

**Niche modelling the distributions of
large *Acacia nigrescens* and *Sclerocarya
birrea* trees**

by

ALAIN SMITH

Submitted in fulfillment of the academic requirements for the degree of
Master of Science in the School of Biological & Conservation Sciences,
University of KwaZulu-Natal Durban Westville

December 2011

As the candidate's supervisor I have approved this dissertation for submission.

Signed: _____ Name: _____ Date: _____

Abstract

MaxEnt modelling uses only the known locations of a species to predict the overall distribution of a species. Large trees are important for the functioning of savanna ecosystems, bringing nutrients to the surface, providing shelter to animals and providing a number of ecological functions. Large trees have been identified as declining in density in many southern African reserves, making the conservation of large trees within reserves an issue in park management, such as in Kruger National Park (KNP) and Hluhluwe iMfolzi Parks (HiP). Two species of primary concern are *Acacia nigrescens* and *Sclerocarya birrea*, which have similar distributions in Southern Africa. Effective management of large trees requires understanding their distribution within reserves and any potential distribution changes. By determining the current locations of a species, and using GIS layers of environmental variables to predict the extent of habitats that could support the species, niche models can predict species distribution. Maximum Entropy techniques evaluate the probability of finding the species in raster squares, with values for environmental factors controlling distribution. For this study, the locations of *A. nigrescens* and *S. birrea* trees higher than 5 m were recorded in KNP and HiP, and were used in conjunction with MaxEnt to produce distribution probability maps for both species in each reserve. In HiP, the distribution map was compared with an independent existing data set to determine if the predicted distributions were accurate. The factors effecting their distribution were compared between HiP and KNP to determine why the species were found together in KNP but not in HiP. MaxEnt could predict the locations of the species within HiP, but predictions were better for *A. nigrescens* than *S. birrea*. In both Reserves, rainfall was the best predictor of tree location, along with elevation. The niche overlap was higher in KNP, where both species are well within their total species range, than in HiP where *A. nigrescens* was at the edge of its distribution. These variables that are limiting distribution at a reserve scale will have an influence on the overall distribution of the species. Niche models can be used to inform the establishment of botanical reserves or other management strategies that can help preserve large trees within reserves.

PREFACE

The experimental work described in this dissertation was carried out in the School of Life & Environmental Sciences, University of Natal, Durban, from January 1996 to December 1997, under the supervision of Professor Rob Slotow and Mr Bruce Page.

These studies represent original work by the author and have not otherwise been submitted in any form for any degree or diploma to any tertiary institution. Where use has been made of the work of others it is duly acknowledged in the text.

DECLARATION 1 - PLAGIARISM

I, Alain Roland Smith declare that

1. The research reported in this thesis, except where otherwise indicated, is my original research.
2. This thesis has not been submitted for any degree or examination at any other university.
3. This thesis does not contain other persons' data, pictures, graphs or other information, unless specifically acknowledged as being sourced from other persons.
4. This thesis does not contain other persons' writing, unless specifically acknowledged as being sourced from other researchers. Where other written sources have been quoted, then:
 - a. Their words have been re-written but the general information attributed to them has been referenced
 - b. Where their exact words have been used, then their writing has been placed in italics and inside quotation marks, and referenced.
5. This thesis does not contain text, graphics or tables copied and pasted from the Internet, unless specifically acknowledged, and the source being detailed in the thesis and in the References sections.

Signed:

DECLARATION 2 - PUBLICATIONS

DETAILS OF CONTRIBUTION TO PUBLICATIONS that form part and/or include research presented in this thesis (include publications in preparation, submitted, *in press* and published and give details of the contributions of each author to the experimental work and writing of each publication)

Publication 1:

Accepted: Ecosphere

Using Maximum Entropy Modelling to predict actual and potential distributions of large trees for conservation planning and management, Alain Smith, Bruce Page, Kevin Duffy, Rob Slotow

Design: A. Smith

Data Collection: A Smith with assistance from P. Tshibase and P. Birkett. Elephant location points were contributed by Prof K Duffy

Analyses: A. Smith and assistance from Dr. F. Smith with calculating the index of dispersion

Writing: A. Smith

Editing and commenting: B. Page, Prof K. Duffy, Prof. R. Slotow

Publication 2:

Submitted: **Journal of Biogeography**

Local and range level limiting factors of two sympatric large savanna trees, Alain Smith, Bruce Page, Rob Slotow

Design: A. Smith

Data Collection: Dr. G. Shannon and Dr D. Druce in KNP. A Smith with assistance from P. Tshibase and P. Birkett in HiP

Analyses: A. Smith

Writing: A. Smith

Editing and commenting: B. Page, Prof. R. Slotow

Signed..... Date:

Table of Contents

Contents

General Introduction	1
Conservation	1
Niche Theory	2
Niche models	3
Large Trees	4
Study Species	5
<i>Acacia nigrescens</i>	5
<i>Sclerocaryea birrea</i>	5
Factors affecting Distribution	5
Aims and Objectives	8
Study Sites	9
Chapter 2	10
Using Maximum Entropy modelling to predict the potential distributions of large trees for conservation planning	10
Abstract	10
Introduction	11
Methods	14
Results	19
Discussion	29
Acknowledgments	33
Chapter 3	41
Local and range level limiting factors of two sympatric large savanna trees	41
Introduction	42
Methods	44
Results	47
Discussion	54
Acknowledgments	56
Chapter 4	61
Concluding Chapter	61
Niches	61
Site History and Distribution in HiP	62

Conservation Applications.....	63
Continued Scope for Research.....	66
Conclusion	68
References.....	69

ACKNOWLEDGEMENTS

I would like to acknowledge my Parents for supporting me and encouraging me to continue studying. Tark Bodasing, Simon Morgan and Enrico Di Minin for all the advice and entertainment given. Ruth Howison for the use of her geology, soil and vegetation maps. Phinda Tshibase and Patricia Birkett for helping with field work. Ezemvelo KZN Wildlife for accommodation and guarding. Amarula Elephant Research Program and the National Research Foundation (Grant to RS: FA2006032300024) for funding. Dr Corrie Schoeman and Dr François Smith for advice and assistance with analyses. Cyrille Chatelain and the Conservatoire et Jardin botaniques & South African National Biodiversity Institute for use of the species records in their database

Chapter 1

General Introduction

Conservation

The conservation of natural spaces and resources dates far back in human history, with various cultures dating back to antiquity realising that the control of natural resources was required to ensure their persistence (Thomson 1986). Conservation faces a number of challenges from human driven transformation and land uses, these include both rural and urban (Margules and Pressey 2000). As human populations have grown the amount of land left undeveloped has continued to shrink (Tilman et al. 1994). The fragmentation of areas of natural habitat by transformation has left previously connected areas separated by impassable barriers for species (Fahrig 2003). The reduction in the extent of species ranges due to habitat fragmentation makes conservation of species in small isolated reserves a reality of conservation at this time (Simberloff and Abele 1976).

Views of conservation have changed from those expressed in works such as Ron Thompsons “On Wildlife “Conservation”, in which conservation is described as the maintenance of species. Current conservation initiatives are focused on the conservation of natural systems, and the conservation of biodiversity in particular (Margules and Pressey 2000). Systematic biodiversity conservation is the planning of conservation initiatives and areas in such a way as to prioritize areas of importance (Margules and Pressey 2000). Conservation planning can take place at large scales from global (Myers et al. 2000) to regional scales (Cowling et al. 2003). All conservation planning requires the geographic locations in which species are found to be known, to prioritize areas by their biodiversity value (Myers et al. 2000).

Knowing the distribution of species spatially on the earth is important for planning conservation efforts (Myers et al. 2000, Samraat Pawar et al. 2007). The ranges of species can be divided into two categories, the “extent of occurrence” and the “actual occurrence” (Gaston 1991). These two terms describe the total area in which the species is found and the areas within this general area the species are found (Gaston 1994). These different categories are used by the *International Union for Conservation of Nature* (IUCN) for the red list of species in danger of extinction (Resources, International Union for Conservation of Nature and Natural, 2001). These categories

of distribution represent different scales of management, the extent of occurrence might be used to plan conservation at a broad scale, but the implementation of conservation at a reserve scale will require knowing distribution in terms of occurrence. This study looks at using niche models to determine the locations in which a species can be found within a reserve at a very fine scale, relative to distributions over continents, it predicts the extent of occurrence of the two species.

Changes in species assemblages over time should be taken into account when planning conservation areas during systematic biodiversity planning. The species composition and community assemblages are not static in time at any one place on the earth's surface (Hobbs and Huenneke 1992). These changes may occur due to a number of factors, such as fires, predation and herbivory and changes in climate (Hobbs and Huenneke 1992). Knowing species distributions can assist the management of species and conservation efforts to take into account and better plan to manage shifts. Management strategies can then manage populations in such a way as to ensure persistence of species over large time frames.

Managers of protected areas in southern Africa must take into account a number of human manageable factors controlling the recruitment and protection of large trees. Fires are important for determining the structure of savanna systems (Bond et al. 2005). The management of fire in protected areas is an important tool in the maintenance of habitat heterogeneity, but also a strong factor controlling recruitment of large trees (Shackleton and Scholes 2000, Van Wilgen et al. 2000, Balfour 2003). Herbivory is also a strong factor controlling species assemblages in savanna systems as the utilization of particular species can affect the distribution of these species (Sankaran et al. 2008). Climatic changes must be incorporated into conservation plans by integrating range shift into reserve planning (Midgley et al. 2002, Araújo et al. 2004).

Niche Theory

The theory of niches of organisms controlling distribution dates back to 1924 in a paper written by Joseph Grinnell (1924), in which he describes the niche of a species as the distribution in which a species can be found (Vandermeer 1972). Grinnell focused on the abiotic factors controlling the distribution of species (Vandermeer 1972). Charles Elton developed a theory by which a species occupied a niche that was both the biotic and abiotic influences on distribution, as determined by interactions such as feeding and predation (Vandermeer 1972). In 1957 G. E. Hutchinson described Niches, which can be defined as the "N-dimensional space" describing a

“hypervolume” a species occupies in the environment. Hutchinsons’ “N-dimensional space” is defined by the resources individuals of the species require and the tolerance of the species to environmental factors (Hutchinson 1957). Factors affecting niches can be broken into two categories (Hutchinson 1959). Environmental factors, including temperature, salinity or any other environmental aspect of the habitat which dictates the presence or absence of a species called the “potential” niche of the species (Hutchinson 1957). Biological factors, which are the interactions between species including, competition, predation and other interactions, called the “realized” niche (Hutchinson 1957). The potential niche is therefore larger than the realized niche of the species as the interactions with other species prevent access to resources (Hutchinson 1957). These theories on the niche of species come from the Darwinian concept of species having a place in the world, for which they are shaped by evolution (Darwin 1859).

Niche models

One of the oldest form of niche modelling is Grinnell in 1917 who describes the distribution of species according to the environments and habitats in which they are found (Grinnell 1917a, b). Systematic descriptions of the factors limiting the distribution of species dates as far back as the Greek scientist Theophrastus who was Aristotle’s successor and described the distribution of a number of plant species in his works titled “Enquiry into Plants” (Woodward and Williams 1987). Niches describe the habitat conditions a species is found within, the distribution of a species is therefore linked to the geographic distribution of these conditions (Peterson 2006). Niche models used the limitations imposed on the distribution on species by the habitat requirements to determine the possible distribution of the species (Peterson 2006). The possible uses of niche models are varied (Guisan and Zimmerman, 2000, Guisan and Thuiller, 2005, Elith and Leathwick, 2009) but they can play an important role in understanding the factors effecting species distribution in different environments, as well as describing the difference between species (Warren et al. 2010). The principal reason for the development of niche modelling has been for biogeographic and conservation planning studies. Predicting the accurate distribution of a species from a few records, can be used to ensure the conservation of threatened or rare species in a conservation plan (Godown and Peterson 2000, Benito et al. 2009, Costa et al. 2010, Newbold 2010). An additional use of niche models has been in predicting the locations within countries in which invasive alien plants and animals will invade (Peterson and Vieglais 2001, Peterson et al. 2003, Giovanelli et al. 2008).

Niche models have seen a huge growth in popularity in South Africa with their uses ranging from the prediction of changes in distribution with climate change (Erasmus et al. 2000, Midgley et al. 2002), producing distribution maps (Monadjem et al. 2010), predicting the distribution of disease vectors (Moffett et al. 2007) and determining possible areas of invasion by alien species (Trethowan et al. 2010). An important question concerning the use of niche models is at what scale the models should be used to predict distribution. The niche models which have been used thus far in South Africa have been largely at the scale of the biome or regional space. This study models distribution at a fine scale. Reserve scale models could be important in determining the use of management strategies to protect species within protected spaces in southern Africa.

Large Trees

Large trees are important contributors to habitat structural diversity, and are therefore important for overall biodiversity (Manning et al. 2006). There has been a change in the approach of conservation, from the conservation of specific species to the conservation of ecosystems (Franklin 1993). This is largely due to the acknowledgment that the protection of species is futile without the protection of the habitats and environments within which they are found (Primack 2010). Large trees are important in the environment, as they increase the heterogeneity of habitats within areas (Manning et al. 2006). This heterogeneity is important for the conservation of high numbers of species in areas (Tews et al. 2004). The removal of large trees by elephant *Loxodonta africana* has been linked to a decrease in biodiversity in reserves where the canopies formed in woodlands have been removed (Cumming et al. 1997). Large trees provide microhabitats which are used by other species (Raman et al. 1998, Dean et al. 1999). Large trees also play an important role in increasing the nutrient content of surrounding grasses (Ludwig et al. 2004, Treydte et al. 2007)

Due to plants being largely immobile, it is important to understand the growth of trees and their recruitment to understand where they occur. For a tree to grow large the environment in which it is located must support the needs of the tree (Harcombe 1987). Tree growth can be linked to the tree's acquisition of resources, and its interaction with other elements of the environment, such as temperature or precipitation, which cause stresses (Dobbertin 2005). The trees modelled in this study would be within the mature tree category of life models constructed, as they are

reproductively active (Harcombe 1987). Large trees are important to the continued survival of species in an area as they produce large numbers of seeds (Greene and Johnson 1994).

Study Species

Acacia nigrescens

Acacia nigrescens is most commonly 8 m to 15 m high but can reach a height of 20 m (Coates-Palgrave and Coates-Palgrave 2002). The range is said to correspond with low altitude woodlands and wooded grasslands near to water sources (Coates-Palgrave and Coates-Palgrave 2002). This species is commonly utilised by many browser species which impact on the survival of individuals from seedling to large trees (Fornara and du Toit 2007).

Sclerocarya birrea

S. Birrea is described as being a tree that ranges from 10 m high to 15 m high (Coates-Palgrave and Coates-Palgrave 2002). The habitat of *S. Birea* is described as ranging from medium to low altitude open woodlands and bush (Coates-Palgrave and Coates-Palgrave 2002). *S. Birrea* trees are an important forage source for a variety of animals, producing large amounts of large fruit in a season (Lewis 1987) which are high in vitamin C and an important food source for many species including monkeys and baboons (Coates-Palgrave and Coates-Palgrave 2002). This species has also become important to people as a species which can be cultivated and a large number of uses exist for these trees (Shackleton et al. 2002). The high germination temperature of the species from 27 °C to 37 °C (Lewis 1987) is likely to play a role in limiting the distribution of the species spreading farther south, with current temperature averages.

Factors affecting Distribution

Aspect

Aspect is an important factor influencing the distribution of plants, as it influences the amount of direct sunlight which reaches a place on the earth throughout the year (MacArthur 1972). Due to southern Africa being in the southern hemisphere the sun will be most direct over the tropic of Capricorn at the summer equinox. Slopes that face the north will therefore receive more direct sunlight throughout the year than those that face the south. North facing slopes are therefore usually drier and hotter (Fig. 1.).

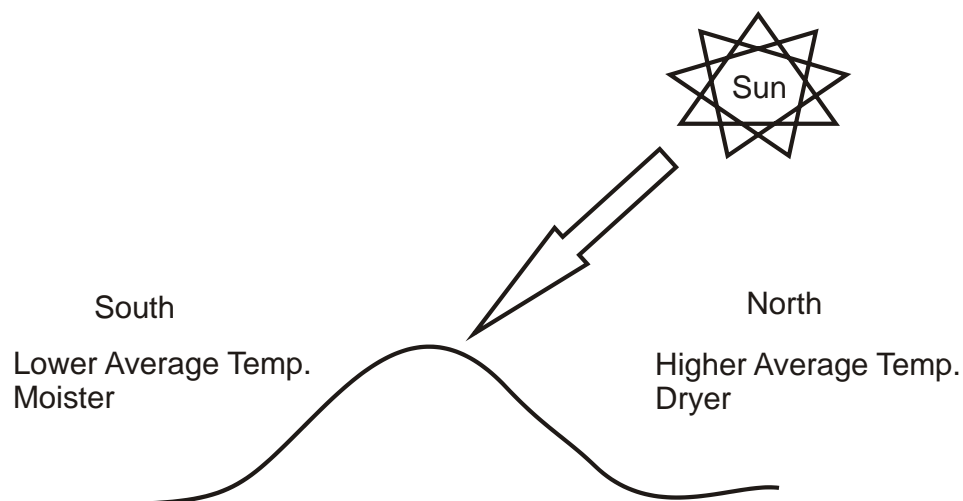


Fig. 1. The influence of aspect on the microclimate of areas in the southern hemisphere.

Geology

Geology is an important factor controlling the distribution of many species (Du Puy and Moat 1996). Geology influences the distribution of species by influencing the soil types which are found above the parent rock. Parent rocks below the soil layer erode to form soil, and the composition of the overlying soil is therefore determined by the underlying geology of an area (Skempton 1953). Geology can also influence the amount of available ground water in an area.

Elevation

Elevation is negatively correlated with temperature at large gradients (MacArthur 1972). Due to topographic rainfall at small scales elevation can be positively correlated with rainfall, due to moisture in air condensing as wind is swept up a slope (Fig. 2.), forming clouds and precipitation (MacArthur 1972). On the reverse side of a slope there may then be a rain shadow (MacArthur 1972).

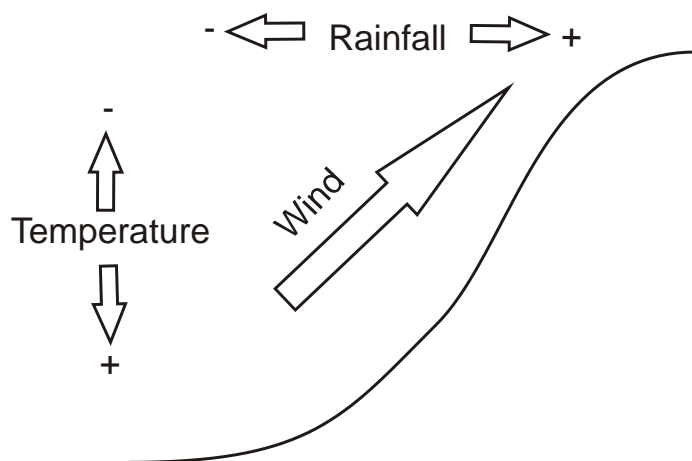


Fig. 2. Figure showing the influence of topography and elevation on rainfall and temperature.

Soil Type

The various adaptations that a species has undergone to adapt to soil types restrict the distribution of that species (John et al. 2007). Plants are strongly influenced by soil type and large tree species occurrence has been linked to soil nutrients (John et al. 2007). Due to the inability of plants to move from the position in which they sprout the soil in a location must provide a rooting foundation as well as nutrients. Soil structures are important in particular the clay content of many soils as clay content is important for cation exchange from the roots of plants (Högberg and Read 2006).

Slope

Slope is an important factor effecting the distribution of plants as it indicates the strength of gravity to move things location. In particular the movement of water along slopes is important, water runs down slopes and the greater the angle of the slope the greater the energy of water moving down (Fig. 3.). Greater energy allows the water to carry soil and erode the slope and will allow less water to percolate through into the soil, and steeper slopes are therefore usually drier slopes. Slopes influence soil characteristics of an area by determining the amount of clay that is present in the soil and its mineral concentration.

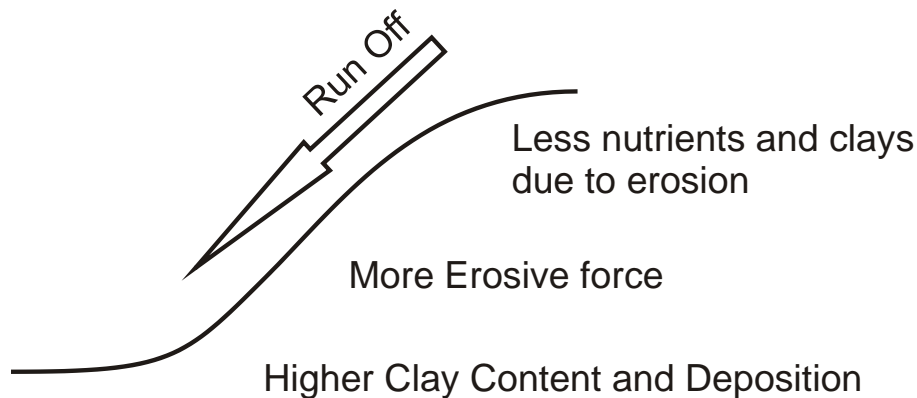


Fig. 3. Figure showing the influence of slope on plant resources.

Rainfall

Rainfall is the primary source of water for plants, and a strong determinant of woody plant structure in savannas (Sankaran et al. 2005). Water percolates down into the soil, and it is absorbed through the root system. Water is used to transport nutrients from the ground up to the leaves through transpiration (Grace 2009). A lack of water is therefore limiting to plants and the tolerances of different species to differing levels of desiccation are a strong influence on the distribution of species (Grace 2009).

Vegetation Type

The interactions of species with other species and amongst individuals of their own species can be an important factor determining their distribution in the landscape and time (Hutchinson 1959). These biological interactions are the basis for assembly rules which govern the inclusion of species in the communities at any given location (Diamond 1975). Vegetation maps are created to show the spatial distribution and extent of different plant communities (Mucina and Rutherford 2006). By using a layer for the vegetation communities in the analyses, the biological interactions between the modeled species and communities in the habitat can be included in the analyses.

Aims and Objectives

The aim of this study was to determine the distributions trees ≥ 5 m of *A. nigrescens* and *S. birrea* in Hluhluwe iMfolozi Park and Kruger National Park using niche modelling to determine whether the factors affecting distribution were the same in both reserves. The objectives of this study were to (1) Using MaxEnt niche modelling software model the distribution of each species

in each reserve using a similar set of environmental variables for each reserve. (2) Compare the resulting distribution map in HiP with unbiased data. (3) Determine the fine scale factors that are controlling the distribution of each species at the reserve scale. (4) Compare distributions of each species in each reserve.

Study Sites

Hluhluwe Imfolozi Park

Of the two reserves used in the study HiP is the smallest with an area of 900 km². The reintroduction of elephant (*Loxodonta africana*) into the reserve and their rapid increase in number (Mackey et al. 2006) fuelled the need for a number of studies looking at the impacts of elephants on the vegetation within the reserve (Balfour 2003, Boundja and Midgley 2010). In HiP, previous studies have shown that the impacts of elephant on *A. nigrescens* were relatively low (Balfour 2003), while the impacts on *S. birrea* indicated that it was a species that may be targeted for toppling which increases the likelihood of the tree dying (Helm et al. 2011). The distribution of *A. nigrescens* in HiP may be more strongly influenced by changes of climate within HiP, while impacts on *S. birrea* indicate that there may be a greater risk of elephant impacts removing the species from the reserve (Boundja and Midgley 2010).

Kruger National Park

The utilization of both *A. nigrescens* and *S. birrea* by elephant has been a concern since the increase in elephant population within the park (Whyte et al. 2003). The increasing numbers of elephants in the reserve made their impacts on vegetation a concern and studies on both tree species date back to 1979 (Whyte et al. 2003). Both species were shown to be utilised in KNP (Shannon et al. 2008). The mortality of *S. birrea* trees greater than five meters in KNP between year 2001 and 2008, was 3.7 % (Helm et al. 2009), comparable to a study in three small reserves adjacent to KNP in which 2 % were found to be killed (Gadd 2002). In KNP, a number of studies have shown that there is a link between the utilisation of a tree by elephants, both tree pushing and debarking, which make the tree more susceptible to fire damage (Helm et al. 2011, Shannon et al. 2011).

Chapter 2

Using Maximum Entropy modelling to predict the potential distributions of large trees for conservation planning

Alain Smith^{*}, Bruce Page^{*}, Kevin Duffy^{**}, Rob Slotow^{*}

^{*}*School of Biological and Conservation Sciences, University of KwaZulu-Natal, Durban, 4041, South Africa*

^{**}*Institute of Systems Science, DUT Durban, 4041, South Africa*

Rob Slotow

School of Biological and Conservation Sciences, University of KwaZulu-Natal Westville, Durban, 4041, South Africa

Tel: + 031-260 5199

e-mail: Slotow@ukzn.ac.za

MaxEnt, Niche Modelling, *Acacia nigrescens*, *Sclerocarya birrea*, Hluhluwe-Imfolozi Park, Conservation Planning, Elephant

Abstract

Large trees, as keystone structures, are functionally important in savanna ecosystems and low recruitment and slow growth makes their conservation important. Understanding factors influencing their distribution is essential for mitigation of excessive mortality, for example from management fires or large herbivores. We recorded the locations of large trees in Hluhluwe-

Imfolozi Park (HiP) using GPS to record trees along 43 km of 10 m-wide transects. Maximum entropy modelling (MaxEnt) uses niche modelling to predict the distribution of a species from the probability of finding it within raster squares, based on environmental variables and recorded locations. MaxEnt is typically applied at a regional spatial scale, and here we assessed its usefulness when predicting the distribution of species at a small (local) scale. HiP has variable topography, heterogeneous soils, and a strong rainfall gradient, resulting in a wide variety of habitat types. We used locations of 179 *Acacia nigrescens* and 106 *Sclerocarya birrea*, (large trees $\geq 5\text{m}$), and the variables: aspect, elevation, fire frequency, geology, rain, slope, soil and vegetation. *A. nigrescens* was largely restricted to the Imfolozi section, while *S. birrea* had a wider distribution across the reserve. Ground truthing demonstrated that the predicted distribution for *A. nigrescens* was more accurate than that for *S. birrea*. Understanding the interaction of environmental variables dictating tree distribution may facilitate habitat restoration, and will assist planning decisions for persistence of large trees within reserves, including options to reduce fire frequency or herbivore impacts.

Introduction

Large trees play many important roles in the functioning and structural heterogeneity of ecosystems and habitats in African savannas (Belsky 1994, Dean *et al.* 1999, Manning *et al.* 2006). They play important roles in that they bring nutrients to the surface (Ludwig *et al.* 2004), provide shade and protection for a number of animals, especially when nesting and roosting, particularly for large raptors and bats (Galindo-Gonzalez *et al.* 2000, Roche 2006). Large trees are important in maintaining habitat heterogeneity, which in turn, maintains species diversity within protected areas (Dunn 2000). They are keystone structures (Manning *et al.* 2006) and have an effect on the distribution of other species in the landscape (Dunn 2000). The contribution

of large trees to both species and structural diversity makes understanding the factors controlling their distribution essential (Shannon *et al.* 2008).

The managers of protected areas have expressed concern over an observed decline in large tree abundance in savannas (Eckhardt *et al.* 2000, Whyte *et al.* 2003) linked to the destruction of vegetation by large herbivores, particularly elephant *Loxodonta africana* (Coetzee *et al.* 1979, Dominy *et al.* 1998, Jacobs and Biggs 2002b, O'Connor *et al.* 2007). The current density and distribution of large trees may be a result of historically low browser densities or a low frequency of fire prior to establishment of the protected area (Baxter and Getz 2005, Shackleton and Scholes 2008), sporadic recruitment of trees (Young and Lindsay 1988, Sankaran *et al.* 2005), or most likely a combination of factors, both spatial and temporal (Scholes and Archer 1997). In smaller protected areas subjected to fluctuating environmental conditions, fine scale management to prevent extirpation of species from the area is necessary (Shafer 1995, Turner 1996).

Understanding the factors effecting the distribution and abundance of large trees within protected areas allows managers to plan actions such as burns, and the manipulation of the densities of large mammals by culling or altering water point distribution, to increase the likelihood of the establishment and survival of large tree species (Bond *et al.* 2001, Sankaran *et al.* 2008).

Niche models have become an important tool to predict the distributions of species, and are thus useful for the planning and management of biodiversity conservation (Austin and Meyers 1996, Zaniwski *et al.* 2002, Benito *et al.* 2009). The relatively small number of data points required for niche modelling using maximum entropy (MaxEnt) modelling makes MaxEnt an attractive tool (Elith *et al.* 2006, Phillips and Dudík 2008). Time in the field and data collection time can be reduced as the models can predict distributions over large areas using existing environmental datasets (Dudík 2007). Previously, MaxEnt has been used to predict the distributions of entire

species rather than for modelling the distribution in a small part of the total range (Murray-Smith *et al.* 2008, Benito *et al.* 2009), but we believe that there is no reason why it cannot be used at a finer scale, provided a sufficient breadth of the determining niche axes are sampled. Increasingly, protected area managers are setting targets for population size (Parrish *et al.* 2003), or establishing population ‘thresholds of concern’ that trigger management actions (Biggs *et al.* 2008). Niche models not only facilitate better prediction of where a species may occur both within and outside of protected areas, thereby enabling more efficient censusing and monitoring (Wilgen *et al.* 1998, Gillson and Duffin 2007), but also enhance predictions of where optimal habitats occur, thus enabling management to implement actions that facilitate higher recruitment and survival of species threatened with extirpation.

Whilst several studies have focused on the interaction between the woody and grass components of savannas (Bond and Midgley 2000, Steven I. Higgins *et al.* 2000, Bond *et al.* 2005), few have examined the determinants of woody cover in savannas, and these have largely focused at the biome level (Bond *et al.* 2005, Sankaran *et al.* 2005). Autecological studies of single woody species are very rare. Quantifying of the effects of environmental variables on the distribution and abundance of individuals using niche modelling establishes the importance of particular variables in determining the distribution of individuals. It also investigates the relationship between these variables and the probability of finding an individual at a particular location (Rebelo and Jones 2010) (Phillips and Dudík 2008).

We therefore aimed to determine the factors affecting the distribution of two well-utilized, large tree species with different distributions within a protected area. We (1) sampled the distribution of each species and then (2) linked these data to the environmental conditions at each location to predict a potential distribution using a MaxEnt niche model. (3) We tested the model predictions

using a discrete data set. (4) We used the MaxEnt response curves for each species to determine the differences in the environmental determinants of the distribution of each species. (5) These results were then used to establish what mitigating measures might be possible to reduce the loss of large trees in protected areas, which conserve large mammalian herbivores. Finally, (6) to introduce an application of niche modelling of large trees to the planning of conservation measures in reserves, we used the movement of elephant to demonstrate how botanical reserves could be planned within a game reserve, guided in part by areas that could support large trees.

Methods

The study was carried out in Hluhluwe-Imfolozi Park (HIP), KwaZulu-Natal, South Africa (28°02'24"S 32°03'36"E) covering 900 km². The park has a strong rainfall gradient from 990 mm of rainfall in the north eastern Hluhluwe section, to 635 mm in the south western Imfolozi section. Temperatures range between 13 and 35 °C, and elevation ranges from 60 m in Imfolozi to 600 m in Hluhluwe. The topography of the reserve can be split into three broad categories, from the steep slopes in the northern Hluhluwe section to the rolling hills of the central corridor section, and the river basins of the Mfolozi Rivers in the Imfolozi section. One hundred and seventy two elephant were introduced into the reserve between 1981 and 1993, with the population in 2010 estimated at 550. They were extirpated from the region 91 years ago (Dominy *et al.* 1998), and probably occurred at low densities for a few decades before this. Several other large browser species occur, including black rhino *Diceros bicornis* (198), giraffe *Giraffa camelopardalis* (874), Greater kudu *Tragelaphus strepsiceros* (717), nyala *Tragelaphus angasii* (4082) and impala *Aepyceros melampus* (14054), with smaller browsers, including red duiker *Cephalophus natalensis* and grey duiker *Sylvicapra grimmia*, at low densities. The current distribution and abundance of large trees within the reserve is therefore influenced by 28 years of

relatively low elephant impacts as numbers increased (Jacobs and Biggs 2002a, Shannon *et al.* 2008), following from their previous absence (Spinage and Guinness 1971).

Two tree species, *Acacia nigrescens* Oliver (Fabacea) and *Sclerocarya birrea* (A. rich.) Hochst. subsp. *caffra* (Sond.) Kokwaro (Anacardiaceae), were selected for the study. Both species are used intensively and impacted on by elephant (Jacobs and Biggs 2002a, Boundja and Midgley 2010). The seedlings are also browsed by other species (Moe *et al.* 2009). The two species have different distributions with *A. nigrescens* being more clumped within the reserve, while *S. birrea* trees are found at lower densities over a wider area. The currently observed loss of these species to browsing pressure from animals, and pushing and debarking from elephant, has raised concern about threats of extirpation (Coetzee *et al.* 1979, Jacobs and Biggs 2002a, Fornara and Toit 2007). *A. nigrescens* can reach a height of up to 20 m, though 8 m to 10 m trees are more common, and they are found in low-altitude woodlands and wooded grasslands (Coates-Palgrave and Coates-Palgrave 2002). *S. birrea* are shorter than *A. nigrescens* trees, ranging from 7 m to 10 m in height, and are associated with medium to low altitude open woodland and bush (Coates-Palgrave and Coates-Palgrave 2002).

Sampling was conducted in February 2010. The transect lines used for sampling were those used by the park management for animal census counts (Fig. 1). We sampled all individuals of the two selected species ≥ 5 m in height within a 5 m width on either side of the line. We located and walked transect lines using a Trimble 2005 Geo XM™ and ESRI Arc pad™ in which the previously digitized transect lines and 5 m buffers were stored. We estimated the height of individual trees relative to the known height of a field assistant (Shannon *et al.* 2008). We noted

whether the tree was dead or alive, and the mortality was ascribed to elephant, fire, porcupine *Hystrix africaeaustralis* debarking, moisture stress, disease or old age. These transects were originally laid out to adequately sample the different habitat types and to cover the spatial extent of the reserve (Kraus 1997). We sampled 20 transects with an average length of 2.15 km and covering a total length of 43.06 km.

In this study, we chose environmental variables, including three categorical variables: geological, soil and vegetation type; and four continuous variables: aspect, elevation, slope, and predicted rainfall. The geology, soils and vegetation maps were after Howison (2009). We created the aspect, elevation, slope layers using ESRI Arc Map™ and the national 1:50 000 topographic map layers. For rainfall patterns, we used the South African rainfall atlas map (Zucchini and Nenadić 2006). We used the map with the smallest raster squares as a base map to clip the other maps in ESRI Arc Map™, which resulted in the maps having a raster cell size of 45.1 m x 45.1 m.

Maximum entropy modelling (MaxEnt) uses techniques developed from machine learning, allowing empirical data to be used to predict the probability of finding something under certain conditions distributed in space (Dudík 2007). MaxEnt uses presence only data by generating random test points. We ran the model 50 times for each species, using cross validation to test accuracy. For this analysis, we used the suggested default settings, which have been shown to yield robust results. (Phillips and Dudík 2008). An important part of determining the ability of niche models to predict the distribution of a species is having a measure of fit. A common method for determining the fit of a model is using the AUC (area under the curve) of the receiver operator curve (ROC) (Phillips and Dudík 2008). For this purpose, MaxEnt uses a percentage of points of occurrence of individuals selected randomly from the data set to test against. A model with AUC values greater than 0.75 is predicting the distribution of test points accurately (Phillips

and Dudík 2008). To generate the final maps and response curves, we then ran the model using all data points, i.e. including the test data, and run 50 times with cross validation.

A problem identified with this testing a model using AUC is the autocorrelation of points used to test and build the model (Jorge *et al.* 2008, Veloz 2009). A more powerful method to test the model is the use of an alternative data set to test against (Fielding 1997). For ground testing, we used a separate set of vegetation quadrats to test the accuracy of the model. These quadrats were sampled in 1999 and covered a large proportion of the study area (Boundja and Midgley 2010). Quadrats were 50 m x 50 m, which is comparable to the cell size for the model of 45.1 m x 45.1 m, located randomly and thus not influenced by the results of the MaxEnt analyses. We split these quadrats into presence and absence, according to whether individuals of the particular species (taller than 5 m), occurred in the quadrat or not. We used a 10th percentile threshold to classify the raster cells in the MaxEnt output as presence or absence (Raes *et al.* 2009, Rebelo and Jones 2010). The quadrats could then be split into categories of absence or presence and incorrectly classified or correctly classified by the model. To assess the ability of the model to correctly predict whether or not a quadrat included the particular species, we constructed a confusion matrix (Fielding 1997). Five measures of fit were used to assess the ability of the model to classify quadrats. Kappa statistics range from -1 to +1 with higher values (closer to one) indicating that the model is predicting better than random, zero indicating that the accuracy could be a result of chance, and anything below zero indicating that the model is predicting presence and absence worse than random. Other measures of fit included accuracy, which is the rate of correctly classified quadrats; sensitivity, which is the likelihood that the probability map would correctly predict presence in test quadrats indicating omission errors; and specificity, which is the probability map that will correctly predict absence quadrats indicating commission

errors (Allouche *et al.* 2006). The fifth indicator calculated was the TSS (true skills statistic), which is the specificity plus the sensitivity, minus one, which is an indicator of the total model performance. In addition, we divided MaxEnt scores into 0.1 intervals and the number of presence and absence quadrats associated with each score class. This is related to the frequency of scores in each class, and the percentage of present and absent transects in each MaxEnt probability class calculated.

Initially, we ran the model and tested the kappa statistic calculated as outlined above. The optimal regularization multiplier variable was determined by changing regularization multipliers in steps of 1; increasing from 1 to 10, and running the model 10 times for each change with crossvalidation. We then used the test quadrats to calculate a Kappa score for each run. We plotted these scores in a graph, and used the point in the graph which had the highest Kappa, to calculate distributions in the final map. For *A. nigrescens*, the highest Kappa statistic was at a regularization of 2, and for *S. birrea*, at a regularization of 1. A higher Kappa statistic indicates that the results of the model better fit the predictions made for the presence and absence in the test quadrats. Graphical results were calculated using the optimal regularization multiplier.

We used data from five GPS-collared, adult female elephant in HiP, each representing a separate herd. Location were recorded at 30 min intervals, from October 2006 to September 2008. This produced 149238 recorded locations. We used these points to create a kernel density raster map using ESRI Arc Map™ Spatial Analyst™ kernel analysis tool. A high density of points in an area is likely to indicate that the elephants were utilizing this area as elephant spend large amounts of time feeding (Beekman and Prins 1989). Kernel densities have been used in a number of studies to determine the spatial utilization of the landscape by animals (Worton 1989, Seaman and Powell 1996). For this study we simplified the analyses by combining all the data

collected for all elephants. We summed the raster grid densities for *A. nigrescens* and *S. birrea* to give a single raster map. Thus, each cell indicates the probability of occurrence of both species, with a maximum density of two. We then divided these values by two, to make the map values a fraction of one. The elephant point density values for each raster square were divided by the highest density to calculate the proportion of the highest density of each raster cell. If elephant point density is considered to show the most likely location in which elephant impacts will be high, the elephant point map can be combined with the MaxEnt probability maps for the trees in two ways. 1) The elephant point density can be added to the MaxEnt probability map to show where trees are more likely to be threatened by elephant. 2) If elephant impacts are considered negative, point density can be subtracted from the MaxEnt probability map to show where there is least conflict. This map, together with the elephant distributions, can be used to estimate the placement of a botanical reserve that would optimize the conservation of both tree species and elephants, by identifying refuges for trees outside of key forage areas for elephant.

Results

We recorded 179 *A. nigrescens* trees and 106 *S. birrea* trees in the 20 ca. 2 km long transects.

The AUC values for both *A. nigrescens* (0.93) and *S. birrea* (0.797) indicated that the model fitted well to the data used (i.e. > 0.75), and that the model for *A. nigrescens* was likely to be predicting somewhat better than the model for *S. birrea*. The probability distribution maps produced by MaxEnt indicated distinct differences in the spatial distribution of each species. The niche model prediction for *A. nigrescens* indicated that the species is restricted to the iMfolozi section, with only a small patch in the Hluhluwe and Corridor sections (Fig. 2). *S. birrea* had a wider predicted distribution than *A. nigrescens*; where it was predicted to be most common in the

corridor section of the park, in small areas in the Hluhluwe section, and over a wider area in the Imfolozi section, although with lower probability (Fig. 2).

The AUC values that use a percentage of the recorded locations to construct the model are likely to be autocorrelated and give higher AUC values (Veloz, 2009). Thus, we required the use of another source of data to test the model.

We calculated the proportion of quadrats which were correctly predicted by the MaxEnt map using the 10th percentile threshold of presence, by extracting MaxEnt probabilities for each quadrat and separating those that were above and below the threshold (Fig. 3). The proportion of test quadrats that correctly matched model output are shown in Table 1, and the test statistics derived from this are shown in Table 2. The model for *A. nigrescens* had a higher accuracy than the model for *S. birrea*. Both species had similar values for sensitivity which were not high, indicating that the models were both over-fitting the data and omission errors were occurring (Table 2). The specificity statistic for both species was higher than the sensitivity score and the value for *A. nigrescens* was higher than *S. birrea*, which indicates that the model produced fewer commission errors (Table 2). As expected, the Kappa statistic and TSS had similar values. Both measures take into account the variability in the model that could exist by chance, but TSS is less sensitive to prevalence in the data set. Both measures showed that the model for *A. nigrescens* was predicting the distribution better than that for *S. birrea* (Table 2). The results from the model for *S. birrea* using these test results indicated that though it was a relatively poor fit to the quadrat data the AUC predicted that the model was accurate. It is therefore imperative that studies using these techniques use independent test data to evaluate the accuracy of models.

Table 1. Numbers of Plots which were correctly identified as possible present and absent areas by the model

		MaxEnt Model Predicted	50 x 50 m plots Observed Absent	50 x 50 m plots Observed Present
<i>A. nigrescens</i>	Absent	254	229	60
	Present	85	25	55
<i>S. birrea</i>	Absent	231	147	84
	Present	136	80	56

Table 2. Five Model evaluation statistics for *Acacia nigrescens* and *Sclerocarya birrea*. Values closer to one indicate a better result

	Accuracy	Sensitivity	Specificity	TSS	Kappa Statistic
<i>A. nigrescens</i>	0.77	0.48	0.9	0.38	0.41
<i>S. birrea</i>	0.52	0.39	0.65	0.05	0.04

To make sense of the low Kappa statistic and TSS, we examined the distribution of transects of both types across the MaxEnt probability spectrum. A large proportion of the test quadrats with individuals present overlapped the 0 - 10% probability raster squares (Fig. 4), suggesting weak prediction. However, the distribution of areas within each probability class predicted by the model showed that there was a high proportion of the area in low probability classes represented by the available proportion (Fig. 4). Thus, we used a relative measure, which resulted in the percentage of all quadrats in each probability class in which individuals were present, having a better predictive ability (Fig 5). This indicated that the model for *A. nigrescens* was more accurate than *S. birrea* (Fig 5).

The AUCs calculated for each variable had a higher value for *A. nigrescens* than *S. birrea*, except for soil type. Aspect, slope, geology, soil and vegetation had relatively low AUC for both species. Of these variables, aspect was slightly higher for *A. nigrescens* and soil, for *S. birrea*. The variable with the second highest AUC was elevation, and the highest was rainfall. Highest AUC values were obtained with all variables included, with little difference when any one variable was excluded, indicating that the variables were correlated to some degree. In the model, the absence of rainfall caused the lowest drop in AUC, indicating that a larger proportion of the predictive power of the model was due to this variable. Elevation was the next most important as a predictor.

The probability of occurrence of both species declined with increasing slope, from 0° for *A. nigrescens* and from 4° for *S. birrea*. The two species responded differently to aspect, where the probability of occurrence for *A. nigrescens* peaked at 50° (East North East), and *S. birrea* from 300° to 360° (West North West to North). *S. birrea* occupied a wider range of elevation than *A. nigrescens*, peaking at about 140m to 150m, before dropping and then increasing in probability

of occurrence from 300m to 500m. In contrast, *A. nigrescens* peaked at 50 m, before dropping down sharply. As expected, the probability of occurrence was strongly influenced by vegetation type. *A. nigrescens* had a higher probability of occurring in fine leaved woodland, riverine forest and broad leaved woodland, while *S. birrea* had a high probability of occurring in induced thicket, riverine forest and fine leaved woodland.

The elephant point density map was combined with the MaxEnt tree score map (Fig. 6) The combination of these two maps allows for the position of a possible location of a botanical reserve to be evaluated, in which the combined MaxEnt score is high and the density of elephant points is low. Areas in which elephant are spending less time, and where large trees have a high probability of occurring, may provide refuges to large trees. From the relatively low MaxEnt score over the whole reserve, produced when probabilities are summed (Fig. 6 b), it can be assumed that there is not a high degree of distribution overlap between tree species.

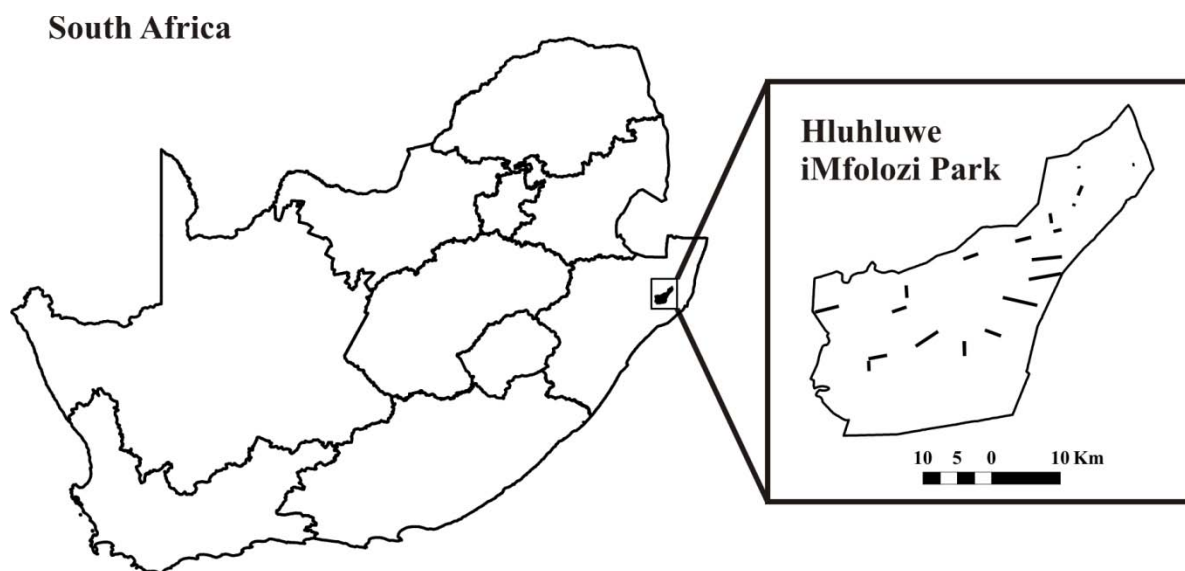


Fig. 1. The location of Hluhluwe–Imfolozi Park and the large tree transects within the park.

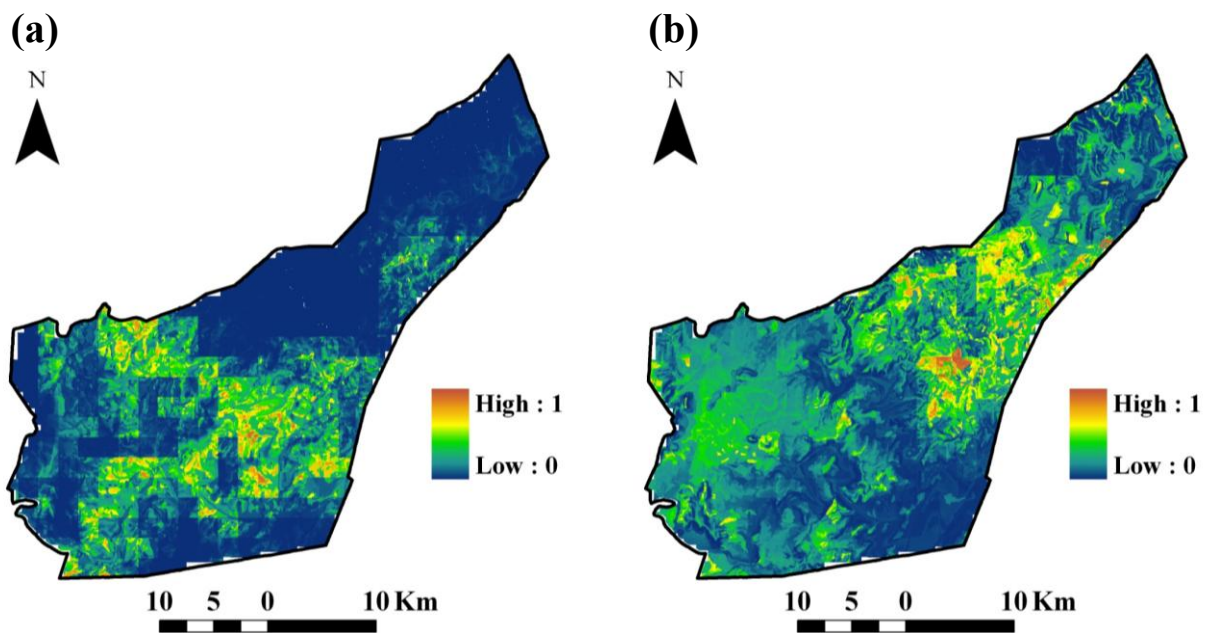


Fig. 2. Probability of occurrence or habitat suitability maps produced by MaxEnt for (a) *Acacia nigrescens* and (b) *Sclerocarya birrea*. A probability of one indicates a high likelihood of finding the species within the raster square, and zero indicates that it is unlikely that the species will be found there.

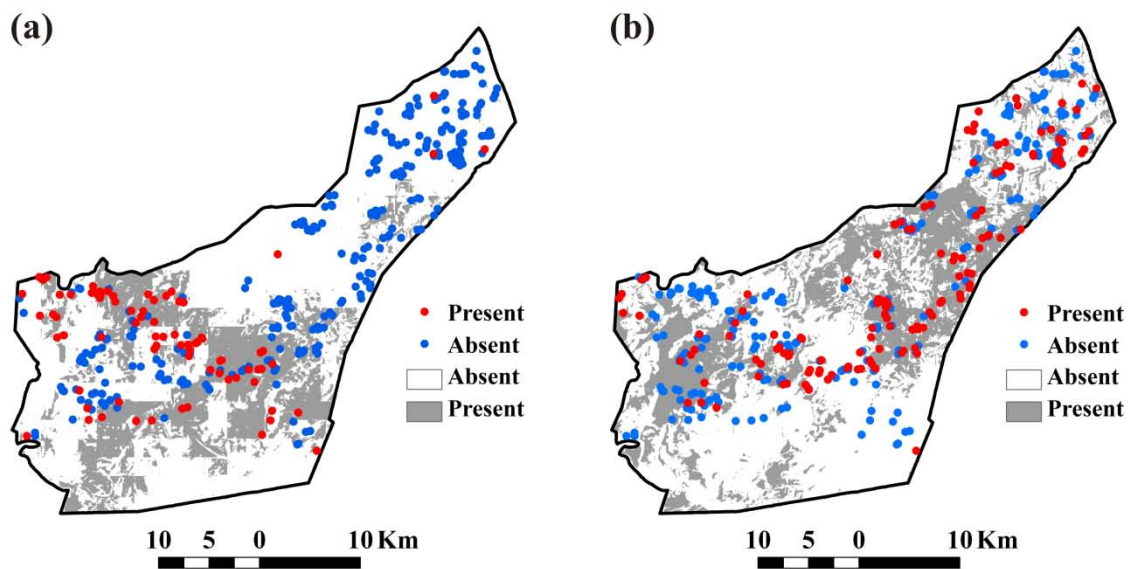
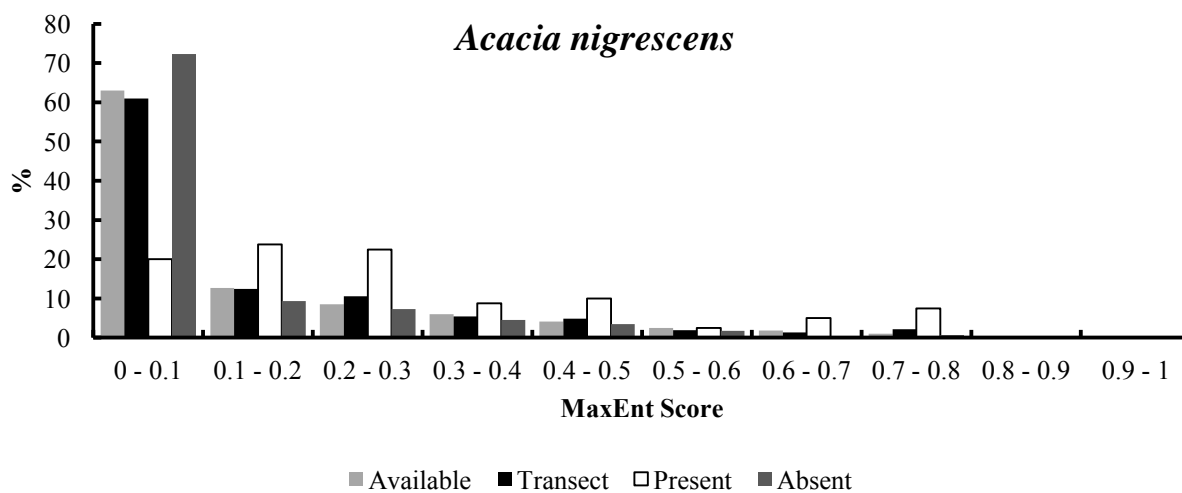


Fig. 3. The predicted distribution for *Acacia nigrescens* and *Sclerocarya birrea* from the MaxEnt model versus their presence or absence in independent sampling quadrats.



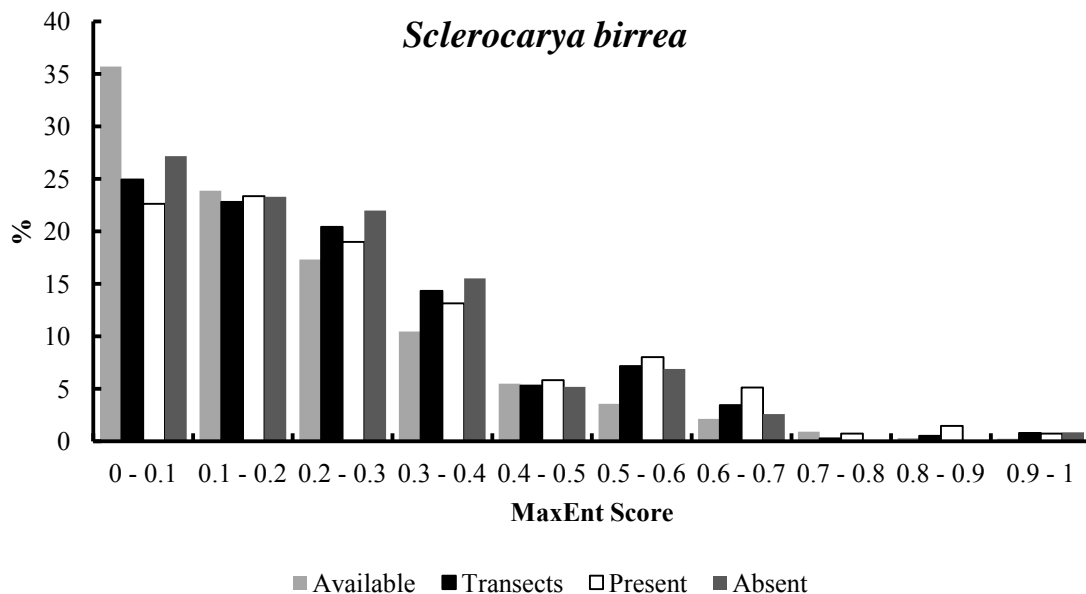


Fig. 4. The distribution of a quadrats with and without each species present, compared to the availability of areas within probability categories and the distribution of transects within the MaxEnt categories. The expected trend would be that presence quadrats would have a greater distribution in higher MaxEnt probability classes and absence quadrats would have a higher proportion in low MaxEnt probability classes. Available = the number of test plots overlapping cells that fell into each MaxEnt probability class as a percentage of the total number of cells in the map. Transects = the number of test quadrats overlapping cells in each MaxEnt score range as a percentage of the total number of test quadrats in the reserve. Present = the number of test quadrats with individuals of the species present, overlapping cells in the probability range. This is calculated as a percentage of the total number of test quadrats with the species present in the reserve. Absent = the number of test quadrats with individuals absent, overlapping cells in the probability range. This is calculated as a percentage of the total number of test quadrats in which the species was absent in the reserve.

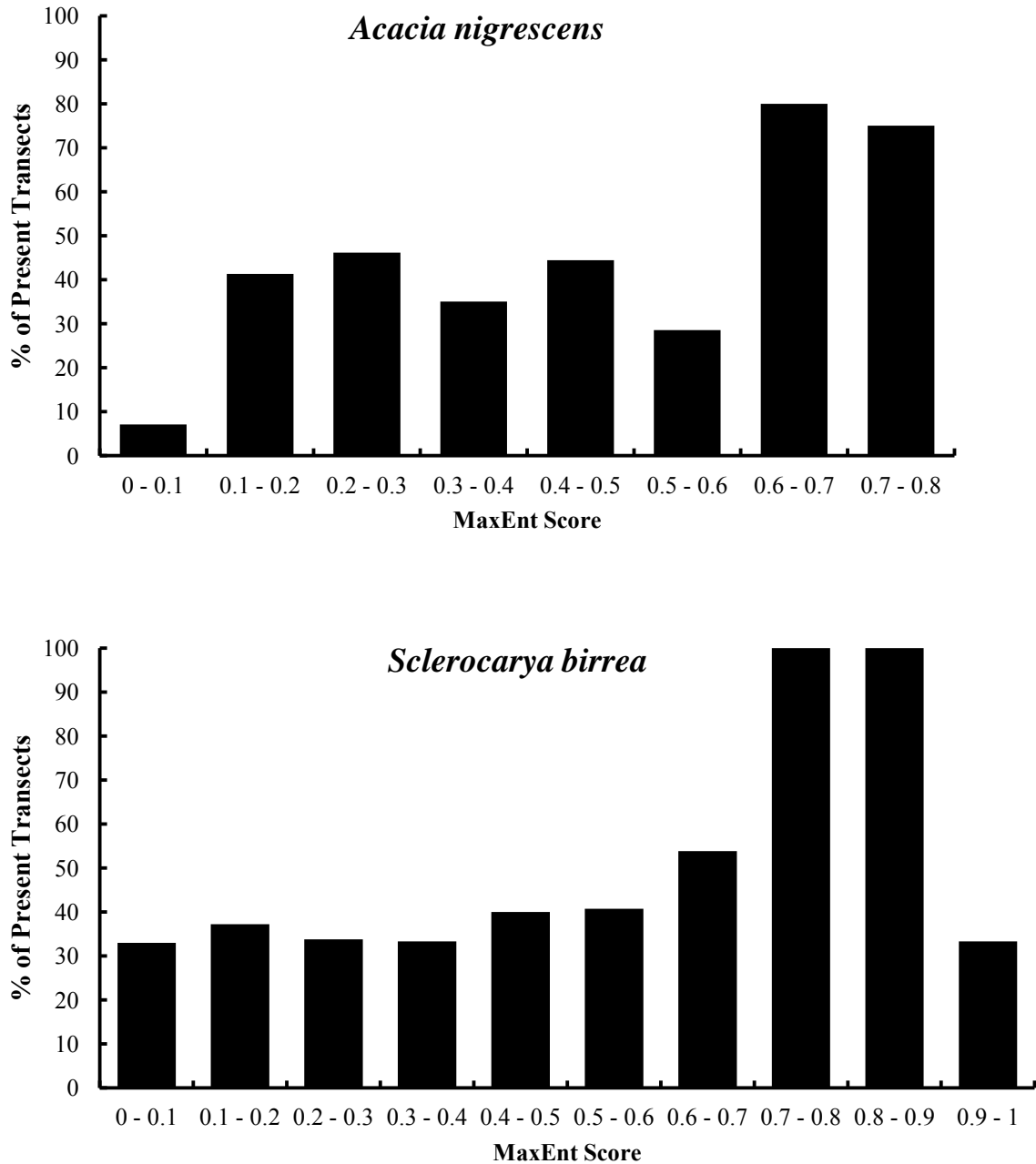
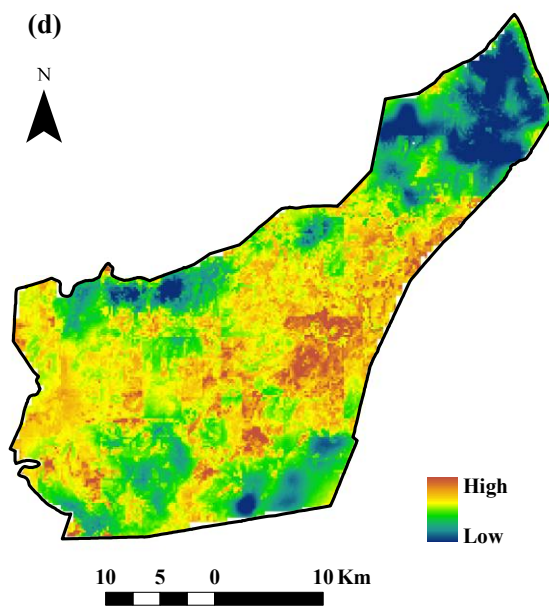
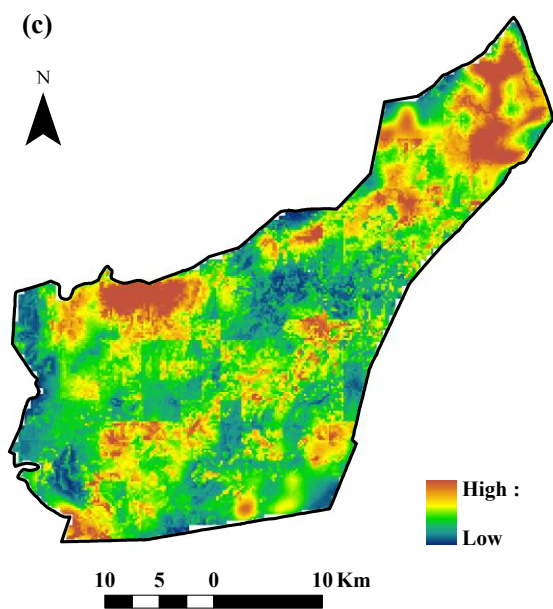
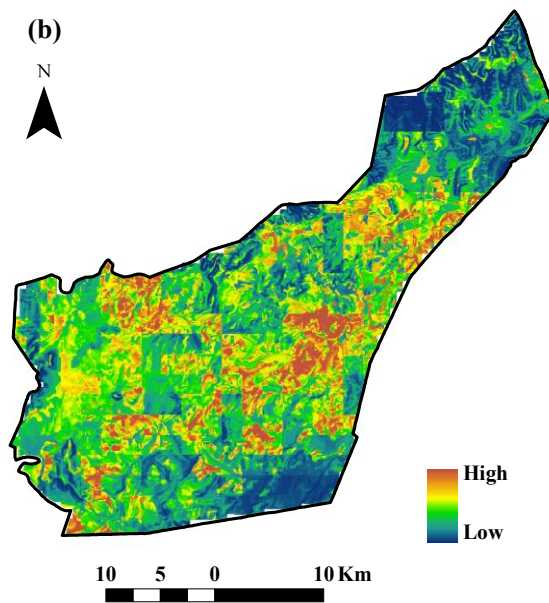
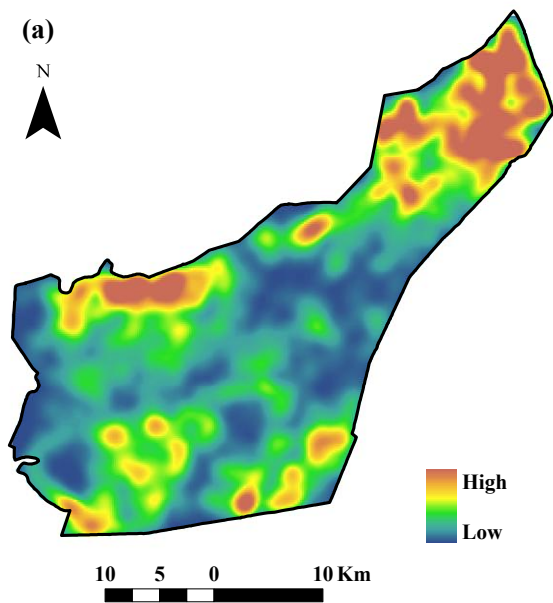


Fig. 5. The number of test quadrats in which the species occurred that overlapped each MaxEnt score range. This is given as a proportion of the total number of test quadrats that overlapped each probability range. An increasing percentage should occur as the MaxEnt score category increases.



scores to indicate areas of conflict with high elephant usage; and (d) the elephant point density subtracted from the MaxEnt probability to show areas with least conflict. This map can be used to assist in the placement of potential botanical reserves which simultaneously protect large trees and minimize the exclusion of elephants.

Discussion

The use of GPS and GIS to sample transects for large trees was successful, allowing transects to be sampled quickly and efficiently (see Druce *et al.* 2008). This permitted a large enough area to be sampled in order to give a representative distribution of the species modelled in the study.

Due to the relatively low density of trees ≥ 5 m within the savanna system, it was imperative that the methods used would allow a large area to be sampled. Traditional methods of sampling transects, such as the use of a tape to measure distance and to keep the transect in a straight line (Bauer 1936), would have taken a large amount of time. However, possible inaccuracies introduced by our method include inaccuracy of GPS coordinates due to factors such as signal reflection, poor satellite geometry and poor signal quality, which are usually a result of tree cover or atmospheric conditions (Rempel *et al.* 1995). A negative impact of using transects to sample for MaxEnt analyses is the autocorrelation caused by sampling within transects, since this causes clumping of recorded points which have a non random distribution (Jorge *et al.* 2008, Veloz 2009). This causes inflated AUCs which would usually be used as an indication of model accuracy.

Interpreting probability maps is complicated by the lack of definitive thresholds, when deciding at what threshold above zero an individual may be found (Liu *et al.* 2005). Our ground testing methods used a double-blind method, as opposed to the testing methods used by Rebelo and

Jones (2010), who used transects to ground truth the probability distribution maps for *Barbastella barbastellus* bats in Spain. The distributions of test quadrats in this study were random, with relatively few falling within high probability MaxEnt score categories. The results from the Kappa analyses of the presence/absence of the species in quadrats were therefore not as high as they may have been if data were collected with larger numbers of transects in the high probability categories. The ability of niche models to better predict the locations of species which have more restricted distributions, has been shown in previous studies (Brotons *et al.* 2004). The Kappa statistic indicated that the model for *A. nigrescens* fitted the test quadrat data better and is likely to be more accurate than for *S. birrea*. This may be because the variables selected to construct the models are more relevant to the distribution of *A. nigrescens* on a fine scale i.e at the scale of the reserve. In addition, in terms of the distribution of each species, HiP is located close to the southern extent of the distribution of *A. nigrescens*, while the distribution of *S. birrea* reaches farther south (Boon 2010). The topographic and environmental variable such as rainfall may be a stronger factor influencing the distribution of *A. nigrescens* than *S. birrea*, which is more likely to be found throughout the reserve. The locations of *S. birrea* may therefore be more strongly linked to the fire regime or herbivore pressures within the reserve, rather than simply to environmental variables.

The difference in preferred elevation is likely to cause the split in distribution of the species, with *S. birrea* being found at intermediate elevations and *A. nigrescens* being restricted to the lower lying areas in iMfolozi. The split is likely to be correlated with rainfall, since there is a rainfall gradient present (Skowno *et al.* 1999). The response curves for rainfall indicate that *A. nigrescens* is restricted to areas of lower rainfall, which occur in the south of the reserve; and *S.*

birrea has a much wider tolerance for rainfall within the reserve. Using rainfall in isolation, the AUC for *A. nigrescens* was higher than for *S. birrea*, which indicates that rainfall is restricting the distribution strongly. The large square patches within the predicted distribution of *A. nigrescens* are likely to be a result of the model predicting a low probability of this species' occurrence within those rainfall raster cells.

The variables used as niche descriptors in the model in this study are all surrogates or indirect measures of the actual limiting resources and conditions that define the niche (Peterson 2001). They also comprise a subset of the full niche description. Despite this, the model prediction provided was adequate for planning and management purposes, at least in the context of large trees in protected areas, and these two species in particular. The low correspondence between the presence of individuals in relatively small test quadrats, and the model output in the same size small cells, is not surprising, and does not nullify the suitability of the method as tool in this instance. There are many reasons why individuals might be absent from suitable habitat, in reality as well as that defined by the model. The random events that influencing both seedling and adult mortality, such as fire occurrence, browsing pressure, episodic droughts and floods (Ben-Shahar 1991), can result in a suitable site not being occupied. The question addressed here is whether the predictions are of a suitable quality to enable effective conservation measures to be implemented that might ensure the persistence of large trees. Effective management actions are those that result in increased recruitment and survival of recruits and adults (Muller, 2002). Such actions comprise activities such as increased seed dispersal by human agents, or by removing seed predators or reducing browser numbers in order to control the effects of herbivores on vegetation (Lombard *et al.* 2001). Three methods have been proposed: the

establishment of botanical reserves (Lombard *et al.* 2001); culling (Gordon *et al.* 2004); and the removal and improved planning of water point locations (Thrash 1998).

Establishing botanical reserves to protect vegetation from large herbivores can be achieved by placing fences around sensitive vegetation types in order to exclude herbivores, particularly elephant (Lombard *et al.* 2001). In this study, we show how knowledge of botanical reserve placement can be guided by niche models, indicating large tree recruitment areas. Our results indicate that it would be more difficult to create a single botanical reserve within HiP to conserve both species. However, the establishment of more than one botanical reserve, covering optimal zones which target each species individually, may enhance the conservation of these trees. The application for this type of model to the conservation of large trees in reserves is through the planning of refuges and areas in which recruitment can occur. Two important factors influencing recruitment are fire and herbivory (Dublin *et al.* 1990, Langevelde *et al.* 2003, Sankaran *et al.* 2008); fire, through the frequency and intensity of burns (Williams *et al.* 1999, Higgins *et al.* 2000) and herbivory, through its intensity, which is controlled by abundance of resources and herbivore density (Baxter and Getz 2005, Sankaran *et al.* 2005). Both factors can be controlled to a certain extent by management interventions, which employ measures to ensure the persistence of large trees in conservation areas. Fire management in southern Africa has a long history dating back to Iron Age people burning veld (Acocks 1988), to the implementation of burning strategies by reserves intended to maintain the balance between grasses and trees (Higgins *et al.* 2007). Current trends in fire management have shifted from block burning and set fire frequencies used in the past by management, to policies that take into account other outcomes and are used to create heterogeneous environments in parks (Bond and Archibald 2003). By shaping these

strategies to take into account areas which are most likely to support the growth of large trees, niche models can influence fire regimes and guide adaptive management strategies (Van Wilgen *et al.* 1998).

Our results of the MaxEnt model predictions show that niche models can be used at finer scales. Considering the relatively poor functioning of the model for *S. birrea*, we recommend testing models thoroughly with independent data (Veloz, 2009). The requirements in terms of changing the regularization factor of the model to decrease over-fitting indicated that increased parameter optimization may be required to improve model fitting at fine scales (Phillips and Dudík 2008). The relative ease in which the above methods can be applied to manageable reserve size areas make niche modelling an important tool, as management applications can stretch towards managing many different species. The two species that have been modelled are of importance to conservation endeavors in many southern African reserves. Moreover, the application of these techniques can be applied in different geographic areas, and will improve the conservation and management of rare species and, as in our case, species ‘of concern’. The extension of these techniques and models into predicting distributions outside of reserves can allow conservation to take a broader view of species conservation expanded outside of fenced areas. This may include the rehabilitation of previously transformed land, by informing the choices of species to be reintroduced. Moreover, the use of predictive climate models can be applied to niche models with relative ease, allowing predictions to be made about changes in species distribution from climate change (Beaumont *et al.* 1995, Willis *et al.* 2009).

Acknowledgments

E. Di Minin for assisting me with MaxEnt and helping with many GIS related queries. R. Howison for the use of her geology, soil and vegetation maps. P. Tshibase and P. Birkett for

helping with field work. Ezemvelo KZN Wildlife for accommodation and guarding. I thank EKZWN for the use of the monitoring transect data and the Earthwatch, UKZN and other volunteers for collecting the data. Amarula Elephant Research Program and the National Research Foundation (Grant to RS: FA2006032300024) for funding. Dr C. Schoeman and Dr F. R. Smith for advice and assistance with analyses. P. Birkett for manuscript editing.

Appendix: Supplemental material for Using Maximum Entropy Modelling to predict the potential distributions of large trees for conservation planning and management

Maxent Software:

MaxEnt was developed for predicting the distributions of species using niche modelling techniques (Phillips *et al.* 2006). Niche distribution models use the statistical relationship between the recorded locations of individuals of a particular species, and environmental variables at that location, in order to predict the probability of finding a species at a given location (Ben-Shahar 1991, Hirzel *et al.* 2002). MaxEnt uses a grid (raster) based approach in which occurrence and environmental conditions are recorded in cells of defined size. The relative likelihood of finding a species in each cell is calculated and plotted as a distribution probability map ranging from zero to one with increasing likelihood of finding the species in the cell. MaxEnt predicts the probability of finding the species within each raster square by finding the distribution of maximum entropy constrained by the expected value of each predictive variable, matched to its empirical average over the value at presence sites (Phillips *et al.* 2004). The version of MaxEnt used was version 3.3.0.

To determine the strength of each variable in predicting the distribution of a species, MaxEnt uses jackknife runs with only one variable, and then uses all other variables to determine how well the variable determines species distributions on its own, and how correlated that variable is with the other variables in the model (Phillips *et al.* 2004). The strength of prediction is measured by the area under the curve AUC of each model (Phillips and Dudík 2008). Higher AUC values indicate that the model is predicting the location of the species more accurately than those with lower AUC values. A model with a single variable and a lower AUC than other

single-variable models, indicates a stronger predictor of distribution. The difference between the model without one variable, but all other variables, and those with all the variables, indicates the level of correlation between that variable and other variables within the model (Phillips and Dudík 2008). When MaxEnt runs a model, variables are run in sequence and correlation effects are reduced by determining the individual contribution of variables in explaining the total variation in distribution (Phillips and Dudík 2008).

Generating the Topographic Layers

The starting point for the topographic layers was the south african national topographic maps. The vector version of the elevation isoclines was used to create a digital elevation model for the reserve using ESRI Arc Map. The elevation DEM was then used to create the aspect and slope layers using ESRI Arc Map.

Supplementary outputs:

Selection of an optimal regularization multiplier (Fig. 1) was chosen as multiplier of 2 for *A. Nigrescens*, and the default value of 1 was used for *S. birrea*.

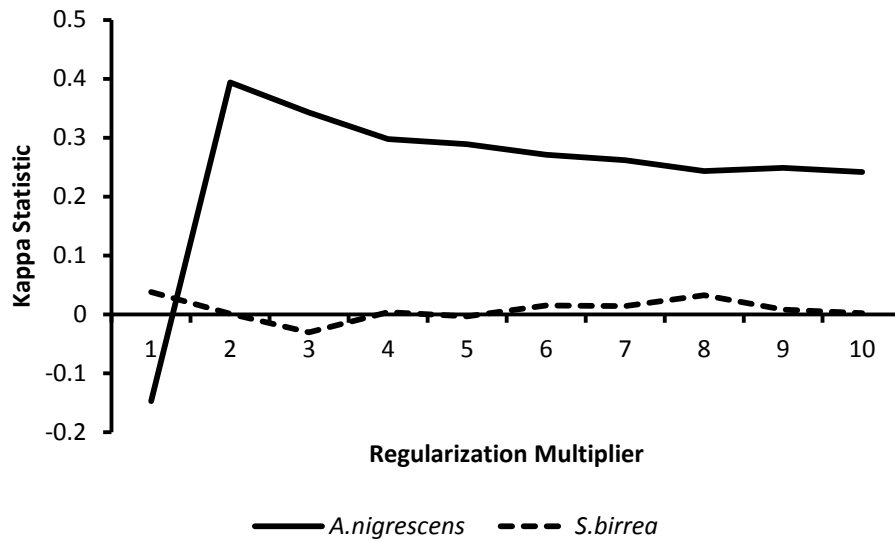


Fig. 1 Variation in the Kappa statistic for each species as the regularization multiplier variable is increased. The regularization number which yielded the highest Kappa statistic was used in the model.

Jackknife graphs are an important tool for evaluating the variables which have been used in the analyses (Fig. 2). They show which variables can predict the distribution well, as well as those which do not. By comparing the AUC for each species with the AUC for the whole model, the correlation between the variable, and the other variables in the model, can be determined.

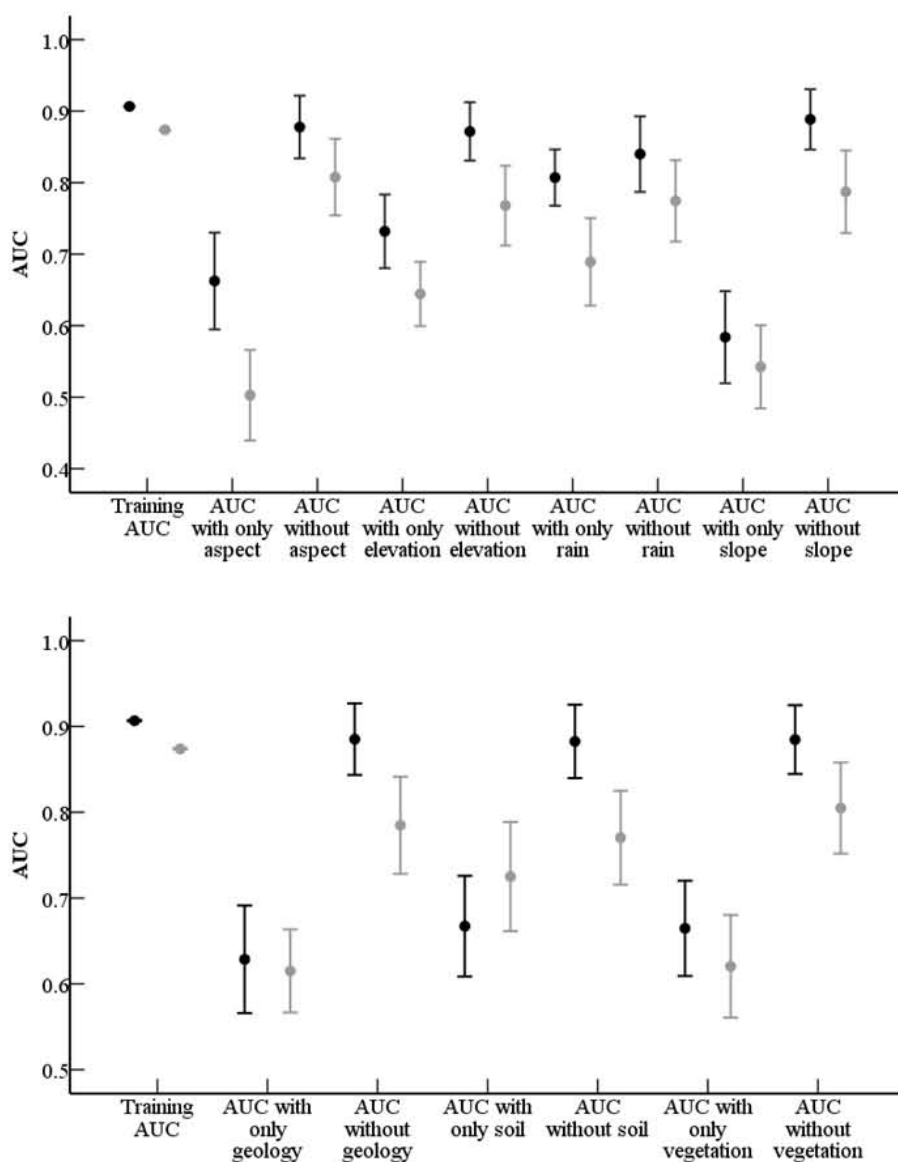


Fig. 2. Comparison of AUC values for different variable combinations, placed in two plots for purposes of clarity. The black points and bars are for *A. nigrescens* and the grey points and bars are for *S. birrea*. Shown are the mean \pm 95% Confidence Limits, based on the 50 times that the

model was run. The above graph is for continuous variables, the graph bellow for categorical variables.

The response curves produced by Maxent are an important means to understand the relationship between the probability of finding the species and the variables used in the models. The response curves for each species being presented together to allow a comparison to be made between the species in terms of the probability of finding them in a place, and the value of each variable (Figs 3 & 4).

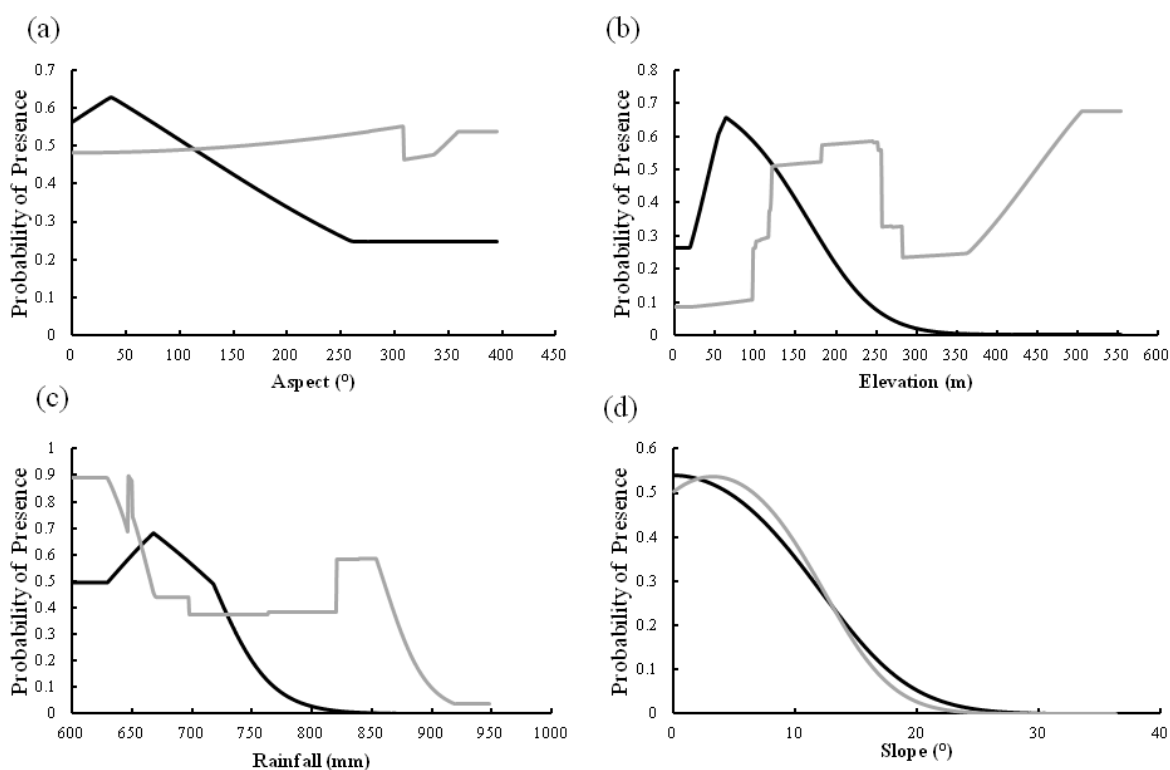


Fig. 3. Response curves for the continuous variables used in the MaxEnt analyses, indicating the manner in which each variable used in the analysis affected the distribution of the species in question. (a) for aspect, (b) for elevation, (c) for rainfall and (d) for slope. The black lines represent *A. nigrescens* and grey, *S. birrea*.

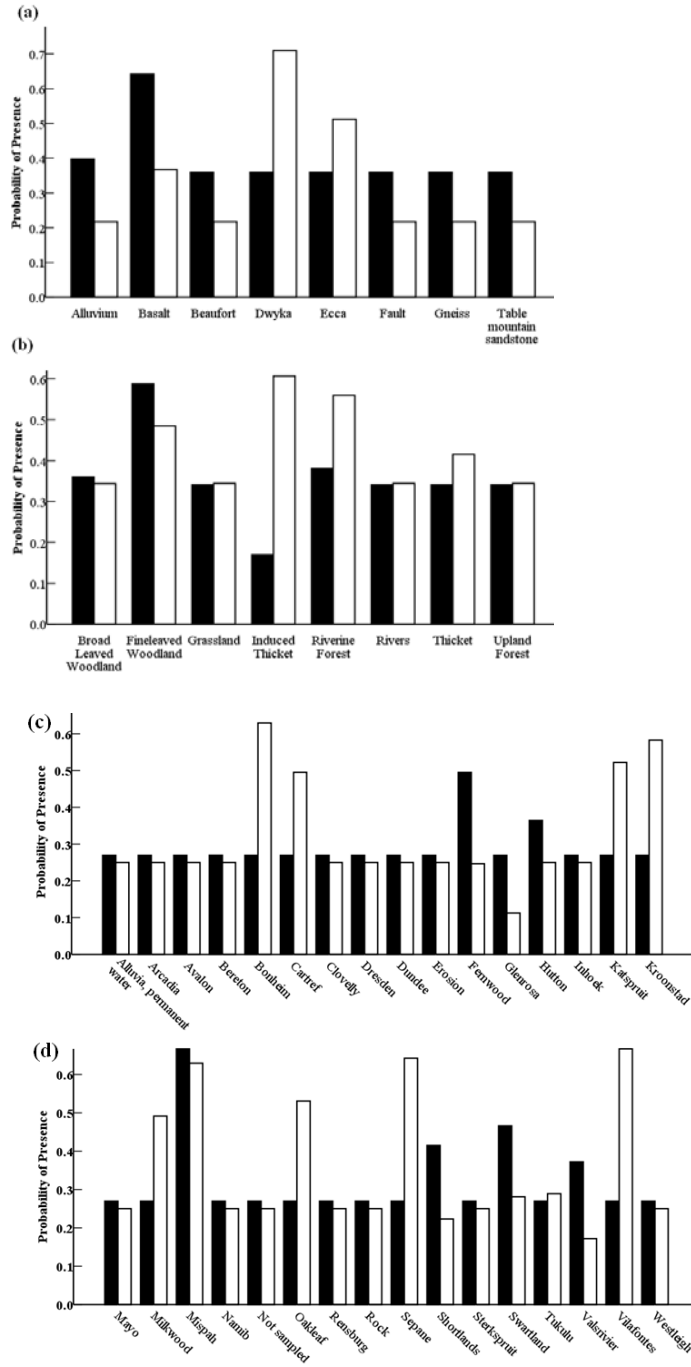


Fig. 4. Response curves for categorical variables used in the MaxEnt predictions of probability. Categorical variables include: (a) geology, (b) Vegetation, and (c) and (d) the soils map, used in the analyses.

Chapter 3

Local and range level limiting factors of two sympatric large savanna trees

Alain Smith, Bruce Page, Rob Slotow

Amarula Elephant Research Program, School of Biological and Conservation Sciences, University of KwaZulu-Natal, Durban, 4041, South Africa

Rob Slotow

School of Biological and Conservation Sciences, University of KwaZulu-Natal Westville, Durban, 4041, South Africa

Tel: +278337707080

e-mail: Slotow@ukzn.ac.za

Key Words: MaxEnt, Niche Modelling, Hluhluwe Imfolozi, Kruger National Park, Distributions, *Acacia nigrescens*, *Sclerocarya birrea*

Aim (i) To predict the fine scale distributions of two large tree species, *Acacia nigrescens* and *Sclerocarya birrea*, which are threatened with extirpation from several protected areas in southern Africa, in two protected areas, from a small sample of known locations. (ii) To determine which variables from a suite of previously selected ones are responsible for the differences in overlap of the ranges of the two species in the two different localities. (iii) To determine which of the variables affect the distribution limits of the two species within each reserve, (iv) To determine if it is possible to predict the distributions of the two species at a fine scale within each reserve, for the purpose of managing the impacts on the populations within the two protected areas.

Location Kruger National Park (KNP) which lies well within the distribution range of the two species, and Hluhluwe Imfolozi Park (HiP), being within the distribution of *Sclerocarya birrea*, and at the edge of the range of *Acacia nigrescens*.

Methods We used MaxEnt to model tree distributions as a function of the distribution of determining variables in the environmental layers. The differences in probable distribution of

each species were compared, as well as the responses of each species to the different environmental variables within reserves and between the different reserves. Nonlinear multidimensional scaling was used to compare the sites in which the species were found in each reserve. The results were verified by examining the co-occurrence of the two species in transects in Pongola Nature reserve, 60 km North of HiP.

Results *A. nigrescens* has a limited distribution in HiP and is more widespread in KNP. In HiP, it is limited by soil moisture, as influenced by rainfall and topography. In KNP the main factor limiting the distribution of *A. nigrescens* is also soil moisture, but the influence of soil type overrides topographic effect. *S. birrea* is more widely distributed in both reserves, and is limited by soils and geology.

Main conclusions The differences in distribution between the two species in the two reserves is likely to be due to an increasing rainfall gradient in HiP, as one moves south and west, which thus limits the southern distribution of *A. nigrescens*.

Introduction

The factors determining the distribution of species act at different scales (Rahbek and Graves 2001, Rahbek 2005, Field et al. 2009). These factors range from environmental to biological (Grinnell 1917a, Hutchinson 1957). Environmental determinants can have marked effects at a fine scale and can be used to predict species distribution (Bugmann 1996, Guisan et al. 1998). At broad scales, vegetation is primarily controlled by climate (Woodward and Williams 1987), but at the local scale it is controlled by geology and soil types (Kruckeberg 2002). By understanding the effects of different variables on the distribution of species, predictions can be made about their geographic distribution (Peterson 2006) under different climate change scenarios (Midgley et al. 2003). These predictions can be made at broad or narrower geographic scales. In this paper, we examine the fine scale differences in environmental variables that effect the distribution of species that are well within the range or near the edge.

A species' niche can be partially described by the biotic and abiotic variables that characterize the habitat in which it occurs, and can be represented as an n-dimensional hypervolume (Hutchinson 1957). Describing the niche enables tolerances along each of the differences dimensions of the niche space to be identified. If the spatial distribution of these limits is known,

this can be used to determine the potential distribution of the species (Pulliam 2000). Niche modelling uses recorded locations of a species, in conjunction with spatially explicit layers of environmental variables to identify the limiting variables within the list of those recorded, and to predict the probability of finding a species at any location within the extent of the supplied layers (Jorge and Peterson 2005). Measuring Niche overlap is an important way to compare the niches of species, and to predict where competition, exclusion and other interactions of species are likely to be occurring (Abrams 1980). Niche modelling is also a useful tool to determine what separates species at fine and broad scales (Wilson and Lee 1994, Costa et al. 2002). The response curves correlation between the abundance of the species in samples to the different levels of different environmental variables. When combined with the different layers of environmental variables, MaxEnt produces a probability of finding the species in a particular grid cell (Phillips 2006). The response curves therefore describe the n-dimensional niche space.

The decline of large trees in some protected areas has become a major concern (Eckhardt et al. 2000, Whyte et al. 2003). The two species selected for the study are considered keystone species and indicator diagnostic species and occur in a range of community types (Mucina and Rutherford 2006). This study was conducted in Kruger National Park, where both species are at the centre of their ranges, and co-occur in the same localities and habitat; and Hluhluwe iMfolozi Park, where *Acacia nigrescens* Oliver (Fabacea) is at the edge of its range while *Sclerocarya birrea* (A. rich.) Hochst. subsp. *caffra* (Sond.) Kokwaro (Anacardiaceae) is still well within its range, and where the species are not locally sympatric. We used Niche modelling to compare the distribution of both species in both reserves, and determine which environmental variables were causing the split in distribution in HiP. By comparing the abundances at two different locations separated by some 300 km, important drivers that locally limit their distribution can be determined. These models can be used to predict change in distribution within protected areas over time, and under different regional (e.g. climate change) and or local (e.g. fire regimes) influences, enabling effective planning and management. The presence of adult trees in high numbers is an indication of the suitability of the habitat for that species' persistence and productivity (Manning et al. 2006)

Methods

The Hluhluwe-Imfolozi Park is located in KwaZulu-Natal, South Africa (28°02'24"S 32°03'36"E); Kruger National Park is 284 km north of HiP (24°0'41"S 31°29'7"E) in the Limpopo and Mpumalanga provinces. Although the entire KNP covers approximately 19 000 km², the model was run for the southern section of the reserve covering 4637 km² (~ 25 % of the park). The model was run for the entire HiP, which has an area of 896 km² (~ 19 % of the study area in KNP). The vegetation in the southern section of KNP is shaped strongly by the geology of the area, with granitic soils on the west and basaltic soils on the east (Venter et al. 2003). The vegetation in HiP is strongly influenced by a rainfall gradient, with the long-term mean ranging from 985 mm in the north to 650 mm in the south. There is also a decrease in elevation from the highest regions (550 m) in the north to the lowest in the south (19 m) (Howison 2009). Rainfall in KNP varies from 719 mm in the west to 537 mm in the east of the southern section (Venter et al. 2003). Elevation ranges from 236 m on the Lebombo Mountains to the east, with the lowest points occurring along the river valleys at 140 m.

In KNP, *S. birrea* and *A. nigrescens* occur within the broad national scale vegetation type, Tshokwane-Hlane Basalt Lowveld (Mucina and Rutherford 2006), in which they are dominant species. In HiP, *A. nigrescens* and *S. birrea* occur within Zululand Lowveld vegetation. However, in HiP, the two species were found to occupy separate areas and vegetation types (habitats), as a result of differences in rainfall across the reserve. To determine the reasons for this difference in the association of the two species, we compared the results of niche modelling of each species in both reserves to identify differences in the realized niches of each species in the two localities, and the reasons for the two species growing in close proximity in one locality and widely separated in the other. Niche theory suggests that the species should co-occur in both reserves since the fundamental niche should be the same in each reserve. However, the realized niches might be different.

We identified and measured all trees ≥ 5 m along 10 m wide transects (Druce et al. 2008). We used a Garmin GPS 12 XLTM to walk transects, using bearings in KNP, and a Trimble Geo XM 2005TM GPS running ESRI ArcPadTM to set a 5 m buffer around the transect lines in HiP. We sampled 3082 trees along 22 transects, totaling 67 km in the southern KNP in 2007 (Druce et al. 2008; Fig. 1), and 1998 trees along 16 transects, totaling 43 km in HiP (Fig. 1). We recorded the

dimensions of each tree, including the diameter of stems and the canopy. We also noted the impacts of browsing by large herbivores, with emphasis on the intensity of browsing by elephant (*Loxodonta africana*), and the visible impacts of fire (Druce et al. 2008).

In both reserves, raster layers for aspect, elevation and slope were created using the 3D analyst™ extension in the ESRI ARCMAP™ GIS from 20 m contour lines in the national 1:50 000 topographic maps from the Surveyor General. In KNP, geology and soils maps (Venter 1982) and vegetation types (Mucina and Rutherford 2006) were used in the model. The geology map was created for HiP by combining two different source maps: the Imfolozi section created by B.H Downing in 1980 and the Hluhluwe section of the reserve created by L. King in 1970 (Howison 2009). In HiP, the soils map was created by combining the soil types recorded in three different maps: the Imfolozi section mapped in 1980 by B.H Downing, the Hluhluwe section surveyed by S.N Barrows in 1984, and the corridor section of the reserve, mapped by students from the University of KwaZulu-Natal, Pietermaritzburg, supervised by Prof. Jeff Hughes from 1998 to 2001 (Howison 2009). The vegetation map used in modelling for HiP was a structural map prepared by R. Howison (Howison 2009) by reducing the complexity of an older vegetation map (Whately and Porter 1983).

The Bioclim (Hijmans et al. 2005) data for predicted mean average rainfall in each grid cell was used for modelling, as it is a well used model (Godown and Peterson 2000, Peterson 2001, Beaumont et al. 2005). Although the rainfall averages for the reserves from the Bioclim model are high, the spatial pattern reflected those recorded by rainfall stations. The variables selected to detect environmental controls on the distribution of species, and of tree growth, should reflect ecological processes which are affecting the distribution and growth of trees (Austin and Meyers 1996). These environmental variables must also be mapped at a fine enough scale to closely match the sampling scale used to collect the tree distribution data. Four of the variables were continuous: aspect, elevation, rainfall and slope, while the other three were categorical data: geology, soil and vegetation. In KNP, elevation ranged from 174 m to 500 m with an average of 323 m, slope ranged from 0° to 38.7° (average 2.5°), and rainfall ranged from 935 mm to 595 mm. The raster layers for HiP ranged from 19 m to 550 m for elevation, 0° to 36° for slope, and 826 mm to 983 mm for rainfall.

MaxEnt uses the machine learning techniques of maximum entropy modelling described by Jaynes (Jaynes 1957). It can therefore use presence only data to build a model and predict the distribution of a species (Phillips et al. 2006). The presence data are used to create a model, using environmental variables to produce empirical averages for recorded presence sites, which are then used to predict the probability of finding the species in other cells according to their attributes (Phillips and Dudík 2008). Unlike other methods used for Environmental Niche Models (ENM's) which use regression analyses to determine probabilities in other cells from the effects of environmental variables, MaxEnt uses random background points to predict the probabilities in different cells as samples in the model (Phillips and Dudík 2008). In its use as an ENM, MaxEnt has been shown to predict the locations of species accurately, in comparison with other ENM techniques and algorithms (Elith et al. 2006, Rebelo and Jones 2010). We ran the model 50 times for each species in each reserve, using cross validation to ensure that the predicted results were robust and thus likely to indicate the true distribution of the species (Phillips 2006).

To compare the resulting probability distributions from the MaxEnt models for the two species in each reserve separately, we used ENM Tools to determine the niche overlap and the distribution overlap (Warren et al. 2008). We used four different methods of calculating the similarity of the maps. The *I* overlap was calculated by normalizing the probability of finding the species to 1, and then comparing the probability maps with one another (Warren et al. 2010). The range overlap used the average 10th percentile threshold for both species to determine the likely overlap between their ranges within each reserve. We also ran the relative ranking in ENM Tools to compare species distribution within each reserve.

We ran Nonlinear Multidimensional Scaling in Primer 6TM (Clarke and Gorley 2006) on the environmental variables for each tree within each reserve, to determine if there was a difference between the niche separation of each species. We chose Nonlinear Multidimensional Scaling because it can display the dissimilarity or similarity of points, and is less sensitive to categorical data than ordination methods (Kenkel and Orloci 1986). We used both Bray-Curtis and Euclidean distance to determine the distribution of the points. The Euclidean distance had a lower stress value, and was used to produce the final plots.

In order to assess whether distance from the edge of the range, or local conditions were driving our results, we used an existing vegetation database from a reserve about 150 km north of HiP. A vegetation type *Acacia*, Marula woodland was mapped at a fine scale in Pongola Game Reserve (27° 25' 6"S 31° 50' 43"E) by B. Page and K. Duffy. Forty-three 50 m transects were used to create the vegetation map for PGR (Shannon et al. 2006), and we assessed the percentage of transects in which both species occurred, and compared this with HiP for the percentage of 50 * 50 m plots where both species occurred in 1999 (Boundja and Midgley 2010).

Results

During the study, we recorded 827 *Acacia nigrescens* and 350 *Sclerocarya birrea* trees in KNP, while in HiP we recorded 179 *A. nigrescens* and 106 *S. birrea* trees. The MaxEnt model run for each reserve had an area under the curve (AUC) of the receiver operator curve (ROC) of 0.891 for *A. nigrescens* and 0.889 for *S. birrea* in KNP; in HiP *A. nigrescens* had an AUC of 0.916 and *S. birrea* of 0.794. The AUC values from the models indicated models that are predicting distribution well (values greater than 0.75 are considered to be a good indication of a model that is predicting well (Phillips and Dudík 2008)). The resultant probability maps indicated that the distribution of the species was separate in HiP, but that in KNP they were likely to co-occur (Fig. 2). To compare the distribution of both species, we used MaxEnt to calculate the 10th percentile threshold, and illustrate the areas in which the probability was above the threshold value (Fig. 3).

Both the Jack Knife responses and response curves for each species produced by the model were used to understand the relationship between the variable and the probability of finding the species in a particular cell. From the Jack Knife responses for both reserves, aspect had a low AUC (meaning it was not a strong predictor in the model) except for *A. nigrescens* in HiP, where it was higher (Fig. 4). In KNP, for aspect, both species had similar response curves, peaking at 175° (S). In HiP, response curves for aspect were different for the two species, peaking at 300° (NW) for *S. birrea* and 60° (ENE) for *A. nigrescens* (Fig. 4). Rainfall was the strongest predictor for *A. nigrescens* in both HiP and KNP, but a weaker predictor for *S. birrea* in both reserves (Fig. 4). In KNP, the species shared a similar range in rainfall from 600 mm to 700 mm. In contrast, in HiP there was a difference in the rainfall responses for each species, with *A. nigrescens* peaking at around 860 mm, while *S. birrea* occupied a wider range from 860 mm to 940 mm, and peaked

at 920 mm (Fig. 4). Slope was not a strong variable on its own to determine the location of either species (Fig. 4). However, there was an interesting difference in the response curves in KNP, with *A. nigrescens* having a small peak at low slope angles $< 5^\circ$, but with the largest peak from 25° to 40° ; and *S. birrea* peaked at 3° . In contrast, in HiP, both species had similar response curves indicating that they occur in flat areas, $< 20^\circ$ slope.

Geology was not a strong determinant of either species' distribution in KNP, although it was stronger than in HiP (Fig. 4). The major difference in the response curves between the species in KNP was the high value for fine grained sandstone, mudstone and chert obtained for *A. nigrescens*, and the high value for basalt diabase obtained for *S. birrea*. In HiP, the response curves for the two species were quite different, with *A. nigrescens* occurring on the Basalt deposits and to a lesser extent on alluvial deposits, while *S. birrea* was found on the Eccca and Dwyka metamorphic rocks. *A. nigrescens* was found on Mispah, Swartland, Shortlands, Fernwood, Valsrivier and Hutton soil forms, while *S. birrea* was found on Mispah, Vilafontes, Sepane, Bonheim, Kroonstad, Katspruit, Cartref, Milkwood and Oakleaf soil forms. Vegetation type was not a strong predictor of species distribution probability in KNP or HiP, although it was stronger in KNP. In KNP, both species were found in the vegetation type, Granite Lowveld, but *A. nigrescens* peaked in Delagoa Lowveld and was also found in Pretoriuskop Sour Bushveld. *S. birrea* peaked in Gabbro Grassy Bushveld. The two species overlapped in Fineleaved Woodland and Riverine Forest in HiP, but *A. nigrescens* was also found in Broad Leaved Woodland, and *S. birrea* was found in Induced Thicket.

The values from the ENM tools analyses of niche overlap indicated that there was a greater overlap in KNP than in HiP (Table 1. Niche overlap D and I). Both the D and I overlap was nearly twice as large in KNP as in HiP. The value for the range overlap was calculated using the tenth percentile value from the MaxEnt analyses considered to be the threshold of presence. The overlap of areas in each reserve within this 10th percentile threshold for each species (Fig. 6), was compared using ENM tools, this overlap was calculated to be 0.81 in KNP and 0.39 in HiP (Table 1). The value for the relative rank comparing the species was 0.69 for KNP and 0.44 for HiP (Table 1).

Table 1. Results of niche overlap and range overlap analyses performed using Environmental Niche Modelling Tools. Both indices indicated that there was more overlap between the species in Hluhluwe-iMfolozi than in Kruger National Park.

Overlap Statistic	Kruger National Park	Hluhluwe-iMfolozi Park
D niche overlap	0.63	0.32
I niche overlap	0.85	0.59
Range overlap	0.81	0.39
Relative rank statistic	0.69	0.44

The multi dimensional scaling figures showed that in KNP, *A. nigrescens* and *S. birrea* are poorly split and distributed along a single plain, with only a few points for *A. nigrescens* splitting away from the plane (Fig. 5). There was greater separation of the points in HiP, with *A. nigrescens* concentrated more in the top left half of the distribution and *S. birrea* occurring below (Fig. 5). This indicates that the species have greater overlap in KNP than in HiP.

When contrasting the distributions of the two species in the Pongola Nature Reserve, which is closer to HiP, the percentage of transects which had both *A. nigrescens* and *S. birrea* was 5.7 % in HiP and 32.6 % in PNR. This indicates that the two species are more likely to be found together in PNR than in HiP.

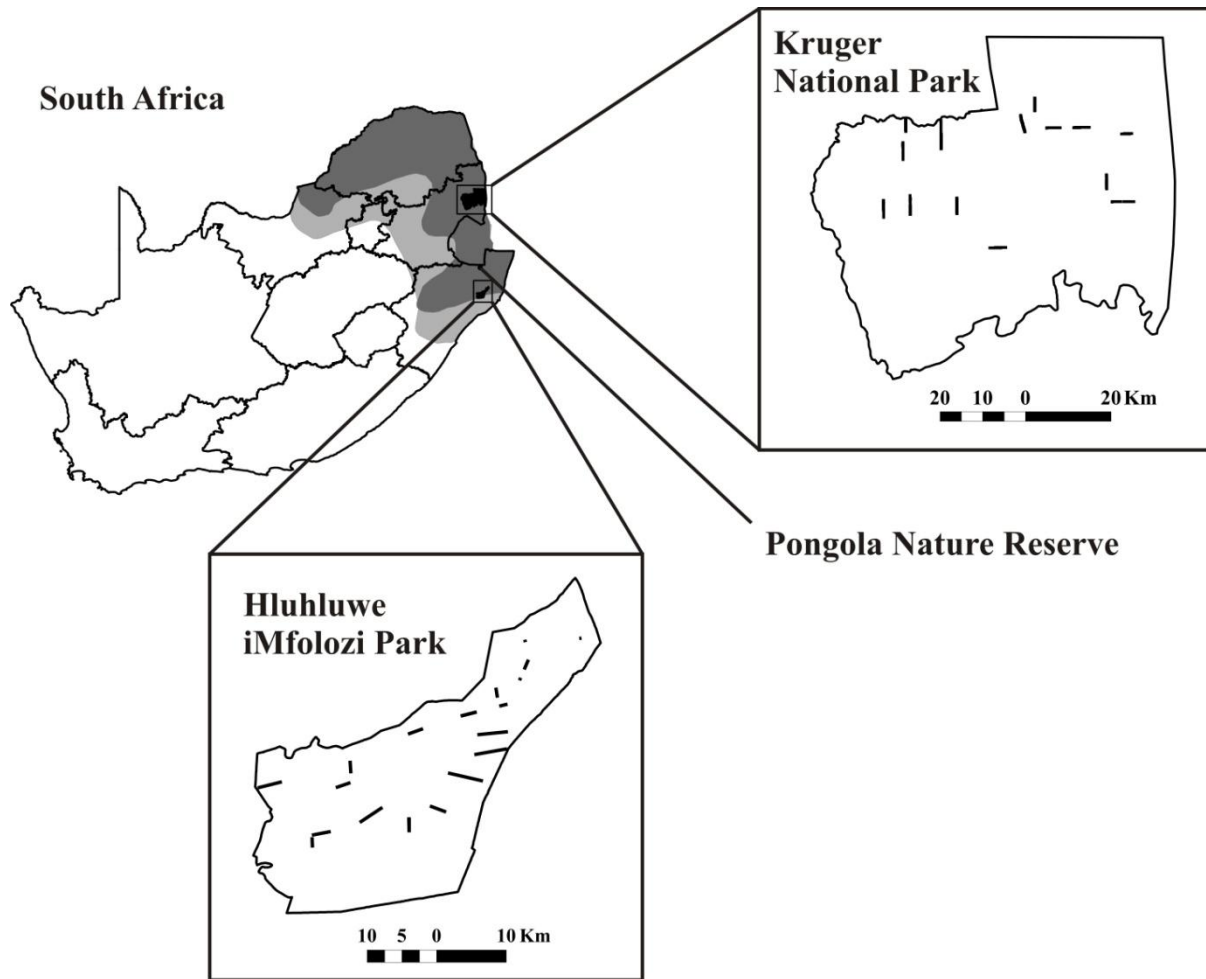


Figure 1. The position of Kruger National Park, Pongola Game Reserve and Hluhluwe-iMfolozi Park in relation to the distribution range of the two study species (Thomas and Grant, 2007), and the locations of transects sampled within each reserve. Dark grey shows the distribution of both species and light grey shows the extended distribution of just *Sclerocarya birrea*.

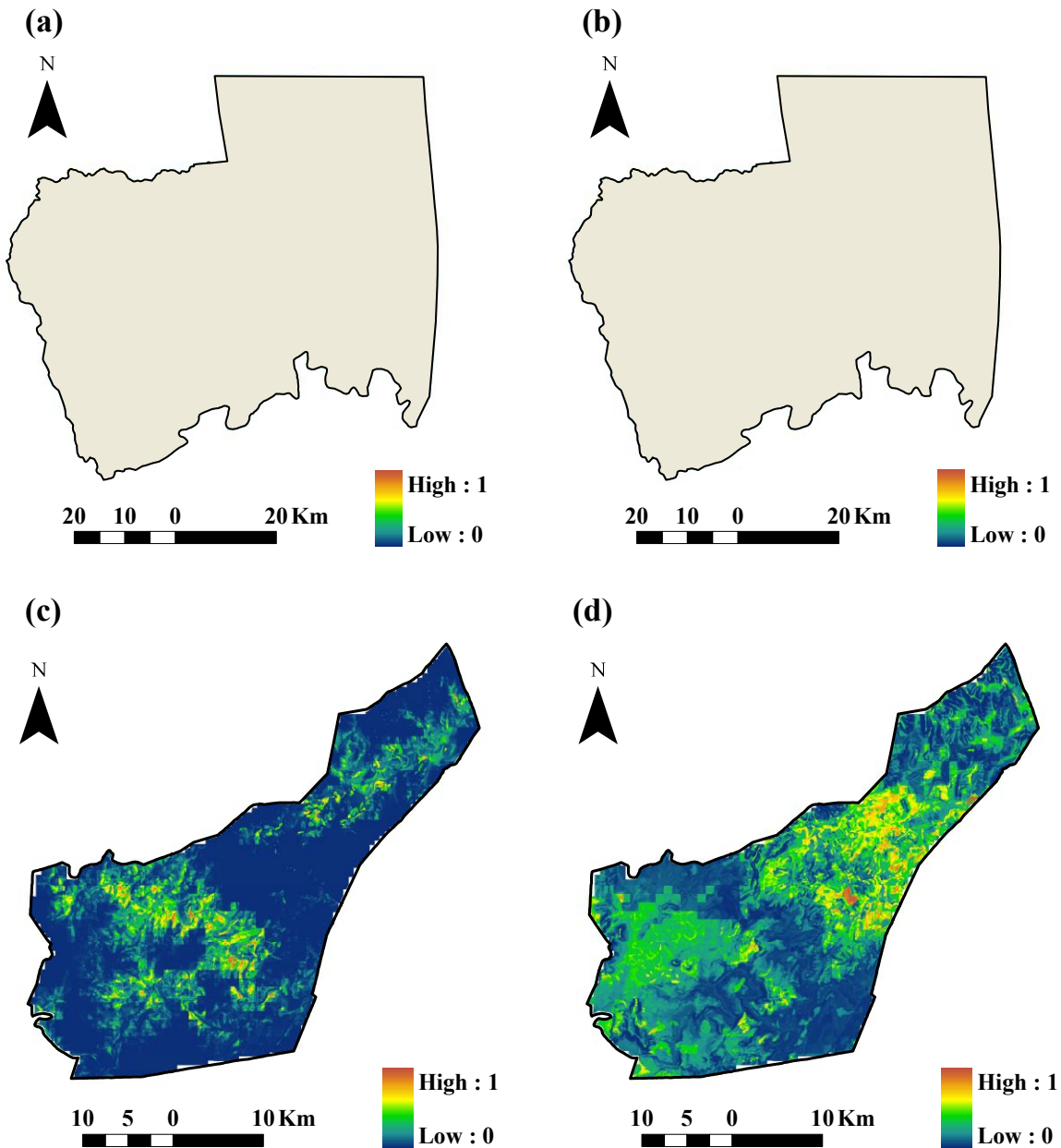


Figure 2. Distribution maps produced by MaxEnt analyses of the predicted location of each species in KNP and HiP. (a) *Acacia nigrescens* in KNP, (b) *Sclerocarya birrea* in KNP, (c) *Acacia nigrescens* in HiP and (d) *Sclerocarya birrea* in HiP. Red shading = areas with a high probability of finding the species; Blue shading = low probability of finding the species.

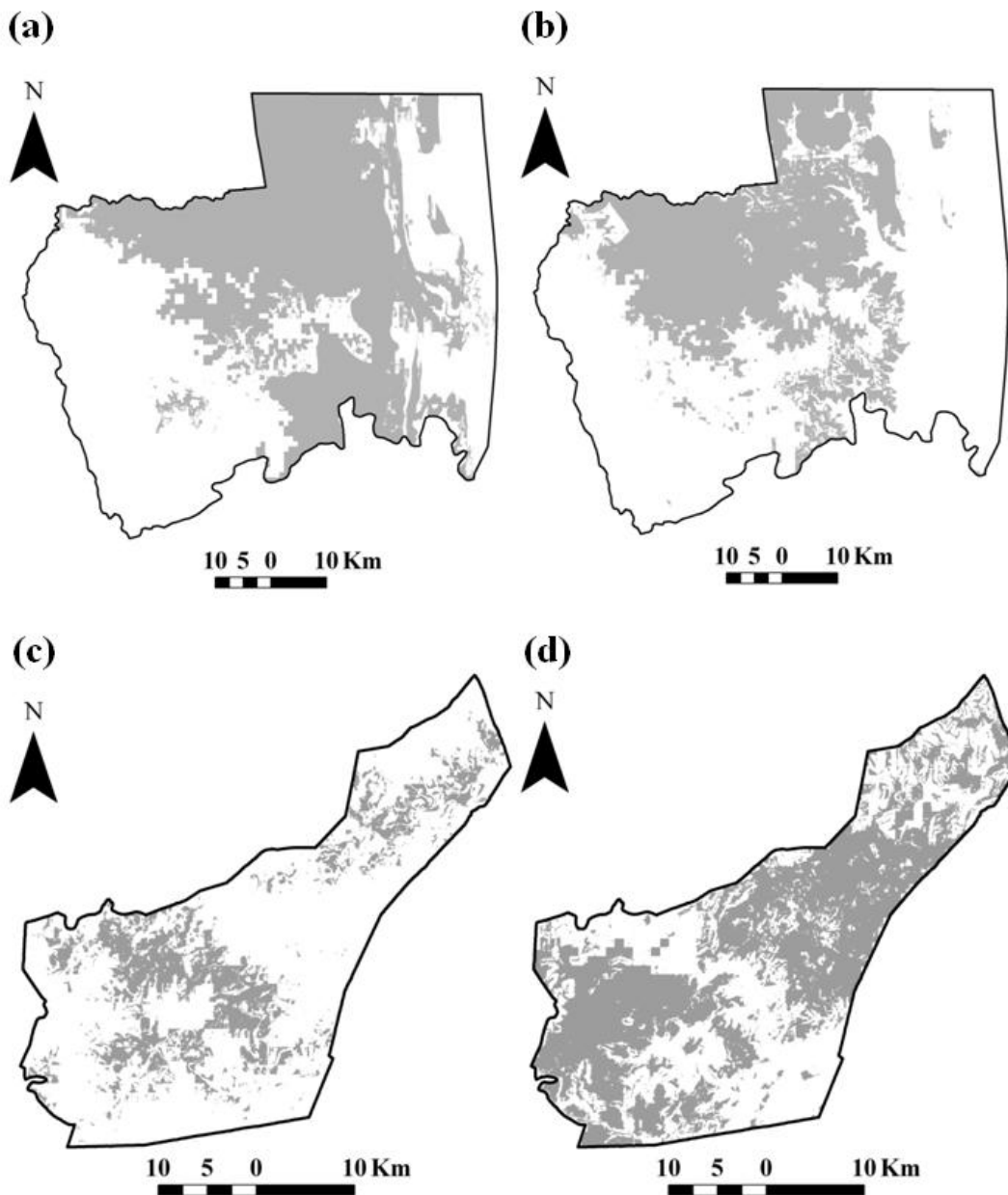


Figure 3. The likely distribution of each species using the 10th percentile threshold for presence and absence. (a) *Acacia nigrescens* in KNP, (b) *Sclerocarya birrea* in KNP, (c) *Acacia nigrescens* in HiP and (d) *Sclerocaryea birrea* in HiP. Grey shading indicates areas which are over the 10th percentile probability, and therefore are considered places in which the species may be present.

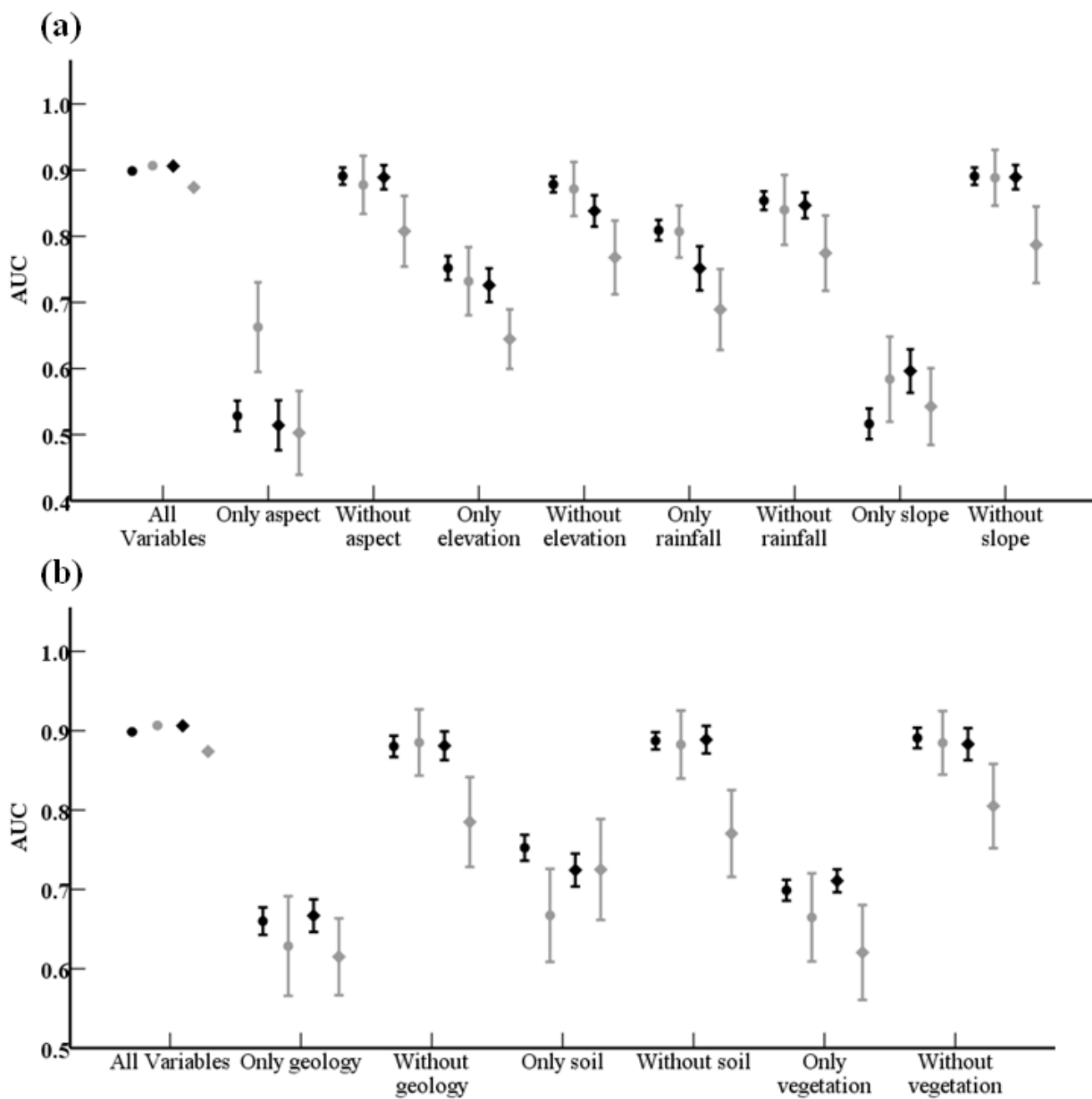


Figure 4. The results from the Jackknife comparisons made between variables used in the MaxEnt analyses conducted for each species. The greater the AUC, the better the model is predicting the distribution of test points using just that variable, in comparison to? the model without that variable and the AUC of the model with all variables. Circles represent *Acacia nigrescens* and diamonds represent *Sclerocarya birrea*, Black represents KNP and Grey represents HiP.

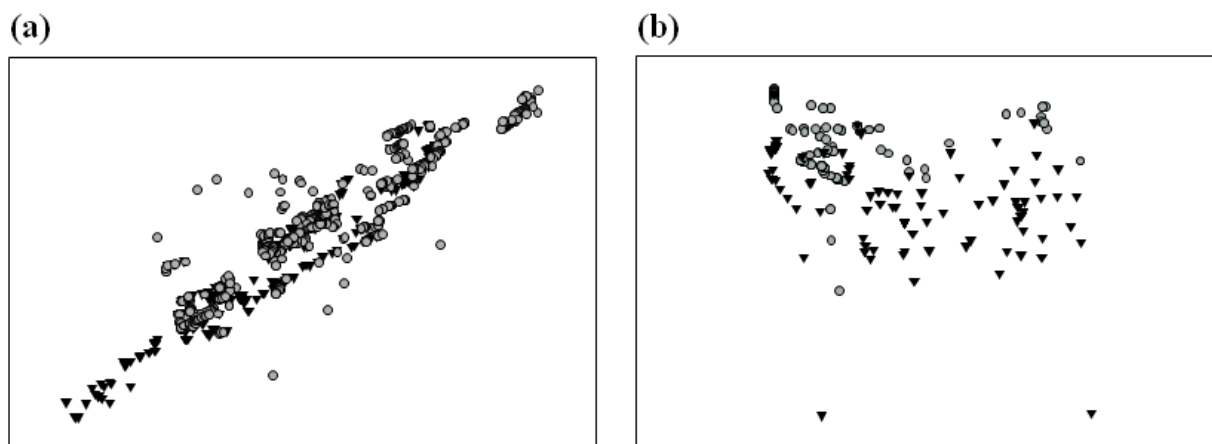


Figure 5. Multi dimensional Scaling plots for (a) KNP and (b) HiP. Circles represent *Acacia nigrescens* and triangles represent *Sclerocarya birrea*. The stress value for KNP was 0.01 and the stress value for HiP was 0.02, indicating that the models fitted the data well. The spread of points for KNP indicated that the points were spread along a single plane with a few *Acacia nigrescens* points lying off this plane, while for HiP, the points were spread in more than one plane and there was more clumping in *Acacia nigrescens* points, with *Sclerocarya birrea* points occurring? below.

Discussion

In HiP, the species occurred separately and in KNP they co-occurred; as confirmed by both the niche models and multi dimensional scaling analyses. The location of the reserves in relation to the overall distribution of the species is likely to be an important factor driving the differences in niches between the reserves. *A. nigrescens* is closer to the edge of its distribution in HiP, while *S. birrea* is still well within its range. In KNP, both species are well within their ranges.

Temperature and climate are likely to be important factors in determining the broad distribution within the reserve, while at a finer scale, geology and soils may play an important role in determining local distributions (Kruckeberg 2002).

In KNP, the soil types on which both species were found were similar to each other. However, *A. nigrescens* was found on Solonchic duplex soil which is not a strongly productive soil for plant growth, and can hinder the growth of grasses and other vegetation (Cairns and Bowser 1977), and *S. birrea* also occurred on smectitic expansive clay soils which have a high clay content. In HiP, there was a split between the soil types each species was found on, since *A. nigrescens*

occurred on sandy loam soils; in particular, shallow newly developed soils, and *S. birrea* occurred on grey clayey soil types. There was a wide overlap in the geology types that each species was found on in KNP. Both species had a higher probability of occurring on southerly facing slopes in KNP. This is due to southern facing slopes in the southern hemisphere being cooler and likely to have a higher soil moisture content than on slopes facing north (Armesto and Martínez 1978). In HiP, the two species were found on slopes facing different directions, but angled towards the north. This might be because the two species are less constrained since there is higher rainfall in HiP than in KNP. The potential importance of moisture on the distribution of both species, in both reserves is indicated by the high AUC when used alone. The overlap of response curves for rainfall in KNP will contribute to the similarity of the species' distribution in KNP. In contrast, in HiP there is a distinct difference in the rainfall response curves for the species, with *A. nigrescens* favoring dryer areas of the reserve.

KNP extends across the core of both species' range within South Africa (Coates-Palgrave and Coates-Palgrave 2002). Although, the distribution of *S. birrea* stretches more southward than HiP (Boon 2010), HiP is near the southern tip of the *A. nigrescens* distribution (Coates-Palgrave and Coates-Palgrave 2002, Boon 2010). As you move south through KwaZulu Natal, the temperature becomes progressively colder, and there is higher rainfall (Schulze 1986). Therefore, at the southern range limit of *A. nigrescens*, at a local scale, the species may favor the dryer, hotter areas of HiP, including the lower altitude, north-facing slopes of the Imfolozi section. Given that *S. birrea*'s distribution stretches the length of HiP and extends further south beyond the HiP boundary, it may not be as constrained as *A. nigrescens*.

To explain the differences in association between the two species in HiP and KNP, we compared the data from PGR with that in these two reserves. The vegetation in PGR is similar to that of southern Kruger (Acocks 1988). Although it is closer to HiP than KNP, PNR is also located further from the edge of the distribution of both species, whereas HiP is close to the edge of *A. nigrescens* distribution (Coates-Palgrave and Coates-Palgrave 2002, Thomas and Grant 2007, Boon 2010). In the 90 km from HiP to PNR, the temperature average remains similar, with an average of 21.5 °C in HiP and 21.7 °C in PNR (Schulze 2008). However, precipitation decreases from 887 mm in HiP to 669 mm in PNR (Zucchini and Nenadić 2006). This suggests that whilst temperature may be an important factor determining the broad scale distribution of these species,

rainfall, in combination with soil type, slope, aspect, and elevation, as the ultimate determinants of soil moisture, determine distribution at the local scale.

Niche models can be used to predict changes in distribution due to climate change (Hijmans and Graham 2006, Keith et al. 2008), and the application of these models to small scale reserves will allow the prediction of local extinctions where efforts are being made to preserve species. Changes in the distribution of these two species can then be predicted using different predictive rainfall maps. In particular, the effect of global warming needs to be taken into consideration in future models (Gottfried et al. 1999). Due to the challenges facing biodiversity conservation, understanding the factors affecting species distribution at broad scales is important for implementing strategies at regional scales (Cowling et al. 2003). However, the implementation of these strategies at ground level will require an understanding of the distributions of species? at finer scales (Pyke et al. 2005). The management strategies at a reserve level need to adapt to changes in environmental conditions in the future. This study shows that a broad scale distribution map of a species (Díaz et al. 1998) may not be the best means to predict distributions at reserve scales, and that over relatively short distances (eg areas covered by PGR and HiP), environmental conditions such as topography can become important factors in predicting species distributions (Clark et al. 1999, Higgins et al. 1999). Ultimately, the location of a specific reserve in relation to the distribution range of a species, in addition to the fine scale topographic differences between reserves; may be important factors in preserving species. Niche modelling facilitates the prediction of which species are likely to be lost from protected areas, allowing an opportunity to implement conservation strategies that do not rely on small protected areas as the only place of refuge for species (Koh and Sodhi 2004).

Acknowledgments

To SANParks and Ezemvelo KZN Wildlife for guarding, accommodation and for access to reserves and data coverage's for each reserve. E. Di Minin assistance with MaxEnt and helping with many GIS related queries. R. Howison for the use of her geology, soil and vegetation maps. Amarula Elephant Research Program and the National Research Foundation (Grant to RS: FA2006032300024) for funding. Dr C. Schoeman for advice. Dr's G. Shannon and D. Druce for data collection in KNP, and P. Tshibase and P. Birkett for assisting in the field in HiP. P. Birkett for manuscript editing.

Appendix

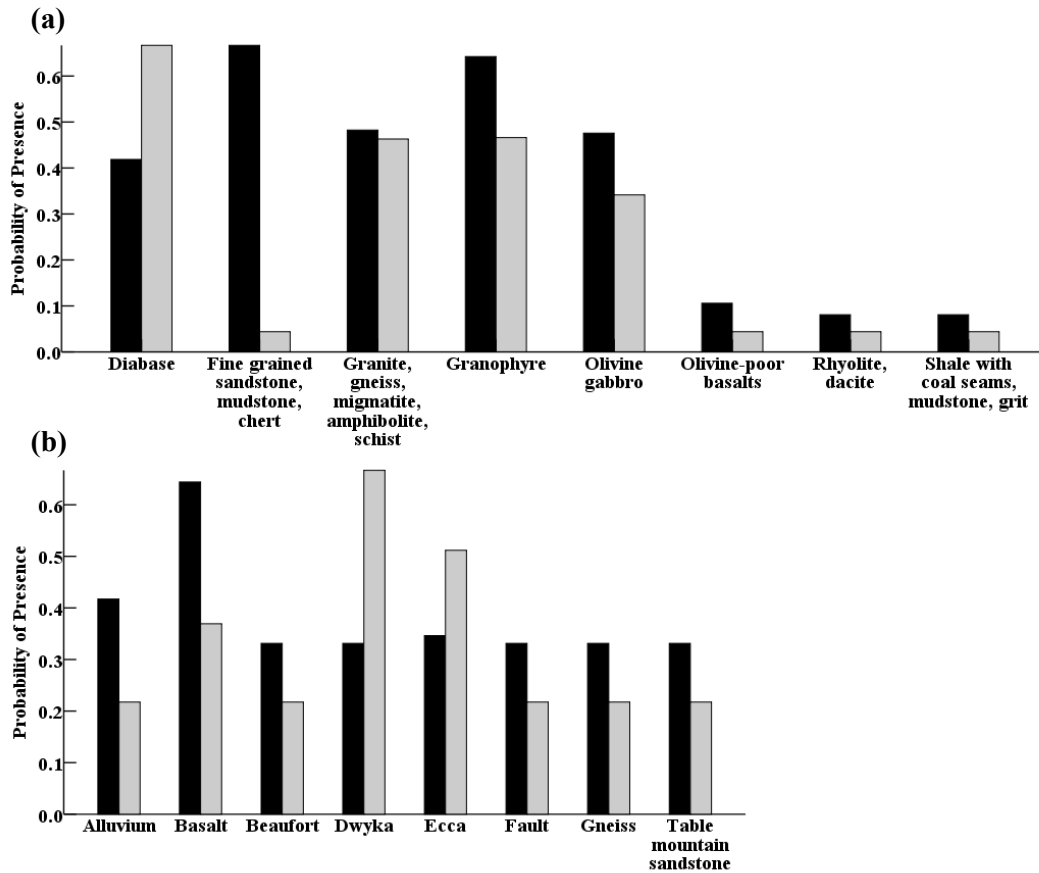


Fig. 1. Response curve created by MaxEnt for geology in both reserves (a) Kruger National Park and (b) Hluhluwe iMfolozi Park. Black columns represent *A. nigrescens* and grey columns, *S. birrea*. The probability of presence indicates the relationship between the presence of the species and the variables in the model.

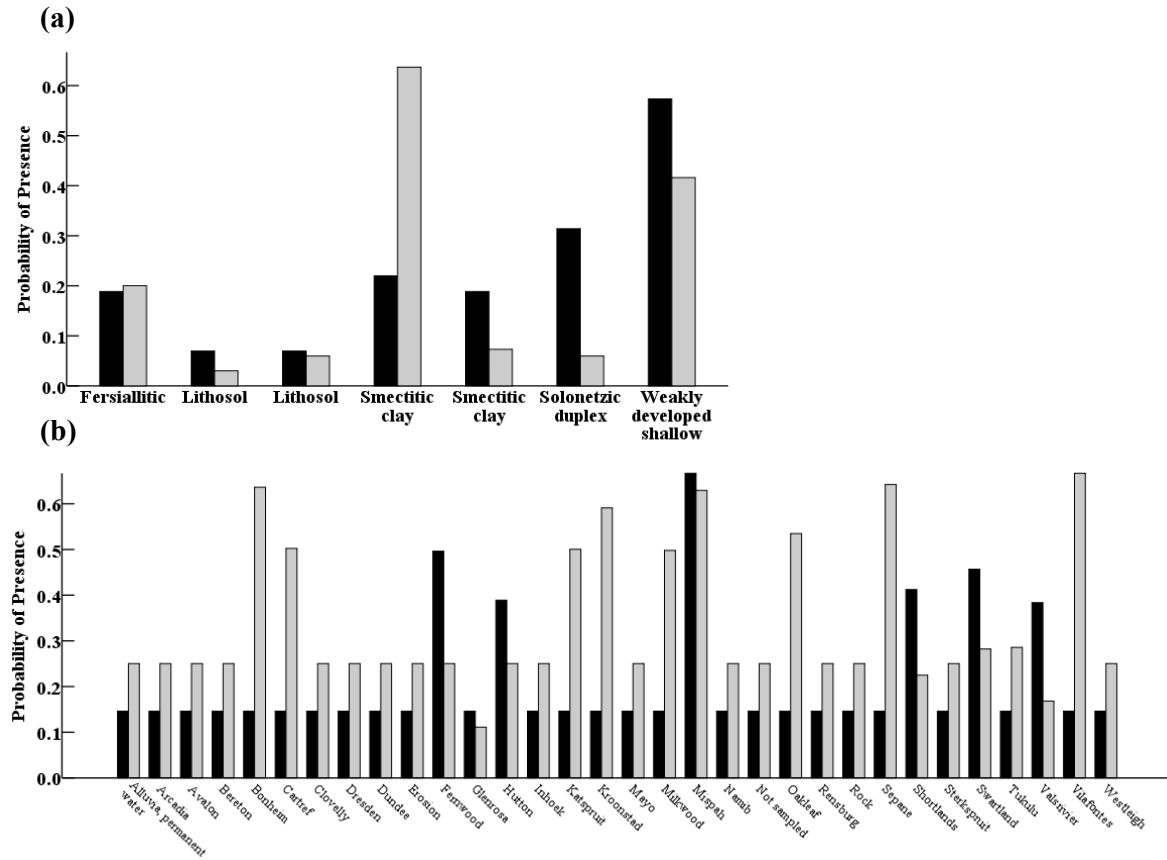


Fig. 2. Response curve created by MaxEnt for soil type in both reserves (a) Kruger National Park and (b) Hluhluwe iMfolozi Park. Black columns represent *A. nigrescens* and grey columns, *S. birrea*. The probability of presence indicates the relationship between the presence of the species and the variables in the model.

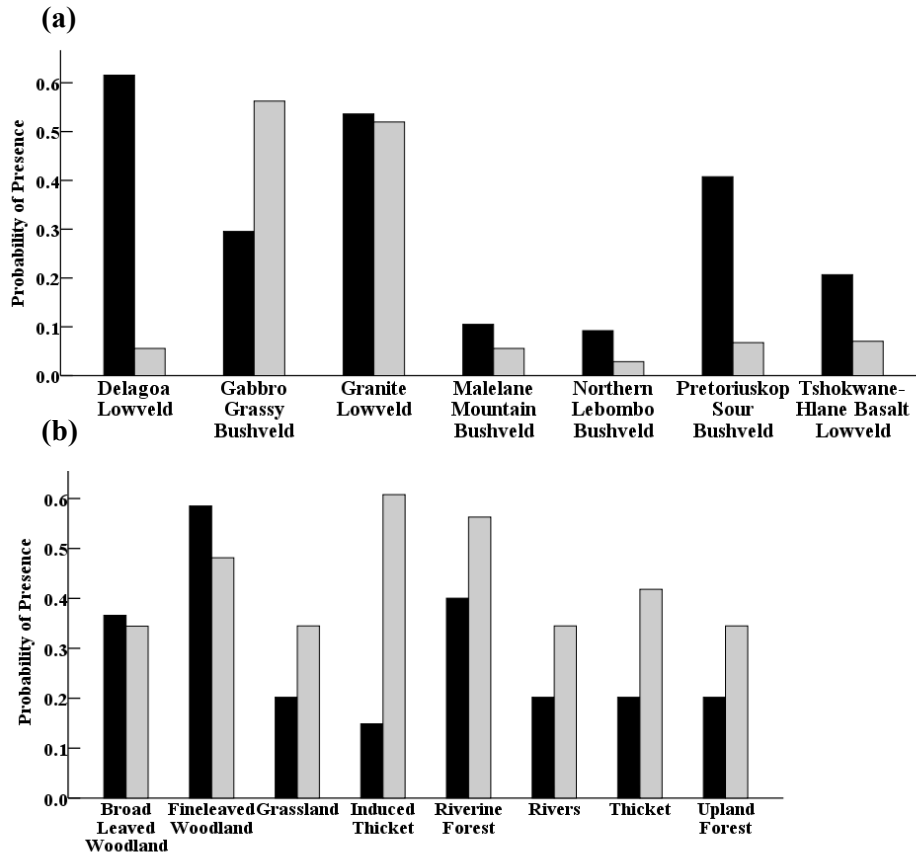


Fig. 3. Response curve created by MaxEnt for vegetation type in both reserves (a) Kruger National Park and (b) Hluhluwe iMfolozi Park. Black columns represent *A. nigrescens* and grey columns, *S. birrea*. The probability of presence indicates the relationship between the presence of the species and the variables in the model.

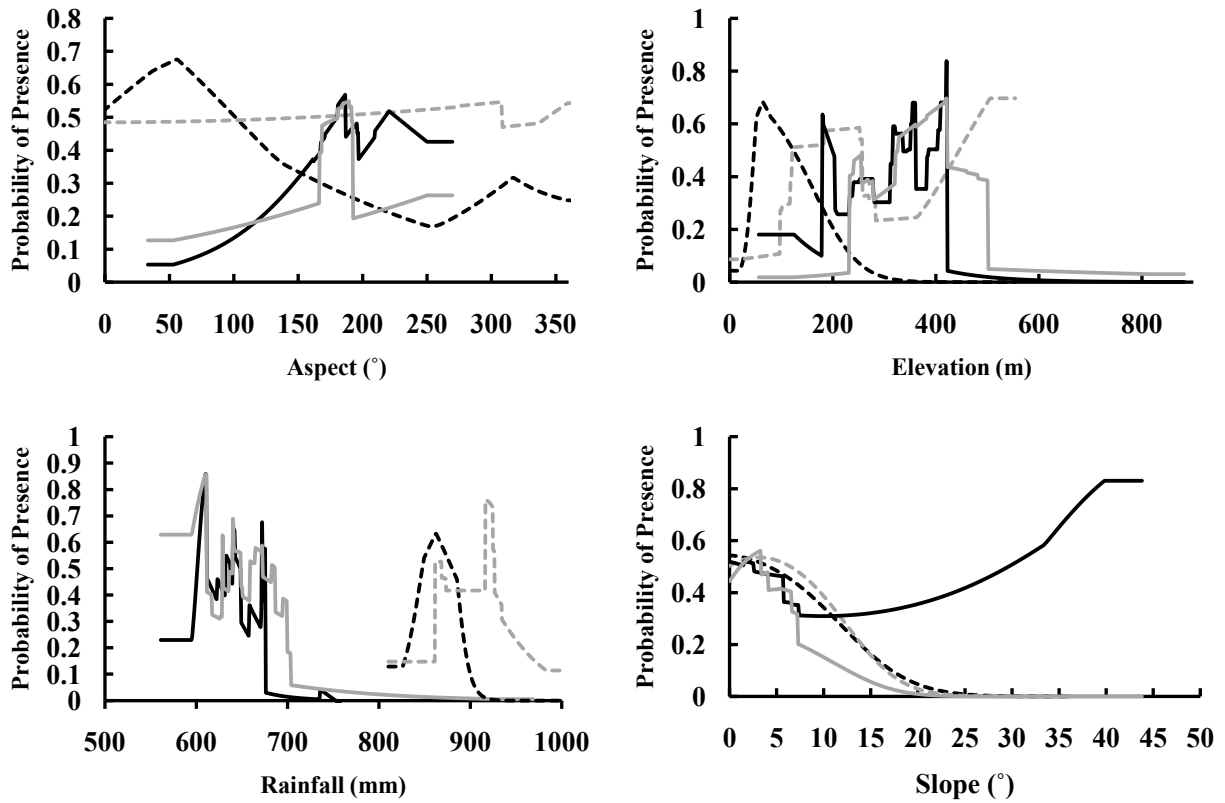


Fig. 4. Response curves created by MaxEnt for categorical variables used in the models. Solid lines represent Kruger National Park and dotted lines, Hluhluwe iMfolozi Park. Black lines represent *A. nigrescens* and grey lines, *S. birrea*. The probability of presence indicates the relationship between the presence of the species and the variables in the model.

Chapter 4

Concluding Chapter

It is essential that models that are used in conservation have firm support by cross validation using data not used in the model (Bart 1995). All ecological models can be criticized as taking into account relatively few variables in systems that are open, and where patterns are governed by large number of interacting effects (Oreskes et al. 1994). It is therefore imperative that the outcomes of models are used with an understanding of the flaws and the inherent weakness in simplifying ecological systems (Edward J 1996). The models in this study were tested using a number of different techniques to corroborate their results. The results of testing showed that these models could be used as they have been applied in the study. But models should be tested against independent data to ensure that results are accurate.

MaxEnt models have been used mainly to look at the distributions of species over larger scales than reserve (Suarez - Seoane et al. 2008, Kumar and Stohlgren 2009, Wang et al. 2010). At large scale it was shown to be a good predictor of species distribution (Elith et al. 2006, Rebelo and Jones 2010). The default settings in MaxEnt were set to determine distributions at large scales (Phillips and Dudík 2008). The use of MaxEnt on as fine a scale as reserve scale needed to be tested, and the results of the MaxEnt model for HiP were tested against existing plot data. The testing indicated that at a fine scale these models can predict the distribution of species, but predicted distribution for species with limited distributions are most accurate. At a fine scale it was shown that the model could also over fit data, to limit the predicted distribution below the true area that the species occupies in the reserve. It is therefore imperative that models are compared to data which can be used to fine tune the models responses.

Niches

When comparing the distributions of both species between KNP and HiP, the MaxEnt models allowed fine scale differences between the two species niches to be shown. The location of the species topographically showed that the two species shared a similar range of elevations in KNP with *S. birrea* being found at slightly higher altitudes than *A. nigrescens*. This is due to their occurring on the hills in the west of the reserve. In HiP there was a difference in the elevations at which each species occurred, with *A. nigrescens* occurring at lower altitudes. These areas are in

Imfolozi, which are hotter and drier. The opposite trend is seen between reserves when looking at the slopes on which the different species were recorded in KNP there was a difference between the species with *A. nigrescens* being on steeper slopes and *S. birrea* being on flatter areas. In HiP, both species are found on flatter areas. In KNP the fine scale soil patterns are dictated by slope. *A. nigrescens* favors Certref, Longlands, Fernwood and Wesbank grey sandy soils of the mid slope while *S. birrea* favors Griffin, Hutton and Clovelly red and yellow sands of the flatter crests (Venter et al. 2003).

There was a wide overlap in the geology types that each species is found on in KNP with the only difference being that *A. nigrescens* was found on metamorphic sandstones and cherts and mudstones, whereas *S. birrea* was found on the Diabase or worn basalts. Soils are an important factor for predicting the distribution of plant species and communities (Venter et al. 2003). The soil maps used in this study for KNP and HiP are at different scales, the map for KNP being at a broader scale than the one for HiP. The fine scale of the soil map for HiP allows the fine scale topographic features, such as where on a slope the soil is positioned, to influence the distribution of soil types. The differences in soil characteristics influence the distribution of species. The soil types both species were found on in KNP were similar to each other, but *A. nigrescens* was found on Solonchic duplex soil which are not strongly productive soils for plant growth and can hinder the growth of grasses and other vegetation (Cairns and Bowser 1977), *S. birrea* also occurred on smectitic expansive clay soils which have a high clay content. In HiP there is a split between the soil types each species is using with *A. nigrescens* being found on sandy loam soils in particular shallow newly developed soils and *S. birrea* being on grey clayey soil types. In Gertenbach's Landscapes of the Kruger Park, he describes type 19 as Dwarf *Acacia nigrescens* Savanna found in the central regions of the reserve, dominated by *A. nigrescens* on the midslopes growing in a dwarfed (2 m – 4 m) state due to the clayey soils retention of water decreasing growth rate (Gertenbach 1983), this could explain the occurrence of *A. nigrescens* on sandy soils in HiP and not the clayey soils or higher rainfall areas that *S. birrea* favour.

Site History and Distribution in HiP

Although it was not considered in this study, in HiP, the distribution of both species may have been influenced by anthropogenic effects. Both species are utilized by people, *A. nigrescens* is used for fence poles and fire wood, while *S. birrea* is used for both the fruit and seeds which are

eaten (Coates-Palgrave and Coates-Palgrave 2002). The utilization of the fruit of *S. birrea* fruit and the use of bark, leaves and the wood of the tree by rural people is an incentive for people to plant or maintain *S. birrea* trees close to homesteads and fields (Shackleton *et al.* 2002). People introduced fire, to which both species are sensitive (Enslin *et al.* 2008), to reduce woody cover and promote the growth of grass rather than trees (Bond *et al.* 2005). Fires, combined with the destructive use of *A. nigrescens* by people, will mean that near rural settlements *A. nigrescens* is more likely to be scarce. The Hluhluwe and Imfolozi sections were proclaimed in 1895, both reserves being managed separately. The corridor between these reserves, was previously used and managed by rural people, was proclaimed in 1989, and the three components integrated (Charlton-Perkins and Harpe 1995). For this reason, the absence of *A. nigrescens* in the corridor section and the relatively high predicted density of *S. birrea* in the corridor section may be due to the previous management of the land, as well as climatic and topographic variables as predicted by the model. There was also a reduction in the number of ungulate species in the reserve which caused a change in the vegetation in the reserve towards more open woodlands (Thomson 1986).

Conservation Applications

A large number of studies have assessed increasing elephant numbers on tree decline across southern Africa (Coetzee *et al.* 1979, Ben-Shahar 1998, Calenge *et al.* 2002, Gadd 2002, Edkins *et al.* 2007). These studies cite the removal of large trees in particular as a concern. This is due to the manner in which elephant feed, being particularly destructive in terms of tree pollarding and pushing trees over, resulting in the death of trees (Jacobs and Biggs 2002a, Vanak *et al.* 2011). Previous methods for the control of elephant impacts on vegetation was the implementation of culling to reduce the elephant population in a reserve to below carrying capacity to prevent overutilization (Barnes 1983). For this reason the monitoring of large trees is becoming of important in setting the thresholds of concern for large trees, and for monitoring to ensure their conservation within reserves (Druce *et al.* 2008).

Although elephant are responsible for large proportions of large tree mortality in *S. birrea* (Helm *et al.* 2009), the structure of the populations in many reserves shows a skewed demographic (Jacobs and Biggs 2002b). The distribution of height classes have large trees present but few smaller individuals found, this indicates the presence of these large trees has interaction effects between recruitment and mortality in particularly in smaller height classes (Lewis 1987). Fire is

a major factor controlling the recruitment of large trees into savanna systems (Sharam et al. 2006, Mourik et al. 2007). The use of fire as a savanna structure manipulator by humans in southern Africa predates its use in conservation areas, during which time it was used to improve the grazing potential of savannas (Dublin et al. 1990). A fire management policy within reserves could be implemented in such a way as to make the recruitment of large trees and the filling of the “missing” height classes to ensure large trees are replaced in the environment (Van Wilgen et al. 1998). Knowing where recruitment can occur, by using niche models can help guide these decisions.

Herbivory is important factor controlling vegetation structure and assemblages (Peel et al. 2005). In particular the growth of elephant populations in reserves is of concern to managers (Coetzee et al. 1979, Ben-Shahar 1993, Dominy et al. 1998, Shannon et al. 2008). The practice of culling of elephant was practiced to control their numbers in reserves and mitigate impacts on the vegetation in reserves (Van Aarde et al. 1999). This was practiced until these methods were brought into question and culling of elephants was banned (Van Aarde et al. 1999). Revised methods of culling elephants in Kruger take the heterogeneity of different impacted environments into account and rather than focus on across the board culling the reserve is split into sections with different strategies including botanical reserves in which elephant numbers are reduced (Whyte et al. 1999). Culling of elephants can also combined with culling of smaller herbivores to reduce the numbers of smaller browsers and mixed feeders that impact on the recruitment of large trees (Levick and Rogers 2008). The third method to control the distribution of herbivores would be to control water sources a major controller of animal distributions (Brits et al. 2002, Chamaille-Jammes 2007, Shannon et al. 2009). The planning of botanical reserves, culling and water points can all be influenced by knowing where in the environment large trees can be established, which can be illustrated by niche modelling of current locations of large trees.

There are strong links between the use of niche models and the predictions of changes in species distribution due to changes in climate (Midgley et al. 2002, Beaumont et al. 2005, Hijmans and Graham 2006). By using models that predict changes in rainfall and temperature due to climate change, the distribution changes of these trees can be predicted. These models can be used to determine which species are likely to be poorly protected from extinction, and to assess new

areas in which reserves can be created (Araújo et al. 2004). Current models are at scales larger than the reserve scale, and look at changes in distribution at a broad scale (Beaumont et al. 2005, Hole et al. 2009). Extinction risk due to predicted range reduction can be assessed (Midgley et al. 2002). Predicted changes at these scales can be inaccurate due to coarse grid sizes (Seo et al. 2009). These fine scale models of the distribution of large trees, could be combined with an envelope modelling approach to make predictions of the likelihood of the parks conserving the species.

Modelling species distributions changes with climate envelopes at fine scales such as those in the study are likely to have relatively poor predictive capabilities if conducted in isolation. In a study by Beale et al. (Beale et al. 2008), which looked at distributions predicted for a number of birds in Europe. Beale et al. showed that there was poor fit between the climate envelope models and the actual distribution of species. This result was then challenged by Araújo et al. (Araújo et al. 2009) who showed that if the data use was broadened to include a wider number of occurrence data, the predictions were more likely to be correct. The contradicting results of these two studies will indicate a likely problem when attempting to use climate change models at a fine scale. Fine scale models are likely not to be representative of the full tolerances of the species, if response curves for only current distribution in the reserve are used to predict distribution change.

Fine scale niche models can be used to assess the factors which limit distributions. By using both fine and broad scale models the determinants of a species distribution can be assessed in more detail. Predicted distribution maps were created for both species using a continent wide database of locations stored in a Conservatoire et Jardin botaniques & South African National Biodiversity Institute database (Fig. 1). These maps were comparable with current distribution maps for each species, but the predicted distribution projected further south than the current distribution of either species. By considering the results of studies in HiP and KNP it could be deduced that the reasons for this may be that the climate model does not take into account all interactions between species and the landscape. Factors such as soil types and geology which were included in the fine scale model are not included in this broad scale environmental envelope model.

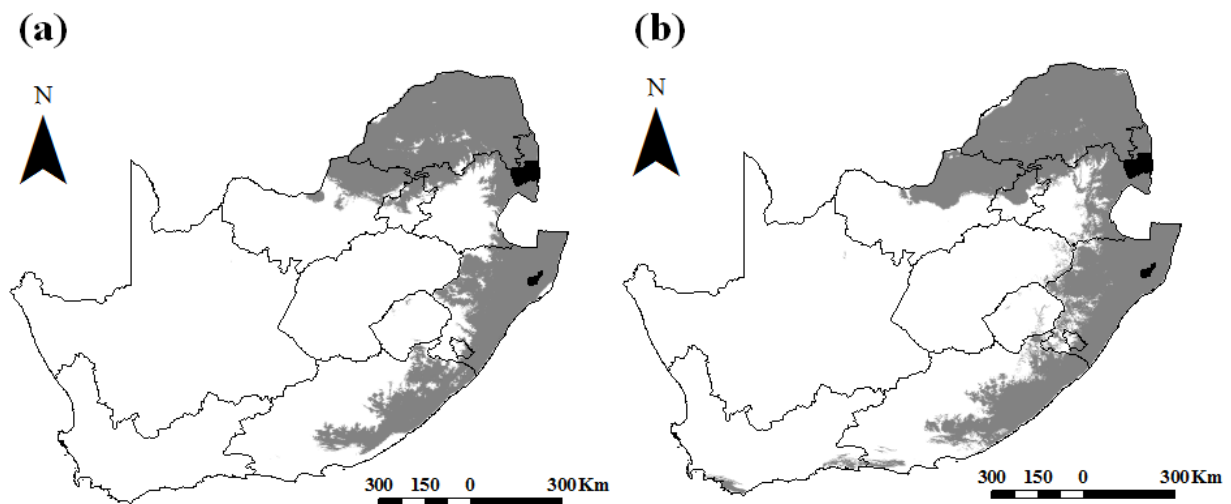


Fig. 1. Distribution maps created by niche modelling the location points recorded in the Conservatoire et Jardin botaniques & South African National Biodiversity Institute database for each species. These models used the 30 second resolution Bioclim Database as environmental layers. (a). *A. nigrescens* (b). *S. birrea*. The grey areas show the areas the species would be present in when using the 10th percentile threshold of presence.

Continued Scope for Research

The limitations of these simple interaction models, used in this study are that they only take into account one aspect of niches, which are the potential niche of each species. This is important in determining where recruitment may be occurring, but vegetation communities are also controlled by the interactions of species. The physical habitat restricted by the interactions between species will dictate the realized niche of the species (Soberon and Peterson. 2005). Using both a niche method and the vegetation plots may allow the interactions between large tree species as communities to be determined. By modelling a number of species, calculating the niche overlap, determining possible community assemblages and testing for these species assemblages in the plot data. If the assemblages of species with high overlap do not occur then this may be an indication of competition between these species.

There is also the possibility of using niche modelling to predict where elephant impacts are likely to be high in the reserves. These data were collected during field work. There are recorded locations of specific types and amounts of impact by elephants on trees. These predictions can be tested using the plot data once more. If the model does not predict well the plot data can be included in the model and it can be re-run. These areas of high predicted probability can be combined with the predictions of tree niches to determine which species are likely to be most affected by elephant impacts and mortality in particular. These species are therefore the ones which management strategies should pay the most attention to when elephant management strategies are being formulated.

Another approach could also be to determine the factors affecting the distribution of a number of species in each reserve using the Akaike information criterion (AIC) approach and Generalized Linear models (GLMs) (Austin, 2002). The results of the GLMs can be used to create distribution maps. These results could be compared to those using MaxEnt in HiP and using the plot data to calculate the Kappa statistic and other indicators for the predictive power of each model. This comparison has been done between model approaches (Tsoar *et al.* 2005), but not at small spatial scales such as in this study. Using GLMs allow different models to be constructed, and models could be created which can test the responses of the species to specific climatic changes in the reserve. Using location points collected over a continent wide scale such as those in the Conservatoire et Jardin botaniques & South African National Biodiversity Institute database, the wide scale environmental tolerance of each species can be calculated. These climatic tolerance models could then be used to determine possible distribution changes in the reserve. By using predictive models which aim to predict climatic changes during the current trends of Global warming, the persistence of the species can be predicted. Species have four different responses to Climate change these are; tolerance, habitat shift, migration and extinction (Dawson *et al.* 2011). Climate envelope models will predict the changes due to migration and extinction as species are constrained by climate envelopes in which they are adapted. The responses to changes in climate which will add to the variability in the accuracy of envelope models when predicting species distribution are, tolerance and habitat shift, these responses will result in changes which are not predicted by current climate envelope models.

Conclusion

This study has shown that niche models can predict the distribution of species at fine scales. The results from tests in HiP show that the models are most accurate at predicting the distribution of the most restricted species. These models can therefore be used to predict the distribution of species within reserves. Rare species are often the ones which management plans are most influenced by and therefore knowing their locations can inform the management plans used to conserve them. By looking at the factors controlling the two species within HiP and KNP it can be seen that the factors which are likely to control the regional distribution of the species can be determined if the reserves fall within and near the edge of the species total distribution. The factor limiting the distribution of *A. nigrescens* in HiP was rainfall which is associated with the change in elevation across the reserve. This trend in rainfall limiting *A. nigrescens* in HiP may be the reason for the southern tip of distribution of the species. By comparing the distributions in the distributions of the species in these two reserves possible factors controlling their overall distribution can be determined.

References

- Van Aarde, R., I. Whyte, and S. Pimm. 1999. Culling and the dynamics of the Kruger National Park African elephant population. *Animal Conservation* **2**:287-294.
- Abrams, P. 1980. Some Comments on Measuring Niche Overlap. *Ecology* **61**:44-49.
- Acocks, J. P. H. 1988. *Veld Types of South Africa* 3rd edn. Botanical Research Institute, Pretoria.
- Allouche, O., A. Tsoar, and R. Kadmon. 2006. Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). *Journal of Applied Ecology* **43**:1223-1232.
- Araújo, M. B., M. Cabeza, W. Thuiller, L. Hannah, and P. H. Williams. 2004. Would climate change drive species out of reserves? An assessment of existing reserve-selection methods. *Global Change Biology* **10**:1618-1626.
- Araújo, M. B., W. Thuiller, and N. G. Yoccoz. 2009. Reopening the climate envelope reveals macroscale associations with climate in European birds. *Proceedings of the National Academy of Sciences* **106**:E45-E46.
- Armesto, J. J. and J. A. Martínez. 1978. Relations between vegetation structure and slope aspect in the mediterranean region of Chile. *Journal of Ecology* **66**:881-889.
- Austin, M. P. and J. A. Meyers. 1996. Current approaches to modelling the environmental niche of eucalypts: implication for management of forest biodiversity. *Forest Ecology and Management* **85**:95-106.
- Austin, M. P. 2002. Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. *Ecological Modelling* **157**:101-118.
- Balfour, D. A. 2003. *Acacia demography, fire and elephants in a South African savanna*. University of Cape Town, Cape Town.
- Barnes, R. F. W. 1983. Effects of elephant browsing on woodlands in a Tanzanian National Park: measurements, models and management. *Journal of Applied Ecology* **20**:521-539.
- Bart, J. 1995. Acceptance criteria for using individual-based models to make management decisions. *Ecological Applications* **5**:411-420.
- Bauer, H. L. 1936. Moisture relations in the chaparral of the Santa Monica Mountains, California. *Ecological Monographs* **6**:409-454.

- Baxter, P. W. J. and W. M. Getz. 2005. A Model-Framed evaluation of elephant effects on tree and fire dynamics in African savannas. *Ecological Applications* **15**:1331–1341.
- Beale, C. M., J. J. Lennon, and A. Gimona. 2008. Opening the climate envelope reveals no macroscale associations with climate in European birds. *Proceedings of the National Academy of Sciences* **105**:14908-14912.
- Beaumont, L. J., L. Hughes, and M. Poulsen. 2005. Predicting species distributions: use of climatic parameters in BIOCLIM and its impact on predictions of species' current and future distributions. *Ecological Modelling* **186**:251-270.
- Beekman, J. H. and H. H. T. Prins. 1989. Feeding strategies of sedentary large herbivores in East Africa, with emphasis on the African buffalo, *Syncerus coffer*. *African Journal of Ecology* **27**:129-147.
- Belsky, A. J. 1994. Influences of trees on savanna productivity: tests of shade, nutrients, and tree-grass competition. *Ecology* **75**:922-932.
- Ben-Shahar, R. 1991. Abundance of trees and grasses in a woodland savanna in relation to environmental factors. *Journal of Vegetation Science* **2**:345.
- Ben-Shahar, R. 1993. Patterns of elephant damage to vegetation in northern Botswana. *Biological Conservation* **65**:249-256.
- Ben-Shahar, R. 1998. Changes in structure of savanna woodlands in Northern Botswana following the impacts of elephants and fire. *Plant Ecology* **136**:189-194.
- Benito, B. M., M. M. Martínez-Ortega, L. M. Muñoz, J. Lorite, and J. Peñas. 2009. Assessing extinction-risk of endangered plants using species distribution models: a case study of habitat depletion caused by the spread of greenhouses *Biodiversity and Conservation* **18**:2509-2520.
- Biggs, H. C., R. Slotow, B. Scholes, J. Carruthers, R. van Aarde, G. Kerley, W. Twine, D. Grobler, H. Bertschinger, R. Grant, H. Lötter, J. Bignaut, L. Hopkinson, and M. Peel. 2008. Towards integrated decision-making for elephant management. Pages 537-586 in R. Scholes and K. Mennell, editors. *Assessment of South African Elephant Management*. Witwatersrand University Press, Johannesburg.
- Bond, W. J. and S. Archibald. 2003. Confronting complexity: fire policy choices in South African savanna parks. *International Journal of Wildland Fire* **12**:381 - 389.

- Bond, W. J. and G. F. Midgley. 2000. A proposed CO²-controlled mechanism of woody plant invasion in grasslands and savannas. *Global Change Biology* **6**:865-869.
- Bond, W. J., K.-A. Smythe, and D. A. Balfour. 2001. Acacia species turnover in space and time in an African savanna. *Journal of Biogeography* **28**:117-128.
- Bond, W. J., F. I. Woodward, and G. F. Midgley. 2005. The global distribution of ecosystems in a world without fire. *New Phytologist* **165**:525-538.
- Boon, R. 2010. *Pooley's Trees of Eastern South Africa*. Flora and Fauna Trust, Pinetown.
- Boundja, R. P. and J. J. Midgley. 2010. Patterns of elephant impact on woody plants in the Hluhluwe-Imfolozi park, Kwazulu-Natal, South Africa. *African Journal of Ecology* **48**:206-214.
- Brits, J., M. W. Van Rooyen, and N. Van Rooyen. 2002. Ecological impact of large herbivores on the woody vegetation at selected watering points on the eastern basaltic soils in the Kruger National Park. *African Journal of Ecology* **40**:53-60.
- Brotons, L., W. Thuiller, M. B. Araújo, and A. H. Hirzel. 2004. Presence-absence versus presence-only modelling methods for predicting bird habitat suitability. *Ecography* **27**:437-448.
- Bugmann, H. K. M. 1996. A simplified forest model to study species composition along Climate gradients. *Ecology* **77**:2055-2074.
- Cairns, R. R. and W. E. Bowser. 1977. *Solonchic soils and their management*. Agriculture Canada : obtainable from Information Division, Canada Dept. of Agriculture (Ottawa)
- Calenge, C., D. Maillard, J.-M. Gaillard, L. Merlot, and R. Peltier. 2002. Elephant damage to trees of wooded savanna in Zakouma National Park, Chad. *Journal of Tropical Ecology* **18**:599-614.
- Chamaille-Jammes, S. 2007. Managing heterogeneity in elephant distribution : interactions between elephant population density and surface - water availability. *Journal of Applied Ecology* **44**:625-633.
- Charlton-Perkins, W. and R. D. Harpe. 1995. *Hluhluwe-Umfolozi Park*. Struik.
- Clark, D. B., M. W. Palmer, and D. A. Clark. 1999. Edaphic factors and the landscape-scale distributions of tropical rain forest trees. *Ecology* **80**:2662-2675.
- Clarke, K. and R. Gorley. 2006. *PRIMER v6: User Manual/Tutorial*. PRIMER-E, Plymouth.

- Coates-Palgrave, K. and M. Coates-Palgrave. 2002. *Trees of Southern Africa*. 3 edition. Struik, South Africa.
- Coetzee, B. J., A. H. Engelbrecht, S. C. J. Joubert, and P. F. Retief. 1979. Elephant impact on *Sclerocarya Caffra* trees in *Acacia Nigrescens* tropical plains Thornveld of the Kruger National Park. *Koedoe* **22**:39-60
- Costa, G., C. Nogueira, R. Machado, and G. Colli. 2010. Sampling bias and the use of ecological niche modeling in conservation planning: a field evaluation in a biodiversity hotspot. *Biodiversity and Conservation* **19**:883-899.
- Costa, J., A. T. Peterson, and C. B. Beard. 2002. Ecologic niche modeling and differentiation of populations of *Triatoma brasiliensis* neiva, 1911, the most important Chagas' disease vector in northeastern Brazil (hemiptera, reduviidae, triatominae). *The American Journal of Tropical Medicine and Hygiene* **67**:516-520.
- Cowling, R. M., R. L. Pressey, M. Rouget, and A. T. Lombard. 2003. A conservation plan for a global biodiversity hotspot—the Cape Floristic Region, South Africa. *Biological Conservation* **112**:191-216.
- Cumming, D. H. M., M. B. Fenton, I. L. Rautenbach, R. D. Taylor, G. S. Cumming, M. S. Cumming, J. M. Dunlop, G. S. Ford, M. D. Hovorka, D. S. Johnston, M. C. Kalcounis, Z. Mahlanga, and C. V. Portfors. 1997. Elephants, woodlands and biodiversity in southern Africa. *South African Journal of Science* **93**:231-236.
- Darwin, C. 1859. *The origin of species by means of natural selection or the preservation of favored races in the struggle for life*. Murray, London.
- Dawson, T. P., S. T. Jackson, J. I. House, I. C. Prentice, and G. M. Mace. 2011. Beyond predictions: biodiversity conservation in a changing climate. *Science* **332**:53-58.
- Dean, W. R. J., S. J. Milton, and F. Jeltsch. 1999. Large trees, fertile islands, and birds in arid savanna. *Journal of Arid Environments* **41**:61-78.
- Diamond, J. 1975. *Assembly of species communities*. Harvard University Press, Cambridge, Massachusetts, USA.
- Díaz, S., M. Cabido, and F. Casanoves. 1998. Plant functional traits and environmental filters at a regional scale. *Journal of Vegetation Science* **9**:113-122.
- Dobbertin, M. 2005. Tree growth as indicator of tree vitality and of tree reaction to environmental stress: a review. *European Journal of Forest Research* **124**:319-333.

- Dominy, N. J., N. S. Ferguson, and A. Maddock. 1998. Modelling elephant (*Loxodonta africana*) population growth in Hluhluwe-Umfolozi Park to predict and manage limits. *South African Journal of Wildlife Research* **28**:61.
- Druce, D. J., G. Shannon, B. R. Page, R. Grant, and R. Slotow. 2008. Ecological thresholds in the savanna landscape: developing a protocol for monitoring the change in composition and utilisation of large trees. *Plos One* **3**:e3979.
- Du Puy, D. J. and J. Moat. 1996. A refined classification of the primary vegetation of Madagascar based on the underlying geology : using GIS to map its distribution and to assess its conservation status. W. R. Lourenço, editor. *Biogéographie de Madagascar = Biogeography of Madagascar*. ORSTOM, Paris. 205-218
- Dublin, H. T., A. R. E. Sinclair, and J. McGlade. 1990. Elephants and fire as causes of multiple stable states in the serengeti-mara woodlands. *The Journal of Animal Ecology* **59**:1147-1164.
- Dudík, M. 2007. Maximum entropy density estimation with generalized regularization and an application to species distribution modeling. *Journal of Machine Learning Research* **8**:1217.
- Dunn, R. R. 2000. Isolated trees as foci of diversity in active and fallow fields. *Biological Conservation* **95**:317-321.
- Eckhardt, H. C., B. W. Van Wilgen, and H. C. Biggs. 2000. Trends in woody vegetation cover in the Kruger National Park, South Africa, between 1940 and 1998. *East African Wild Life Society, Africa Journal of Ecology* **38**:108–115.
- Edkins, M. T., L. M. Kruger, K. Harris, and J. J. Midgley. 2007. Baobabs and elephants in Kruger National Park: nowhere to hide. *African Journal of Ecology* **46**:119–125.
- Edward J, R., Jr. 1996. Testing ecological models: the meaning of validation. *Ecological Modelling* **90**:229-244.
- Elith, J., C. H. Graham, R. P. Anderson, M. Dudík, S. Ferrier, A. Guisan, R. J. Hijmans, F. Huettmann, J. R. Leathwick, A. Lehmann, L. Jin, L. G. Lohmann, B. A. Loiselle, G. Manion, C. Moritz, M. Nakamura, Y. Nakazawa, J. McC. Overton, A. T. Peterson, and S. J. Phillips. 2006. Novel methods improve prediction of species distributions from occurrence data. *Ecography* **29**:129-151.

- Elith, J. and J. R. Leathwick. 2009. Species distribution models: ecological explanation and prediction across space and time. *Ecology, Evolution, and Systematics* **40**:677-697.
- Enslin, B. W., A. L. F. Potgieter, H. C. Biggs, and R. Biggs. 2008. Long term effects of fire frequency and season on the woody vegetation dynamics of the *Sclerocarya birrea*/*Acacia nigrescens* savanna of the Kruger National Park. *Koedoe - African Protected Area Conservation and Science*; **43**, .
- Erasmus, B. F. N., M. Kshatriya, M. W. Mansell, S. L. Chown, and A. S. V. Jaarsveld. 2000. A modelling approach to antlion (Neuroptera: Myrmeleontidae) distribution patterns. Entomological Society of Southern Africa, Pretoria, Afrique Du Sud.
- Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics* **34**:487-515.
- Field, R., B. A. Hawkins, H. V. Cornell, D. J. Currie, J. A. F. Diniz-Filho, J.-F. Guégan, D. M. Kaufman, J. T. Kerr, G. G. Mittelbach, T. Oberdorff, E. M. O'Brien, and J. R. G. Turner. 2009. Spatial species-richness gradients across scales: a meta-analysis. *Journal of Biogeography* **36**:132-147.
- Fielding, A. H. and J. F. Bell. 1997. A review of methods for the assessment of prediction errors in conservation presence / absence models. *Environmental Conservation* **24**:38.
- Fornara, D. A. and J. T. D. Toit. 2007. Browsing lawns? responses of *Acacia nigrescens* to ungulate browsing in an african savanna. *Ecology* **88**:200-209.
- Franklin, J. F. 1993. Preserving biodiversity: species, ecosystems, or landscapes? *Ecological Applications* **3**:202-205.
- Gadd, M. E. 2002. The impact of elephants on the marula tree *Sclerocarya birrea*. *African Journal of Ecology* **40**:328-336.
- Galindo-Gonzalez, J., S. Guevara, and V. J. Sosa. 2000. Bat- and bird-generated seed rains at isolated trees in pastures in a tropical rainforest. *Conservation Biology* **14**:1693-1703.
- Gaston, K. J. 1991. How large is a species' geographic range? *Oikos* **61**:434-438.
- Gaston, K. J. 1994. Measuring geographic range sizes. *Ecography* **17**:198-205.
- Gertenbach, W. P. D. 1983. Landscapes of the Kruger National Park. *Koedoe* **26**:9 - 121.
- Gillson, L. and K. I. Duffin. 2007. Thresholds of potential concern as benchmarks in the management of African savannahs. *Philosophical transactions - Royal Society. Biological sciences* **362**:27-37

- Giovanelli, J., C. Haddad, and J. Alexandrino. 2008. Predicting the potential distribution of the alien invasive American bullfrog (*Lithobates catesbeianus*) in Brazil. *Biological Invasions* **10**:585-590.
- Godown, M. E. and A. T. Peterson. 2000. Preliminary distributional analysis of US endangered bird species. *Biodiversity and Conservation* **9**:1313-1322.
- Gordon, I. J., J. H. Alison, and M. Festa-Bianchet. 2004. The management of wild large herbivores to meet economic, conservation and environmental objectives. *Journal of Applied Ecology* **41**:1021-1031.
- Gottfried, M., H. Pauli, K. Reiter, and G. Grabherr. 1999. A fine-scaled predictive model for changes in species distribution patterns of high mountain plants induced by climate warming. *Diversity and Distributions* **5**:241-251.
- Grace, J. 2009. Plant Water Relations. Pages 28-50 *Plant Ecology*. Blackwell Publishing Ltd.
- Greene, D. F. and E. A. Johnson. 1994. Estimating the mean annual seed production of trees. *Ecology* **75**:642-647.
- Grinnell, J. 1917a. Field tests of theories concerning distributional control. *The American Naturalist* **51**:115-128.
- Grinnell, J. 1917b. The Niche-Relationships of the California Thrasher. *The Auk* **34**:427-433.
- Grinnell, J. 1924. Geography and Evolution. *Ecology* **5**:225-229.
- Guisan, A., J.-P. Theurillat, and F. Kienast. 1998. Predicting the potential distribution of plant species in an alpine environment. *Journal of Vegetation Science* **9**:65-74.
- Guisan, A. and N. E. Zimmermann. 2000. Predictive habitat distribution models in ecology. *Ecological Modelling* **135**:147-186.
- Harcombe, P. A. 1987. Tree Life Tables. *BioScience* **37**:557-568.
- Helm, C., G. Wilson, J. Midgley, L. Kruger, and E. T. F. Witkowski. 2011. Investigating the vulnerability of an African savanna tree (*Sclerocarya birrea ssp. caffra*) to fire and herbivory. *Austral Ecology* **36**: 964–973.
- Helm, C. V., E. T. F. Witkowski, L. Kruger, M. Hofmeyr, and N. Owen-Smith. 2009. Mortality and utilisation of *Sclerocarya birrea subsp. Caffra* between 2001 and 2008 in the Kruger National Park, South Africa. *South African Journal of Botany* **75**:475-484.
- Higgins, S. I., W. J. Bond, E. C. February, A. Bronn, D. I. W. Euston-Brown, B. Enslin, N. Govender, L. Rademan, S. O'Regan, A. L. F. Potgieter, S. Simon, R. Sowry, L. Trollope,

- and S. W. T. Winston. 2007. Effects of four decades of fire manipulation on woody vegetation structure in savanna. *Ecology* **88**:1119-1125.
- Higgins, S. I., D. M. Richardson, R. M. Cowling, and T. H. Trinder-Smith. 1999. Predicting the landscape-scale distribution of alien plants and their threat to plant diversity. *Conservation Biology* **13**:303-313.
- Hijmans, R. J., S. E. Cameron, J. L. Parra, P. G. Jones, and A. Jarvis. 2005. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* **25**:1965 - 1978.
- Hijmans, R. J. and C. H. Graham. 2006. The ability of climate envelope models to predict the effect of climate change on species distributions. *Global Change Biology* **12**:2272-2281.
- Hirzel, A. H., J. Hausser, D. Chessel, and N. Perrin. 2002. Ecological - niche factor analysis : how to compute habitat - suitability maps without absence data. *Ecology* **83**:2027.
- Hobbs, R. J. and L. F. Huenneke. 1992. Disturbance, diversity, and invasion: implications for Conservation. *Conservation Biology* **6**:324-337.
- Högberg, P. and D. J. Read. 2006. Towards a more plant physiological perspective on soil ecology. *Trends in Ecology & Evolution* **21**:548-554.
- Hole, D. G., S. G. Willis, D. J. Pain, L. D. Fishpool, S. H. M. Butchart, Y. C. Collingham, C. Rahbek, and B. Huntley. 2009. Projected impacts of climate change on a continent-wide protected area network. *Ecology Letters* **12**:420-431.
- Howison, R. A. 2009. Food preferences and feeding interactin smong browsers and the effect of an exotic invasive weed *Chromolaena odorata* on the endangered black rhino (*Diceros Bicornis*), in an African Savanna. University of KwaZulu-Natal, Durban.
- Hutchinson, G. E. 1957. Concluding remarks. Pages 415 - 457 in Cold Spring Harbor Symposium on Quantitative Biology.
- Hutchinson, G. E. 1959. Homage to Santa Rosalia or why are there so many kinds of animals? *The American Naturalist* **93**:145-159
- Jacobs, O. S. and R. Biggs. 2002a. The Impact of African elephant on marula trees in the Kruger National Park. *South African Journal of Wildlife Research* **32**:13-22.
- Jacobs, O. S. and R. Biggs. 2002b. The status and population structure of the marula in the Kruger National Park. *South African Journal of Wildlife Research* **32**:1-12.

- Jaynes, E. T. 1957. Information theory and statistical mechanics. *The Physical Review* **106**:620-630.
- John, R., J. W. Dalling, K. E. Harms, J. B. Yavitt, R. F. Stallard, M. Mirabello, S. P. Hubbell, R. Valencia, H. Navarrete, M. Vallejo, and R. B. Foster. 2007. Soil nutrients influence spatial distributions of tropical tree species. *Proceedings of the National Academy of Sciences* **104**:864-869.
- Jorge, M. L., V. Alberto Jimenez, and R. Raimundo. 2008. AUC : a misleading measure of the performance of predictive distribution models. *Global Ecology and Biogeography* **17**:145-151.
- Keith, D. A., H. R. Akçakaya, W. Thuiller, G. F. Midgley, R. G. Pearson, S. J. Phillips, H. M. Regan, M. B. Araújo, and T. G. Rebelo. 2008. Predicting extinction risks under climate change: coupling stochastic population models with dynamic bioclimatic habitat models. *Biology Letters* **4**:560-563.
- Kenkel, N. C. and L. Orloci. 1986. Applying metric and nonmetric multidimensional scaling to ecological studies: some new results. *Ecology* **67**:919-928.
- Koh, L. P. and N. S. Sodhi. 2004. Importance of reserves, fragments, and parks for butterfly conservation in a tropical urban landscape. *Ecological Applications* **14**:1695-1708.
- Kraus, J. 1997. Counting furtive beasts by computer. *Communications of the Acm* **40**:20.
- Kruckeberg, A. R. 2002. *Geology And Plant Life: The effects of landforms and rock types on plants*. University of Washington Pr, Washington.
- Kumar, S. and T. Stohlgren. 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.
- Levick, S. and K. Rogers. 2008. Patch and species specific responses of savanna woody vegetation to browser exclusion. *Biological Conservation* **141**:489-498.
- Lewis, D. M. 1987. Fruiting patterns, seed germination, and distribution of *Sclerocarya caffra* in an elephant-inhabited woodland. *Biotropica* **19**:50-56.
- Liu, C., P. M. Berry, T. P. Dawson, and R. G. Pearson. 2005. Selecting thresholds of occurrence in the prediction of species distributions. *Ecography* **28**:385-393.

- Lombard, A. T., C. F. Johnson, R. M. Cowling, and R. L. Pressey. 2001. Protecting plants from elephants: botanical reserve scenarios within the Addo Elephant National Park, South Africa. *Biological Conservation* **102**:191–203.
- Ludwig, F., H. d. Kroon, F. Berendse, and H. H. T. Prins. 2004. The influence of savanna trees on nutrient, water and light availability and the understorey vegetation. *Plant Ecology* **170**:93–105.
- MacArthur, R. H. 1972. *Geographical Ecology: Patterns in the distribution of species*. Princeton University Press, Princeton New Jersey.
- Mackey, R. L., B. R. Page, K. J. Duffy, and R. Slotow. 2006. Modelling elephant population growth in small, fenced, South African reserves. *South African Journal of Wildlife Research* **36**:33-43
- Manning, A. D., J. Fischer, and D. B. Lindenmayer. 2006. Scattered trees are keystone structures – Implications for conservation. *Biological Conservation* **132**:311–321.
- Margules, C. R. and R. L. Pressey. 2000. Systematic conservation planning. *Nature* **405**:243-253.
- Midgley, G. F., L. Hannah, D. Millar, M. C. Rutherford, and L. W. Powrie. 2002. Assessing the vulnerability of species richness to anthropogenic climate change in a biodiversity hotspot. *Global Ecology and Biogeography* **11**:445-451.
- Midgley, G. F., L. Hannah, D. Millar, W. Thuiller, and A. Booth. 2003. Developing regional and species-level assessments of climate change impacts on biodiversity in the Cape Floristic Region. *Biological Conservation* **112**:87-97.
- Moe, S. R., L. P. Rutina, H. Hytteborn, and J. T. Du Toit. 2009. What controls woodland regeneration after elephants have killed the big trees? *Journal of Applied Ecology* **46**:223-230.
- Moffett, A., N. Shackelford, and S. Sarkar. 2007. Malaria in Africa : vector species niche models and relative risk maps. *Plos One* **2**.
- Monadjem, A., P. J. Taylor, F. P. D. Cotterill, and C. Schoeman. 2010. *Bats of Southern and Central Africa: A Biogeographic and Taxonomic Synthesis*. Wits University Press, Wits University South Africa.
- Mourik, A. A., F. v. Langevelde, E. v. Telling, I. M. A. Heitkönig, and I. Gaigher. 2007. Stability of wooded patches in a South African nutrient-poor grassland: do nutrients, fire or herbivores limit their expansion? *Journal of Tropical Ecology* **23**:529–537.

- Mucina, L. and M. C. Rutherford. 2006. The vegetation of South Africa, Lesotho and Swaziland. South African Biodiversity Institute, Pretoria.
- Murray-Smith, C., N. A. Brummit, A. T. Oliviera-Filho, S. Bachman, J. Moat, E. M. N. Lughadha, and E. J. Lucas. 2008. Plant Diversity Hotspots in the Atlantic Coastal Forests of Brazil. *Conservation Biology* **23**:151–163.
- Myers, N., R. A. Mittermeier, C. G. Mittermeier, G. A. B. da Fonseca, and J. Kent. 2000. Biodiversity hotspots for conservation priorities. *Nature* **403**:853-858.
- Newbold, T. 2010. Applications and limitations of museum data for conservation and ecology, with particular attention to species distribution models. *Progress in Physical Geography* **34**:3-22.
- O'Connor, T. G., P. S. Goodman, and B. Clegga. 2007. A functional hypothesis of the threat of local extirpation of woody plant species by elephant in Africa. *Biological Conservation* **136**:329-345.
- Oreskes, N., K. Shrader-Frechette, and K. Belitz. 1994. Verification, validation, and confirmation of numerical models in the earth sciences. *Science* **263**:641-646.
- Parrish, J. D., D. P. Braun, and R. S. Unnasch. 2003. Are we conserving what we say we are? Measuring ecological integrity within protected areas. *BioScience* **53**:851-860.
- Peel, M. J. S., J. M. Kruger, and P. J. K. Zacharias. 2005. Environmental and management determinants of vegetation state on protected areas in the eastern Lowveld of South Africa. *African Journal of Ecology* **43**:352-361.
- Peterson, A. T. 2001. Predicting species' geographic distributions based on ecological niche modeling. *The Condor* **103**:599-605.
- Peterson, A. T. 2006. Uses and requirements of ecological niche models and related distributional models. **3**:59-72
- Peterson, A. T., M. Papes, and D. A. Kluza. 2003. Predicting the potential invasive distributions of four alien plant species in North America. *Weed Science* **51**:863-868.
- Peterson, A. T. and D. A. Vieglais. 2001. Predicting Species invasions using ecological niche modeling: new approaches from bioinformatics attack a pressing problem. *BioScience* **51**:363-371.
- Phillips, S. 2006. A Brief Tutorial on Maxent AT&T Research, www.cs.princeton.edu/~schapire/maxent/tutorial/tutorial.doc.

- Phillips, S. J., R. P. Anderson, and R. E. Schapire. 2006. Maximum entropy modeling of species geographic distributions. *Ecological Modelling* **190**:231–259.
- Phillips, S. J. and M. Dudík. 2008. Modeling of species distributions with Maxent : new extensions and a comprehensive evaluation. *Ecography* **31**:161-175.
- Phillips, S. J., M. Dudík, and R. E. Schapire. 2004. A maximum entropy approach to species distribution modeling. Proceedings of the twenty-first international conference on Machine learning. ACM, Banff, Alberta, Canada.
- Primack, R. B. 2010. *Essentials of Conservation Biology*. Sinauer Associates, Massachusetts, USA.
- Pulliam, H. R. 2000. On the relationship between niche and distribution. *Ecology Letters* **3**:349.
- Pyke, C. R., S. J. Andelman, and G. Midgley. 2005. Identifying priority areas for bioclimatic representation under climate change: a case study for Proteaceae in the Cape Floristic Region, South Africa. *Biological Conservation* **125**:1-9.
- Raes, N., M. C. Roos, J. W. F. Slik, E. E. Van Loon, and H. t. Steege. 2009. Botanical richness and endemism patterns of Borneo derived from species distribution models. *Ecography* **32**:180-192.
- Rahbek, C. 2005. The role of spatial scale and the perception of large-scale species-richness patterns. *Ecology Letters* **8**:224-239.
- Rahbek, C. and G. R. Graves. 2001. Multiscale assessment of patterns of avian species richness. *Proceedings of the National Academy of Sciences* **98**:4534-4539.
- Raman, T. R. S., G. S. Rawat, and A. J. T. Johnsingh. 1998. Recovery of tropical rainforest avifauna in relation to vegetation succession following shifting cultivation in Mizoram, north-east India. *Journal of Applied Ecology* **35**:214-231.
- Rebelo, H. and G. Jones. 2010. Ground validation of presence-only modelling with rare species: a case study on *barbastelles* *Barbastella barbastellus* (Chiroptera: Vespertilionidae). *Journal of Applied Ecology* **47**:410-420.
- Rempel, R. S., A. R. Rodgers, and K. F. Abraham. 1995. Performance of a GPS animal Location system under boreal forest canopy. *The Journal of Wildlife Management* **59**:543-551.
- Resources, International Union for Conservation of Nature and Natural. 2001. *IUCN Red List Categories and Criteria Version 3.1*. Information Press, Oxford, UK, The NatureBureau, Newbury, UK.

- Roche, C. 2006. Breeding records and nest site preference of Hooded Vultures in the greater Kruger National Park. *Ostrich* **77**:99-101.
- Samraat Pawar, Michelle S. Koo, Chris Kelley, M. Firoz Ahmed, Sujoy Chaudhurid, and S. Sarkar. 2007. Conservation assessment and prioritization of areas in Northeast India : priorities for amphibians and reptiles. *Biological Conservation* **136**:346–361.
- Sankaran, M., N. P. Hanan, R. J. Scholes, J. Ratnam, D. J. Augustine, B. S. Cade, J. Gignoux, S. I. Higgins, X. Le Roux, F. Ludwig, J. Ardo, F. Banyikwa, A. Bronn, G. Bucini, K. K. Caylor, M. B. Coughenour, A. Diouf, W. Ekaya, C. J. Feral, E. C. February, P. G. H. Frost, P. Hiernaux, H. Hrabar, K. L. Metzger, H. H. T. Prins, S. Ringrose, W. Sea, J. Tews, J. Worden, and N. Zambatis. 2005. Determinants of woody cover in African savannas. *Nature* **438**:846-849.
- Sankaran, M., J. Ratnam, and N. Hanan. 2008. Woody cover in African savannas: the role of resources, fire and herbivory. *Global Ecology and Biogeography* **17**:236-245.
- Scholes, R. J. and S. R. Archer. 1997. Tree-Grass Interactions in Savannas. *Annual Review of Ecology, Evolution, and Systematics* **28**:517–544.
- Schulze, B. R. 1986. *Climate of South Africa part 8 general survey*. 6 edition. Weather Burea, Pretoria.
- Schulze, R. E. 2008. *South African atlas of climatology and agrohydrology*. South Africa. Water Research Commission., Pretoria.
- Seaman, D. E. and R. A. Powell. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. *Ecology* **77**:2075-2085.
- Seo, C., J. H. Thorne, L. Hannah, and W. Thuiller. 2009. Scale effects in species distribution models: implications for conservation planning under climate change. *Biology Letters* **5**:39-43.
- Shackleton, C. M. and R. J. Scholes. 2000. Impact of fire frequency on woody community structure and soil nutrients in the Kruger National Park. *Koedoe* **43**:75-81.
- Shackleton, C. M. and R. J. Scholes. 2008. Impact of fire frequency on woody community structure and soil nutrients in the Kruger National Park. *Koedoe* **43**:75-81.
- Shackleton, S., C. Shackleton, T. Cunningham, C. Lombard, C. Sullivan, and T. Netshiluvhi. 2002. Knowledge on *Sclerocarya birrea subsp. caffra* with emphasis on its importance as

- a non-timber forest product in South and southern Africa: a summary. Part 1: Taxonomy, ecology and role in rural livelihoods. *Southern African Forestry Journal* **194**:27-40.
- Shafer, C. L. 1995. Values and Shortcomings of Small Reserves. *BioScience* **45**:80-88.
- Shannon, G., D. J. Druce, B. R. Page, H. C. Eckhardt, R. Grant, and R. Slotow. 2008. The utilization of large savanna trees by elephant in southern Kruger National Park. *Journal of Tropical Ecology* **24**:281-289.
- Shannon, G., W. S. Matthews, B. R. Page, G. E. Parker, and R. J. Smith. 2009. The affects of artificial water availability on large herbivore ranging patterns in savanna habitats: a new approach based on modelling elephant path distributions. *Diversity and Distributions* **15**:776-783.
- Shannon, G., B. Page, R. Slotow, and K. Duffy. 2006. African elephant home range and habitat selection in Pongola Game Reserve, South Africa. *African Zoology* **41**:37-44.
- Shannon, G., M. Thaker, A. Vanak, B. Page, R. Grant, and R. Slotow. 2011. Relative Impacts of Elephant and Fire on Large Trees in a Savanna Ecosystem. *Ecosystems* **14**:1372-1381.
- Sharam, G., A. R. E. Sinclair, and R. Turkington. 2006. Establishment of broad-leaved thickets in Serengeti, Tanzania: The influence of fire, browsers, grass competition, and elephants. *Biotropica* **35**:599–605.
- Simberloff, D. S. and L. G. Abele. 1976. Island biogeography theory and conservation Practice. *science* **191**:285-286.
- Skempton, A. W. 1953. Soil mechanics in relation to geology. *Proceedings of the Yorkshire Geological Society* **29**:33-62.
- Soberon, J. and A. T. Peterson. 2005. Interpretation of Models of Fundamental Ecological Niches and Species Distributional Areas. University of Kansas, Informatics Biodiversity Research Center. **2**:1-10
- Spinage, C. A. and F. E. Guinness. 1971. Tree survival in the absence of elephants in the Akagera National Park, Rwanda. *Journal of Applied Ecology* **8**:723-728.
- Steven I. Higgins, William J. Bond, and W. S. W. Trollope. 2000. Fire, resprouting and variability : a recipe for grass - tree coexistence in savanna. *Journal of Ecology* **88**:213.
- Suarez - Seoane, S., E. L. Garcia de la Morena, M. B. Morales Prieto, P. E. Osborne, and E. de Juana. 2008. Maximum entropy niche - based modelling of seasonal changes in little bustard (*Tetrax tetrax*) distribution. *Ecological Modelling* **219**:17-29.

- Tews, J., U. Brose, V. Grimm, K. Tielbörger, M. C. Wichmann, M. Schwager, and F. Jeltsch. 2004. Animal species diversity driven by habitat heterogeneity / diversity : the importance of keystone structures. *Journal of Biogeography* **31**:79–92.
- Thomas, V. and R. Grant. 2007. *SAPPI Tree Spotting: Lowveld*. Jacana, Johannesburg.
- Thomson, R. 1986. *On Wildlife "Conservation"*. United Publishers International, South Africa.
- Thrash, I. 1998. Impact of water provision on herbaceous vegetation in Kruger National Park, South Africa. *Journal of Arid Environments* **38**:437–450.
- Tilman, D., R. M. May, C. L. Lehman, and M. A. Nowak. 1994. Habitat destruction and the extinction debt. *Nature* **371**:65-66.
- Trethowan, P. D., M. P. Robertson, and A. J. McConnachie. 2010. Ecological niche modelling of an invasive alien plant and its potential biological control agents. *South African Journal of Botany* **77**:137-146.
- Treydte, A. C., I. M. A. Heitkonig, H. H. T. Prins, and F. Ludwig. 2007. Trees improve grass quality for herbivores in African savannas. *Perspectives in Plant Ecology, Evolution and Systematics* **8**:197–205.
- Tsoar, A., O. Allouche, O. Steinitz, D. Rotem, and R. Kadmon. 2007. A comparative evaluation of presence-only methods for modelling species distribution. *Diversity and Distributions* **13**:397-405.
- Turner, I. M. 1996. Species Loss in Fragments of Tropical Rain Forest: A Review of the Evidence. *Journal of Applied Ecology* **33**:200-209.
- van Langevelde, F., C. A. D. M. van de Vijver, L. Kumar, J. v. d. Koppel, N. de Ridder, J. van Andel, A. K. Skidmore, J. W. Hearne, L. Stroosnijder, W. J. Bond, H. H. T. Prins, and M. Rietkerk. 2003. Effects of Fire and Herbivory on the Stability of Savanna Ecosystems. *Ecology* **84**:337-350.
- Vanak, A. T., G. Shannon, M. Thaker, B. Page, R. Grant, and R. Slotow. 2011. Biocomplexity in large tree mortality: interactions between elephant, fire and landscape in an African savanna. *Ecography*:no-no.
- Vandermeer, J. H. 1972. Niche Theory. *Annual Review of Ecology and Systematics* **3**:107-132.
- Veloz, S. D. 2009. Spatially autocorrelated sampling falsely inflates measures of accuracy for presence-only niche models. *Journal of Biogeography* **36**:2290-2299.

- Venter, F. J. 1982. Schematic soil map of Kruger National Park. National Parks Board. Unpublished, Skukuza, South Africa.
- Venter, F. J., R. J. Scholes, and H. C. Eckhardt. 2003. The abiotic template and its associated vegetation pattern. Pages 83-129 in J. T. du Toit, K. H. Rogers, and H. C. Biggs, editors. *The Kruger Experience*. Island Press, Washington.
- Wang, X. Y., X. L. Huang, L. Y. Jiang, and G. X. Qiao. 2010. Predicting potential distribution of chestnut phylloxerid (Hemiptera: Phylloxeridae) based on GARP and Maxent ecological niche models. *Journal of Applied Entomology* **134**:45-54.
- Warren, D. L., R. E. Glor, and M. Turelli. 2008. Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. *Evolution* **62**:2868-2883.
- Warren, D. L., R. E. Glor, and M. Turelli. 2010. ENMTools: a toolbox for comparative studies of environmental niche models. *Ecography* **33**:607-611.
- Whately, A. and R. Porter. 1983. Woody vegetation communities of Hluhluwe-Umfolozi-Corridor Game Reserve Complex. *Bothalia* **14**:745 – 758.
- Whyte, I. J., R. J. Van Aarde, and S. L. Pimm. 2003. Kruger's elephant population: its size and consequences for ecosystem heterogeneity. Pages 332-348 in J. D. Toit, H. Biggs, and K. H. Rogers, editors. *The Kruger experience: ecology and management of savanna heterogeneity*. Island Press, Washington.
- Whyte, I. J., H. C. Biggs, A. Gaylard, and L. E. O. Braack. 1999. A new policy for the management of the Kruger National Park's elephant population. *Koedoe* **42**.
- Van Wilgen, B. W., H. C. Biggs, S. P. O'Regan, and N. Mare. 2000. A fire history of the savanna ecosystems in the Kruger National Park, South Africa, between 1941 and 1996 *South African Journal of Science* **96**:167-178.
- Van Wilgen, B. W., H. C. Biggs, and A. L. F. Potgieter. 1998. Fire management and research in the Kruger National Park, with suggestions on the detection of thresholds of potential concern. *Koedoe* **41**:69-87.
- Williams, R. J., G. D. Cook, A. M. Gill, and P. H. R. Moore. 1999. Fire regime, fire intensity and tree survival in a tropical savanna in northern Australia. *Australian Journal of Ecology* **24**:50-59.
- Wilson, J. B. and W. G. Lee. 1994. Niche Overlap of Congeners: A test using plant altitudinal distribution. *Oikos* **69**:469-475.

- Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* **70**:164-168.
- Woodward, F. I. and B. G. Williams. 1987. Climate and plant distribution at global and local scales. *Plant Ecology* **69**:189-197.
- Young, T. P. and K. W. Lindsay. 1988. Role of even-age population structure in the disappearance of *Acacia xanthophloea* woodlands. *African Journal of Ecology* **26**:67-72.
- Zaniewski, A. E., A. Lehmann, and J. M. Overton. 2002. Predicting species spatial distributions using presence - only data : a case study of native New Zealand ferns. *Ecological Modelling* **157**:261–280.
- Zucchini, W. and O. Nenadić. 2006. A Web-based rainfall atlas for Southern Africa. *Environmetrics* **17**:269-283.