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CHAPTER 3

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Vulnerability of South African animal taxa to climate change

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Abstract

The responsiveness of South African fauna to climate change events is poorly documented and not routinely incorporated into regional conservation planning. We model the likely range alterations of a representative suite of 179 animal species to climate change brought about by the doubling of CO₂ concentrations. This scenario is expected to cause a mean temperature increase of 2°C. We applied a multivariate climate envelope approach and evaluated model performance using the most comprehensive bird data set. The results, based on distribution records from South Africa only, were encouraging although model performance was inconsistent in the eastern coastal area of the country. The levels of climate change-induced impacts on species ranges varied from little impact to local extinction. Some 17% of species expanded their ranges, 80% displayed range contraction (0 – 98%) and 3% showed no response. The majority of range shifts (41%) were in an easterly direction, reflecting the east-west aridity gradient across the country. Species losses were highest in the west. Substantially smaller westward shifts were present in some eastern species. This may reflect a response to the strong altitudinal gradient in this region, or may be a model artifact. Species range change (composite measure reflecting range contraction and displacement) identified selected species that could act as climate change indicator taxa. Red-data and vulnerable species showed similar responses but were more likely to display range change (58% vs. 43% for all species). Predictions suggest that the flagship Kruger National Park conservation area may lose up to 66% of the species included in this analysis. This highlights the extent of the predicted range shifts, and indicates why conflicts between conservation and other land uses are likely to escalate under conditions of climate change.

Introduction

Large-scale species extinctions and movements were precipitated by major climate events in the past (Gates 1993; Coope 1995; Roy *et al.* 1996). Consequently, prediction of the biodiversity consequences of current and predicted climate change is becoming increasingly important (McNeely *et al.* 1995), especially because such change is not likely to affect all species similarly. Some species are expected to benefit from and others to suffer under altered climatic conditions (Fajer *et al.* 1989; Freedman 1989; Cammell & Knight 1992; Davis *et al.* 1998a,b). Thus, not only are species likely to be affected by such change, but community composition is also likely to be altered because of individualistic species responses (see Coope 1995; Jablonski & Sepkoski 1996 for examples of such changes in the past). If biodiversity is to be conserved (Convention on Biodiversity, UNEP, Rio de Janeiro 1992), an understanding of how species and communities are likely to change under conditions of climate change is essential. Such understanding is particularly important because existing conservation networks, as well as theoretically selected areas, will not perform adequately if species temporal turnover is not taken into consideration (Rodrigues *et al.* 2000). This is likely to be true particularly if current and predicted climate change result in dramatic species movements, as seems likely to be the case (Parmesan *et al.* 1999, Pounds *et al.* 1999). Furthermore, interactions between habitat fragmentation, and changing species distribution patterns imply considerable future conservation conflicts (McNeely 1994, Fearnside 2000), making predictions of likely range shifts all the more important.

In South Africa, early qualitative (McDonald & Midgley 1996), and more recent quantitative (Rutherford *et al.* 2000) analyses of the effects of predicted climate change on the flora have suggested that the species rich biomes in the south-west of the country are likely to suffer substantial biodiversity losses, and that species loss from the existing protected area network will be significant. Despite these rather dramatic predictions, to date no attempts have been made to investigate the likely effects of predicted climate change on the South African fauna. Here we provide a first assessment of individual animal species responses to a climate change scenario in South Africa, by modeling the likely responses of the geographic ranges of a selection of 179 animal species from across the taxonomic spectrum.

The analytical approach we employ is generally referred to as the “climate envelope” approach (Sutherst & Maywald 1985; Sutherst *et al.* 1995; Markham & Malcolm 1996), and explores the extent to which species ranges might shift in response to changes in the

surrounding environment. Our use of this approach does not mean that we are unaware that climate is only one determinant of species distributions. Rather, we reasoned that while other factors, such as both horizontal and vertical linkages in ecosystems (Davis *et al.* 1998a, b; Buse *et al.* 1999; Hochberg & Ives 1999), and the phylogenetic history of taxa (see Myers & Giller 1988; Brown & Lomolino 1998), are likely to influence the geographic distributions of taxa, in the main, geographic distributions are likely to be determined to a large degree by climate (Jablonski *et al.* 1985; Root 1988; Rogers & Williams 1994; Coope 1995; Robinson *et al.* 1997a, b; Chown & Gaston 1999; Spicer & Gaston 1999). Nonetheless, we acknowledge that a full understanding of the consequences of climate-induced range changes for the functioning of local ecosystems is unlikely to be achieved without additional investigations. These include the development of an understanding of the influence of such changes on regional diversity, and in turn its influence on local communities (see Cornell & Lawton 1992; Ricklefs & Schluter 1993; Tokeshi 1999 for review of local and regional interactions), and the effect that novel species interactions, precipitated by range changes, will have at local scales.

However, given the speed with which climate change is taking place (IPCC 1992, 1995, 1997, 2000) and that, within the context of urgent local development needs (e.g. ANC 1994), conservation decisions have to be made (van Jaarsveld *et al.* 1998), the approach we use provides a rapid and initial best estimate of likely responses of species over broad areas (Guisan & Zimmerman 2000). This estimate can be used as a broad guide to the urgent conservation action that is required, while additional, more specific data on species interactions and their change under different climate scenarios are collected (e.g. Masters *et al.* 1998; Buse *et al.* 1999; Fielding *et al.* 1997).

Materials and methods

Species screening and distribution data

Distribution data for birds, mammals, reptiles (snakes, lizards, and tortoises), butterflies, dung beetles (Scarabaeidae), antlions (Neuroptera), jewel beetles (Buprestidae) and termites were collated. The last four invertebrate taxa were grouped together under “other invertebrates” because they are generally poorly known in the subregion (Scholtz & Chown 1995; Koch *et al.* 2000). The species distribution data were obtained from: *birds* (Avian Demography Unit, University of Cape Town), *mammals* (Natural History Museum, Northern

Flagship Institution, Pretoria (NFI); Durban Natural Science Museum; Conservation Planning Unit, University of Pretoria (CUP)), *reptiles* (NFI; Port Elizabeth Museum), *butterflies* (NFI), *antlions* (National Insect collection, ARC Plant Protection Research Institute (NCI)), *jewel beetles* (NFI), *dung beetles* (NCI, NFI, CUP) and *termites* (CUP). Data were generalized to a 15' x 15' grid cell resolution (~25 X 25 km), the finest common resolution between taxa, to generate absence-presence maps. Because many southern African species remain poorly known, both taxonomically and geographically (Scholtz & Chown 1995; van Jaarsveld 2000), taxonomic experts were requested to identify a suite of representative species in their study taxon, to increase the likelihood of including accurate and representative distributions, based on the following criteria: (a) accurate but not necessarily comprehensive distribution patterns, (b) representative geographic range types (e.g. species restricted to winter or to summer rainfall regions), (c) taxonomic clarity, and (d) species known from a reasonable number of records. A total of 34 bird, 19 mammal, 50 reptile, 19 butterfly, and 57 "other invertebrate" species were finally selected (Appendix 1).

Climate data (historic and predicted)

Climate data for South Africa were provided by the Computing Centre for Water Research (CCWR, University of Natal, Pietermaritzburg). The historic data (30 year monthly and annual means: 1960 – 1989) were re-sampled to 15' x 15' grid cells from interpolated climate surfaces available at a minute by minute resolution to conform with the resolution of the species data. The variables employed in the present study are: minimum temperature, maximum temperature, and precipitation seasonality measured as the difference between February and August mean rainfall figures. These months were selected because a factor analysis of the 12 monthly rainfall means showed that February rainfall contributed most to Factor 1, which explained 56% of the variance, and August rainfall contributed most to Factor 2, which explained 37% of the variance in the data. Preliminary analyses with these data indicated that temporal variability is a dominant feature, with annual mean precipitation values tending to disguise seasonal aspects of climate change (Erasmus *et al.* 2000).

Equivalent precipitation and temperature variables were also obtained for a predicted climate change scenario (CCWR). These climate data were derived from climate surfaces produced from GCM (General Circulation Model) predictions. Climate changes values were derived by implementing the Hadley Centre Unified Model with no sulphates, which represents a worst-case scenario for South Africa (Hewitson 1998). This GCM predicts a

temperature increase of 2.5 – 3°C for South Africa with atmospheric CO₂ doubling from pre-industrial levels. Erring on the side of caution, this means that significant climate change can be expected by the year 2050 (Hewitson 1998), and quite possibly earlier.

Species distribution modeling and evaluation

The model we employed is conceptually similar to the one proposed by Jeffree & Jeffree (1994, 1996). The original model was modified to accept multivariate data as input, and to produce a probability surface as output, rather than a simple binary prediction (see Erasmus *et al.* 2000 for a full description). Essentially, on a scatterplot of climate variables (multivariate climate space), the values of climate variables at known records are used to construct a confidence region where there is a high probability that the records reflect the core range of the species. Points falling inside this confidence region are then mapped back to geographic space to represent an interpolated distribution (ID). Climate affected distributions are produced by altering the climate variables of individual cells according to the GCM predictions, i.e. shifting the climate space, and subsequently mapping the predicted climate affected species distributions (CAD) back into geographic space.

Changes in distribution patterns owing to predicted climate change were assessed by comparing interpolated distribution patterns (ID) with climate affected distribution patterns (CAD) using a number of variables:

- a. Species richness pattern – number of species predicted per grid cell using interpolated distributions;
- b. Species range shift – proportion of climate-affected distributions (CAD) inside the interpolated distribution (ID).
- c. Species range contraction – climate-affected distribution (CAD) as a proportion of the interpolated distribution (ID), and
- d. Species range change – the sum of interpolated distribution grid cells lost and additional grid cells added under climate change, expressed as a percentage of the original interpolated distribution (ID). This additional measure provides an integrated assessment of range alterations through the combined effects of range contraction and shift.

These analyses were conducted for each taxonomic group separately, collectively across all species and for Red-data (mammals, birds, butterflies) and vulnerable species (identified as such by taxon experts: reptiles, jewel beetles, dung beetles, termites and antlions). Areas of

the country that are currently more than 50% transformed by human activity (Fairbanks *et al.* 2000) were superimposed on the post climate change species richness map to assess the potential availability of pristine land for accommodating climate-driven species range shifts.

To evaluate our model (Oreskes *et al.* 1994, Guisan & Zimmerman 2000), we compared interpolated distributions with known records. Incomplete distribution data severely limited the extent to which absence data could be included in model evaluation procedures for most taxa. The bird data, resulting from extensive sampling, was the best approximation of true presence-absence data and was used for evaluation. Instead of dichotomising the predicted probability output to predicted presence-absence by applying a threshold probability, which results in loss of information (Deleo 1993, Fielding *et al.* 1997), the actual predicted probabilities were utilized using receiver operating characteristic analyses (ROC). ROC analysis has its origins in engineering in the context of measuring the ability of a detector to detect a particular signal. It has found wide application in clinical medical tests (Fielding *et al.* 1997) and here it is used to measure the performance of a predictive species' distribution model. Kraemer's (1988) critique of ROC application in biology concerns the subjectivity of observations and the inability of the observed characters to be controlled or known with absolute certainty. The bird data set has been subjected to extensive expert vouching procedures and as such presents a close approximation of objective observations (Allan *et al.* 1997, van Jaarsveld *et al.* 1998). Therefore, we regard ROC analyses as suitable for our purposes of evaluation.

ROC analysis primarily concerns the calculation of specificity and sensitivity values. Sensitivity is defined as the number of true occurrences of a species (true positive predictions, TP) divided by the total number of positive predictions, whether true (TP) or not (false negatives predictions, FN). Similarly, specificity is defined as the number of true negative predictions (TN) divided by the total number of negative predictions, whether TN or false positive (FP) predictions (Fielding *et al.* 1997). The area-under-curve (AUC) of a plot of 1-specificity against sensitivity at every given probability of occurrence value is used as a test statistic. The AccuROC® software (Vida 1993) uses the nonparametric method of De Long *et al.* (1988) to determine the statistical significance of the difference between an AUC of 0.5 (corresponding to a random test with no discriminatory ability) and the AUC of every bird species. The confidence interval for the AUC was calculated using the asymptotic method (Obuchowski *et al.* 1998). A random subsample (with no replacement) of 20% of the known records of each species were also taken and used as input to generate probabilities of occurrence. The AUC of the 20% subsample was compared with the AUC based on all

known records (De Long *et al.* 1998). Such cross validation should ideally involve two independent data sets, although subsampling is an acceptable alternative (Guisan & Zimmerman 2000). Owing to a lack of absence data, the ROC analyses were only applied to the bird dataset to evaluate the model's ability to match predicted and observed data. The predicted probabilities generated for the other taxonomic groups had to be dichotomized into presence-absence data after determining a probability of occurrence threshold level from the ROC analyses of the bird data. This threshold was determined by calculating the correct classification rate ($([TP + TN]/[TP+FP+TN+FN])$) for all possible thresholds and selecting an appropriate probability threshold at which to interpret distribution changes.

Results

Model evaluation

The model correctly classified TN and TP predictions at a mean correct classification rate of 0.79 (SD=0.09) using a 50% probability of occurrence threshold for all 34 bird species. Such a high correct classification rate suggests strongly that the model can make useful predictions. Further support for the usefulness of the model (Zweig & Campbell 1993) comes from the construction of a confusion matrix (Fielding & Bell 1997) for the bird data. The results are summarized in Table 1. Mean values of 60% for true positives and 88% for true negatives suggest a reasonable performance of the model. This result is further underscored by the narrow ranges recorded for the variables. Although the mean figures for false positives and false negatives may inspire confidence in the above conclusion, the extremely large ranges recorded for false positives (1 – 44%) suggest that the model is useful for predicting the true ranges of some species but less so for other bird species. For those species where the model performs poorly, the 50% probability of occurrence area may extend markedly beyond the recorded range of the species. The large mean figure obtained for false negative values (38%) can be explained by our application of the 50 % probability of occurrence rule, with many species being recorded at lower probabilities of occurrence than the benchmark 50% level.

Given these considerations, the 50% probability of occurrence figure was considered an acceptable probability of occurrence and was applied to all other taxa. Thus, species were considered present when the model predicted a probability of

occurrence of $\geq 50\%$, and absent below 50%. The application of this general rule was only

Table 1 Percentage prediction reliability at the 50% probability of occurrence level, for the multivariate model (Erasmus *et al.* 2000) used in this study. These estimates are for the bird data only because true distributions of the other taxa are too poorly known.

	True positives	True negatives	False positives	False negatives
Mean \pm S.D.	60.3 \pm 5.2	87.8 \pm 10.3	12.2 \pm 10.3	39.7 \pm 5.2
Range	49.1 – 69.3	56.0 – 98.6	1.4 – 44.0	30.7 – 50.9

(AUC) values significantly different ($p < 0.05$, ranging from 0.0553 to 0.9131) from an AUC of 0.5 (see Fig. 1 for an example). The number of known records for each species was a significant difference (probability of type I error 0.1, probability of type II error 0.1) between an AUC of 0.5 and 0.85 was found to be lower (44) than the number of records for the species with the least number of records (49 for the Drakensberg Bustard). The remaining 30 bird species had larger ranges with the number of known records varying from 98 to 1593 with a mean of 697. It is clear that differences between the minimum values and an AUC of 0.5 are small and narrow, that is, they are close to the values of a random model with no discriminatory skill.

For 24 of the 34 bird species, the AUC values based on a subsample of known records were not significantly different from the values derived from the complete data set of known records for each bird. The remaining 10 species (all non-passerine and of relatively large body size) had AUC values significantly different (values ranging from 0.0553 to 0.9131) from the AUC values based on the complete data set of known records for each species. This result suggests that these 10 species might experience range limitations due to other factors than climate, such as resource quality or resource availability.

Species distribution changes

The species richness pattern for all taxa, revealed using the unspatial distribution model, differs markedly from the richness pattern using climate alone as a predictor. The unspatial model predicts that the most species-rich areas in the country are the southern coastal region, with significant species losses occurring in the southern coastal region. This is in contrast to the general decline in the size of species area and a corresponding decline in species richness with increasing elevation. This pattern of species loss with increasing elevation was a consistent outcome of the model across all taxa, even when the

occurrence of $\geq 50\%$, and absent below 50%. The application of this general rule accounts for losses of species from many areas of the country. Thus, a 100% species loss in any one area in effect means that no species were present in that area at a $\geq 50\%$ probability of occurrence.

Although ROC analyses performed on the bird data could not be applied to other taxa due to a lack of absence data, the results from these analyses provided further support for the usefulness of the model's predictions. Model evaluation using the area under the ROC curve as a test statistic found that all 34 bird species in the ROC analyses had area-under-curve (AUC) values significantly different ($p < 0.05$, ranging from 0.6357 to 0.9665, mean 0.85) from an AUC of 0.5 (see Fig. 1 for an example). The number of known records needed to detect a significant difference (probability of type I error 0.1, probability of type II error, 0.5) between an AUC of 0.5 and 0.85 was found to be lower (44) than the number of known records for the species with the least number of records (49 for the Drakensberg Siskin). The remaining 33 bird species had larger ranges with the number of known records varying from 98 to 1573 with a mean of 697. This means that differences between the measured AUC values and an AUC of 0.5 are real and that the model performs significantly better than a random model with no discriminatory ability.

For 24 of the 34 bird species, the AUC values derived from analyses using a 20% subsample of known records were not significantly different ($p < 0.05$) from the AUC values derived from the complete data set of known records for each bird. The remaining 10 species (all non-passerine and of relatively large body size) had AUC values significantly different (p values ranging from 0.0553 to 0.9131) from the AUC values based on the complete data set of known records for each species. This result suggests that these 10 species might experience range limitation due to other factors than climate, such as resource quality or resource availability.

Species distribution changes

Fig. 1 An example of a ROC curve. The area under the curve has a mean AUC of 0.85.

The species richness pattern for all taxa, produced using the interpolated distributions (ID), differs markedly from the richness pattern using climate affected data (CAD) (Fig. 2). The model predicts that the most speciose areas in the country will be concentrated on the eastern escarpment, with significant species losses occurring in the western, arid regions (Fig. 2b). A general decline in the size of speciose areas and a concentration of species around the eastern escarpment was a consistent outcome of the model across all taxonomic groups, and reflects

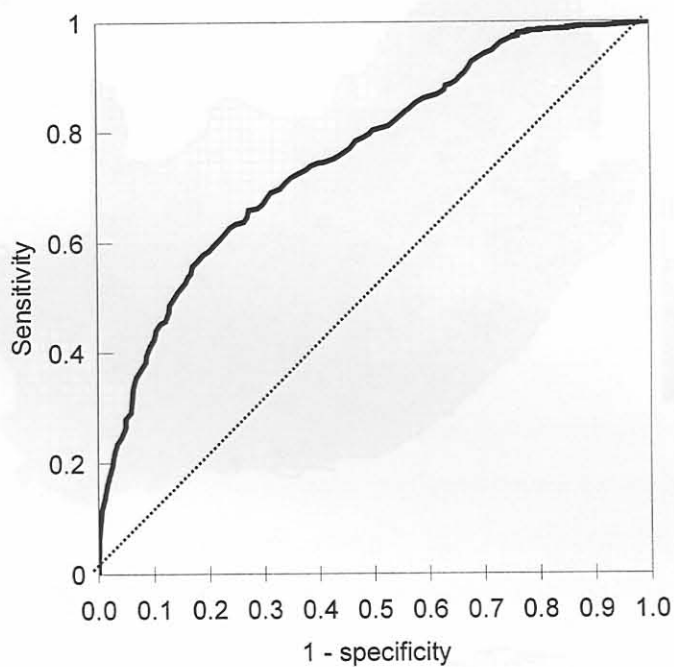
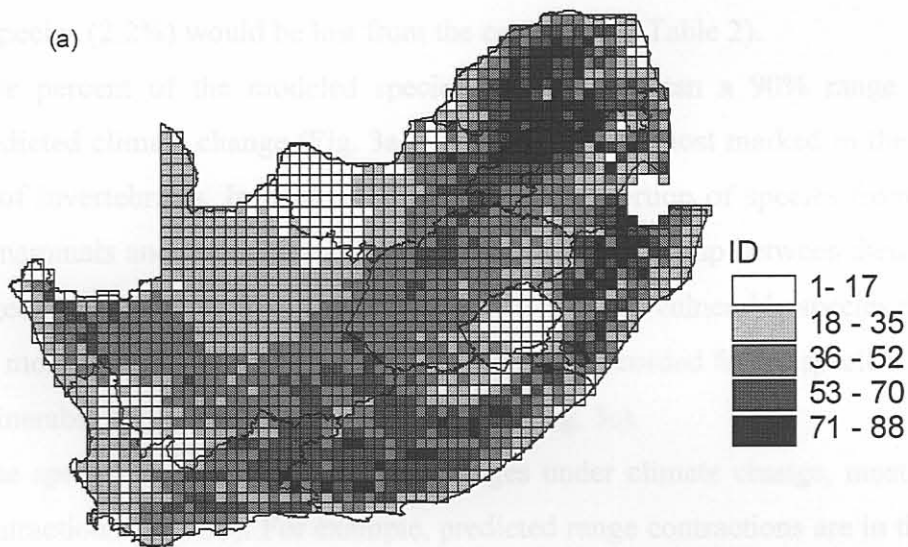


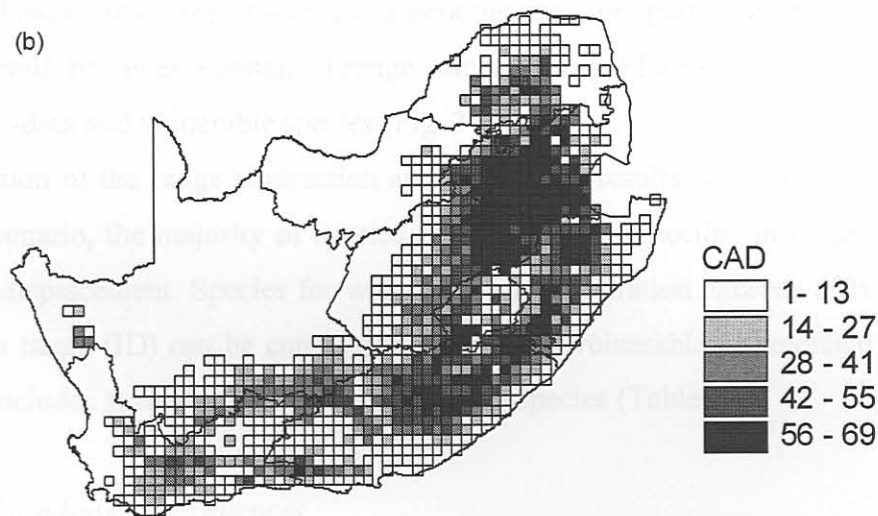
Fig. 1 An example of a ROC curve. The area under the dotted line represents an AUC of 0.5, which would translate into a test with discriminatory ability. The area under the solid black line represents the AUC for this particular species, the South African shelduck.

distributions (CAD) for all 179 species included in this study

(a)



(b)



300 0 300 600 Kilometers



Fig. 2 Species richness patterns for (a) interpolated distributions (ID), (b) climate affected distributions (CAD) for all 179 species included in this study.

to some extent, the likely western movement of most species and also movement of species up altitudinal gradients towards the eastern and south-eastern highlands. Similar patterns were found for the red-data and vulnerable species. Nonetheless, the model outputs suggested that only four species (2.2%) would be lost from the country (see Table 2).

Twenty-five percent of the modeled species show more than a 90% range shift in response to predicted climate change (Fig. 3a). This pattern was most marked in the reptiles and a number of invertebrates. In contrast, a substantial proportion of species from groups such as birds, mammals and butterflies show more than a 50% overlap between their present and predicted geographic ranges. The proportion of Red-data and vulnerable species that shift their ranges by more than 90% approaches 40% vs. the 25% recorded for all species, and few Red-data or vulnerable species displayed no range shift (Fig. 3c).

While some species appear to expand their ranges under climate change, most species show range contractions (Fig. 3b). For example, predicted range contractions are in the order of 40% of the ID for butterflies, and this is generally true of most of the invertebrate taxa. On the other hand, this figure can be both much higher (98% for the lizard *Homopholis wahlbergi*) and lower (0%, see Table 2) depending on the particular taxon under investigation. Overall, however, substantial range contractions are likely to occur, and this is true also of the red-data and vulnerable species (Fig. 3c)

The combination of the range contraction and range shift results suggests that, under a climate change scenario, the majority of species will show both a decline in range size and substantial range displacement. Species for which this range alteration exceeds 50% of their extant distribution range (ID) can be considered particularly vulnerable to predicted climate change, and this includes several red-data and vulnerable species (Table 3).

Conservation and land-use consequences

Figure 4 indicates areas in South Africa where existing land-use practices have transformed natural land-cover by more than 50%. These areas are concentrated in the southern coastal belt (South-Western Cape), across the Northern Provinces (Free State, Gauteng, Mpumalanga, North-West and Northern Province) as well as parallel to the eastern shores (KwaZulu-Natal and Eastern Cape). The areas where most overlap between transformed areas and regions likely to form species richness 'hotspots' under conditions of climate change is likely to occur are in the northern Free State, Gauteng, Mpumalanga and Northern Province. This overlap between climate affected species richness 'hotspots' and areas

Table 2. Species included in the present study that the model predicted would likely go locally extinct in South Africa following climate change (< 50% probability of occurrence throughout the country).

Species
<i>Stolotermes</i> – termite genus
<i>Epirinus gratus</i> - canthonine dung beetle
<i>Chrysospalax trevelyani</i> – golden mole
<i>Cordylus macrophallus</i> – armoured lizard

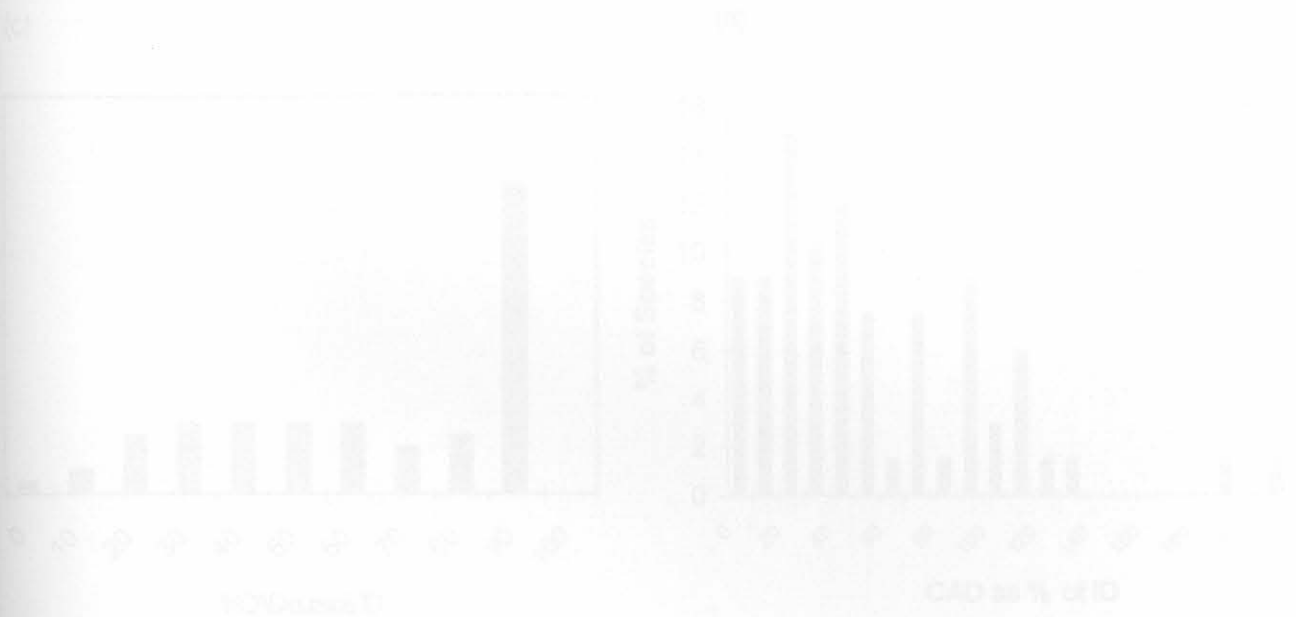


Fig. 3 Percentage of species that exhibit range shifts (expressed as percentage of their affected distribution outside the interpoint) (a) all species and (b) red data and vulnerable species. Percentage of species that exhibit range shifts (c) distribution expressed as a percentage of the interpoint (d) all species and (d) red data and vulnerable species.

3. South African fauna and climate change

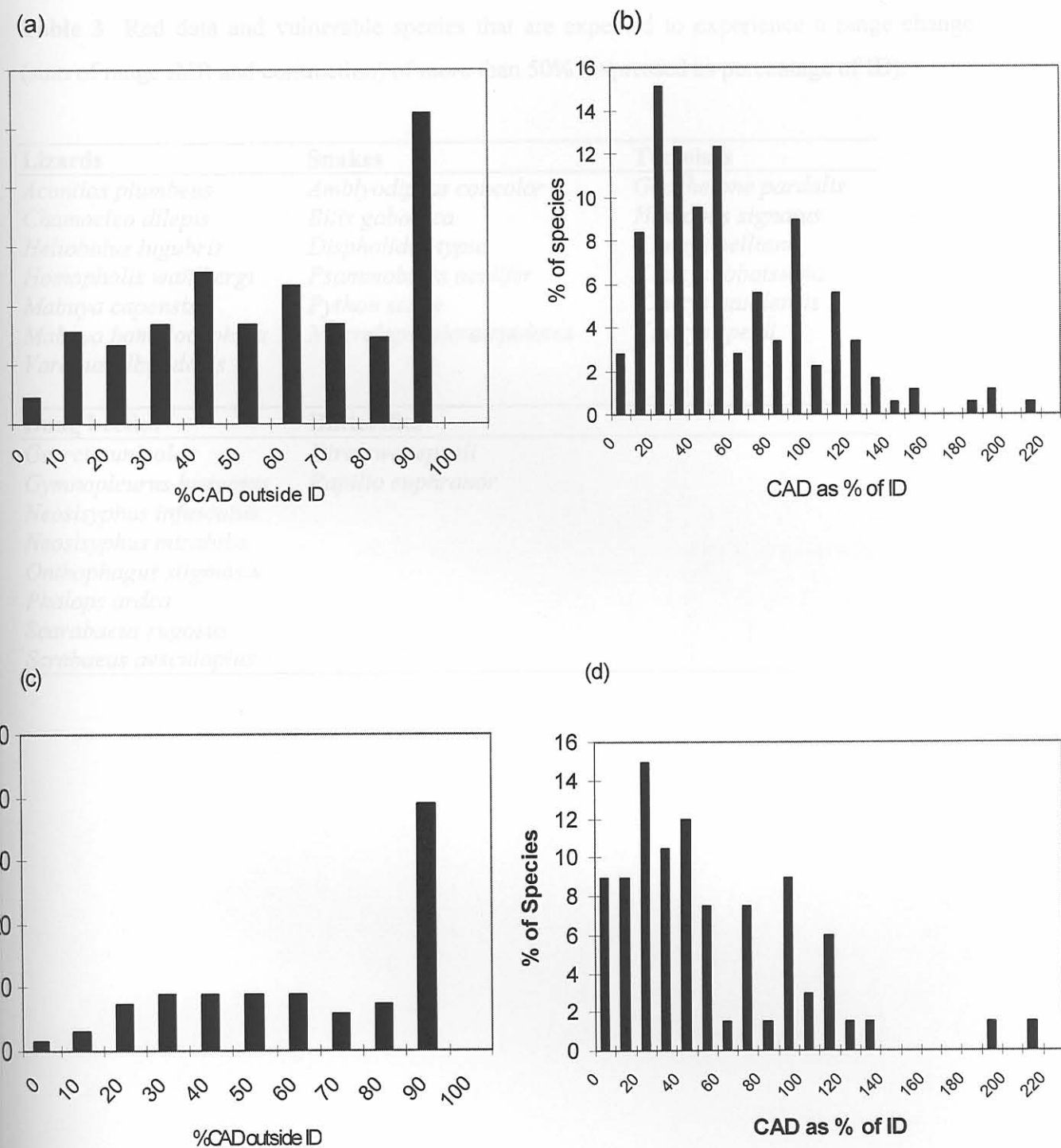


Fig. 3 Percentage of species that exhibit range shifts (expressed as percentage of climate affected distribution outside the interpolated distribution) for (a) all species and (c) red-data and vulnerable species. Percentage of species that exhibit range contraction (climate affected distribution expressed as a percentage of the interpolated distribution) predicted for (b) all species and (d) red data and vulnerable species.

Table 3 Red data and vulnerable species that are expected to experience a range change (sum of range shift and contraction) of more than 50% (expressed as percentage of ID).

Lizards	Snakes	Tortoises
<i>Acontias plumbeus</i>	<i>Amblyodipsas concolor</i>	<i>Geochelone pardalis</i>
<i>Chamaeleo dilepis</i>	<i>Bitis gabonica</i>	<i>Homopus signatus</i>
<i>Heliobolus lugubris</i>	<i>Dispholidus typus</i>	<i>Kinixys belliana</i>
<i>Homopholis wahlbergi</i>	<i>Psammobates oculifer</i>	<i>Kinixys lobatsiana</i>
<i>Mabuya capensis</i>	<i>Python sebae</i>	<i>Kinixys natalensis</i>
<i>Mabuya homalocephala</i>	<i>Macrelaps microlepidotus</i>	<i>Kinixys spekii</i>
<i>Varanus albigularis</i>		
Dung beetles	Butterflies	
<i>Garreta unicolor</i>	<i>Dira swanepoeli</i>	
<i>Gymnopleurus humanus</i>	<i>Papilio euphranor</i>	
<i>Neosisyphus infuscatus</i>		
<i>Neosisyphus mirabilis</i>		
<i>Onthophagus stigmosis</i>		
<i>Phalops ardea</i>		
<i>Scarabaeus rugosus</i>		
<i>Scarabaeus aesculapius</i>		

Fig. 4 Predicted climate affected (CA) species richness and diversity patterns in South Africa. Areas coloured in black are predicted to be degraded.

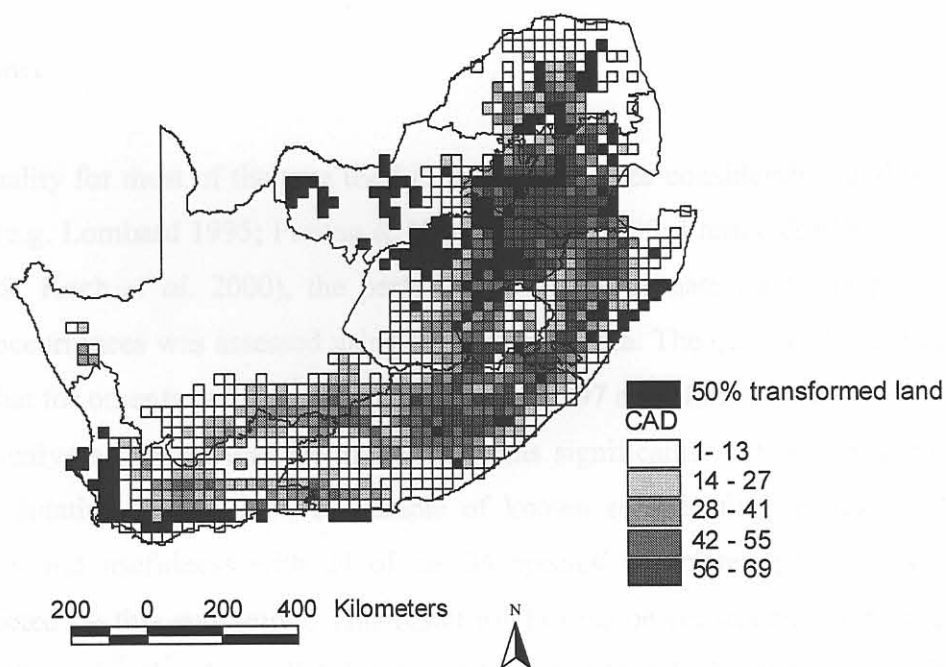


Fig. 4 Predicted climate affected (CAD) species richness patterns and extant land-cover patterns in South Africa. Areas coloured in black are at least 50% transformed and/or degraded.

presently subjected to cultivation and land transformation points to an increased potential for land-use conflict (Wessels *et al.* 2000) between agents of land transformation and conservation advocates.

Discussion

Model performance

Because data quality for most of the taxa used in this study varies considerably, and is often relatively poor (e.g. Lombard 1995; Freitag & Van Jaarsveld 1995; Freitag & Mansell 1997; Hull *et al.* 1998; Koch *et al.* 2000), the performance of the climate model in predicting known species occurrences was assessed using the bird atlas data. The quality of these data is far superior to that for other taxa (compare Harrison *et al.* 1997 and Hull *et al.* 1998).

The ROC analyses showed that the model performs significantly better than a random model. Cross validation with a 20% subsample of known records further supported the model's accuracy and usefulness with 24 of the 34 species' complete distributions being accurately predicted by this subsample. This result might thus be considered an estimate of the proportion of species that have distributions determined largely by climate, and hence provide insight into the broader applicability of the approach. If the model is valid for approximately 70% of the species in the taxa we have selected, then we consider the outcome of this exercise a useful first take at the likely impacts of climate change on animal distributions in South Africa. In some instances, the model did not perform well, especially in predicting presence/absence data for eastern parts of South Africa. This may well be due to the biogeographic complexity of the region and its strong altitudinal gradient that has a considerable influence on animal distribution patterns (see Low & Rebelo 1996; van Wyk 1996; Schulze *et al.* 1997; Oatley & Arnott 1998; Poynton 1961; White 1983; Poynton & Boycott 1996; Davis 1997; Eeley *et al.* 1999; Van Rensburg *et al.* 2000)

Notwithstanding these problems, we are of the opinion that the model used here represents a best estimate for a provisional study of the likely impacts of climate change on the South African higher invertebrate and vertebrate terrestrial fauna. We hold this view for a variety of reasons. First, despite what appear to be poor model performances on the east coast, the mean values for false presences and absences at a countrywide level were generally low, while those for true presence and absence data were not unreasonable (60, and 87%,

respectively). Second, given the resolution of the available data, and the quality of the data available for most taxa, this model is currently the only way in which the potential impacts of climate change can be investigated for a reasonable “shopping basket of taxa” (Hammond 1994).

The effects of climate change: model outputs and biological implications

Under the climate change scenario associated with a doubling in pre-industrial CO₂ levels, impacts on the fauna of South Africa range from minimal (six species showed no change in range size) to severe (four species were predicted to go extinct). Nonetheless, it appears that many species will show a range alteration characterized by a marked range shift from west to east, a somewhat smaller shift from east to west, and a substantial reduction in absolute range size.

Eastward range shifts

Range shifts from west to east are a common prediction of the model, and are characteristic of approximately 41% of all the taxa we examined. Given the pronounced aridity gradient in an east-west direction across the country (Rutherford & Westfall 1994; Schulze et al. 1997), the general decline in species richness in this direction (e.g. Drinkrow & Cherry 1995; Gelderblom *et al.* 1995; Freitag & Van Jaarsveld 1995, but also Gelderblom & Bronner 1995; Branch *et al.* 1995), and replacements over this gradient of species that differ markedly in their physiological tolerances (e.g. Le Lagadec *et al.* 1998), these changes are undoubtedly a realistic reflection of the likely impacts of climate change. In this context it is significant that range shifts as substantial as those predicted here have already been documented over the past century in western Europe (Parmesan *et al.* 1999), and similar range shifts are predicted elsewhere (e.g. Kerr & Packer 1998).

The extent to which such predicted eastward shifts in range will translate into realized alterations in range position will obviously also vary between taxa. For example, in species that are dependent on surface water for drinking, such as many southern African dove species, eastward shifts in range may not take place at all if agricultural practices continue to involve the surface provision of artesian water to livestock. Likewise, if species are capable of adapting to local conditions by behavioural or physiological means, realised range shifts may not be as pronounced as those predicted. However, information on the relationships

between species ranges and behavioural patterns and physiological tolerances, and the extent to which behavioural and physiological flexibility influence species ranges is limited to just a few South African taxa (e.g. Lovegrove & Wissel 1988; Richter *et al.* 1997; LeLagadec *et al.* 1998).

Landscape alterations in the eastern and central portions of South Africa will also have a marked impact on the extent to which the predicted changes will be realised. Extensive habitat alteration and fragmentation could prevent eastward range shifts from taking place because of the unavailability of suitable habitat patches (see also Hill *et al.* 1999; Parmesan *et al.* 1999), and because of large distances between suitable patches (see Brown & Lomolino 1998; Thomas *et al.* 1999; Tokeshi 1999; Channell & Lomolino 2000 for further discussion of the influence of these parameters on species occurrences). This interaction between species range alterations and habitat transformation is amongst the most significant consequences of climate change in a landscape that has been transformed by humans. If a species is unable to move into an area because of a lack of suitable habitat, or because that area is too distant from the closest source population of that species, then that area is effectively unavailable to the species and local extinction (or extirpation) is the most likely outcome. In effect this means that range contractions predicted by the current model may be underestimates.

Westward range shifts

Although there are good reasons for doubting the ability of the model to predict reliably range changes in the eastern coastal areas, it seems likely that at least some of the predicted westward range shifts will be real, rather than model artifacts. In particular, the shift of species up the altitudinal gradient (i.e. a gradient of increasing water availability and decreasing temperature) in this region does not seem unlikely. Such shifts already take place on a seasonal basis in a number of local avian migrants (see discussion in Harrison *et al.* 1997; Oatley & Arnott 1998), and have been documented in the Neotropics (Pounds *et al.* 1999). At least amongst the ectotherms, such shifts are likely to be more pronounced for coastal than for interior species. It appears that it is an inability to tolerate low temperatures that prevents the more tropical species from expanding their range up the elevational gradient (Gaston & Chown 1999). Thus, an increase in temperature in this region will undoubtedly lead to an expansion of the ranges of the tropical species.

Range alteration as a whole

Of the 179 species we examined, 30 species expanded their ranges, while 143 species showed range contractions varying between 0 and 98%. Few species showed no response or little response in terms of changes to their absolute range size. Because so many of the species we examined here showed substantial range contractions, it is this facet of range alterations that is of most concern. This concern is especially warranted if it is borne in mind that although the range contractions we have predicted here, are in some instances quite dramatic, they may actually be underestimates because landscape transformation has not been explicitly factored into the model. In practice, theoretical range shifts into transformed landscapes may mean local extinction. On the other hand, it is also possible that some of the dramatic predicted range changes may be mitigated by species immigration from outside the modelled area. Ideally, the geographic extent of the model area should be bounded physiographically, i.e. coastal boundaries for terrestrial animals, and not by political boundaries. In the real world, however, data availability dictated the use of political boundaries for this particular study. The effects of this artificial partition in species' ranges on modelled output have yet to be investigated.

The major reasons for significant concerns regarding range contractions have to do with the negative relationship between range size and extinction probability (Jablonski 1991; Gaston 1994). A reduction in the absolute range size of a species will almost inevitably mean an increase in its risk of extinction. There are several reasons for this. First, a decrease in range size will mean that smaller catastrophic events affect a larger proportion of the species total population. If a species is restricted to just a few sites, then a local catastrophic event could easily cause the extinction of that species (Gaston 1994; see also Lawton & May 1995). Second, the generally positive interspecific relationship between population size and range size is such that population size increases at a disproportionately faster rate with increasing range size, and hence local density also increases with increasing range size (Brown 1995, Gaston *et al.* 1997). Thus a decrease in range size is likely to effect a reasonably rapid decline in population size, and consequently extinction rate will increase for the usual small population reasons, susceptibility to stochastic variation being amongst the most important (see Gaston 1994; Caughley & Gunn 1996). Contraction of species' ranges towards the centre of their original distributions, as predicted by the model used here, is also unlikely to be entirely realistic given landscape transformation. Channell & Lomolino (2000) recently showed that in many of the 245 species they examined, which have recently shown range

contractions, the peripheral, rather than central populations of the species have survived. This means that range fragmentation is likely to be more pronounced than that predicted by our model. Such fragmentation is in itself of considerable conservation concern.

Conclusions

In summary, our model suggests that climate change will have a profound impact on terrestrial animal species in South Africa. Moreover, even this assessment is likely to be conservative given that population growth in South Africa is in the order of 1.9% per year (Anonymous 1998), and that the concomitant increases in population density are likely to result in additional, profound landscape transformation (perhaps exacerbated by high and increasing prevalence of AIDS, Williams *et al.* 2000). Mitigation of the impacts of climate change is ultimately a function of political will to confront difficult issues such as land-use and population planning. However, from a conservation and research perspective several actions can be taken. These include: better communication of findings to politicians, substantial improvements in the quality of information on animal diversity and distribution in South Africa, integration of this information into land-use planning, time-series data for at least some taxa, and the need for substantial improvement of knowledge of the causal links between climate and animal distributions. Of these, the first remains most critical.

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References

- Allan DG, Harrison JA, Herremans M, *et al.* (1997) Southern African geography: its relevance to birds. In: *The Atlas of Southern African Birds*. (eds Harrison JA, Allan DG, Underhill LG *et al.*), pp. 1xv-ci. Birdlife South Africa, Johannesburg.
- African National Congress (1994) *The Reconstruction and Development Programme*. Umanyano, Johannesburg.
- Anonymous (1998) *White Paper on Population Policy*. http://www.polity.org.za/govdocs/white_papers/popwp.html.
- Branch WR *et al.* (1995) The tortoises (Testudinidae) and terrapins (Pelomedusidae) of southern Africa: their diversity, distribution and conservation. *South African Journal of Zoology*, **30**, 91-102.
- Brown JH (1995) *Macroecology*. University of Chicago Press, Chicago, 269 pp.
- Brown JH, Lomolino MV (1998) *Biogeography*. Sinauer Associates, Sunderland, 691 pp.
- Buse A *et al.* (1999) Effects of elevated temperatures on multi-species interactions: the case of pedunculate oak, winter moth and tits. *Functional Ecology*, **13**, 74-82.
- Cammell ME, Knight JD (1992) Effects of climate change on the population dynamic of crop pests. *Advances in Ecological Research*, **22**, 117-162.
- Caughley G, Gunn A, (1996) *Conservation Biology in Theory and Practice*. Blackwell Science, Oxford, 459pp.
- Channell R, Lomolino MV (2000) Dynamic biogeography and conservation of endangered species. *Nature*, **403**, 84-86.
- Chown SL, Gaston K (1999) Exploring links between physiology and ecology at macro-scales: the role of respiratory metabolism in insects. *Biological Reviews*, **74**, 87-120.
- Coope GR (1995) Insect faunas in ice age environments: why so little extinction? In: *Extinction Rates*. (eds Lawton JH, May RM), pp. 55-74. Oxford University press, Oxford.
- Cornell HV, Lawton JH (1992) Species interactions, local and regional processes, and limits to the richness of ecological communities: A theoretical perspective. *Journal of Animal Ecology*, **61**, 1-12.
- Davis ALV (1997) Climatic and biogeographical associations of southern African dung beetles (Coleoptera: Scarabaeidae s. str.). *African Journal of Ecology*, **35**, 10-38.
- Davis AJ *et al.* (1998a) Making mistakes when predicting shifts in species range in response to global warming. *Nature*, **391**, 783-786.

- Davis AJ *et al.* (1998b) Individualistic species responses invalidate simple physiological models of community dynamics under global environmental change. *Journal of Animal Ecology*, **67**, 600-612.
- Deleo, JM. (1993) Receiver operating characteristic laboratory (ROCLAB): software for developing decision strategies that account for uncertainty. In: *Proceedings of the Second International Symposium on Uncertainty Modelling and Analysis*, pp. 318-325. College park, MD: IEEE Computer Society Press.
- Delong ER, Delong DM, Clarke-Pearson DL (1988) Comparing thr areas under two or more correlated receiver operating characteristic curves: a nonparametric approach. *Biometrics*, **44**, 837-845.
- Drinkrow DR, Cherry MI (1995) Anuran distribution, diversity and conservation in South Africa, lesotho and Swaziland. *South African Journal of Zoology*, **30**, 82-90.
- Eeley HAC, *et al.* (1999) The influence of climate change on the distribution of indigenous forest in Kwazulu-Natal, South Africa. *Journal of Biogeography*, **26**, 595-617.
- Erasmus, BFN, Kshatriya M, Mansell MW, Chown SL, Van Jaarsveld, AS (2000) A modelling approach to antlion (Neuroptera: Myrmeleontidae) distribution patterns. *African Entomology*, **8**, 157-168.
- Fairbanks DHK *et al.* (2000) The South African land-cover characteristics database: a synopsis of the landscape. *South African Journal of Science*, **96**, 69-82.
- Fearnside, PM (1999) Biodiversity as an environmental service in Brazil's Amazonian forests: risks, value and conservation *Environmental Conservation*, **26**, 305-321.
- Fielding, AH, Bell, JF (1997) A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation*, **24**, 38-49.
- Fajer ED *et al.* (1989) The effects of enriched carbon dioxide atmospheres on plant-insect herbivore interactions. *Science*, **243**, 1198-1200.
- Freedman B (1989) *Environmental Ecology: the Impacts of Pollution and other Stresses on Ecosystem Structure and Function*. Academic Press, San Diego, 424 pp.
- Freitag S, Mansell MW (1997) The distribution and protection status of selected antlion species (Neuroptera: Myrmeleontidae) in South Africa. *African Entomology*, **5**, 205-216.
- Freitag S, Van Jaarsveld AS (1995) Towards conserving regional mammalian species diversity: a case study and data critique. *South African Journal of Zoology*, **30**, 136-144.
- Gaston KJ (1994) *Rarity*. Chapman & Hall, London, 205 pp.

- Gaston KJ *et al.* (1997) Interspecific abundance-range size relationships: an appraisal of mechanisms, *Journal of Animal Ecology* **66**, 579-601.
- Gaston KJ, Chown SL (1999) Elevation and climatic tolerance: a test using dung beetles. *Oikos*, **86**, 584-590.
- Gates DM (1993) *Climate Change and its Biological Consequences*. Sinauer Associates, Sunderland, Mass., 280 pp.
- Gelderblom CM, Bronner GN (1995) Patterns of distribution and protection status of endemic mammals in South Africa. *South African Journal of Zoology*, **30**, 127-135.
- Gelderblom CM *et al.* (1995) Patterns of distribution and current protection status of the Carnivora, Chiroptera and Insectivora in South Africa. *South African Journal of Zoology*, **30**, 103-114.
- Guisan A, Zimmerman NE (2000) Predictive habitat distribution models in ecology. *Ecological Modelling*, **135**, 147-186.
- Hammond P (1994) Practical approaches to the estimation of the extent of biodiversity in speciose groups. *Philosophical Transactions of the Royal Society of London B*, **345**, 119-136.
- Harrison JA *et al.* (1997) *The atlas of southern African birds*. Birdlife South Africa, Johannesburg, vol I 732 pp., vol II 785 pp.
- Hewitson BC (1998) South African National Assessment for the Framework Convention for Climate Change: Climate Change Scenarios <http://tie.egs.uct.ac.za/fccc/hadcm2.html>
- Hill JK *et al.* (1999) Climate and habitat availability determine 20th century changes in a butterfly's range margin. *Proceedings of the Royal Society of London B*, **266**, 1197-1206.
- Hochberg ME, Ives AR (1999) Can natural enemies enforce geographical range limits? *Ecography*, **222**, 268-276.
- Hull HE *et al.* (1998) Identification and evaluation of priority conservation areas for Buprestidae (Coleoptera) in South Africa, Lesotho, Swaziland and Namibia. *African Entomology*, **6**, 265-274.
- IPCC (1992) *IPCC Supplement: Scientific Assessment of Climate change. Report prepared by Working Group 1. WHO-UNEP.* (eds Houghton JT, Callender BA, Varney S). Cambridge University Press, Cambridge.
- IPCC (1995) *IPCC Second Assessment Synthesis of Scientific-Technical Information Relevant to Interpreting Article 2 of the UN Framework Convention on Climate Change.* <http://www.ipcc.ch/pub/sarsyn.html>.

- IPCC (1997) *Summary for Policymakers: The Regional Impacts of Climate Change – an Assessment of Vulnerability*. <http://www.ipcc.ch/pub/sr97.html>
- IPCC (2000) *Summary for Policymakers: Emissions Scenarios*. <http://www.ipcc.ch/pub/reports.htm>
- Jablonski D (1991) Extinctions: A paleontological perspective. *Science*, **253**, 754-757.
- Jablonski D, Sepkoski JJ (1996) Paleobiology, community ecology and scales of ecological pattern. *Ecology*, **77**, 1367-1378.
- Jablonski D *et al.* (1985) Biogeography and paleobiology. *Paleobiology*, **11**, 75-90.
- Jeffree CE, Jeffree EP (1996) Redistribution of the potential geographical ranges of Mistletoe and Colorado Beetle in Europe in response to the temperature component of climate. *Functional Ecology* **10**, 562-577.
- Jeffree EP, Jeffree CE (1994) Temperature and the biogeographical distribution of species. *Functional Ecology*, **8**, 640-650.
- Kerr J, Packer L (1998) The impact of climate change on mammal diversity in Canada. *Environmental Monitoring and Assessment*, **49**, 263-270.
- Koch SO *et al.* (2000) Conservation strategies for poorly surveyed taxa: a dung beetle (Coleoptera, Scarabaeidae) case study from southern Africa. *Journal of Insect Conservation*, **4**, 45-56.
- Kraemer HC (1988) Assessment of 2 x 2 association: generalisations of signal-detection methodology. *The American Statistician*, **42**, 37-49.
- Lawton JH, May RM (1995) *Extinction Rates*. Oxford University Press, Oxford, 233 pp.
- Le Lagadec MD *et al.* (1998) Desiccation resistance and water balance in southern African keratin beetles (Coleoptera, Trogidae): the influence of body size and habitat. *Journal of Comparative Physiology B*, **168**, 112-122.
- Lombard AT (1995) The problems with multi-species conservation: do hotspots, ideal reserves and existing reserves coincide? *South African Journal of Zoology*, **30**, 145-163.
- Lovegrove BG, Wissel C (1998) Sociality in mole-rats, metabolic scaling and the role of risk sensitivity. *Oecologia*, **74**, 600-606.
- Low AB, Rebelo AG (1996.) *Vegetation of South Africa, Lesotho, and Swaziland*. Department of Environmental Affairs and Tourism, Pretoria, South Africa.
- Markham A, Malcolm J (1996) Wildlife and biodiversity impact and adaptation assessment. In: *Vulnerability and Adaptation Assessment: an International Handbook* (eds Benioff R, Guill S, Lee J), pp. 5-107 – 5-133. Kluwer Academic, London.

- Masters GJ *et al.* (1998) Direct and indirect effects of climate change on insect herbivores: Auchenorrhyncha (Homoptera). *Ecological Entomology*, **23**, 45-52.
- McDonald IAW, Midgley GF (1996) Impacts and implications for nature conservation. In: *Global Climate Change and South Africa*. (eds Shackleton LY, Lennon SJ, Tosen GR) pp. 83-86. Environmental Scientific Association, Cleveland, South Africa.
- McNeely JA (1994) Protected areas for the 21st century: working to provide benefits to society *Biodiversity and Conservation*, **3**, 390-405.
- McNeely JA (1995) Keep all the pieces: Systematics 2000 and world conservation. *Biodiversity and Conservation*, **4**, 510-519.
- Myers AA, Giller PS. (1988) *Analytical Biogeography. An Integrated Approach to the Study of Animal and Plant Distributions*. Chapman & Hall, London, 578 pp.
- Oatley T, Arnott G (1998) *Robins of Africa*. Acorn Books, Randburg and Russel Friedman Books, Halfway House.
- Oreskes N *et al.* (1994) Verification, validation and confirmation of numerical models in the earth sciences. *Science*, **263**, 641-644.
- Osborne PE, Tigar BJ (1992) Interpreting bird atlas data using logistic models: an example from Lesotho, Southern Africa. *Journal of Applied Ecology*, **29**, 55-62.
- Parmesan C, Ryrholm N, Stefanescu C *et al.* (1999) Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature*, **399**, 579-583.
- Pounds JA *et al.* (1999) Biological response to climate change on a tropical mountain. *Nature*, **398**, 611-615.
- Poynton JC (1961) Biogeography of south-east Africa. *Nature*, **189**, 801-803.
- Poynton JC, Boycott RC (1996) Species turnover between Afromontane and eastern African lowland faunas: patterns shown by amphibians. *Journal of Biogeography*, **23**, 669-680.
- Richter TA *et al.* (1997) Limits to the distribution of the southern African Ice rat (*Otomys sloggettii*): thermal physiology or competitive exclusion? *Functional Ecology*, **11**, 240-246.
- Ricklefs RE, Schluter D (1993) *Species Diversity in Ecological Communities: Historical and Geographical Perspectives*. University of Chicago Press, Chicago, 414 pp.
- Robinson T *et al.* (1997a) Univariate analysis of tsetse habitat in the common fly belt of southern Africa using climate and remotely sensed vegetation data. *Medical and Veterinary Entomology*, **11**, 223-234.

- Robinson T *et al.* (1997b) Mapping tsetse habitat suitability in the common fly belt of southern Africa using multivariate analysis of climate and remotely sensed vegetation data. *Medical and Veterinary Entomology*, **11**, 235-245.
- Rodrigues ASL *et al.* (2000) Robustness of reserve selection procedures under temporal species turnover. *Proceedings of the Royal Society London B*, **267**, 49-55.
- Rogers DJ, Williams BG (1994) Tsetse distribution in Africa: seeing the wood *and* the trees. In: *Large-Scale Ecology and Conservation Biology*. (eds Edwards PJ, May RM, Webb, NR) pp. 247-271. Blackwell Scientific Publications, Oxford.
- Root T (1988) Environmental factors associated with avian distribution boundaries. *Journal of Biogeography*, **15**, 489-505.
- Roy K *et al.* (1996) Scales of climatic variability and time averaging in Pleistocene biotas: implications for ecology and evolution. *Trends in Ecology and Evolution*, **11**, 458-463.
- Rutherford MC, Westfall RH (1994) Biomes of southern Africa: an objective categorization. *Memoirs of the Botanical Survey of South Africa*, **63**, 1-94.
- Rutherford MC *et al.* (2000) Climate change in conservation areas of South Africa and its potential impact on floristic composition: a first assessment. *Diversity & Distributions*, **5**, 253-262.
- Scholtz CH, Chown SL (1995) Insects in southern Africa: How many species are there? *South African Journal of Science*, **91**, 124-126.
- Schulze R *et al.* (1997) *South African Atlas of Agrohydrology and Climatology*. CSIR, Pretoria, 276 pp.
- Spicer JJ, Gaston KJ (1999) *Physiological Diversity and its Ecological Implications*. Blackwell Science, Oxford, 241 pp.
- Sutherst RW, Maywald GF (1985) A computerized system for matching climates in ecology. *Agriculture, Systems and Environment*, **13**, 281-299.
- Sutherst RW *et al.* (1995) Predicting insect distributions in a changed climate. In: *Insects in a Changing Environment* (eds Harrington R, Stork NE) pp. 59-91. Academic Press, London.
- Thomas JA *et al.* (1999) Intraspecific variation in habitat variability among ectothermic animals near their climatic limits and their centres of range. *Functional Ecology*, **13**, 55-64.
- Tokeshi M (1999) *Species Coexistence. Ecological and Evolutionary Perspectives*. Blackwell Science, Oxford.

- Van Jaarsveld AS *et al.* (1998) Throwing biodiversity out with the binary data? *South African Journal of Science*, **94**, 210-214.
- Van Jaarsveld AS (2000) Biodiversity: conserving the building blocks of environmental health. In: *The sustainability challenge for southern Africa* (ed Whitman J), pp. 265-290. McMillan Press, London, UK.
- Van Rensburg BJ *et al.* (2000) Testing generalities in the shape of patch occupancy frequency distributions. *Ecology*, **8**, 3163-3177.
- Van Wyk AE (1996) Biodiversity of the Maputland Centre. In: *The Biodiversity in African Savannas*. (eds van der Maesen LJG, van der Burgt XM, van Medenbach de Rooy JM), pp. 198-207. Kluwer Academic Publishers, Dordrecht.
- Vida S (1993) A computer program for non-parametric receiver operating characteristic analysis. *Computer Methods and Programs in Biomedicine*, **40**, 95-101.
- Wessels KJ *et al.* (2000) Incorporating land cover information into regional biodiversity assessments in South Africa. *Animal Conservation*, **3**, 67-79.
- White F (1983) *The Vegetation of Africa: a Descriptive Memoir to Accompany the UNESCO/AETFAT/ UNSO Vegetation Map of Africa*. Natural Resources Research XX. UNESCO, Paris.
- Williams BG *et al.* (2000) Where are we now? Where are we going? The demographic impact of HIV/AIDS in South Africa. *South African Journal of Science*, **96**, 297-300.
- Zweig MH, Campbell G (1993) Receiver-operating characteristic (ROC) plots: a fundamental evaluation tool in clinical medicine. *Clinical Medicine*, **39**, 561-577.

Appendix 1 List of 179 species included in the analyses.

Birds	
Common name	Scientific name
Anteater Chat	<i>Myrmecocichla formicivora</i>
Blackchested Prinia	<i>Prinia flavicans</i>
Blackheaded Canary	<i>Serinus alario</i>
Blackthroated Canary	<i>Serinus atrogularis</i>
Blue Korhaan	<i>Eupodotis caerulescens</i>
Buffstreaked Chat	<i>Oenanthe bifasciata</i>
Bully Canary	<i>Serinus sulphuratus</i>
Cape Bunting	<i>Emberiza capensis</i>
Cape Canary	<i>Serinus canicollis</i>
Crimsonbreasted Shrike	<i>Laniarius artococcineus</i>
Dark Chanting Goshawk	<i>Melierax metabates</i>
Drakensberg Siskin	<i>Pseudochloroptila symonsi</i>
Dusky Sunbird	<i>Nectarinia fusca</i>
Forest Canary	<i>Serinus scotops</i>
Ground Woodpecker	<i>Geocolaptes olivaceus</i>
Kalahari Robin	<i>Erythropygia paena</i>
Karoo Korhaan	<i>Eupodotis vigorsii</i>
Karoo Robin	<i>Erythropygia coryphaeus</i>
Larklike Bunting	<i>Emberiza impetuani</i>
Longtailed Shrike	<i>Corvinella melanoleuca</i>
Ludwig's Bustard	<i>Neotis ludwigii</i>
Malachite Sunbird	<i>Nectarinia famosa</i>
Pale Chanting Goshawk	<i>Melierax canorus</i>
Redcrested Korhaan	<i>Eupodotis ruficrista</i>
Redeyed Bulbul	<i>Pycnonotus nigricans</i>
Rock Bunting	<i>Emberiza tahapisi</i>
Rock Kestrel	<i>Falco tinnunculus</i>
South African Cliff Swallow	<i>Hirundo spilodera</i>
South African Shelduck	<i>Tadorna cana</i>
Stanley's Bustard	<i>Neotis denhami</i>
Streakyheaded Canary	<i>Serinus gularis</i>
Tractrac Chat	<i>Cercomela tractrac</i>
Whitethroated Canary	<i>Serinus albogularis</i>
Yellow Canary	<i>Serinus flaviventris</i>

Mammals

Common name	Scientific name
Cape pangolin	<i>Manis temminckii</i>
Cape serotine bat	<i>Eptesicus capensis</i>
Caracal	<i>Felis caracal</i>
Giant golden mole	<i>Chrysothalax trevelyani</i>
Grant's rock mouse	<i>Aethomys granti</i>
Gunning's golden mole	<i>Amblysomus gunningi</i>
Hottentot golden mole	<i>Amblysomus hottentotus</i>
Meller's mongoose	<i>Rhynchogale melleri</i>
Namaqua rock mouse	<i>Aethomys namaquensis</i>
Red duiker	<i>Cephalophus natalensis</i>
Riverine rabbit	<i>Bunolagus monticularis</i>
Rock dassie	<i>Procavia capensis</i>

South African lesser bushbaby	<i>Galago moholi</i>
Striped polecat	<i>Ictonyx striatus</i>
Suricate	<i>Suricata suricatta</i>
Verreaux's mouse	<i>Myomyscus verreauxii</i>
Wahlberg's epauletted fruit bat	<i>Epomophorus wahlbergi</i>
Water mongoose	<i>Atilax paludinosus</i>
Yellow mongoose	<i>Cynictis penicillata</i>

Butterflies

Abantis bicolor
Acraea natalica
Belenois aurota
Catopsilia florella
Charaxes jasius
Colias electo
Colotis danae
Danaus chrysippus
Dira swanepoeli
Eurema brigitta
Freyeria trochylus
Henotesia perspicua
Lepidochrysops bacchus
Papilio dardanus
Papilio demodocus
Papilio euphranor
Papilio nireus
Pontia helice
Zizeeria knysna

Reptiles

Lizards	Snakes	Tortoises
<i>Acontias plumbeus</i>	<i>Amblyodipsas concolor</i>	<i>Geochelone pardalis</i>
<i>Bradypodium damaranum</i>	<i>Bitis atropos</i>	<i>Homopus areolatus</i>
<i>Chamaeleo dilepis</i>	<i>Bitis caudalis</i>	<i>Homopus boulengeri</i>
<i>Chamaeleo namaquensis</i>	<i>Bitis cornuta</i>	<i>Homopus femoralis</i>
<i>Chamaesaura aneae</i>	<i>Bitis gabonica</i>	<i>Homopus signatus</i>
<i>Chondrodactylus angulifer</i>	<i>Causus defilippii</i>	<i>Kinixys belliana</i>
<i>Cordylus giganteus</i>	<i>Dasypeltis inornata</i>	<i>Kinixys lobatsiana</i>
<i>Cordylus macrophallus</i>	<i>Dispholidus typus</i>	<i>Kinixys natalensis</i>
<i>Heliobolus lugubris</i>	<i>Hemachatus haemachatus</i>	<i>Kinixys spekii</i>
<i>Homopholis wahlbergi</i>	<i>Homoroselaps dorsalis</i>	<i>Psammobates geometricus</i>
<i>Mabuya capensis</i>	<i>Lamprophis aurora</i>	<i>Psammobates oculifer</i>
<i>Mabuya homalocephala</i>	<i>Lamprophis inornatus</i>	<i>Psammobates tentorius</i>
<i>Nucras lalandei</i>	<i>Lycodonomorphus rufulus</i>	
<i>Nucras livida</i>	<i>Macrelaps microlepidotus</i>	
<i>Pedioplanis laticeps</i>	<i>Naja nivea</i>	
<i>Pedioplanis namaquensis</i>	<i>Psammophis subtaeniatus</i>	
<i>Scelotes mirum</i>	<i>Python sebae</i>	
<i>Tropidosaura montana</i>	<i>Typhlops bibronii</i>	
<i>Varanus albigularis</i>	<i>Typhlops fornasinii</i>	

Other invertebrates**Dung beetles**

Chironitis audens
Copris cornifrons
Epirinus flagellatus
Epirinus gratus
Garreta unicolor
Gymnopleurus humanus
Metacatharsius marani
Neosisyphus infuscatus
Neosisyphus mirabilis
Onitis minutus
Onthophagus asperulus
Onthophagus binodis
Onthophagus cameloides
Onthophagus immundus
Onthophagus stigmosis
Phalops ardea
Scarabaeus garipepinus
Scarabaeus rugosus
Scarabaeus aesculapius

Jewel beetles

Acmaeodera albovilloso
Acmaeodera grata
Julodis cirrosa
Julodis viridipes
Lampetis gregaria
Lampetis viridimarginata
Megactenodes reticulata
Monosacra lalandei
Neojulodis tomentosa
Phlocteis exasperata
Pseudophlocteis vidua
Scaptelytra aliena
Sphenoptera brincki
Sternocera orissa

Antlions

Cymothales bouvieri
Cymothales illustris
Golafrus oneili
Palparellus festivus
Palpares annulatus
Palpares cataractae
Palpares lentus
Palpares sobrinus
Palpares sparsus
Palpares speciosus
Pamexis karoo

Termites

Stolotermes
Porotermes
Fulleritermes
Apicotermes
Macrotermes (4 species)
Termes
Allodontotermes
Cryptotermes (2 species)
Hodotermes