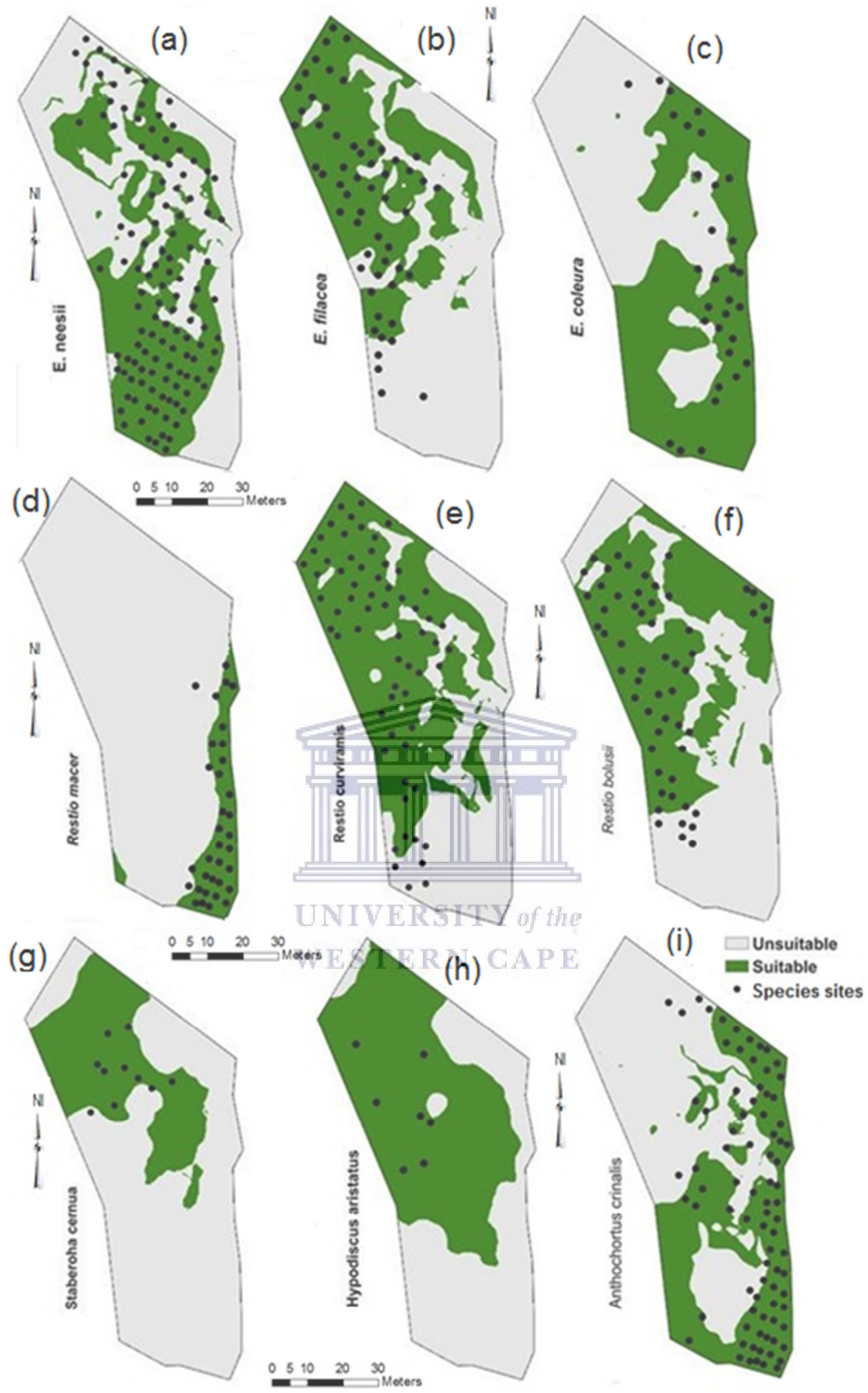


Figure 6.14. Species niches at the New Years Peak site (a) *E. neesii,* (b) *E. filacea,* (c) *E. coleura,* (d) *R. macer,* (e) *R. curviramis,* (f) *R. boluscii,* (g) *S. cernua*, (h) *H. aristatus*, (i) *A. crinalis*.

6.3.2.6 Riverlands

Overall, the MaxEnt SDMs were successful at discriminating between suitable and unsuitable hydrological niches at the Riverlands site for 12 out of 14 Restionaceae species. AUC values in Table 6.11 show SDMs for *S. distachyos, E. filacea, H. willdenowia, E. nuda, R. capensis, R. monanthos, T. punctatus, W. arescens, R. quinquefarius* and *R. vimineus* yielded better than random results with average test AUC values ranging from 0.60 to 0.98.*C. parviflora* and *R. sporadicus* models were considered random based on their Test AUC values and were not discussed any further. Table 6.11 also reveals that restioids in Riverlands responded differently to hydrological conditions. It shows that *E. filacea*, *E. nuda*, *R. macer*, *R. monanthos*, *R. vimineus* and *T. punctatus* were sensitive to water table depth changes (MWTD). Likewise, *R. capensis*, *S. distachyos*, *W. arescens* and *W. sulcata* were strongly influenced by SEVd. Finally, the distribution of *R. quinquefarius* is mainly influenced by SEVa. Table 6.12 shows the hydrological profiles (i.e., the range of preference of the different hydrological variables) for all species at the Riverlands site. Figure 6.15 depicts the hydrological niches of restioids in Riverlands modelled using MWTD, elevation, SEVd and SEVa values.

T. punctatus and *W. arescens* share the same realised niche space and seem to cohabit successfully based on current distributions of both species with this modelled space. Likewise, *R. capensis* (Figure 6.15a) is not a good competitor in the presence of *E. nuda* (Figure 6.15e) and *S. distachyos* (Figure 6.15k) which in turn tolerate each other and cohabit successfully.

Table 6.11. Percentage contribution of environmental variables, model performance and the habitat suitability thresholds for each species model at Riverlands site.

Species	Test AUC ± SD	Percentage variable contribution			
		Elevation	SEVa	SEVd	MWTD
Cannomois parviflora	0.39 ± 0	4.34	**45.66**	0	0
Elegia filacea	0.74± 0.04	4.91	3.41	3.47	**88.21**
Elegia nuda	0.75 ± 0.05	5.32	25.71	4.36	**64.61**
Hypodiscus willdenowia	0.83 ± 0.04	3.70	23.85	**39.72**	**32.72**
Restio capensis	0.65 ± 0.09	18.21	6.50	**52.92**	22.37
Restio macer	0.60 ± 0.08	10.32	5.47	13.87	**70.34**
Restio monanthos	0.84 ± 0.03	**55.34**	2.63	**40.04**	1.99
Restio quinquefarius	0.98 ± 0	29.79	**51.18**	0.99	18.04
Restio sporadicus	0.48 ± 0	0	0	**100**	0
Restio vimineus	0.78 ± 0.05	8.97	0.18	**39.33**	**51.52**
Staberoha distachyos	0.75 ± 0.03	5.68	12.94	**72.72**	8.66
Thamnochortus punctatus	0.80 ± 0.02	1.13	2.55	37.20	**59.11**
Willdenowia arescens	0.84 ± 0.03	4.09	4.16	**88.43**	3.32
Willdenowia sulcata	0.91 ± 0.03	2.42	6.17	**82.73**	8.68

SEVa = aeration stress SEVd = drought stress MWTD = mean water table depth

Table 6.12. Preferred range of occurrence of species for each hydrological variable at Riverlands site.

Species	Elevation	SEVa	SEVd	MWTD
Cannomois parviflora	0.9 - 1.3	**0.0 - 0.3**	14.9 - 23.1	0.6 - 0.9
Elegia filacea	0.0 - 0.7	0.0 - 0.9	14.7 - 17.8	**0.6 - 0.8**
Elegia nuda	0.0 - 0.7	0.0 - 0.9	14.7 - 17.8	**0.6 - 0.8**
Hypodiscus willdenowia	0.2 - 0.9	0.0 - 0.2	**15.3 - 19.2**	**0.7 - 0.8**
Restio capensis	0.1 - 1.3	0.0 - 0.7	**14.9 - 22.9**	0.6 - 0.9
Restio macer	0.0 - 1.0	0.0 - 0.6	15.0 - 20.8	**0.6 - 0.8**
Restio monanthos	**0.6 - 1.7**	0.0 - 0.0	**16.1 - 23.4**	0.7 - 0.9
Restio sporadicus	0.1 - 0.9	0.0 - 0.5	**15.0 - 18.6**	0.6 - 0.8
Restio vimineus	0.1 - 0.8	0.0 - 0.8	**14.8 - 19.1**	**0.6 - 0.8**
Staberoha distachyos	0.2 - 1.6	0.0 - 0.5	**15.1 - 23.4**	0.6 - 0.9
Thamnochortus punctatus	0.4 - 1.7	0.0 - 0.1	15.9 - 23.4	**0.7 - 0.9**
Willdenowia arescens	0.3 - 1.6	0.0 - 0.2	**15.4 - 23.4**	0.7 - 0.9
Willdenowia sulcata	0.8 - 1.7	0.0 - 0.0	**18.6 - 23.4**	0.8 - 0.9

SEVa = aeration stress SEVd = drought stress MWTD = mean water table depth

Figure 6.15. Hydrological niches of Restionaceae species at the Riverlands site: (a) *Restio capensis*, (b) *Restio monanthos*, (c) *Restio quinquefarius*, (d) *Restio vimineus*, (e) *Elegia nuda*, (f) *Elegia filacea*, (g) *Hypodiscus willdenowia*, (h) *Thamnochortus punctatus*, (i) *Willdenowia arescens*, (j) *Wiildenowia sulcata*, (k) *Staberoha distachyos*.

6.3.2.7 Silvermine

Table 6.13 shows the model performance (Test AUCs) for *Elegia filacea*, *Hypodiscus aristatus*, *Restio capensis*, *Restio cincinnatus* and *Staberoha cernua* were better than random with AUC value ranging between 0.62 and 0.77 at the Silvermine site. The percentage contribution of environmental variables to predicting species potential distributions varied. Elevation was the most influential in discriminating *H. aristatus* and *R. capensis* showing 42.1% and 56.0% contributions, respectively. The wetness index (SEVa) contributed the most in discriminating *R. cincinnatus* (78.3%) and the dryness index (SEVd) was most influential in modelling both *E. filacea* (65.8%) and *S. cernua* (57.7%). The preferred hydrological range of each species model is shown in Table 6.14.

Figure 6.16 shows the hydrological niches of the Restionaceae species. The observed species occurrences in the field are restricted within the predicted hydrological niches space. However, most species occupy a fraction of the predicted niche possibly as a response to external constraints. The most adaptable species is *R. cincinnatus* (Figure 6.16d) as it is the most widespread species without any restriction by environmental conditions. *E. filacea* and *S. cernua* seem to cohabit successfully as both plants share the same fundamental niche space. Meanwhile, *H. aristatus* (Figure 6.16b) seems to segregate within its fundamental niche space possibly due to biotic influences.

Table 6.13. Percentage contribution of environmental variables, model performance and the habitat suitability thresholds for each species model at the Silvermine site

Species	Test AUC±SD	Variable percentage contribution to models			
		Elevation	SEVa	SEVd	MWTD
Elegia filacea	0.72 ± 0.09	20.01	8.62	**65.79**	5.58
Hypodiscus aristatus	0.77 ± 0.05	**42.05**	**32.03**	20.79	5.12
Restio capensis	0.65 ± 0.08	**56.03**	3.13	10.41	**30.43**
Restio cincinnatus	0.62 ± 0.04	6.76	**78.31**	2.03	12.90
Staberoha cernua	0.65 ± 0.19	15.05	3.52	**57.73**	23.69

SEVa = aeration stress SEVd = drought stress MWTD = mean water table depth

Table 6.14. The preferred hydrological range of occurrence of species at the Silvermine site

Species	Elevation	SEVa	SEVd	MWTD
Elegia filacea	1.0 – 5.1	0.0 - 1.1	**15.2 - 22.2**	0.7 – 0.9
Hypodiscus aristatus	**1.1 – 5.4**	**0.0 - 0.6**	15.9 - 21.7	0.7 – 0.9
Restio capensis	**0.9 - 6.0**	0.0 - 0.5	15.8 - 21.8	**0.7 – 0.9**
Restio cincinnatus	0.0 - 6.2	**0.0 - 1.0**	15.1 - 22.2	0.7 – 0.9
Staberoha cernua	1.7 - 5.9	0.0 - 0.9	**15.5 - 21.7**	0.7 – 0.9

SEVa = aeration stress SEVd = drought stress MWTD = mean water table depth

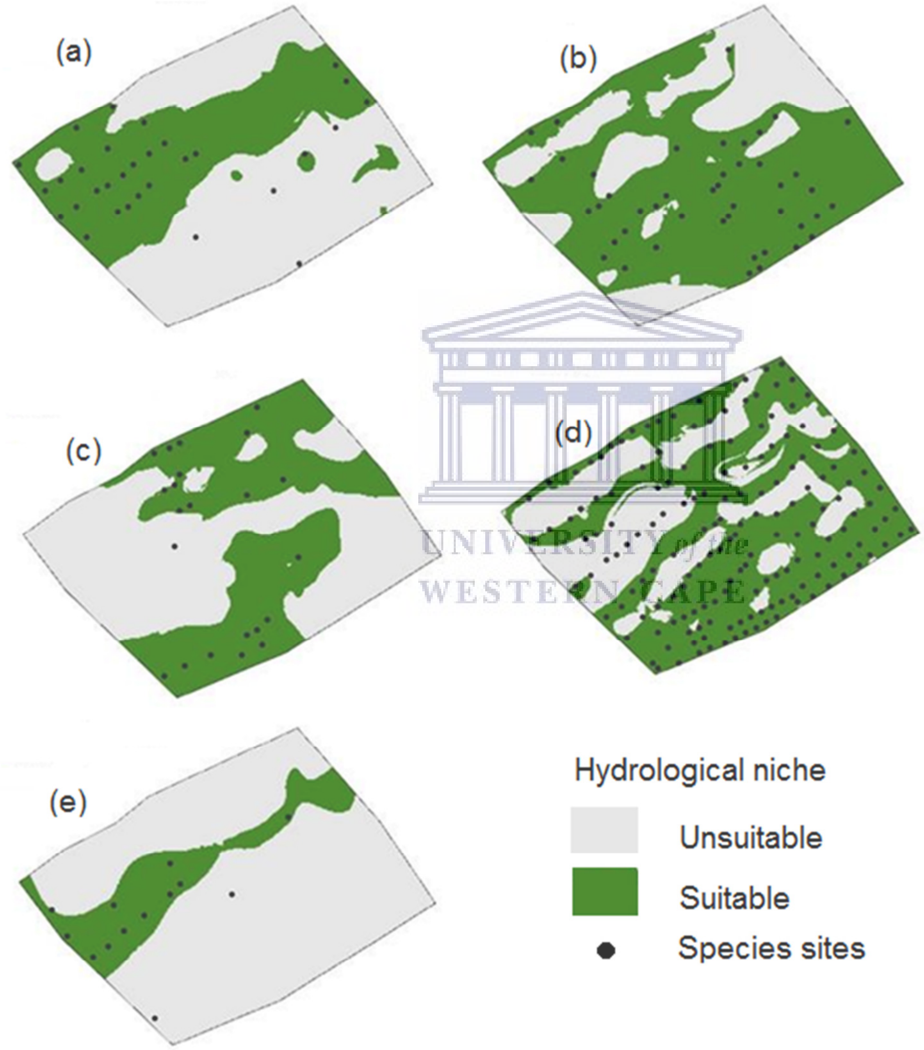


Figure 6.16. Hydrological niches of five Restionaceae species at the Silvermine plot site: (a) *Elegia filacea*, (b) *Hypodiscus aristatus*, (c) *Restio capensis*, (d) *Restio cincinnnatus*, (e) *Staberoha cernua*.

6.3.2.8 Theewaterskloof

Table 6.15 indicates that MaxEnt species model outputs at Theewaterskloof provided highly accurate and satisfactory results (AUCs ranged between 0.60 and 0.95) based on the given set of training and test data but for *R. curviramis* with AUC below 0.6. The percentage contribution of hydrological variables to species distribution is shown in Table 6.15. MWTD contributed the most in defining *S. distachyos* (59.99%). SEVd contributed the most in defining hydrological models for *E. neesii* (40.0%), *R. curviramis* (62.21%) and *S. cernua* (62.63%). Finally, waterlogging conditions seem to influence the distribution of 6 out of 11 species present here. SEVa influenced the modelling of the majority of models viz. *A. crinalis* (77.21%), *E. capensis* (91.49%), *E. thyrsifera* (82.71%), *Platycaulos callistachyus* (57.12%), *R. pedicellatus* (76.67%) and *T. fruticosus* (96.06%).

Table 6.16 shows the preferred ranges of individual species for each hydrological variable based on current distributions. Figure 6.17 shows the hydrological niches of restioids at Theewaterskloof plot modelled using hydrological variables. Most species show current occurrence within the predicted fundamental niche space. In general, most species occupy only a fraction of the expected niche space which could be the result of a number of constraints. *E. neesii* (Figure 6.17c) is the most adaptable species as it spreads over most of its modelled niche space amidst competitions from cohabiting species. *A. crinalis* (Figure 6.17a), *E. asperiflora* (Figure 6.17b), *E. thyrsifera* (Figure 6.17d) and *R. pedicellatus* (Figure 6.17f) have a common hydrological niche. However, *A. crinalis* is the best competitor followed by *E. thyrsifera* as these two species have a better relative abundance in this common niche space. *S. cernua* has adapted to unfavourable environmental conditions and where it flourishes probably due to the absence of stiff competition. Meanwhile, *S. distachyos* seems to be the only species occupying a specialised niche where there are relatively few competitors in its supposed niche space.

Table 6.15. Percentage contribution of environmental variables, model performance and the habitat suitability thresholds for each species model at Theewaterskloof site

Species	Test AUC±SD	Percentage contribution of variables			
		Elevation	SEVa	SEVd	MWTD
Anthochortus crinalis	0.92 ± 0.03	0.16	**77.21**	14.16	8.47
Elegia asperiflora	0.95 ±-1	**99.57**	0.43	0	0
Elegia capensis	0.82 ±-1	4.24	**91.49**	1.62	2.64
Elegia neesii	0.65 ± 0.05	**38.13**	18.94	**40.00**	2.93
Elegia thyrsifera	0.94 ± 0.03	0.84	**82.71**	11.49	4.96
Platycaulos callistachyus	0.87 ± 0.04	14.64	**57.12**	22.14	6.09
Restio curviramis	0.54 ± 0.04	12.73	11.36	**62.21**	13.69
Restio pedicellatus	0.86 ± -1	23.33	**76.67**	0	0
Staberoha cernua	0.74 ± 0.03	9.81	4.56	**62.63**	23.01
Staberoha distachyos	0.79 ± 0.08	12.87	14.27	12.87	**59.99**
Thamnochortus fruticosus	0.60 ± 0.12	0	**93.06**	6.945	0

SEVa = aeration stress SEVd = drought stress MWTD = mean water table depth

Table 6.16. Preferred range of occurrence of species for each hydrological variable at Theewaterskloof site

Species	Elevation	SEVa	SEVd	MWTD
Anthochortus crinalis	-2.6 - -1.9	**1.8 – 2.8**	10.7 – 11.3	0.4 - 0.5
Elegia asperiflora	**-2.6 - -2.1**	1.2 - 2.6	11.0 - 11.3	0.4 - 0.5
Elegia capensis	-2.1 - -1.6	**1.7 – 2.6**	11.0 – 11.6	0.4 – 0.5
Elegia neesii	**-2.6 - -0.6**	0.0 - 2.6	**10.9 - 15.4**	0.4 - 0.7
Elegia thyrsifera	-2.6 - -1.8	**1.6 - 2.8**	10.7 - 11.4	0.4 - 0.5
Platycaulos callistachyus	-2.4 - -1.6	**0.4 – 2.7**	10.9 - 11.6	0.4 - 0.5
Restio curviramis	-2.6 - -0.5	0.0 - 2.6	**11.0 - 15.6**	0.4 - 0.7
Restio pedicellatus	-2.6 - -2.0	**2.0 - 2.7**	10.9 - 11.3	0.4 - 0.5
Staberoha cernua	-2.6 - -0.5	0.0 - 2.1	**11.2 - 15.6**	0.5 - 0.7
Staberoha distachyos	-2.6 - -0.9	0.0 - 2.4	11.2 - 13.2	**0.5 - 0.6**
Thamnochortus fruticosus	-1.8 - -0.6	**0.0 - 0.7**	11.5 - 15.3	0.5 - 0.7

SEVa = aeration stress SEVd = drought stress MWTD = mean water table depth

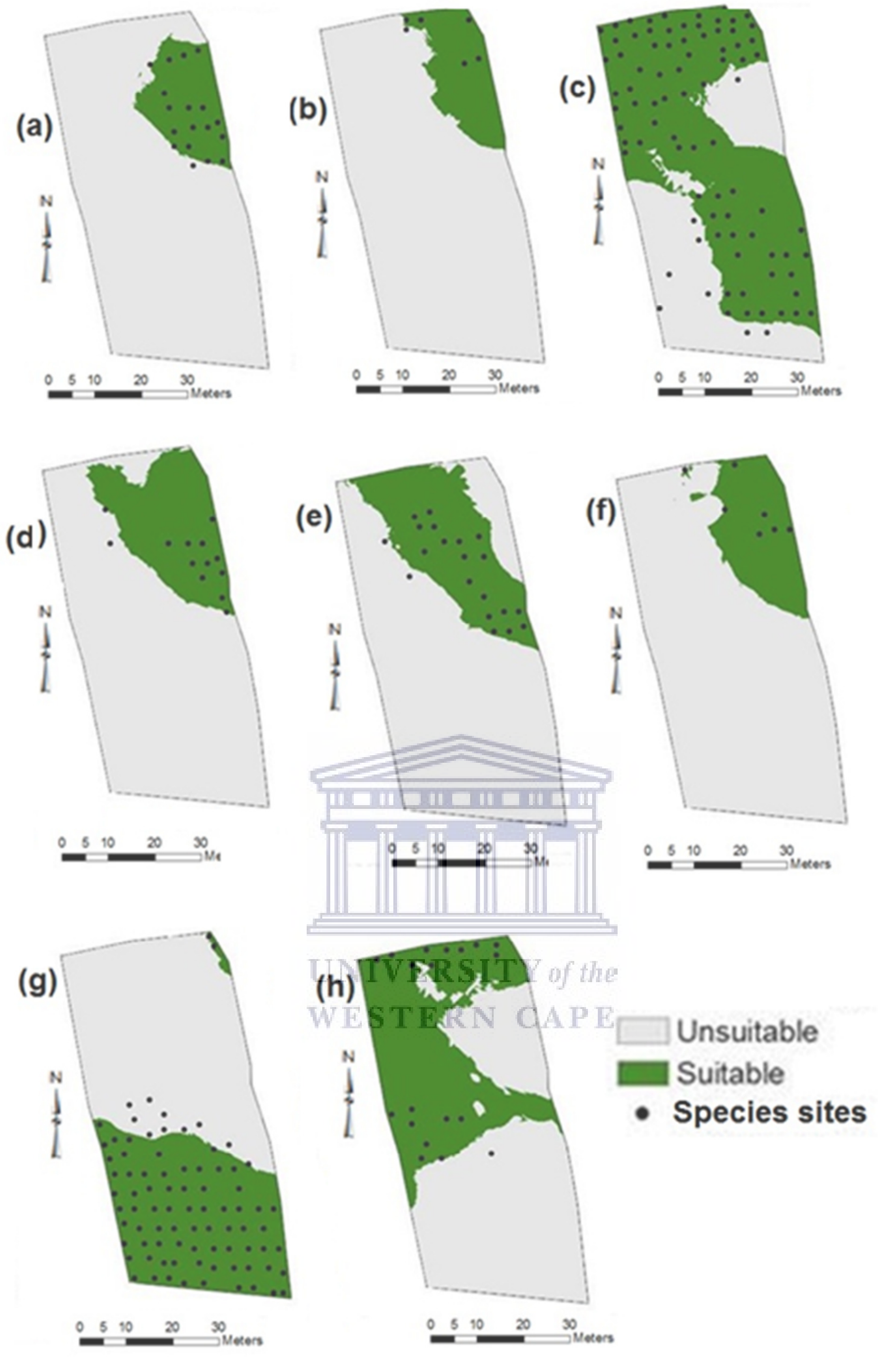


Figure 6.17. Hydrological niches of Restionaceae species at the Theewaterskloof site. (a) *Anthochortus crinalis* (b) *Elegia asperiflora* (c) *Elegia neesii* (d) *Elegia thyrsifera* (e) *Platycaulos callistachyus* (f) *Restio pedicellatus* (g) *Staberoha cernua* (h) *Staberoha distachyos*.

6.3.2.9 Synthesis

As can be seen from Section 6.3.2, some Restionaceae species prefer wetter conditions, and some drier, while others tolerate a wide range of hydrological conditions. Species are seen to exhibit varied preferred hydrological ranges at different sites. Each individual species has its defined hydrological niche based on their niche requirements. However, there are also possibilities of coexistence as species do share the same ecological niche spaces with eminent competition for the shared hydrological resources. Appendix 4 shows a combined table of the potential predictability and relative percentage contribution of environmental variables in modelling the MaxEnt hydrological niche model.

6.3.3 Comparative analysis of some frequent species models (common to many sites)

In all eight study sites were examined for SDM analysis. Most frequent species were considered to be species that occur in three or more of these plots. *Restio capensis*, *Restio curviramis* and *S. distachyos* are three Restionaceae species that fall in this category and a comparative analysis of the species models between corresponding sites was done. Climate variables contributed differently in defining the hydrological niches of these species between the sites.

6.3.3.1 Restio capensis

Restio capensis occurs at the Bastiaanskloof, Riverlands and Silvermine sites. Overall, the SDMs were successful at discriminating between suitable and unsuitable hydrological niches at all three sites. Satisfactory model predictions (AUC > 0.6) were achieved (Table 6.17). MaxEnt Jack-knife test of variable importance in showed that *R. capensis* model is significantly favoured by MWTD and SEVd. Both parameters contributed 33.1% and 36.6% on average, respectively, during the discrimination which signifies that these two parameters play a vital role in the distribution of this species. The species occurs within a MWTD range of 0.5 to 0.9 m and SEVd of 14.4 to 23.1 m.wk (see Table 6.17). These values indicate that *R. capensis* prefers drier soil conditions. The species cohabits with *R. curviramis* and *S. distachyos, E. nuda*, and *R. cincinnatus* but competes poorly within the shared niche. It is not a very adaptable species as it retreats to a specialised niche where competition is minimal.

Table 6.17. Model performances and percentage contributions of the microclimatic variables for *Restio capensis* niche models.The values shown are averages over four replicate runs.

Site + Test AUC	Measure	MWTD	SEVd	SEVa	Elev.
Bastiaanskloof	% contribution	**46.5**	**46.5**	2.8	4.2
0.635±0.055	Preferred range	0.5 – 0.9	14.4 – 23.1	0.0 – 1.3	0.3 – 2.5
Riverlands	% contribution	**22.4**	**52.9**	6.5	18.2
0.653±0.052	Preferred range	0.6 - 0.9	14.9 – 22.9	0.0 – 0.7	0.1 – 1.3
Silvermine	% contribution	**30.4**	10.4	3.1	**56**
0.652±0.084	Preferred range	0.7 - 0.9	15.8 – 21.8	0.0 – 0.5	0.9 - 6.0
General		33.1%	36.6%	4.1%	26.1%
		0.5 – 0.9	14.4 – 23.1	0.0 – 1.3	0.1 – 6.0

6.3.3.2 Restio curviramis

Restio curviramis occurs at Bastiaanskloof, New Years Peak (NYP) and Theewaterskloof. The MaxEnt models for *R. curviramis* performed above random with a combined average AUC value of 0.701 (± 0.038 SD) for all three sites (Table 6.18). Table 6.18 shows that microclimatic variables contribute differently to the modelling of *R. curviramis* niche at each of the sites. The Jack-knife training gain results in Table 6.18 show that MWTD contributed the most (i.e. 64% of the required information during modelling) towards modelling *R. curviramis* at Bastiaanskloof. SEVd contributed over 62% at Theewaterskloof while SEVa is the most useful microclimatic variable at NYP where it contributed 45.5% of the required information during modelling. Meanwhile, the preferred MWTD for this species is shown to be between 0.4 and 0.9 m. The species prefers drought stress (dry) conditions within the range 0.9 – 23 m.wk. Conversely, it performs minimally in saturated conditions showing a preferred range between 0 and 5 m.wk. This pattern is confirmed by the high regularised training gain and training AUC for these variables at these sites.

Table 6.18.Model performances and percentage contributions of microclimatic variables in *Restio curviramis* nichemodels.The values shown are averages over four replicate runs

Site + test AUC	Measure	MWTD	SEVd	SEVa	Elev.
Bastiaanskloof	% contribution	**64**	9.5	10.1	15.6
0.787 ± 0.072	Preferred range(m)	0.5 – 0.9	14.3 – 23.4	0.0 – 1.3	0.3 – 2.5
NYP	% contribution	1	9	**45.5**	**44.6**
0.772 ± 0.020	Preferred range(m)	0.4 – 0.7	9.0 – 13.4	0.0 – 1.7	1.6 – 5.1
Theewaterskloof	% contribution	13.7	**62.2**	11.4	12.7
0.545 ± 0.024	Preferred range(m)	0.4 – 0.7	11.0 – 15.6	0.0 – 2.6	0.0–2.1
General	% contribution	26.2%	26.9%	22.3%	24.3%
	Preferred range	0.4 – 0.9	9.0 – 23.4	0.0 – 2.6	0.0 – 5.1

6.3.3.3 Staberoha distachyos

Suitable hydrological niches for *S. distachyos* were predicted at the Bastiaanskloof, Cape Point, Kogelberg and Riverlands sites. Overall, the SDMs were successful at discriminating between suitable and unsuitable hydrological niches for *S. distachyos* at all four sites (AUCs> 0.6 were achieved) (Table 6.19). This means that meaningful comparative analogies could be made out of these results. MaxEnt's Jack-knife test of variable importance showed that both MWTD and SEVd contribute significantly to *S. distachyos* models at three out of four sites (Table 6.19). MWTD contributed 49.4% of the information needed to hydrological niches for *S. distachyos* while SEVd contributed 60.8% and 72.7%, respectively (see Table 6.19). Based on the occurrence behaviour of the species at three (majority) sites, and the fact that MWTD and SEVd are mainly covariates, it could be inferred that *S. distachyos* thrive better under dryer moisture conditions where the mean depth to the water table exceeds 0.5 m below the surface. The species distribution is best explained by waterlogged conditions at the Cape Point site though still within a water table depth range between 0.5 and 0.7 m below surface.

Table 6.19. Model performances and percentage contributions of microclimatic variables in *Staberoha distachyos* niche models. Values shown are averages over four replicate runs.

Staberoha distachyos

Site + test AUC	Measure	MWTD	SEVd	SEVa	Elev.
Bastiaanskloof	% contribution	**49.4**	9	36.3	5.4
0.645±0.046	Preferred range	0.5 – 0.9	14.3 – 23.4	0.0 – 1.2	0.3 – 2.5
Cape Point	% contribution	3.8	5.2	**65.1**	25.9
0.644±0.043	Preferred range	0.5 – 0.7	11.4 – 13.9	0.0 – 1.0	0.0 – 1.5
Kogelberg	% contribution	2.8	**60.8**	2.7	33.8
0.730±0.035	Preferred range	0.6 – 0.8	15.3 - 19.2	0.0 – 0.9	-1.0 – 2.1
Riverlands	% contribution	8.7	**72.7**	12.9	5.7
0.749±0.010	Preferred range	0.6 – 0.9	15.1 – 23.4	0.0 – 0.5	0.2 – 1.6
General	% contribution	16.2	36.9	29.3	17.7
	Preferred range	0.5 – 0.9	11.4 – 23.4	0.0 – 1.2	-1.0 – 2.5

6.4 Discussion

Over the years, many attempts to explain the how and why species assumed current distribution patterns have centred on the presence of a hydrological gradient (Glaser et al., 1990, Wassen and Joosten, 1996, Peters et al., 2007, Bartelheimer et al., 2010). In this study, the existence of hydrological gradients was clearly established in all experimental study plots based on the mean water table depths and soil moisture content data collated from field measurements.

First, elevation maps (Figures 6.1 to 6.8) clearly reveal a topographic gradient across each plot which is a key physical requirement for the existing moisture gradient in the experimental landscape. The presence of these gradients is significant in defining subsurface hydraulics which in turn influences species occurrences. Generally, soil moisture flows downslope and the shape of the water table usually conforms to the surface topography (Dingman, 2015). Moisture tends to accumulate at the lower end of the slope resulting in a hydrological gradient (Silvertown et al., 1999, Araya et al., 2011).

While topography has a direct influence on the moisture gradient it has an indirect influence on the species distribution. The presence of such a gradient impacts plant species because plants rely on the soil for anchorage and resources such as water and mineral nutrients (Araya and Garcia-Baquero, 2007). In a study to investigate the possible impact of bulk water abstraction from the TMG aquifer, Aston (2007) distinguished between the xylem pressure potential between aquifer-fed seeps (located at lower slope) and perched seeps (located at relatively higher altitude) and found that, shallower rooted seep species are likely to be the first to be impacted when water levels decline possibly due to bulk abstraction. Furthermore, a number of studies have identified the impacts of hydrological gradients in species distributions both at small or large scale. Bledsoe and Shear (2000) used ordination methods and showed that the differences between two alluvial forest stands were primarily the result of variations in elevation alongside growing season, flooding frequency, percent base saturation, exchangeable acidity and soil physical properties.Magee and Kentula, (2005) examined plant assemblages in order to understand if the hydrologic requirements of native and introduced species are critical to sustaining native plant communities in wetlands of disturbed landscapes. The most common species were identified to belong in different response groups with unique occurrence/abundance and exhibited unique responses in relation to water level variability, but were abundant over a wide range of water table depth. The realized niches of other species in each response group were more restricted and confined to narrower ranges of water table depth and variability. Moser et al., (2007) explored the relationship between induced microtopography, hydrology and plant species richness/diversity in non-tidal freshwater wetlands and found that plant diversity correlated with tortuosity and limiting elevation difference, in both created and natural wetland settings. Meadow plants segregate along hydrological gradients (Silvertown et al., 1999). Dwire et al., (2006) examined meadow plant species distributions in three riparian plant communities along short topographical gradients. Species richness negatively correlated with mean water table depth suggesting that biological diversity often observed in montane riparian meadows is strongly related to steep environmental gradients in hydrology.

Restionaceae are tolerant to a wide range of hydrological regimes. There are species that are tolerant to moist through to dry environmental conditions (Araya et al., 2011). As expected, the species which were identified in this study have different hydrological preferences with a range of wet and dry conditions (Silvertown et al. 2014). In order to examine the relationship between the species and the hydrological variables, species habitat distributions are modelled to show the hydrological niche of species (Franklin, 2010). Maximum Entropy Modelling software (MaxEnt version 333k) (Phillips et al., 2006) successfully created species distribution models for each sampled plot in parts of the floristic region with hydrological variables being the main controls (Phillips et al., 2006). MaxEnt algorithms made use of both the presence and absence of species at locations in these plots

(Elith et al., 2006) to successfully estimate habitat suitability models for Restionaceae in eight Fynbos wetland communities.

Being the products of defined explanatory boundaries (physical phenomena), species models defined the fundamental niche space of every species examined (Hutchinson, 1957). In essence, the MaxEnt model predicts only the fundamental niche after being trained by the environmental conditions under which some populations of the species seemed to thrive. It considers only species presence data (i.e. niche-based) thereby predicting the species fundamental niche rather than the realized niche (Pearson, 2007, Kumar and Stohlgren, 2009). By definition, the fundamental niche, as opposed to realised niches of the species, is the set of all environmental conditions that allow for optimal survival, whereas the realized niches which are a subset of the fundamental niche, form the niche space that is actually occupied by the species (Hutchinson, 1957). This means that the potential species niche can comfortably serve as an extrapolation of the fundamental niches beyond the extent of the perceived or observed realized niche by relating species presence to environmental predictors (Franklin, 1995). The realised niche mimics the actual species distribution observed in the field (Pidwirny, 2006, Pearson, 2007). These Restionaceae species hydrological niche models are realised niches or predictions of the potential habitat of the species amidst biotic interferences and the prevailing environmental constraints within the wetland communities. Predicted species distribution maps for most species at all sites demonstrate that the niches do spread beyond the actual observed occurrence ranges that were observed in the field. This creates the impression of an over-estimation of the predicted potential distribution of these species. In effect, this would rather be the result of intraspecific as well as interspecific competition which results in biotic exclusion and adaptation. On the other hand, species existence outside of their suitability zones could be attributed to adaptation or resilience to changing hydrology.

The predicted species occurrences are in coicide with the occurrence data for most species across all sites. However, according to the potential distribution in all sites, the area suitable for Restionaceae species growth is wider than the area defined by the occurrence points. This may be an indication that most species have experienced some form of limitation possibly due to competition, exclusion or specialisation. Again, the potential species habitats or fundamental niches for most species varied across sites showing a conflicting affinity for environmental variables. Conversely, in many instances, Restionaceae species have been plotted outside of their modelled suitability zones which could be attributed to adaptation or resilience to changing hydrology after adapting to previous wetter or drier years at the establishment phase. Such species are definitely not expected to be threatened by the changing hydrological conditions.

The absence of a species from suitable habitats may be attributed to local extinctions or dispersion barriers or lack thereof, or even due to limited propagation rates (Guisan and Thuiller, 2005). Species dispersal might have been limited due to geographic barriers, human disturbance or associated competitive species. Restrictions prevent species from optimally exploiting environmental conditions which lead them to their full ecological potential (Pulliam 2000). Also, this could simply be the result of an error during sampling in the field where specimens might have been overlooked or missed in the field. The selection of optimal areas within the fundamental niche may also limit the extent of the realized niche (Hutchinson 1978). Those portions of the fundamental niche which are currently not occupied by the specific species are the candidate areas for further research to understand why these absences.

As can be seen from the results, some Restionaceae species prefer waterlogged conditions, and some drier, while some tolerate a wide range of hydrological conditions. Each individual species has its hydrological niche with its niche requirements, but also coexist with some other species within the same ecological niche, and competing for the same hydrological resources. This also suggests niche segregation in the community structure (Silvertown et al. 1999) although the mechanisms through individual plants segregate remain obscure. Bathelheimer et al. (2010) have attributed this dynamic to species genetically defined preference or the result of current subsurface competition within the community.

The water table depth and the dryness threshold values seem to have the most influence in determining the distribution of Restionaceae species in most of these wetland sites where species presence were repeated (Guo et al., 2015, Guo et al., 2016a). Interestingly, there is a high correlation between these two variables as these explain similar environmental conditions. The water table depth fluctuates seasonally with lowest levels measured during the dry summer months. This implies that there are multiple shifts in optimal ranges for residents exposing all species to competition and adaptation. Most species have segregated and aggregated in clusters separate from any interference from other competitors, an evidence of adapting to a specific edaphic condition.

The performance of this model was not affected by the spatial scale at which investigations were done. This achievement is in line with earlier results for Silvermine in the region at minute scale (Guo et al. 2015). In most cases, such studies have focused mainly on the regional to global and hardly at such minute scale as portrayed by Guo et al. (2015) and Guo et al. (2016b). Whereas many similar studies have successfully modelled species niches with large-scale bioclimatic variables (Pearson, 2007), this study modelled hydrological niches at very fine scale habitats which composed of minute sample sizes.

The performance test for Restionaceae model yielded results which ranged from poor to satisfactory based on the perceived AUC values from plot to plot (Thuiller et al., 2005). The AUCs ranged from 0.42 to 0.92 giving an average AUC of 0.67 indicating that the potential predictability of the Restionaceae models was good although it varied across sites. Some studies have attributed the attainment of high AUC values as an indication of the presence of widely spread species distributions (McPherson and Jetz, 2007, Evangelista et al., 2008) although such an observation remains inconclusive in this study. Meanwhile, AUC values for each species' model differed across the sites.

The percentage influence of environmental variables to species distribution in the models varied for each species and differed across the sites (Table 6.19). Likewise, the change in model gain differed for each environmental variable among species and across sites when used in isolation or when omitted during modelling which makes it difficult to single out one variable as the most influential for a species across all its habitats. Furthermore, based on this observation, it remains a challenge to ascertain the best environmental variable range for each species simply based on the percentage variable contributions. For example, Table 6.19 shows a comparison of species habitat models of species which occur repeatedly in three or more sites. The table reveals that MWTD and SEVd are the most influential hydrological variables in the model predicting habitats for species that are common in three or more sites. The soil dryness and waterlogging threshold are both correlative and dependent on the water table depth which means that any changes in MWTD due to climate change, would directly impact species niches (Guo et al. 2015).

6.5 Conclusion

In this study, GIS techniques were used to generate hydrological layers, in order to explore the hydrological niche of Restionaceae species. The results show that species response to hydrological variables varied across localities. Citing an example of the Silvermine study area, the water table depth is identified as the main hydrological factor responsible for species niches there. This highlights the presence of hydrological requirements specific to individual species, which at the same time coexist and share the same broader hydrological niche area.

These results have a direct impact on the conservation of species richness. Because should there be any climate change, the water table depth could become greater, it could mean a reduction in species richness, as some species might not survive a change in the water table depth or moisture conditions and might probably need to move along the gradient. Considering that South Africa is a semi-arid environment, and with the threat of urbanization and groundwater extraction and more boreholes; this will ultimately cause a change in the hydrology and therefore impacts on Restionaceae niches.

This study assessed and modelled the effectiveness of using hydrological variables in determining species hydrological niche, at a microclimate level in a Mediterranean-type environment. It identified hydrological regimes of species. it also provided evidence of the importance of hydrology to conservation and future climate change impact analysis, because any changes in the hydrological variables, will cause changes in the hydrological niche and a major change in the species richness index. The results of this study are invaluable in the assessment and monitoring plant species due to hydrological changes.

Restionaceae are tolerant to a wide range of hydrological regimes, meaning that there are species that are tolerant to different sites along a moisture gradient (Araya et al., 2011). As expected, the species which are identified for use in this study have different hydrological preferences with a range of wet and dry conditions (Silvertown et al. 2014). In order to examine the relationship between the species and the hydrological variables, species habitat distributions are modelled to show the hydrological niche of species.

MaxEnt has proven to be very efficient in modelling the hydrological species of Restionaceae and remains a valuable tool in biodiversity conservation and management in relation to climate change. Species distribution modelling predicted the spatial relationship between Restionaceae species niches and soil hydrological conditions at sampled sites (Franklin, 2010). MaxEnt version 333k (Phillips et al., 2006) successfully estimated habitat suitability models for Restionaceae in the Fynbos wetland communities (Elith et al., 2006). The performance of this model was not affected by the spatial scale at which investigations were done. In most occasions, similar studies were done on a regional to global and not at such a minute scale as portrayed by Guo et al. (2015). This study successfully produced hydrological niches for species at plot (minute) scale which makes it different from the more commonly practised large-scale alternatives that have not gone down to such minute scale nor have they utilised minute sample sizes (Pearson, 2007).

Based on the observed spatial distribution of species models which seem to be influenced by environmental factors, one can speculate that species ranges will experience severe shifts, typically contractions and considerably altered geographic distributions for the majority of the shallow-rooted Restionaceae species. Through such findings, an idea about the species at risk could be attained and these should inform decisions for future biodiversity management and biodiversity conservation strategies. However, these results presented this study do not take current or on-going habitat destruction patterns that are related to human activities into account which introduces an uncertainty factor warranting even more rapid remedial action.

CHAPTER 7 PROJECTING FUTURE DISTRIBUTIONS OF SELECTED RESTIONACEAE SPECIES WITHIN THE CFR

7.1 Introduction

This chapter is the second of two parts wherein species distribution models were used to investigate the impact of climate change on the distribution of Restionaceae species in parts of the CFR. It involves a comparative analysis of the projected distributions of selected species (generated in Chapter 6) for an RCP2.6 and RCP8.5 future climate change scenario. Species models for both current and future climates were assessed to create distributional change maps which illustrated the possible species expansions, contractions, or stability into the future. An expansion or gain in the species range is an indication that expected changes in climate would be suitable for such species while species that are disfavoured will experience losses or contractions in their species ranges. Some species will not show any range changes. Where a species range expands or remains unchanged from the current to the future will signify that species is stable or resilient to climate change. These distributional change maps facilitate visualisation of the extent of areal change in species in sampled experimental sites. They give an indication of the ability of Fynbos wetland communities to cope with projected climate change. Finally, species models might serve as reliable objects for use in biodiversity planning and management of the Restionaceae in CFR.

7.1.1 Projected species response to climate change

Historical evidence has shown significant changes in species assemblages over time due mainly to perceived environmental factors. Changes in natural systems have been attributed to anthropogenic climate change (Walther et al., 2002, Rosenzweig et al., 2014). Studies which have projected possible changes in the future show that there would be substantial changes in species ranges in the near to distant future if current trends in climate persist (Huntley et al., 2006, Mason et al., 2015). Most predictions project a net reduction in the distributional ranges of plant species due to climate change and rapid urbanisation. There is an increased risk of extinction for species which are likely to migrate in upslope or pole ward directions within continents (Thomas et al., 2004b, Midgley et al., 2005, Hickling et al., 2006, Lenoir and Svenning, 2015, Mason et al., 2015). The limitations upslope include a possible net reduction in suitable habitat due to montane geometry (Lenoir and Svenning, 2015). Similarly, with decreasing habitat suitability space towards the poles, migrating plant species would be isolated and eventually become extinct resulting in lower levels of both endemism and species richness (Walther et al., 2005). Some species have shifted their ranges at rates reflecting local rates of climate change warming (Parmesan et al., 1999, Chen et al., 2011), whereas others have lagged behind climate changes (Menéndez et al., 2006, Devictor et al., 2008, Valladares et al., 2014, Mason et al., 2015). These responses may as well be different between taxonomic groups of species caused by variability of habitats, resource requirements, dispersal patterns, life history and pre-warming ranges (Angert et al., 2011, Mason et al., 2015). Instances of large inter- and intra-specific variation within taxonomic groups in response to climate change include Mair et al. (2012), Mair et al. (2014). The projected complex outcome of species distribution ranges in the future obviously poses a challenge to biodiversity management and conservation planning in the CFR as well (Rouget et al., 2003, Midgley et al., 2005). This chapter investigates the future predicted SDMs and accompanying possible distributional changes of successfully modelled Restionaceae species (with test AUCs > 0.6) from Chapter 6 based on future RCP26 and RCP85 GCM scenarios.

The difference between the SDM modelling process in the previous chapter and the current chapter is that, while the previous chapter focussed on potential distribution of species based on the actual microclimatic/environmental conditions that prevailed during species sampling, the current chapter predicts the potential distribution of the sampled species data when subjected to changing microclimatic conditions in the near to distant future. This introduces uncertainty as the latter lacks observations of species occurrence data from the future which could have served to directly train or test the validity of predictions (Elith and Leathwick, 2009). Another source of uncertainty is that there might be projected climate or environmental conditions in the future landscape that may not be analogous to the conditions of today (outside of the current ranges). For example, some regions may be colder and wetter than any existing spot on today's landscape. These conditions are outside the range represented in the training data. Model projections onto such conditions are questionable, and a solution would be to limit projections at the limit of the corresponding training range (Phillips et al., 2006, Phillips et al., 2009). MaxEnt addresses this problem by 'clamping', in which variables outside the training data range are identified (displayed on a clamping image). Furthermore, MaxEnt down-weights the clamped areas in the final niche prediction and make these areas less likely to be labelled as suitable niches. Although clamping does not eliminate uncertainty in the forecasting processes, it aids to point out areas where extreme caution should be exercised during interpretation. Nonetheless, in many instances, these uncertainties are simply ignored since conservation and management outweigh the errors from uncertainties (Wiens and Bachelet, 2010).

SDMs are prolific at integrating climate change into conservation management by projecting how the distributions of species may change under different climate change scenarios (AkÇAkaya et al., 2006, Botkin et al., 2007, Lawler et al., 2009, Bellard et al., 2012). As climatic or environmental conditions change, species may respond in different ways, including: (i) becoming resilient and adapting to the changing conditions (ii) shift their distribution ranges in pursuit of their preferred environmental conditions (iii) becoming extinct (Holt, 1990, Theurillat and Guisan, 2001, Wiens et al., 2009, Huey et al., 2012).

The ability to adjust range as in (ii) above is instrumental in modelling future potential species distributions (Botkin et al., 2007, Franklin, 2010). Species distribution models compute potential distributions by correlating the location of species and the prevailing environmental conditions. Similarly, projections into the future are possible as well when correlations are based upon expected future environmental conditions. This has been applicable in assessing the potential impacts of climate change upon a wide range of species (Barange et al., 2014, Pacifici et al., 2015, Urban, 2015).

7.1.2 Assumptions and limitations of SDM in changing environments

SDMs are merely representations of the potential distribution range of the species based on prevailing environmental or climate conditions. When subjected to changed environmental conditions, plants are assumed to respond in a number of ways to ensure survival.

Through dispersal, species may be able to spread and establish at foreign locations with favourable conditions (Pearson and Dawson, 2003, Bradley et al., 2016, Weber, 2017, Suppo et al., 2018). However, species dispersal may be limited by dispersal barriers created through anthropogenic activities or by patchy landscapes with varying degrees of suitability (Araújo et al., 2006, Midgley et al., 2006, Thuiller et al., 2006, Miller and McGill, 2018). Also, where the environmental conditions change more rapidly than the dispersal rate, as by slow-moving organisms like plants, species' dispersal capacity may be compromised (McLachlan et al., 2007). In this case migration, corridors may be a plausible solution to addressing this disrupted habitat connectivity (McLachlan et al., 2007, Seddon et al., 2014, Seddon et al., 2015). SDMs cannot ascertain the actual reaction of species or infer whether or not these species will be able to migrate to new areas that are suitable for their survival. They merely give the possibilities if current observations are considered.

Easily, the choice of spatial scale for SDM can depend on the scale of the available modelling data. However, the influence of environmental and climate factors appear to be more significant at large spatial scales while biotic interactions within the species are effective at fine-scale (Pulliam, 2000). Whereas at a macro scale, climatic conditions dominate in structuring the distribution of species thereby reducing the impact of biotic interactions, the opposite obtains at the microscale (Pearson and Dawson, 2003, Pearson et al., 2004). This introduces a dilemma on what spatial scale to use in SDM modelling. Logically, SDMs that model fine-scale features are more likely to capture the factors that determine the actual realised distribution of a species. Hence, alternative environmental variables/determinants aside from climate need to be utilised if biotic interactions were to be incorporated somewhat in the final analysis. This thesis uses hydrological conditions of the soil (viz. mean water table depths, saturation and drought stress measurements) measured on site, also impacted by climate change, to assess the potential response of Restionaceae species at microscale communities.

Additionally, despite the rate of current and future environmental change exceeding the dispersion capacity of most species, there are instances where species are capable of rapid evolutionary change (Franks et al., 2007). Indeed some species have shown the capacity to adapt to changing conditions without shifting distributions (Root et al., 2003) and the SDM cannot predict such outcomes and only allow for inferences based on available knowledge. So far, attempts to incorporate physiological traits and the spatial data in order to better explain the niche distribution have been made through mechanistic means (Kearney and Porter, 2009). This compelled by the fact that species distributions respond individualistically to environmental factors, and community is merely a reflection of the juxtaposition of species distributions (Gleason, 1926). Deterministic means might not adequately serve to explain species distribution due to the possible presence of indeterminate factors. So far, correlative SDM does not account for biotic interactions between species in natural communities though they may be useful to some extent (Gutiérrez et al., 2005, Guisan et al., 2006, Araújo and Luoto, 2007).

The quality of SDMs may be affected by the quality, quantity and source of data in use. The problem of spatial autocorrelation and other issues related to species occurrence data discussed in Chapter Six could also render the quality of the GCM data used for projection of the potential future distribution questionable. For example, the quality of downscaled data may be influenced by the spatial and temporal resolution of the GCM data used to construct it. Furthermore, any incoherence in scale between the species occurrence data and the grid/cell size of the bioclimatic variable (and other environmental data) used during species change modelling would add to the uncertainties related to the analyses (Root and Schneider, 1993, Wiens and Bachelet, 2010). In modelling species habitat shifts and other changes due to future change, it has been recommended that the climate change projections should closely correspond with the scale of the species occurrence data (Wiens and Bachelet, 2010). It is impractical to rely on coarser grained climate data in a micro scale biodiversity assessment as in the current study. Additionally, it gets even more problematic making climate change projections for hydrological niche modelling at a microscale (1m x 1m) where grids at such scale are hardly available. For this reason only, in situ hydrological parameter readings were customised to the appropriate local scale following the interpolation procedures described in Chapter Six.

Realistically, the choice of data to use largely depends on the availability and even the access to the data despite all the above uncertainties (Beaumont et al., 2008). Also, correlative SDMs are currently the best practical options for exploring the future responses of a wide range of species to an already changing climate at varying scales (Pearson and Dawson, 2003). However, care must be taken in interpreting the outputs from these models as inferences for different purposes can be affected by different levels of uncertainty present (Elith and Leathwick, 2009). The level of uncertainty could be improved with constant modification of models (Elith and Leathwick, 2009, Franklin, 2010, Wiens and Bachelet, 2010). Indeed, incorporating dispersal, demography and the mechanistic constructs of species' responses to bio(hydro)geophysical factors will enhance the ecological realism of habitat suitability modelling (Pearson et al., 2006, Thuiller et al., 2006, Lawler et al., 2009).

A few existing means are being used at present to improve the use of habitat models for extrapolation and to reduce the sources of error. Examples include the use of ensemble forecasting (Araújo and New, 2007), retrospective testing of predictions (Araújo and New, 2007) or the reduction of differences between models by consensus (Pearson et al., 2006). Where possible, aspects like evolutionary and physiological change, dispersal, landscape and/or population models can be incorporated in species models in order to represent potential processes of change (Keith et al., 2008, Kearney and Porter, 2009). However, considerable challenges still remain, especially with respect to modelling the consequences of anthropogenic climate change (Thuiller, 2007) and the likely change in biotic interactions as climate changes (Elith and Graham, 2009).

7.1.3 Climate change scenarios

Changes in the spatial distribution of species are directly linked with the variations in the prevailing eco-physical conditions including climate. Climate change scenarios are possible future climates that have been constructed to determine the long-term impacts of climate change on resources and the (ecological) environment (Beaumont et al., 2008). Hence, in order to predict the possible impacts of climate change on species distributions, climate scenarios with appropriate spatial resolutions are required to sufficiently represent potential changes across the landscape. Generally, two types of climate scenarios are used for impact modelling purposes. These include: (i) idealised and (ii) simulated climate scenarios.

Idealised scenarios are similar to sensitivity analysis where a range of change possibilities in climatic variables are conducted to explore the responses of species as well as to identify thresholds above which species may be adversely affected by changing conditions (Williams et al., 2003, Fernando et al., 2014). This approach is limited in that it assumes a simplistic linear relationship between species and environmental variables. Furthermore, it implies some form of uniformity in the change in climate across the regions of interest. Finally, it does not incorporate a temporal dimension in the analysis of species response. Despite these limitations, idealised scenarios of increases in greenhouse gases over a range of possible future climates have been used as intermediate steps in assessing a species response and then refined further by using simulated scenarios (Beaumont et al., 2008). E.g. Nineteen climate models have been used to evaluate idealised 1%/yr. CO_2 increase climate change (Senior et al., 2016).

Simulated scenario models are derived from emission scenarios or estimates of future concentrations of greenhouse gas of GCM (Beaumont et al., 2008). GCMs or Climate models simulate oceanic, atmospheric, land surface, seasonal snow cover and ice dynamics both continentally at seasonal to decadal time scales (Randall et al., 2007) and regionally at daily time scales (Perkins et al., 2007). The Intergovernmental Panel on Climate Change (IPCC) is the global authority providing up to date information on the physical, human and environmental effects of climate change (Barros et al., 2014, Field et al., 2014). Through its assessment reports, the IPCC has projected the nature of climate changes and its impacts on the physical environment, social and economic activity, and on ecosystems biodiversity e.g. Barros et al., (2014). The IPCC Fifth Assessment Report (IPCC AR5) of 2013 and 2014 is the most recent report which comprehensively presents the most recent evidence of climate change and details its consequences (Barros et al., 2014, Edenhofer et al., 2014, Field et al., 2014, Pachauri et al., 2014, Stocker et al., 2014). The IPCC AR5 report developed four emission scenario possibilities or emission pathways that associate greenhouse gas concentration with radiative forcing, referred to as Representative Concentration Pathways (RCPs) to generate climate models. The four RCP scenarios were (i) 8.5 W/m^2 - very high emission scenario where emissions continue to rise through the 21st century; (ii) 6 W/m^2 – high stabilisation scenario where emissions peak around 2080; (iii) 4.5 Wm^{-2} – intermediate stabilisation scenario where emissions peak around 2040, then decline; (iv) 2.6 Wm^{-2} – assumes that emissions peak between 2010-2020 and substantially subsides thereafter. And so, each RCP scenario is aligned to a socio-economic scenario. The model that was used for the analyses in this thesis was derived from one of the climate models within the Fifth Assessment Report (AR5) of the IPCC and only scenario (i) and (iv) representing extremes were utilised.

7.1.4 Some limitations of climate models in species distribution modelling

SDM algorithms represent the correlative relationship between the species being modelled and a set of environmental conditions. Hence, a potential shift in the distribution of species due to climate change is possible. Species models that incorporate future environment conditions or GCM projections can project potential shifts in a species' distribution. There exist a variety of GCM scenarios that aim to represent the dynamics of atmospheric circulation, ocean effects and feedbacks between surfaces and the atmosphere. The individual climate algorithms rely on different parameters and functions which makes them unique and different from one another. Hence, different future climate projections do exist for a given level of greenhouse gas emissions this depending on the GCM being used.

Climate change is believed to operate differently at different scales; being driven mainly by dynamics that operate at global and continental scales. Its effects alter climate and weather at the regional and local scales (Pearson and Dawson, 2003). Consequently, its impacts may affect biological systems of different scales in different ways. Although GCMs may provide realistic representations of the large-scale aspects of climate, they generally do not adequately/readily simulate climate at the regional and local scales (Hawkins and Sutton, 2009) which are necessary for the assessment of potential impacts of climate change upon species distributions (Benestad, 2004). Furthermore, in their simulations, GCMs consider cloud cover and topography as homogeneous within each grid cell, thereby overlooking the actual complexities and heterogeneities of climate and landscapes that may exist for small areas found within grids (Wiens and Bachelet, 2010). This limitation with respect to detail in

GCM grids is problematic for small-scale biodiversity and management studies whose heterogeneity and the impact of climate may be missed (Kremen et al., 2008). In this thesis, the Restionaceae species segregating at fine-scale hydrological gradients (Araya et al. 2011) are of key focus. The quest for finer grid future climate scenarios is a necessity for the scope of this study. High-resolution future climate scenarios are possible through the downscaling of GCMs (Jones et al., 2004, Guo et al., 2018, Mearns et al., 2018).

7.1.5 Downscaling GCMs

Future and past climate data are being generated with varied GCMs each giving different results. The weather simulated by GCMs depends in part on the assumed atmospheric concentration of greenhouse gases. Projected future atmospheric concentrations of greenhouse gases are referred to as emission scenarios. Meaning, projected weather for the future depends on the chosen model and the emission scenario used as well on the model run (each run is different as the weather is partly a stochastic phenomenon). Most habitat suitability models use readily available GCM data from global or regional databases such as the WorldClim dataset (http://www.worldclim.org/bioclim, Hijmans et al., 2005) to predict optimal species ranges. GCMs are used to assess the impacts of climate change at regional or large scales but the potential impacts of climate change are better appreciated at finer local or plot scale levels (Root and Schneider, 1993). This makes global or regional scale data layers not suitable for fine-scale impact assessment studies (Hannah, 2015). Moreover, there have been increasing demands for climatic predictions of the regional and local changes that would impact ecosystems or communities.

Data at high ($\leq 1km^2$) spatial resolution is necessary to capture local environmental variability that is sometimes lost at lower resolutions and where there are steep environmental gradients. GCMs are mostly available at coarse resolutions and consequently not readily applicable to resolve features at regional or local scale. Downscaling refines them to finer scale in order to capture sub-grid cell heterogeneity (Wilby et al., 2015). In this process, the empirical relationships among variables derived from GCM data or weather station observations are reconfigured in order to incorporate greater spatial variability into the climate change scenarios (Wilby et al., 1998b, Wilby et al., 2004). One of either statistical or dynamical downscaling of the GCM is necessary for aligning the coarse-grained GCM grids with local finer-scaled vegetation cover and topography grids necessary for impact assessment studies.

Dynamical downscaling requires running high-resolution climate models on a regional sub-domain, using observational data or lower-resolution climate models output as a boundary condition. This computationally heavy procedure uses outputs from the GCM to drive Regional Climate Models (RCMs) (RCM is basically, a GCM of higher resolution and additional environmental local information) to enable a better representation of the landscape climate or environmental processes (Fowler et al., 2007, Jakob Themeßl et al., 2011). Statistical downscaling on the other hand is computationally less demanding. It reanalysis observational data of global and regional climate models down to point or station scale level. This method heavily relies on the availability of current estimates of climate variables from spatially distributed observational points and largely assumes that the small-scale spatial distribution will not change significantly in a modified climate. It also assumes that past relationships between regional climate and local weather persist into the future.

RCMs perform like GCMs but only at a smaller scale but as a consequence of computational intensity their availability is limited (Jones et al., 2004, Di Luca et al., 2012). Empirical statistical downscaling can be used to cover different locations or plots representing wetland communities as homogenous climatic zones (Mtongori et al., 2016).

7.1.6 RCMs for the winter rainfall region of southern Africa

The location of the CFR is in the semi-arid region west of the southern tip of southern Africa which makes it easily susceptible to the impacts of climate change. Over the last decade and beyond, major improvements in the understanding the predictability of southern Africa's seasonal rainfall has emerged. There are instances of regional climate modelling in Southern Africa (e.g. Hewitson and Crane, 2006, Shongwe et al., 2009, Shongwe et al., 2011).

Generally, downscaling of GCMs have not been as prolific in Africa as in other parts of the world (Hulme et al., 2005). In their attempt to fix uncertainties in current GCM forecasts of rainfall for Southern Africa, Landman and Tennant (2000) used statistical means to downscale the Centre for Ocean Land Atmosphere (COLA) T30 GCM data for the sub-region. The retroactive real-time forecasts generated coincided well with other observational studies mostly for the highveld and lowveld regions of South Africa. Through the use of cluster analyses on monthly rainfall data recorded in stations in the country, seven near-homogenous rainfall regions were determined (including the western interior, south-western Cape, south coast, east coast, lowveld, central interior and the north-eastern interior (Landman and Tennant, 2000). A little later, Landman and Goddard (2002) used statistical means to recalibrate ECHAM3.6 GCM to observe regional rainfall for the December-January-February season in southern Africa. Shongwe et al., (2006) reiterate the need to recalibrate GCM predictions for use at smaller spatial scales in southern Africa. Using statistical means they were able to improve the predictability of ECHAM4.5 GCM through recalibration. Landman (2012) compared the forecast performances of 3 coupled systems and showed that the 2-tiered ECHAM4.5v3 of the Modular Ocean Model (MOM3-DC2), and the ECHAM4.5-GML-NCEP Coupled Forecast System (CFS SST) outperformed the ECHAM4.5 atmospheric model for South Africa.

7.1.7 The Fifth Coupled Model Intercomparison Project (CMIP5) and the Max-Planck Institute Earth System Model (MPI-ESM) Model

Model intercomparison projects have been employing improved methods of assessing the uncertainty and robustness of predictive models. The coupled model intercomparison project (CMIP) focuses particularly on assessing climate change. Currently at its fifth phase, the CMIP5, this project adds a new experimental framework to the previous CMIP phases in addressing things like climate change projections for scenarios of the future or even decadal climate predictions (Taylor et al., 2012). An important inclusion to the CMIP5 is idealised simulations which are designed to advance understanding (Giorgetta et al., 2013). The CMIP5 also makes use of RCP scenarios which incorporate a wider range of social developments to define climate policies (Moss et al., 2010, Van Vuuren et al., 2011). Anthropogenic CO_2 emissions are the main drivers of climate change under a number of RCP concentration scenarios.

Max-Planck Institute for Meteorology used the CMIP5 protocols to develop the Max-Planck Institute Earth System Model (MPI-ESM) consisting of a model structure that couples the general circulation models of the atmosphere - ECHAMS6 (Stevens et al., 2013), the oceans - MPIOM (Mikolajewicz et al., 2013), land and vegetation subsystem models - JSBACH (Reick et al., 2013, Schneck et al., 2013) and a marine biogeochemistry component - HAMOCC5 (Ilyina et al., 2013). The main novelty from its predecessors is inclusion of a ‘dynamic vegetation’ or climate consistent development of the geographical distribution of vegetation (Brovkin et al., 2009, Reick et al., 2013), with all carbon fluxes from natural vegetation and soils (Schneck et al., 2013) and from anthropogenic land use and land use change (Pongratz et al., 2009), incorporated (Giorgetta et al., 2013).

The MPI-ESM model system is configured with a variety of configurations which differ in resolution. The low-resolution version (MPI-ESM-LR) is widely applicable in simulations while the mixed resolution (MR) version, MPI-ESM-MR, has realisation and temporal limitations and is not used for experiments driven by CO_2 emissions. Finally, the land and vegetation setup version (MPI-ESM-P) is used for CMIP5 palaeo-environmental and long-term core experiments (Giorgetta et al., 2013). Core experiments are used to assess climate sensitivity and transient climate change for the period 2006 - 2100, and partly to 2300.

The MPI-ESM-LR model has been widely used in most CMIP5 experiments to evaluate and compare model performance. Among the many sets of experiments are the RCP set of experiments that were developed by Moss et al. (2010). MPI-ESM was used to calculate projections for RCP2.6 (Van Vuuren et al., 2011), RCP4.5 (Thomson et al., 2011) and RCP8.5 (Riahi et al., 2011).

Although better than its ECHAM/MPIOM predecessor, the MPI-ESM-LR still has systematic errors in key parameters like annual mean surface temperature and precipitation with a cold bias in the equatorial Pacific SST or warm biases in the subtropical ocean basin, where the strato-stimulus cloud is insufficiently simulated. The differences in precipitation in South America and Africa are clearly related to the net productivity and consequently to the surface albedo. MPI-ESM-LR is capable of simulating the main modes of tropical variability as shown for the Madden-Julian Oscillation and El Niño.

7.1.8 The challenges of managing changing biodiversity due to climate change

SDM products have been incorporated in the management of biodiversity by identifying species at risk and in establishing biodiversity reserves where policy is used to protect the available biota from the threats of destruction. Nature reserves have therefore been the centre of modern conservation efforts despite the varied nature of the response of individual species to environmental perturbations (Watson et al., 2014). So far current reserves have been established based on relatively stable climate with little consideration for possible changes in species geographic ranges in response to climate change (Hannah et al., 2002, Williams and Jackson, 2007).

Over the years, the establishment of conservation reserves has been based on the paradigm that individual species and their biological attributes are inextricably linked to their location and not as much on the maintenance of biological diversity (Hannah, 2010). Even with the shift in paradigm in recent years to include biodiversity, it is still linked to location as each ecoregion is unique in its suite of species and ecosystems that required conservation. Unfortunately, these protected areas are becoming increasingly isolated due to habitat destruction by natural and anthropogenic forces, and some species are shifting their ranges thereby highlighting the need to sustainably conserve biodiversity into the future (Pressey et al., 2007, Hannah, 2008, Hannah, 2010). The imminent effects of changing climate could simply add to the trend of reduction of species range and the overall biodiversity (Thomas et al., 2004a, Hannah et al., 2005, Hannah et al., 2007). This poses a challenge to current conservation efforts as conservation strategies would have to be revised in order for them to remain relevant. Novel mechanisms of planning and new adaptation management strategies must be backed by thorough research to cope effectively with these changes (Hannah et al., 2002, Scott et al., 2002, Klausmeyer and Shaw, 2009, Vitt et al., 2010).

However, it does seek to take the first steps of forecasting the potential future distributions (suitable climate space) for Restionaceae. This study examines how hydrological variables contribute to defining plant hydrological niches at a micro scale. The primary objective was to assess and model the effectiveness of hydrological variables as determinants of species niches in a gradient environment. The outcomes of analysis would be clues to future climate change impacts and inform conservation strategies.

7.2 Methods

7.2.1 Regional climate models

For the future statistically downscaled GCM data for 2020 – 2100 was provided by the CGIAR Research Program on Climate Change Agriculture and Food Security (CCAFS). CCAFS – climate data were downloaded at <www.ccafs-climate.org>. The study uses the Raw GCM CMIP5 daily data set that is calibrated using the AgMerra (Modern-Era Retrospective Analysis for Research and Applications - MERRA) or AgCFSR observational dataset and is bias corrected using the 'nudging' (bias correction) approach (Gudmundsson et al., 2012a, Hawkins et al., 2013). This data is readily available for use as time series point data. It consists of three climatic variables, namely, precipitation in mm, temperature in ^{o}C and solar radiation in W/m^2 units.

Precipitation is a primary source of the moisture that makes up soil water. It is the result of and can be considered as representative of, the synoptic-scale processes in the atmosphere including changes in air humidity and movement of air masses (Linderson et al., 2004). Precipitation also reflects climate signals due to anthropogenic activities (Wilby et al., 1998a) and it represents processes not explained by atmospheric circulation. Generally, the spatial resolution of the atmospheric components of GCMs roughly ranges from 0.5^{o} to 4^{o}

(Taylor et al., 2012). Downscaling future rainfall projections were achieved by using GCM daily rainfall simulations for the period 2020 – 2100.

The MPI-ESM model was chosen because it is well suited for predictions of Southern Africa climate including other significant advantages it has over the others (Santer et al., 1989, Connolley and Bracegirdle, 2007). Projected simulations forced with two representative pathways (i.e. RCP2.6 and RCP8.5) were used. These RCPs simulate a possible range of radiative forcing values in the future relative to pre-industrial values, of +2.6 W/m^2 and +8.5 W/m^2, respectively. RCP2.6 assumes that global annual emissions measured in CO_2-equivalents peak by 2020 and then decline thereafter, and RCP 8.5 assumes emissions continue to rise throughout the 21st century (Lamarque et al., 2011, Van Vuuren et al., 2011). The RCP2.6 scenario is good but an unlikely future scenario, while the RCP8.5 is a more realistic future scenario based on the present human activity. They were used as comparative future scenarios to reasonably reflect the lower and upper extremes of modelled possible changes in solar irradiations (Rogelj et al., 2012).

7.2.2 Preparation of future climate data layers

The SDM analyses for this study focused on the potential of changes in Restionaceae habitats due to different possible scenarios of change in climate in the future. The choice of models enabled comparison between current observations and those projected for the RCP2.6 and RCP8.5 future scenarios by the turn of the century. Future climate data used represented simulations for changes in climate at selected wetland communities in the CFR under study recalling that the current study investigates the possible impact of a change in the hydrological gradient on the distribution of Restionaceae at plot scale. Moisture content in the soil is directly controlled by fluctuations in the depth to water table along with its gradient and is in turn influenced by available moisture from rainfall. Precipitation is considered the sole input source for moisture that infiltrates to the soil. Hence, rainfall simulations were incorporated in physical models to derive projected water table depth variations in the future.

Several steps were involved in the derivation of future depth to water table. The RCM data obtained consisted of daily rainfall (P), temperature (T) and solar radiation (R) records from the year 2020 to 2100 in a tabular format. First, annual averages for P were computed for the periods representative of the current (2009 to 2010) and future (2099 to 2100) climates. Secondly, a climate signal was calculated between the current and the future climates by finding the ratio between the current and future annual average P and multiplying this by the observed MWTD to obtain the future climate signal (i.e. future MWTD) for each quadrat on each site (Guo et al., 2016b). The above computational steps are lumped up in Equation 7.1 which calculates the climate signal. Computation of future SEVs based on current and future moisture scenarios proved complicated and were abandoned during this study. As such variable values for SEVd, SEVd and elevation were left constant, making MWTD the only varying variable in use during all computations into the future. The newly derived future MWTD and the unchanged data for SEVa, SEVd and elevation together formed the environmental inputs during SDM projections. The data were saved as comma separated values (**.csv*) files in readiness for conversion into continuous raster grid layers to be used in MaxEnt. Though they do not contribute to any changes in the analysis, the other variables needed to be included to satisfy computational requirements of MaxEnt.

$$Future\ MWTD = \left(\frac{C}{F}\right) * MWTD \qquad \text{Equation 7.1}$$

Where, MWTD is water table depth, C is the current precipitation; F is the future total precipitation.

The MaxEnt model requires that all the environmental data inputs must be in raster grid (ASCII) format, of the exact same cell size, spatial extent and coordinate reference system (geographic or UTM) in order to smoothly execute the model. Microclimatic signals in **.csv* format were converted into continuous raster grids in ArcGIS using the Kriging interpolation function of the Spatial Analyst Tools within ArcToolbox and later into ASCII grids using the 'Raster to ASCII' function of the Conversion Tools within the ArcToolbox. The interpolation procedures were fully explained in Section 6.2.1.3. The resulting ASCII grids constituted the future microclimatic data for future SDM analyses.

7.2.3 Projecting future distributions of species using MaxEnt

The potential distribution model of each species under the RCP scenarios was generated within MaxEnt by using the model trained on the suite of microclimatic variables for the current climate (Chapter 6) and 'projecting' it by applying it to a new suite of corresponding microclimatic variables for the RCP 2.6 and 8.5 scenarios. MaxEnt interface requires the species location data, a directory of predictor variables for the current climate (as used in Chapter 6) and another directory of corresponding predictor variables for the future RCP scenarios. Apart from this single modification, the procedure and configuration settings in MaxEnt were identical to those used for the generation of the potential current distribution models in Section 6.2.2.

The projected future species distribution of each species was expressed as a probability distribution map with pixels illustrating the probability of occurrence of suitable habitats for the Restionaceae species of interest. The model results also included an accompanying grid map which showed the effects of 'clamping' upon the projected future distribution.

7.2.4 Hydrological (habitat niche) suitability maps for the RCP2.6 W/m^2 and RCP8.5 W/m^2 scenarios and distributional change maps

Post-analytical processes included the derivation of hydrological (habitat niche) suitability maps for the RCP2.6 W/m^2 and RCP8.5 W/m^2 scenarios and distributional change maps. The species binary maps for both the RCP2.6 and RCP8.5 scenarios were created using the same procedures that were used to create binary maps for current microclimatic conditions described in Chapter 6. Each of these maps represented the projected suitable space (presence denoted as 1), and unsuitable space (absence denoted 0) of species based on modelled interactions with environmental variables.

The distributional change between the current and the future species models for each species was computed by subtracting the current potential (binary) distribution from the future RCP scenario projections using the *Map Algebra* tool of ArcGIS' ArcToolbox tool suite. (E.g. the following expression in the Map Algebra calculation window ["*species1*_rcp85.tif"-"*species1*_cur.tif"] calls for a change raster map where 'species1_rcp85' is the new future potential distribution of a species and 'species1_cur' is the current potential distribution of a species). The result was a change map which contained pixels that extended beyond the current range and vice versa. The resulting raster maps depict predicted expansion (gain '+1' in species occurrences), contraction (or loss '-1' of habitat), and areas of stability which showed no change ('0') in the species distribution. The change maps were overlain on the current species distribution layer to give a spatial impression of these changes in ArcGIS' ArcMap window. These change maps illustrated the anticipated changes in each species' distribution range from the potential current distribution to the projected distribution by the end of the century (2100). Explaining these results further: (i) -1 = range contraction i.e.

species does not occur in the future (ii) 0 = no occupancy (species is absence in both periods) (iii) 1 = expansion i.e. species occurs in the future.

Additionally, for each species, the number of pixels for which future species models increased beyond or decreased below the current presence pixels was noted from Attributes Tables of each model. Projected future and present presence pixels noted and the Raster Calculator tool of ArcGIS was used to calculate the proportion (%) of gain or loss for each species model. Similarly, the same procedures were used to calculate the proportion (%) of the site that was projected to experience novel climate conditions for each microclimatic variable (in this case MWTD only). These data were also mapped in ArcGIS 10.3 to show the location of these novel climate conditions across the sites.

Species responses based upon anticipated changes in the distribution range of the species compared to the area of its potential present distribution range were categorised into winners', 'losers', 'shifters' and 'stable' based on Walmsley et al. (2007). As the names suggest, the 'winners' are species that showed a projected increase in their distribution range while 'losers' experienced a decrease of 20% or more of the area occupied by their present distribution ranges. The 'shifters' are species whose projected distribution ranges show both noticeable contraction compared to potential present ranges and potential expansions into unoccupied areas. Finally, the 'stable' are species with no projected change in their potential present distribution under the RCP scenarios.

Alternatively, distributional changes in species hydrological niches could be examined from the current and future binary SDMs in ArcGIS 10.3 using the *Distribution Changes Between Binary SDMs* tool of SDMtoolbox v1.0 (Brown, 2014). To measure the predicted distributional changes for each species, the binary SDMs are projected to an equal area projection e.g. the Africa Albers Equal-Area Cylindrical projection in ArcMap 10.3 (ESRI 2015) at specified spatial resolutions for each experimental site. This tool calculates the distributional changes between two binary SDMs (e.g. current and future SDMs) at a time by subtracting future and current SDMs from each other, and areas of contraction, expansion, and stability were identified. The resulting raster maps depict predict aerial gain in species occurrences (expansion), contraction (or loss of habitat), and areas of stability which show no change in the species distribution. Meanwhile, table outputs are used to estimate distributional range shifts (percentage distributional abundances) of impacted species.

7.3 Results

In presenting the results of this chapter, first, some key concepts in use would be defined in the context of this chapter. The results mainly show the modelled potential change patterns of Restionaceae species which were selected for impact assessments from the previous chapter. Species richness refers to the number of co-existing Restionaceae present in plots area (density) and not the total density of all species on the plots. It recalled that the potential future distribution just like was the potential species distributions, and is merely projections of possible occurrence based on the availability of suitable habitat conditions both in the present and in the future. These predictions do not foretell the species ability to disperse nor does it predict where the species will actually occur in the future since these processes certainly depend on a number of variables which cannot be covered simply by SDM analyses based on a few physical variables. The term site refers to systematically sampled plot at a location; hereafter used interchangeably referring to the same thing.

7.3.1 Anticipated changes in microclimatic variables from present to RCP scenarios in the future

Microclimate signals which reflected the hydrological variations in terms of the depths to the water table (MWTD) were successfully derived. The projected microclimatic variables and the current records differed significantly at all sites except at Bastiaanskloof (Table 7.1 and Table 7.2). Generally, the mean difference in the microclimate variable between now and the projected future would be higher for the more extreme RCP8.5 scenario compared with RCP2.6 scenario projections. According to the results, Bastiaanskloof showed the least change in the expected mean increase in depth of soil water levels (shown by the mean difference in Table 7.1 and Table 7.2) while Riverlands would seem to be the most affected for both projected climatic scenarios. Additionally, Table 7.3 shows that projected novel climate conditions (outside the range of present climate) were experienced differently at the sites.

Table 7.1 Differences in microclimate variables and associated the statistics between the present and the projected RCP2.6 future climate scenarios.

Site	**N**	**Current**	**RCP2.6**	**Mean Diff.**	**q**	**Significant? P < 0.05?**
Bastiaanskloof	200	0.7347 ± 0.1372	0.7363 ± 0.1375	-0.0016	0.13	No
Cape Point	916	0.5833 ± 0.0549	0.9558 ± 0.0900	-0.3726	91.44	Yes
Jonkershoek	190	0.5837 ± 0.0891	0.7460 ± 0.1139	-0.1623	13.82	Yes
Kogelberg	821	0.6922 ± 0.0521	0.8115 ± 0.0612	-0.1192	37.91	Yes
New Years Peak	493	0.4637 ± 0.1339	0.4919 ± 0.1420	-0.0282	3.00	Yes
Riverlands	294	0.7516 ± 0.0905	1.6470 ± 0.1983	-0.8953	63.80	Yes
Silvermine	200	0.7956 ± 0.0605	0.8942 ± 0.0681	-0.0986	14.30	Yes
Theewaterskloof	395	0.5779 ± 0.0997	0.6732 ± 0.1162	-0.0954	11.47	Yes

Table 7.2 Differences in microclimate variables and associated the statistics between the present and the projected RCP8.5 future climate scenarios.

Site	**N**	**Current**	**RCP8.5**	**Mean Diff.**	**q**	**Significant? P < 0.05?**
Bastiaanskloof	200	0.7347 ± 0.1372	0.3587 ± 0.0669	0.3760	31.7	Yes
Cape Point	916	0.5833 ± 0.0549	1.1480 ± 0.1081	-0.5649	138.7	Yes
Jonkershoek	190	0.5837 ± 0.0892	0.8884 ± 0.1357	-0.3047	25.94	Yes
Kogelberg	821	0.6922 ± 0.0522	1.0030 ± 0.0756	-0.3105	98.72	Yes
New Years Peak	493	0.4637 ± 0.1339	0.5711 ± 0.1648	-0.1073	11.43	Yes
Riverlands	294	0.7516 ± 0.0905	1.6470 ± 0.1983	-0.8953	63.8	Yes
Silvermine	200	0.7956 ± 0.0606	1.0150 ± 0.0773	-0.2195	31.83	Yes
Theewaterskloof	395	0.5779 ± 0.0997	0.7672 ± 0.1324	-0.1893	22.77	Yes

7.3.2 Future species distribution map and distributional changes showing ‘losers’, ‘winners’, ‘shifters’ and ‘grounded’ species

A comparative analysis has been made between species hydrological niches distributions modelled for the year 2100 based on the two irradiative forcing climate scenarios (RCP2.6 and RCP8.5). Change maps (Figure 7.1 to Figure 7.8) show the difference between the potential present and future modelled distributions with respect to the varying climate scenarios for individual species at all sites. These maps show the spatial distributional changes while the percentage change in the ranges of species or proportional distributions ate shown in Tables (Table 7.3 to Table 7.10). Distributional change maps show different colour codes for each change response: ‘loses’ as red, ‘gains’ as yellow, and ‘stable or no change’ species remain in the green shade. The black dots indicate sampled species occurences. The changes in species density are also discussed in the subsections that follow. Species richness generates quantitative predictions of the number of coexisting species.

7.3.2.1 Bastiaanskloof

At the Bastiaanskloof there will be noticeable differences in the responses of species when exposed to varying conditions of climate by 2100 (Figure 7.1). Whereas a number of species are projected to show shifts in their distributional ranges with RCP2.6 scenario conditions by this time, for the RCP8.5 scenario in contrast, in addition to shifts, there is also the potential of total extermination of a majority of species at these sites. Based on the RCP2.6 scenario projections, only *Elegia coleura* is expected to solely lose over 2% (Table 7.3) of its habitat. *Restio capensis*, *Restio curviramis*, *Restio sporadicus* and *Staberoha distachyos* show potential shifts while *Thamnochortus sporadicus* and *Willdenowia sulcata* could remain unchanged. For the RCP8.5 scenario, on the other hand, no shifts in ranges are projected. Species are shown to either contract or expand their ranges compared to current ranges including cases of possible extermination which are most probable. *E. coleura*, *R. capensis*, *R. curviramis* and *S. distachyos* are expected to lose more than 80% of their current ranges while *R. sporadicus* and *T. sporadicus* might experience over 20% increase to their current ranges. *W. sulcata* is the only species which seems unaffected by any coming changes in climatic conditions as it remains almost unchanged in both possible climatic scenarios. Generally, judging from the relatively small percentage changes of species in the RCP2.6 scenarios compared with the marked changes in the RCP8.5 ones, it could be concluded that the future would be better for most species here if humanity reduces emission rates. Ultimately, the perceived shifts in geographical distributions are an issue which would better direct management strategies.

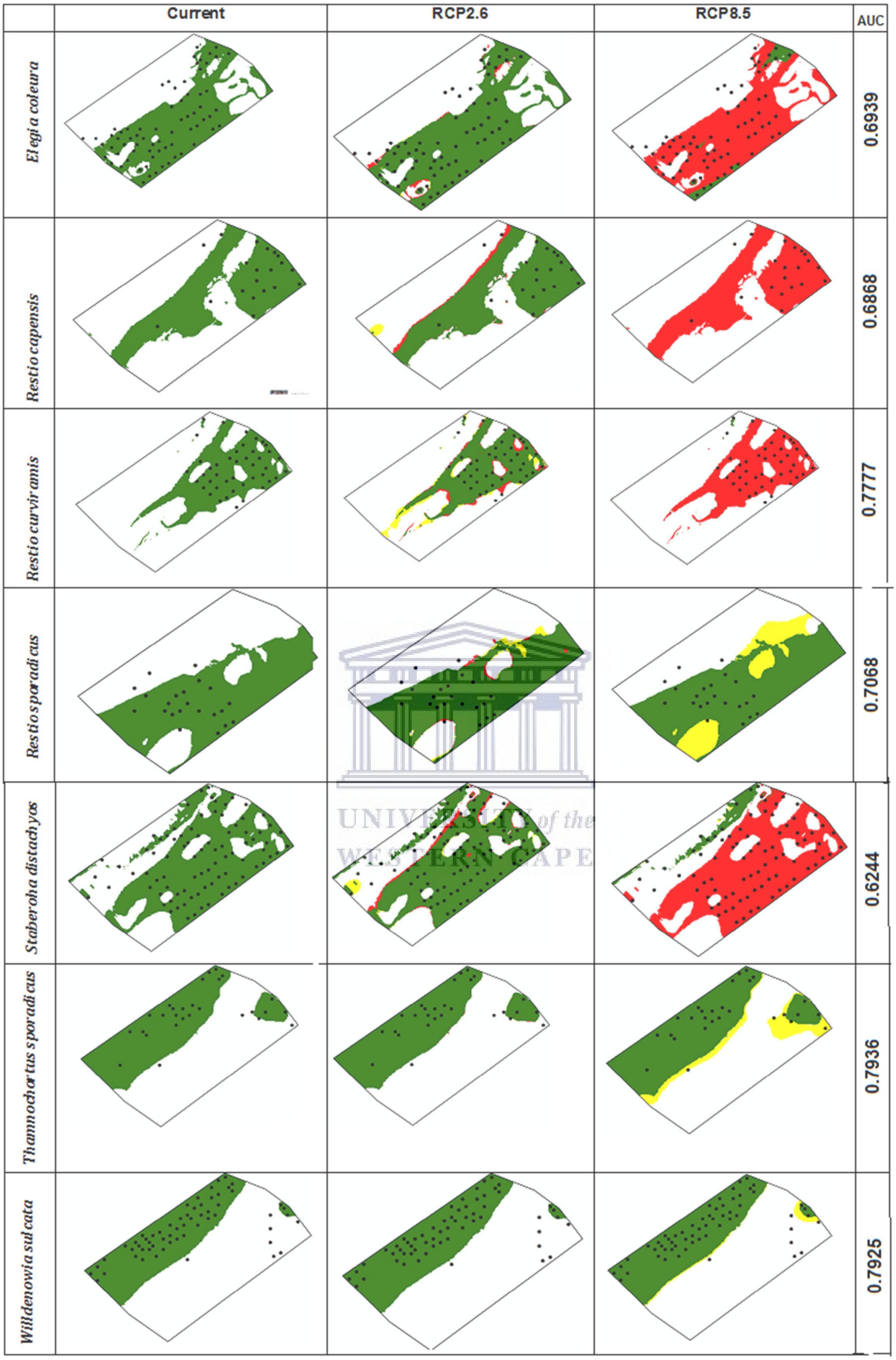


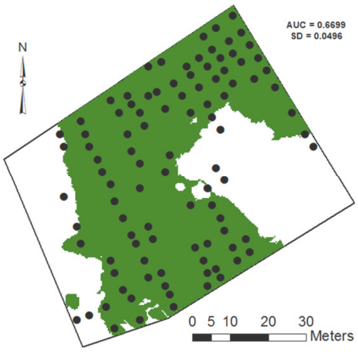
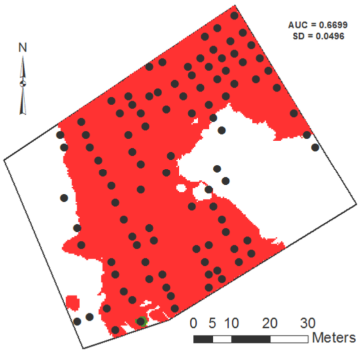
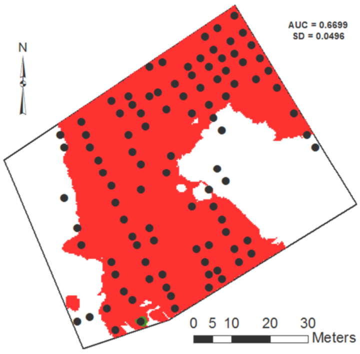
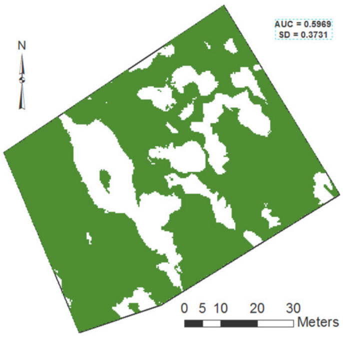
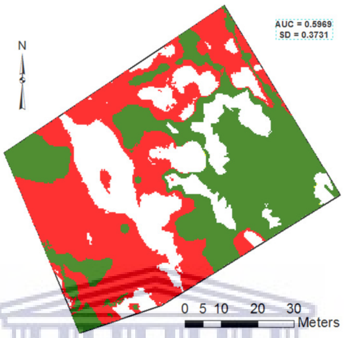
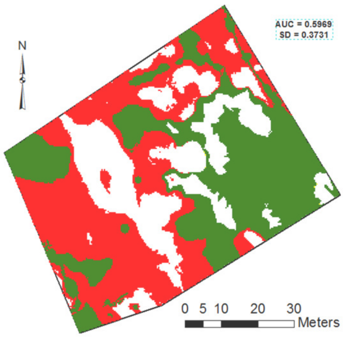
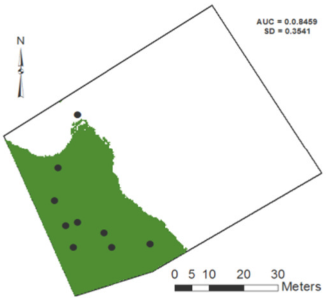
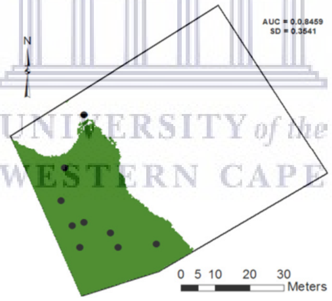
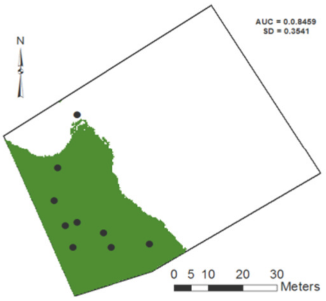
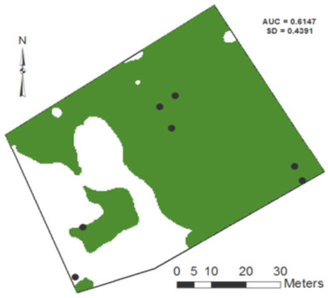
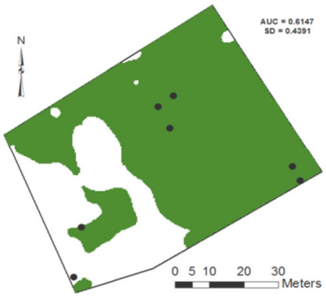
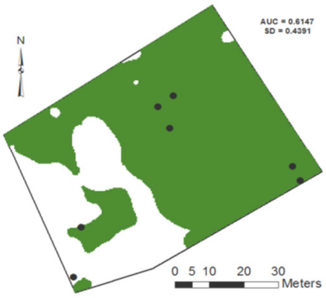
Figure 7.1. Bastiaanskloof site: Distributional change under two climate change scenarios

Table 7.3 Projected distributional change relative to current distributions at the Bastiaanskloof.

	RCP2.6 scenario				RCP8.5 scenario			
Species	**Gain %**	**Loss %**	**Net change %**	**Remark**	**Gain %**	**Loss %**	**Net change %**	**Remark**
E. coleura	0.35	-2.19	-1.84	Loss	0	-93.11	-93.11	Loss
R. capensis	1.68	-4.91	-3.23	Loss	0	-100	-100	Loss
R. curviramis	9.51	-6.90	2.61	Gain	0	-98.93	-98.93	Loss
R. sporadicus	3.24	-1.43	1.81	Gain	27.09	0	27.09	Gain
S. distachyos	2.18	-4.51	-2.33	Loss	0.39	-91.06	-90.67	Loss
T. sporadicus	0.09	-0.14	-0.05	Loss	20.72	0	20.72	Gain
W. sulcata	0	0	0	Stable	5.05	0	5.05	Gain

7.3.2.2 Cape Point

Based on their AUC values of 0.6 or more, eight Restionaceae species models from the Cape Point site were further analysed for climate change impacts. As shown in Figure 7.2, the responses of species to new (dryer) hydrological conditions are projected to be varying. The projected distributions of two species, *Elegia nuda* and *Hypodiscus aristatus,* remain unchanged for both RCP2.6 and RCP8.5 scenarios implying that these two species would be stable and unaffected by projected hydrological changes (Table 7.4). The rest of the species are expected to experience losses of varying amounts relative to their current distribution ranges. The most affected species would be *Elegia cuspidata* (99% loss), *Restio dodii* (99% loss) and *Restio tenuissisimus* (95% loss) with losses above 95%, followed by *Elegia filacea* (51% loss), *Restio quinquefarius* (48%). *Staberoha distachyos* is expected to be minimally affected with just over 6% decrease on its current potential distributions. Interestingly, it is possible that species responses will be the same during both moderate (RCP2.6) and extreme (RCP8.5) climate change scenarios as responses are uniform (Table 7.4 and Figure 7.2).

	Current	**RCP 2.6**	**RCP 8.5**	**AUC**
Elegia cuspidata				**0.6699**
Elegia filacea				**0.6069**
Elegia nuda				**0.8459**
Hypodiscus aristatus				**0.6147**

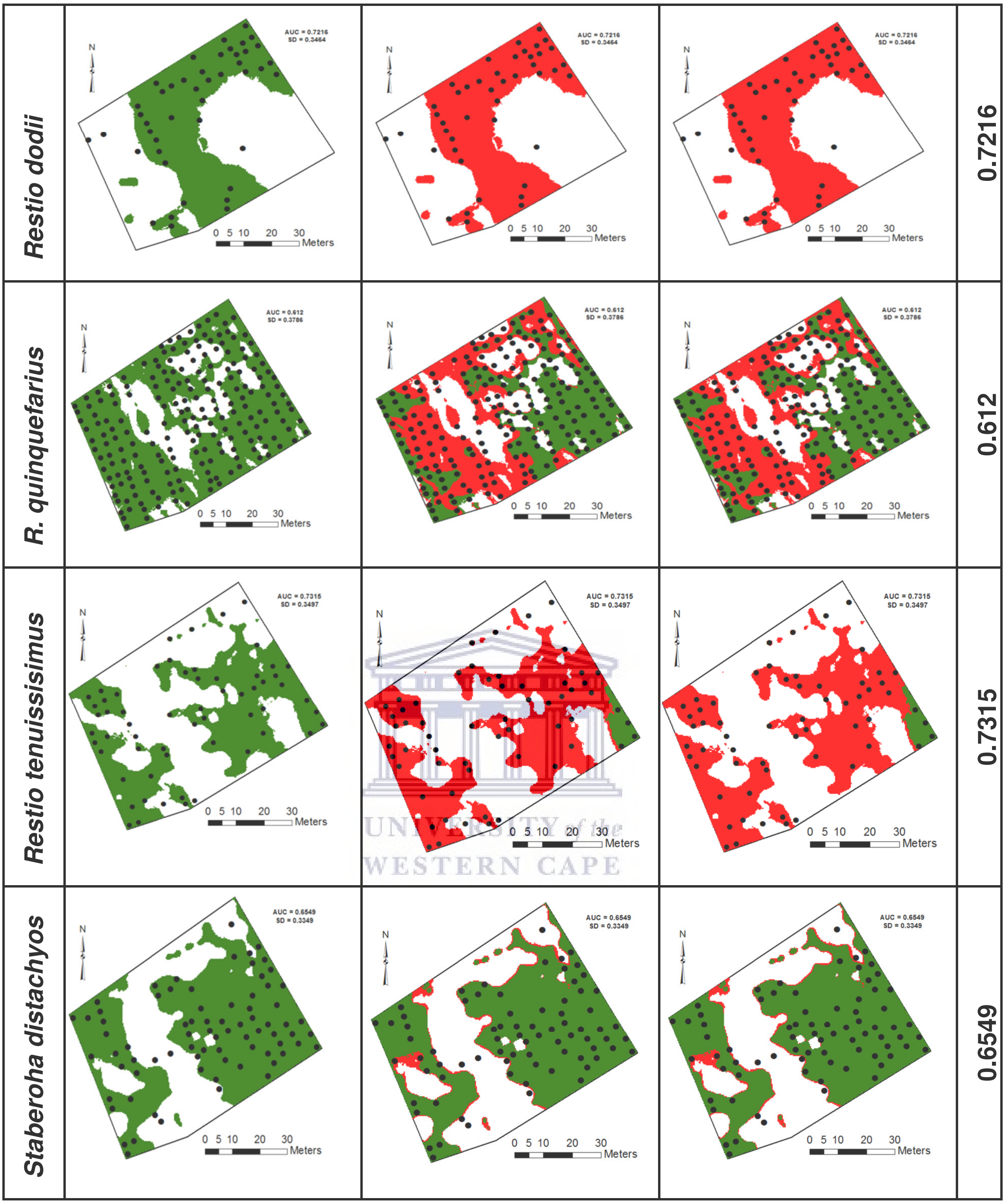


Figure 7.2 Cape Point site: Distributional change under two climate change scenarios. Map legend: Green = stable, red = contracted area, dots = current species locations.

Table 7.4 Projected distributional change relative to current distributions at Cape Point.

	RCP 2.6				RCP8.5			
Species	Gain %	Loss %	Net change	Remark	Gain %	Loss %	Net change	Remark
E.cus	0.00	-99.78	-99.77	Loss	0.00	-99.78	-99.77	Loss
E.fila	0.02	-51.25	-51.23	Loss	0.02	-51.25	-51.23	Loss
E.nuda	0.00	0.00	0.00	Stable	0.00	0.00	0.00	Stable
H.aris	0.00	0.00	0.00	Stable	0.00	0.00	0.00	Stable
R.dodi	0.00	-99.99	-99.99	Loss	0.00	-99.99	-99.99	Loss
R.quin	0.00	-48.41	-48.41	Loss	0.00	-48.41	-48.41	Loss
R.tenu	0.00	-95.00	-95.00	Loss	0.00	-95.00	-95.00	Loss
S.dist	0.00	-6.77	-6.77	Loss	0.00	-6.77	-6.77	Loss

7.3.2.3 Jonkershoek

At the Jonkershoek site, six Restionaceae species were subjected to climate change impact analysis based on their satisfactory prediction powers from Chapter 6. The predicted change in response to climate-induced hydrological changes is shown in Figure 7.3 and in Table 7.5. Of all species examined, only *Elegia juncea* showed signs of a possible distribution shift in the future. Its range may contract by 16% and expand by about 1% as a response to climate-induced hydrological changes. Three species, *Elegia asperiflora, Hypodiscus alboaristatus and Hypodiscus aristatus,* are expected to contract in the future. *Elegia asperiflora* would be the most affected losing 68%, followed by *H. aristatus*, *E. juncea* and *H. alboaristatus*. Two species might be favoured by climate change and expand their distributions. These are *Restio filiformis* and *Staberoha cernua* with range expansions of over 56% and 100%, respectively. Again, it is observed that changes in species remain similar in both climate change scenarios.

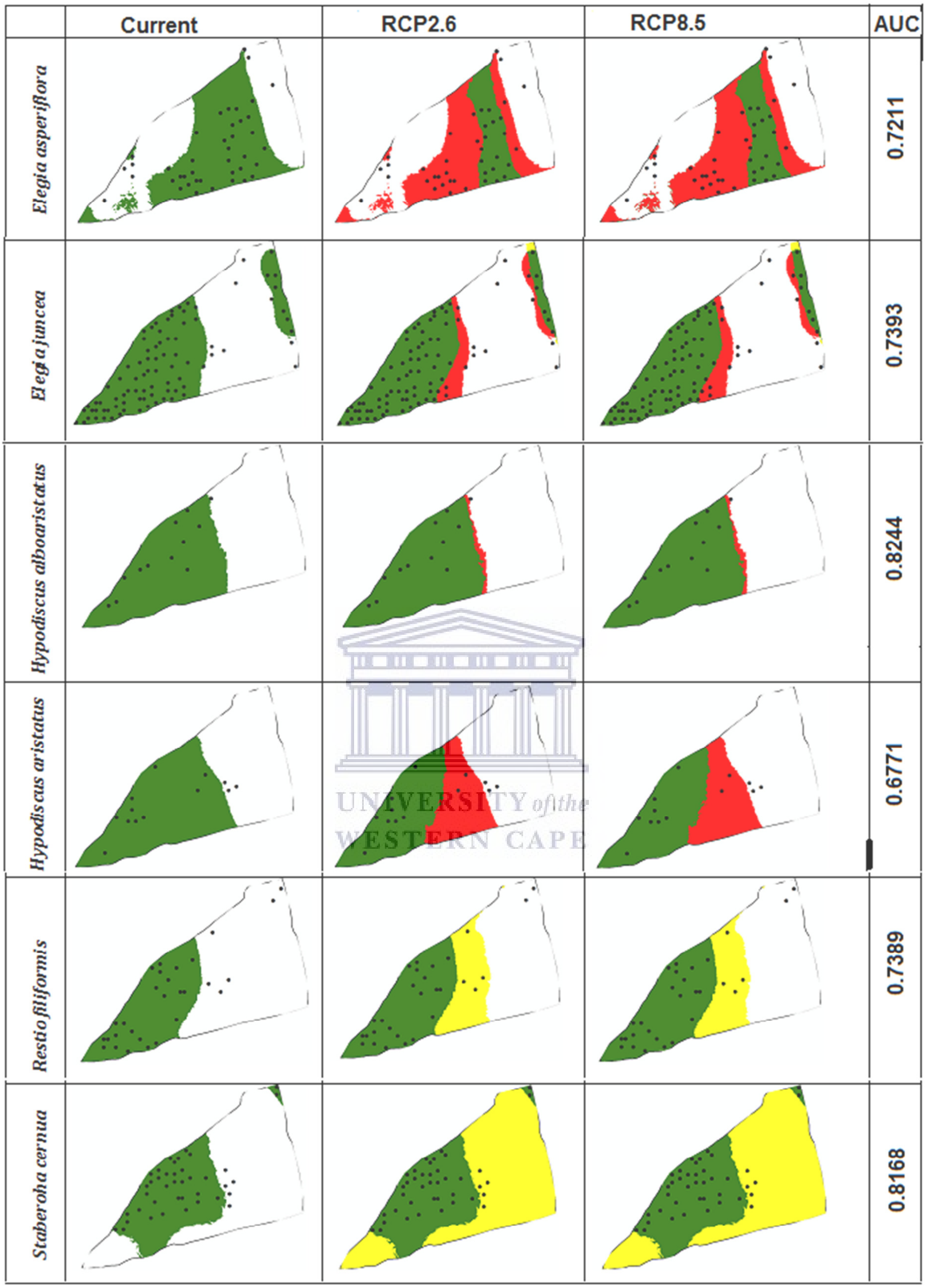


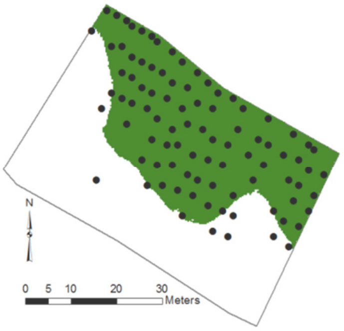
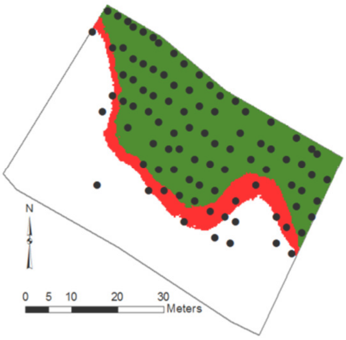
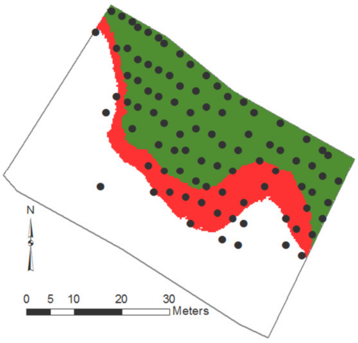
Figure 7.3 Projected distributional changes for two climatic scenarios at the Jonkershoek site

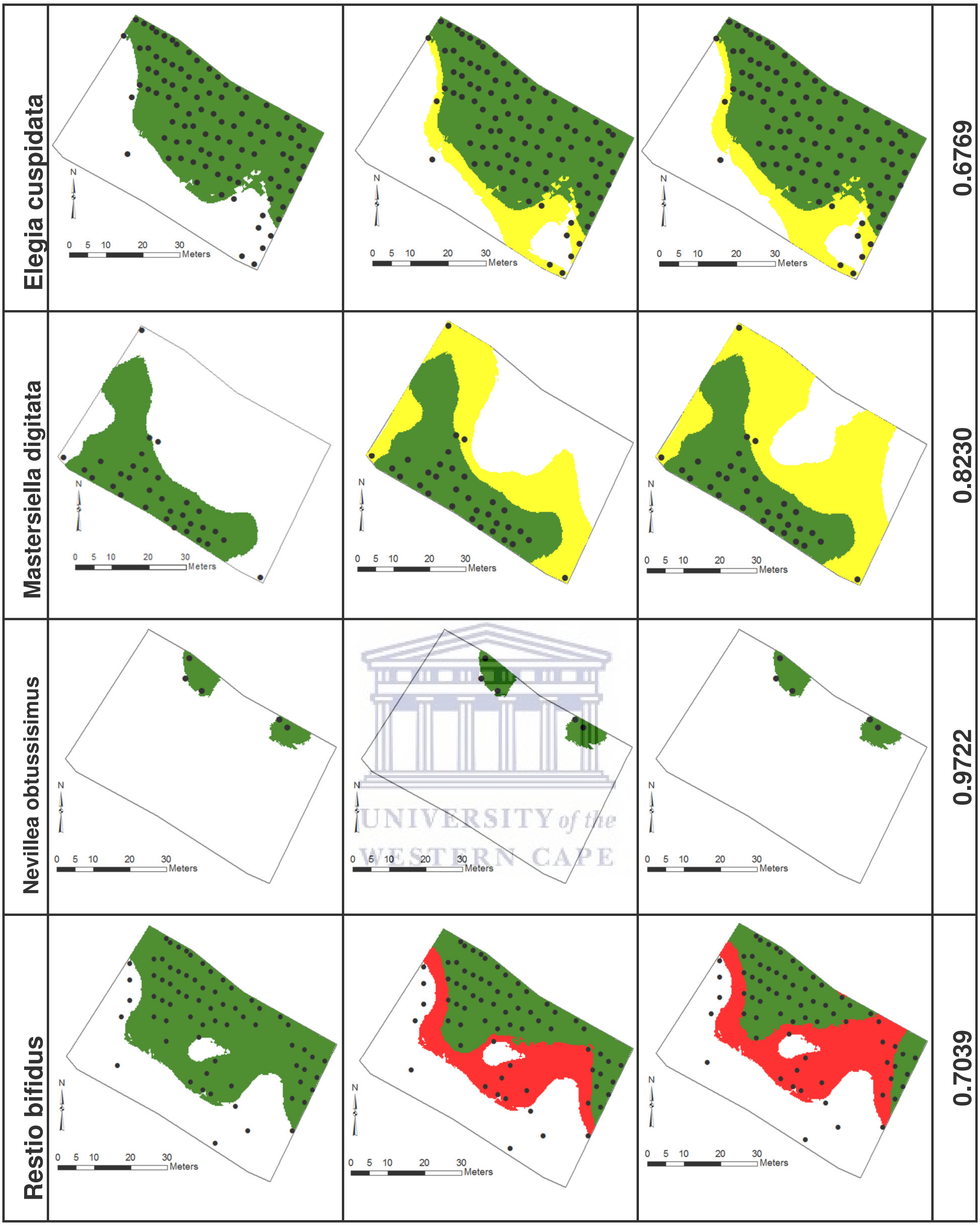
Table 7.5 Projected distributional change relative to current distributions at the Jonkershoek

	RCP 2.6				RCP8.5			
Species	Gain %	Loss %	Net change	Remark	Gain %	Loss %	Net change	Remark
E. asperiflora	0.00	-68.66	-68.66	Loss	0.00	-68.47	-68.47	Loss
E. juncea	1.49	-18.21	-16.72	Loss	1.49	-19.60	-18.11	Loss
H. alboaristatus	0.01	-3.77	-3.76	Loss	0.01	-3.76	-3.75	Loss
H. aristatus	0.00	-39.60	-39.60	Loss	0.00	-39.70	-39.70	Loss
R. filiformis	56.32	0.00	56.32	Gain	56.32	0.00	56.32	Gain
S. cernua	155.84	0.00	155.84	Gain	155.84	0.00	155.84	Gain

7.3.2.4 Kogelberg

Nine Restionaceae species from the Kogelberg site were further analysed for climate change impacts. As shown in Figure 7.4, the responses of species to drier conditions on site are projected to be varying in the future. Further details into the proportional changes by each species are shown in Table 7.6. *Elegia caespitosa, Restio bifidus* and *Staberoha distachyos* might lose between 18-29%, 41-51% and 61-81%, respectively, of their current ranges, based on future climate-induced hydrological changes (Figure 7.4 and Table 7.6). On the other hand, there is a chance that *Elegia cuspidate* (25-28% gain), *Mastersiella digitata* (92-137% gain) and *Restio hyalinus* (156-231% gain) might expand to occupy the space vacated by the retreating counterparts under these same climate-related hydrological perturbations (Figure 7.4). The trend of resilience continues with *Restio dispar* which shows a slight chance of expanding while *Nevillea obtusissimus* and *Restio nudiflorus* might remain grounded and not respond to any form of hydrological change. When compared, the magnitude of change is expected to be more severe in a more extreme climate trajectory.

	Current	**RCP 2.6**	**RCP 8.5**	**AUC**
Elegia caespitosa				**0.6895**


Elegia cuspidata
0.6769
Mastersiella digitata
0.8230
Nevillea obtussisimus
0.9722
Restio bifidus
0.7039
N
0 5 10 20 30
Meters

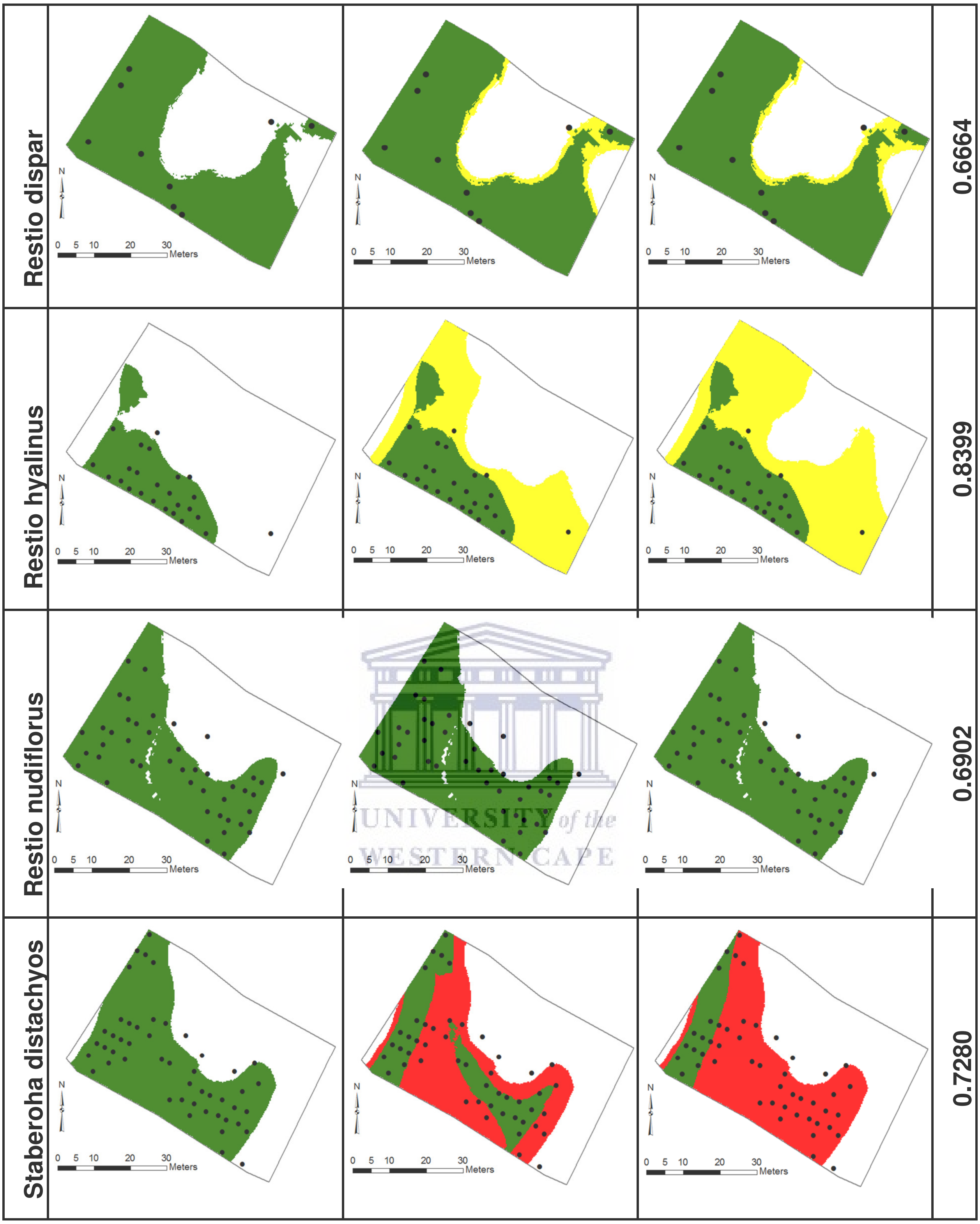


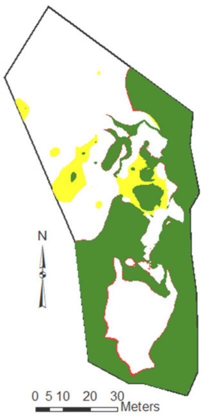
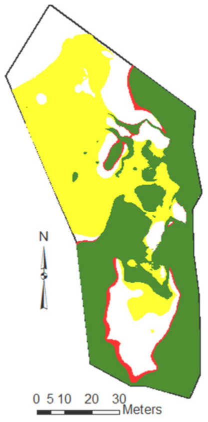
Figure 7.4 Projected distributional changes for two climatic scenarios at the Kogelberg site

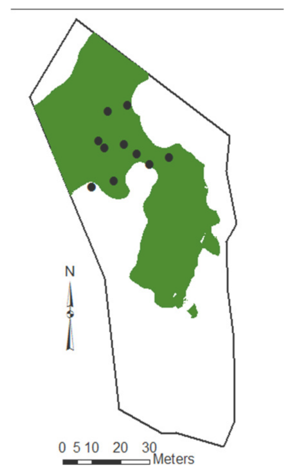
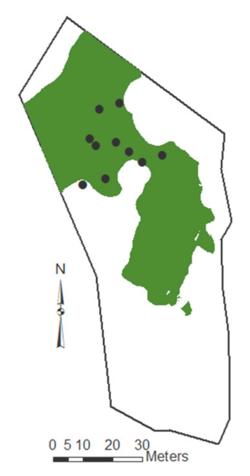
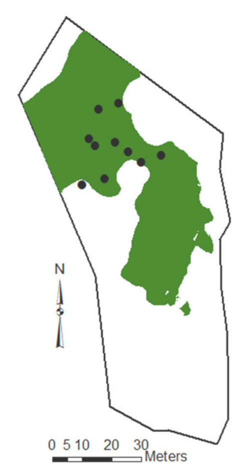
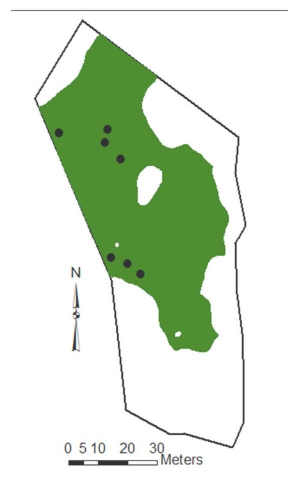
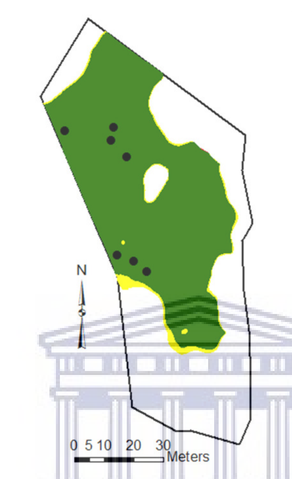
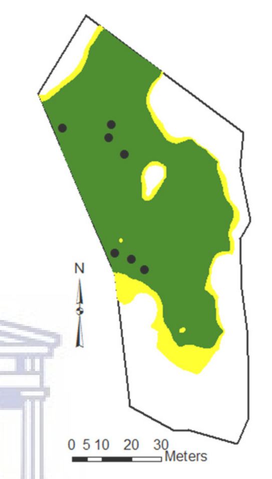
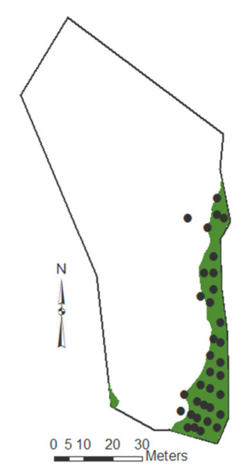
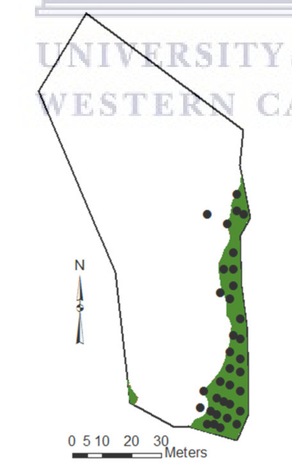
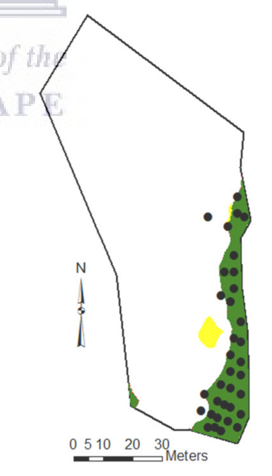
Table 7.6 Projected distributional change relative to current distributions at the Kogelberg.

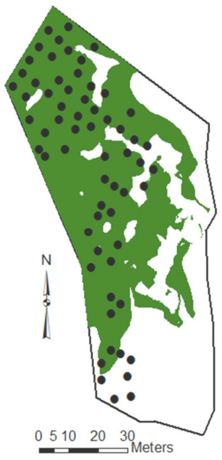
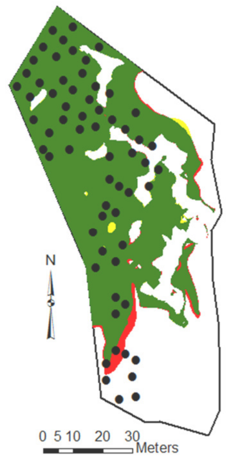
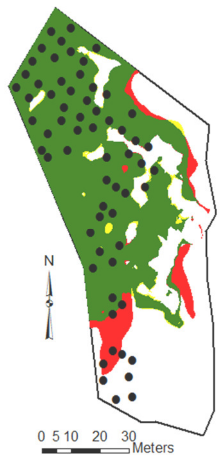
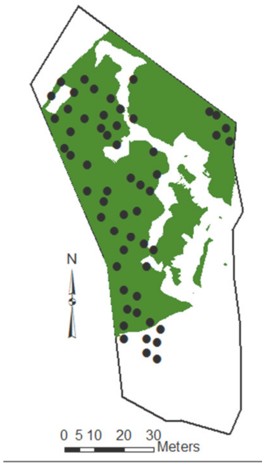
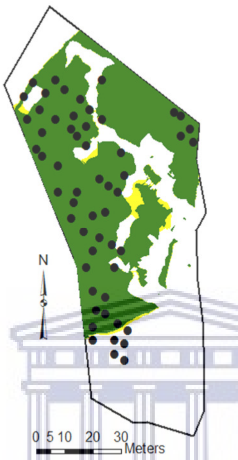
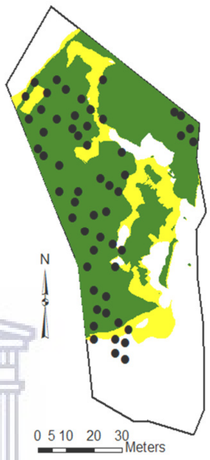
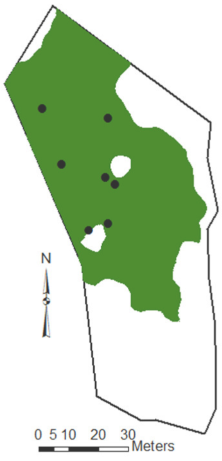
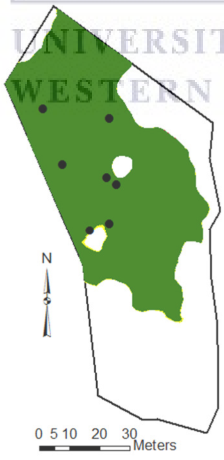
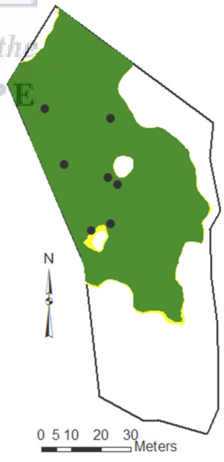
Kogelberg	RCP2.6 (%)				RCP8.5 (%)			
Species	Gain (%)	Loss (%)	Net change	Remark	Gain (%)	Loss (%)	Net change	Remark
E. caespitosa	0.00	-18.09	-18.09	Loss	0.00	-29.59	-29.59	Loss
E. cuspidata	25.63	0.00	25.63	Gain	28.34	0.00	28.34	Gain
M. digitata	92.42	0.00	92.42	Gain	137.93	0.00	137.93	Gain
N. obtissisimus	0.00	0.00	0.00	Stable	0.00	0.00	0.00	Stable
R. bifidus	0.00	-41.48	-41.48	Loss	0.00	-53.82	-53.82	Loss
R. dispar	10.30	0.00	10.30	Gain	15.23	0.00	15.23	Gain
R.hyalinus	156.09	0.00	156.09	Gain	231.11	0.00	231.11	Gain
R.nudiflorus	0.00	0.00	0.00	Stable	0.00	0.00	0.00	Stable
S. distachyos	0.00	-61.47	-61.47	Loss	0.00	-81.98	-81.98	Loss

7.3.2.5 New Years Peak

Of the 10 species considered for post modelling analysis for the NYP site, two species, i.e. *Hypodiscus aristatus* and *Staberoha cernua*, remained unchanged or relatively unchanged (Figure 7.5). Species seen to possibly experience shifts included *Anthochortus crinalis*, *Elegia coleura*, *Elegia neesii*, *Hypodiscus aristatus*, *Restio curviramis* and *Restio obtusissimus* (Table 7.7). Three species might invade new territory. These include *Elegia filiformis, R. boluscii* and *Restio miser* seem to be favoured by new climatic conditions due to climate change (Table 7.7). All forms of change will be more severe under the RCP8.5 scenario conditions. The most significant loses would be experienced by *E. coleura* with up to 24% loss of habitat (Figure 7.5 and Table 7.7). The rest of the species models exhibit relatively minute change compared with their current ranges.

	Current	RCP 2.6	RCP 8.5	AUC
Anthochortus crinalis				**0.7967**

Staberoha cernua				**0.8019**
Restio obscurus				**0.6629**
Restio miser				**0.9317**

Restio curviramis				**0.7600**
Restio boluscii				**0.6992**
Hypodiscus aristatus				**0.6786**

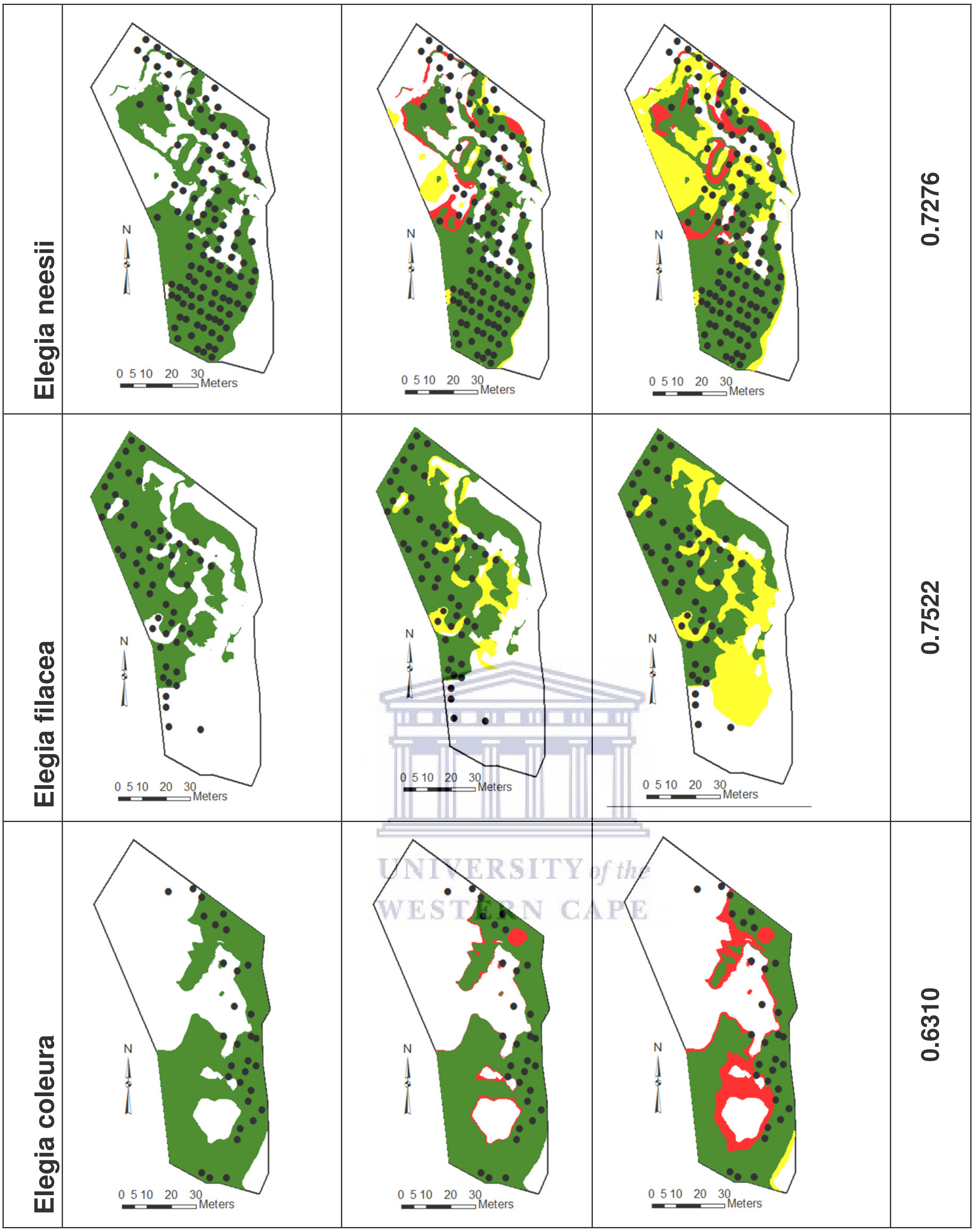


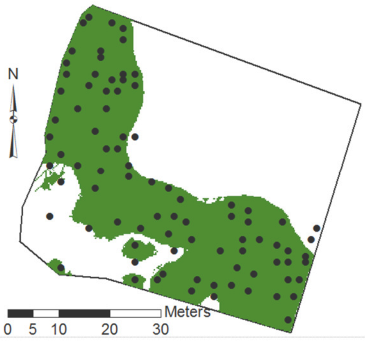
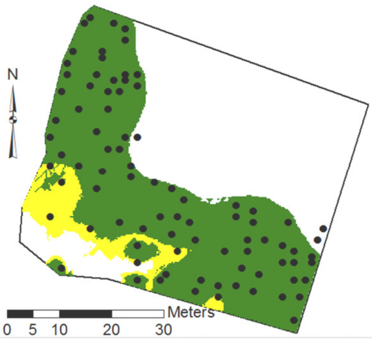
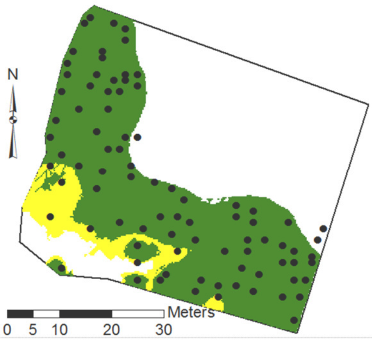
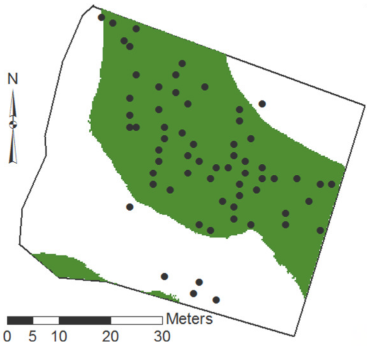
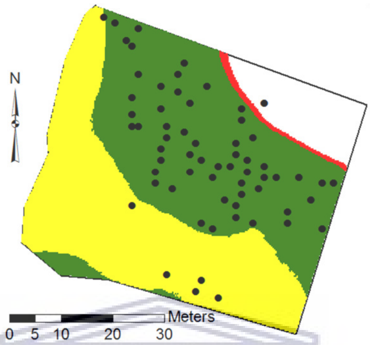
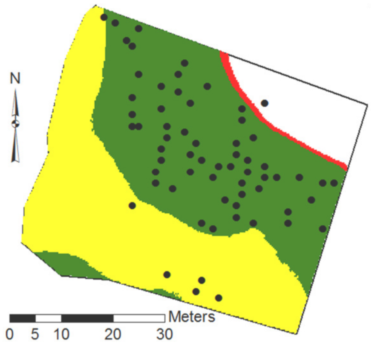
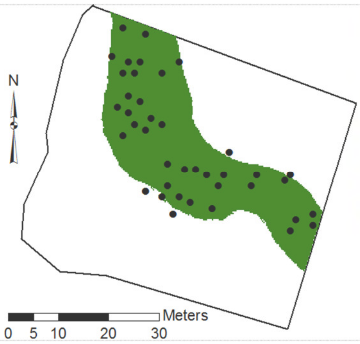
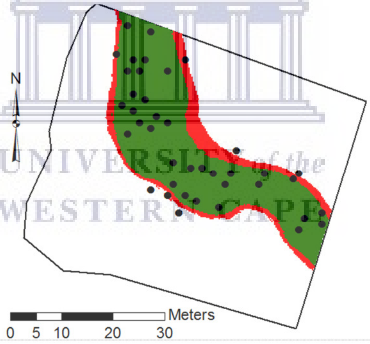
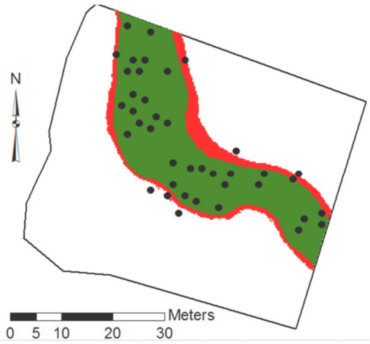
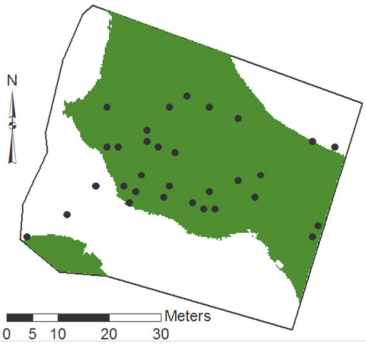
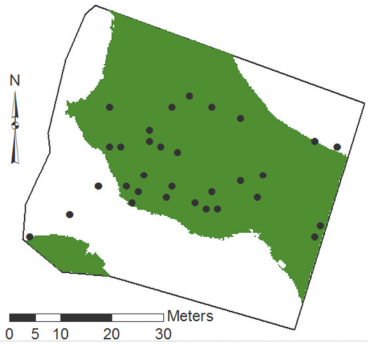
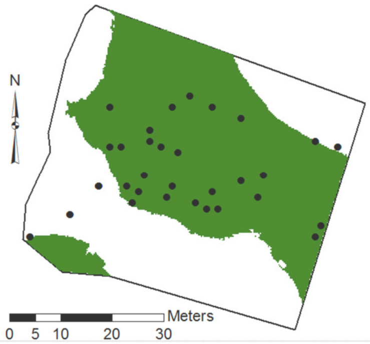
Figure 7.5 Projected distributional changes for two climatic scenarios at the New Years Peak site

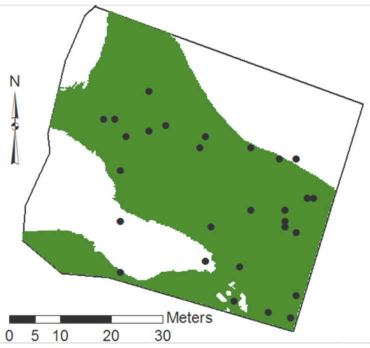
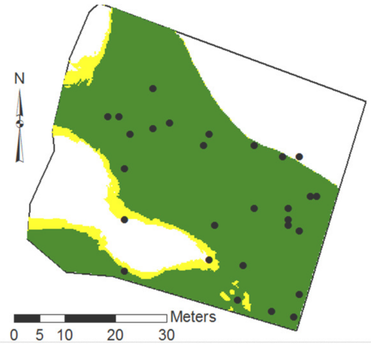
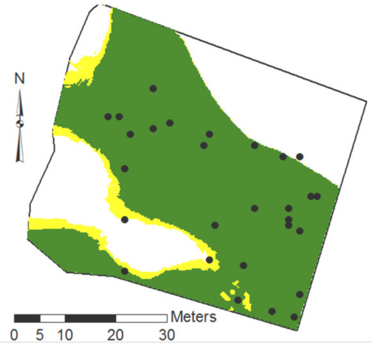
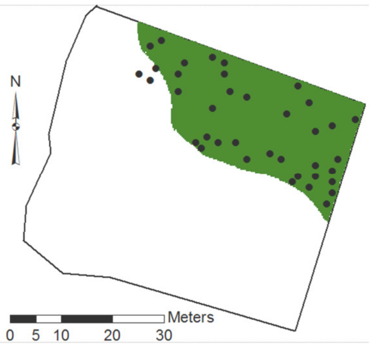
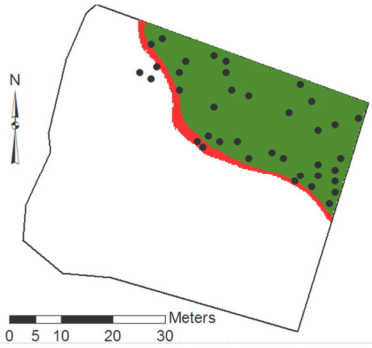
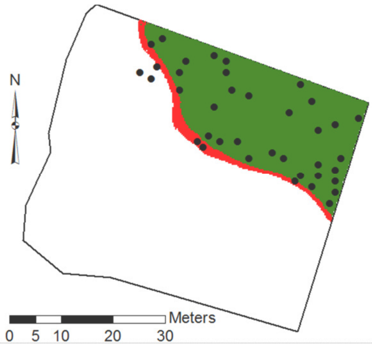
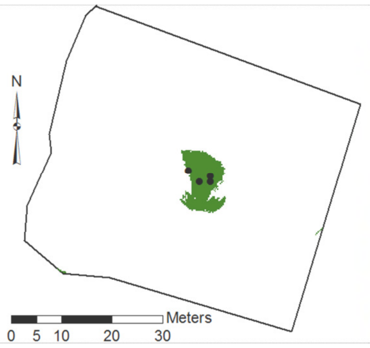
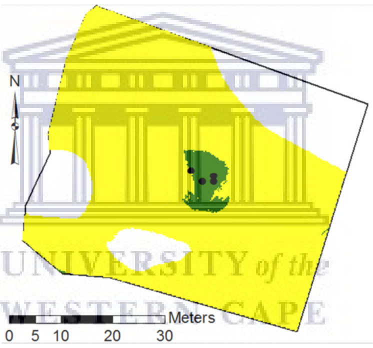
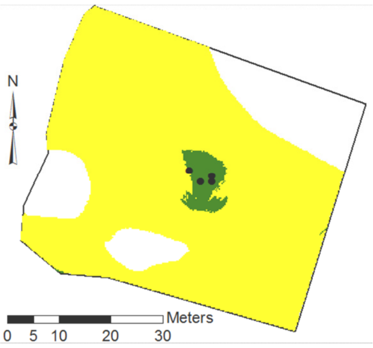
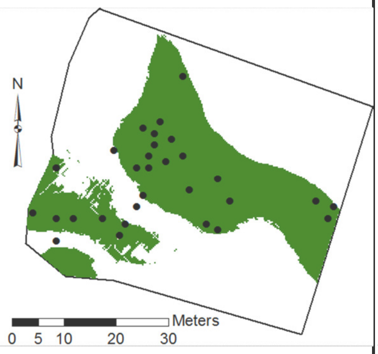
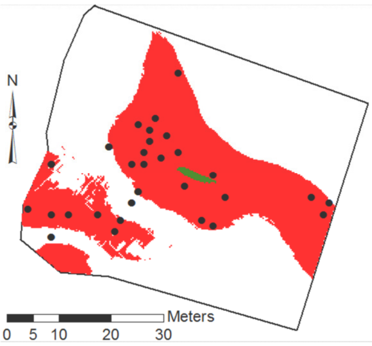
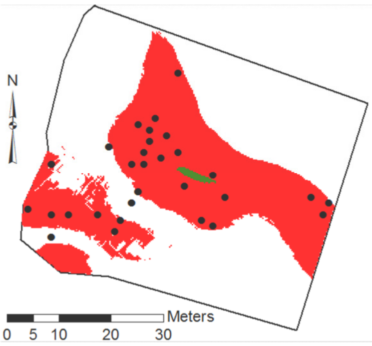
Table 7.7 Projected distributional change relative to current distributions at the New Years Peak.

	RCP2.6 scenario				**RCP8.5 scenario**			
Species	**Gain (%)**	**Loss (%)**	**Net change**	**Remark**	**Gain (%)**	**Loss (%)**	**Net change**	**Remark**
A. crinalis	13.32	-2.36	10.96	Gain	80.62	-5.62	75.00	Gain
E. coleura	0.98	-5.52	-4.54	Loss	1.65	-26.15	-24.49	Loss
E. filiformis	19.42	0.00	19.42	Gain	52.90	0.00	52.90	Gain
E. neesii	9.65	-8.78	0.87	Gain	48.16	-12.17	35.99	Gain
H. aristatus	0.71	-0.01	0.70	Gain	2.31	0.00	2.31	Gain
R. bolusii	3.84	0.00	3.84	Gain	25.88	0.00	25.88	Gain
R. curviramis	0.97	-3.64	-2.67	Loss	2.38	-9.99	-7.61	Loss
R. miser	0.00	-0.18	-0.18	Loss	9.12	-0.55	8.57	Gain
R. obscurus	4.57	-0.01	4.55	Gain	15.21	0.00	15.21	Gain
S. cernua	0.00	0.00	0.00	Stable	0.00	0.00	0.00	Stable

7.3.2.6 Riverlands

At the Riverlands site, the twelve species models examined showed losing, gaining, shifting and stable models due to climate change impacts (Figure 7.6 and Table 7.8). Only Elegia nudiflorus shows possible shifts. Three species might remain unchanged. These include *Restio capensis, Staberoha distachyos* and *Willdenowia arescens* (Figure 7.6). Gaining species e.g. *Elegia filacea*, *Thamnochortus punctatus* and *Willdenowia sulcata* extended their hydrological niches towards remnants of previously moist locations. Meanwhile, *Restio quinquefarius,* previously restricted to the centre of the plot, seems to show the most gain as it is expected to expand its range by more than 100% into the entire space (Figure 7.6). *Restio monanthos*, *Hypodiscus aristatus* are reduced slightly while *Restio vimineus* will be the most adversely affected species as its models show there might be a complete disappearance of its hydrological niches (Figure 7.6 and Table 7.8).

	Current	RCP 2.6	RCP 8.5	AUC
Elegia filacea				**0.7313**
Elegia nuda				**0.7609**
H. willdenowia				**0.8408**
Restio capensis				**0.6828**

Restio macer				0.617
Restio monanthos				0.8504
Restio quinquefarius				0.9867
Restio vimineus				0.7467

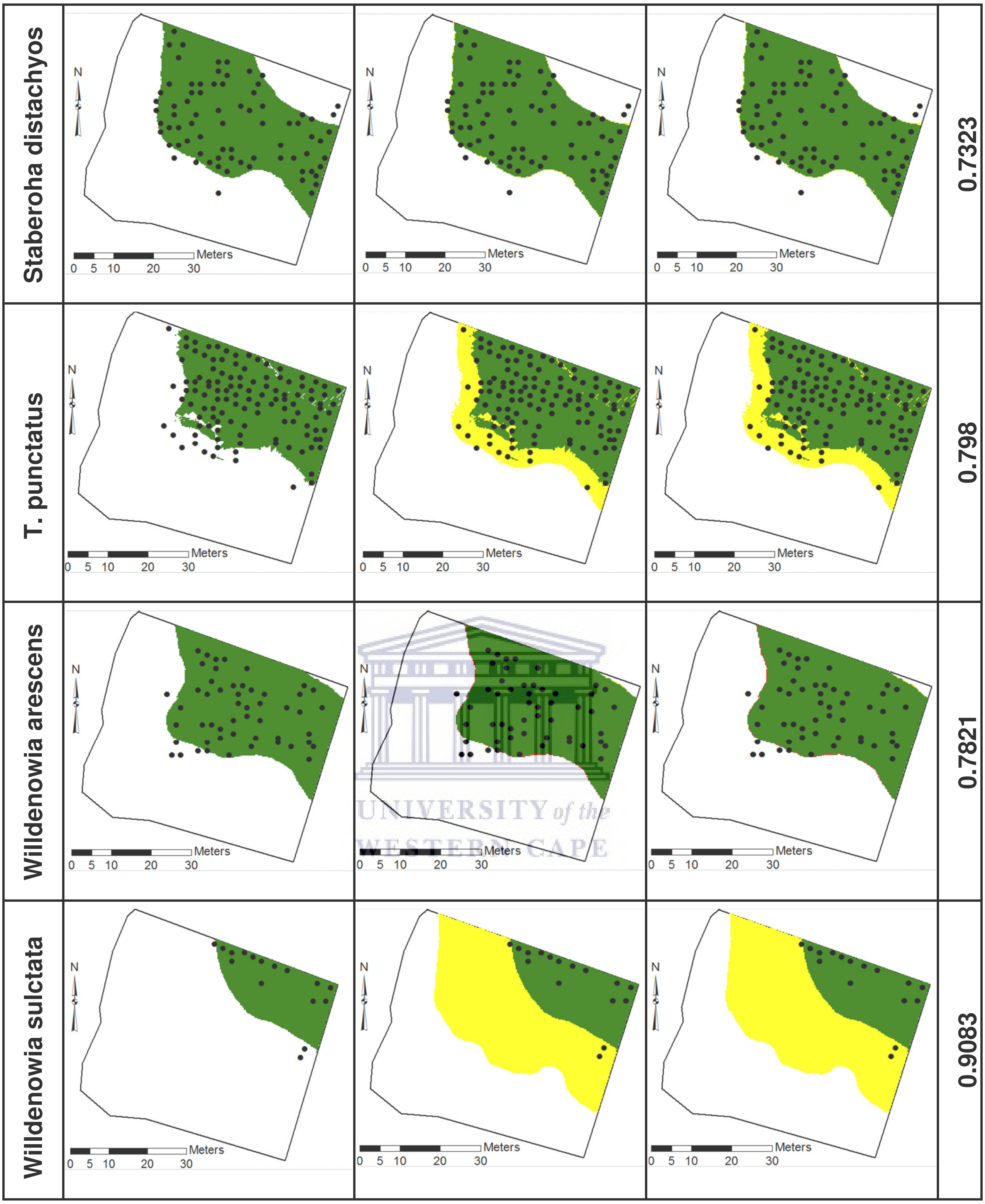


Figure 7.6. Projected distributional changes for two climatic scenarios at the Riverlands site

Table 7.8.Projected distributional change relative to current distributions at Riverlands.

	RCP 2.6				RCP8.5			
Species	Gain %	Loss %	Net change	Remark	Gain %	Loss %	Net change	Remark
E. filacea	14.20	0.00	14.20	Gain	14.20	0.00	14.20	Gain
E. nudiflorus	79.55	-2.37	77.18	Gain	79.55	-2.37	77.18	Gain
H. willdenowia	0.00	-18.98	-18.98	Loss	0.00	-18.98	-18.98	Loss
R. capensis	0.00	-0.12	-0.12	Stable	0.00	-0.12	-0.12	Stable
R. macer	8.98	0.00	8.98	Gain	8.98	0.00	8.98	Gain
R. monanthos	0.00	-8.91	-8.91	Loss	0.00	-8.91	-8.91	Loss
R. quinquefarius	100.00	0.00	100.00	Gain	100.00	0.00	100.00	Gain
R. vimineus	0.00	-99.12	-99.12	Loss	0.00	-99.12	-99.12	Loss
S. distachyos	1.03	0.00	1.03	Stable	1.03	0.00	1.03	Stable
T. punctatus	36.55	0.00	36.55	Gain	36.55	0.00	36.55	Gain
W. arescens	0.11	-0.68	-0.57	Stable	0.11	-0.68	-0.57	Stable
W. sulcata	100.00	0.00	100.00	Gain	100.00	0.00	100.00	Gain

7.3.2.7 Silvermine

Figure 7.7 and Table 7.9 show varying levels of response to climate-induced hydrological changes at the Silvermine in the future. There is a general loss of habitat as conditions become drier over time. By the turn of the century, species concentrate mostly at the remnants of previously very wet points. Shifters include *Hypodiscus aristatus*, *Restio capensis* and *Restio cincinnatus*. *H. aristatus* and *R. capensis* seem to show some loss but would generally expand their ranges especially under RCP8.5 conditions. *R. capensis* benefits the most as it keeps expanding from about 44%, if in the RCP2.6 scenario, to above 100% increase in its range, if the RCP8.5 climate scenario alternative prevails (Table 7.9). *R. cincinnatus* shows a very interesting pattern of change. There is a chance it might expand under the RCP2.6 conditions but this fades away in the RCP8.5 conditions in the favour of contractions. Hypodiscus willdenowia remains unchanged. *Elegia filacea, Restio cincinnatus*, *Staberoha cernua* and *Thamnochortus gracilis* stand the risk of eradication in the future especially under RCP8.5 climatic conditions compared with RCP2.6 scenarios. In all instances of change, the species models show the magnitude of change is greater for the RCP8.5 than over the RCP2.6 projected conditions.

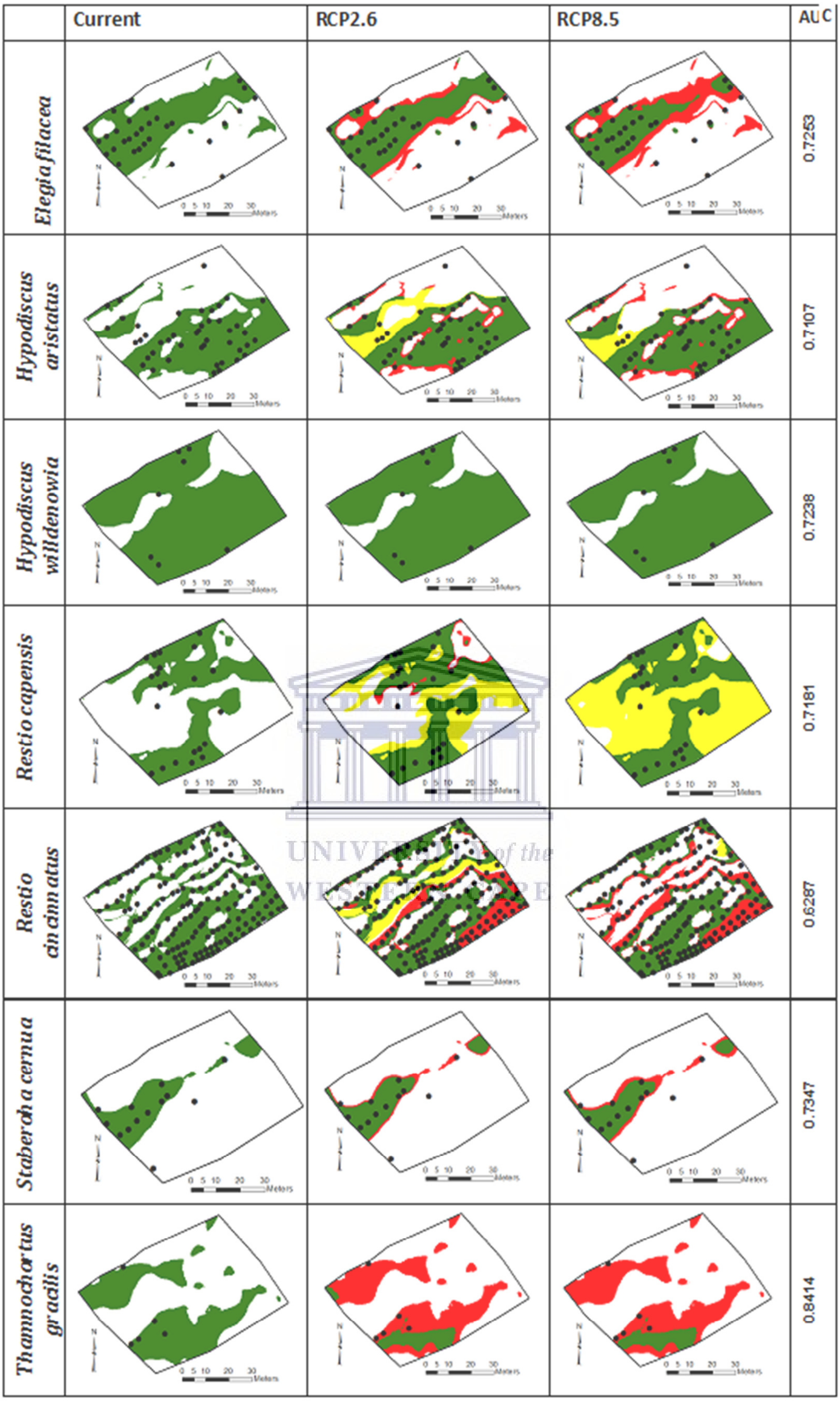


Figure 7.7 Projected distributional changes for two climatic scenarios at the Silvermine site

Table 7.9 Projected distributional change relative to current distributions at the Silvermine site.

	RCP 2.6				RCP8.5			
Species	Gain %	Loss %	et change	Remark	Gain %	Loss %	et change	Remark
E. filacea	0.00	-26.08	-26.08	Loss	0.00	45.53	-45.53	Loss
H. aristatus	21.52	-11.42	10.11	Gain	11.11	14.09	-2.98	Loss
H. willdenowia	0.00	0.00	0.00	Stable	0.00	0.00	0.00	Stable
R. capensis	48.77	-4.73	44.04	Gain	125.50	0.00	125.50	Gain
R. cincinnatus	19.68	-25.48	-5.80	Loss	1.43	37.25	-35.80	Loss
S. cernua	0.00	-20.68	-20.68	Loss	0.00	31.66	-31.66	Loss
T. gracillis	0.00	-82.18	-82.18	Loss	0.00	111.39	-111.39	Loss

7.3.2.8 Theewaterskloof

Figure 7.8 and Table 7.10 show the results of change impact analysis for ten Restionaceae species models (deemed qualified from Chapter 6) at the Theewaterskloof site. *Anthochortus crinalis*, *Elegia capensis* and *Staberoha cernua* might contract at varying degrees and these responses will be more severe for the RCP8.5 than for the RCP2.6 future climate scenario. Four other species remain stable (*Elegia thyrsifera*, *Platycaulos callistachyos*, *Restio pedicellatus* and *Thamnochortus fruticosus*) (Table 7.10). These stable species maintain the same patterns as shown in Chapter 6 and are not shown in Figure 7.8 for the purpose of space. Finally, *Elegia neesii* and *Staberoha distachyos* are expected to experience a shift in range towards the remnants of moist sections of the now drier plot. Interestingly, *S. distachyos* is prone to expand extensively under RCP2.6 condition and contract relatively less and might end up with a net gain in change. Under RCP8.5 conditions, the species might expand less, resulting in a net loss of habitat space as result of the change.

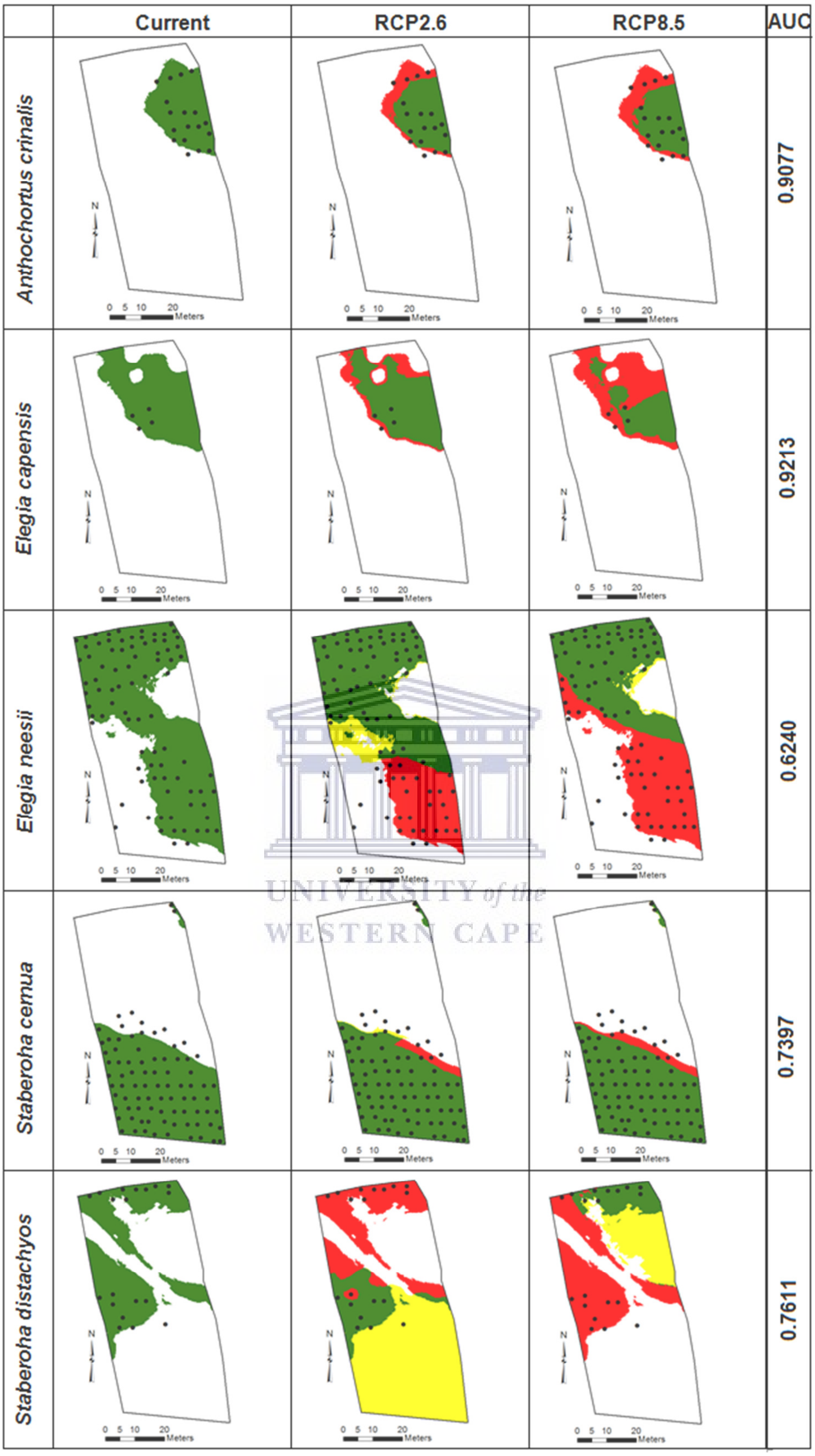


Figure 7.8. Projected distributional changes for two climatic scenarios at the Theewaterskloof site

Table 7.10. Projected distributional change relative to current distributions at the Theewaterskloof

	RCP 2.6				RCP8.5			
Species	Gain (%)	Loss (%)	Net change	Remark	Gain (%)	Loss (%)	Net change	Remark
A. crinalis	0.00	-29.09	-29.09	Loss	0.00	-37.57	-37.57	Loss
E. asperiflora	0.00	0.00	0.00	Stable	0.00	0.00	0.00	Stable
E. capensis	0.00	-22.66	-22.66	Loss	0.00	-60.28	-60.28	Loss
E. neesii	10.21	-31.82	-21.61	Loss	2.25	-47.60	-45.35	Loss
E. thyrsifera	0.00	0.00	0.00	Stable	0.00	0.00	0.00	Stable
P. callistachyos	0.00	0.00	0.00	Stable	0.00	0.00	0.00	Stable
R. pedicellatus	0.00	0.00	0.00	Stable	0.00	0.00	0.00	Stable
S. cernua	1.30	-5.03	-3.72	Loss	0.10	-7.79	-7.70	Loss
S. distachyos	141.65	-62.64	79.00	Gain	43.31	-75.38	-32.07	Loss
T. fruticosus	0.00	0.00	0.00	Stable	0.00	0.00	0.00	Stable

7.3.2.9 Conclusion

Future RCP climate scenarios values differed significantly in the study area. Both RCPs, in turn, caused significant changes in the hydrological niches of most sites by 2100. In comparison, RCP 8.5 scenarios result in more significant changes than RCP 2.6. Most species have shown to have their own hydrological niches, which indicates that they each have individual hydrological requirements although they all coexist in their habitats. The impact of climate change on species varied for individual species across the sites. Different environmental variables acted differently on the species niches at these different sites. Species showed the full range of possible changes that might occur as responses to climate change including gains, losses, shifts and stability in the projected ranges. In general, the changes appear not to result in the loss of species but rather in range shifts. Care is, however, taken when making general inferences based on the perceived species responses from modelling because these models were created from trained conditions. In most sites, the change in climate is expected to introduce novel conditions which are totally outside of the hydrological ranges known today. Hence, there is uncertainty and any inferences on the behaviour of species in the future at this stage remain grossly speculative. Additional experiments would be required to ascertain the actual hydrological regimes of species and the behavioural trends alongside alterations of these regimes in order to effectively conclude on plant possible migratory response to change. Again, plant response behaviour is not exclusive to the influence hydrological variables but also due to the presence of other environmental factors which could be included in future experimental designs. The next section attempts a comparison of common species.

7.3.3 Species richness

Species richness across communities of all the sites was observed to vary for the present as well as for the future (Figure 7.9 – 7.16). Species richness values ranged from 0 designating low species richness areas to maximum depending on the species numbers for the site. Equally, some parts of plots were projected to remain low in species density while others increased in richness in the future.

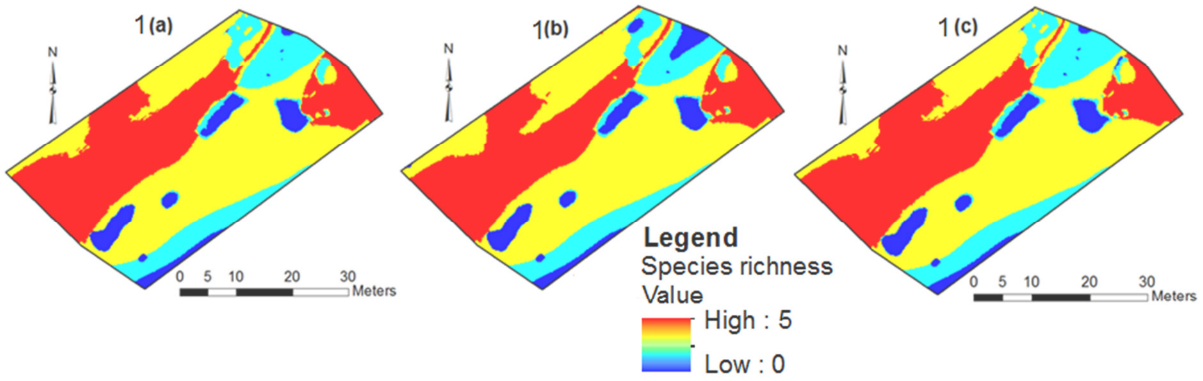


Figure 7.9 Changes in species richness for(1a) Current, (1b) future GCM RCP2.6, (1c) future GCM RCP8.5 climatic scenarios at the Bastiaanskloof site.

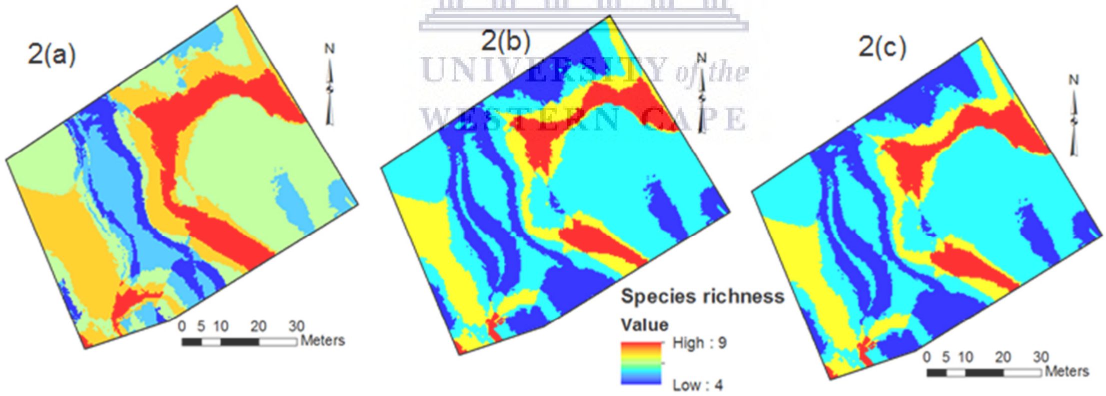


Figure 7.10.Changes in species richness from current to future climatic scenarios at the Cape Point site (2a) Current, (2b) GCM RCP2.6, (2c) GCM RCP8.5 scenario.

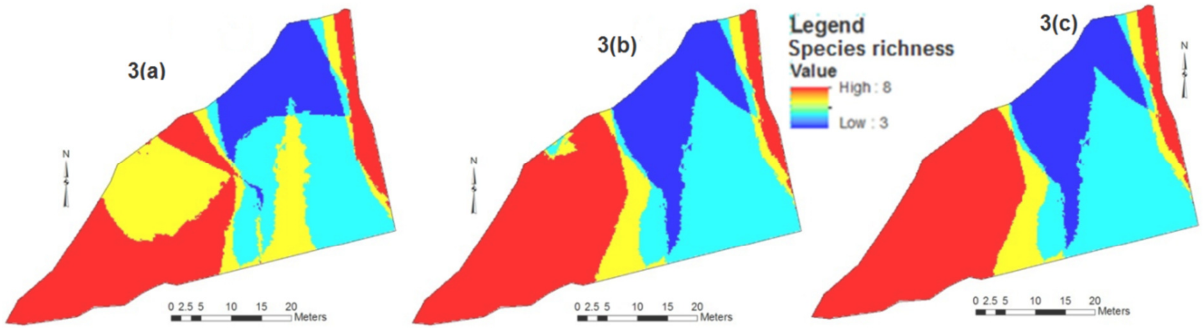


Figure 7.11.Changes in species richness from current to future climatic scenarios at the Jonkershoek site (3a) Current, (3b) GCM RCP2.6, (3c) GCM RCP8.5 scenario.

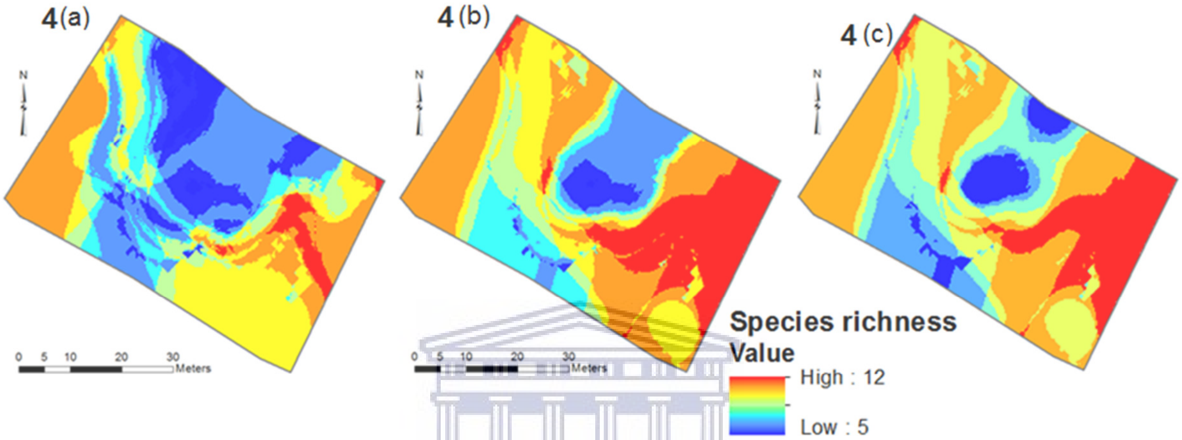


Figure 7.12.Changes in species richness from current to future climatic scenarios at the Kogelberg site (4a) Current, (4b) GCM RCP2.6, (4c) GCM RCP8.5 scenario.

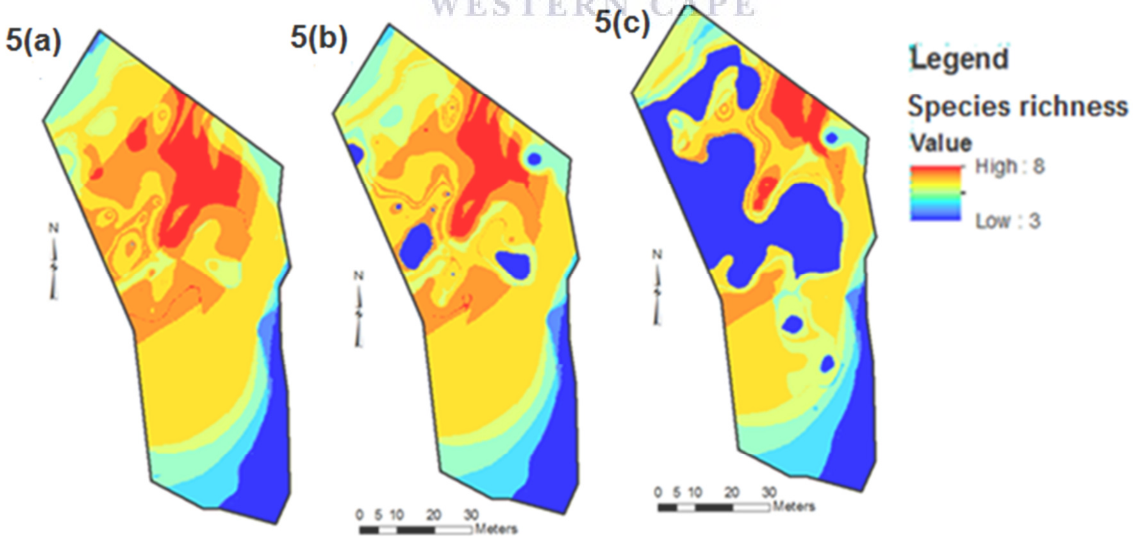


Figure 7.13.Changes in species richness from current to future climatic scenarios at the New Years Peak site (5a) Current, (5b) GCM RCP2.6, (5c) GCM RCP8.5 scenario.

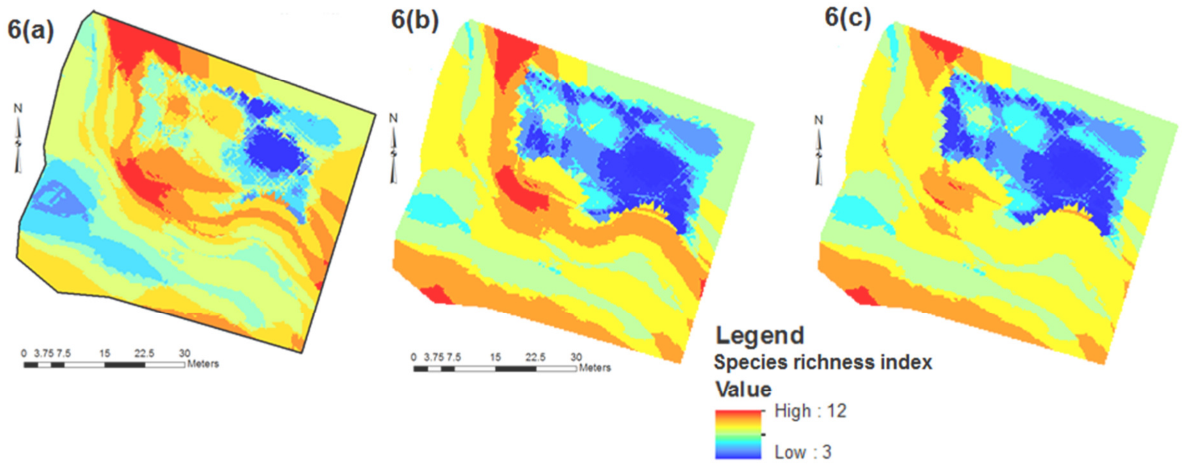


Figure 7.14.Changes in species richness from current to future climatic scenarios at the Riverlands site (6a) Current, (6b) GCM RCP2.6, (6c) GCM RCP8.5 scenario.

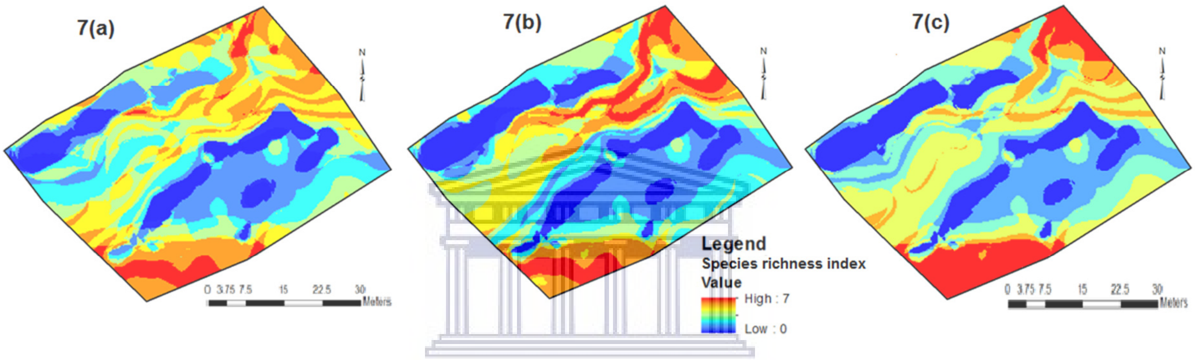


Figure 7.15 Changes in species richness from current to future climatic scenarios at the Silvermine site (7a) Current, (7b) GCM RCP2.6, (7c) GCM RCP8.5 scenario.

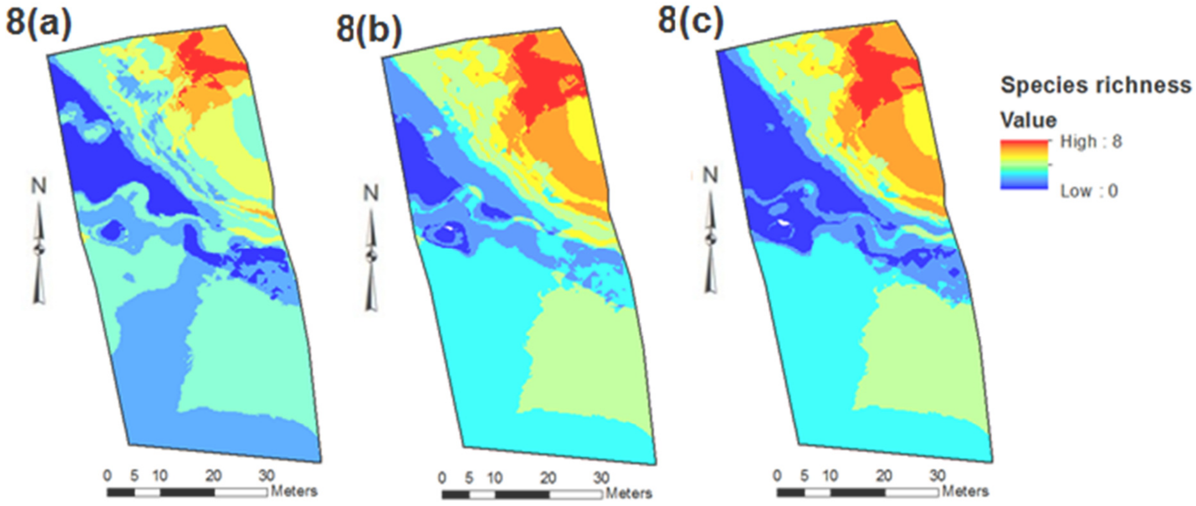


Figure 7.16. Changes in species richness from current to future climatic scenarios at the Theewaterskloof (8a) current (8b) GCM RCP2.6 (8c) GCM RCP8.5 scenario.

7.3.4 Comparative analysis of some frequent species models (common to many sites)

Elegia filacea, *Restio capensis*, *Restio curviramis* and *Staberoha distachyos* were considered for examination as frequently occurring species. In regard to the future distribution of the frequently occurring Cape Restionaceae modelling suggests that their geographical distribution ranges will change under predicted levels of climate change. RCP 2.6 and RCP 8.5 scenarios respectively predict generally warmer conditions which would enhance evaporation and render lowered soil water levels leading to drier soil conditions. An overview of the net distributional change by three most frequently occurring species is shown in Appendix 5.

7.3.4.1 Restio capensis

Restio capensis occurs at the Bastiaanskloof, Riverlands and Silvermine sites. Overall, the SDMs were successful at discriminating between suitable and unsuitable hydrological niches at all three sites. Satisfactory model predictions (AUC > 0.6) were achieved (Table 7.1) which makes the results valid for further inferences.

MaxEnt Jack-knife test of variable importance in showed that *R. capensis* model is significantly favoured by MWTD and SEVd. These two variables had the highest gains when used in isolation and equally decreased the gain the most when omitted which appears to mean that these variables have the most useful information to influence the modelling processes. Considering the average contributions of these parameters at sites where they were sampled, it is seen that MWTD and SEVd still contributed 33.1% and 36.6%, respectively, during the discrimination process at which signifies that these two parameters play a vital role in the species distribution. As such, it could be considered that *R. capensis* occurs within a MWTD range of 0.5 to 0.9 m and SEVd of 14.4 to 23.1 m.wk (see Table 7.1). These values indicate that *R. capensis* prefers drier soil conditions. Although the species cohabits successfully with *R. curviramis* and *S. distachyos, E. nuda*, and *R. cincinnatus*, It is not a very adaptable species as it retreats to a specialised niche where competition is minimal. It competes poorly within the shared niche. Generally, *R. capensis* would lose its habitat based on future climate change projections. Faced with a drop in moisture levels due to climate change, the species could lose about 4% of its current habitat at Riverlands and 10.5% at Silvermine.

7.3.4.2 Restio curviramis

The hydrological niche model data for *Restio curviramis* comes from Bastiaanskloof, New Years Peak (NYP) and Theewaterskloof. The MaxEnt models for *R. curviramis* performed above random with a combined average AUC value of 0.701 (+/-0.038 SD) for all three sites where it was sampled (Table 7.2). These AUC values validate the quality of these models and allow for valid inferences to be made on the preferred hydrological ranges and the possible range shifts due to climate changes of this species.

The Jack-knife training gain for *R. curviramis* shows that microclimatic variable contributed differently to defining the hydrological niches of *R. curviramis* at different locations as shown in Table 7.2. At Bastiaanskloof MWTD is most important (64% contribution). At NYP SEVa and relative elevation equally contributed (45.5% by SEVa and 44.6% by Elev.) while MWTD only contributed 1%. At Theewaterskloof, SEVd contributed 62.2% and the other variables did just over 10% contributions.

Based on the variable performances in these instances, none of the variables can exclusively explain the spatial distribution of this species. However, the preferred hydrological ranges for these variables could be inferred. Generally, *R. curviramis* would likely occupy niches with MWTD between 0.4 and 0.9 m, dryness thresholds (SEVd) between 9 and 23.4 m.wk, and wetness thresholds (SEVa) between 0 and 2.6 m.wk. Meanwhile, SEVa is the most useful microclimatic variable at NYP where it contributed 45.5% of the required information during modelling.

Based on future climatic emission scenarios, there is a chance of a shift in the ranges of *R. curviramis* at Bastiaanskloof by 2100 with the species disappearing from places and appearing in others. At NYP *R. curviramis* completely disappears from its current preferred habitats with a calculated net loss of up to 30.7% predicted as the site dries up further. At Theewaterskloof there is would be a significant range shift from current locations and seek suitable dry areas in the future similar to present habitat conditions. Considering the vast areal change to more arid conditions, an equally high percentage expansion is expected to inhabit these spaces in future. The habitat suitability of *R. curviramis* increased slowly with increases in the mean water table depths (MWTD) up the elevation gradient but quickly drops to a minimum beyond the maximum MWTD range.

7.3.4.3 Staberoha distachyos

Suitable hydrological niches for *S. distachyos* were predicted at Bastiaanskloof, Cape Point, Kogelberg and Riverlands sites. The preferred microclimatic variable ranges differed for this species at different sites. However, in general, the species would prefer a MWTD range between 0.5 and 0.9 m, SEVd range of 11.4 to 23.4 m.wk and preferably SEVa ranges of 0.0 to 1.2 m.wk. Clearly, this species prefers drier soil conditions. Averaged future predictions for *S. distachyos* niches for the four plots show shifts in hydrological niches for 2100for both RCP2.6 and RCP8.5 emission scenarios. There could be ~20% gain against an ~5% loss in habitats at Bastiaanskloof; approx. 30% gain in Cape Point. Conversely, it might experience ~30 to 50% loss of habitat at Kogelberg and Riverlands. The probability of the presence of *S. distachyos* increased with an increase in MWTD and SEVa but would decrease sharply if conditions got drier.

7.4 Discussion

The study focused on microclimatic (hydrological) niches of Restionaceae species at selected wetland communities in the Cape Floristic Region of the SW of the Western Cape Province, South Africa. Restionaceae was chosen because it is a versatile species with shallow root systems and habits a wide spectrum of environmental conditions (hydrological regimes). Hence the family is of great ecological importance (Taylor, 1978) and an ideal specimen for studying shallow water table depth variation and their impacts on plant distributions. Hydrological change dynamics in wetlands are important for modelling climate-induced inundation patterns in terrestrial ecosystems in the region and relating this to the distribution patterns of a number of species. Climate projections for southern Africa region suggest a geographic pattern of warming air temperature changes, with greater winter and summer-autumn warming (Van Wilgen et al., 2016). Species models predict how far the suitable habitat for species may be extended into areas where conditions are not currently suitable or disappear from currently suitable areas as they become unsuitable. The current study specifically modelled the distribution of Restionaceae in the Cape Floristic Region, which is unique in this part of the globe, based on future climate projections. Hence, caution is necessary if the resulting models are extrapolated to other regions which may have diagnosed the presence of these species.

The trend in species distributions in response to climate change may be exacerbated by the encroachment of alien and anthropogenic elements into Fynbos biomes. While the rate and nature of spread may be influenced naturally, natural physical barriers or sudden changes in the substrate conditions may hinder propagation. Human activities might facilitate or favour survival and reproduction. Natural barriers and increased urbanisation introduce new pressures or steep natural competition in the habitat space while introduced alien species end up outcompeting local endemics (Parmesan, 1996).

All wetland communities were considered to be in equilibrium with current climatic conditions alongside other factors like biotic interactions, species dispersal ability although these were not incorporated in the analysis. It would have been very useful if the role played by fire, ants and other agents on the dispersal potential were accounted for in the models (e.g. Nathan and Muller-Landau, 2000).

Climatic effects were summarised to annual rates which smoothened out climatic extremes or temporary anomalies. This climatic dimension suited the long-term projections of the study which focused on modelling the possible response of the Restionaceae species to prevailing future environmental conditions. The future was modelled using the RCP2.6 and the RCP8.5 scenarios as comparative scenarios of possible change.

7.4.1 Species modelling at a microscale

In projecting possible differences in suitable hydrological niche space for Restionaceae species in this study, a number of conceptual challenges were dealt with in the methodology due to the uniqueness of the micro-spatial scale used. It has been established that different factors influence species distributions at different scales. Whereas climate has an overarching influence on a larger scale, biotic interactions dominate at the local scale (Pearson and Dawson, 2003, Wiens and Bachelet, 2010). So far, most SDM studies have commonly been done at regional scales where regional-scale climate models are used and such regional scale models may not be suitable in representing processes at individual terrestrial wetlands communities. If used directly to represent environmental phenomena, it might lead in deficiencies in the ability to model the underlying relationships between environmental variables with perceived species distributions (Wilby et al., 1998a). Nonetheless, the methodology for modelling species distributions at microscale was guided by those mostly used in large-scale settings (Wilby et al., 1998a). For this to happen, there was a need to downscale climatic influences from global down to landscape or local scales to better simulate local-scale ecological dynamics (Benestad, 2004, Linderson et al., 2004, Gudmundsson et al., 2012a). The use of downscaled model outputs enabled the creation of potential species distribution models at fine scale.

Investigating the impact of climate change in plant communities at local scale would forcefully require that the climate signature (normally available at regional scale) be available at the appropriate scale too. From Chapter 4, it was firmly concluded that landscape topography and hydrological variables controlled the spatial patterns of species assemblages in all wetland communities under examination (Araya et al. 2011; Silvertown et al. 2016). A plausible idea was to device a relationship which integrates overarching climatic influences with local environmental gradients in order to derive a localised climate signature for species distribution modelling purposes. In the current study species distribution is hinged on the moisture gradient which is actually an artefact of the landscape topography. While acknowledging the contributions of soil moisture variation, precipitation was considered the sole climatic factor of change as it is being considered the primary source of moisture input into the subsurface components of the hydrological cycle. Integrating precipitation as a climatic variable with local hydrological gradients sufficiently provided the required environmental signature or microclimatic gradients for testing the possible variability in species distributions with respect to changing climate.

7.4.2 Discrepancy between current and future climatic data

Generally, WorldClim climate grids are best suited for SDM analysis but they are usually coarse-grained and require downscaling to a finer grid in order to be representative of local to microscale climatic variations. Statistical downscaling allows for the obtaining of point data which are a more realistic representation of climate features in response to the biotic interactions which prevail at a microscale. In this study, sampling was done on $1m^2$ grid and statistically downscaled MPI-ESM-LR RCM model data were interpolated to this grid size resolution. The derived high-resolution grids were representative of the micro topography, climate and vegetation gradient on the selected experimental sites.

7.4.3 The distributional changes

A range of responses to climate change was observed (Table 7.1). Some species models projected stable distributions (‘grounded’ species) under the RCP scenarios, while a good majority showed some form of a shift, loss or gain. Particularly large contractions in potential distribution range were projected for the most species under future conditions (Figures 7.1 to 7.8). The percentage range reductions are included in Table 7.3 - 7.10. As seen in Table 7.3, almost half of the species within these sites would suffer net losses of 25% or more in area if Fynbos cover remains as it was during 2009. However, there are suggestions that species response to changing climate may be individualistic and that the composition of communities which exist today might likely be different to those of a future changed climate (Huntley, 1991, Davis et al., 1998, Pearson and Dawson, 2003, Chen et al., 2011, Hannah et al., 2014, Rapacciuolo et al., 2014, Maguire et al., 2015). The drivers of distribution changes are varied and inter-dependent. Some of these include climate, biotic interactions such as dispersal and competition, physiological requirements and genetic properties of the species (Pearson and Dawson, 2003, Hampe, 2004). However, information on the above drivers hardly exist, hence SDMs content with using locational records for species presence to forecast species response to climate change. The hydrological niches of Restionaceae at fine scale have been modelled (Guo et al., 2015) and the impacts of climate change also projected for species in some wetland communities in south-western sections of the CFR (Guo et al., 2016b). In this study, identical patterns for these same species have been observed.

7.4.4 Species response to future climatic scenarios

The species distribution models predict that there would be a significant change in the hydrological niche for most Restionaceae around the CFR as a result of climate change in the future with possibilities that the examined Restionaceae species may respond by expanding or contracting their habitat ranges over the next 70 or so years. The degree of change is expected to vary depending on the severity of the climatic scenario i.e. whether harsh or mild climate change effects. The results of the SDM analyses showed that the majority of these species generally appeared to prefer or will be adaptable to the relatively milder RCP2.6 climate conditions than to the more extreme RCP8.5 scenario.

7.4.5 The influence of hydrological parameters

The species distribution models suggest that there would be a significant change in hydrological niches of most Restionaceae around the CFR as a result of climate change in the future. This implies that hydrological change dynamics in wetlands are important for modelling the physical conditions in this region and relating this to the distribution patterns of a number of species. There is a possibility of the examined Restionaceae responding by expanding or contracting their habitat ranges over the next 70 or so years. The degree of change is expected to vary depending on the severity of the climatic scenario i.e. whether harsh or mild climate change effects.

The use of downscaled model outputs enabled the creation of potential species distribution models at a fine scale at the assessed wetland communities in the CFR. GCMs operate at regional scales and may not be suitable in representing wetland processes at this scale. And so, if used to represent certain conditions in wetlands, there may be deficiencies in the ability to model the underlying physical influences that underpin the relationships perceived in species distributions.

However, it has been found that the hydrological gradient is a strong phenomenon which shapes the distribution of Restionaceae niches in these communities (Araya et al. 2011). Therefore, a relationship that established climatic influences on the moisture gradient is established for the GCM scenarios in order to generate wetland conditions for the future. Notwithstanding any shortcomings from the above, it is important to note that the species models in this study are not a definitive analysis of where species would spread, but just a demonstration of the potential spread based on the projected environmental suitability (Jarnevich et al., 2015). Even the projected future hydrological niches were validated to the present day distributions based on recorded occurrences which may not be absolutely correct due to sampling errors.

The hydrological niche alone may not fully predict Restionaceae species distributions (Soberon and Peterson, 2005), and for a complete picture, there are many factors to consider other than those included in this study. A number of boundary conditions may prevent species from establishing in predicted suitable habitats. For example, wind-spread tree species of North America might not be able to withstand the climate change because the natural wind-driven spread of many species will occur at a significantly slower pace than that which will be required to cope with the changes in surface temperature (primarily essential for increased fecundity and advance maturity), and so they will not spread to all of the areas deemed suitable (Chen et al., 2011, Nathan et al., 2011). Additional factors such as substrate type, species interactions and local nutrition may diminish the suitability status of an area earlier projected to be suitable (Cook et al., 2013). For example, overlaying the habitat suitability projections over maps of substrate type would show the specific areas in which the species may become established. Indeed, the inclusion of other related factors would certainly improve the description of species distributions in relation to the physical environment but this would go out of the scope of this study. Alternatively, where an assessed species tend to specialise in a particular habitat (hydrological) niche, its results could be extrapolated to other regions of similar conditions.

Climate-induced competition would affect the existing community by eliminating some species or even cause the introduction of new ones (especially aliens) if the resources that could facilitate the successful invasion of non-native plants become available. E.g. in the Western United States warming climate will cause various species to migrate to higher elevations but some native species that will not be able to migrate upward at the same pace would be lost as a result (Tausch, 2008).

7.4.6 Influence of elevation within the sites

Apart from moisture availability which is the main influence of variations in hydrological variables, elevation at the microscale (microtopography) is being perceived as another contributor to the species distributional change. Generally, moisture variation in the subsurface is directly influenced by the topography but just like climate, its influence can only be clearly assessed at larger scales rather than at micro scale. As a response to gravity, moisture flows from higher to lower elevations. Hence, the landscape rather than the microtopography is the main control of the moisture gradients that is perceived in the study sites. A few species models at some sites do show elevation as the key influence in the distribution of the species.

7.4.7 Caution with respect to interpretations

Species distribution models must be interpreted with appropriate caution due to the presence of uncertainties (Jarnevich et al., 2015). Although sufficient effort has been put in the sampling to avoid sampling bias or autocorrelation errors, the effects of human error cannot be quantified in species models. Alternatively, more mechanistic modelling approaches can be used (Kearney and Porter, 2009). However, the MaxEnt algorithm is relatively simple and effective for modelling fine scale communities even with small sample numbers relative to other distribution models (Phillips et al., 2005, Guo et al., 2016b). A study comparing different species distribution modelling techniques found MaxEnt to be one of the most robust, including for small sample sizes (Elith et al., 2006, Phillips et al., 2006, Pearson, 2007).

The current study was specific in modelling the distribution of Restionaceae which is unique in this part of the globe based on climate projections in the Cape Floristic Region. Hence, care is necessary if the resulting models are extrapolated to other regions which may have diagnosed the presence of these species. In addition, modelling of individual species in local wetland communities required the use fine scale resolution grids. This was not in congruence with most practice that use coarse grain data although its local scale approach may serve as a basis for projecting larger scale suitability predictions (upscaling) (e.g.

(Pearson and Dawson, 2003, Araújo and Luoto, 2007). There was no need to import readily available (higher resolution) bioclimatic data as suitable fine scale similar alternatives were generated by means of interpolation of downscaled GCM point data.

This study investigated the expected long-term impacts of climate change on species distributions. The scope of this study did not include the intermediate temporal succession trends as the years went through towards the turn of the century. For example, it would have been useful to include the impact of climate scenarios in the intermediate 2040 – 2060 as is the case with Pacifici et al. (2015). However, a simple visualisation of the current species habitat structure compared with the expected future distribution should be sufficient to inform the appropriate biodiversity and conservation management strategies.

Mean water table depth is predicted to have diverse effects on Restionaceae which have been known to segregate at very fine scale moisture gradients (Araya et al. 2011). The introduction of harsher conditions or even those which fall outside of the preferred range of a species, there is the risk of extinction or migration of species to more favourable areas (Tausch, 2008). The effects of these parameters on individuals and ecosystems are complex and so further research will help to understand the complexities affecting spread, survival and population persistence of species.

There are a number of sources of uncertainty that will affect these results. These sources of uncertainty may stem from the methodology, the underlying climate projections, and the species distribution modelling approach or from its training data. A full quantification of uncertainty is outside the scope of this study although they are briefly discussed here. Climate projection uncertainty typically includes the choice of emission scenario. Here two radiative forcing scenarios, RCP2.6 and RCP8.5, are compared. The choice of model uncertainty arises as a single GCM; the MPI-ESM is used. And finally, the model parameter uncertainty which is inherent in the choice of model used. In this study, the results only give an estimate of the possible future climate including the full range of possible Restionaceae models. The implications of the underlying climate and the species modelling approach uncertainties could be explored in future works through the use of multi-model approach (e.g. Tebaldi and Knutti, 2007).

The limitations of sampling by Restionaceae experts during systematic sampling are indeterminate. If a species has not realised its full fundamental niche (i.e. partially occurs in its potential suitable habitat space as seen in this study), then it is difficult to make predictions about its future distribution, as the predicted niche may be smaller than the full 'realisable' potential niche (Phillips et al., 2006). Further, systematic sampling is expected to have dealt away with any autocorrelation or sampling bias (Phillips et al., 2006) because equally spaced same size quadrats were sampled for species presence at all parts of the plots. This gives a better chance that the recorded species occurrence was a representation of the actual (whole) species niche, even when very few occurrence data points were recorded.

MaxEnt provided the added advantage of modelling even relatively small numbers of species occurrences thereby affording the analysis of scarce species. The only shortcoming is the unavailability of sufficient data to train and validate the species models thereby ascertaining the accuracy of modelling techniques and the authenticity of forecasts thereof.

Although wetland ecosystems can be resilient to some changes, or maybe succumb to loss, the impact can only be determined by increased monitoring and screening of the ecosystem. The introduction of novel microclimates from future projections ushers in a source of uncertainty in the generated species models. Evidently, the appearance of areas with novel hydrological conditions seems to be in correlation with the areas of most contraction or disappearance. This could be explained. As these new conditions are out of the range of the current microclimate where species responses are predictable, there is the likelihood that they are considered as unsuitable conditions in the future. One doubts the accuracy of such species models because they were not created based on a known set of training conditions although MaxEnt algorithms attempt to deal with the problem through a clamping procedure (Pearson, 2007). Clamping does not include these novel conditions in the modelling process but treats them as being at the limit of their training range.

Conversely, projected presence models do not coincide with the novel environmental conditions but instead occur within areas that are projected to experience climate conditions within the present climate range. Such areas of presence are therefore associated with relatively less uncertainty.

7.4.8 Potential of incorporating wetland ecological into future conservation strategies

It is important to note that the species models in this study are not a definitive analysis of where species would spread, but just a demonstration of the potential spread based on the projected environmental suitability (Jarnevich et al., 2015). Projected future suitable habitats were modelled based on the present day recorded species occurrences which may not be absolute distributions. The co-operation of private landowners should be encouraged in order to facilitate the establishment of biodiversity corridors and connectivity zones. Alien vegetation clearing and managed fire burning could control alien vegetation growth. Solutions are also required to address:(i) the intense competition for already limited land that is required for settlement, agriculture, industry and other anthropogenic activity and any development of conservation strategies involving the management of areas for the future survival of these species will require scientific inputs, political will and co-operation from the private stakeholders who may own the lands which border the peripheries of the biodiversity reserves. However, before any recommendation can be made with respect to the area of land which will be needed to ensure the future survival of these species into the future, further analyses (involving the use climate data derived from multiple GCMs) which are beyond the scope of this thesis are needed. Notwithstanding the survival of many species in the long term would depend on several factors including (i) the stabilisation of greenhouse gas concentrations and (ii) the prevention of encroachment of the nature reserves by anthropogenic activity. Assuming that (ii) was possible, any further climate change beyond the levels used in these analyses would likely result in a further reduction or even disappearance of the climate space of these species.

It would require a more comprehensive modelling approach involving the construction of model ensembles based on multiple SDM algorithms (Araújo and New, 2007) as well as climate data derived from multiple GCMs.

7.4.9 Projections

The loss of biodiversity due to extinctions and species range shifts has been taking place quite rapidly in time (Pimm and Jenkins, 2010). In conjunction with projections by the IPCC, future climate data from the CFR region show increased evapotranspiration rates and reduced precipitation amounts. The impact of climate change to biodiversity caused by the changes in the natural habitats of species and hence in their natural distribution is clearly visible from research results (Millenium Ecosystem Assessment, 2005, Kéfi et al., 2007). In order to mitigate the impacts of climate change on ecosystems, and hence, conserve biodiversity, monitoring and quantification of losses has been necessary (Balmford and Bond, 2005, Scheffer et al., 2009, Scheffer et al., 2012, Carpenter et al., 2011). Modelling species distribution has provided a useful means of quantifying conservation needs (Guisan and Thuiller, 2005).

This chapter specifically investigated the impact of future climate change on the hydrological niches of Restionaceae species. It reports possible shifts in species ranges and highlights species that might be at risk or habitat conditions that might be favourable to new species and even invasive. The acquired results would guide the strategic steps to be taken by conservation specialists and biodiversity managers as they know the degree of vulnerability of Restionaceae species to future changes in climate.

7.5 Conclusion

In this study, GIS techniques were used to generate hydrological layers, in order to explore the hydrological niche of Restionaceae species. Determining the species hydrological niches required the use of the statistical algorithms in MaxEnt species distribution model, to create representative surfaces which show results of the interactions between species and physical principles. The suitability of niches to future changes in climate was calculated under two climate change scenarios. Climate change is a global phenomenon whose impact is experienced by all organisms, although the degree to which species and ecological communities are affected would be different (Dawson et al., 2011).

The results show that species response to hydrological variables varied across localities. Citing an example of the Silvermine study area, the water table depth is identified as the main hydrological factor responsible for species niches there. This highlights the presence of hydrological requirements specific to individual species, which at the same time coexist and share the same broader hydrological niche area. These results have a direct impact on the conservation of species richness. Because should there be any climate change, the water table depth could become greater, it could mean a reduction in species richness, as some species might not survive in situ with a low water table and these need to migrate along the gradient. Considering that South Africa is a semi-arid environment, and with the threat of urbanization and groundwater extraction and more boreholes; this will ultimately cause a change in the hydrology and therefore impacts on Restionaceae niches.

This study assessed and modelled the effectiveness of using hydrological variables in determining species hydrological niche, at a microclimate level in a Mediterranean-type environment. It identified hydrological regimes of species. It also provided evidence of the importance of hydrology to conservation and future climate change impact analysis, because any changes in the hydrological variables, will cause changes in the hydrological niche and a major change in the species richness index. The results of this study are invaluable in the assessment and monitoring plant species due to hydrological changes. It contributes to the growing knowledge base available, aimed at understanding the underlying factors that underpin the Restionaceae community structure as well as the future implications as changes occur in the environmental parameters. The results of this study will enable managers of protected areas to identify high-risk species and implement management programmes.

Restionaceae are tolerant to a wide range of hydrological regimes, meaning that there are species that are tolerant to different sites along a moisture gradient (Araya et al., 2011). As expected, the species which are identified for use in this study have different hydrological preferences with a range of wet and dry conditions (Silvertown et al. 2014). In order to examine the relationship between the species and the hydrological variables, species habitat distributions are modelled to show the hydrological niche of species.

MaxEnt has proven to be very efficient in modelling the hydrological species of Restionaceae and remains a valuable tool in biodiversity conservation and management in relation to climate change. Species distribution modelling predicted the spatial relationship between Restionaceae species niches and soil hydrological conditions at sampled sites (Franklin, 2010). MaxEnt version 333k (Phillips et al., 2006) successfully estimated habitat suitability models for Restionaceae in the Fynbos wetland communities (Elith et al., 2006). The performance of this model was not affected by the spatial scale at which investigations were done. In most occasions, similar studies were done on a regional to global and not at such a minute scale as portrayed by Guo et al. (2015). This study successfully modelled species hydrological niches at plot (minute) scale differentiating it from similar studies which have not gone down to such minute scale nor have they utilised minute sample sizes (Pearson, 2007).

Species ranges will experience severe shifts, typically contractions, and for the majority of Restionaceae species, geographic distributions will be considerably altered. Through these findings, an idea about the species at risk has been attained and these should inform decisions for future biodiversity management and biodiversity conservation strategies. However, these results do not take current or on-going habitat destruction patterns relate to human activities into account which brings in an uncertainty factor.

CHAPTER 8 SYNTHESIS AND CONCLUSION

This chapter synthesises the main outcomes and attempts to interconnect the main conclusions from the chapters in this thesis. It includes a summary of the chapters followed by a view on the conservation implications following the envisaged impacts of changes in the hydrological gradient. It shall also discuss some of the limitations of the processes in the thesis as well as state some suggestions for future work.

8.1 Summary of results

The overall objective of this thesis was to investigate the possible water regime requirements and to envision the potential impact of a change in local shallow hydrological systems on the distribution of Restionaceae in selected wetland communities the Cape Floristic Region (CFR). With the main hypothesis being that hydrological factors play the major part determining the species niches due to the semi-arid nature of Southern Africa, the study objectives aimed to do the following:

Objective (i): assessment of the distribution and ecology of many fynbos wetland Restionaceae species in order to decipher the underlying factors that underpin the range of these species along hydrological gradients. In Chapter three, statistical means were used to explore the role of hydrological factors as drivers of community structure in wetland communities and identify the variables which best define the hydrological niche of the Restionaceae species. This was done through ANOVA to test if hydrological niches occupied by Restionaceae species where they are present were significantly different from those where these species were absent; and if Restionaceae species occupied significantly different hydrological niches at each site of study. Canonical Discriminant Analysis differentiated species into groups based on the influences of environmental variables. It was found that at most sites, the soils that were occupied by Restionaceae species were significantly hydrologically different from the soils where the species were absent with just a few exceptions of where some species occurred irrespective of hydrological conditions (ubiquitous species) (Table 3.2 – Table 3.9 and Figure 3.1 – Figure 3.8). This confirms the primary role played by hydrological variables in determining the distribution patterns of the Restionaceae. Additionally, canonical discriminant analysis indicated the hydrological variables contributed differently to this dynamic between the different sites. This suggests slight differences in species-specific water relations which enable them to co-exist. On the whole, statistical analysis demonstrated that species segregation in wetland communities in the southwestern CFR is significantly explained by the soil hydrology. The findings show that hydrological gradients play a major role in the maintenance of species of the Restionaceae in fynbos wetland communities. This relationship between species distribution and hydrological gradients makes it possible to predict the impacts of potential hydrological changes on species distributions.

These results provided a statistical perspective for comparison with the results of machine learning Species Distribution Models (SDM). They also, aided in the interpretation of SDM analyses at the plot scale in the absence of sufficient support from existing literature. There is sufficient literature that supports the continental 'macro-scale' SDM as the widely accepted dimension at which climate-driven impacts are most represented in the distribution of species. Literature support for the fine-scale alternative in explaining climate-driven impacts on plants is relatively scarce.

Objective (ii): To quantify the nature of evapotranspiration (ET) as the main driver of soil hydrology in this semi-arid region now and in the future. The hypothesis here is that ET is a key process of moisture escape and hence has significant control of the soil moisture storage. Also that ET rates are expected to increase with projected increases in temperature and radiation into the future due to climate change. Hence estimates of ET in situ provided an assessment of the rate of moisture loss in the present and allow for predictions in the future. Additionally, in-situ ET (microscale ET) at the wetland communities would later be used as an input in a simple soil-water budget model for these same wetland communities. In Chapter four, estimates of potential ET rates were made using the Jensen-Haise ET model a method which was calibrated based on arid/semi-arid conditions in the western USA and assumes an evaporative surface within an adequately watered arid/semi-arid area.

Results in Section 4.3 clearly showed that there were statistically significant differences in evapotranspiration rates at the different stations that were studied. Average relative humidity from all sites in this study revealed extremely high levels of atmospheric moisture in the region but a strong wind presence at high altitudes (like at NYP 1080 m) should favour maximal levels of soil moisture escape through evapotranspiration. Furthermore, the strong seasonal patterns in prevailing winds are an important climatic influence in the region. The future scenario revealed possible significant increases in potential evapotranspiration levels of up to 2 mm which would be a 71% increase in the future if the current projected climatic trends persist. Rates would, however, be slightly lower if CO_2 emissions were to subside (based on RCP2.6 scenario) beyond 2020, relative to higher levels for the RCP8.5 scenario where CO_2 emissions do not subside going forward. Solar radiation directly influences evapotranspiration rates to a greater extent than climate variables like temperature on the surface. Incidentally, global climate model projections reveal increased solar radiation in the future which, in turn, should be directly responsible for the increased evapotranspiration rates. Unfortunately, it is the more likely that ET rates are bound to increase in the future based climate projections considering current anthropogenic trends. The consequence of this would be dire to the soil moisture balance system which has an integral influence on terrestrial ecosystems.

Both potential and reference evapotranspiration rate estimates were derived. However, according to studies, the potential evapotranspiration alternative is preferred as inputs in water budget 'bucket' models. Hence, in addition to precipitation which is the main input of moisture, evapotranspiration becomes the next key component to include in the water budget to model water levels both currently and in the future.

Objective (iii): To derive soil parameters and test for predictability of a workable soil moisture model which simulates variations in soil moisture contents with the aim of replicating the hydrological framework at other study sites. Soil moisture regimes are defined based on the water table level and the duration of presence or absence of available water for plant use. The hypothesis here was that changing conditions of hydrological variables directly influence the changes in moisture of the soil. This brings to focus the role of hydrological variables in changing the richness and diversity within fynbos wetland communities over time.

In Chapter 5 the moisture flux between compartments of the soil water system was modelled using bi-weekly aggregates of rainfall and evapotranspiration (ET) amounts as the only inputs while soil water level records were used for calibrating the model simulations. The primary objective which was to derive a replicable model was partially achieved because the soil moisture model was successfully applied only at one site, - the New Years Peak site (Section 5.3.1.2). Notwithstanding, the intended (best) parameter values for the NYP site were deduced and the outcome of the soil moisture model was satisfactory. Using the available rainfall and estimated evapotranspiration (from Chapter 4), the water table fluctuation within a 65 week period was simulated. Soil moisture levels peaked during the winter months of June, July and August (Figure 5.4d). The model results were deemed satisfactory (Table 5.2) and could be recommended for future simulations of soil moisture and hydrological fluxes under changing climatic conditions particularly at the NYP site. Some slight mismatch persisted between the simulations and the observed records. The precision of the model could be improved through additional testing and model validation using additional measurements on site.

Objective (iv): to develop models of the potential distributions of Restionaceae species under present microclimatic (hydrological) conditions using the Maximum Entropy (MaxEnt) species distribution modelling algorithms. Species models were to express the spatial relationships between these species and the hydrological (environmental) phenomena that underpin the existing community structure at plot scale (or micro scale). Beyond this, the achieved models were used to predict the impact of the future climate dynamics on the composition of the Restionaceae community. This made up the body of the material in Chapter Six.

MaxEnt model algorithms successfully generated hydrological niche models based on moisture gradients of microscale experimental plots. The model used novel bioclimatic grids specially customised for use at the microscale. The procedures used to generate novel microclimatic layers are described in Section 6.2.1 and the outcomes are in Section 6.3.1. MaxEnt effectively created robust species models from limited data and at very fine spatial scale. The predictive quality of the models as indicated by the AUC values varied for the same species between the experimental sites (Table 6.3 – Table 6.18). Visual assessment confirmed the proximity of actual (observed) sampled occurrences to the predicted (modelled) locations on spatial maps, so these species models were considered valid (Figure 6.9 – Figure 6.16). Most valid outputs are fit for the interpretation of community structure and deemed fit for predicting the potential future species distributions based on novel environmental conditions introduced by climate change. Furthermore, like with the ecological analyses that were conducted in Chapter 3, the MaxEnt algorithm indicated that mean water table depth (MWTD) and to a lesser extent dryness or drought conditions (SEVd) appeared to be the main drivers of the potential present distribution of most of these species.

Objective (v) was to (a) forecast the potential future distributions of the selected Restionaceae species using robust species model outputs from Chapter 6 and to (b) compute distributional change maps which highlight areas that are expected to lose, gain or maintain the population structure of species when the RCP2.6 and RCP8.5 future climate scenarios are considered.

Projected species change results in Chapter 7 revealed that the majority of Restionaceae species would experience some form of change and differ from their current distribution. The prospect of species disappearing was the most prominent outcome based on the reduction in suitable microclimatic space for a number of species. Future species models predicted instances of resilience (by either remaining unchanged or by expanding their ranges) and of catastrophe (disappearance) at certain sites. The maintenance of diversity or possible expansion is most probable for the RCP2.6 GCM scenario. The severity of catastrophe on species occurrence is expected to be high if the RCP8.5 GCM scenarios persist into the future. Generally, the response of most species whether positively or negatively to climate change cannot be predicted with certainty due to the variedness in the nature of the expected distributional changes. For instance, *Staberoha distachyos* (Rottb.) Kunth might remain stable at altitudinal conditions (Figure 7.6 and Table 7.9) but is mostly predicted to disappear at most places where they presently occur (see Figures 7.1, 7.2, 7.4 and Tables 7.4, 7.5, 7.7, respectively). Additionally, the species is seen to expand in population under RCP2.6 scenario conditions but on the other hand shrink under RCP8.5 scenario conditions (see Figure 7.8 and Table 7.11). A similar trend is expected for *Elegia filacea* Mast. (Figures 7.2, 7.5, 7.6, 7.7), *Hypodiscus aristatus* (Thunb.) C. Krauss (Figures 7.2, 7.3, 7.5) and *Staberoha cernua* (L.f.) T.Durand & Schinz (see Figure 7.3, 7.5, 7.7).

Based in their contributions to defining species models, hydrological factors are considered ecologically important to account for the expected differences in the response of individual species and for species diversity in these fynbos wetland communities.

Because of the very fine scale and localized nature of this study, distribution trends could not be aligned with numerous established outcomes at large scales which have reported the poleward and upslope migration of species in response to climate change (Hickling et al., 2006, Chen et al., 2011, Freeman and Class Freeman, 2014, Lenoir and Svenning, 2015, Lenoir et al., 2017). Species distribution has mainly been underpinned by a moisture gradient rather than by the overarching climatic variations seen in larger settings. Finally, the results derived from different possible climatic scenarios may guide future decisions on conservation. While the direction to which species change would definitely take remains uncertain in the future, these results are a firm pointer towards the most likely occurrences and guide to maintain the survival of these species into the distant future.

8.2 Implications, limitations and some recommendations

Conclusions from this research have important implications for the management and conservation of fynbos in general and the Restionaceae in particular in the CFR. It has been shown that species abundances would change either positively or negatively, but would be largely negatively affected under drier conditions. It is expected that there will be shifts in species occurrences, expansion and reductions in response to climate change all of which have different implications for the biodiversity of the future.

Also, it has shown that the distribution of the Restionaceae is mostly influenced by the depth of the water table over which some control could be exerted through adequate monitoring and control in order to maintain the natural species abundance trends and the availability of a habitat. This adds to a better understanding of variation in response to climate change.

8.2.1.1 Experimental framework

A systematic survey framework of quadrats in the various sites was used to sample the Restionaceae (Section 3.2). This provided both spatially unbiased locational botanical data for SDM analysis and some sort of baseline inventory of the existing Restionaceae in selected Fynbos wetland communities. The use of spatially unbiased occurrence data for SDM derivation ascertains their appropriateness for use in strategic planning into the future as opposed to relying on herbarium specimens which might be spatially biased and may not accurately represent the distribution of given species (Schulman et al., 2007).

Furthermore, the choice of using micro scale-size plots provided the added advantage of realistically and strategically sampling across the entire study surface area; whereas the same effort will yield less convincing results at larger scale schemes merely due to the size (Feeley and Silman, 2011).

The data collected from structured vegetation surveys are suitably used to analyse the ecological dynamics of the vegetation community within fynbos wetlands (Chapter 3, 6 and 7). Such analyses are invaluable to ecological studies in general as they can serve to assess the environmental parameters that are important drivers of perceived ecological change in the vegetation communities.

A drawback to the above intensive approach has been the financial and logistic expenses that were incurred including the taxonomic expertise that was required.

8.2.1.2 Issues of scale

Within the set of factors which are thought to influence the distribution of species across a range of scales, climate is thought to be important at a regional or macro scale level, while biotic interactions have an impact at the local scale level (Pearson and Dawson, 2003, Wiens et al., 2009, Wiens and Bachelet, 2010). The results of this study have confirmed that it is possible to generate SDMs at micro scale settings in the presence of both spatial and data limitations. Precipitation driven hydrological variables influenced species distributions. By incorporating climatic parameters like precipitation into environmental variables as bio–climatic or hydro-climatic inputs of SDMs, one indirectly accounts for the role of climate in species distributions and the impact of them changing. Similarly, it is obviously possible to forecast future species distributions based on changes in climate at the micro scales.

8.2.1.3 Issues with correlative species distribution models

To understand the potential utility of SDMs for accurate biodiversity inferences and management, an assessment of the model's efficiency or quality is necessary. One would need to assess the goodness of fit of the species model curve to the observed data. Frequently used metrics like the Area Under the receiver Curve (AUC) do not sufficiently evaluate the goodness of fit of habitat suitability values (Hijmans, 2012). At best, these metrics assess the effectiveness of discriminating between suitable and non-suitable of habitats at any scale. They do not sufficiently tell if the modelled habitat suitability value is proportional to the actual suitability habitat.

8.2.1.4 Models of ubiquitous species

One prominent limitation with SDMs is the production of poor or less robust models by ubiquitous species. These are non-restricted species with unlimited suitable range in the sampled space. While such models might be a problem when assessing widely occurring species that may be of ecological importance, they are advantageous for the assessment of range-restricted endemics or rare species.

However, the implementation of ensemble modelling could improve the confidence on the models of ubiquitous species (Araújo and New 2007). The same applies to the treatment of species projections which were based on novel conditions that are introduced by climate change. Model ensembles make use of several species modelling algorithms at once, predictor variables, and other initial and future conditions to predict relatively robust forecasts. Here, the products from individual species models are examined for overlaps and the zones of greater model overlap are considered areas of high probability for the appearance of the set species (Araújo and New 2007). This improves the confidence and flexibility in decision making compared to the same guidance which might be offered by individual model algorithms. Ensemble models have successfully projected the distribution of plants species into the future under a number of climatic scenarios (Araújo and New, 2007). As such, they can be efficient tools for the management of invasive species (e.g. Lei et al., 2017). Other applications of ensemble models include projecting future climates (Wang et al., 2016), risk assessment (e.g. Rosenzweig et al., 2014), projecting future expansion of invasive (Mainali et al., 2015), extinction risk of species in the future (Zhang et al., 2017), resource monitoring (Vanderhoeven et al., 2017), resource allocation (e.g. Carvalho et al., 2011), bio-assessments (Rose et al., 2015), improving the use of species distribution models in conservation planning and management under climate change (Porfirio et al., 2014), etc. Optimization of forest sampling strategies for woody plant species distribution modelling at the landscape scale (Mateo, 2018)

The current study did not warrant the implementation of ensemble modelling since it merely needed an exploratory approach to satisfy the study objective which was to determine the hydrological regimes and the impacts of possible changes in the physical gradients into the future. A similar emphasis was not placed on seeking for appropriate management policies for which ensembles could have been most advantageous (Akçakaya et al., 2006).

8.2.1.5 Bias in data

The bias background treatment algorithms incorporated in MaxEnt reduce the effect of spatial bias in the data in use if any (Phillip et al., 2009). Current literature, lower AUC test scores as poor but does not define an acceptable range that defines the limits of the robustness (Elith et al., 2011). Additionally, MaxEnt SDM techniques were developed with the intention of generating species models under observed current conditions although its use has been extended to predicting the future. It is not yet known if the future projections are accurate since the future is in itself indeterminate. It should be noted that the solutions provided by bias treatments in MaxEnt are meant to reduce the effects of data bias rather not to eliminate them entirely.

One probable solution that works is the implementation of proper unbiased sampling design as indicated in earlier discussions. Additionally, MaxEnt model also implements its own calibration procedures in the model run thereby eliminating the need for additional data to serve in the calibration of its results.

8.2.1.6 GCM representative scenario

The current study made use of Representative Concentration Pathways (RCP) scenarios from the 5th Climate Monitoring Intercomparison Project (CMIP5) which were published alongside the 5th Assessment Reports (AR5) (Stocker et al., 2014). These scenarios are representations of possible future conditions based on possible greenhouse gas emission rates, demography, economic data, emerging technology, land cover changes, land use and environmental changes (Meehl et al., 2014, Kraucunas et al., 2015). RCPs were well suited for climate change impact and adaptation studies. They are applied in the form of representative pathways which are direct estimations of radiative levels to provide projections of future climate change. On the whole, this data set satisfactorily contributed to modelling climate impacted changes in the distribution of species in the distant future.

8.3 Further research

It should be noted that the results which have been described in this study are just for selected Restionaceae Fynbos plants sampled in wetlands. They represent just a group of the great biome of Fynbos, and more so of individuals that are found in selected temporal wetland habitats. These, therefore, do not in any way represent the impact of changes in the hydrological gradient on all species of Fynbos in the CFR. It is possible that the same analytical procedures performed on an expanded set of ecosystems would certainly reveal quite plausible results. This is confirmed in the variability of the results shown by the same species sampled at different wetland communities. This would necessitate additional monitoring over a long range of time to provide more reliable data from further sampling.

Compound modelling is seen to be advantageous in providing definitive species models which hitherto would be accounted for by individual models. The so-called ensemble approach compensates for the limitations of individual models enabling a more refined output in the end. Further work should, therefore, consider the use of such ensemble models and the outputs compared with the current achieved results.

8.4 Conclusions

This study's results, though on a spatial scale that is far smaller than many other studies which are conducted in continental settings, have also indicated that there will likely be alterations in the distribution of many species due to climate changes. This distribution change would probably reduce biodiversity. The results show that climate change scenarios would certainly introduce novel climate conditions which are foreign to current settings, the result of which will be the realignment of biodiversity to adjust to such environmental adversities. A range of possible changes is expected which include shifts to environmentally suitable sites by Restionaceae species which experience a loss of their preferred niche base. Such species might be managed by allowing for biodiversity corridors through which species might replace lost niches. Alternatively, there might also be disastrous losses as a result of inadaptability by some of these species. Management might consider translocations of such species as a means to ensure continued survival. On the positive side, there are also species which will be unaffected by any perturbations in the future.

APPENDICES

Appendix 1. Data input, pre-processing and ET estimation with Jensen & Haise and Makkink models for Riverlands site

```
> Data directory
# C:\\ETestimates\\Observed\\RIV
>
> # create a new dataframedata.frame
> lat <- -33.486889
> lat_rad <- -0.584456469298
> Elev <- 120
> lambda <- 2.45
> Gsc <- 0.0820
> Z <- 2
> sigma <- 4.903*10^-3
> Roua <- 1.2
> Ca <- 0.001013
> G <- 0
> constants <- data.frame(lat_rad, Elev, lambda, Gsc, Z, sigma, Roua, Ca, G)
> constants
     lat_rad Elev lambda   Gsc Z    sigma Roua       Ca G
1 -0.5844565  120   2.45 0.082 2 0.004903  1.2 0.001013 0

> # ReadInputs climate data
> setwd("C:\\ETestimates\\Observed\\RIV")
>
> climatedata <- read.csv("C:\\ETestimates\\Observed\\RIV\\RIV_AWS_inputs.csv",
+ header=T) #read csv file
> head(climatedata)
  Year Month Day Tmax.daily Tmin.daily RHmax.daily RHmin.daily Rs.daily u2.daily Precip.daily
1 2007     1  16     20.870     20.870    43.03333    43.03333 50.37120       NA            0
2 2007     1  17     18.900     18.900    60.32500    60.32500 27.20952       NA            0
3 2007     1  18     21.975     21.975    55.22500    55.22500 25.83576       NA            0
4 2007     1  19     22.825     22.825    62.62500    62.62500 27.31752       NA            0
5 2007     1  20     21.675     21.675    71.10000    71.10000 22.82904 1.360730            0
6 2007     1  21     19.575     19.575    76.15000    76.15000 25.89840 1.402385            0

> data <- ReadInputs(climatedata, constants,
+                    stopmissing=c(10,10,3),
+                    timestep="daily",
+                    interp_missing_days = T,
+                    interp_missing_entries = T,
+                    interp_abnormal = T,
+                    missing_method = "DoY average",
+                    abnormal_method = "DoY average")
The maximum acceptable percentage of date indices is 10 %
The maximum acceptable percentage of missing data is 10 %
The maximum acceptable percentage of continuous missing data is 3 %
Warning: missing values in 'Tmax.daily' (daily maximum temperature)
Number of missing values in Tmax.daily:  7
% missing data:  1 %
Maximum duration of missing data as percentage of total duration:  1 %
Warning: missing values in 'Tmin.daily' (daily minimum temperature)
Number of missing values in Tmin.daily:  7
% missing data:  1 %
Maximum duration of missing data as percentage of total duration:  1 %
Warning: missing values in 'u2.daily'
Number of missing values in u2.daily:  11
% missing data:  2 %
Maximum duration of missing data as percentage of total duration:  1 %
Warning: missing values in 'Rs.daily'
Number of missing values in Rs.daily:  9
% missing data:  1 %
Maximum duration of missing data as percentage of total duration:  1 %
Warning: missing values in 'Precip.daily' (daily precipitation)
Number of missing values in Precip.daily:  7
% missing data:  1 %
Maximum duration of missing data as percentage of total duration:  1 %
Warning: missing values in 'Precip.daily' (daily precipitation)
Number of missing values in Precip.daily:  7
% missing data:  1 %
Maximum duration of missing data as percentage of total duration:  1 %
```

```
        Warning: missing values in 'RHmax.daily' (daily maximum relative humidity)
        Number of missing values in RHmax.daily:  7
        % missing data:  1 %
        Maximum duration of missing data as percentage of total duration:  1 %
        Warning: missing values in 'RHmin.daily' (daily minimum relative humidity)
        Number of missing values in RHmin.daily:  7
        % missing data:  1 %
        Maximum duration of missing data as percentage of total duration:  1 %

        > # Call ET.Jensen-Haise under the generic function ET
        > results.JenH <- ET.JensenHaise(data, constants, ts="daily", solar="data")
        Jensen-Haise Potential ET
        Solar radiation data have been used for calculating evapotranspiration
        Timestep: daily
        Units: mm
        Time duration: 2007-01-16 to 2008-12-16
        701 ET estimates obtained
        Basic stats
        Mean: 3.89
        Max: 12.27
        Min: 0.15

        > # Call ET.Makkink under the generic function ET
        > results.Makk <- ET.Makkink(data, constants, ts="daily", solar="data")
        Makkink Reference crop ET
        Solar radiation data have been used directly for calculating evapotranspiration
        Timestep: daily
        Units: mm
        Time duration: 2007-01-16 to 2008-12-16
        701 ET estimates obtained
        Basic stats
        Mean: 2.87
        Max: 8.6
        Min: -0.03

        > # Plot the estimated Jensen-Haise PET against Makkink ETo
        > ETComparison(results.JenH, results.Makk, type = "Monthly", ylim=c(0,300),
        +              labs=c("Riverlands","Riverlands"))
        Hit <Return> to see next plot:
        Hit <Return> to see next plot:

        >  #  Plot  the  estimated  Jensen-Haise
potential  evapotranspiration  against  average
temperature e.g.
        > ETForcings(data, results.JenH, forcing = "Rs")
        >
        > # Plot the estimated Makkink reference evapotranspiration against average
temperature e.g.
        > ETForcings(data, results.Makk, forcing = "Rs")
```

Appendix 2. Data processing with ReadInputs() and ET estimation with ET.JensenHaise() and ET.Makkink() for the NYP site

```
        >climatedata<- read.csv("C:\\ETestimates\\Observed\\NYP\\NYP_AWS_inputs.csv", header=T) #read
        data
        > head(climatedata)
          Year Month Day Tmax.daily Tmin.daily RHmax.daily RHmin.daily Rs.daily U2.daily Precip.daily
        1 2007     2  28      21.10      21.10       62.50       62.50 32.64192 1.602329         0.00
        2 2007     3   1      17.73      17.73       80.43       80.43 22.99795 0.958065         0.00
        3 2007     3   2      18.20      18.20       69.35       69.35 26.23795 1.527350         0.00
        4 2007     3   3      10.48      10.48       96.23       96.23  2.81664 2.832540        21.43
        5 2007     3   4       8.00       8.00       87.13       87.13 15.67123 1.818935         0.93
        6 2007     3   5      11.05      11.05       83.48       83.48 18.59328 1.041375         0.00

        > data <- ReadInputs(climatedata, constants,
        +                    stopmissing=c(10,10,3),
        +                    timestep="daily",
        +                    interp_missing_days = T,
        +                    interp_missing_entries = T,
        +                    interp_abnormal = T,
        +                    missing_method = "DoY average",
        +                    abnormal_method = "DoY average")
        The maximum acceptable percentage of date indices is 10 %
```

```
The maximum acceptable percentage of missing data is 10 %
The maximum acceptable percentage of continuous missing data is 3 %
Warning: missing values in 'Tmax.daily' (daily maximum temperature)
Number of missing values in Tmax.daily:  7
% missing data:  1 %
Maximum duration of missing data as percentage of total duration:  0.7 %
Warning: missing values in 'Tmin.daily' (daily minimum temperature)
Number of missing values in Tmin.daily:  7
% missing data:  1 %
Maximum duration of missing data as percentage of total duration:  0.7 %
Warning: missing values in 'Rs.daily'
Number of missing values in Rs.daily:  8
% missing data:  1 %
Maximum duration of missing data as percentage of total duration:  0.9 %
Warning: missing values in 'Precip.daily' (daily precipitation)
Number of missing values in Precip.daily:  2
% missing data:  0.3 %
Maximum duration of missing data as percentage of total duration:  0.1 %
Warning: missing values in 'Precip.daily' (daily precipitation)
Number of missing values in Precip.daily:  2
% missing data:  0.3 %
Maximum duration of missing data as percentage of total duration:  0.1 %
Warning: missing values in 'RHmax.daily' (daily maximum relative humidity)
Number of missing values in RHmax.daily:  7
% missing data:  1 %
Maximum duration of missing data as percentage of total duration:  0.7 %
Warning: missing values in 'RHmin.daily' (daily minimum relative humidity)
Number of missing values in RHmin.daily:  7
% missing data:  1 %
Maximum duration of missing data as percentage of total duration:  0.7 %

> NYP.JenH <- ET.JensenHaise(data, constants, ts="daily", solar="data")
Jensen-Haise Potential ET
Solar radiation data have been used for calculating evapotranspiration
Timestep: daily
Units: mm
Time duration: 2007-02-28 to 2009-01-16
689 ET estimates obtained
Basic stats
Mean: 2.97
Max: 13.52
Min: 0.01

> # Call ET.Makkink under the generic function ET
> NYP.Makk <- ET.Makkink(data, constants, ts="daily", solar="data")
Makkink Reference crop ET
Solar radiation data have been used directly for calculating evapotranspiration
Timestep: daily
Units: mm
Time duration: 2007-02-28 to 2009-01-16
689 ET estimates obtained
Basic stats
Mean: 2.59
Max: 10.49
Min: -0.1

> # Plot the estimated Jensen-Haise PET against Makkink ETo
> ETComparison(NYP.JenH, NYP.Makk, type = "Monthly", ylim=c(0,300),
+ labs=c("New Years Peak","New Years Peak"))
Hit <Return> to see next plot:
Hit <Return> to see next plot:

> # Plot the estimated Jensen-Haise potential evapotranspiration against average temperature e.g.
> ETForcings(data, NYP.JenH, forcing = "Rs")
>
> # Plot the estimated Makkink reference evapotranspiration against average temperature e.g.
> ETForcings(data, NYP.Makk, forcing = "Rs")

> # Plot the estimated Jensen-Haise PET against Makkink ETo
>  ETComparison(NYP.JenH, NYP.Makk, results.JenH, results.Makk, type = "Monthly", ylim=c(0,400),
+ Sdate = "2007-02-28",
+               Edate = "2008-12-16",
+ labs=c("New Years Peak","New Years Peak", "Riverlands", "Riverlands"))
Hit <Return> to see next plot:
Hit <Return> to see next plot:
```

```
# create a new data frame data frame
lat_rad <- -0.5879806
Elev <- 1080
```

```
lambda <- 2.45
Gsc <- 0.0820
constants <- data.frame(lat_rad, Elev, lambda, Gsc)
constants

# ReadInputs climate data
setwd("C:/GCMdata")

climatedata <- read.csv("C:\\GCMdata\\bc_ts_rcp85_mpi_esm_lr.csv", header=T)

#read csv file
head(climatedata)

str(climatedata)

#
data <- ReadInputs(climatedata, constants,
                   stopmissing=c(10,10,3),
                   timestep="daily",
                   interp_missing_days = F,
                   interp_missing_entries = F,
                   interp_abnormal = F,
                   missing_method = NULL,
                   abnormal_method = NULL)


# Call ET.Jensen-Haise under the generic function ET
results <- ET.JensenHaise(data, constants, ts="daily", solar="data")
head(results)

# Call ET.Makkink under the generic function ET
results <- ET.Makkink(data, constants, ts="daily", solar="data")
```

Appendix 3. Example of a typical session of data processing with ReadInputs() and ET estimation with ET.JensenHaise() and ET.Makkink() for the NYP site

Computation of reference crop evapotranspiration ET using the Jensen-Haise model
ET.JensenHaise   Jensen-Haise Formulation

Description
Implementing the Jensen-Haise formulation for estimating potential evapotranspiration

Usage
S3 method for class 'JensenHaise'
ET(data, constants, ts="daily", solar="sunshine hours", ...)

Arguments

data	A list of data which contains the following items (climate variables) required by Jensen-Haise formulation: Tmax, Tmin, Rs or n or Cd
constants	A list named constants consists of constants required for the calculation of Jensen-Haise formulation which must contain the following items: Elev - ground elevation above mean sea level in m,

lambda - latent heat of vaporisation = 2.45 MJ.kg^-1,
lat_rad - latitude in radians,
Gsc - solar constant = 0.0820 MJ.m^-2.min^-1.

The following constants are also required when argument solar has value of sunshine hours:
as - fraction of extra-terrestrial radiation reaching earth on sunless days,
bs - difference between fraction of extra-terrestrial radiation reaching full-sun days and that on sunless days.

ts	Must be either daily, monthly or annual, which indicates the desired time step that the output ET estimates should be on. Default is daily.
solar	Must be either data, sunshine hours, cloud or monthly precipitation: data indicates that solar radiation data is to be used directly for calculating evapotranspiration; sunshine hours indicates that solar radiation is to be calculated using the real data of sunshine hours; cloud sunshine hours is to be estimated from cloud data; monthly precipitation indicates that solar radiation is to be calculated directly from monthly precipitation. Default is sunshine hours.
...	Dummy for generic function, no need to define.

Details
This formulation provides a single calculation method with no alternatives available.

Value
The function prints a calculation summary to the screen containing the following elements:

- ET model name and ET quantity estimated
- Option for calculating solar radiation (i.e. the value of argument solar)
- Time step of the output ET estimates (i.e. the value of argument ts)
- Units of the output ET estimates
- Time duration of the ET estimation
- Number of ET estimates obtained in the entire time-series
- Basic statistics of the estimated ET time-series including mean, max and min values.

The function also generates a list containing the following components, which is saved into a csv file named as ET_JensenHaise.csv in the working directory:

ET.Daily	Daily aggregated estimations of Jensen-Haise potential evapotranspiration.
ET.Monthly	Monthly aggregated estimations of Jensen-Haise potential evapotranspiration.
ET.Annual	Annually aggregated estimations of Jensen-Haise potential evapotranspiration.
ET.MonthlyAve	Monthly averaged estimations of daily Jensen-Haise potential evapotranspiration.
ET.AnnualAve	Annually averaged estimations of daily Jensen-Haise potential evapotranspiration.
ET_formulation	Name of the formulation used which equals to Jensen-Haise.
ET_type	Type of the estimation obtained which is Potential Evapotranspiration.

References
Jensen, M.E.Haise, H.R. 1963, Estimating evapotranspiration from solar radiation. Proceedings of the American Society of Civil Engineers, Journal of the Irrigation and Drainage Division, vol. 89, pp. 15-41.
Prudhomme, C.Williamson, J. 2013, Derivation of RCM-driven potential evapotranspiration for hydrological climate change impact analysis in Great Britain: a comparison of methods and associated uncertainty in future projections. Hydrol. Earth Syst. Sci., vol. 17, no. 4, pp. 1365-1377.
Xu, C.Y.Singh, V.P. 2000, Evaluation and generalization of radiation-based methods for calculating evaporation., Hydrological Processes, vol. 14, no. 2, pp. 339-349.

Examples
```
# Use processed existing data set and constants from site
data("processeddata")
data("constants")
# Call ET.JensenHaise under the generic function ET
```

```
results<- ET.JensenHaise(data, constants, ts="daily", solar="data")
```

Computation of reference crop evapotranspiration ETo using the Makkink model algorithm

ET.Makkink Makkink Formulation

Description

Implementing the Makkink formulation for estimating reference crop evapotranspiration.

Usage

```
## S3 method for class 'Makkink'
ET(data, constants, ts="daily", solar="data", ...)
```

Arguments

data	A list of data which contains the following items (climate variables) required by Makkink formulation: Tmax, Tmin, Rs or n or Cd
constants	A list named constants consists of constants required for the calculation of Makkink formulation which must contain the following items: Elev - ground elevation above mean sea level in m, lambda - latent heat of vaporisation = 2.45 MJ.kg^-1, lat_rad - latitude in radians, Gsc - solar constant = 0.0820 MJ.m^-2.min^-1. The following constants are also required when argument solar has value of sunshine hours: as - fraction of extraterrestrial radiation reaching earth on sunless days, bs - difference between fracion of extraterrestrial radiation reaching full-sun days and that on sunless days.
ts	Must be either daily, monthly or annual, which indicates the desired time step that the output ET estimates should be on. Default is daily.
solar	Must be either data, sunshine hours, cloud or monthly precipitation: data indicates that solar radiation data is to be used directly for calculating evapotranspiration; sunshine hours indicates that solar radiation is to be calculated using the real data of sunshine hours; cloud sunshine hours is to be estimated from cloud data; monthly precipitation indicates that solar radiation is to be calculated directly from monthly precipitation. Default is sunshine hours.
...	Dummy for generic function, no need to define.

Details

The alternative calculation options can be selected through argument solar, please see Arguments for details.

Value

The function prints a calculation summary to the screen containing the following elements:

- ET model name and ET quantity estimated
- Option for calculating solar radiation (i.e. the value of argument solar)
- Time step of the output ET estimates (i.e. the value of argument ts)
- Units of the output ET estimates
- Time duration of the ET estimation
- Number of ET estimates obtained in the entire time-series
- Basic statistics of the estimated ET time-series including mean, max and min values.

The function also generates a list containing the following components, which is saved into a csv file named as ET_Makkink.csv in the working directory:

ET.Daily	Daily aggregated estimations of Makkink reference crop evapotranspiration.
ET.Monthly	Monthly aggregated estimations of Makkink reference crop evapotranspiration.
ET.Annual	Annually aggregated estimations of Makkink reference crop evapotranspiration.

ET.MonthlyAve	Monthly averaged estimations of daily Makkink reference crop evapotranspiration.
ET.AnnualAve	Annually averaged estimations of daily Makkink reference crop evapotranspiration.
ET_formulation	Name of the formulation used which equals to Makkink.
ET_type	Type of the estimation obtained which is Reference crop evapotranspiration.
message1	A message to inform the users about how solar radiation has been calculated by using which data.

References

McMahon, T., Peel, M., Lowe, L., Srikanthan, R. & McVicar, T. 2012. Estimating actual, potential, reference crop and pan evaporation using standard meteorological data: a pragmatic synthesis. Hydrology and Earth System Sciences Discussions, 9, 11829-11910.

De Bruin, H. 1981. The determination of (reference crop) evapotranspiration from routine weather data.Evaporation in relation to hydrology, pp. 25-37.

Example

```
# Use processed existing data set and constants from NYP site, CFR
Data <- read.csv("climatedata.csv")
data("constants")

# Call ET.Makkink under the generic function ET
results<- ET.Makkink(data, constants, ts="daily", solar="data")
```

Appendix 4. Potential predictability and relative percentage contribution of environmental variables in modelling the MaxEnt hydrological niche model

Site	Species	AUC ± SD	SEVa	SEVd	MWTD	Elev
Bastiaanskloof	*E. coleura*	0.710 ± 0.023	23.9	61.1	3.6	11.4
	R. capensis	0.635 ± 0.055	2.8	46.5	46.5	4.2
	R. curviramis	0.787 ± 0.072	10.1	9.5	64	15.6
	R. sporadicus	0.765 ± 0.078	24.2	19.6	9.2	47
	S. distachyos	0.645 ± 0.046	36.3	9	49.4	5.4
	T. sporadicus	0.742 ± 0.077	8.1	63.9	26	2
	W. sulcata	0.794 ± 0.026	0.7	88.5	9.2	1.5
Cape Point	*S. distachyos*	0.644 ± 0.043	65.1	5.2	3.8	25.9
	R. tenuissimus	0.722 ± 0.048	47.4	9.3	16.5	26.7
	R. quinquefarius	**0.578 ± 0.02**	**66.9**	**15.7**	**6.7**	**10.6**
	R. dodii	0.684 ± 0.047	11.4	5.3	48	35.3
	R. bifurcus	0.626 ± 0.025	66.4	12.2	8.2	13.2
	H. aristatus	**0.456 ± 0.241**	**82**	**17.1**	**0**	**0**
	E. nuda	0.864 ± 0.03	0	88	0	12
	E. filacea	0.602 ± 0.014	60.3	11.8	8.5	19.4
	E. cuspidata	0.699 ± 0.051	10.2	3.2	48.7	37.9
Jonkershoek	*E. asperiflora*	0.641 ± 0.059	2.4	83.5	0.7	13.4
	E. juncea	0.744 ± 0.034	78.2	9.4	1.4	11.1
	H. alboaristatus	0.822 ± 0.022	0	100	0	0

	H. aristatus	0.689 ± 0.098	10.1	79.3	8.7	1.8
	R. distachus	**0.522 ± 0.022**	**0**	**0**	**0**	**50**
	R. filiformis	0.797 ± 0.067	79.8	0.4	4.1	15.7
	R. triticeus	**0.587 ± 0.021**	**2.8**	**10.8**	**62**	**24.4**
	S. cernua	0.796 ± 0.052	41	42.1	3.1	13.7
Kogelberg	*C. hyalina*	0.795 ± 0.034	1.3	58.1	1.3	39.3
	C. nudiflora	0.688 ± 0.037	6.2	59.4	0	34.4
	E. caespitosa	0.707 ± 0.029	1.5	64.6	25.6	8.3
	E. cuspidata	0.708 ± 0.036	1.3	86	4.8	8
	E. filacea	**0.536 ± 0.020**	**6.3**	**1.5**	**4.2**	**88**
	E. hookeriana	**0.418 ± 0.02**	**48.2**	**5.2**	**25.1**	**21.6**
	M. digitata	0.849 ± 0.046	1.5	70.7	2.8	25
	N. obtussisimus	0.923 ± 0.042	17.1	82.9	0	0
	R. bifurcus	0.72 ± 0.082	9.5	59.9	5.2	25.4
	R. dispar	0.673 ± 0.079	86.6	0.4	13	0
	R. distichus	**0.582 ± 0.036**	**5.9**	**57.7**	**3.9**	**32.5**
	R. distachyos	0.73 ± 0.035	2.7	60.8	2.8	33.8
New Years Peak	*A. crinalis*	0.786 ± 0.031	21.3	48.5	10.2	20
	E. coleura	0.681 ± 0.063	6.1	36.7	32.2	25
	E. filacea	0.780 ± 0.033	31.3	8.6	13.5	46.6
	E. neesii	0.721 ± 0.031	40.6	18.3	20.5	20.5
	H. aristatus	**0.578 ± 0.207**	**77.9**	**0**	**1.1**	**21**
	R. bolussi	0.66 ± 0.03	21.7	1.9	25.1	51.2
	R. curviramis	0.772 ± 0.02	45.5	9	1	44.6
	R. micer	0.924 ± 0.045	11	5.8	52.9	30.3
	R. obscurus	0.606 ± 0.022	60.4	0	35.9	3.7
	R. pedicellatus	**0.539 ± 0.063**	**62.9**	**7.6**	**16.7**	**12.8**
	S. cernua	0.752 ± 0.114	68.7	0	2.1	29.2
Riverlands	***C.parviflora***	**0.398 ± 0.102**	**45.7**	**0**	**0**	**4.3**
	E. filacea	0.736 ± 0.027	3.4	3.5	88.2	4.9
	E. nuda	0.753 ± 0.032	25.7	4.4	64.6	5.3
	H. willdenowia	0.827 ± 0.021	23.9	39.7	32.7	3.7
	R. capensis	0.653 ± 0.052	6.5	52.9	22.4	18.2
	R. macer	0.605 ± 0.122	5.5	13.9	70.3	10.3
	R. monanthos	0.838 ± 0.012	2.6	40	2	55.3
	R. quinquefarius	0.982 ± 0.012	51.2	1	18	29.8
	R. sporadicus	0.480 ± 0.133	0	100	0	0
	R. vimineus	0.779 ± 0.049	0.2	39.3	51.5	9
	S. distachyos	0.749 ± 0.010	12.9	72.7	8.7	5.7
	T. punctatus	0.803 ± 0.022	2.5	37.2	59.1	1.1
	W. arescens	0.841 ± 0.042	4.2	88.4	3.3	4.1
	W. sulcata	0.905 ± 0.039	6.2	82.7	8.7	2.4
Silvermine	*E. filacea*	0.720 ± 0.076	8.6	65.8	5.6	20
	E. hokeriana	**0.413 ± 0.08**	**93.7**	**0**	**0**	**6.3**
	H. aristatus	0.775 ± 0.057	32	20.8	5.1	42.1

	H. willdenowia	0.909 ± 0.031	0	100	0	0
	R. capensis	0.652 ± 0.084	3.1	10.4	30.4	56
	R. cincinnatus	0.618 ± 0.025	78.3	2	12.9	6.8
	S. cernua	0.652 ± 0.144	3.5	57.7	23.7	15
	T. arenarius	**0.423 ± 0.048**	**0**	**0**	**0**	**75**
	T. gracilis	0.636 ± 0.173	68.3	0	4.1	27.5
Theewaterskloof	*T. crinalis*	0.918 ± 0.010	14.2	77.2	8.5	0.2
	E. asperiflora	0.953 ± 0.068	0	0.4	0	99.6
	E. capensis	0.823 ± 0.070	1.6	91.5	2.6	4.2
	E. neesii	0.653 ± 0.016	40	18.9	2.9	38.1
	E. thyrsifera	0.944 ± 0.034	11.5	82.7	5	0.8
	E. vaginulata	**0.583 ± 0.048**	**0**	**0**	**75**	**0**
	P. callistachyus	0.866 ± 0.034	22.1	57.1	6.1	14.6
	R. curviramus	**0.545 ± 0.024**	**62.2**	**11.4**	**13.7**	**12.7**
	R. pedicellatus	0.857 ± 0.049	0	76.7	0	23.3
	S. cernua	0.744 ± 0.039	62.6	4.6	23	9.8
	S. distachyos	0.798 ± 0.075	12.9	14.3	60	12.9
	T. fruticosus	0.602 ± 0.050	6.9	93.1	0	0

Appendix 5. An overview of the net distributional change shown by three most frequently occurring species

Species	BK	CP	KB	NP	RL	SM	TK	Remarks
Elegia filacea		Loss		Gain	Gain	Loss		Moderate
Restio capensis	Loss				Loss	Gain		Concern
S. distachyos[a]	Loss	Loss	Loss		Loss		Loss	Critical

[a] *Staberoha distachyos*. BK = Bastiaanskloof, CP = Cape Point, KB = Kogelberg, NP = New Years Peak, RL = Riverlands, SM = Silvermine, TK = Theewaterskloof

REFERENCES

ACREMAN, M. C., BLAKE, J. R., BOOKER, D. J., HARDING, R. J., REYNARD, N., MOUNTFORD, J. O. & STRATFORD, C. J. 2009. A simple framework for evaluating regional wetland ecohydrological response to climate change with case studies from Great Britain. *Ecohydrology,* 2**,** 1-17.

AHMADI, S. H. & SEDGHAMIZ, A. 2008. Application and evaluation of kriging and cokriging methods on groundwater depth mapping. *Assess Environmental Monitoring and Assessment : An International Journal Devoted to Progress in the Use of Monitoring Data in Assessing Environmental Risks to Man and the Environment,* 138**,** 357-368.

AKÇAKAYA, H. R., BUTCHART, S. H. M., MACE, G. M., STUART, S. N. & HILTON-TAYLOR, C. 2006. Use and misuse of the IUCN Red List Criteria in projecting climate change impacts on biodiversity. *Global change biology,* 12**,** 2037-2043.

ALLEN, R. G., HOWELL, T. A., PRUITT, W. O., WALTER, I. A. & JENSEN, M. E. 1991. Lysimeters for evapotranspiration and environmental measurements. ASCE.

ALLEN, R. G., PEREIRA, L. S., RAES, D. & SMITH, M. 1998. Crop evapotranspiration: guidelines for computing crop requirements. *FAO Irrigation and Drainage Paper*.

ALLEN, R. G., SMITH, M., PEREIRA, L. S. & PERRIER, A. 1994. An update for the calculation of reference evapotranspiration *ICID Bulletin,* 43**,** 35 - 92.

ANGERT, A. L., CROZIER, L. G., RISSLER, L. J., GILMAN, S. E., TEWKSBURY, J. J. & CHUNCO, A. J. 2011. Do species' traits predict recent shifts at expanding range edges? *Ecology Letters,* 14**,** 677-689.

ARAÚJO, M. B. & LUOTO, M. 2007. The importance of biotic interactions for modelling species distributions under climate change. *Global Ecology and Biogeography,* 16**,** 743-753.

ARAÚJO, M. B. & NEW, M. 2007. Ensemble forecasting of species distributions. *Trends in Ecology & Evolution,* 22**,** 42-47.

ARAÚJO, M. B., THUILLER, W. & PEARSON, R. G. 2006. Climate warming and the decline of amphibians and reptiles in Europe. *Journal of Biogeography,* 33**,** 1712-1728.

ARAYA, Y. N. 2005. *Influence of soil water regime on nitrogen availability and plant competition in wet meadows.* Open University;.

ARAYA, Y. N. & GARCIA-BAQUERO, G. 2007. Ecology of water relations in plants. *eLS*.

ARAYA, Y. N., SILVERTOWN, J., GOWING, D. J., MCCONWAY, K. J., PETER LINDER, H. & MIDGLEY, G. 2011. A fundamental, eco-hydrological basis for niche segregation in plant communities. *New Phytologist,* 189**,** 253-258.

ARNELL, N. W., VAN VUUREN, D. P. & ISAAC, M. 2011. The implications of climate policy for the impacts of climate change on global water resources. *Global Environmental Change,* 21**,** 592-603.

ASSESSMENT, M. E. 2005. *Ecosystems and Human Well-Being: Our Human Planet: Summary for Decision Makers*, Island Press.

ASTON, T. 2007. Geohydrological characteristics of TMG aquifer-fed seeps and plant ecophysiological consequences. Unpublished Masters thesis.

AUSTIN, M. 2002. Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. *Ecological Modelling,* 157**,** 101-118.

AUSTIN, M. 2007. Species distribution models and ecological theory: A critical assessment and some possible new approaches. *Ecological Modelling,* 200**,** 1-19.

BAI, J., GAO, H., XIAO, R., WANG, J. & HUANG, C. 2012. A review of soil nitrogen mineralization as affected by water and salt in coastal wetlands: issues and methods. *CLEAN–Soil, Air, Water,* 40**,** 1099-1105.

BALMFORD, A. & BOND, W. 2005. Trends in the state of nature and their implications for human well-being. *Ecology Letters,* 8**,** 1218-1234.

BALTZER, J. L., DAVIES, S. J., BUNYAVEJCHEWIN, S. & NOOR, N. 2008. The role of desiccation tolerance in determining tree species distributions along the Malay–Thai Peninsula. *Functional Ecology,* 22**,** 221-231.

BARANGE, M., MERINO, G., BLANCHARD, J., SCHOLTENS, J., HARLE, J., ALLISON, E., ALLEN, J., HOLT, J. & JENNINGS, S. 2014. Impacts of climate change on marine ecosystem production in societies dependent on fisheries. *Nature Climate Change,* 4**,** 211.

BARBER, K., LEEDS-HARRISON, P., LAWSON, C. & GOWING, D. 2004. Soil aeration status in a lowland wet grassland. *Hydrological Processes,* 18**,** 329-341.

BARROS, D. & ALBERNAZ, A. 2014. Possible impacts of climate change on wetlands and its biota in the Brazilian Amazon. *Brazilian Journal of Biology,* 74**,** 810-820.

BARROS, V., FIELD, C., DOKKEN, D., MASTRANDREA, M., MACH, K., BILIR, T., CHATTERJEE, M., EBI, K., ESTRADA, Y. & GENOVA, R. 2014. IPCC, 2014: Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part B: Regional Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

BARRY, S. & ELITH, J. 2006. Error and uncertainty in habitat models. *Journal of Applied Ecology,* 43**,** 413-423.

BARTELHEIMER, M., GOWING, D. & SILVERTOWN, J. 2010. Explaining hydrological niches: the decisive role of below-ground competition in two closely related Senecio species. *Journal of Ecology,* 98**,** 126-136.

BARTELHEIMER, M. & POSCHLOD, P., 2016. Ellenberg's water table experiment put to the test: species optima along a hydrological gradient. Oecologia, 181(4), pp.1163-1172.

BARTHOLOMEUS, R. 2009. *Moisture matters. Climate-proof and process-based relationships between water, oxygen and vegetation.* PhD PhD Thesis, Free University.

BEAUMONT, L. J., HUGHES, L. & PITMAN, A. J. 2008. Why is the choice of future climate scenarios for species distribution modelling important? *Ecology Letters,* 11**,** 1135-1146.

BELLARD, C., BERTELSMEIER, C., LEADLEY, P., THUILLER, W. & COURCHAMP, F. 2012. Impacts of climate change on the future of biodiversity. *Ecology Letters,* 15**,** 365-377.

BENDIX, J. & HUPP, C. R. 2000. Hydrological and geomorphological impacts on riparian plant communities. *Hydrological Processes,* 14**,** 2977-2990.

BENESTAD, R. E. 2004. Empirical-statistical downscaling in climate modeling. *Eos, Transactions American Geophysical Union,* 85**,** 417-422.

BLEDSOE, B. P. & SHEAR, T. H. 2000. Vegetation along hydrologic and edapic gradients in a North Carolina coastal plain creek bottom and implications for restoration. *Wetlands,* 20**,** 126-147.

BOND, W. J. & KEELEY, J. E. 2005. Fire as a global `herbivore': the ecology and evolution of flammable ecosystems. *Trends in Ecology & Evolution,* 20**,** 387-394.

BOOTH, T. H., NIX, H. A., BUSBY, J. R. & HUTCHINSON, M. F. 2014. BIOCLIM: the first species distribution modelling package, its early applications and relevance to most current MAXENT studies. *Diversity and Distributions,* 20**,** 1-9.

BOSSI, L., JARMAN, M., CAMPBELL, B., BOUCHER, C., COWLING, R. & MOLL, E. 1984. Description of major vegetation categories in and adjacent to the Fynbos biome. National Scientific Programmes Unit: CSIR.

BOTKIN, D. B., SAXE, H., ARAÃŠJO, M. B., BETTS, R., BRADSHAW, R. H. W., CEDHAGEN, T., CHESSON, P., DAWSON, T. P., ETTERSON, J. R., FAITH, D. P., FERRIER, S., GUISAN, A., HANSEN, A. S., HILBERT, D. W., LOEHLE, C., MARGULES, C., NEW, M., SOBEL, M. J. & STOCKWELL, D. R. B. 2007. Forecasting the Effects of Global Warming on Biodiversity. *BioScience,* 57**,** 227-236.

BOUCHER, C. 1978. Cape Hangklip area. II The Vegetation. *Bothalia***,** 455 - 497.

BOWEN, I. S. 1926. The Ratio of Heat Losses by Conduction and by Evaporation from any Water Surface. *Physical Review,* 27**,** 779-787.

BRADLEY, B. A., CURTIS, C. A. & CHAMBERS, J. C. 2016. Bromus response to climate and projected changes with climate change. *Exotic brome-grasses in arid and semiarid ecosystems of the western US.* Springer.

BREIMAN, L. 2001. Random forests. *Machine learning,* 45**,** 5-32.

BREIMAN, L. 2017. *Classification and regression trees*, Routledge.

BREMER, K. 2002. Gondwanan evolution of the grass alliance of families (Poales). *Evolution,* 56**,** 1374-1387.

BRIONES, O., MONTAÑA, C. & EZCURRA, E. 1996. Competition between three Chihuahuan desert species: evidence from plant size-distance relations and root distribution. *Journal of Vegetation Science,* 7**,** 453-460.

BROCCA, L., MORBIDELLI, R., MELONE, F. & MORAMARCO, T. 2007. Soil moisture spatial variability in experimental areas of central Italy. *Journal of Hydrology,* 333**,** 356-373.

BROTONS, L., THUILLER, W., ARAÚJO, M. B. & HIRZEL, A. H. 2004. Presence-absence versus presence-only modelling methods for predicting bird habitat suitability. *Ecography,* 27**,** 437-448.

BROVKIN, V., RADDATZ, T., REICK, C. H., CLAUSSEN, M. & GAYLER, V. 2009. Global biogeophysical interactions between forest and climate. *Geophysical Research Letters,* 36.

BROWN, J. L. 2014. SDMtoolbox: a python-based GIS toolkit for landscape genetic, biogeographic and species distribution model analyses. *Methods in Ecology and Evolution,* 5**,** 694-700.

BROWN, J. L. & YODER, A. D. 2015. Shifting ranges and conservation challenges for lemurs in the face of climate change. *Ecology and Evolution,* 5**,** 1131-1142.

BUSCH, D. E., LOFTUS, W. F. & BASS, O. L. 1998. Long-term hydrologic effects on marsh plant community structure in the southern Everglades. *Wetlands,* 18**,** 230-241.

CARMER, S. G. & SWANSON, M. R. 1973. An evaluation of ten pairwise multiple comparison procedures by Monte Carlo methods. *Journal of the American Statistical Association,* 68**,** 66-74.

CARPENTER, G., GILLISON, A. & WINTER, J. 1993. DOMAIN: a flexible modelling procedure for mapping potential distributions of plants and animals. *Biodiversity & Conservation,* 2**,** 667-680.

CARPENTER, S. R., COLE, J. J., PACE, M. L., BATT, R., BROCK, W. A., CLINE, T., COLOSO, J., HODGSON, J. R., KITCHELL, J. F., SEEKELL, D. A., SMITH, L. & WEIDEL, B. 2011. Early warnings of regime shifts: A whole-ecosystem experiment. *Science,* 332**,** 1079-1082.

CARVALHO, S. B., BRITO, J. C., CRESPO, E. G., WATTS, M. E. and POSSINGHAM, H. P. 2011. Conservation planning under climate change: Toward accounting for uncertainty in predicted species distributions to increase confidence in conservation investments in space and time. *Biological Conservation*, 144, 7, 2020-2030.

CASTELLI, R. M., CHAMBERS, J. C. & TAUSCH, R. J. 2000. Soil-plant relations along a soil-water gradient in Great Basin riparian meadows. *Wetlands,* 20**,** 251-266.

CHASE, B. M. & MEADOWS, M. E. 2007. Late Quaternary dynamics of southern Africa's winter rainfall zone. *Earth-Science Reviews,* 84**,** 103-138.

CHEFAOUI, R. M. & LOBO, J. M. 2008. Assessing the effects of pseudo-absences on predictive distribution model performance. *Ecological Modelling,* 210**,** 478-486.

CHEN, I.-C., HILL, J. K., OHLEMÜLLER, R., ROY, D. B. & THOMAS, C. D. 2011. Rapid range shifts of species associated with high levels of climate warming. *Science,* 333**,** 1024-1026.

CHOU, C., CHEN, C. A., TAN, P. H. & CHEN, K. T. 2012. Mechanisms for global warming impacts on precipitation frequency and intensity. *Journal of Climate,* 25**,** 3291-3306.

CHRISTENSEN, J. H., HEWITSON, B., BUSUIOC, A., CHEN, A., GAO, X., HELD, R., JONES, R., KOLLI, R. K., KWON, W. & LAPRISE, R. 2007. Regional climate projections. *Climate Change, 2007: The Physical Science Basis. Contribution of Working group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change, University Press, Cambridge, Chapter 11.*

CLULOW, A. D., EVERSON, C. S., MENGISTU, M. G., JARMAIN, C., JEWITT, G. P. W., PRICE, J. S. & GRUNDLING, P. L. 2012. Measurement and modelling of evaporation from a coastal wetland in Maputaland, South Africa. *Hydrol. Earth Syst. Sci.,* 16**,** 3233-3247.

COBBEN, M., VAN TREUREN, R., CASTAÑEDA-ÁLVAREZ, N. P., KHOURY, C. K., KIK, C. & VAN HINTUM, T. J. 2015. Robustness and accuracy of Maxent niche modelling for Lactuca species distributions in light of collecting expeditions. *Plant Genetic Resources,* 13**,** 153-161.

CONNOLLEY, W. M. & BRACEGIRDLE, T. J. 2007. An Antarctic assessment of IPCC AR4 coupled models. *Geophysical Research Letters,* 34.

COWLING, R. & HEIJNIS, C. 2001. The identification of Broad Habitat Units as biodiversity entities for systematic conservation planning in the Cape Floristic Region. *South African Journal of Botany,* 67**,** 15-38.

COWLING, R., RICHARDSON, D. & MUSTART, P. 1997. Fynbos. *Vegetation of southern Africa***,** 99-130.

COWLING, R. M. & BOND, W. J. 1991. How small can reserves be? An empirical approach in Cape Fynbos, South Africa. *Biological Conservation,* 58**,** 243-256.

COWLING, R. M. & HOLMES, P. M. 1992. Flora and vegetation. *In:* COWLING, R. M. (ed.) *The Ecology of Fynbos, Nutrients and Diversity.* Cape Town: Oxford University Press.

COWLING, R. M., HOLMES, P. M. & REBELO, A. G. 1992. Plant diversity and endemism. *The ecology of fynbos: Nutrients, fire and diversity***,** 62-112.

COWLING, R. M., RUNDEL, P. W., LAMONT, B. B., KALIN ARROYO, M. & ARIANOUTSOU, M. 1996. Plant diversity in mediterranean-climate regions. *Trends in Ecology & Evolution,* 11**,** 362-366.

CURRIE, D. J. 1991. Energy and large-scale patterns of animal-and plant-species richness. *American Naturalist***,** 27-49.

DALY, C., GIBSON, W. P., TAYLOR, G. H., JOHNSON, G. L. & PASTERIS, P. 2002. A knowledge-based approach to the statistical mapping of climate. *Climate research,* 22**,** 99-113.

DAVIS, A. J., LAWTON, J. H., SHORROCKS, B. & JENKINSON, L. S. 1998. Individualistic species responses invalidate simple physiological models of community dynamics under global environmental change. *Journal of Animal Ecology,* 67**,** 600-612.

DAVIS, S. M. & OGDEN, J. C. 1994. *Everglades: the ecosystem and its restoration*, CRC Press.

DAWSON, T. E. 1996. Determining water use by trees and forests from isotopic, energy balance and transpiration analyses: The roles of tree size and hydraulic lift. *Tree physiology,* 16**,** 263-272.

DAWSON, T. P., JACKSON, S. T., HOUSE, J. I., PRENTICE, I. C. & MACE, G. M. 2011. Beyond predictions: Biodiversity conservation in a changing climate. *Science,* 332**,** 53-58.

DE'ATH, G. & FABRICIUS, K. E. 2000. Classification and regression trees: a powerful yet simple technique for ecological data analysis. *Ecology,* 81**,** 3178-3192.

DE BRUIN, H. 1981. The determination of (reference crop) evapotranspiration from routine weather data. Proceedings of Technical Meeting. 25-37.

DE CHAZAL, J. & ROUNSEVELL, M. D. A. 2009. Land-use and climate change within assessments of biodiversity change: A review. *Global Environmental Change,* 19, 306-315.

DEBUSK, W. & REDDY, K. 2003. Nutrient and hydrology effects on soil respiration in a northern Everglades marsh. *Journal of environmental quality,* 32, 702-710.

DENSLOW, J. S., ELLISON, A. M. & SANFORD, R. E. 1998. Treefall gap size effects on above-and below-ground processes in a tropical wet forest. *Journal of Ecology,* 86, 597-609.

DEVICTOR, V., JULLIARD, R., COUVET, D. & JIGUET, F. 2008. Birds are tracking climate warming, but not fast enough. *Proceedings of the Royal Society of London B: Biological Sciences,* 275, 2743-2748.

DI LUCA, A., DE ELÍA, R. & LAPRISE, R. 2012. Potential for added value in precipitation simulated by high-resolution nested Regional Climate Models and observations. *Climate Dynamics,* 38, 1229-1247.

DINGMAN, S. L. 2015. *Physical hydrology*, Waveland press.

DIRZO, R. & RAVEN, P. H. 2003. Global state of biodiversity and loss. *Annual Review of Environment and Resources,* 28, 137-167.

DONOHUE, R. J., MCVICAR, T. R. & RODERICK, M. L. 2010. Assessing the ability of potential evaporation formulations to capture the dynamics in evaporative demand within a changing climate. *Journal of Hydrology,* 386, 186-197.

DOORENBOS, J. & PRUITT, W. 1977. Irrigation and drainage. *Irrigation and Drainage*.

DUQUE-LAZO, J., VAN GILS, H., GROEN, T. & NAVARRO-CERRILLO, R. 2016. Transferability of species distribution models: The case of Phytophthora cinnamomi in Southwest Spain and Southwest Australia. *Ecological modelling,* 320, 62-70.

DWAF 2006. A Guide to Verifying the Extent of Existing Lawful Water Use. Available online: www.dwaf.gov.za/WAR/documents/VerificationGuide2EdNov06.pdf (accessed on 1 2016). Pretoria.

DWIRE, K. A., KAUFFMAN, J. B. & BAHAM, J. E. 2006. Plant species distribution in relation to water-table depth and soil redox potential in montane riparian meadows. *Wetlands,* 26, 131-146.

DYMOND, C. C. & JOHNSON, E. A. 2002. Mapping vegetation spatial patterns from modeled water, temperature and solar radiation gradients. *ISPRS Journal of Photogrammetry and Remote Sensing,* 57, 69-85.

EARLY, R. & SAX, D. F. 2014. Climatic niche shifts between species' native and naturalized ranges raise concern for ecological forecasts during invasions and climate change. *Global Ecology and Biogeography,* 23, 1356-1365.

EDENHOFER, O., PICHS-MADRUGA, R., SOKONA, Y., FARAHANI, E., KADNER, S., SEYBOTH, K., ADLER, A., BAUM, I., BRUNNER, S. & EICKEMEIER, P. 2014. IPCC, 2014: summary for policymakers. *Climate change*.

EHRLÉN, J. & MORRIS, W. F. 2015. Predicting changes in the distribution and abundance of species under environmental change. *Ecology Letters,* 18, 303-314.

EHRLÉN, J., MORRIS, W. F. & BUCKLEY, Y. 2015. Predicting changes in the distribution and abundance of species under environmental change. *Ecology Letters,* 18, 303-314.

ELITH, J. & GRAHAM, C. H. 2009. Do they? How do they? WHY do they differ? On finding reasons for differing performances of species distribution models. *Ecography,* 32, 66-77.

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. M., TOWNSEND PETERSON, A., PHILLIPS, S. J, RICHARDSON, K., 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.

ELITH, J., KEARNEY, M. & PHILLIPS, S. 2010. The art of modelling range-shifting species. *Methods in Ecology and Evolution,* 1, 330-342.

ELITH, J. & LEATHWICK, J. R. 2009. Species distribution models: ecological explanation and prediction across space and time. *Annual review of ecology, evolution, and systematics,* 40, 677-697.

ELITH, J., LEATHWICK, J. R. & HASTIE, T. 2008. A working guide to boosted regression trees. *Journal of Animal Ecology,* 77, 802-813.

ELITH, J., PHILLIPS S.J, HASTIE, T, DUDIK, M., CHEE, Y.E., YATES, C.J. 2011. A statistical explanation of MaxEnt for ecologists. *Diversity and Distributions*,17, 43-57.

ELENBERG, H., 1953. Physiologisches und okologisches Verhalten serselben Pflanzenarten. *Ber. Deut. Botan. Ges*., 65, 351-362.

ELLIS, S. & MELLOR, T. 2002. *Soils and environment*, Routledge.

ENGELBRECHT, B. M., COMITA, L. S., CONDIT, R., KURSAR, T. A., TYREE, M. T., TURNER, B. L. & HUBBELL, S. P. 2007. Drought sensitivity shapes species distribution patterns in tropical forests. *Nature,* 447**,** 80-82.

ERWIN, K. L. 2009. Wetlands and global climate change: the role of wetland restoration in a changing world. *Wetlands Ecology and Management,* 17**,** 71.

ESRI, 2015. ARCGIS 10.3.1. Environmental Systems Research Institute, Inc. Redlands.

ESTRADA-MEDINA, H., SANTIAGO, L. S., GRAHAM, R. C., ALLEN, M. F. & JIMENEZ-OSORNIO, J. J. 2013. Source water, phenology and growth of two tropical dry forest tree species growing on shallow karst soils. *Trees-Structure and Function,* 27**,** 1297-1307.

EVANGELISTA, P. H., KUMAR, S., STOHLGREN, T. J., JARNEVICH, C. S., CRALL, A. W., NORMAN III, J. B. & BARNETT, D. T. 2008. Modelling invasion for a habitat generalist and a specialist plant species. *Diversity and Distributions,* 14**,** 808-817.

EVERSON, C., CLULOW, A. & MENGITSU, M. 2009. *Feasibility Study on the Determination of Riparian Evaporation in Non-Perennial Systems*, Water Research Commission.

FAHRIG, L. 2003. Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics,* 34**,** 487-515.

FEBRUARY, E. C., MATIMATI, I., HEDDERSON, T. A. & MUSIL, C. F. 2013. Root niche partitioning between shallow rooted succulents in a South African semi desert: implications for diversity. *Plant Ecology,* 214**,** 1181-1187.

FEELEY, K. J. & SILMAN, M. R. 2011. Keep collecting: accurate species distribution modelling requires more collections than previously thought. *Diversity and Distributions,* 17**,** 1132-1140.

FERNANDO, V., SILVIA, M., FRANÇOIS, G., B., A. M., LUIS, B., MARTA, B. G., WILL, C., ERNESTO, G., MARK, K., E., N. D., B., N. A., HENDRIK, P. & A., Z. M. 2014. The effects of phenotypic plasticity and local adaptation on forecasts of species range shifts under climate change. *Ecology Letters,* 17**,** 1351-1364.

FERREIRA, S., DEACON, A., SITHOLE, H., BEZUIDENHOUT, H., DAEMANE, M. & HERBST, M. 2011. From numbers to ecosystems and biodiversity: A mechanistic approach to monitoring. *Koedoe,* 53**,** 187-198.

FIELD, C. B., BARROS, V. R., DOKKEN, D., MACH, K., MASTRANDREA, M., BILIR, T., CHATTERJEE, M., EBI, K., ESTRADA, Y. & GENOVA, R. 2014. IPCC, 2014: Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

FIELDING, A. H. & BELL, J. F. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental conservation,* 24**,** 38-49.

FILELLA, I. & PENUELAS, J. 2003. Partitioning of water and nitrogen in co-occurring Mediterranean woody shrub species of different evolutionary history. *Oecologia,* 137**,** 51-61.

FLINT, L. E. & FLINT, A. L. 2012. Downscaling future climate scenarios to fine scales for hydrologic and ecological modeling and analysis. *Ecological Processes,* 1**,** 2.

FLORY, A. R., KUMAR, S., STOHLGREN, T. J. & CRYAN, P. M. 2012. Environmental conditions associated with bat white-nose syndrome mortality in the north-eastern United States. *Journal of Applied Ecology,* 49**,** 680-689.

FOOLADMAND, H. R. & HAGHIGHAT, M. 2007. Spatial and temporal calibration of Hargreaves equation for calculating monthly ETo based on Penman-Monteith method. *Irrigation and Drainage,* 56**,** 439-449.

FOURCADE, Y., ENGLER, J. O., RÖDDER, D. & SECONDI, J. 2014. Mapping species distributions with MAXENT using a geographically biased sample of presence data: a performance assessment of methods for correcting sampling bias. *PloS one,* 9**,** e97122.

FOWLER, H. J., BLENKINSOP, S. & TEBALDI, C. 2007. Linking climate change modelling to impacts studies: recent advances in downscaling techniques for hydrological modelling. *International Journal of Climatology,* 27**,** 1547-1578.

FRANKLIN, J. 1995. Predictive vegetation mapping: geographic modelling of biospatial patterns in relation to environmental gradients. *Progress in physical geography,* 19**,** 474-499.

FRANKLIN, J. 2010. Mapping species distributions: spatial inference and prediction, Cambridge University Press.

FRANKS, S. J., SIM, S. & WEIS, A. E. 2007. Rapid evolution of flowering time by an annual plant in response to a climate fluctuation. *Proceedings of the National Academy of Sciences,* 104**,** 1278-1282.

FREEMAN, B. G. & CLASS FREEMAN, A. M. 2014. Rapid upslope shifts in New Guinean birds illustrate strong distributional responses of tropical montane species to global warming. *Proceedings of the National Academy of Sciences,* 111**,** 4490-4494.

FRIEDMAN, J. H. 2001. Greedy function approximation: a gradient boosting machine. *Annals of statistics*, 1189-1232.

FU, B., POLLINO, C. A., CUDDY, S. M. & ANDREWS, F. 2015. Assessing climate change impacts on wetlands in a flow regulated catchment: A case study in the Macquarie Marshes, Australia. *Journal of Environmental Management,* 157, 127-138.

GIORGETTA, M. A., JUNGCLAUS, J., REICK, C. H., LEGUTKE, S., BADER, J., BÖTTINGER, M., BROVKIN, V., CRUEGER, T., ESCH, M., FIEG, K., GLUSHAK, K., GAYLER, V., HAAK, H., HOLLWEG, H.-D., ILYINA, T., KINNE, S., KORNBLUEH, L., MATEI, D., MAURITSEN, T., MIKOLAJEWICZ, U., MUELLER, W., NOTZ, D., PITHAN, F., RADDATZ, T., RAST, S., REDLER, R., ROECKNER, E., SCHMIDT, H., SCHNUR, R., SEGSCHNEIDER, J., SIX, K. D., STOCKHAUSE, M., TIMMRECK, C., WEGNER, J., WIDMANN, H., WIENERS, K.-H., CLAUSSEN, M., MAROTZKE, J. & STEVENS, B. 2013. Climate and carbon cycle changes from 1850 to 2100 in MPI-ESM simulations for the Coupled Model Intercomparison Project phase 5. *Journal of Advances in Modeling Earth Systems,* 5, 572-597.

GLASER, P. H., JANSSENS, J. A. & SIEGEL, D. I. 1990. The response of vegetation to chemical and hydrological gradients in the Lost River peatland, northern Minnesota. *The Journal of Ecology*, 1021-1048.

GLEASON, H. A. 1926. The individualistic concept of the plant association. *Bulletin of the Torrey botanical club*, 7-26.

GOLDBLATT, P. & MANNING, J. C. 2002. Plant diversity of the Cape region of southern Africa. *Annals of the Missouri Botanical Garden*, 281-302.

GÓMEZ-PLAZA, A., MARTıNEZ-MENA, M., ALBALADEJO, J. & CASTILLO, V. 2001. Factors regulating spatial distribution of soil water content in small semiarid catchments. *Journal of Hydrology,* 253, 211-226.

GOODCHILD, M. F. 1993. The state of GIS for environmental problem-solving. *Environmental modeling with GIS*, 8-15.

GOOVAERTS, P. 1997. *Geostatistics for natural resources evaluation*, Oxford University Press on Demand.

GOWING, D. & SPOOR, G. 1998. The effect of water table depth on the distribution of plant species on lowland wet grassland. *United Kingdom floodplains. Westbury Academic and Scientific Publishing, Otley*, 185-196.

GOWING, D., YOUNGS, E., GILBERT, J. & SPOOR, G. 1998. Predicting the effect of change in water regime on plant communities. *Hydrology in a Changing environment,* 1, 473-484.

GOWING, D. T. G., LAWSON, C. S., YOUNGS, E. G., BARBER, K. R., RODWELL, J. S., PROSSER, M. V., WALLACE, H. L., MOUNTFORD, J. O. & SPOOR, G. 2002. The water regime requirements and the response to hydrological change of grassland plant communities. DEFRA-commissioned project BD1310. Final report to the Department for Environment, Food and Rural Affairs. Institute of Water and Environment Silsoe Bedford MK45 4DT UK.

GOWING, G. J. W. & YOUNG, M. D. B. 1997. “Computer Simulation as a Tool for Technology Transfer: Interpreting and Extending Experimental Results on RWH for Maize Production”. *Proc. 1st Int. Conf. Southern and Eastern Africa Society of Agricultural Engineers (SEASAE), Arusha, Oct. 1996.*

GRACE, J. B. & WETZEL, R. G. 1981. Habitat partitioning and competitive displacement in cattails (*Typha*): experimental field studies. *American Naturalist*, 463-474.

GRACE, J. B. & WETZEL, R. G. 1982. Niche differentiation between two rhizomatous plant species: *Typha latifolia* and *Typha angustifolia*. *Canadian Journal of Botany,* 60, 46-57.

GRIESER, J., GOMMES, R. & BERNARDI, M. 2006. *New LocClim-the local climate estimator of FAO*. In Geophysical research abstracts, 8, 2).

GRINNELL, J. 1917. The niche-relationships of the California Thrasher. *The Auk,* 34, 427-433.

GROOM, P. K. 2004. Rooting depth and plant water relations explain species distribution patterns within a sandplain landscape. *Functional Plant Biology,* 31, 423-428.

GUDMUNDSSON, L., BREMNES, J., HAUGEN, J. & ENGEN-SKAUGEN, T. 2012a. Downscaling RCM precipitation to the station scale using statistical transformations-a comparison of methods. *Hydrology and Earth System Sciences,* 16, 3383.

GUDMUNDSSON, L., BREMNES, J. B., HAUGEN, J. E. & ENGEN-SKAUGEN, T. 2012b. Technical Note: Downscaling RCM precipitation to the station scale using statistical transformations – a comparison of methods. *Hydrol. Earth Syst. Sci.,* 16, 3383-3390.

GUISAN, A., EDWARDS, T. C. & HASTIE, T. 2002. Generalized linear and generalized additive models in studies of species distributions: setting the scene. *Ecological Modelling,* 157, 89-100.

GUISAN, A., LEHMANN, A., FERRIER, S., AUSTIN, M., OVERTON, J. M. C., ASPINALL, R. & HASTIE, T. 2006. Making better biogeographical predictions of species’ distributions. *Journal of Applied Ecology,* 43, 386-392.

GUISAN, A. & THUILLER, W. 2005. Predicting species distribution: offering more than simple habitat models. *Ecology Letters,* 8, 993-1009.

GUNDERSON, L. H. 1994. Vegetation of the Everglades: determinants of community composition. *Everglades: the ecosystem and its restoration (SM Davis and JC Ogden, eds.) St. Lucie Press, Delray Beach, FL. 848pp*, 323-340.

GUO, D., ARNOLDS, J. L., MIDGLEY, G. F. & FODEN, W. B. 2016a. Conservation of quiver trees in Namibia and South Africa under a changing climate. *Journal of Geoscience and Environment Protection,* 4, 1-8.

GUO, D., GUO, R. & THIART, C. 2007. Predicting air pollution using fuzzy membership grade Kriging. *Computers, environment and urban systems,* 31, 33-51.

GUO, D., MIDGLEY, G. F., ARAYA, Y. N., SILVERTOWN, J. & MUSIL, C. F. 2016b. Climate change impacts on hydrological niches of Restionaceae species in Jonkershoek, South Africa. *Journal of Water Resource & Hydraulic Engineering,* 5, 20-28.

GUO, D., MUSIL, C. F., MIDGLEY, G. F. & AYUK, J. 2015. Hydrological Niche of Restionaceae Species in Silvermine South Africa. *JWRHE Journal of Water Resource and Hydraulic Engineering,* 4, 286-292.

GUO, D., THIART, C., GUO, R. & CUI, Y. 2011. *Imprecise Uncertainty Modelling of Air Pollutant PM10*, INTECH Open Access Publisher.

GUO, D., WESTRA, S. & MAIER, H. R. 2016c. An R package for modelling actual, potential and reference evapotranspiration. *Environmental Modelling & Software,* 78, 216-224.

GUO, J., HUANG, G., WANG, X., LI, Y. & LIN, Q. 2018. Dynamically-downscaled projections of changes in temperature extremes over China. *Climate Dynamics,* 50, 1045-1066.

GUTIÉRREZ, D., FERNÁNDEZ, P., SEYMOUR, A. S. & JORDANO, D. 2005. Habitat distribution models: are mutualist distributions good predictors of their associates? *Ecological Applications,* 15, 3-18.

HAAKSMA, E. D. & LINDER, P. H. 2000. *Restios of the Fynbos,* Cape Town, Botanical Society of South Africa.

HÁJEK, M., HÁJKOVÁ, P., KOČÍ, M., JIROUŠEK, M., MIKULÁŠKOVÁ, E. & KINTROVÁ, K. 2013. Do we need soil moisture measurements in the vegetation–environment studies in wetlands? *Journal of Vegetation Science,* 24, 127-137.

HAMPE, A. 2004. Bioclimate envelope models: what they detect and what they hide. *Global Ecology and Biogeography,* 13, 469-471.

HANNAH, L. 2008. Protected areas and climate change. *Annals of the New York Academy of Sciences,* 1134, 201-212.

HANNAH, L. 2010. A global conservation system for climate-change adaptation. *Conservation Biology,* 24**,** 70-77.

HANNAH, L. 2015. Chapter 2 - The climate system and climate change. *Climate Change Biology (Second Edition).* Boston: Academic Press.

HANNAH, L., FLINT, L., SYPHARD, A. D., MORITZ, M. A., BUCKLEY, L. B. & MCCULLOUGH, I. M. 2014. Fine-grain modeling of species' response to climate change: holdouts, stepping-stones, and microrefugia. *Trends in Ecology & Evolution,* 29**,** 390-397.

HANNAH, L., MIDGLEY, G., ANDELMAN, S., ARAÚJO, M., HUGHES, G., MARTINEZ-MEYER, E., PEARSON, R. & WILLIAMS, P. 2007. Protected area needs in a changing climate. *Frontiers in Ecology and the Environment,* 5**,** 131-138.

HANNAH, L., MIDGLEY, G., HUGHES, G. & BOMHARD, B. 2005. The view from the Cape: extinction risk, protected areas, and climate change. *BioScience,* 55**,** 231-242.

HANNAH, L., MIDGLEY, G. F., LOVEJOY, T., BOND, W. J., BUSH, M., LOVETT, J. C., SCOTT, D. & WOODWARD, F. I. 2002. Conservation of biodiversity in a changing climate. *Conservation Biology,* 16**,** 264-268.

HARDY, C. R., MOLINE, P. & LINDER, H. P. 2008. A phylogeny for the African restionaceae, and new perspectives on morphology's role in generating complete species phylogenies for large clades. *Int. J. Plant Sci,* 169**,** 377-90.

HARGREAVES, G. H. & SAMANI, Z. A. 1985. Reference crop evapotranspiration from temperature. *Applied engineering in agriculture,* 1**,** 96-99.

HARRISON, S. P. & PRENTICE, C. I. 2003. Climate and CO_2 controls on global vegetation distribution at the last glacial maximum: analysis based on palaeovegetation data, biome modelling and palaeoclimate simulations. *Global change biology,* 9**,** 983-1004.

HASTIE, T., TIBSHIRANI, R. & FRIEDMAN, J. 2009. Unsupervised learning. *The elements of statistical learning.* Springer.

HASTIE, T. J. & TIBSHIRANI, R. J. 1990. Generalized additive models, volume 43 of Monographs on Statistics and Applied Probability. Chapman & Hall, London.

HAWKINS, E., OSBORNE, T. M., HO, C. K. & CHALLINOR, A. J. 2013. Calibration and bias correction of climate projections for crop modelling: An idealised case study over Europe. *Agricultural and Forest Meteorology,* 170**,** 19-31.

HAWKINS, E. & SUTTON, R. 2009. The Potential to Narrow Uncertainty in Regional Climate Predictions. *Bulletin of the American Meteorological Society,* 90**,** 1095-1108.

HAYHOE, K., WAKE, C. P., HUNTINGTON, T. G., LUO, L., SCHWARTZ, M. D., SHEFFIELD, J., WOOD, E., ANDERSON, B., BRADBURY, J. & DEGAETANO, A.

2007. Past and future changes in climate and hydrological indicators in the US Northeast. *Climate Dynamics,* 28**,** 381-407.

HENSON, I., JENSEN, C. & TURNER, N. 1989. Leaf Gas Exchange and Water Relations of Lupins and Wheat. I. Shoot Responses to Soil Water Deficits. *Functional Plant Biology,* 16**,** 401-413.

HESS, T. M. 1998. Trends in reference evapo-transpiration in the North East Arid Zone of Nigeria, 1961-91. *Journal of Arid Environments,* 38**,** 99-115.

HEWITSON, B. & CRANE, R. 2006. Consensus between GCM climate change projections with empirical downscaling: precipitation downscaling over South Africa. *International Journal of Climatology,* 26**,** 1315-1337.

HICKLING, R., ROY, D. B., HILL, J. K., FOX, R. & THOMAS, C. D. 2006. The distributions of a wide range of taxonomic groups are expanding polewards. *Global change biology,* 12**,** 450-455.

HIGGINS, K., LAMB, A. & VAN WILGEN, B. 1987. Root systems of selected plant species in mesic mountain fynbos in the Jonkershoek Valley, south-western Cape Province. *South African Journal of Botany,* 53**,** 249-257.

HIJMANS, R. J. 2012. Cross-validation of species distribution models: removing spatial sorting bias and calibration with a null model. *Ecology,* 93**,** 679-688.

HIJMANS, R. J., CAMERON, S. E., PARRA, J. L., JONES, P. G. & JARVIS, A. 2005. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology,* 25**,** 1965-1978.

HIJMANS, R. J. & GRAHAM, C. H. 2006. The ability of climate envelope models to predict the effect of climate change on species distributions. *Global change biology,* 12**,** 2272-2281.

HOFSTETTER, R. H. & PARSONS, F. The ecology of sawgrass in the Everglades of southern Florida. Proceedings of 1st Conference on Scientific Research in the National Parks, US Department of Interior, National Park Service Transaction and Proceedings Series, 1979. 165-170.

HOLSTE, E. K., KOBE, R. K. & VRIESENDORP, C. F. 2011. Seedling growth responses to soil resources in the understory of a wet tropical forest. *Ecology,* 92**,** 1828-1838.

HOLT, R. D. 1990. The microevolutionary consequences of climate change. *Trends in Ecology & Evolution,* 5**,** 311-315.

HUEY, R. B., KEARNEY, M. R., KROCKENBERGER, A., HOLTUM, J. A. M., JESS, M. & WILLIAMS, S. E. 2012. Predicting organismal vulnerability to climate warming: roles of behaviour, physiology and adaptation. *Philosophical Transactions of the Royal Society B: Biological Sciences,* 367, 1665-1679.

HULME, M., DOHERTY, R., NGARA, T., NEW, M. & LISTER, D. 2005. Global warming and African climate change: a reassessment. *Climate change and Africa*, 29-40.

HUNTLEY, B. 1991. How plants respond to climate change: Migration rates, individualism and the consequences for plant communities. *Annals of Botany,* 67, 15-22.

HUNTLEY, B., COLLINGHAM, Y. C., GREEN, R. E., HILTON, G. M., RAHBEK, C. & WILLIS, S. G. 2006. Potential impacts of climatic change upon geographical distributions of birds. *Ibis,* 148, 8-28.

HUTCHINSON, G. E. 1957. Cold Spring Harbor Symposium on Quantitative Biology. *Concluding remarks,* 22, 415-427.

HUTCHINSON, G. E. 1959. Homage to Santa Rosalia or why are there so many kinds of animals? *The American Naturalist,* 93, 145-159.

ILYINA, T., SIX, K. D., SEGSCHNEIDER, J., MAIER-REIMER, E., LI, H. & NÚÑEZ-RIBONI, I. 2013. Global ocean biogeochemistry model HAMOCC: Model architecture and performance as component of the MPI-Earth system model in different CMIP5 experimental realizations. *Journal of Advances in Modeling Earth Systems,* 5, 287-315.

IPCC 2007. Summary for Policymakers. *In:* SOLOMON, S., D. QIN, M. MANNING, Z. CHEN, M. MARQUIS, K.B. AVERYT, M.TIGNOR AND H.L. MILLER (ed.) *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change.* Cambridge, United Kingdom and New York, NY, USA: Cambridge University Press.

ISAAKS, E. & SRIVASTAVA, R. M. 1989. Applied Geostatisties. Oxford Univ. Press. New York, USA.

JACKSON, P. C., MEINZER, F. C., BUSTAMANTE, M., GOLDSTEIN, G., FRANCO, A., RUNDEL, P. W., CALDAS, L., IGLER, E. & CAUSIN, F. 1999. Partitioning of soil water among tree species in a Brazilian Cerrado ecosystem. *Tree physiology,* 19, 717-724.

JAKOB THEMEßL, M., GOBIET, A. & LEUPRECHT, A. 2011. Empirical-statistical downscaling and error correction of daily precipitation from regional climate models. *International Journal of Climatology,* 31, 1530-1544.

JARNEVICH, C. S., STOHLGREN, T. J., KUMAR, S., MORISETTE, J. T. & HOLCOMBE, T. R. 2015. Caveats for correlative species distribution modeling. *Ecological Informatics,* 29, 6-15.

JENSEN, M. E., BURMAN, R. D. & ALLEN, R. (eds.) 1990. *Evaporation and Irrigation Water Requirements,* New York, NY.

JENSEN, M. E. & HAISE, H. R. 1963. Estimating evapotranspiration from solar radiation. *Proceedings of the American Society of Civil Engineers, Journal of the Irrigation and Drainage Division,* 89**,** 15-41.

JOHNSON, W. C., BOETTCHER, S. E., POIANI, K. A. & GUNTENSPERGEN, G. 2004. Influence of weather extremes on the water levels of glaciated prairie wetlands. *Wetlands,* 24**,** 385-398.

JOHNSON, W. C., MILLETT, B. V., GILMANOV, T., VOLDSETH, R. A., GUNTENSPERGEN, G. R. & NAUGLE, D. E. 2005. Vulnerability of northern prairie wetlands to climate change. *BioScience,* 55**,** 863-872.

JOHNSON, W. C., WERNER, B., GUNTENSPERGEN, G. R., VOLDSETH, R. A., MILLETT, B., NAUGLE, D. E., TULBURE, M., CARROLL, R. W., TRACY, J. & OLAWSKY, C. 2010. Prairie wetland complexes as landscape functional units in a changing climate. *BioScience,* 60**,** 128-140.

JONES, R., NOGUER, M., HASSELL, D., HUDSON, D., WILSON, S., JENKINS, G. & MITCHELL, J. 2004. Generating high resolution climate change scenarios using PRECIS. *Met Office Hadley Centre, Exeter, UK,* 40.

JOVANOVIC, N., MASIYANDIMA, M., NAIKEN, V., DZIKITI, S. & GUSH, M. 2012. Remote sensing applications in water resources management—Desktop validation and draft paper. *CSIR Rep. No. CSIR/NRE/ECOS/IR/2011/0097/A*.

KEARNEY, M. & PORTER, W. 2009. Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. *Ecology Letters,* 12**,** 334-350.

KEDDY, P. A. 2010. *Wetland ecology: principles and conservation*, Cambridge University Press.

KÉFI, S., RIETKERK, M., ALADOS, C. L., PUEYO, Y., PAPANASTASIS, V. P., ELAICH, A. & DE RUITER, P. C. 2007. Spatial vegetation patterns and imminent desertification in Mediterranean arid ecosystems. *Nature,* 449**,** 213.

KEITH, D. A., AKÇAKAYA, H. R., THUILLER, W., MIDGLEY, G. F., PEARSON, R. G., PHILLIPS, S. J., REGAN, H. M., ARAÚJO, M. B. & REBELO, T. G. 2008. Predicting extinction risks under climate change: coupling stochastic population models with dynamic bioclimatic habitat models. *Biology Letters,* 4**,** 560-563.

KELLY, A. E. & GOULDEN, M. L. 2008. Rapid shifts in plant distribution with recent climate change. *Proceedings of the National Academy of Sciences,* 105**,** 11823-11826.

KLAUSMEYER, K. R. & SHAW, M. R. 2009. Climate Change, Habitat Loss, Protected Areas and the Climate Adaptation Potential of Species in Mediterranean Ecosystems Worldwide. *PloS one,* 4**,** e6392.

KOBE, R. K. 1999. Light gradient partitioning among tropical tree species through differential seedling mortality and growth. *Ecology,* 80**,** 187-201.

KONAR, M., JASON TODD, M., MUNEEPEERAKUL, R., RINALDO, A. & RODRIGUEZ-ITURBE, I. 2013. Hydrology as a driver of biodiversity: Controls on carrying capacity, niche formation, and dispersal. *Advances in Water Resources,* 51**,** 317-325.

KOTOWSKI, W., THÖRIG, W., DIGGELEN, R. & WASSEN, M. J. 2006. Competition as a factor structuring species zonation in riparian fens-a transplantation experiment. *Applied Vegetation Science,* 9**,** 231-240.

KRAUCUNAS, I., CLARKE, L., DIRKS, J., HATHAWAY, J., HEJAZI, M., HIBBARD, K., HUANG, M., JIN, C., KINTNER-MEYER, M., VAN DAM, K. K., LEUNG, R., LI, H.-Y., MOSS, R., PETERSON, M., RICE, J., SCOTT, M., THOMSON, A., VOISIN, N. & WEST, T. 2015. Investigating the nexus of climate, energy, water, and land at decision-relevant scales: the Platform for Regional Integrated Modeling and Analysis (PRIMA). *Climatic Change,* 129**,** 573-588.

KREMEN, C., CAMERON, A., MOILANEN, A., PHILLIPS, S., THOMAS, C., BEENTJE, H., DRANSFIELD, J., FISHER, B., GLAW, F. & GOOD, T. 2008. Aligning conservation priorities across taxa in Madagascar with high-resolution planning tools. *Science,* 320**,** 222-226.

KRUGER, A. C. & SHONGWE, S. 2004. Temperature trends in South Africa: 1960–2003. *International Journal of Climatology,* 24**,** 1929-1945.

KRUGER, F. J. 1983. Plant community diversity and dynamics in relation to fire. *Mediterranean-type ecosystems.* Springer.

KULMATISKI, A. & BEARD, K. H. 2013. Root niche partitioning among grasses, saplings, and trees measured using a tracer technique. *Oecologia,* 171**,** 25-37.

KUMAR, S. & STOHLGREN, T. J. 2009. Maxent modeling for predicting suitable habitat for threatened and endangered tree Canacomyrica monticola in New Caledonia. *Journal of Ecology and natural Environment,* 1**,** 094-098.

LAMARQUE, J., MASUI, T., MEINSHAUSEN, M., NAKICENOVIC, N., SMITH, S. & ROSE, S. 2011. The representative concentration pathways: an overview. *Clim Chang,* 109**,** 531.

LANDMAN, S., 2012. A multi-model ensemble system for short-range weather prediction in South Africa (Doctoral dissertation, University of Pretoria).

LANDMAN, W.A. and GODDARD, L., 2002. Statistical recalibration of GCM forecasts over southern Africa using model output statistics. Journal of Climate, 15(15), pp.2038-2055.

LANDMAN, W.A. and TENNANT, W.J., 2000. Statistical downscaling of monthly forecasts. International Journal of Climatology, 20(13), pp.1521-1532.

LATIMER, A. M., SILANDER, J. A. & COWLING, R. M. 2005. Neutral ecological theory reveals isolation and rapid speciation in a biodiversity hot spot. *Science,* 309**,** 1722-1725.

LAWLER, J. J., SHAFER, S. L., WHITE, D., KAREIVA, P., MAURER, E. P., BLAUSTEIN, A. R. & BARTLEIN, P. J. 2009. Projected climate-induced faunal change in the Western Hemisphere. *Ecology,* 90**,** 588-597.

LEI, J., CHEN, L. & LI, H. 2017. Using ensemble forecasting to examine how climate change promotes worldwide invasion of the golden apple snail (*Pomacea canaliculata*). *Environmental monitoring and assessment*, 189, 404.

LENOIR, J., HATTAB, T. & PIERRE, G. 2017. Climatic microrefugia under anthropogenic climate change: implications for species redistribution. *Ecography,* 40**,** 253-266.

LENOIR, J. & SVENNING, J. C. 2015. Climate-related range shifts – a global multidimensional synthesis and new research directions. *Ecography,* 38**,** 15-28.

LI, J. & HEAP, A. D. 2014. Spatial interpolation methods applied in the environmental sciences: A review. *Environmental Modelling & Software,* 53**,** 173-189.

LINDER, H. P., BRIGGS, B. G. & JOHNSON, L. A. S. 1998. Restionaceae. *In:* KUBITZKI, K. (ed.) *The Families and Genera of Vascular Plants IV. Flowering Plants: Monocotyledons.* Berlin: Springer.

LINDERSON, M.-L., ACHBERGER, C. & CHEN, D. 2004. Statistical downscaling and scenario construction of precipitation in Scania, southern Sweden. *Hydrology Research,* 35**,** 261-278.

LIU, S., GRAHAM, W. D. & JACOBS, J. M. 2005. Daily potential evapotranspiration and diurnal climate forcings: influence on the numerical modelling of soil water dynamics and evapotranspiration. *Journal of hydrology,* 309**,** 39-52.

LOWRY, C. S., LOHEIDE, S. P., MOORE, C. E. & LUNDQUIST, J. D. 2011. Groundwater controls on vegetation composition and patterning in mountain meadows. *Water Resources Research,* 47.

MAGEE, T. K. & KENTULA, M. E. 2005. Response of wetland plant species to hydrologic conditions. *Wetlands Ecology and Management,* 13**,** 163-181.

MAGUIRE, K. C., NIETO-LUGILDE, D., FITZPATRICK, M. C., WILLIAMS, J. W. & BLOIS, J. L. 2015. Modeling Species and Community Responses to Past, Present, and Future Episodes of Climatic and Ecological Change. *Annual review of ecology, evolution, and systematics,* 46**,** 343-368.

MAHALANOBIS, P. C. On the generalized distance in statistics. 1936. National Institute of Science of India.

MAIDMENT, D. R. 1992. *Handbook of hydrology*, McGraw-Hill Inc.

MAINALI, K. P., WARREN, D. L., DHILEEPAN, K., MCCONNACHIE, A., STRATHIE, L., HASSAN, G., KARKI, D., SHRESTHA, B. B. & PARMESAN, C. 2015. Projecting future expansion of invasive species: comparing and improving methodologies for species distribution modeling. *Global change biology,* 21**,** 4464-4480.

MAIR, L., HILL, J. K., FOX, R., BOTHAM, M., BRERETON, T. & THOMAS, C. D. 2014. Abundance changes and habitat availability drive species' responses to climate change. *Nature climate change,* 4**,** 127.

MAIR, L., THOMAS, C. D., ANDERSON, B. J., FOX, R., BOTHAM, M. & HILL, J. K. 2012. Temporal variation in responses of species to four decades of climate warming. *Global change biology,* 18**,** 2439-2447.

MAKKINK, G. 1957. Testing the Penman formula by means of lysimeters. *J. Inst. Water Eng,* 11**,** 277-288.

MALCOLM, J. R., LIU, C., NEILSON, R. P., HANSEN, L. & HANNAH, L. 2006. Global warming and extinctions of endemic species from biodiversity hotspots. *Conservation Biology,* 20**,** 538-548.

MALIVA, R. & MISSIMER, T. 2012. *Arid Lands Water Evaluation and Management,* Berlin Heidelberg, Springer-Verlag.

MANNING, S. J. & BARBOUR, M. G. 1988. Root Systems, Spatial Patterns, and Competition for Soil Moisture between Two Desert Subshrubs. *American Journal of Botany,* 75**,** 885-893.

MASON, S. C., PALMER, G., FOX, R., GILLINGS, S., HILL, J. K., THOMAS, C. D. & OLIVER, T. H. 2015. Geographical range margins of many taxonomic groups continue to shift polewards. *Biological Journal of the Linnean Society,* 115**,** 586-597.

MATEO, R. G., GASTÓN, A., AROCA-FERNÁNDEZ, M. J., SAURA, S. and GARCIA-VIŇAS, J. I., 2018. Optimization of forest sampling strategies for woody plant species distribution modelling at the landscape scale. Forest Ecology and Management, 410, pp.104-113.

MCGILL, B. M., SUTTON-GRIER, A. E. & WRIGHT, J. P. 2010. Plant trait diversity buffers variability in denitrification potential over changes in season and soil conditions. *PLoS One,* 5**,** e11618.

MCKANE, R. B., JOHNSON, L. C., SHAVER, G. R., NADELHOFFER, K. J., RASTETTER, E. B., FRY, B., GIBLIN, A. E., KIELLAND, K., KWIATKOWSKI, B. L. & LAUNDRE, J. A. 2002. Resource-based niches provide a basis for plant species diversity and dominance in arctic tundra. *Nature,* 415**,** 68-71.

MCLACHLAN, J. S., HELLMANN, J. J. & SCHWARTZ, M. W. 2007. A framework for debate of assisted migration in an era of climate change. *Conservation Biology,* 21**,** 297-302.

MCLAUGHLIN, F., CARMACK, E., PROSHUTINSKY, A., KRISHFIELD, R. A., GUAY, C., YAMAMOTO-KAWAI, M., JACKSON, J. M. & WILLIAMS, B. 2011. The rapid response of the Canada Basin to climate forcing: From bellwether to alarm bells. *Oceanography,* 24**,** 146-159.

MCMAHON, T., PEEL, M., LOWE, L., SRIKANTHAN, R. & MCVICAR, T. 2013. Estimating actual, potential, reference crop and pan evaporation using standard meteorological data: a pragmatic synthesis. *Hydrology and Earth System Sciences,* 17**,** 1331.

MCPHERSON, J. & JETZ, W. 2007. Effects of species' ecology on the accuracy of distribution models. *Ecography,* 30**,** 135-151.

MEARNS, L. O., BUKOVSKY, M., PRYOR, S. C. & MAGAÑA, V. 2018. Downscaling of climate information. *Climate Modelling.* Springer.

MEEHL, G. A., MOSS, R., TAYLOR, K. E., EYRING, V., STOUFFER, R. J., BONY, S. & STEVENS, B. 2014. Climate model intercomparisons: Preparing for the next phase. *Eos, Transactions American Geophysical Union,* 95**,** 77-78.

MEINZER, F. C., ANDRADE, J. L., GOLDSTEIN, G., HOLBROOK, N. M., CAVELIER, J. & WRIGHT, S. J. 1999. Partitioning of soil water among canopy trees in a seasonally dry tropical forest. *Oecologia,* 121**,** 293-301.

MENDIVELSO, H. A., CAMARERO, J. J., OBREGON, O. R., GUTIERREZ, E. & TOLEDO, M. 2013. Differential Growth Responses to Water Balance of Coexisting Deciduous Tree Species Are Linked to Wood Density in a Bolivian Tropical Dry Forest. *PLoS One,* 8.

MENÉNDEZ, R., MEGÍAS, A. G., HILL, J. K., BRASCHLER, B., WILLIS, S. G., COLLINGHAM, Y., FOX, R., ROY, D. B. & THOMAS, C. D. 2006. Species richness changes lag behind climate change. *Proceedings of the Royal Society of London B: Biological Sciences,* 273**,** 1465-1470.

MEROW, C., SMITH, M. J., EDWARDS, T. C., GUISAN, A., MCMAHON, S. M., NORMAND, S., THUILLER, W., WÜEST, R. O., ZIMMERMANN, N. E. & ELITH, J. 2014. What do we gain from simplicity versus complexity in species distribution models? *Ecography,* 37**,** 1267-1281.

MIDGLEY, G. F., CHAPMAN, R. A., HEWITSON, B., JOHNSTON, P., DE WIT, M., ZIERVOGEL, G., MUKHEIBIR, P., VAN NIEKERK, L., TADROSS, M., VAN WILGEN, B. W., KGOPE, B., MORANT, P. D., THERON, A., SCHOLES, R. J. & FORSYTH, G. G. 2005. A status quo, vulnerability and adaptation assessment of the physical and socio-economic effects of climate change in the western Cape. Report to the Western Cape Government, Cape Town, South Africa. CSIR Report No. ENV-S-C 2005-073, CSIR Environmentek. Stellenbosch.

MIDGLEY, G. F., HANNAH, L., MILLAR, D., THUILLER, W. & BOOTH, A. 2003. Developing regional and species-level assessments of climate change impacts on biodiversity in the Cape Floristic Region. *Biological Conservation,* 112**,** 87-97.

MIDGLEY, G. F., HUGHES, G. O., THUILLER, W. & REBELO, A. G. 2006. Migration rate limitations on climate change-induced range shifts in Cape Proteaceae. *Diversity and Distributions,* 12**,** 555-562.

MIKOLAJEWICZ, U., NOTZ, D. & VON STORCH, J. 2013. Characteristics of the ocean simulations in MPIOM, the ocean component of the MPI-earth system model. *J Adv Model Earth Syst. doi: http://dx. doi. org/10.1002/jame,* 20023.

MILLENIUM ECOSYSTEM ASSESSMENT 2005. Dryland Systems.

MILLER, K. M. & MCGILL, B. J. 2018. Land use and life history limit migration capacity of eastern tree species. *Global Ecology and Biogeography,* 27**,** 57-67.

MILLER, S. P. & BEVER, J. D. 1999. Distribution of arbuscular mycorrhizal fungi in stands of the wetland grass *Panicum hemitomon* along a wide hydrologic gradient. *Oecologia,* 119**,** 586-592.

MINTZ, Y. & WALKER, G. 1993. Global fields of soil moisture and land surface evapotranspiration derived from observed precipitation and surface air temperature. *Journal of Applied Meteorology,* 32**,** 1305-1334.

MITSCH, W. J. & GOSSELINK, J. G. 2007. Wetlands. 4th ed. Hoboken: NJ: John Wiley & Sons, Inc.

MOLL, E. & BOSSI, L. 1984. Assessment of the extent of the natural vegetation of the fynbos biome of South Africa. *South African Journal of Science,* 80**,** 355-358.

MORENO-GUTIÉRREZ, C., DAWSON, T. E., NICOLÁS, E. & QUEREJETA, J. I. 2012. Isotopes reveal contrasting water use strategies among coexisting plant species in a Mediterranean ecosystem. *New Phytologist,* 196**,** 489-496.

MOSER, K., AHN, C. & NOE, G. 2007. Characterization of microtopography and its influence on vegetation patterns in created wetlands. *Wetlands,* 27**,** 1081-1097.

MOSS, R. H., EDMONDS, J. A., HIBBARD, K. A., MANNING, M. R., ROSE, S. K., VAN VUUREN, D. P., CARTER, T. R., EMORI, S., KAINUMA, M., KRAM, T., MEEHL, G. A., MITCHELL, J. F. B., NAKICENOVIC, N., RIAHI, K., SMITH, S. J., STOUFFER, R. J., THOMSON, A. M., WEYANT, J. P. & WILBANKS, T. J. 2010. The next generation of scenarios for climate change research and assessment. *Nature,* 463**,** 747.

MTONGORI, H. I., STORDAL, F. & BENESTAD, R. E. 2016. Evaluation of Empirical Statistical Downscaling Models’ Skill in Predicting Tanzanian Rainfall and Their Application in Providing Future Downscaled Scenarios. *Journal of Climate,* 29**,** 3231-3252.

MU, Q., HEINSCH, F. A., ZHAO, M. & RUNNING, S. W. 2007. Development of a global evapotranspiration algorithm based on MODIS and global meteorology data. *Remote sensing of Environment,* 111**,** 519-536.

MUCINA, L. & RUTHERFORD, M. C. 2006. *The vegetation of South Africa, Lesotho and Swaziland*, South African National Biodiversity Institute.

MYERS, N., MITTERMEIER, R. A., MITTERMEIER, C. G., DA FONSECA, G. A. & KENT, J. 2000. Biodiversity hotspots for conservation priorities. *Nature,* 403**,** 853-858.

NATHAN, R. and MULLER-LANDAU, H.C. 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. Trends in ecology & evolution, 15, 278-285.

NATHAN, R., HORVITZ, N., HE, Y., KUPARINEN, A., SCHURR, F. M. & KATUL, G. G. 2011. Spread of North American wind-dispersed trees in future environments. *Ecology Letters,* 14**,** 211-219.

NEW, M., HEWITSON, B., STEPHENSON, D. B., TSIGA, A., KRUGER, A., MANHIQUE, A., GOMEZ, B., COELHO, C. A. S., MASISI, D. N., KULULANGA, E., MBAMBALALA, E., ADESINA, F., SALEH, H., KANYANGA, J., ADOSI, J., BULANE, L., FORTUNATA, L., MDOKA, M. L. & LAJOIE, R. 2006. Evidence of trends in daily climate extremes over southern and west Africa. *J. Geophys. Res.,* 111**,** D14102.

NIPPERT, J. B. & KNAPP, A. K. 2007. Soil water partitioning contributes to species coexistence in tallgrass prairie. *Oikos,* 116**,** 1017-1029.

NIX, H. A. 1986. A biogeographic analysis of Australian elapid snakes. *Atlas of elapid snakes of Australia,* 7**,** 4-15.

NOBEL, P. 1997. Root distribution and seasonal production in the northwestern Sonoran Desert for a C3 subshrub, a C4 bunchgrass, and a CAM leaf succulent. *American Journal of Botany,* 84**,** 949-949.

O'GORMAN, P. A. & SCHNEIDER, T. 2009. The physical basis for increases in precipitation extremes in simulations of 21st-century climate change. *Proceedings of the National Academy of Sciences,* 106**,** 14773-14777.

OELOFSE, A. & VAN AVERBEKE, W. 2012. *Nutritional value and water use of African leafy vegetables for improved livelihoods*, Water Research Commission.

OLLIS, D., EWART-SMITH, J., DAY, J., JOB, N., MACFARLANE, D., SNADDON, C., SIEBEN, E., DINI, J. & MBONA, N. 2015. The development of a classification system for inland aquatic ecosystems in South Africa. *Water SA,* 41**,** 727-745.

PACHAURI, R. K., ALLEN, M. R., BARROS, V. R., BROOME, J., CRAMER, W., CHRIST, R., CHURCH, J. A., CLARKE, L., DAHE, Q. & DASGUPTA, P. 2014. *Climate change 2014: synthesis report. Contribution of Working Groups I, II and III to the fifth assessment report of the Intergovernmental Panel on Climate Change*, IPCC.

PACIFICI, M., FODEN, W. B., VISCONTI, P., WATSON, J. E. M., BUTCHART, S. H. M., KOVACS, K. M., SCHEFFERS, B. R., HOLE, D. G., MARTIN, T. G., AKÇAKAYA, H. R., CORLETT, R. T., HUNTLEY, B., BICKFORD, D., CARR, J. A., HOFFMANN, A. A., MIDGLEY, G. F., PEARCE-KELLY, P., PEARSON, R. G., WILLIAMS, S. E., WILLIS, S. G., YOUNG, B. & RONDININI, C. 2015. Assessing species vulnerability to climate change. *Nature climate change,* 5**,** 215.

PARMESAN, C., RYRHOLM, N., STEFANESCU, C., HILL, J. K., THOMAS, C. D., DESCIMON, H., HUNTLEY, B., KAILA, L., KULLBERG, J. & TAMMARU, T. 1999. Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature,* 399**,** 579.

PARMESAN, C., 1996. Climate and species' range. Nature, 382, 6594, 765

PAROLIN, P. 2001. Morphological and physiological adjustments to waterlogging and drought in seedlings of Amazonian floodplain trees. *Oecologia,* 128**,** 326-335.

PARRY, M. L. 2007. *Climate Change 2007: Impacts, Adaptation and Vulnerability: Working Group II Contribution to the Fourth Assessment Report of the IPCC Intergovernmental Panel on Climate Change*, Cambridge University Press.

PEARSON, R. G. 2007. Species' distribution modeling for conservation educators and practitioners. *Lessons in Conservation* (*LinC*), 3,54-89.

PEARSON, R. G. & DAWSON, T. P. 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography,* 12, 361-371.

PEARSON, R. G., DAWSON, T. P. & LIU, C. 2004. Modelling species distributions in Britain: a hierarchical integration of climate and land-cover data. *Ecography,* 27, 285-298.

PEARSON, R. G., THUILLER, W., ARAÚJO, M. B., MARTINEZ-MEYER, E., BROTONS, L., MCCLEAN, C., MILES, L., SEGURADO, P., DAWSON, T. P. & LEES, D. C. 2006. Model-based uncertainty in species range prediction. *Journal of Biogeography,* 33, 1704-1711.

PENMAN, H. L. 1948. Natural evaporation from open water, bare soil and grass. *Proceedings of the Royal Society of London. Series A. Mathematical and Physical Sciences,* 193, 120-145.

PERKINS, S. E., PITMAN, A. J., HOLBROOK, N. J. & MCANENEY, J. 2007. Evaluation of the AR4 climate models' simulated daily maximum temperature, minimum temperature, and precipitation over Australia using probability density functions. *Journal of Climate,* 20, 4356-4376.

PETERS, J., DE BAETS, B., VERHOEST, N. E., SAMSON, R., DEGROEVE, S., DE BECKER, P. & HUYBRECHTS, W. 2007. Random forests as a tool for ecohydrological distribution modelling. *Ecological Modelling,* 207, 304-318.

PETITPIERRE, B., BROENNIMANN, O., KUEFFER, C., DAEHLER, C. & GUISAN, A. 2017. Selecting predictors to maximize the transferability of species distribution models: lessons from cross-continental plant invasions. *Global Ecology and Biogeography,* 26, 275-287.

PHILLIPS, S., DUDIK, M. & SCHAPIRE, R. 2005. Maxent software for species distribution modeling. *www. cs. princeton.edu/schapire/maxent*.

PHILLIPS, S. J., ANDERSON, R. P. & SCHAPIRE, R. E. 2006. Maximum entropy modeling of species geographic distributions. *Ecological Modelling,* 190, 231-259.

PHILLIPS, S. J. & DUDÍK, M. 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography,* 31, 161-175.

PHILLIPS, S. J., DUDÍK, M., ELITH, J., GRAHAM, C. H., LEHMANN, A., LEATHWICK, J. & FERRIER, S. 2009. Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. *Ecological applications,* 19, 181-197.

PHILLIPS, S. J., DUDÍK, M. & SCHAPIRE, R. E. 2004. A maximum entropy approach to species distribution modeling. Proceedings of the twenty-first international conference on Machine learning. ACM, 83.

PIDWIRNY, M. 2006. Physical properties of water. *Fundamentals of Physical Geography*.

PIMM, S. L. & JENKINS, C. N. 2010. Extinctions and the practice of preventing them. *Conservation biology for all,* 1**,** 181-98.

POFF, N. L. & ZIMMERMAN, J. K. 2010. Ecological responses to altered flow regimes: a literature review to inform the science and management of environmental flows. *Freshwater Biology,* 55**,** 194-205.

POIANI, K. A. & JOHNSON, W. C. 1993. A spatial simulation model of hydrology and vegetation dynamics in semi-permanent prairie wetlands. *Ecological applications***,** 279-293.

POIANI, K. A., JOHNSON, W. C., SWANSON, G. A. & WINTER, T. C. 1996. Climate change and northern prairie wetlands: simulations of long-term dynamics. *Limnology and Oceanography,* 41**,** 871-881.

PONGRATZ, J., REICK, C., RADDATZ, T. & CLAUSSEN, M. 2009. Effects of anthropogenic land cover change on the carbon cycle of the last millennium. *Global Biogeochemical Cycles,* 23.

PORFIRIO, L. L., HARRIS, R. M. B., LEFROY, E. C., HUGH, S., GOULD, S. F., LEE, G., BINDOFF, N. L. & MACKEY, B. 2014. Improving the use of species distribution models in conservation planning and management under climate change. *PloS one,* 9**,** e113749.

PRESSEY, R. L., CABEZA, M., WATTS, M. E., COWLING, R. M. & WILSON, K. A. 2007. Conservation planning in a changing world. *Trends in Ecology & Evolution,* 22**,** 583-592.

PRIESTLEY, C. H. B. & TAYLOR, R. J. 1972. On the assessment of surface heat flux and evaporation using large-scale parameters. *Monthly Weather Review,* 100**,** 81-92.

PRUDHOMME, C. & WILLIAMSON, J. 2013. Derivation of RCM-driven potential evapotranspiration for hydrological climate change impact analysis in Great Britain: a comparison of methods and associated uncertainty in future projections. *Hydrology and Earth System Sciences,* 17**,** 1365.

PULLIAM, H. R. 2000. On the relationship between niche and distribution. *Ecology Letters,* 3**,** 349-361.

QIU, Y., FU, B., WANG, J. & CHEN, L. 2001. Spatial variability of soil moisture content and its relation to environmental indices in a semi-arid gully catchment of the Loess Plateau, China. *Journal of Arid Environments,* 49, 723-750.

R DEVELOPMENT CORE TEAM 2015. R: A language and environment for statistical computing. 3.12 ed. Vienna, Austria: R Foundation for Statistical Computing.

RAMOELO, A., MAJOZI, N., MATHIEU, R., JOVANOVIC, N., NICKLESS, A. & DZIKITI, S. 2014. Validation of global evapotranspiration product (MOD16) using flux tower data in the African savanna, South Africa. *Remote Sensing,* 6, 7406-7423.

RANDALL, D. A., WOOD, R. A., BONY, S., COLMAN, R., FICHEFET, T., FYFE, J., KATTSOV, V., PITMAN, A., SHUKLA, J. & SRINIVASAN, J. 2007. Climate models and their evaluation. *Climate change 2007: The physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the IPCC (FAR).* Cambridge University Press.

RAPACCIUOLO, G., MAHER, S. P., SCHNEIDER, A. C., HAMMOND, T. T., JABIS, M. D., WALSH, R. E., IKNAYAN, K. J., WALDEN, G. K., OLDFATHER, M. F., ACKERLY, D. D. & BEISSINGER, S. R. 2014. Beyond a warming fingerprint: individualistic biogeographic responses to heterogeneous climate change in California. *Global change biology,* 20, 2841-2855.

RAULINGS, E., MORRIS, K., ROACHE, M. & BOON, P. 2010. The importance of water regime operating at small spatial scales for the diversity and structure of wetland vegetation. . *Freshwater Biology,* 55, 701-715.

RAY, D., BEHERA, M. D. & JACOB, J. 2017. Evaluating ecological niche models: A comparison between Maxent and GARP for predicting distribution of *Hevea brasiliensis* in India. *Proceedings of the National Academy of Sciences, India Section B: Biological Sciences*.

RAZALI, N. M. & WAH, Y. B. 2011. Power comparisons of shapiro-wilk, kolmogorov-smirnov, lilliefors and anderson-darling tests. *Journal of statistical modeling and analytics,* 2, 21-33.

REBELO, A. G., BOUCHER, C., HELME, N. A., MUCINA, L. & RUTHERFORD, M. C. 2006. Fynbos biome. *In:* MUCINA, L. & RUTHERFORD, M. C. (eds.) *The Vegetation of South Africa, Lesotho and Swaziland.* Pretoria: South African National Biodiversity Institute

REICK, C., RADDATZ, T., BROVKIN, V. & GAYLER, V. 2013. Representation of natural and anthropogenic land cover change in MPI-ESM. *Journal of Advances in Modeling Earth Systems,* 5, 459-482.

REYER, C. P., LEUZINGER, S., RAMMIG, A., WOLF, A., BARTHOLOMEUS, R. P., BONFANTE, A., DE LORENZI, F., DURY, M., GLONING, P. & ABOU JAOUDÉ, R. 2013. A plant's perspective of extremes: terrestrial plant responses to changing climatic variability. *Global Change Biology,* 19**,** 75-89.

REYNOLDS, H. L., PACKER, A., BEVER, J. D. & CLAY, K. 2003. Grassroots ecology: plant-microbe-soil interactions as drivers of plant community structure and dynamics. *Ecology,* 84**,** 2281-2291.

REYNOLDS, J. F., VIRGINIA, R. A., KEMP, P. R., DE SOYZA, A. G. & TREMMEL, D. C. 1999. Impact of drought on desert shrubs: Effects of seasonality and degree of resource island development. *Ecological Monographs,* 69**,** 69-106.

RIAHI, K., KREY, V., RAO, S., CHIRKOV, V., FISCHER, G., KOLP, P., KINDERMANN, G., NAKICENOVIC, N. & RAFAI, P. 2011. RCP-8.5: exploring the consequence of high emission trajectories. *Climatic Change. doi,* 10**,** 1007.

RICHARDS, M. B., COWLING, R. M. & STOCK, W. D. 1997. Soil nutrient dynamics and community boundaries in the Fynbos vegetation of South Africa. *Plant Ecology,* 130**,** 143-153.

RODERICK, M. L., HOBBINS, M. T. & FARQUHAR, G. D. 2009. Pan evaporation trends and the terrestrial water balance. II. Energy balance and interpretation. *Geography Compass,* 3**,** 761-780.

RODRIQUEZ-ITURBE, I., VOGEL, G. K., RIGON, R., ENTEKHABI, D., CASTELLI, F. & RINALDO, A. 1995. On the spatial organisation of soil moisture fields. . *Geophysical Research Letters,* 22**,** 2757 - 2760.

ROGELJ, J., MEINSHAUSEN, M. & KNUTTI, R. 2012. Global warming under old and new scenarios using IPCC climate sensitivity range estimates. *Nature climate change,* 2**,** 248-253.

ROOT, T. L., PRICE, J. T., HALL, K. R., SCHNEIDER, S. H., ROSENZWEIG, C. & POUNDS, J. A. 2003. Fingerprints of global warming on wild animals and plants. *Nature,* 421**,** 57.

ROOT, T. L. & SCHNEIDER, S. H. 1993. Can Large-Scale Climatic Models Be Linked with Multiscale Ecological Studies?*. *Conservation Biology,* 7**,** 256-270.

ROSENZWEIG, C., ELLIOTT, J., DERYNG, D., RUANE, A. C., MÜLLER, C., ARNETH, A., BOOTE, K. J., FOLBERTH, C., GLOTTER, M. & KHABAROV, N. 2014. Assessing agricultural risks of climate change in the 21st century in a global gridded crop model intercomparison. *Proceedings of the National Academy of Sciences,* 111**,** 3268-3273.

ROSENZWEIG, M. L. 1995. *Species diversity in space and time*, Cambridge University Press.

ROSS, M. S., REED, D. L., SAH, J. P., RUIZ, P. L. & LEWIN, M. 2003. Vegetation: environment relationships and water management in Shark Slough, Everglades National Park. *Wetlands Ecology and Management,* 11**,** 291-303.

ROUGET, M., RICHARDSON, D. M., COWLING, R. M., LLOYD, J. W. & LOMBARD, A. T. 2003. Current patterns of habitat transformation and future threats to biodiversity in terrestrial ecosystems of the Cape Floristic Region, South Africa. *Biological Conservation,* 112**,** 63-85.

SANTER, B., WIGLEY, T., SCHLESINGER, M. & MITCHELL, J. 1989. Max-Planck-Institut fur Meteorologie. *Report,* 45.

SCHEFFER, M., BASCOMPTE, J., BROCK, W. A., BROVKIN, V., CARPENTER, S. R., DAKOS, V., HELD, H., VAN NES, E. H., RIETKERK, M. & SUGIHARA, G. 2009. Early-warning signals for critical transitions. *Nature,* 461**,** 53.

SCHEFFER, M., CARPENTER, S. R., LENTON, T. M., BASCOMPTE, J., BROCK, W., DAKOS, V., VAN DE KOPPEL, J., VAN DE LEEMPUT, I. A., LEVIN, S. A., VAN NES, E. H., PASCUAL, M. & VANDERMEER, J. 2012. Anticipating Critical Transitions. *Science,* 338**,** 344-348.

SCHEMSKE, D. W., HUSBAND, B. C., RUCKELSHAUS, M. H., GOODWILLIE, C., PARKER, I. M. & BISHOP, J. G. 1994. Evaluating approaches to the conservation of rare and endangered plants. *Ecology,* 75**,** 584-606.

SCHNECK, R., REICK, C. H. & RADDATZ, T. 2013. Land contribution to natural CO_2 variability on time scales of centuries. *Journal of Advances in Modeling Earth Systems,* 5**,** 354-365.

SCHULMAN, L., TOIVONEN, T. & RUOKOLAINEN, K. 2007. Analysing botanical collecting effort in Amazonia and correcting for it in species range estimation. *Journal of Biogeography,* 34**,** 1388-1399.

SCHULZE, R. 1997. South African atlas of agrohyrdology and climatology. Tech. Rep., Report TT82/96, Water Research Commission, Pretoria, South Africa.

SCHULZE, R., MAHARAJ, M., WARBURTON, M., GERS, C., HORAN, M., KUNZ, R. & CLARK, D. 2007. South African atlas of climatology and agrohydrology. *Water Research Commission, Pretoria, RSA, WRC Report,* 1489**,** 06.

SCHULZE, R. & MARARAJ, M. 2007. Rainfall seasonality. In: Schulze, R.E. (Ed.), 2007/8. South African Atlas of Climatology and Agrohydrology. Water Research Commission, Pretoria, South Africa, Report 1489/1/06, Section 3.4.

SCHWINNING, S. & EHLERINGER, J. R. 2001. Water use trade-offs and optimal adaptations to pulse-driven arid ecosystems. *Journal of Ecology,* 89**,** 464-480.

SCOTT, D., MALCOLM, J. R. & LEMIEUX, C. 2002. Climate change and modelled biome representation in Canada's national park system: implications for system planning and park mandates. *Global Ecology and Biogeography,* 11**,** 475-484.

SEDDON, P. J., GRIFFITHS, C. J., SOORAE, P. S. & ARMSTRONG, D. P. 2014. Reversing defaunation: restoring species in a changing world. *Science,* 345**,** 406-412.

SEDDON, P. J., MORO, D., MITCHELL, N. J., CHAUVENET, A. L. & MAWSON, P. R. 2015. Proactive conservation or planned invasion? Past, current and future use of assisted colonisation. *Advances in reintroduction biology of Australian and New Zealand fauna***,** 105-126.

SENIOR, C. A., ANDREWS, T., BURTON, C., CHADWICK, R., COPSEY, D., GRAHAM, T., HYDER, P., JACKSON, L., MCDONALD, R. & RIDLEY, J. 2016. Idealized climate change simulations with a high-resolution physical model: HadGEM3-GC2. *Journal of Advances in Modeling Earth Systems,* 8**,** 813-830.

SHAPIRO, S. S. & WILK, M. B. 1965. An analysis of variance test for normality (complete samples). *Biometrika,* 52**,** 591-611.

SHONGWE, M.E., LANDMAN, W.A. and MASON, S.J., 2006. Performance of recalibration systems for GCM forecasts for southern Africa. International journal of climatology, 26(12), pp.1567-1585.

SHONGWE, M. E., VAN OLDENBORGH, G. J., VAN DEN HURK, B. & AALST, M. V. 2011. Projected changes in mean and extreme precipitation in Africa under global warming. Part II: East Africa. *Journal of Climate,* 24**,** 3718-3733.

SHONGWE, M. E., VAN OLDENBORGH, G. J., VAN DEN HURK, B. J. J. M., DE BOER, B., COELHO, C. A. S. & VAN AALST, M. K. 2009. Projected changes in mean and extreme precipitation in Africa under global warming. Part I: Southern Africa. *Journal of Climate,* 22**,** 3819-3837.

SIEBEN, E., BOUCHER, C. & MUCINA, L. 2004. Vegetation of high-altitude fens and restio marshlands of the Hottentots Holland Mountains, Western Cape, South Africa. *Bothalia,* 34**,** 141-153.

SILVERTOWN, J. 2004. Plant coexistence and the niche. *Trends in Ecology & Evolution,* 19**,** 605-611.

SILVERTOWN, J., ARAYA, Y. & GOWING, D. 2015. Hydrological niches in terrestrial plant communities: a review. *Journal of Ecology,* 103**,** 93-108.

SILVERTOWN, J., ARAYA, Y. N., LINDER, H. P. & GOWING, D. J. 2012. Experimental investigation of the origin of fynbos plant community structure after fire. *Annals of botany,* 110**,** 1377-1383.

SILVERTOWN, J., DODD, M. E., GOWING, D. J. G. & MOUNTFORD, J. O. 1999. Hydrologically defined niches reveal a basis for species richness in plant communities. *Nature,* 400**,** 61-63.

SILVERTOWN, J., MCCONWAY, K., GOWING, D., DODD, M., FAY, M. F., JOSEPH, J. A. & DOLPHIN, K. 2006. Absence of phylogenetic signal in the niche structure of meadow plant communities. *Proceedings of the Royal Society B: Biological Sciences,* 273**,** 39-44.

SMALL, C. 2003. High spatial resolution spectral mixture analysis of urban reflectance. *Remote Sensing of Environment,* 88**,** 170-186.

SOBERON, J. & PETERSON, A. T. 2005. Interpretation of models of fundamental ecological niches and species' distributional areas.

SOLOMON, S., QIN, D., MANNING, M., MARQUIS, M., AVERYT, K. & TIGNOR, M. 2007. Climate change 2007: The physical science basis. Contribution of Working Group I to the fourth assessment report of the Intergovernmental Panel on Climate Change.

STEVENS, B., GIORGETTA, M., ESCH, M., MAURITSEN, T., CRUEGER, T., RAST, S., SALZMANN, M., SCHMIDT, H., BADER, J. & BLOCK, K. 2013. Atmospheric component of the MPI-M Earth System Model: ECHAM6. *Journal of Advances in Modeling Earth Systems,* 5**,** 146-172.

STOCKER, T., QIN, D., PLATTNER, G., TIGNOR, M., ALLEN, S. & BOSCHUNG, J. 2014. IPCC 2013: Summary for Policymakers. Climate Change 2013—The Physical Science Basis, Working Group I Contribution to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge: Cambridge University Press.

STOCKWELL, D. 1999. The GARP modelling system: problems and solutions to automated spatial prediction. *International journal of geographical information science,* 13**,** 143-158.

STRATTON, L. C., GOLDSTEIN, G. & MEINZER, F. C. 2000. Temporal and spatial partitioning of water resources among eight woody species in a Hawaiian dry forest. *Oecologia,* 124**,** 309-317.

STRENGERS, B., LEEMANS, R., EICKHOUT, B., DE VRIES, B. & BOUWMAN, L. 2004. The land-use projections and resulting emissions in the IPCC SRES scenarios scenarios as simulated by the IMAGE 2.2 model. *GeoJournal,* 61**,** 381-393.

STROH, P., MOUNTFORD, J. O., ARAYA, Y. & HUGHES, F. R. 2013. Quantifying soil hydrology to explain the development of vegetation at an ex-arable wetland restoration site. *Wetlands,* 33, 311-320.

SUMNER, D. M. & JACOBS, J. M. 2005. Utility of Penman–Monteith, Priestley–Taylor, reference evapotranspiration, and pan evaporation methods to estimate pasture evapotranspiration. *Journal of Hydrology,* 308, 81-104.

SUPPO, C., ROBINET, C., PERDEREAU, E., ANDRIEU, D. & BAGNÈRES, A.-G. 2018. Potential spread of the invasive North American termite, *Reticulitermes flavipes*, and the impact of climate warming. *Biological Invasions,* 20, 905-922.

TAKHTAJAN, A. 1986. Floristic regions of the world. *Berkeley, etc.:(Transl. by TJ Crovello.) Univ. Calif. Press,* 581, 1.

TAUSCH, R. J. 2008. Invasive plants and climate change. *Washington, DC: US Department of Agriculture, Forest Service, Climate Change Resource Center*.

TAYLOR, H. C. 1978. Capensis. *In:* WERGER, M. J. A. (ed.) *Biogeography and ecology of Southern Africa.* Junk, The Hague: Springer.

TAYLOR, K. E., STOUFFER, R. J. & MEEHL, G. A. 2012. An Overview of CMIP5 and the Experiment Design. *Bulletin of the American Meteorological Society,* 93, 485-498.

TEBALDI, C. & KNUTTI, R. 2007. The use of the multi-model ensemble in probabilistic climate projections. *Philosophical transactions of the royal society A: mathematical, physical and engineering sciences*, 365, 2053-2075.

THEURILLAT, J. P. & GUISAN, A. 2001. Potential Impact of Climate Change on Vegetation in the European Alps: A Review. *Climatic Change,* 50, 77-109.

THOM, A. & OLIVER, H. 1977. On Penman's equation for estimating regional evaporation. *Quarterly Journal of the Royal Meteorological Society,* 103, 345-357.

THOMAS, C. D., CAMERON, A., GREEN, R. E., BAKKENES, M., BEAUMONT, L. J., COLLINGHAM, Y. C., ERASMUS, B. F., DE SIQUEIRA, M. F., GRAINGER, A. & HANNAH, L. 2004a. Extinction risk from climate change. *Nature,* 427, 145-148.

THOMAS, C. D., FRANCO, A. & HILL, J. K. 2006. Range retractions and extinction in the face of climate warming. *Trends in Ecology & Evolution,* 21, 415-416.

THOMAS, J. A., TELFER, M. G., ROY, D. B., PRESTON, C. D., GREENWOOD, J., ASHER, J., FOX, R., CLARKE, R. T. & LAWTON, J. H. 2004b. Comparative losses of British butterflies, birds, and plants and the global extinction crisis. *Science,* 303, 1879-1881.

THOMSON, A. M., CALVIN, K. V., SMITH, S. J., KYLE, G. P., VOLKE, A., PATEL, P., DELGADO-ARIAS, S., BOND-LAMBERTY, B., WISE, M. A. & CLARKE, L. E. 2011.

RCP4. 5: a pathway for stabilization of radiative forcing by 2100. *Climatic Change,* 109, 77.

THORNTON, P. E., RUNNING, S. W. & WHITE, M. A. 1997. Generating surfaces of daily meteorological variables over large regions of complex terrain. *Journal of Hydrology,* 190, 214-251.

THUILLER, W. 2007. Climate change and the ecologist. *Nature,* 448, 550.

THUILLER, W., F. MIDGLEY, G., ROUGETI, M. & M. COWLING, R. 2006. Predicting patterns of plant species richness in megadiverse South Africa. *Ecography,* 29, 733-744.

THUILLER, W., LAVOREL, S., ARAÚJO, M. B., SYKES, M. T. & PRENTICE, I. C. 2005. Climate change threats to plant diversity in Europe. *Proceedings of the National Academy of Sciences of the United States of America,* 102, 8245-8250.

TODD, M. J., MUNEEPEERAKUL, R., MIRALLES-WILHELM, F., RINALDO, A. & RODRIGUEZ-ITURBE, I. 2012. Possible climate change impacts on the hydrological and vegetative character of Everglades National Park, Florida. *Ecohydrology,* 5, 326-336.

TODD, M. J., MUNEEPEERAKUL, R., PUMO, D., AZAELE, S., MIRALLES-WILHELM, F., RINALDO, A. & RODRIGUEZ-ITURBE, I. 2010. Hydrological drivers of wetland vegetation community distribution within Everglades National Park, Florida. *Advances in Water Resources,* 33, 1279-1289.

TYSON, P. D. & PRESTON-WHYTE, R. A. 2000. *The weather and climate of southern Africa*, Oxford University Press.

UNESCO 2009. Case Studies on Climate Change and World Heritage. *In:* CENTRE, U. W. H. (ed.). Paris, France: http://whc.unesco.org

URBAN, M. C. 2015. Accelerating extinction risk from climate change. *Science,* 348, 571-573.

VALLADARES, F., MATESANZ, S., GUILHAUMON, F., ARAÚJO, M. B., BALAGUER, L., BENITO-GARZÓN, M., CORNWELL, W., GIANOLI, E., KLEUNEN, M. & NAYA, D. E. 2014. The effects of phenotypic plasticity and local adaptation on forecasts of species range shifts under climate change. *Ecology Letters,* 17, 1351-1364.

VAN DER KNAAP, Y. A., DE GRAAF, M., VAN EK, R., WITTE, J.-P. M., AERTS, R., BIERKENS, M. F. & VAN BODEGOM, P. M. 2015. Potential impacts of groundwater conservation measures on catchment-wide vegetation patterns in a future climate. *Landscape Ecology,* 30, 855-869.

VAN VUUREN, D. P., EDMONDS, J., KAINUMA, M., RIAHI, K., THOMSON, A., HIBBARD, K., HURTT, G. C., KRAM, T., KREY, V. & LAMARQUE, J.-F. 2011. The representative concentration pathways: an overview. *Climatic change,* 109**,** 5.

VAN WILGEN, N.J., GOODALLI, V., HOLNESS, S., CHOWN, S.L. and MCGEOCH, M.A. 2016. Rising temperatures and changing rainfall patterns in South Africa's national parks. International Journal of Climatology, 36, 706-721.

VANDERHOEVEN, S., ADRIAENS, T., DESMET, P., STRUBBE, D., BARBIER, Y., BROSENS, D., CIGAR, J., COUPREMANNE, M., DE TROCH, R. & HEUGHEBAERT, A. 2017. Tracking Invasive Alien Species (TrIAS): Building a data-driven framework to inform policy. *Research Ideas and Outcomes,* 3**,** e13414.

VARNER, J. & DEARING, M. D. 2014. The Importance of biologically relevant microclimates in habitat suitability assessments. *PloS one,* 9**,** e104648.

VERHEYEN, K., BULTEEL, H., PALMBORG, C., OLIVIÉ, B., NIJS, I., RAES, D. & MUYS, B. 2008. Can complementarity in water use help to explain diversity–productivity relationships in experimental grassland plots? *Oecologia,* 156**,** 351-361.

VERHEYEN, W. &De La ROSA, D. 2005. Mediterranean soils, in land use and land cover. Encyclopedia of Life Support Systems (EOLSS). UNESCO - EOLSS Publishers, Oxford, UK.

VIESSMAN, W., LEWIS, G. L., KNAPP, J. W. & HARBAUGH, T. E. 2003. *Introduction to hydrology*, Prentice Hall NJ.

VITT, P., HAVENS, K., KRAMER, A. T., SOLLENBERGER, D. & YATES, E. 2010. Assisted migration of plants: Changes in latitudes, changes in attitudes. *Biological Conservation,* 143**,** 18-27.

VOGIATZAKIS, I. N. 2003. *GIS-based modelling and ecology: a review of tools and methods*, Citeseer.

WALTHER, G.-R., BERGER, S. & SYKES, M. T. 2005. An ecological 'footprint' of climate change. *Proceedings of the Royal Society B: Biological Sciences,* 272**,** 1427-1432.

WALTHER, G.-R., POST, E., CONVEY, P., MENZEL, A., PARMESAN, C., BEEBEE, T. J. C., FROMENTIN, J.-M., HOEGH-GULDBERG, O. & BAIRLEIN, F. 2002. Ecological responses to recent climate change. *Nature,* 416**,** 389-395.

WANG, T., WANG, G., INNES, J., NITSCHKE, C. & KANG, H. 2016. Climatic niche models and their consensus projections for future climates for four major forest tree species in the Asia–Pacific region. *Forest Ecology and Management,* 360**,** 357-366.

WALMSLEY, C. 2007. Monarch (Modelling Natural Resource Responses to Climate Change: *a Synthesis for Biodiversity Conservation*, UKCIP.

WARREN, D. L. 2012. In defense of ‘niche modeling’. *Trends in Ecology & Evolution,* 27**,** 497-500.

WASSEN, M. & JOOSTEN, J. 1996. In search of a hydrological explanation for vegetation changes along a fen gradient in the Biebrza Upper Basin (Poland). *Plant Ecology,* 124**,** 191-209.

WATSON, J. E. M., DUDLEY, N., SEGAN, D. B. & HOCKINGS, M. 2014. The performance and potential of protected areas. *Nature,* 515**,** 67.

WAY, D. A. & PEARCY, R. W. 2012. Sunflecks in trees and forests: from photosynthetic physiology to global change biology. *Tree physiology,* 32**,** 1066-1081.

WEBER, E. 2017. *Invasive plant species of the world: a reference guide to environmental weeds*, CABI.

WEBSTER, R. & OLIVER, M. A. 2007. *Geostatistics for environmental scientists*, John Wiley & Sons.

WELTZIN, J. F., LOIK, M. E., SCHWINNING, S., WILLIAMS, D. G., FAY, P. A., HADDAD, B. M., HARTE, J., HUXMAN, T. E., KNAPP, A. K. & LIN, G. 2003. Assessing the response of terrestrial ecosystems to potential changes in precipitation. *BioScience,* 53**,** 941-952.

WELTZIN, J. F. & MCPHERSON, G. R. 1997. Spatial and temporal soil moisture resource partitioning by trees and grasses in a temperate savanna, Arizona, USA. *Oecologia,* 112**,** 156-164.

WERNER, B. A., JOHNSON, W. C. & GUNTENSPERGEN, G. R. 2013. Evidence for 20th century climate warming and wetland drying in the North American Prairie Pothole Region. *Ecology and evolution,* 3**,** 3471-3482.

WESSELING, J. & VAN WIJK, W. R. (eds.) 1957. *Soil physical conditions in relation to drain depth. Drainage of Agricultural Lands,* Madison, WI: American Society for Agronomy.

WESSELING, J. & VAN WIJK, W. R. 1975. Soil physical conditions in relation to drain depth. *In Drainage of Agricultural Lands. LuthinJN (ed.). American Society of Agronomy: Madison***,** 461-504.

WHITE, F. 1983. The vegetation of Africa: a descriptive memoir to accompany the UNESCO/AETFAT/UNSO vegetation map of Africa. *Natural Resources Research Report XX, UNESCO, Paris, France*.

WHITTAKER, R. H. 1965. Dominance and diversity in land plant communities numerical relations of species express the importance of competition in community function and evolution. *Science,* 147**,** 250-260.

WHITTAKER, R. H., LEVIN, S. A. & ROOT, R. B. 1973. Niche, habitat, and ecotope. *The American Naturalist,* 107, 321-338.

WIENS, J. A. & BACHELET, D. 2010. Matching the multiple scales of conservation with the multiple scales of climate change

Adecuación de las Múltiples Escalas de Conservación con las Múltiples Escalas de Cambio Climático. *Conservation Biology,* 24, 51-62.

WIENS, J. A., STRALBERG, D., JONGSOMJIT, D., HOWELL, C. A. & SNYDER, M. A. 2009. Niches, models, and climate change: Assessing the assumptions and uncertainties. *Proceedings of the National Academy of Sciences,* 106, 19729-19736.

WILBY, R., CHARLES, S., ZORITA, E., TMBAL, B., WHETTON, P. & MEARNS, L. 2015. Guidelines for use of climate scenarios developed from statistical downscaling methods. Procedures for the Preparing, Review, Acceptance, Adoption, Approval, and Publication of IPCC Reports.

WILBY, R. L., CHARLES, S., ZORITA, E., TIMBAL, B., WHETTON, P. & MEARNS, L. 2004. Guidelines for use of climate scenarios developed from statistical downscaling methods. *Supporting material of the Intergovernmental Panel on Climate Change, available from the DDC of IPCC TGCIA,* 27.

WILBY, R. L., HASSAN, H. & HANAKI, K. 1998a. Statistical downscaling of hydrometeorological variables using general circulation model output. *Journal of Hydrology,* 205, 1-19.

WILBY, R. L., WIGLEY, T., CONWAY, D., JONES, P., HEWITSON, B., MAIN, J. & WILKS, D. 1998b. Statistical downscaling of general circulation model output: a comparison of methods. *Water resources research,* 34, 2995-3008.

WILCOX, C. S., FERGUSON, J. W., FERNANDEZ, G. C. J. & NOWAK, R. S. 2004. Fine root growth dynamics of four Mojave Desert shrubs as related to soil moisture and microsite. *Journal of Arid Environments,* 56, 129-148.

WILLIAMS, C. J., KNIVETON, D. R. & LAYBERRY, R. 2010. Assessment of a climate model to reproduce rainfall variability and extremes over Southern Africa. *Theoretical and Applied Climatology,* 99, 9-27.

WILLIAMS, J. W. & JACKSON, S. T. 2007. Novel climates, no-analog communities, and ecological surprises. *Frontiers in Ecology and the Environment,* 5, 475-482.

WILLIAMS, S. E., BOLITHO, E. E. & FOX, S. 2003. Climate change in Australian tropical rainforests: an impending environmental catastrophe. *Proceedings of the Royal Society of London. Series B: Biological Sciences,* 270, 1887-1892.

WILSON, A. M. & SILANDER, J. A. 2014. Estimating uncertainty in daily weather interpolations: a Bayesian framework for developing climate surfaces. *International Journal of Climatology,* 34, 2573-2584.

WINTER, T. C. 2000. The vulnerability of wetlands to climate change: A hydrologic landscape perspective 1. *Journal of the American Water Resources Association,* 36, 305 - 311.

WOOD, S. N. 2006. *Generalized additive models: an introduction with R*, Chapman and Hall/CRC.

WOODWARD, F. I. & WILLIAMS, B. G. 1987. Climate and plant distribution at global and local scales. *Vegetatio,* 69, 189-197.

XU, C.-Y., GONG, L., JIANG, T., CHEN, D. & SINGH, V. 2006. Analysis of spatial distribution and temporal trend of reference evapotranspiration and pan evaporation in Changjiang (Yangtze River) catchment. *Journal of Hydrology,* 327, 81-93.

XU, C. Y. & SINGH, V. P. 2000. Evaluation and generalization of radiation-based methods for calculating evaporation. *Hydrological Processes,* 14, 339-349.

YATES, C. J., ELITH, J., LATIMER, A. M., LE MAITRE, D., MIDGLEY, G. F., SCHURR, F. M. & WEST, A. G. 2010. Projecting climate change impacts on species distributions in megadiverse South African Cape and Southwest Australian Floristic Regions: opportunities and challenges. *Austral Ecology,* 35, 374-391.

ZANIEWSKI, A. E., LEHMANN, A. & OVERTON, J. M. 2002. Predicting species spatial distributions using presence-only data: a case study of native New Zealand ferns. *Ecological Modelling,* 157, 261-280.

ZEDLER, J. B. 2009. How frequent storms affect wetland vegetation: a preview of climate-change impacts. *Frontiers in Ecology and the Environment,* 8, 540-547.

ZHANG, J., NIELSEN, S. E., CHEN, Y., GEORGES, D., QIN, Y., WANG, S. S., SVENNING, J. C. & THUILLER, W. 2017. Extinction risk of North American seed plants elevated by climate and land-use change. *Journal of Applied Ecology,* 54, 303-312.

ZWEIG, C. & KITCHENS, W. 2009. Multi-state succession in wetlands: a novel use of state and transition models. *Ecology,* 90, 1900-1909.

ZWEIG, C. L. & KITCHENS, W. M. 2008. Effects of landscape gradients on wetland vegetation communities: information for large-scale restoration. *Wetlands,* 28, 1086-1096.