esa ECOSPHERE

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

ALAIN SMITH,[1] BRUCE PAGE,[1] KEVIN DUFFY,[2] AND ROB SLOTOW[1,]†

[1]*School of Biological and Conservation Sciences, University of KwaZulu-Natal Westville, Durban 4041 South Africa*
[2]*Institute of Systems Science, Durban University of Technology, Durban 4041 South Africa*

Citation: Smith, A., B. Page, K. Duffy, and R. Slotow. 2012. Using Maximum Entropy modeling to predict the potential distributions of large trees for conservation planning. Ecosphere 3(6):56. http://dx.doi.org/10.1890/ES12-00053.1

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 modeling (MaxEnt) uses niche modeling 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 $\geq$ 5m), and raster environmental layers for: aspect, elevation, geology, annual rainfall, slope, soil and vegetation. *A. nigrescens* was largely restricted to the Imfolozi section, while *S. birrea* had a wider distribution across the reserve. 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. Though the AUC (Area Under the Curve) values used to test model predictions were high for both species, the ground truthing test data showed that distribution for *A. nigrescens* was more accurate than that for *S. birrea,* highlighting the need for independent test data to assess model accuracy. We emphasize that MaxEnt can be used at finer spatial scales than those typically used for species occurrence, but models must be tested using spatially independent test data.

Key words: *Acacia nigrescens*; conservation planning; elephant; Hluhluwe-Imfolozi Park; MaxEnt; niche modeling; *Sclerocarya birrea*.

Received 22 February 2012; revised 28 March 2012; accepted 29 March 2012; final version received 29 May 2012; **published** 28 June 2012. Corresponding Editor: C. Kwit.

† **E-mail:** Slotow@ukzn.ac.za

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, including nesting and roosting 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 2002*b*, 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, Zaniewski et al. 2002, Benito et al. 2009). The relatively small number of data points required for niche modeling using maximum entropy (MaxEnt) modeling 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 et al. 2007). Previously, MaxEnt has been used to predict the distributions of entire species rather than for modeling 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 (van 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, 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 rare. Quantifying the effects of environmental variables on the distribution and abundance of individuals using niche modeling can help allude to 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 (Phillips and Dudík 2008, Rebelo and Jones 2010).

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 that conserve large mammalian herbivores. Finally, (6) to introduce an application of niche modeling 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 km^2. 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 at population sizes greater than ~200 individuals, including black rhino (*Diceros bicornis*), giraffe (*Giraffa camelopardalis*), Greater kudu (*Tragelaphus strepsiceros*), nyala (*Tragelaphus angasii*) and impala (*Aepyceros melampus*), 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 2002*a*, Shannon et al. 2008), following from their previous absence (Spinage and Guinness 1971).

Two tree species, *Acacia nigrescens* Oliver (Fabaceae) and *Sclerocarya birrea* (A. rich.) Hochst. subsp. *caffra* (Sond.) Kokwaro (Anacardiaceae), were selected for the study. Both species are used intensively and impacted, by elephant (Jacobs and Biggs 2002*a*, Boundja and Midgley 2010), especially when bark removal by elephants is followed by fire (Moncrieff et al. 2008). The seedlings are also browed 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 2002*a*, 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 $\geq$ 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). 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. We recorded 179 *A. nigrescens* trees and 106 *S. birrea* trees.

In this study, we chose environmental raster data to be used by MaxEnt for variables, including three categorical variables (geological, soil, and vegetation type) and four continuous variables (aspect, elevation, slope, and predicted annual rainfall). The geology, soils and vegetation maps were after Howison (2009). We created the aspect, elevation and 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

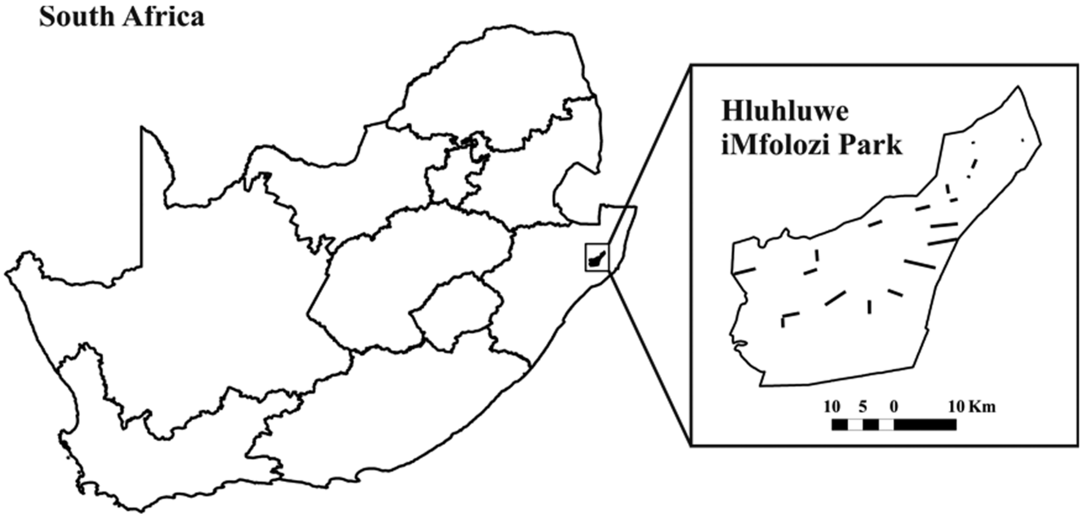


Fig. 1. The location of Hluhluwe–Imfolozi Park and the large tree transects within the park.

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 × 45.1 m.

Maximum entropy modeling (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 et al. 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 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 × 50 m, which is comparable to the cell size for the model of 45.1 × 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 +1) 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 presence/absence map would correctly predict presence in test quadrats indicating omission errors; and specificity, which is the probability of the map 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 models 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. The details of the MaxEnt model, graph showing the Kappa statistic with changes to the regularization multiplier and response curves are shown in the Appendix.

We used data from five GPS-collared, adult female elephant in HiP, each representing a separate herd. Locations were recorded at 30 min intervals, from October 2006 to September 2008. This produced 149,238 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

The AUC values for both *A. nigrescens* (0.93) and *S. birrea* (0.797) indicated that the model fit 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

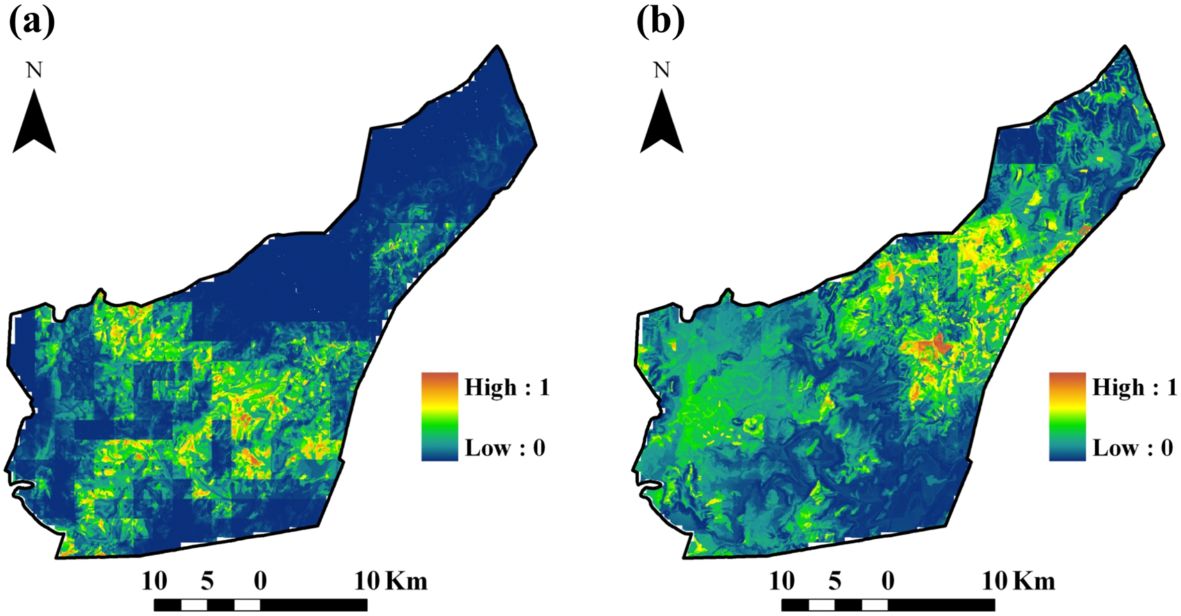


Fig. 2. Probability of occurrence or habitat suitability maps produced by MaxEnt for (a) *Acacia nigrescens* and (b) *Sclerocarya birrea*. A probability of one indicates a high likelihood of finding the species within the raster square, and zero indicates that it is unlikely that the species will be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

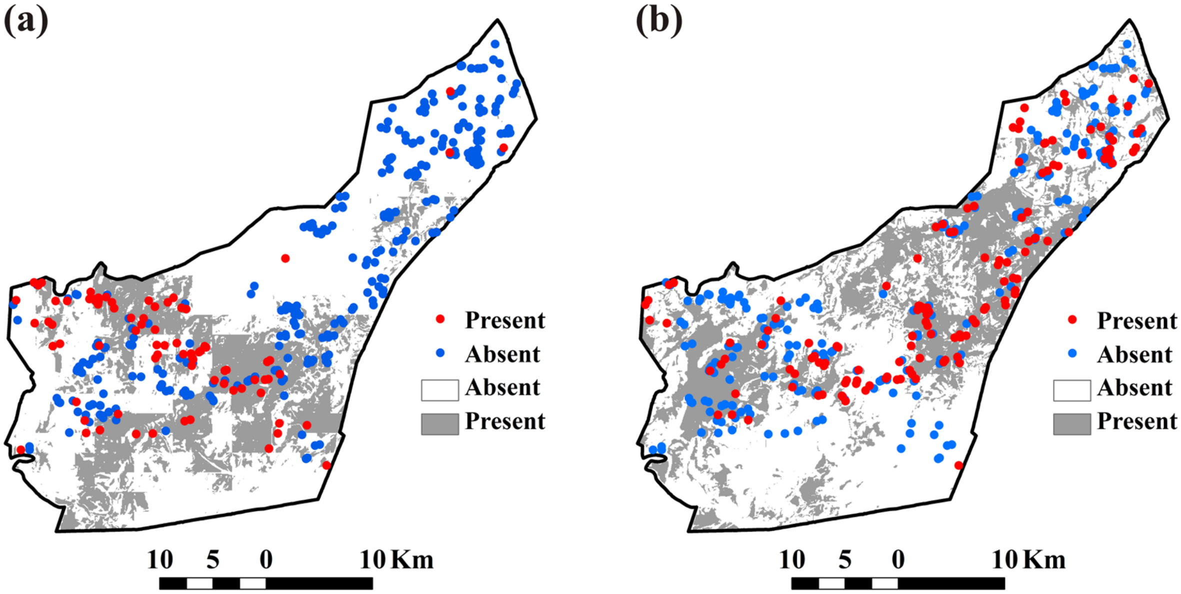


Fig. 3. The predicted distribution for *Acacia nigrescens* and *Sclerocarya birrea* from the MaxEnt model versus their presence or absence in independent sampling quadrats.

Table 1. Numbers of 50 × 50 m plots of *Acacia nigresens* and *Sclerocarya birrea* that were correctly identified as possible present and absent areas by the model.

Species	Presence	MaxEnt model predicted	Plots observed	
			Absent	Present
A. nigrescens	Absent	254	229	60
	Present	85	25	55
S. birrea	Absent	231	147	84
	Present	136	80	56

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.

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

Table 2. Five Model evaluation statistics for *Acacia nigresens* and *Sclerocarya birrea*. Values closer to one indicate a better result. TSS = True Skills Statistic

Species	Accuracy	Sensitivity	Specificity	TSS	Kappa statistic
A. nigrescens	0.77	0.48	0.9	0.38	0.41
S. birrea	0.52	0.39	0.65	0.05	0.04

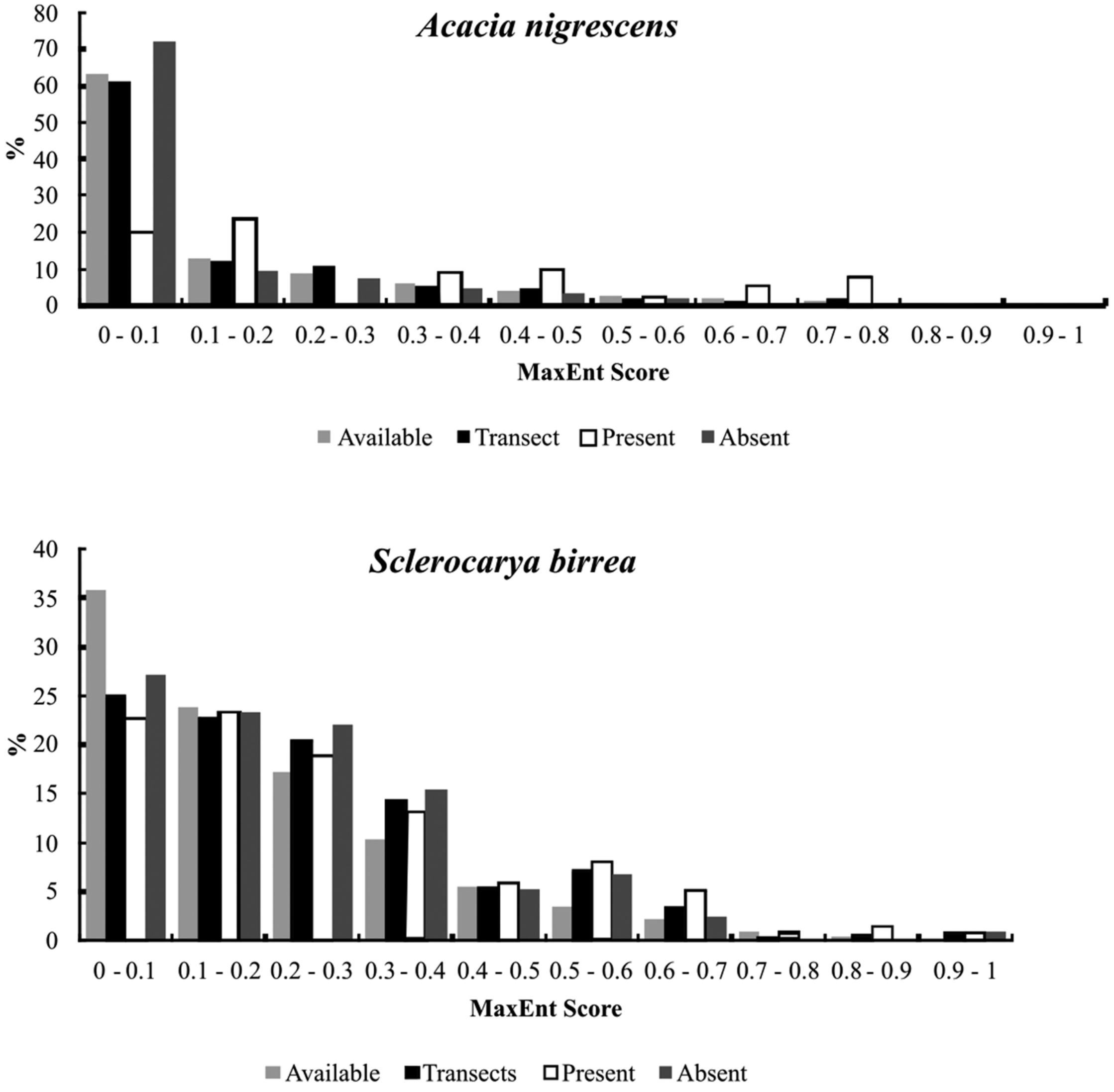


Fig. 4. The distribution of a quadrats with and without each species present, compared to the availability of areas within probability categories and the distribution of transects within the MaxEnt categories. The expected trend would be that presence quadrats would have a greater distribution in higher 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.

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

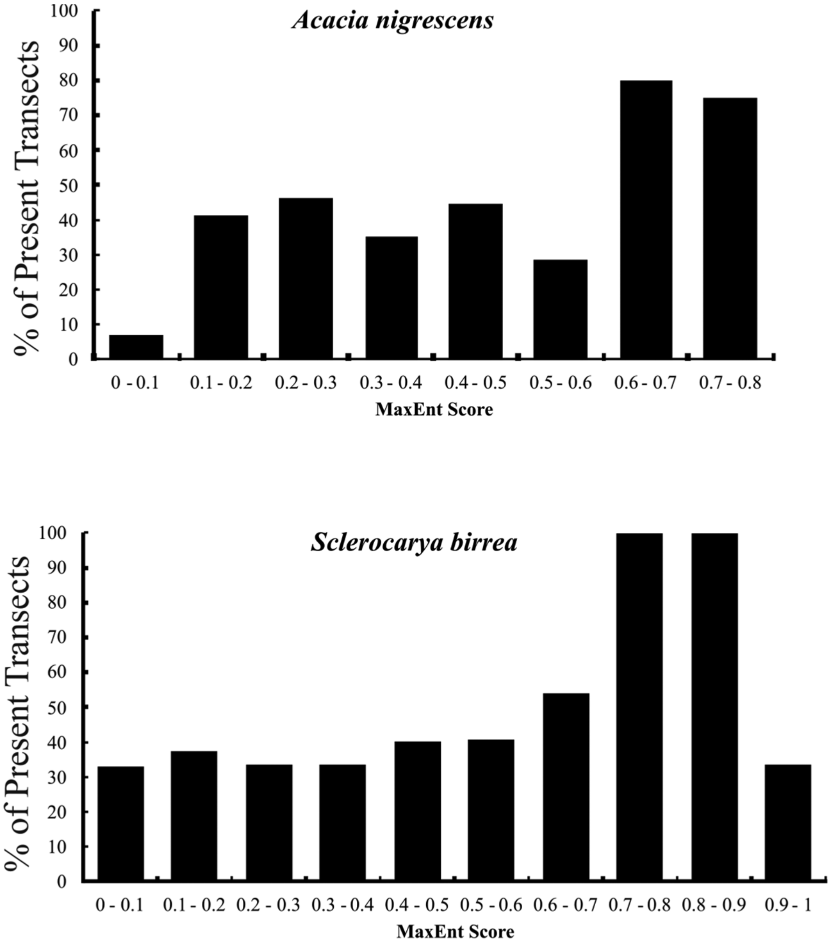


Fig. 5. The number of test quadrats in which the species occurred that overlapped each MaxEnt score range. This is given as a proportion of the total number of test quadrats that overlapped each probability range. An increasing percentage should occur as the MaxEnt score category increases.

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 140–150 m, before dropping and then increasing in probability of occurrence from 300 m to 500 m. 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. 6b), it can

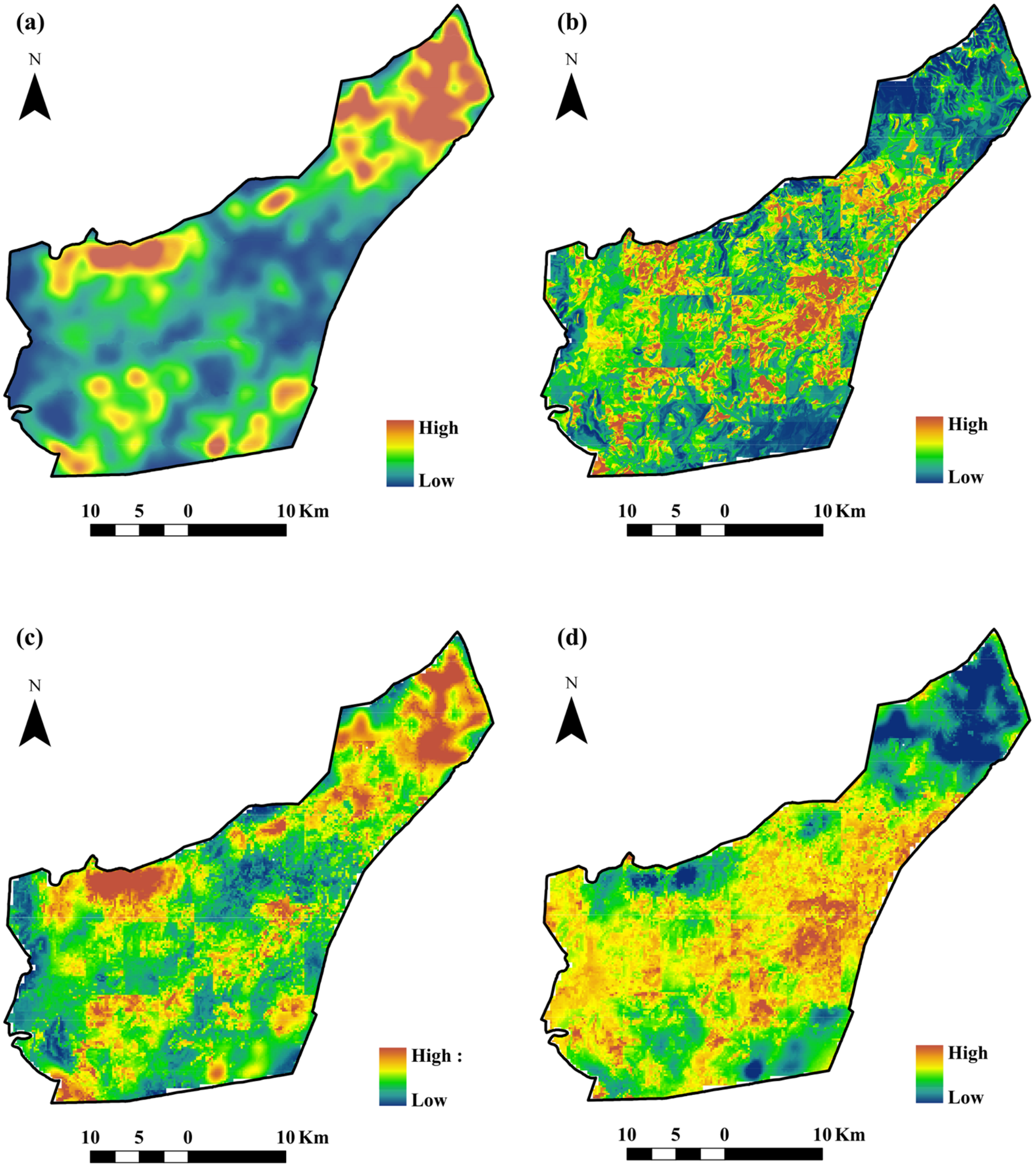


Fig. 6. Map showing the combined MaxEnt probability with elephant density map: (a) the elephant point density map and (b) the combined MaxEnt score for *Acacia nigrescens* and *Sclerocarya birrea*. To combine the two maps, the point density was divided by the highest density to make it a fraction of one. (c) The addition of the MaxEnt and elephant point density 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, orange shows areas of least conflict between elephant presence and possible large tree occurrence. 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. We used a standard deviations color stretch to highlight areas of conflict or areas of least conflict.

be assumed that there is not a high degree of distribution overlap between tree species. Despite a general lack of co-occurrence of the two tree species in raster squares, areas where botanical reserves, or the implementation of other management interventions, may be least or most promising for implementation, are identified (Fig. 6c and d, respectively).

Discussion

The use of GPS and GIS to sample transects for large trees was successful, allowing transects to be sampled quickly and efficiently (Druce et al. 2008). This permitted a large enough area to be sampled in order to give a representative distribution of the species modeled in the study. Due to the relatively low density of trees $\geq$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. Future studies may reduce the impacts of spatial autocorrelation by using a plot format similar to that used by the test data. Plots can be divided into presence and absence which would also allow the use of presence/absence models.

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* fit 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.

A difference in rainfall tolerance is likely to cause the split in distribution of the species, with *S. birrea* being found at intermediate rainfall and *A. nigrescens* being restricted to the lower rainfall areas in iMfolozi. The split is likely to be correlated with elevation, since there is a rainfall gradient present with more rainfall in the higher areas of the park (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. nigerscens* 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. The model prediction provided was more accurate for *A. nigrescens* than for *S. birrea* as shown by their ability to accurately predict presence or absence in test plots. We have used both species to illustrate a possible use of these results for planning and management purposes in the context of large trees in protected areas. 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). The distribution of size classes in reserves is an important consideration when determining the viability of these large tree populations (Helm and Witkowski 2012). With recruitment rates being linked to the production of fruit, it is important that trees which are producing large amounts of fruit are preserved in reserves to ensure that sustainable recruitment rates are taking place (Emanuel et al. 2005, Helm et al. 2011). The majority of research has been focused on assessing the recruitment and distribution of height classes of *S. birrea* due to its commercial usage, but it can be assumed that similar height class distributions will be present for *A. nigrescens*. Both species have been shown to be experiencing losses of individuals in large height classes within protected areas in which elephant are present (Moncrieff et al. 2008, Helm et al. 2009, Shannon et al. 2011). Focusing management strategies and actions on areas which are conducive to the growth of large trees of each species will be important to maintain populations of each species in reserves (Helm and Witkowski 2012). 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), herbivore 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 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, van 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 modeling an important tool, as management applications can stretch towards managing many different species. The two species that have been modeled 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. 2005, Willis et al. 2009).

ACKNOWLEDGMENTS

The authors thank E. Di Minin for assisting 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 and for the use of the monitoring transect data; the Earthwatch, UKZN and other volunteers for collecting the data; the 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; and P. Birkett for manuscript editing.

LITERATURE CITED

Acocks, J. P. H. 1988. Veld types of South Africa. Third edition. Botanical Research Institute, Pretoria, South Africa.

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.

Austin, M. P. and J. A. Meyers. 1996. Current approaches to modeling the environmental niche of eucalypts: implication for management of forest biodiversity. Forest Ecology and Management 85:95–106.

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.

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 Modeling 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 2:345–350.

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. Blignaut, 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, South Africa.

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 CO_2-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, South Africa.

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.

Brotons, L., W. Thuiller, M. B. Araújo, and A. H. Hirzel. 2004. Presence-absence versus presence-only modeling methods for predicting bird habitat suitability. Ecography 27:437–448.

Coates-Palgrave, K. and M. Coates-Palgrave. 2002. Trees of southern Africa. Third 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.

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.

Dominy, N. J., N. S. Ferguson, and A. Maddock. 1998. Modeling elephant (*Loxodonta africana africana*) population growth in Hluhluwe-Umfolozi Park to predict and manage limits. South African Journal of Wildlife Research 28:61–67.

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.

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. Journal of Animal Ecology 59:1147–1164.

Dudík, M., S. J. Phillips, and R. E. Schapire. 2007. Maximum entropy density estimation with generalized regularization and an application to species distribution modeling. Journal of Machine Learning Research 8:1217–1260.

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, African Journal of Ecology 38:108–115.

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.

Emanuel, P. L., C. M. Shackleton, and J. S. Baxter. 2005. Modeling the sustainable harvest of *Sclerocarya birrea* subsp. *caffra* fruits in the South African lowveld. Forest Ecology and Management 214:91–103.

Fielding, A. H. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environmental Conservation 24:38–49.

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.

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.

Gillson, L. and K. I. Duffin. 2007. Thresholds of potential concern as benchmarks in the management of African savannahs. Philosophical Transactions of the Royal Society B 362:309–319.

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.

Helm, C. V., S. L. Scott, and E. T. F. Witkowski. 2011. Reproductive potential and seed fate of *Sclerocarya birrea* subsp. *caffra* (marula) in the low altitude savannas of South Africa. South African Journal of Botany 77:650–664.

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.

Helm, C. V. and E. T. F. Witkowski. 2012. Characterising wide spatial variation in population size structure of a keystone African savanna tree. Forest Ecology and Management 263:175–188.

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., W. J. Bond, and W. S. W. Trollope. 2000. Fire , resprouting and variability: a recipe for grass-tree coexistence in savanna. Journal of Ecology 88:213–299.

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 83:2027–2036.

Howison, R. A. 2009. Food preferences and feeding interaction among 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, South Africa.

Jacobs, O. S. and R. Biggs. 2002*a*. 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. 2002*b*. The status and population structure of the Marula in the Kruger National Park. South African Journal of Wildlife Research 32:1–12.

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.

Kraus, J. 1997. Counting furtive beasts by computer. Communications of the Association Computer Machinery 40:20–23.

van Langevelde, F., C. A. D. M. van de Vijver, L. Kumar, J. van de Koppel, N. de Ridder, J. van de 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.

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.

Manning, A. D., J. Fischer, and D. B. Lindenmayer. 2006. Scattered trees are keystone structures: Implications for conservation. Biological Conservation 132:311–321.

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.

Moncrieff, G. R., L. M. Kruger, and J. J. Midgley. 2008. Stem mortality of *Acacia nigrescens* induced by the synergistic effects of elephants and fire in Kruger National Park, South Africa. Journal of Tropical Ecology 24:655–662.

Muller, S. 2002. Diversity of management practices required to ensure conservation of rare and locally threatened plant species in grasslands: a case study at a regional scale (Lorraine, France). Biodiversity and Conservation 11:1173–1184.

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.

O'Connor, T. G., P. S. Goodman, and B. Clegg. 2007. A functional hypothesis of the threat of local extirpation of woody plant species by elephant in Africa. Biological Conservation 136:329–345.

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.

Peterson, A. T. 2001. Predicting species' geographic distributions based on ecological niche modeling. Condor 103:599–605.

Phillips, S. J., M. Dudík, and R. E. Schapire. 2004. A maximum entropy approach to species distribution modelling. Proceedings of the twenty-first international conference on machine learning. ACM, Banff, Alberta, Canada.

Phillips, S. J., R. P. Anderson, and R. E. Schapire. 2006. Maximum entropy modelling 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.

Raes, N., M. C. Roos, J. W. F. Slik, E. E. van Loon, and H. ter Steege. 2009. Botanical richness and endemicity patterns of Borneo derived from species distribution models. Ecography 32:180–192.

Rebelo, H. and G. Jones. 2010. Ground validation of presence-only modeling 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. Journal of Wildlife Management 59:543–551.

Roche, C. 2006. Breeding records and nest site preference of Hooded Vultures in the greater Kruger National Park. Ostrich 77:99–101.

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.

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.

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., 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.

Skowno, A. L., J. J. Midgley, W. J. Bond, and D. Balfour. 1999. Secondary succession in *Acacia nilotica* (L.) savanna in the Hluhluwe Game Reserve, South Africa. Plant Ecology 145:1–9.

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.

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.

Thrash, I. 1998. Impact of water provision on herbaceous vegetation in Kruger National Park, South Africa. Journal of Arid Environments 38:437–450.

Turner, I. M. 1996. Species loss in fragments of tropical rain forest: A review of the evidence. Journal of Applied Ecology 33:200–209.

Veloz, S. D. 2009. Spatially autocorrelated sampling falsely inflates measures of accuracy for presence-only niche models. Journal of Biogeography 36:2290–2299.

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, D.C., USA.

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.

Willis, S., D. Hole, Y. Collingham, G. Hilton, C. Rahbek, and B. Huntley. 2009. Assessing the impacts of future climate change on protected area networks: a method to simulate individual species' responses. Environmental Management 43:836–845.

Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70:164–168.

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 Modeling 157:261–280.

Zucchini, W. and O. Nenadić. 2006. A Web-based rainfall atlas for Southern Africa. Environmetrics 17:269–283.

SUPPLEMENTAL MATERIAL

APPENDIX

USING MAXIMUM ENTROPY MODELING 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 modeling 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-

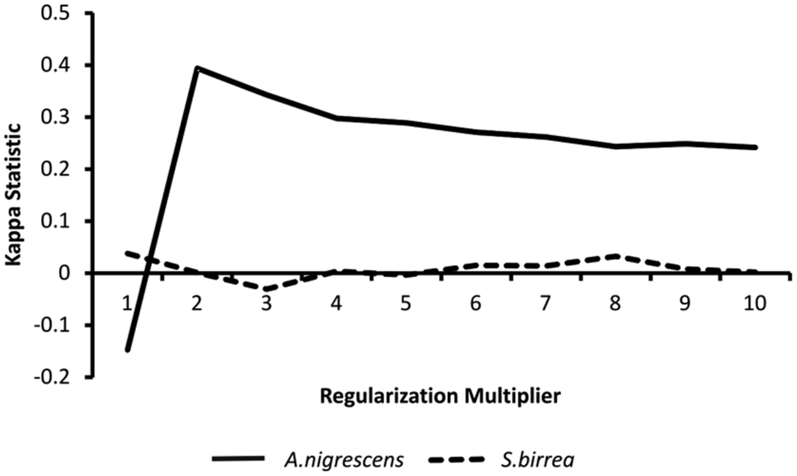


Fig. A1. Variation in the Kappa statistic for each species as the regularization multiplier variable is increased. The regularization number which yielded the highest Kappa statistic was used in the model.

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).

Outputs

Selection of an optimal regularization multiplier (Fig. A1) was chosen as a multiplier of 2 for *Acacia nigrescens*, and the default value of 1 was used for *Sclerocarya birrea*.

Jacknife graphs are an important tool for evaluating the variables which have been used in the analyses (Fig. A2). 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.

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. A3–A5).

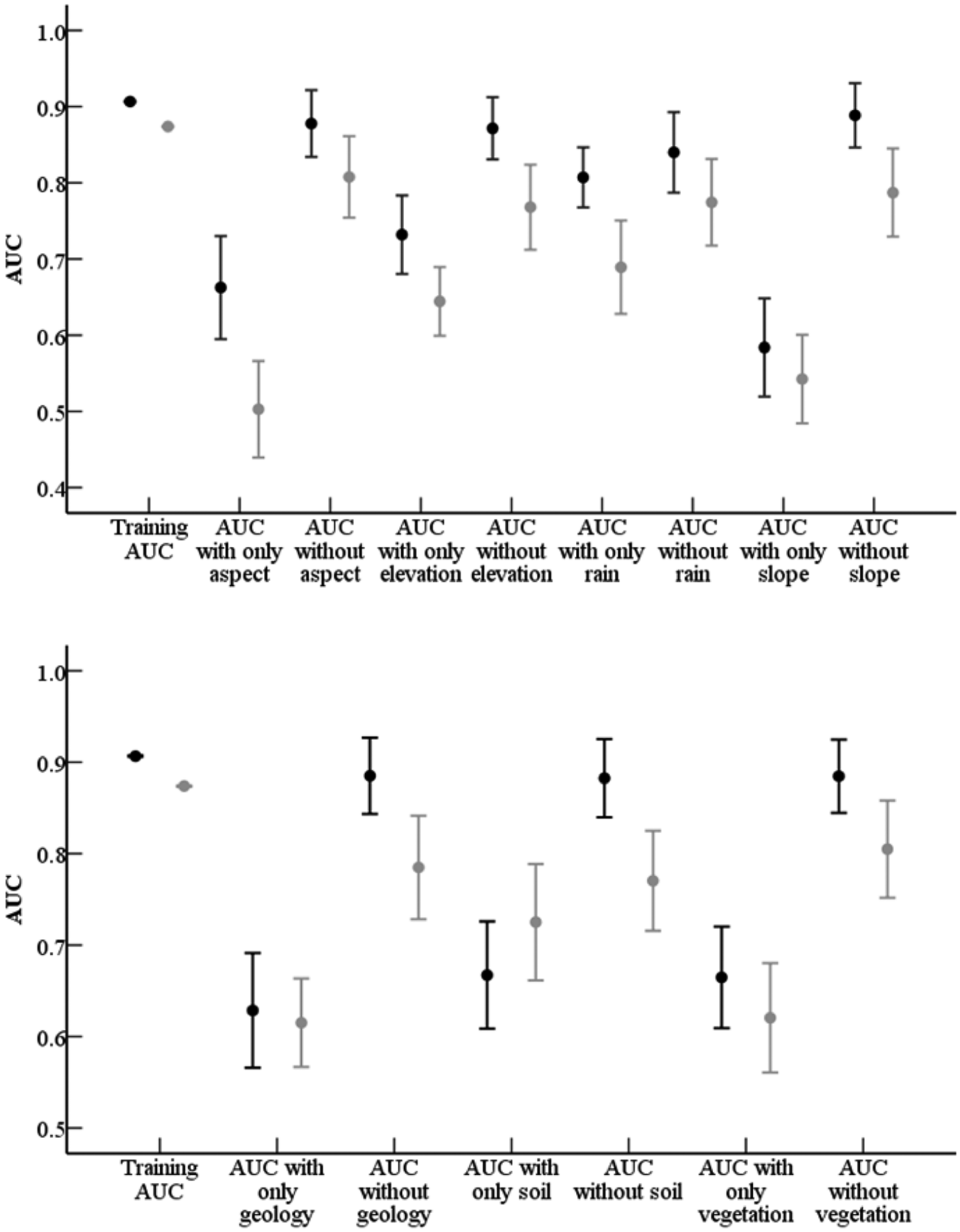


Fig. A2. Comparison of AUC values for different variable combinations, placed in two plots for purposes of clarity. The black points and bars are for *Acacia nigrescens* and the grey points and bars are for *Sclerocarya birrea*. Shown are the mean ±95% confidence limits, based on the 50 times that the model was run. The above graph is for continuous variables, the graph below for categorical variables.

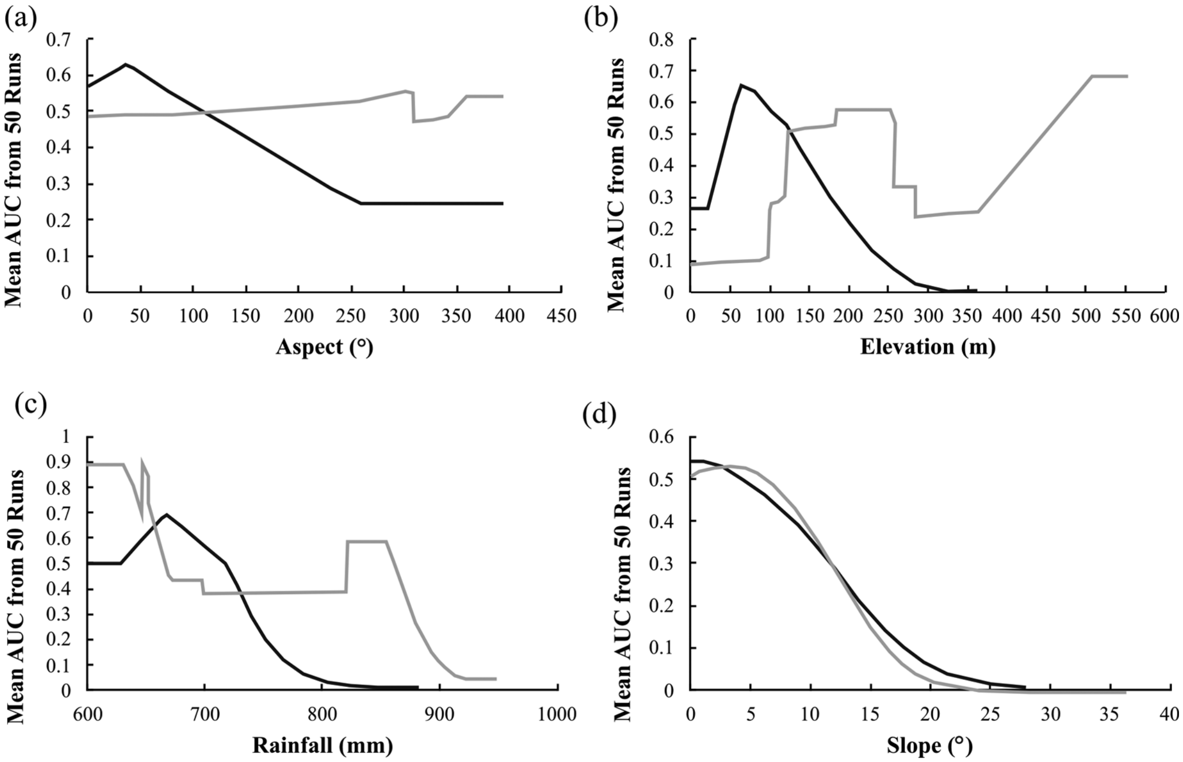
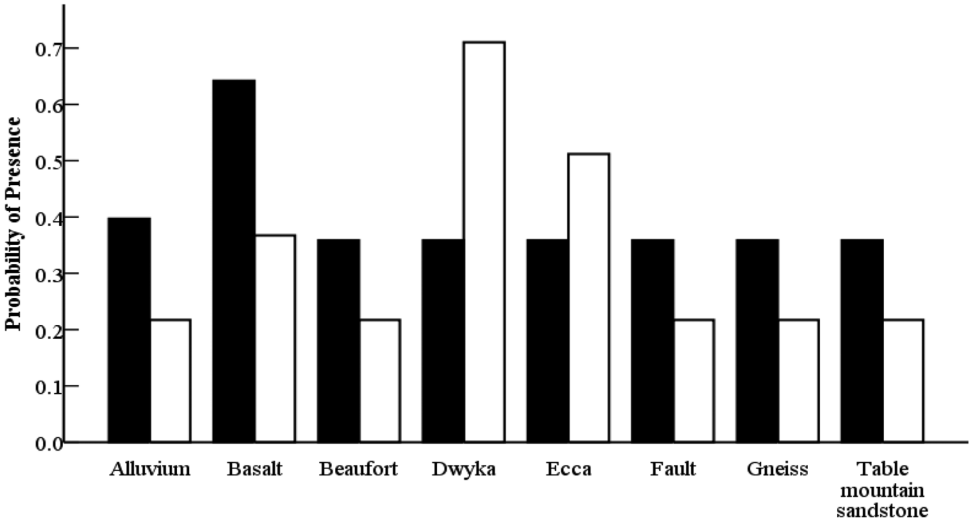


Fig. A3. Response curves for the continuous variables used in the MaxEnt analyses, indicating the manner in which each variable used in the analysis affected the distribution of the species in question. (a) for aspect, (b) for elevation, (c) for rainfall and (d) for slope. The black lines represent *Acacia nigrescens* and grey, *Sclerocarya birrea*.

(a)



(b)

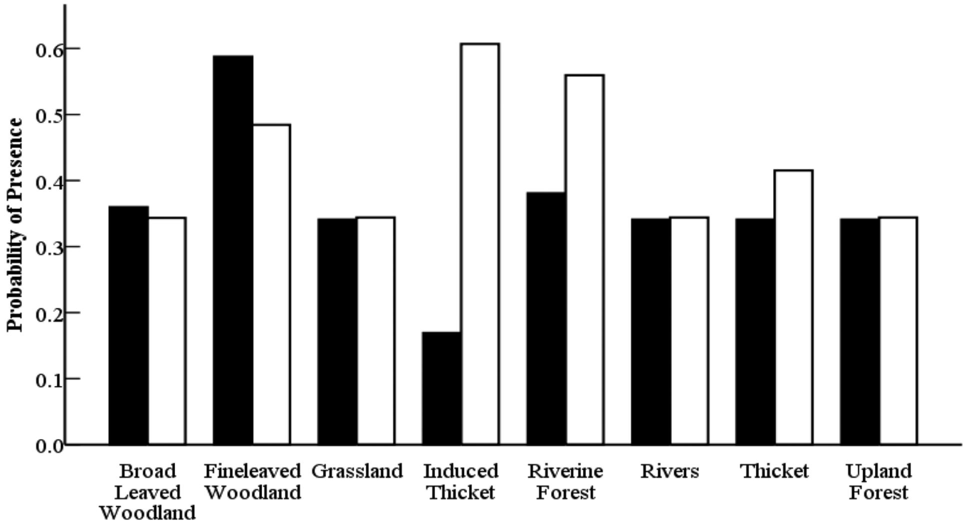


Fig. A4. Response curves for categorical variables used in the MaxEnt predictions of probability. Categorical variables include: (a) geology and (b) vegetation used in the analyses.

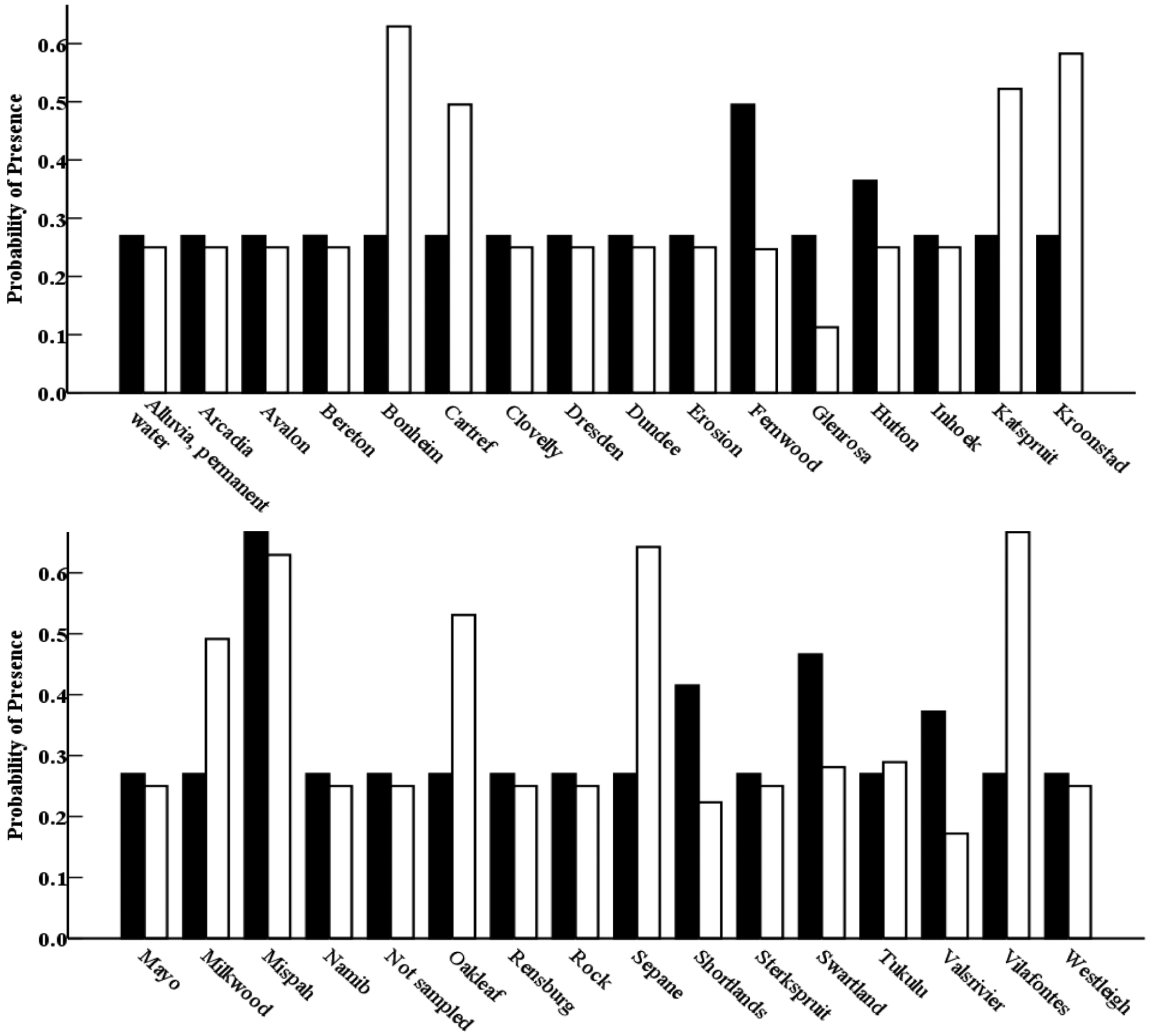


Fig. A5. Response curves for soil as used in the MaxEnt predictions of probability.