Biodiversity and climate change: a South African perspective

by

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Biodiversity and climate change: a South African perspective

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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 exercises. The lack of detailed distribution data for appreciable numbers of taxa demands a modeling solution. We develop a climate envelope model to predict potential distribution range changes. The model can be used to interpolate the distributions of poorly sampled taxa as well as predict responses to a changing climate. It is predicted that species from the more arid western parts of South Africa will be subject to severe range contraction and range shifts whereas the species from the more mesic eastern parts will experience range contraction with limited range shift. Species that could act as climate change indicator taxa are identified based on their predicted extreme range change responses to climate change. Red-data and vulnerable species were more likely to display range change than less threatened species. Without mitigatory action, conservation areas are likely to lose species. The likelihood of successful range shifts will be affected by the nature of novel communities, habitat suitability and the degree of land transformation encountered. Given the extent of the predicted spatial responses, conservation planners can no longer afford to ignore future climate impacts on species distribution patterns. Disease risk profiles are also expected to change with climate; currently, susceptible forestry plantations exist in areas which may be invaded by an economically important pathogen. Resistant clones should be planted in these future high-risk areas. A decrease in precipitation is an important feature of a future climate. This decrease is expected to impact on the agricultural sector by reducing total employment as producers switch to a more extensive production pattern. The total decline in welfare, therefore, will fall disproportionately on the poor. Climate change presents a significant threat to the South African biodiversity estate, and our ability to manage this transition in the face of changing and competing land uses. Adaptation and mitigation options do exist but they are hampered by a lack of definitive analyses, and ultimately, political will to prioritise the threat of climate change.

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Disclaimer

This thesis consists of a series of chapters that have been prepared for submission to, or publication in, a range of scientific journals. As a result styles may vary between chapters in the thesis and overlap may occur to secure publishable entities.

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CHAPTER 1

Introduction

Introduction

Over the past decade, biodiversity and anthropogenic climate change have seen intermittent coverage in the popular media, having to depend on popularly reported links to environmental disasters such as wild fires, droughts, tropical storms and floods to warrant international news worthiness. Scientific interest in climate change issues has been more consistent, if less spectacular from a media point of view. A consensus scientific opinion of the global nature of climate change was first formalized in the First Assessment Report (FAR) of the Intergovernmental Panel on Climate Change (http://www.ipcc.ch) (IPCC 1990a,b,c). At that time, the report had a mandate to review the state of knowledge about climate change, and to present an up-to-date consensus scientific opinion. The report, which consisted of three volumes, placed considerable emphasis on the detection of climate change signals amidst long-term natural climate variation and assessing the evidence for anthropogenic sources for these changes. It is unclear if the 1990 report directly stimulated climate change related investigations but the subsequent political controversy about who is responsible for how much climate change raised the profile of climate change to a legitimate global concern. Although a Second Assessment Report was scheduled for 1995, mounting evidence prompted the IPCC to release Supplements to the Scientific Assessment and Impacts Assessment of FAR in 1992 (IPCC 1992a,b) as well as Special Reports on radiative forcing (IPCC 1994a), national greenhouse gas inventories (IPCC 1994b) and technical guidelines for studying impacts and adaptations to climate change (IPCC 1994c). Further momentum for the global awareness of climate change as a real threat was gained at the Earth Summit in Rio de Janeiro in 1992. At this meeting the United Nations Framework Convention on Climate Change (UNFCCC, http://unfccc.int) was signed by about 170 countries, including the United States, who is responsible for approximately a third of global carbon dioxide emissions. The UNFCCC called for a voluntary reduction of greenhouse gas emissions to 1990 levels by the year 2000. By the time the 1995 Second Assessment Report (SAR) (IPCC 1995a,b,c,d) was released, signatories to the UNFCCC realized that a more binding commitment to the reduction of green house gas emission was needed if any real progress was to be made. As a result, the Kyoto Protocol came into being in 1997, and will become legally binding for signatories as soon as 55 Parties to the Convention ratify (or approve, accept, or accede) the Protocol. These 55 parties have to include enough Annex I Parties (developed countries, or countries transitioning to a market economy, http://unfccc.int/resource/conv/annex1.html), to account for at least 55% of the carbon emissions of all Annex I Parties. As of 6 June 2003, 110 countries have ratified the Protocol, accounting for 43% of 1990 global carbon emission levels (http://unfccc.int/resource/convkp.html#kp).

Although the United States refused to ratify the Kyoto Protocol after initially supporting the UNFCCC, the resultant media coverage catapulted climate change into the limelight and raised global public awareness. This increase in global interest following the SAR in climate change is reflected not only in the number of special reports (five) the IPCC commissioned before the 2001 Third Assessment Report (TAR), but also in the scope covered by these reports: regional impacts (IPCC 1997), aviation (IPCC 1999), technology transfer (IPCC 2000), emissions scenarios (IPCC 2000) and forestry and land use change (IPCC 2000).

The TAR 2001 (IPCC 2001 a,b,c,d) summarised a growing body of evidence that the global climate was indeed changing at an unprecedented rate, most likely due to anthropogenic activities, and that these changes in climate are causing severe, and possibly irreversible, changes in physical and biological systems (IPCC 2001c). Given the severity of the situation, there is a strong focus on assessment of vulnerabilities and an identification of adaptation and mitigation strategies.

It is clear then, that the IPCC reports underwent a shift in focus from just detecting climate change at a global scale, to attributing these changes to anthropogenic activities, to estimating general effects at finer scales, to quantifying effects on specific systems and finally, to adaptation and mitigation strategies. In the context of this thesis, the interest lies in climate change effects on biodiversity. Biodiversity conservation lacks a global coordinating body similar to the IPCC (see Mace et al. 2000) and subsequently, public and scientific awareness of the biodiversity crisis (Pimm 2001) is slower to gain momentum. Seminal papers on vulnerable hotspots (e.g. Myers et al. 2000), the value of biodiversity dependent-ecosystem services (Costanza et al. 1997, Balmford et al. 2002) and specific case studies of the decline of charismatic mammals (e.g. Walsh et al. 2003) all contribute to raising biodiversity awareness. By virtue of its association with sustainable development, biodiversity received a lot of coverage at the recent World Summit on Sustainable Development held in Johannesburg, August 2002. Although this association between biodiversity and sustainable development is not as clear-cut and definitive as publicized catastrophic impacts of climate change, the net effect of raising public awareness was very similar. The IPCC responded to this increased awareness by publishing a Technical Paper on Climate Change and Biodiversity in 2002 in response to a request from the United Nations Convention on Biological Diversity (IPCC 2002).

It is against this backdrop of increased awareness of the immediacy of climate change and the biodiversity crisis that this thesis on the interface between climate change and biodiversity for South Africa is presented. Even without climate change, land-use change poses a serious threat to biodiversity (Schlesinger et al. 2001). In-depth studies of the biodiversity responses to climate change have been identified as a conservation research priority for the next decade (Schlesinger et al. 2001). This thesis is intended as a starting point to address three major shortcomings identified by the IPCC reports: climate change impacts at finer than regional scales, climate change impacts on biodiversity, and finally, climate change impacts on biodiversity at these finer scales. The existing reports on climate change effects at regional scales and climate change effects on biodiversity primarily deal with Africa as a region, with some isolated examples (IPCC 2002). However, conservation planning is usually done at the scale of individual countries (Erasmus et al. 1999) (with the possible exception of transfrontier conservation areas, (see http://www.peaceparks.org)) and therefore country specific studies are critical for climate change-integrated conservation strategies (Hannah et al. 2002).

At any scale, the interface between climate change and biodiversity is by no means a simple one and therefore this study is not meant to be a comprehensive guide to potential climate impacts on South African biodiversity. Instead this thesis has two main foci: first, to quantify the potential responses of biodiversity to climate change and assess the resulting conservation implications, and secondly, to investigate the robustness of the methodologies followed to arrive at these assessments. As such it provides a point of departure for further, more focused studies, as well as a methodological reference.

The first four chapters of this thesis make up the first focus. In chapter 1, a climate envelope model to predict the potential responses of species distributions to climate change is developed. Essentially, this model derives a typical climate envelope for a particular species, and given a changed climate, identifies areas where the changed climate matches the climatic conditions of the climate envelope that was derived from the species' present range. Such areas are then identified as potential novel distribution ranges for the particular species. For illustration purposes, the model is applied to antlion distribution data.

The fact that this approach ignores several other factors that might be critical in determining the final distribution range does not render the approach useless as suggested by Davis et al. (1998), and to a lesser extent by Petchey et al. (1999). Huntley (1998) has shown that climate is an important determinant of species distributions, and that species have responded to climate change in the paleontological past by range shifts. Several studies (Pounds et al. 1999, Parmesan 1996, 1999) and reviews (Hughes 2000, Stenseth et al. 2002, Walther et al. 2002, Parmesan & Yohe 2003, Root et al. 2003) have shown that individual species have already responded to climate change by shifting distributions. Midgley et al. (2002) provides further support for modeling individual species instead of an entire biome. The climate-dependent individual species-based modeling approach that was followed is a hybrid approach between what the IPCC (IPCC 2002) calls an ecosystem movement approach and an ecosystem modification approach. Due to species' differential responses to a changing climate, ecosystems will not move as units, but rather disassemble and form new assemblages (IPCC 2002). By modeling individual species, the ecosystem modification approach was followed, but due to a lack of knowledge on species interactions for any large number of species, only climate was used as a determinant for the new assemblage. The validity of this approach has sparked an ongoing debate in the literature (see critique on Samways et al. 1999 by Sutherst 2003, and the response in Samways 2003), and it will be further elucidated where relevant in each chapter.

Chapter 2 sees the application of the model developed in chapter 1 to a selection of representative South African biodiversity elements. The analysis proceeds on a taxon by taxon basis, and the potential distribution changes for the country as a whole as well as for a flagship conservation area are quantified. A subset of species regarded as vulnerable and/or endangered is also analysed separately. Finally, these potential distribution shifts are put into context by looking at the availability of suitable habitat corridors between current and predicted distribution ranges.

Chapters 3 and 4 have more indirect links to conservation. Conservation is a legitimate land-use that has to compete with other forms of land-use, such as intensive agriculture and forestry, for a limited resource pool. The viability of conservation as an alternative form of land-use will change with a changing climate as conservation goals change with shifting distribution patterns. However, competing land-uses will experience similar climatic constraints, and their response to climate change might be beneficial to conservation, i.e. currently marginal agricultural lands might become too marginal for crop production but still be sufficient for more biodiversity-friendly rangeland farming. Therefore, it is of interest to conservation planners to also have a measure of the potential response of competing land-uses to climate change. Two case studies are presented; chapter 3 predicts the future distribution of two economically important forestry pathogens and chapter 4 investigates the effects of reduced precipitation on the agricultural sector in the Western Cape. Chapter 4 also touches on the social dimension by looking at potential consequences for the labour force as production patterns shift in response to decreased precipitation.

The last two chapters form the second, more methodological, focus area of this thesis. During the analyses in chapters 1 to 4, limitations of the modeling approach were identified and two of these shortcomings were addressed in the last two chapters. Once again, the analyses are not meant to be exhaustive in their description of unwanted model behaviours, but they rather serve as solution oriented case studies. Chapter 5 quantifies the variation associated with any particular probability of occurrence value by using a resampling jackknife procedure. This enables the modeller to use variation in the predicted probabilities of occurrence as an additional constraint to refine predicted distributions.

Finally, chapter 6 compares 3 different kinds of predictive distribution models. The comparisons are done in a spatially explicit manner, and it was found that disagreement between models occurred in an area of ecological transition. Identifying such transition areas prior to a predictive modeling exercise can significantly improve model performance.

I present this work as a point of departure for further, more focused studies of climate change-biodiversity interactions in South Africa. It is not intended as a complete handbook of potential impacts or methods; instead, I hope to elucidate commonalities with IPCC regional assessments and hope that the results will be useful to feed into policymaking processes. As a final product, I summarize lessons learnt from this entire thesis into recommendations for a national study on climate change effects on biodiversity.

References

Balmford A, Bruner A, Cooper P, Costanza R, Farber S, Green RE, Jenkins M, Jefferiss P, Jessamy V, Madden J, Munro K, Myers N, Naeem S, Paavola J, Rayment M, Rosendo S, Roughgarden J, Trumper K & Turner RK (2002) Economic reasons for conserving wild nature. *Science* 297: 950-953.

Costanza R, d'Arge R, de Groot R, Farberk S, Grasso M, Hannon B, Limburg K, Naeem S, O'Neill RV, Paruelo J, Raskin RG, Sutton P & van den Belt M (1997) The value of the world's ecosystem services and natural capital. *Nature* 387:253-260.

Davis AJ, Lawton JH, Shorrocks B & Jenkinson LS (1998) Individualistic species responses invalidate simple physiological models of community dynamics under global environmental change. *Journal of Animal Ecology* 67: 600-612.

Erasmus BFN, Freitag S, Gaston KJ, Erasmus BH, & Van Jaarsveld AS (1999) Scale and conservation planning in the real world. *Proceedings of the Royal Society of London Series B* 266:315-319.

Hannah L, Midgley GF & Millar D (2002) Climate change-integrated conservation strategies. *Global Ecology & Biogeography* 11:485-495.

Hughes L (2000) Biological consequences of global warming: is the signal already apparent? *Trends in Ecology and Evolution* 15: 56-61.

Huntley B (1998) The dynamic response of plants to environmental change and the resulting risks of extinction. In: *Conservation in a changing world*, Mace GM, Balmford A & Ginsberg JR (Eds). Cambridge University Press, UK, pp 69-88.

IPCC (1990a) IPCC First Assessment Report: Scientific Assessment of Climate change – Report of Working Group I. (Eds) Houghton JT, Jenkins GJ & Ephraums JJ. Cambridge University Press, UK, pp 365.

IPCC (1990b) IPCC First Assessment Report: Impacts Assessment of Climate Change – Report of Working Group II. (Eds) McG Tegart WJ, Sheldon GW & Griffiths DC. Australian Government Publishing Service, Australia.

IPCC (1990c) The IPCC Response Strategies – Report of Working Group III. Island Press, USA, pp 270.

IPCC (1992a) Climate Change 1992 - The Supplementary Report to The IPCC Scientific Assessment. (Eds) Houghton JT, Callander BA & Varney SK. Cambridge University Press, UK, pp 205.

IPCC (1992b) Climate Change 1992 - The Supplementary Report to The IPCC Impacts Assessment. (Eds) McG Tegart WJ & Sheldon GW. Australian Government Publishing Service, pp 112.

IPCC (1994a) IPCC Special report: Radiative Forcing of Climate Change and An Evaluation of the IPCC IS92 Emissions Scenarios. (Eds) Houghton JT, Meira Filho LG, Bruce J, Hoesung Lee, Callander BA, Haites E, Harris N & Maskell K. Cambridge University Press, UK, pp 339.

IPCC (1994b) IPCC Guidelines for National Greenhouse Gas Inventories. IPCC Secretariat, Geneva.

IPCC (1994c) IPCC Technical Guidelines for Assessing Climate Change Impacts and Adaptations with a Summary for Policy Makers and a Technical Summary. Carter TR, Parry ML Harasawa H & Nishioka S. Department of Geography, University College London, UK and the Center for Global Environmental Research, National Institute for Environmental Studies, Japan, pp 59.

IPCC (1995a) <u>IPCC Second Assessment Synthesis of Scientific-Technical Information Relevant to Interpreting Article 2 of the UNFCCC</u>. IPCC, Geneva, Switzerland, pp 64.

IPCC (1995b) Climate Change 1995: The Science of Climate Change. Contribution of Working Group I to the Second Assessment of the Intergovernmental Panel on Climate Change. (Eds) Houghton JT, Meira Filho LG, Callender BA, Harris N, Kattenberg A & Maskell K. Cambridge University Press, UK, pp 572.

IPCC (1995c) Climate Change 1995: Impacts, Adaptations and Mitigation of Climate Change: Scientific-Technical Analyses. Contribution of Working Group II to the

Second Assessment of the Intergovernmental Panel on Climate Change. (Eds) Watson RT, Zinyowera MC & Moss RH. Cambridge University Press, UK, pp 878.

IPCC (1995d) Climate Change 1995: Economic and Social Dimensions of Climate Change. Contribution of Working Group III to the Second Assessment of the Intergovernmental Panel on Climate Change. (Eds) Bruce JP, Lee H, Haites EF. Cambridge University Press, UK, pp 448.

IPCC (1997) The Regional Impacts of Climate Change: An Assessment of Vulnerability. (Eds) Watson RT, Zinyowera MC & Moss RH. Cambridge University Press, UK, pp 517.

IPCC (1999) Aviation and the Global Atmosphere. (Eds) Penner JE, Lister DH, Griggs DJ, Dokken DJ & McFarland M. Cambridge University Press, UK, pp 373.

IPCC (2000a) Land Use, Land-Use Change, and Forestry. (Eds) Watson RT, Noble IR, Bolin B, Ravindranath NH, Verardo DJ & Dokken DJ. Cambridge University Press, UK, pp 375.

IPCC (2000b) Emissions Scenarios. (Eds) Nakicenovic N & Swart R. Cambridge University Press, UK, pp 570.

IPCC (2000c) Methodological and Technological Issues in Technology Transfer. (Eds) Metz B, Davidson O, Martens J, Van Rooijen S & Van Wie Mcgrory L. Cambridge University Press, UK, pp 432.

IPCC (2001a) Climate Change 2001: Synthesis Report. (Eds) Watson RT and the Core Writing Team. Cambridge University Press, UK, pp 398.

IPCC (2001b) Climate Change 2001: The Scientific Basis. (Eds) Houghton JT, Ding Y, Briggs DJ, Noguer M, van der Linden PJ & Xiaosu D. Cambridge University Press, UK, pp 944.

IPCC (2001c) Climate Change 2001: Impacts, Adaptation & Vulnerability. (Eds) McCarthy JJ, Canziani OF, Leary NA, Dokken DJ & White KS. Cambridge University Press, UK, pp 1000.

IPCC (2001d) Climate Change 2001: Mitigation. (Eds) Metz B, Davidson O, Swart R & Pan J. Cambridge University Press, UK, pp 700.

IPCC (2002) Climate Change and Biodiversity: IPCC Technical Paper V. (Eds) Gitay H, Suarez A, Watson RT & Dokken DJ. IPCC Secretariat, Geneva, pp.86.

Mace GM, Balmford A, Boitani L, Cowlishaw G, Dobson AP, Faith DP, Gaston KJ, Humphries CJ, Vane-Wright RI, Williams PH, Lawton JH, Margules CR, May RM, Nicholls AO, Possingham HP, Rahbek C & van Jaarsveld AS (2000) It's time to work together and stop duplicating conservation efforts... *Nature* 405(6785):393.

Midgley GF, Hannah L, Millar D, Rutherford MC & Powrie LW (2002) Assessing the vulnerability of species richness to anthropogenic climate change in a biodiversity hotspot. *Global Ecology & Biogeography* 11:445-451.

Myers N, Mittermeier RA, Mittermeier CG, Da Fonseca GAB & Kent J (2000) Biodiversity hotspots for conservation priorities. *Nature* 403:853-858.

Parmesan C (1996) Climate and species' range. *Nature* 382: 765-766.

Parmesan C, Ryrholm N, Stefanescu C, Hill JK, Thomas CD, Descimon H, Huntley B, Kaila L, Kullberg J, Tammaru T, Tennent WJ, Thomas JA & Warren M (1999) Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature* 399: 579-583.

Parmesan C & Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421:37-42.

Petchey OL, McPhearson PT, Casey TM & Morin PJ (1999) Environmental warming alters food-web structure and ecosystem function. *Nature* 402: 69-72.

Pimm S (2001) *The world according to Pimm – a scientist audits the earth.* McGraw-Hill, New York, pp. 285.

Pounds JA, Fogden MPL & Campbell JH (1999) Biological response to climate change on a tropical mountian. *Nature* 398: 611-615.

Root T, Price JT, Hall KR, Schneider SH, Rosenzweig C & Pounds JA (2003) Fingerprints of global warming on wild animals and plants *Nature* 421-57-60

Samways MJ, Osborn R, Hastings H & Hattingh V (1999) Global climate change and accuracy of prediction of species geographical ranges: establishment success of introduced ladybirds (Coccinellidae, Chilocorus spp.) worldwide. *Journal of Biogeography* 26: 795–812.

Samways MJ (2003) Critical response from Professor Michael J. Samways. *Journal of Biogeography* 30:817.

Schlesinger WH, Clark JS, Mohan JE & Reid CD. (2001) Global environmental change – effects on biodiversity. In: *Conservation Biology: research priorities for the next decade,* Soule ME & Orians GH (eds). Island Press, London, pp. 175-223.

Stenseth N Chr, Mysterud A, Ottersen G, Hurrell JW, Chan K-S & Lima M (2002) Ecological effects of climate fluctuations. *Science* 297: 1292-1296

Sutherst RW (2003) Prediction of species geographical ranges. *Journal of Biogeography* 30: 805–816.

Walther G-R, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC, Fromentin J-M, Hoegh-Guldberg O & Bairlein F (2002) Ecological responses to recent climate change. *Nature* 416: 389-395.

CHAPTER 2

A modelling approach to antlion (Neuroptera: Myrmeleontidae) distribution patterns

A modelling approach to antlion (Neuroptera: Myrmeleontidae) distribution patterns

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ABSTRACT

The application of a model modified from Jeffree & Jeffree (1994) for investigating the distribution responses of selected antlion species to a climate change scenario was explored in this study. Modifications include a multivariate capability that facilitates the incorporation of precipitation seasonality, and provides useful outputs in the form of probability of occurrence values for each species. The model can be used to interpolate the distributions of poorly sampled taxa as well as predict responses to a changing climate. It is predicted that species from the more arid western parts of South Africa will be subject to severe range contraction and range shifts whereas the species from the more mesic eastern parts will experience range contraction with limited range shift. The likelihood of successful range shifts will be affected by the nature of novel communities, habitat suitability and the degree of land transformation encountered. Given the extent of the predicted spatial responses, conservation planners can no longer afford to ignore future climate impacts on species distribution patterns.

INTRODUCTION

The conservation of poorly sampled taxa presents special challenges to conservation biology. Information on the geographic distributions of such taxa should ideally be extended through intensive biodiversity surveys before conservation decision-making (Balmford & Gaston 1999), although this strategy is usually confounded by time and resource constraints (Freitag et al. 1998). Acknowledging that the use of poor distribution data may significantly affect land use and related economic efficiency of conservation practice (Balmford & Gaston 1999), an alternative strategy is to model the predicted distributions of species based on suitable broad-scale environmental parameters, e.g. soil, climate and vegetation types (Margules & Redhead 1995). In many instances this approach may require a number of assumptions, including: linear relationships between species' physiological tolerances and their distribution limits, minimal effects of interspecific interactions on species distributions, and that fewer rather than many abiotic variables determine distributions (Chown & Gaston 1999). In the context of the conservation crisis, however, predictive modelling remains one of the few practical alternatives likely to provide information on species distribution patterns and their range dynamics, at a time scale relevant to conservation practitioners.

A recent model developed by Jeffree & Jeffree (1994, 1996) to predict species' distribution patterns and their response to climate change (Intergovernmental Panel on Climate Change 1992) was investigated during this study. The model is straightforward and could potentially be applied to large numbers of taxa in a cost effective manner. The original model was modified by adding a multivariate capability that transcends pure climate matching (Tribe & Richardson 1994; Eeley et al. 1999). The output from this modified model is a spatially explicit set of probabilities of occurrence values for each species.

To demonstrate the potential value of this modified modelling approach, it was used to derive interpolated distributions of selected and poorly surveyed antlion species, and to generate climate-affected distribution patterns for these species under climate change conditions. Because antlions generally prefer arid areas (Mansell 1985a) and climate change models predict general aridification in southern Africa (Hewitson 1998), these neuropteran species were considered appropriate for exploring the value of such a climate-based distribution modelling procedure for poorly sampled taxa.

METHODS

The study was conducted at a subcontinental scale using climate data and antlion (Neuroptera: Myrmeleontidae) distribution data for South Africa. Data resolution was resolved to quarter degree grid cells (approximately 25 km × 25 km). The Computing Centre for Water Research (CCWR, University of Natal) provided climate data for 1858 grid cells encompassing South Africa. Neuroptera distribution data were extracted from the Plant Protection Research Institute (PPRI) database (see Freitag & Mansell 1997) which, for the antlions, comprises 606 records for 49 species. Expert opinion showed that model output based on less than nine sampling records produced spurious predictions and therefore sampling density together with biome representation and expert assessment of sampling bias were used to select appropriate species for inclusion in the model. Five species were selected to test the modelling approach, to illustrate the principles on which the model is based, and to demonstrate the ways in which the model can highlight potential conservation concerns. The selected species were Palpares caffer (Burmeister), a species endemic to southern Africa with the largest proportion of its distribution in the moister eastern parts of South Africa (Mansell, unpubl.); Palpares speciosus (Linnaeus), a species endemic to the Eastern and Western Cape provinces; Palparellus dubiosus (Péringuey), a species endemic to the arid western parts of South Africa; Pamexis luteus (Thunberg), a range-restricted species endemic to the Western Cape Fynbos biome (Low & Rebelo 1996) and Pamexis namaqua (Mansell), a range-restricted species from the Succulent Karoo biome of Namaqualand (Mansell 1985b). Although only five species were selected, they account for 26 % of the 606 records in the PPRI database and were regarded as representative for the purposes of this study.

The climate data initially selected were the mean minimum temperature of the coldest month and the mean maximum temperature of the hottest month for each grid square. Jeffree & Jeffree (1994, 1996) considered these two variables to be sufficient for their models of the distribution changes of European insect and plant species expected under scenarios of climate change. However, exploratory modeling in the present study revealed that these variables were insufficient for realistically describing antlion spatial distributions, partly as a result of the seasonal rainfall patterns in the southern African region. As there are strong east to west rainfall gradients across the subcontinent that have a marked influence on the biota (Schulze 1997; Harrison et al. 1997; Le Lagadec et al. 1998; Davis et al. 2000), and because antlions are generally xerophilous (Mansell 1985a), measures of precipitation were included as additional explanatory variables to increase the predictive power of the proposed model. Mean annual precipitation and precipitation seasonality were included. The latter can be seen as a joint measure reflecting when precipitation occurs as well as the amount recorded. Precipitation seasonality was calculated as the difference between the mean rainfall for February and the mean rainfall for August. These months were selected based on a factor analysis of the 12 monthly rainfall means which showed that February rainfall contributed most to Factor 1, explaining 56 % of the variance in monthly rainfall, and August rainfall contributed most to Factor 2 that explained an additional 37 % of the variance in monthly rainfall. A negative precipitation seasonality value indicates winter rainfall and a positive value summer rainfall. All mean values were calculated from climate data from the last 30 years. Two sets of climate data were used for the four variables employed; one set based on historic climate data and the other on a General Circulation Model (GCM) predicting climate change. The Hadley Centre Unified Model (HadCM2 with no sulphates) (http://www.meto.govt.uk/sec5/NWP/NWP_sys.html) GCM was used because it represents a worst-case scenario for South Africa, predicting the most extreme changes in climate (G. Kiker, pers. comm.). It predicts a temperature rise of 2.5 – 3 °C for South Africa by the time that atmospheric carbon dioxide levels have doubled from their pre-industrial levels. Erring on the side of caution, this means that significant changes in the regional climate can be expected by the year 2050 (Hewitson 1998) but possibly sooner. These changes can be expected to be significant given that climate fluctuations of similar magnitude led to biotic range shifts during the last glacial period (Allen et al. 1999).

The original bivariate Jeffree & Jeffree (1994) modelling approach proceeded as follows. A scatterplot of the values of all grid cells for any two chosen climate variables was defined as the climate space. The grid cells where a particular species was recorded was referred to as the known records (KR). The values of these two climate variables for all KR cells were used to construct an elliptical confidence region that was superimposed on the scatterplot (Fig. 1). The choice of an ellipse to define the confidence region implies the assumption that the shape of the realised niche in climate space is elliptical. The ellipse was chosen partly based on the work of Jeffree & Jeffree (1994, 1996) but also based on the need for a simple basic model that can be used for broad scale modelling for a large number of species. Although it would be possible to build a species-specific model that uses a more complex shape to define the realised niche in climate space, such a model would not be generalisable across species.

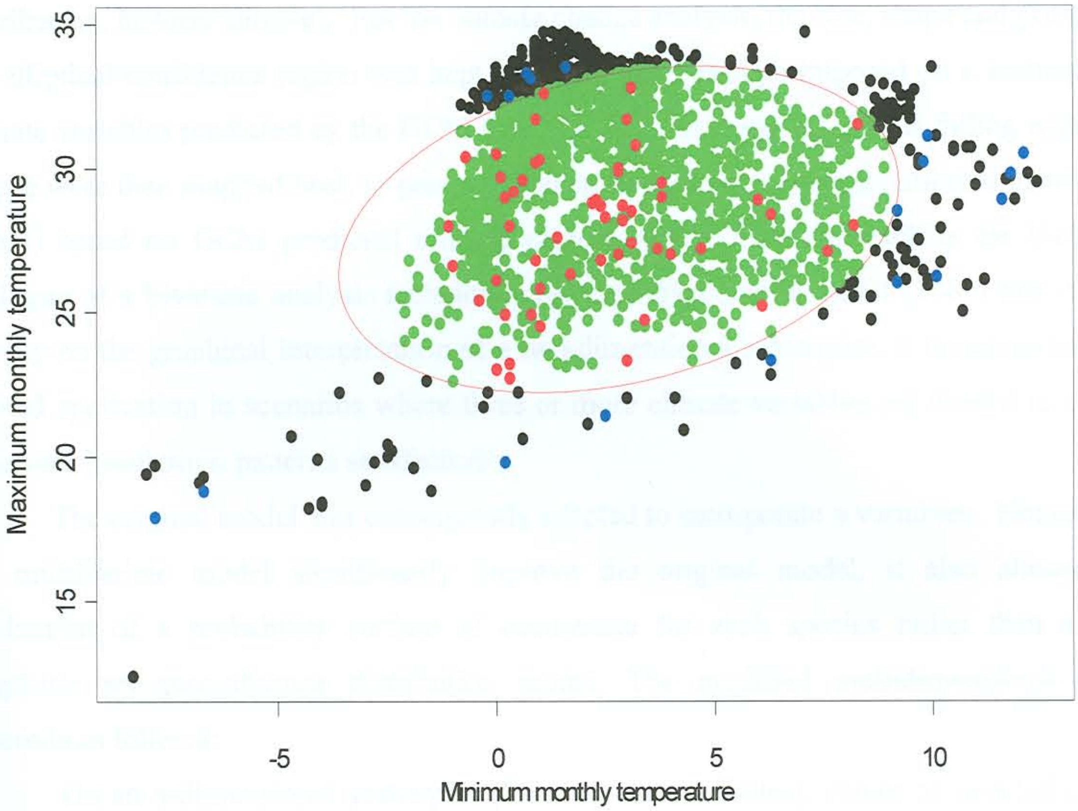

Fig. 1. Scatterplot of the minimum and maximum temperature values for 1858 quarter degree grid squares covering South Africa. Superimposed on this scatterplot is an elliptical confidence region whose size and shape was derived from historic temperature values in grid squares where Palpares caffer was recorded. Red dots represent known records for P. caffer falling inside the confidence region, blue dots represent known records that fall outside the confidence region, green dots represent the distribution predicted for this species by the climate data (interpolated distribution (ID) in the text), and black dots represent the grid squares where this species does not occur and where it was not predicted to occur.

All points falling within this elliptical confidence region were then mapped back on to geographical space to form an interpolated distribution where this species could occur. This interpolated distribution based on historic climate data was referred to as ID (interpolated distribution, historic climate). For the climate change analysis, the size, shape and position of the elliptical confidence region was kept constant, but it is superimposed on a scatterplot of climate variables predicted by the GCM (see Fig. 2 for an example). Points falling within the ellipse were then mapped back to geographical space to depict a climate affected distribution (CAD) based on GCM predicted climate change values. This approach is the biological analogue of a bivariate analysis technique described by Sokal & Rohlf (1981) and it relies heavily on the graphical interpretation of a two-dimensional scatterplot. It therefore has very limited application in scenarios where three or more climate variables are needed to explain observed distribution patterns satisfactorily.

The original model was consequently adapted to incorporate *n* variables. Not only did the multivariate model significantly improve the original model, it also allowed the production of a probability surface of occurrence for each species rather than a more simplistic presence-absence distribution model. The modified multidimensional model proceeds as follows:

On an *n*-dimensional scatterplot (for *n* climate variables), values of selected climate variables were plotted for each KR grid cell and subtracted mean climate values to generate transformed values for each grid cell. This procedure centres values around the origin of the multidimensional scatterplot. An $n \times n$ covariance matrix was calculated and then this matrix was used as an input to calculate eigen values and eigen vectors for the covariance matrix. The climate variable values of all grid cells were then transformed into this eigen vector space. The transformed climate variables were then divided by the eigen values and the distances of these points from the above origin follows a χ^2 distribution. This allows one to read the probability of occurrence of a species in any grid cell off a χ^2 probability table at the appropriate degree of freedom (KR-1). The technique is relatively straightforward and does not require considerable computing power. The outcome of this analysis is a probability of occurrence surface for each species across the country.

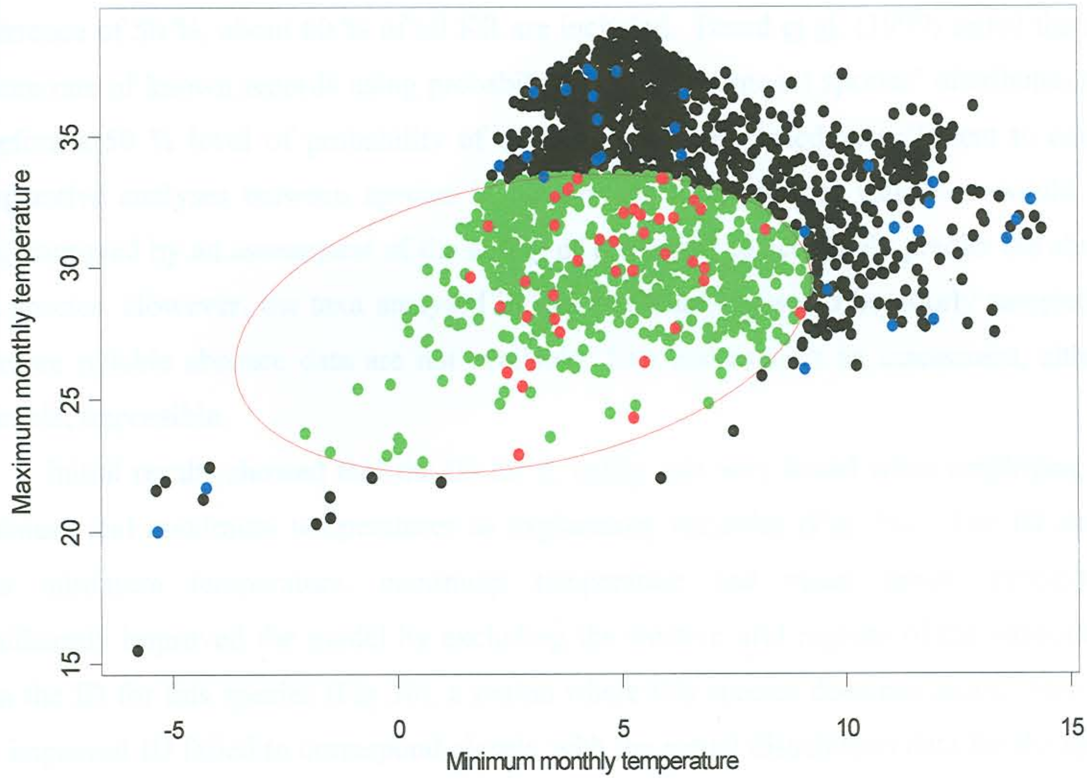

Fig. 2. Scatterplot of the GCM predicted minimum and maximum temperature values for 1858 quarter degree grid squares covering South Africa. Superimposed on this scatterplot is an elliptical confidence region whose size and shape were derived from historic temperature values in grid squares where Palpares caffer was recorded. Red dots represent known records for P. caffer falling inside the confidence region, blue dots represent known records that fall outside the confidence region, green dots represent the distribution predicted for this species by the climate data (climate affected distribution (CAD) in the text), and black dots represent the grid squares where this species does not occur and where it was not predicted to occur.

RESULTS

Because this modified multivariate model (Jeffree & Jeffree 1994) provides a probability of occurrence value for each grid cell, it was necessary to select an appropriate probability level to employ across the study for comparing results from different species. At a probability of occurrence of 50 %, about 60 % of all KR are included. Beard et al. (1999) found the same capture rate of known records using probabilistic models to model species' distributions and therefore a 50 % level of probability of occurrence was regarded as sufficient to conduct comparative analyses between species in the present study. Model validation would have been improved by an assessment of the ability of the model to accurately predict the absence of a species. However, the taxa analysed in this study are known to be poorly sampled and therefore reliable absence data are not available. This makes such an assessment, although desirable, impossible.

Initial results showed that the ID for P. caffer was very broad when employing only minimum and maximum temperatures as explanatory variables (Fig. 3a). The ID derived from minimum temperature, maximum temperature and mean annual precipitation significantly improved the model by excluding the western arid regions of the subcontinent from the ID for this species (Fig 3b), a region where this species does not occur. However, this improved ID failed to correspond closely with the actual distribution data for the species (Fig. 3b) because it predicted that the species would occur in the eastern summer rainfall region of South Africa and along the southern coastal region that has a predominantly winter rainfall pattern. Similar results for the other species confirmed that employing temperature and mean annual rainfall in the model does not adequately represent distributions that are strongly affected by seasonal rainfall patterns. For this reason the mean annual precipitation variable was replaced with a precipitation seasonality value. This resulted in a further improved predicted ID pattern for P. caffer (Fig. 4), using minimum and maximum temperature and precipitation seasonality as explanatory variables. Here the ID is limited to the eastern portions of South Africa, which is more consistent with the distribution data derived from the PPRI database. The improved predictions using precipitation seasonality together with minimum and maximum temperatures were consistent for all species except P. dubiosus, which yielded similar ID's when using either of the precipitation variables in conjunction with minimum and maximum temperatures.

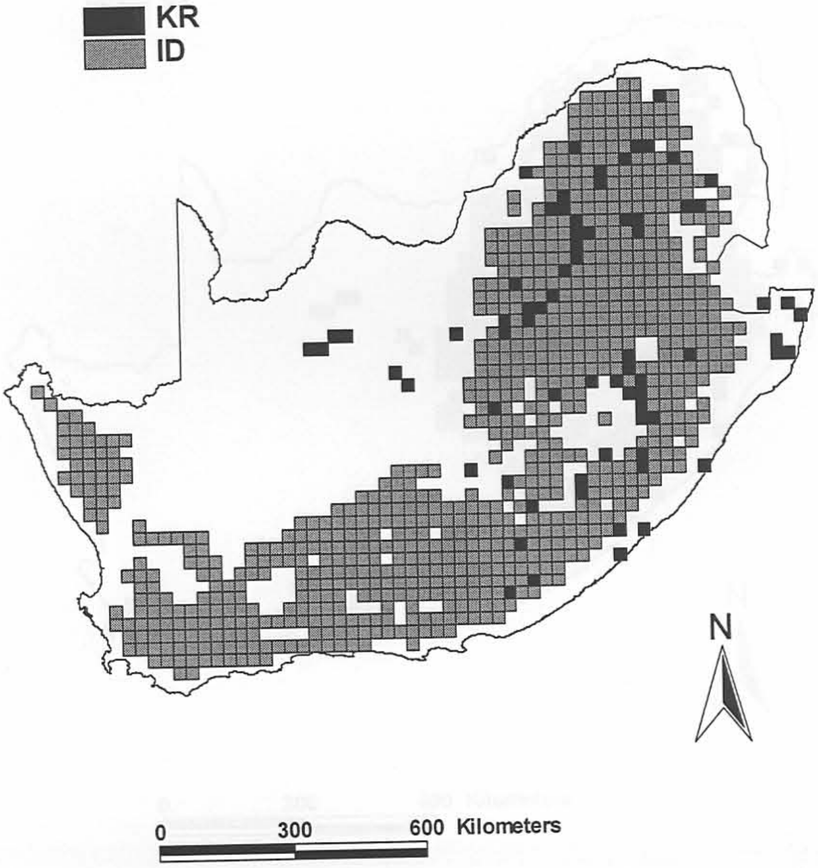

Fig. 3(a). These figures (3a and 3b) illustrate the modelling process. Black squares represent known records (KR) and grey squares represent the interpolated distribution. This figure shows the Interpolated distribution (ID) from historic climate data for Palpares caffer using minimum monthly temperature and maximum monthly temperature.

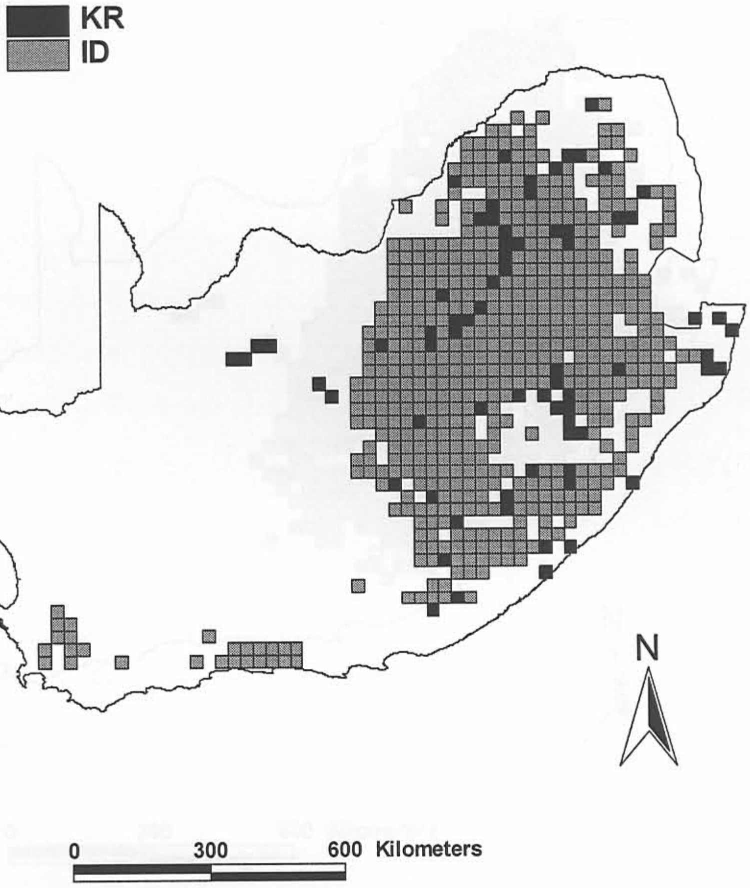

Fig. 3(b) Interpolated distribution (ID) from historic climate data for Palpares caffer using minimum monthly temperature, maximum monthly temperature and mean annual precipitation.

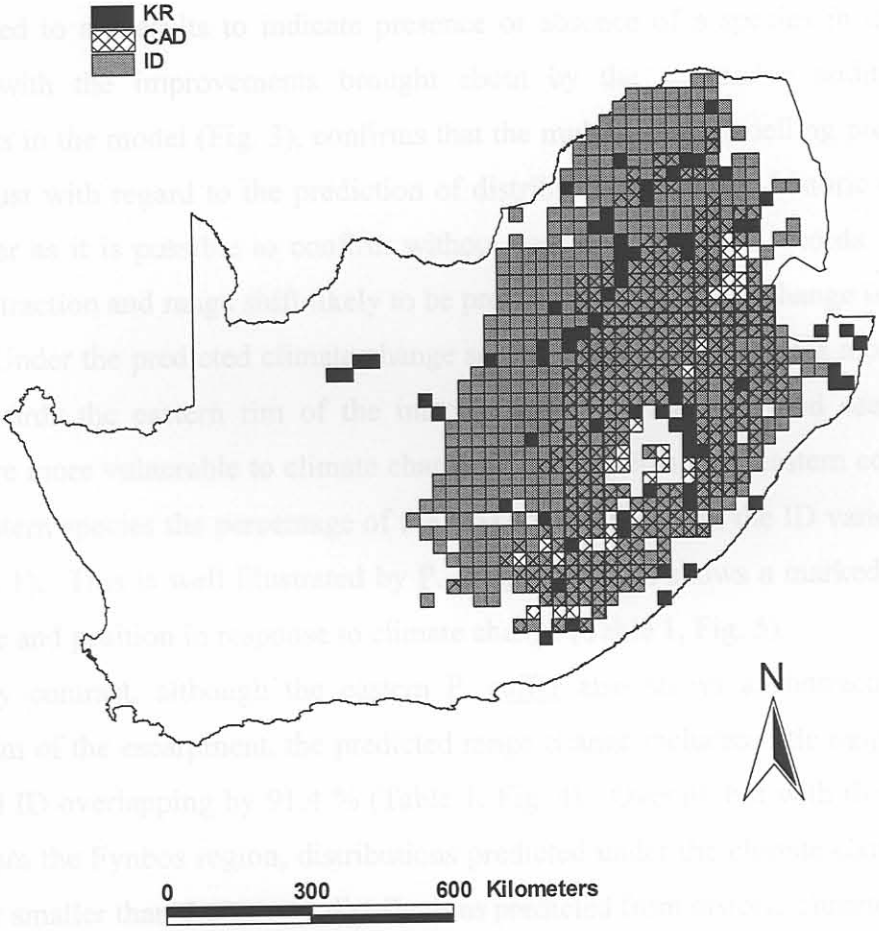

Fig. 4. Predicted distributions for <u>Palpares caffer</u> derived from minimum monthly temperature, maximum monthly temperature and precipitation seasonality. Black squares represent known records (KR) for this species, hatched squares represent the climate affected distribution (CAD) and grey squares represent the interpolated distribution from historic climate data

Nonetheless, following the seasonality-based procedure, on average 51.7 % (± SD 4.9) of the PPRI database-derived records fell within their respective ID's generated by the modified multivariate model. This is consistent with the 50 % probability of occurrence cut-off that was applied to all results to indicate presence or absence of a species in this study. This, together with the improvements brought about by the successive addition of rainfall parameters in the model (Fig. 3), confirms that the multivariate modelling procedure appears to be robust with regard to the prediction of distributions based on historic climate data, at least as far as it is possible to confirm without confirmed absence records. The degree of range contraction and range shift likely to be precipitated by climate change is summarized in Table 1. Under the predicted climate change scenario, the antlion species mostly show range shifts towards the eastern rim of the inland escarpment and it would seem that western species are more vulnerable to climate change (Figs 5-8) than their eastern counterparts.. For these western species the percentage of the CAD coinciding with the ID varies from 0 - 33.8 % (Table 1). This is well illustrated by P. dubiosus which shows a marked change in both range size and position in response to climate change (Table 1, Fig. 5).

By contrast, although the eastern P. caffer also shows a contraction towards the eastern rim of the escarpment, the predicted range change includes little range shift, with the CAD and ID overlapping by 91.4 % (Table 1, Fig. 4). Overall, but with the exception of P. luteus from the Fynbos region, distributions predicted under the climate change scenario are markedly smaller than the current distributions predicted from historic climate data (Table 1)

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DISCUSSION

Model characteristics

It is clear from this analysis that the modified model's ability to accurately predict distributions decreases if the distribution of the species being modelled straddles seasonal rainfall regions. For example, P. speciosus occurs in regions with markedly different seasonal rainfall patterns (Figs 6 & 9) resulting in the disjunct ID in Fig. 6. This distribution is unlikely to be biologically realistic, and clearly some additional improvements to the model are required to adequately deal with species that show this type of distribution pattern. These improvements may include more detailed information on the biology of this particular species to identify appropriate variables that drive its distribution pattern and a subsequent adjustment in the model to include such variables. Such adjustments might include modelling

Table 1. The number of grid cells occupied by each species. The values in brackets indicate percentages. Abbreviations: KR – Known records, ID – interpolated distribution from historical climate data, CAD – Predicted distribution from predicted climate data[1]. The results are from the multivariate improvement on Jeffree & Jeffree (1994) model at a 50% probability of occurrence

Species	KR	ID	CAD (CAD as % of ID)	KR falling inside ID (% of KR)	Overlap between ID and CAD (%CAD inside ID)
Palparellus dubiosus	24	461	59 (12,7)	12 (50)	16 (27,1)
Palpares caffer	74	684	361 (52,8)	43 (58,1)	330 (91,4)
Palpares speciosus	27	187	65 (34,8)	13 (48,1)	22 (33,8)
Pamexis luteus	15	16	18 (112,5)	7 (46,7)	1 (5,3)
Pamexis namaqua	9	12	6 (50,0)	5 (55,6)	0 (0)

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[1] The percentage overlap between ID and CAD was calculated using proportional overlap (Prendergast et al. 1993) where the number of coinciding grids cells is divided by the maximum number of possible overlapping grid cells, ie. the number of grid cells containing records of the smallest distribution.

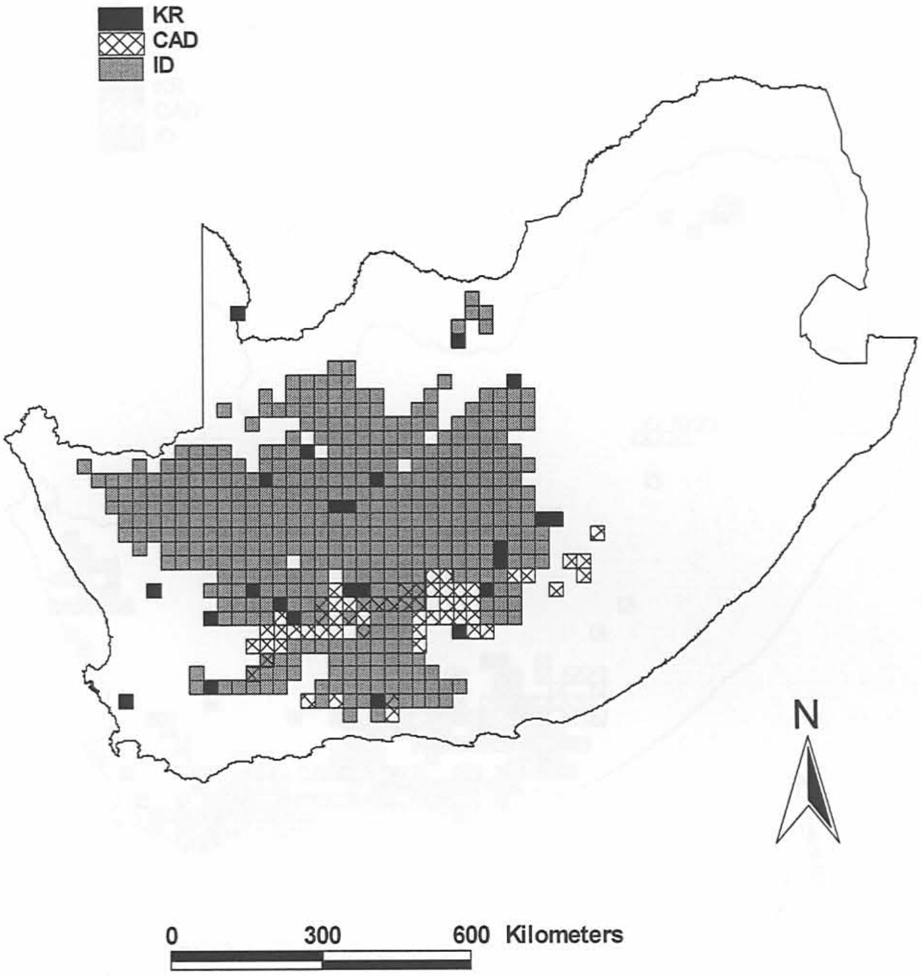

Fig. 5. Predicted distributions for Palparellus dubiosus derived from minimum monthly temperature, maximum monthly temperature and mean annual precipitation. Black squares represent known records (KR) for this species, hatched squares represent the climate affected distribution (CAD) and grey squares represent the interpolated distribution from historic climate data.

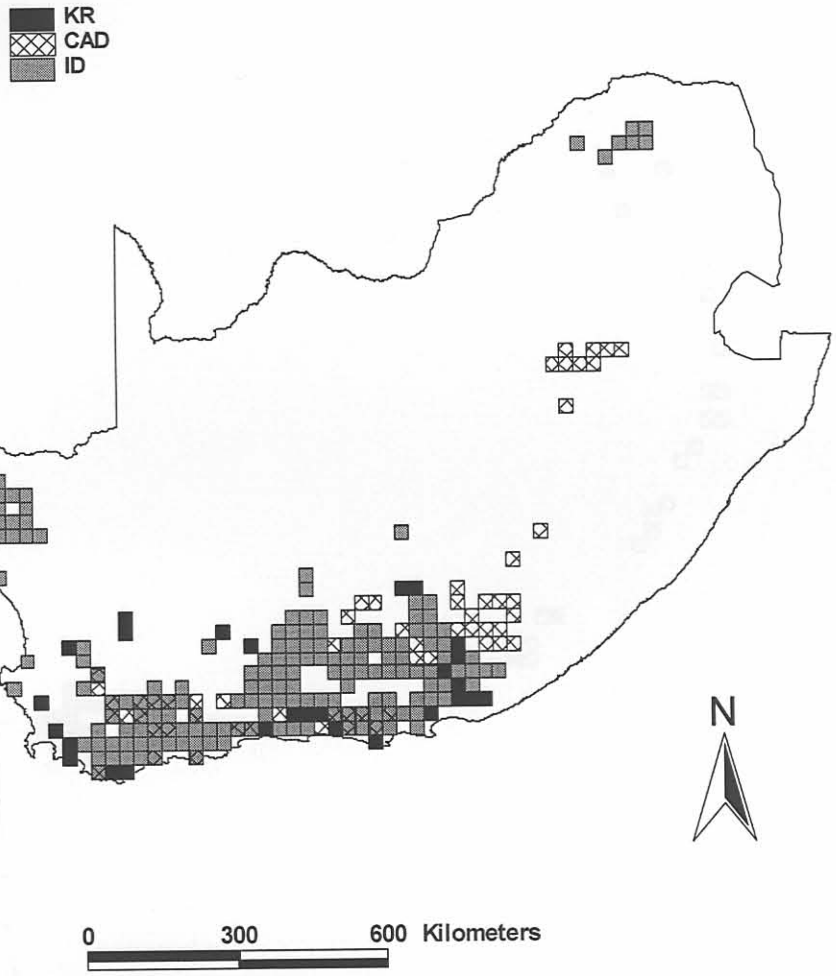

Fig. 6. Predicted distributions for <u>Palpares speciosus</u> derived from minimum monthly temperature, maximum monthly temperature and mean annual precipitation. Black squares represent known records (KR) for this species, hatched squares represent the climate affected distribution (CAD) and grey squares represent the interpolated distribution from historic climate data.

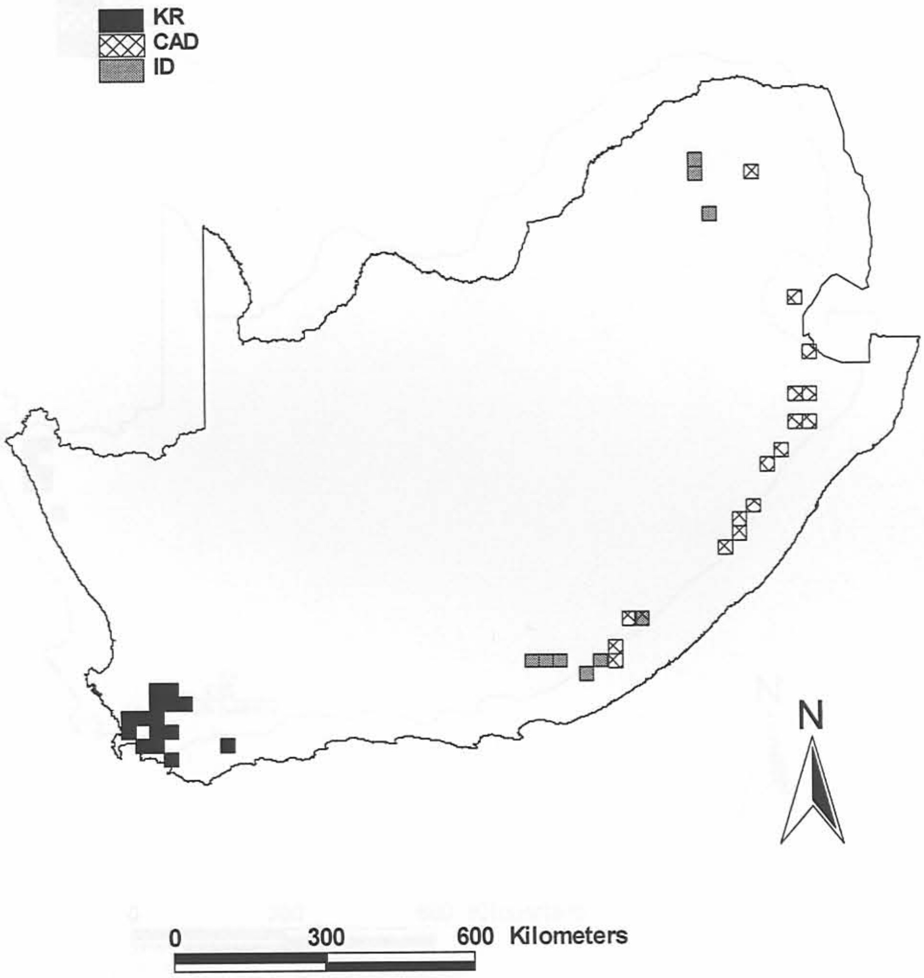

Fig. 7. Predicted distributions for Pamexis luteus derived from minimum monthly temperature, maximum monthly temperature and mean annual precipitation. Black squares represent known records (KR) for this species, hatched squares represent the climate affected distribution (CAD) and grey squares represent the interpolated distribution from historic climate data.

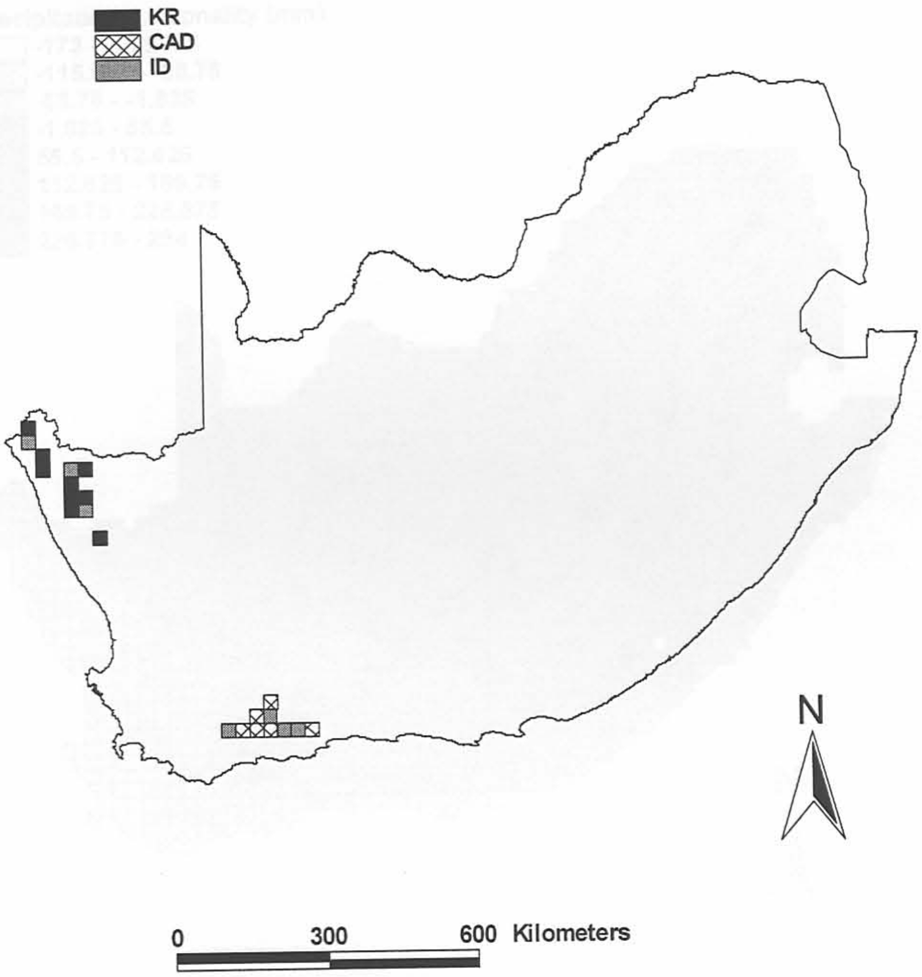

Fig. 8. Predicted distributions for Pamexis namaqua derived from minimum monthly temperature, maximum monthly temperature and mean annual precipitation. Black squares represent known records (KR) for this species, hatched squares represent the climate affected distribution (CAD) and grey squares represent the interpolated distribution from historic climate data.

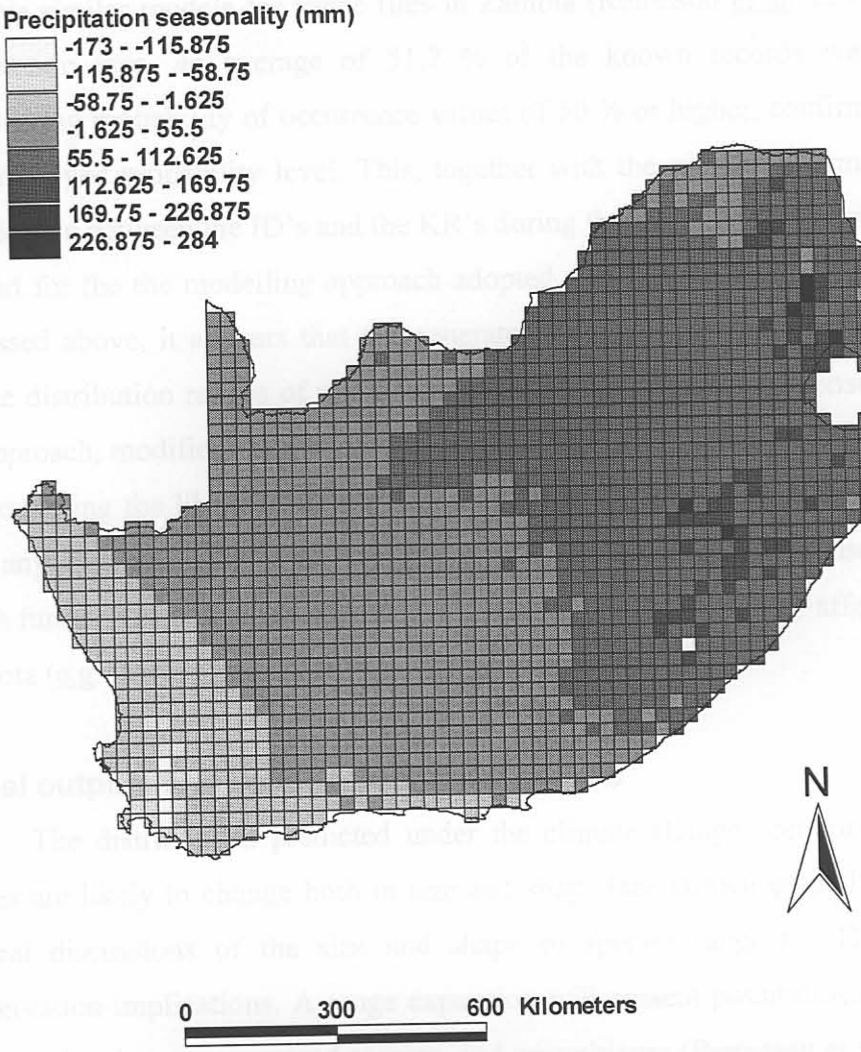

Fig. 9. Precipitation seasonality for South Africa, measured in mm, expressed as the difference in mean rainfall for February and August. A positive value indicates summer rainfall and a negative value winter rainfall.

distributions in the two major climate regions separately, a technique that has been used to improve similar models for tsetse flies in Zambia (Robinson et al. 1997a, b). Despite these problematic taxa, an average of 51.7 % of the known records were captured by IDs representing probability of occurrence values of 50 % or higher, confirming the relevance of this employed probability level. This, together with the progressive improvement in spatial coincidence between the ID's and the KR's during the modelling process (Figs 3a-b), provide support for the the modelling approach adopted. Apart from the obvious model limitations discussed above, it appears that the generated ID's provide reasonably realistic predictions for the distribution ranges of poorly sampled species (Figs 4-8).It consequently appears that the approach, modified from Jeffree & Jeffree (1994, 1996), and presented here will be useful for examining the likely effects of climate change on the distributions of a range of species from any specific region (Van Jaarsveld et al. 2000), and can also be used as a platform from which further, more detailed approaches to understanding the likely affects of climate change on biota (e.g. Davis et al. (1998a,b)), can be undertaken.

Model outputs and conservation implications

The distributions predicted under the climate change scenario suggest that species ranges are likely to change both in size and shape (see Brown et al. 1996; Gaston 1994 for general discussions of the size and shape of species ranges). This has a number of conservation implications. A range expansion will present possibilities of novel interactions with previously unencountered species, and assemblages (Parmesan et al. 1999; Pounds et al. 1999). The likely outcome of such novel interactions is difficult to predict, as the biological invasion and biological control literature illustrates, (Williamson 1996; Lonsdale 1999; McEvoy & Coombs 1999), although many species have survived exposure to such changes in the past (Coope 1979). Nonetheless, some progress could be made toward understanding the outcome of novel interactions by basing microcosm-type experiments (see e.g. Davis et al. 1998a,b), on the new species combinations predicted by climate modelling procedures such as the current one.

Over and above any novel species interactions, of immediate conservation concern is the contraction in range sizes predicted for four of the five species modelled in this study. A reduction in range size may also result in a decline in the local abundance of a species (see Gaston et al. 1996 for a general overview of the range size abundance relationship). Species subjected to both range size contraction and population decline are clearly at substantial conservation risk, the double jeopardy of Gaston (1998). Although P. caffer is vulnerable in terms of range contraction for the reasons outlined above, it may be less susceptible than the other species because it is widespread and shows little range shift under the climate change scenario.

The remaining four species all display range shifts as well as range contractions with ID's and CAD's revealing an average coincidence of 16 % (± SD 16, n = 4, Table 1). Arid-adapted antlion species from the western parts of South Africa will thus experience more severe shifts in distribution than their eastern counterparts (Figs 4-8). This predicted pattern is not unexpected given the general aridification predicted by the HadCM2 general circulation model. However, the likelihood of a species successfully colonising a new habitat during a range shift depends primarily on habitat suitability. In the case of antlions, many of the predicted range shifts are into areas that have been highly transformed for intensive agriculture (Fairbanks et al. 2000). They will consequently be largely unsuitable for antlion colonisation. Predicted range shifts may thus actually represent range contractions, thereby exacerbating the likelihood of species extinction. In effect, our results suggests that arid areas in South Africa may become too arid to support previously xerophilous species, while previously marginal temperate areas may be unsuitable because of land transformation.

Finally, the expected response of P. luteus, the fynbos endemic, raises an important point regarding modelling exercises of this kind (Chown & Gaston 1999). The ID encompasses not only the known records for this species (Fig. 7), but also various habitat patches in what is known as the Afromontane phytogeographical region (Cowling & Hilton-Taylor 1997). Fynbos-related elements do occur in these Afromontane patches in the form of ericaceous shrublands (Killick 1978; White 1978), but P. luteus apparently does not. This example therefore illustrates that although the model is useful for many species, there are clearly cases where other biological variables such as specific habitat requirements will ultimately determine potential habitat occupancy (Chown & Gaston 1999).

A model previously developed for predicting the effects of climate change on insects and plants in Europe is shown here to be applicable to southern Africa, after modification to account for seasonal rainfall patterns. An added advantage of this modified multivariate approach is that the model provides probability of occurrence values for each grid cell in contrast with the presence absence outputs generated by the original bivariate approach (Jeffree & Jeffree 1994). Most importantly, it is shown that range contractions and shifts in the positions of species ranges are likely to be significant consequences of climate change for antlions in South Africa. If this applies to other animal taxa, and it seems that it does (Van Jaarsveld et al. 2000) then the message to the conservation community is clear. The likely impacts of climate change on our ability to conserve our fauna can no longer be ignored, but must now form an integral part of conservation planning.

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REFERENCES

ALLEN, J.R.M., BRANDT, U., BRAUER, A., HUBBERTEN, H., HUNTLEY, B., KELLER, J., KRAML, M., MACKENSEN, A., MINGRAM, J., NEGENDANK, J.F.W., NOWACZYK, N.R., OBERHANSLI, H., WATTS, W.A., WULF, S. & ZOLITSCHKA, B. 1999. Rapid environmental changes in southern Europe during the last glacial period. Nature **400**: 740-743.

BALMFORD, A. & GASTON, K.J. 1999. Why biodiversity surveys are good value. Nature **398**: 204-205.

BEARD, K.H., HENGARTNER, N. & SKELLY, D.K. 1999. Effectiveness of predicting breeding bird distributions using probabilistic models. Conservation Biology **13**: 1108-1116.

BROWN, J. H., STEVENS, G. C. & KAUFMAN, D. M. 1996. The geographic range–size, shape, boundaries, and internal structure. Annual. Review of Ecology and Systematics **22**: 597-623.

CHOWN, S.L. & GASTON, K.J. 1999. Exploring links between physiology and ecology at macro-scales: the role of respiratory metabolism in insects. Biological Review **74**: 87-120.

COOPE, G.R. 1979. Late Cenozoic Coleoptera: Evolution, biogeography and ecology. Annual Review of Ecology and Systematics **10**: 247-267.

COWLING, R.M. & HILTON-TAYLOR, C. 1997. Phytogeography, flora and endemism. In: Cowling, R.M., Richardson, D.M. & Pierce, S.M. (Eds) Vegetation of South Africa 43-61. Cambridge University Press, Cambridge.

DAVIS, A.J., LAWTON, J.H., SHORROCKS, B. & JENKINSON, L.S. 1998a. Individualistic species responses invalidate simple physiological models of community dynamics under global climate change. Journal of Animal Ecology **67**: 600-612.

DAVIS, A.J., JENKINSON, L.S., LAWTON, J.H., SHORROCKS, B. & WOOD, S. 1998b. Making mistakes when predicting shifts in species range in response global warming. Nature **391**: 783-786.

DAVIS, A.L.V., CHOWN, S.L., MCGEOCH, M.A. & SCHOLTZ, C.H. 2000. A comparative analysis of metabolic rate in six Scarabaeus species (Coleoptera: Scarabaeidae) from southern Africa: further caveats when inferring adaptation. Journal of Insect Physiology **46**: 553-562.

EELEY, H.A.C., LAWES, M.J. & PIPER, S.E. 1999. The influence of climate change on the distribution of indigenous forest in KwaZulu-Natal, South Africa. Journal of Biogeography **26**: 595-617..

FAIRBANKS, D.H.K., THOMPSON, M.W., VINK, D.E., NEWBY, T.S., VAN DEN BERG, H.M. & EVERARD, D.A. 2000. The South African land cover characteristics database: a synopsis of the landscape. South African Journal of Science **96**: 69-82.

FREITAG, S. & MANSELL, M.W. 1997. The distribution and protection of selected antlion species (Neuroptera: Myrmeleontidae). African Entomology **5**: 205-216.

FREITAG, S., NICHOLLS, A.O. & VAN JAARSVELD, A.S. 1998. Dealing with established reserve networks and incomplete data sets in conservation planning. South African Journal of Science **94**: 79-84.

GASTON, K.J. 1994. Rarity. Chapman & Hall, London.

GASTON, K.J. 1998. Rarity as double jeopardy. Nature **394**: 229-230.

GASTON, K.J., BLACKBURN, T.M. & LAWTON, J.H. 1996. Interspecific range-size abundance relationships: an appriasal of mechanisms. Journal of Animal Ecology **66**: 579-601.

HARRISON, J.A., ALLAN, D.G., UNDERHILL, L.G., HERREMANS, M., TREE, A.J., PARKER, V. & BROWN, C.J. 1997. The Atlas of Southern African Birds. Birdlife South Africa, Johannesburg.

HEWITSON, B.C. 1998. South African National Assessment for the Framework Convention for Climate Change: Climate Change Scenarios http://tie.egs.uct.ac.za/fccc/hadcm2.html

IPCC (Intergovernmental Panel on Climate Change). 1992. Climatic Change, The IPCC Scientific Assessment. In: Houghton, J.T., Callander, B.A. & Varney, S. (Eds) Report prepared by Working Group 1, WMO-UNEP. Cambridge University Press, Cambridge.

JEFFREE, E.P. & JEFFREE, C.E. 1994. Temperature and the biogeographical distribution of species. Functional Ecology **8**: 640-650.

JEFFREE, C.E. & JEFFREE, E.P. 1996. Redistribution of the potential geographical ranges of Mistletoe and Colorado Beetle in Europe in response to the temperature component of climate change. Functional Ecology **10**: 562-577.

KILLICK, D.J.B. 1978. The Afro-Alpine Region. In: Werger, M.J.A. (Ed.) Biogeography and Ecology of Southern Africa. 515-542. Junk, The Hague.

LE LAGADEC, M.D., CHOWN, S.L. & SCHOLTZ, C.H. 1998. Desiccation resistance and water balance in southern African keratin beetles (Coleoptera, Trogidae): the influence of body size, habitat and phylogeny. Journal of Comparative Physiology B **168**: 112-122.

LOW, A.J. & REBELO, A.G. (Eds) 1996. Vegetation of South Africa, Lesotho and Swaziland. Department of Environmental Affairs and Tourism, Pretoria.

LONSDALE, W.M. 1999. Global patterns of plant invasions and the concept of invasibility. Ecology **80**: 522-1536.

MANSELL, M.W. 1985a. The ant-lions of southern Africa (Neuroptera: Myrmeleontidae). Introduction and genus Bankisus Navás. Journal of the Entomological Society of Southern Africa **48**: 189-212.

MANSELL, M.W. 1985b. Order Neuroptera. In: Scholtz, C.H. & Holm, E. (Eds) Insects of Southern Africa. 181-186. Butterworths, Durban.

MARGULES, C.R. & REDHEAD, T.D. 1995. BioRap: guidelines for using the BioRap Methodology and Tools. CSIRO/ World Bank, Australia.

MCEVOY, P.B. & COOMBS, E. 1999. Biological control of plant invaders: regional patterns, field experiments and structured population models. Ecological Applications **9**: 387-401.

PARMESAN, C., RYRHOLM, N., STEFANESCU, C., HILL, J.K., THOMAS, C.D., DESCIMON, H., HUNTLEY, B., KAILA, L., KULLBERG, J., TAMARU, T.,

TENNET, W.J., THOMAS, J.A. & MARTIN, W. 1999. Poleward shifts in the geographical ranges of butterfly species associated with regional warming. Nature: **399**: 579-583.

POUNDS, J.A., FOGDEN, M.P.L. & CAMPBELL, J.H. 1999. Biological response to climate change on a tropical mountain. Nature: **398**: 611-615.

PRENDERGAST, J.R., QUINN, R.M., LAWTON, J.H., EVERSHAM, B.C. & GIBBONS, D.W. 1993. Rare species, the coincidence of hotspots and conservation strategies. Nature **365**: 335-337.

ROBINSON, T., ROGERS, D. & WILLIAMS, B. 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., ROGERS, D. & WILLIAMS, B. 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.

SOKAL, R.R. & ROHLF, F.J. 1981. Biometry: The Principles and Practice of Statistics in Biological Research. 2nd Edition. W.H. Freeman & Co., San Francisco.

SCHULZE, R. 1997. Climate. In: Cowling, R.M., Richardson, D.M. & Pierce, S.M. (Eds) Vegetation of Southern Africa. 21-41. Cambridge University Press, London.

TRIBE, G.D. & RICHARDSON, D.M. 1994. The European wasp Vespula germanica (Fabricius) (Hymenoptera: Vespidae), in southern Africa and its potential distribution as predicted by ecoclimatic mapping. African Entomology **2**: 1-6.

VAN JAARSVELD, A.S., CHOWN, S.L., ERASMUS, B.F.N., KSHATRIYA, M., & WESSELS, K.J. 2000. Vulnerability and Adaptation Assessment of South African Animal Taxa to Climate Change. Report to the Department of Environmental Affairs and Tourism, Pretoria.

WHITE, F. 1978. The Afro-Alpine Region. In: Werger, M.J.A. (Ed.) Biogeography and Ecology of Southern Africa. 463-513. Junk, The Hague.

WILLIAMSON, M. 1996. Biological Invasions. Chapman & Hall, London.

CHAPTER 3

Vulnerability of South African animal taxa to climate change

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 CO_2 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 CO_2 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

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 ± S.D.	60.3 ± 5.2	87.8 ± 10.3	12.2 ± 10.3	39.7 ± 5.2
Range	49.1 – 69.3	56.0 – 98.6	1.4 – 44.0	30.7 – 50.9

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 form 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

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

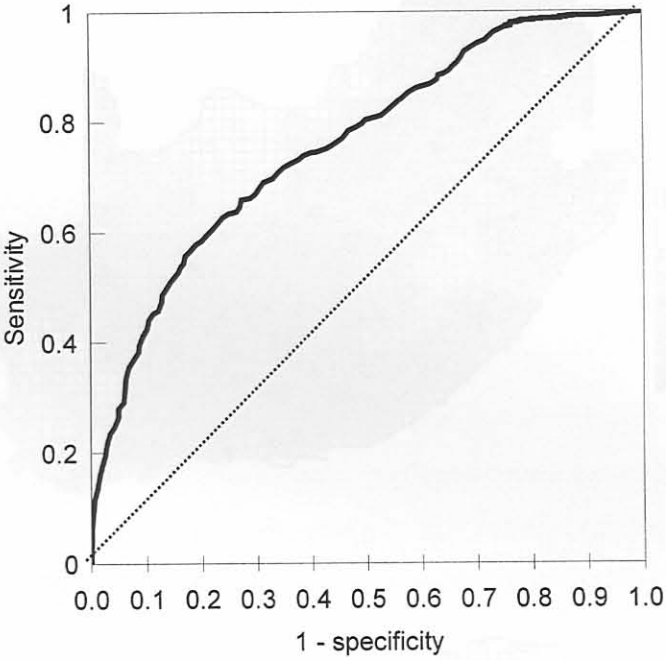

Fig. 1 An example of a ROC curve. The area under the dotted line represents an AUC of 0.5, which would translate into a test with discriminatory ability. The area under the solid black line represents the AUC for this particular species, the South African shelduck.

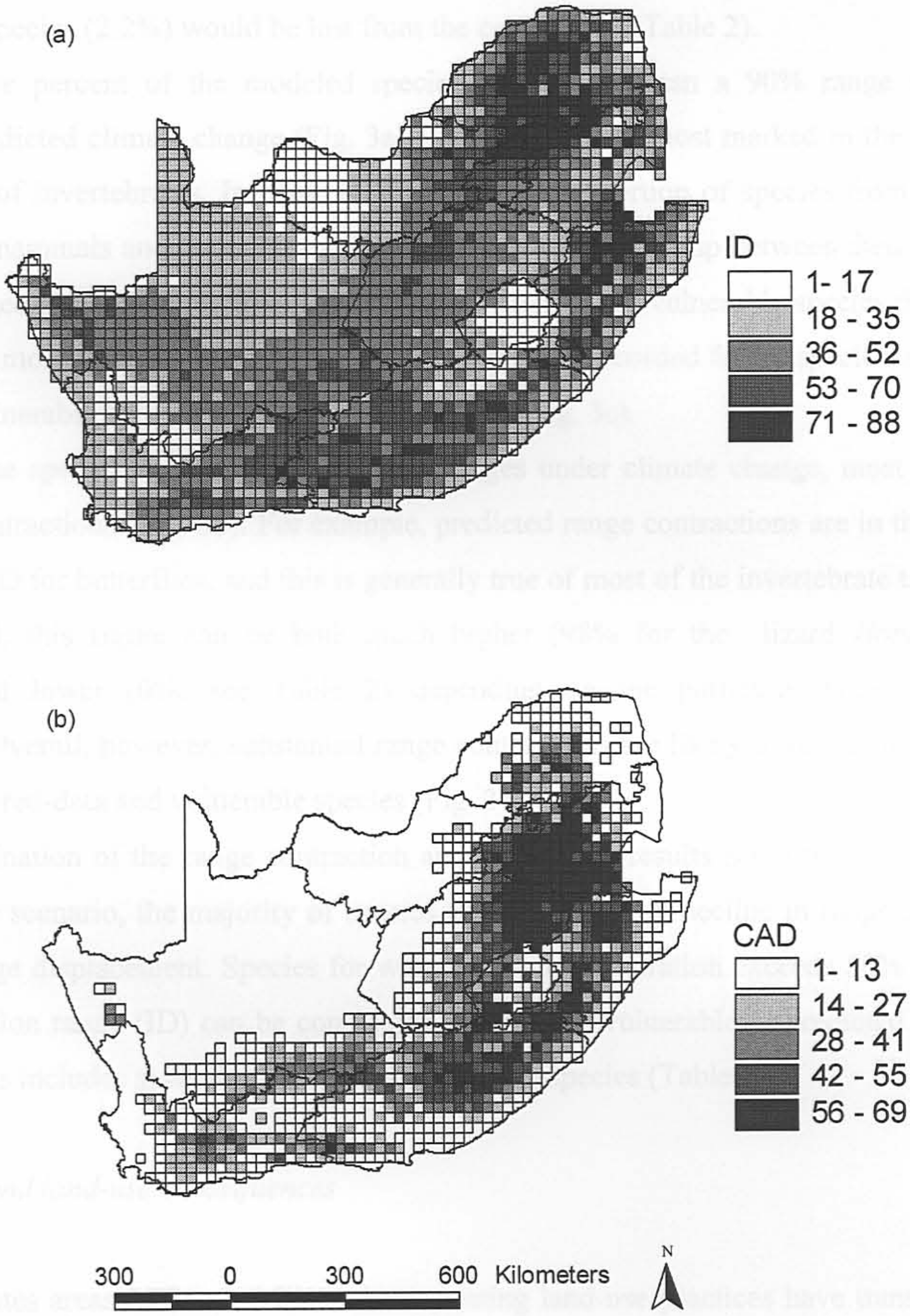

Fig. 2 Species richness patterns for (a) interpolated distributions (ID), (b) climate affected distributions (CAD) for all 179 species included in this study.

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
Stolotermes – termite genus
Epirinus gratus - canthonine dung beetle
Chrysospalax trevelyani – golden mole
Cordylus macrophallus – armoured lizard

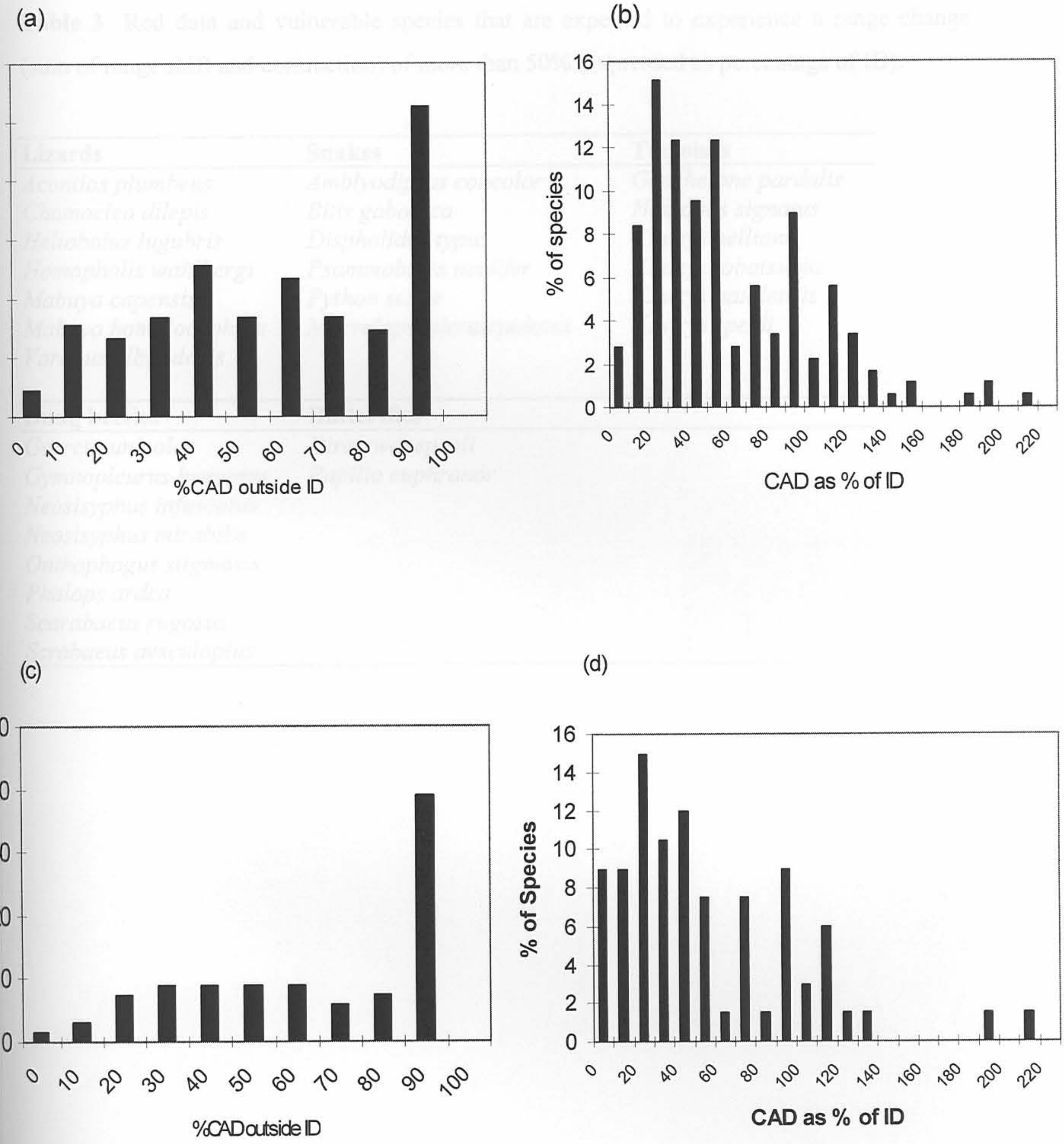

Fig. 3 Percentage of species that exhibit range shifts (expressed as percentage of climate affected distribution outside the interpolated distribution) for (a) all species and (c) red-data and vulnerable species. Percentage of species that exhibit range contraction (climate affected distribution expressed 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**
Acontias plumbeus	*Amblyodipsas concolor*	*Geochelone pardalis*
Chamaeleo dilepis	*Bitis gabonica*	*Homopus signatus*
Heliobolus lugubris	*Dispholidus typus*	*Kinixys belliana*
Homopholis wahlbergi	*Psammobates oculifer*	*Kinixys lobatsiana*
Mabuya capensis	*Python sebae*	*Kinixys natalensis*
Mabuya homalocephala	*Macrelaps microlepidotus*	*Kinixys spekii*
Varanus albigularis		

Dung beetles	**Butterflies**
Garreta unicolor	*Dira swanepoeli*
Gymnopleurus humanus	*Papilio euphranor*
Neosisyphus infuscatus	
Neosisyphus mirabilis	
Onthophagus stigmosis	
Phalops ardea	
Scarabaeus rugosus	
Scrabaeus aesculapius	

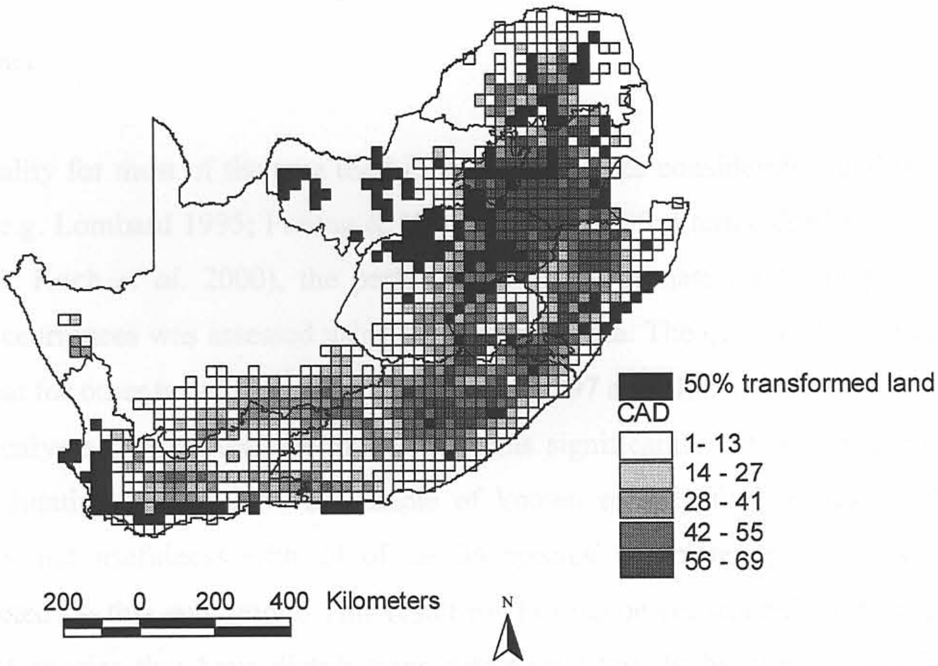

Fig. 4 Predicted climate affected (CAD) species richness patterns and extant land-cover patterns in South Africa. Areas coloured in black are at least 50% transformed and/or degraded.

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 CO_2 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 Review,* **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 sefvice in Brazil's Amazonian forests: risks, value and conservation *Environmetnal 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 mModelling,* **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 persective. *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 Ecolog,y* **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 molerats, 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, Stefanescus 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 selectio 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 JI, 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 Maputaland Centre. In: *The Biodiversity in African Savannahs*. (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 Biopmedicine,* **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
Anteating Chat	*Myrmecocichla formicivora*
Blackchested Prinia	*Prinia flavicans*
Blackheaded Canary	*Serinus alario*
Blackthroated Canary	*Serinus atrogularis*
Blue Korhaan	*Eupodotis caerulescens*
Buffstreaked Chat	*Oenanthe bifasciata*
Bully Canary	*Serinus sulphuratus*
Cape Bunting	*Emberiza capensis*
Cape Canary	*Serinus canicollis*
Crimsonbreasted Shrike	*Laniarius artococcineus*
Dark Chanting Goshawk	*Melierax metabates*
Drakensberg Siskin	*Pseudochloroptila symonsi*
Dusky Sunbird	*Nectarinia fusca*
Forest Canary	*Serinus scotops*
Ground Woodpecker	*Geocolaptes olivaceus*
Kalahari Robin	*Erythropygia paena*
Karoo Korhaan	*Eupodotis vigorsii*
Karoo Robin	*Erythropygia coryphaeus*
Larklike Bunting	*Emberiza impetuani*
Longtailed Shrike	*Corvinella melanoleuca*
Ludwig's Bustard	*Neotis ludwigii*
Malachite Sunbird	*Nectarinia famosa*
Pale Chanting Goshawk	*Melierax canorus*
Redcrested Korhaan	*Eupodotis ruficrista*
Redeyed Bulbul	*Pycnonotus nigricans*
Rock Bunting	*Emberiza tahapisi*
Rock Kestrel	*Falco tinnunculus*
South African Cliff Swallow	*Hirundo spilodera*
South African Shelduck	*Tadorna cana*
Stanley's Bustard	*Neotis denhami*
Streakyheaded Canary	*Serinus gularis*
Tractrac Chat	*Cercomela tractrac*
Whitethroated Canary	*Serinus albogularis*
Yellow Canary	*Serinus flaviventris*

Mammals

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

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

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

Other invertebrates		
Dung beetles	Jewel beetles	Antlions
Chironitis audens	*Acmaeodera albovillosa*	*Cymothales bouvieri*
Copris cornifrons	*Acmaeodera grata*	*Cymothales illustris*
Epirinus flagellatus	*Julodis cirrosa*	*Golafrus oneili*
Epirinus gratus	*Julodis viridipes*	*Palparellus festivus*
Garreta unicolor	*Lampetis gregaria*	*Palpares annulatus*
Gymnopleurus humanus	*Lampetis viridimarginata*	*Palpares cataractae*
Metacatharsius marani	*Megactenodes reticulata*	*Palpares lentus*
Neosisyphus infuscatus	*Monosacra lalandei*	*Palpares sobrinus*
Neosisyphus mirabilis	*Neojulodis tomentosa*	*Palpares sparsus*
Onitis minutus	*Phlocteis exasperata*	*Palpares speciosus*
Onthophagus asperulus	*Pseudophlocteis vidua*	*Pamexis karoo*
Onthophagus binodis	*Scaptelytra aliena*	
Onthophagus cameloides	*Sphenoptera brincki*	
Onthophagus immundus	*Sternocera orissa*	
Onthophagus stigmosis		
Phalops ardea		
Scarabaeus gariepinus		
Scarabaeus rugosus		
Scrabaeus aesculapius		

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

CHAPTER 4

Modelling the spatial distribution of two important South African plantation forestry pathogens

Modelling the spatial distribution of two important South African plantation forestry pathogens

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ABSTRACT

Pathogens, pests and diseases impact heavily on commercial plantation forestry in South Africa, and must thus be considered in any diversified and adaptive management approach. Two important fungal pathogens of Pinus and Eucalyptus species respectively are Sphaeropsis sapinea and Cryphonectria cubensis. The most common disease symptoms associated with S. sapinea infections are shoot blight and top dieback. S. sapinea also exists as an asymptomatic endophyte in healthy tissue of susceptible pine species and can cause disease following predisposition, such as mechanical damage. Canker formation following infection by C. cubensis results in the death of young tress, while older trees with stem cankers are prone to wind breakage. The aim of this study was to explore the use of bioclimatic modelling to predict the habitat distribution for these pathogens, and to consider potential distribution patterns under conditions of climate change. High risk areas identified for Sphaeropsis dieback coincide with the summer rainfall hail belt, emphasising the need for planting resistant Pinus spp. in these regions. A much smaller area of South Africa is predicted to be suitable for the occurrence of C. cubensis than for S. sapinea, but a range shift westward in suitable habitat for C. cubensis is predicted under a climate change scenario. Of concern is that many of these areas are currently being planted with disease susceptible Eucalyptus clones. These preliminary results, and further refinement of the model, will lay a valuable foundation for future risk assessment and strategic planning in the South African forestry industry.

INTRODUCTION

The South African commercial forestry industry is of considerable economic importance to the country, with the value of timber products estimated at US $15 million for 1996 (Hassan, 1999). The industry depends almost exclusively on the planting of exotic Pinus, Eucalyptus and Acacia species, that collectively cover an area of approximately 1.5 million ha (Anonymous, 2001). The extensive use of monocultures has raised concerns regarding the impact of diseases on the future competitiveness and sustainability of the industry (Wingfield et al., 1989). Many fungal pathogens cause diseases in commercial plantation species in South Africa. These account for losses of millions of dollars due to timber damage or tree mortality, excluding impacts due to loss of growth (Zwolinski et al., 1990).

Sphaeropsis sapinea (Fr.:Fr.) Dyko & Sutton [Syn. Diplodia pinea (Desm.) Kickx] is one of the most important and widespread pathogens in pine plantations in South Africa. This pathogen has caused severe damage to pine plantations in many countries, but its notoriety is based on the devastation it has caused in South African plantations of Pinus radiata D.Don and P. patula Schlechtend & Cham., especially after hail injury (Laughton, 1937; Swart et al., 1987b). The fungus is widespread in South Africa, and numerous outbreaks have been reported, mostly from summer rainfall areas following hail damage. The most common disease symptoms associated with S. sapinea infections are shoot blight and top dieback, but canker accompanied by resinosis, bluestain and root disease are also found (Swart et al., 1987b, Swart and Wingfield, 1991a). S. sapinea also exists as an asymptomatic endophyte in healthy tissue of susceptible pine species (Smith et al., 1996; Stanosz et al., 1997), and can cause disease following predisposition. Disease usually affects trees that are wounded by hail, insects or other agents, or physiologically stressed by drought or nutrient deficiencies. Relative humidity, optimum temperatures, the occurrence of rain, temperatures prevailing after rainfall, microclimatic conditions and the season can all influence the dispersal of conidia, spore germination and host penetration by S. sapinea (Swart et al., 1985; Swart et al., 1987a; Swart and Wingfield, 1991a, Swart and Wingfield, 1991b).

In Eucalyptus, canker caused by Cryphonectria cubensis (Bruner) Hodges is one of the most important limitations to plantation success (Bruner, 1916; Boerboom and Maas, 1970; Hodges, 1980). The disease was first discovered in South Africa in 1988 (Wingfield et al.,

1989) and it has subsequently caused significant losses in the sub-tropical Zululand area. Infection generally results in the formation of cankers at the bases and around branch stubs of trees. Basal cankers are characterised by swelling and cracking of the bark, while stem cankers generally result from infection of branch stubs and death of the cambium. Infection of young trees results in death, while older trees with stem cankers are prone to wind breakage (Sharma et al., 1985; Florence et al., 1986). Cryphonectria canker is prevalent in many tropical parts of the world, particularly between 30° north and south of the equator. The growth and spread of the pathogen is promoted by high rainfall, humid conditions, and temperatures above 23°C (Hodges et al., 1979; Sharma et al., 1985).

Plantation disease management relies heavily on the selection of disease tolerant planting material, since chemical control on established trees is generally uneconomical and unreliable. Great success has been achieved in disease management through the selection of disease tolerant clones and hybrids (Denison and Kietzka, 1993; Wingfield et al., 2001). Breeding and selection is often, however, dependent on accurate site species matching. Trees selected for disease tolerance on one site, can be susceptible to the same disease on an unfavourable site. Extensive breeding programmes are thus used to select Eucalyptus clones resistant to Cryphonectria infection for the Zululand area of South Africa (Van Zyl and Wingfield, 1998; Van Zyl and Wingfield, 1999; Van Heerden and Wingfield, 2001).

Pine and eucalyptus plantations in South Africa are distributed mainly along the eastern and south-eastern parts of the country, and include various climatic regions. The distribution and infectivity of both pathogens considered in this study are affected by climatic parameters. Thus, climate studies can promote our understanding of why species are limited to specific regions. If the spatial distribution of a plant is not fully defined, bio-climatic analysis allows the prediction of the probable or theoretical limits of the distribution (Lindenmayer et al., 1991). This could have important implications for developing appropriate management strategies to reduce disease impact or incidence.

Powerful statistical techniques coupled with geographical information systems (GIS), have fostered the development of a host of predictive habitat distribution models. This array of models covers aspects as diverse as biogeography, conservation biology, habitat or species management and climate change research (Guisan and Zimmermann, 2000). A bivariate climate envelope model developed by Jeffree and Jeffree (1994, 1996) for predicting species distribution patterns and the effects of climate change has recently been modified to accept multivariate inputs to yield probability of occurrence maps for species (Erasmus et al., 2000).

The aim of this study was to assess the value of the modified Jeffree and Jeffree model (Erasmus et al., 2000) for predicting the broad habitat distributions of two important South African forestry pathogens, S. sapinea and C. cubensis, and to explore their potential distributions under conditions of climate change. In future, successful plantation disease management will depend on cooperative research involving many disciplines such as pathology, entomology, genetics, soil science and silviculture. A disease modelling system that can aid in the selection or matching of specific clones to specific sites could have a major positive impact on the management of plantation diseases. Our results should form a valuable basis for the development of future spatial disease management systems.

MATERIALS and METHODS

Pathogen distribution records

The distribution records for S. sapinea and C. cubensis were obtained from the disease database of the Tree Pathology Co-operative Programme (TPCP) at the Forestry and Agricultural Biotechnology Institute (FABI), University of Pretoria. The TPCP represents a collaborative venture between the University of Pretoria and all the major players in the South African forestry industry, and manages a centralised database of all important local forest pathogens. In the case of S. sapinea, the data set contained 87 confirmed reports of the fungus identified between 1994 and 1999 on 11 different Pinus species, 66% of which were from either P. patula or P. radiata. For the purposes of this modeling exercise, input data were resolved to 10 x 10 km grid cells, reducing the 87 reports to 48 records. This was due to multiple reports of the pathogen from the same region in different years or from different host species.

For C. cubensis the data set comprised 17 confirmed reports of the pathogen, 14 cases identified on Eucalyptus trees, and 3 from Tibouchina spp. As in the case of S. sapinea, the close proximity of some reports resulted in a reduction of the number of input records for modelling purposes from 17 to 14. As a sampling density of less than nine records is regarded as an unreliable input for the model (Erasmus et al., 2000), these 14 records were considered sufficient for predicting the habitat distribution of C. cubensis.

Climate data

Historic climate data (thirty year means 1960-1990) and a digital elevation model for South Africa were obtained from the Computing Centre for Water Research (CCWR, University of Natal, South Africa). These data comprised interpolated climate surfaces at a minute by minute resolution. Five variables, i.e. altitude, average rainfall of the driest month, average rainfall of the wettest month, average temperature of the hottest month and average temperature of the coldest month were selected for use as model predictors. They were identified from a suite of 11 variables using Pearson's correlation coefficient to select the least correlated variables. It is commonly known that there is a degree of correlation between altitude and temperature; however, this relationship varies in time and space. The fact that both altitude and temperature variables were identified in this least-correlated selection procedure, shows that the correlation is not that strong and that altitude could potentially explain parts of the distribution that temperature can not. However, temperature at similar altitudes may vary considerably due to local conditions, and it should therefore be interpreted with caution.

For predicting distributions under conditions of climate change, two sets of climate data were used. From the available data sets for climate change conditions, only three variables could be employed at a resolution of quarter-degree grid cells (25 x 25 km): (1) minimum temperature of the coldest month, (2) maximum temperature of the hottest month and (3) mean annual precipitation. Although precipitation seasonality has been shown to be a useful predictor variable across South Africa (Erasmus et al. 2000), the study area falls completely within a summer rainfall area, and as such mean annual precipitation was regarded as sufficient for the purposes of this modelling exercise.

One set of data was based on historical climate data and one set on a General Circulation Model (GCM) predicting climate change. The Hadley Centre Unified GCM (HadCM2 with no sulphates) was used, and it predicts significant changes in the regional climate by the year 2050 or sooner, with an average temperature increase of 2.5-3°C expected (Erasmus et al., 2000). Mean annual hail day frequency (HDF) data, derived from HDF, altitude and latitude were available for the summer rainfall region of South Africa and obtained from Le Roux and Olivier (1996).

Climate matching

For comparative purposes in the case of C. cubensis, the global geographic distribution of the pathogen was summarized from existing literature. For each of these localities, the annual rainfall, mean temperature, maximum temperature and minimum temperature were obtained from New et al. (1999, 2000) (http://www.cru.uea.ac.uk/~markn/cru05/cru05_intro.html, http://ipcc-ddc.cru.uea.ac.uk/). Altitude values were determined from a global digital elevation model GTOPO30 with a horizontal spacing of 30 arc seconds developed through a collaborative effort led by the U.S. Geological Survey's EROS Data Centre (http://edcdaac.usgs.gov/gtopo30). Areas predicted to be a suitable habitat for the fungus under local conditions were identified based on homoclime matching. Homoclimes are locations that experience similar climatic conditions (Lindenmayer et al., 1991). Areas within South Africa were identified where the climatic conditions were within the limits of the minimum and maximum values identified globally for each of the five parameters under consideration. From this, a single common area meeting all criteria was defined as a potential habitat for the pathogen, distinct from the Jeffree and Jeffree modelled solution explained below.

Modelling procedure

The adapted Jeffree and Jeffree bioclimatic model can incorporate not only two but multiple climate variables (Erasmus et al., 2000). The input data comprises 11800 grid cells covering South Africa populated with climate variables. The grid cells in which the particular pathogen species was recorded, were termed known records. The model creates a multidimensional scatterplot using the selected climate variables for each known record grid cell, generates a $n \times n$ covariance matrix, transforms the variables according to specified criteria, and maps the generated values back onto geographical space. The output is a probability of occurrence value in every grid cell for a given species. However, such a single probability of occurrence value for each cell gives no indication of the underlying variation in the calculated probability values. This means that although two grid cells may have the same probability of occurrence for a given species, they may differ in their ability to reflect the true distribution pattern of the species in question. Consequently, a statistical re-sampling technique known as jackknifing was incorporated into the model to quantify the variation underlying the calculated probability values. By making use of jackknifing, n probability of occurrence values (n = size of data set) can be generated for each grid cell instead of a single value. This method re-calculates the probability of occurrence n times, each time using a different combination of n-1 of the data set's known records. The jackknife principle uses these n replicates to estimate the variation associated with the probability of occurrence estimates. It calculates an estimated standard error (a measure of absolute variation), and a coefficient of variation (a measure of relative variation), associated with each probability of occurrence value (I. Smit, personal communication).

Model evaluation

The opportunistic nature with which the distribution data for the two fungi were collected precluded rigorous model evaluation with this particular data set. However, this same climate envelope model has been subjected to rigorous evaluation using presence-absence data resulting from a coordinated survey effort. Erasmus et al. (2002) used the distribution records of 34 bird species and tested model performance using receiver operator characteristic analyses (Fielding and Bell, 1997). The model performed significantly better than a random model with no discriminatory ability. The model also accurately predicted the complete known distributions for 24 of the 34 bird species, using a 20% sub-sample of the known records. The remaining 10 bird species distributions are thought to be more determined by habitat and resource preferences than climate. In sum, the model performed satisfactorily and is therefore considered adequate for the present study.

RESULTS

Predicted distribution of Sphaeropsis sapinea

A predicted distribution providing probability of occurrence values for S. sapinea in South Africa was derived from five variables (Fig. 1A). The predicted distribution range decreased as the level of probability was increased. At a probability of occurrence of greater than 0.5, a total of 994 grid cells (10 x 10 km) were selected, which contained 50% of the known

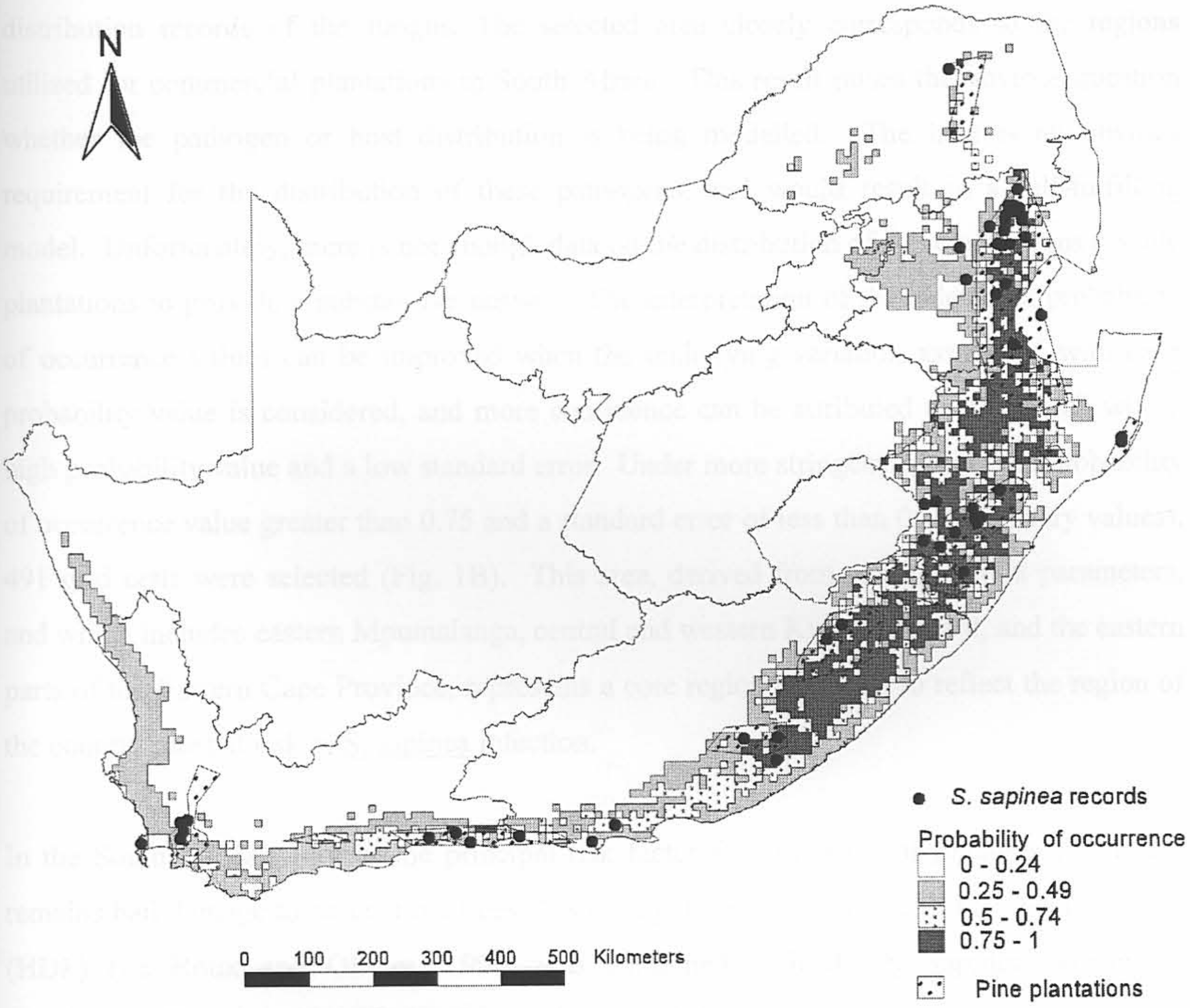

Fig. 1(A) The bioclimatically modelled probability of occurrence surface for Sphaeropsis. sapinea distribution shows the areas at risk of infection. Black dots indicate known distribution records for this species. Perimeters of regions which encompass approximately 90% of commercial pine plantations are indicated.

distribution records of the fungus. The selected area closely corresponds to the regions utilised for commercial plantations in South Africa. This result raises the obvious question whether the pathogen or host distribution is being modelled. The host is an obvious requirement for the distribution of these pathogens, and would result in a self-fulfilling model. Unfortunately, there is not enough data on the distribution of these pathogens outside plantations to provide a substantive answer. The interpretation of the calculated probability of occurrence values can be improved when the underlying variation associated with each probability value is considered, and more confidence can be attributed to a grid cell with a high probability value and a low standard error. Under more stringent criteria of a probability of occurrence value greater than 0.75 and a standard error of less than 0.15 (arbitrary values), 491 grid cells were selected (Fig. 1B). This area, derived from environmental parameters, and which includes eastern Mpumalanga, central and western KwaZulu-Natal, and the eastern parts of the Eastern Cape Province, represents a core region predicted to reflect the region of the country most at risk of S. sapinea infection.

In the South African context the principal risk factor for outbreaks of Sphaeropsis disease remains hail damage to susceptible trees. A spatial pattern of mean annual hail day frequency (HDF) (Le Roux and Olivier, 1996) was combined with the S. sapinea distribution predictions. The areas identified in Mpumalanga and KwaZulu-Natal as high risk regions for S. sapinea infection, also expect more than three occurrences of hail per annum (Fig 1B). This emphasises the management reality that plantation production will necessarily be compromised by a widespread pathogen such as S. sapinea. Furthermore, estimated production targets for such hail-affected regions will have to be weighted accordingly.

Predicted distribution of Cryphonectria cubensis

C. cubensis has been reported from numerous tropical countries of the world, where its distribution is probably determined by humid conditions needed for the growth and spread of the pathogen (Conradie et al., 1990). Environmental conditions prevailing at locations where C. cubensis exists, were thus investigated (Table 1). Using the minimum and maximum values of each climatic parameter as limits, the corresponding homoclime area, which matched these climate values in South Africa was identified (Fig. 2A).

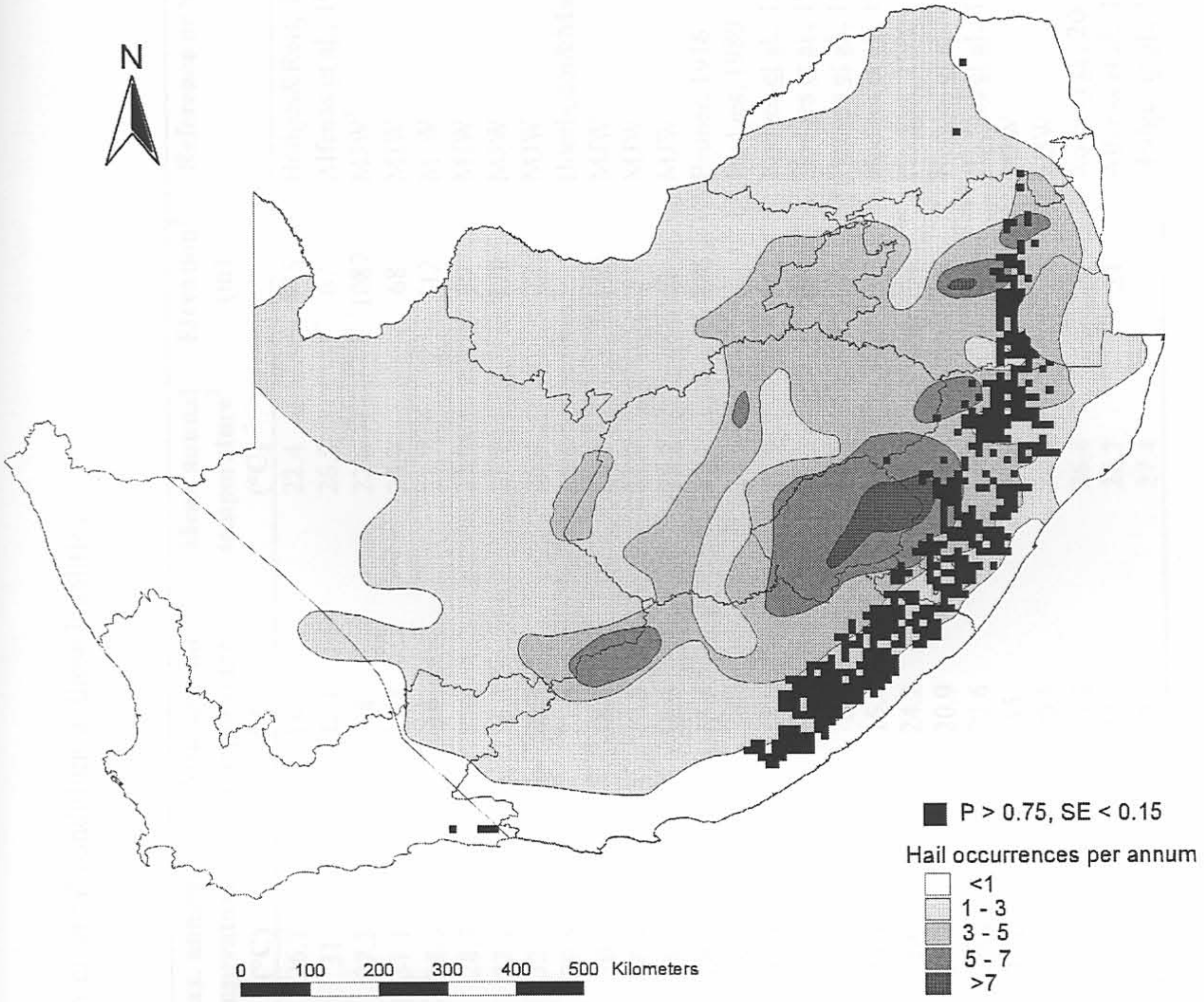

Fig. 1(B) Risk areas for Sphaeropsis sapinea infection in South Africa. Modelled surface with probability of occurrence values greater than 0.75 and a standard error less than 0.15, together with mean annual hail occurrence patterns (adapted from Le Roux and Olivier, 1996).

Table 1 (continued on next page)

Geographical distribution of Cryphonectria cubensis and environmental conditions at these localities

Country	Island/Town/District	Annual rainfall[1] (mm)	Max. annual temperature[1] (°C)	Min. annual temperature[1] (°C)	Mean annual temperature[1] (°C)	Elevation[2] (m)	Reference or Source
Brazil	Sao Paulo	2847	26.7	18.2	22.4	635	Hodges&Reis, 1974
Brazil	Aracruz	1862	31	22.1	26.5	67	Alfenas et al., 1983
Brazil	Brazilia	3030	27.3	18	22.6	1087	MJW[3]
Brazil	Vitoria	1679	31.1	22.8	26.9	68	MJW
Brazil	Piracicaba	2701	28.5	19	23.7	512	MJW
Equador	Quevedo	4307	28.3	15.6	21.9	99	MJW
Colombia	Cali	1643	27.1	16.4	21.7	770	MJW
Argentina	Posadas	1679	32.5	20.3	26.4	72	MJW
Surinam		2920	29.5	21.3	25.1		Boerboom&Maas,1970
Venezuela	Acarigua	438	30.1	18.4	24.2	199	MJW
Mexico	Los Choapas	1424	26.4	17.5	21.9	13	MJW
Mexico	Villahermosa	2008	28.1	18.3	23.2	9	MJW
Cuba	Santiago de las Vegas	694	26.6	15.6	21.1	116	Bruner, 1916
Trinidad & Tobago	Trinidad	767	29.1	20	24.5		Hodges, 1980
Puerto Rico	Toro Negro State Forest	986	25.4	18.5	21.9	543	Hodges et al., 1979
Puerto Rico	Rio Abajo State Forest	986	25.4	18.5	21.9	297	Hodges et al., 1979
USA, Florida	La Belle	767	23.6	13	17.7	7	Hodges et al., 1979
Hawaii	Kauai	1250*	23.7	15.4	19.5		Hodges et al., 1979
Western Samoa	Western Samoa	4709	30	24.2	27.2		Hodges, 1980
Malaysia		1314	29.3	20.9	25.1		Hodges et al., 1986
Indonesia	Bangka Island	3030	29.6	22.6	26.1		Hodges et al., 1986
Indonesia	Prapat	2336	30.6	15	22.8	910	MJW
Indonesia	Bali	3358	29.9	20.1	24.9		MJW
Congo	Pointe-Noire	1898	29.7	23.1	26.4	1	Roux et al., 2000
Cameroon	Edéa	657	31.4	22.1	26.7	21	Alfenas et al., 1983
Tanzania	Zanzibar	876	32	22.9	27.4		Hodges et al., 1986

Country	Island/Town/District	Annual rainfall[1] (mm)	Max. annual temperature[1] (°C)	Min. annual temperature[1] (°C)	Mean annual temperature[1] (°C)	Elevation[2] (m)	Reference or Source
India, Kerala State	Wynad	5217*	30.3*	19.8*	24.9	1100*	Sharma et al., 1985
India, Kerala State	Ernakulam	3008*	30.9*	24.3*	27.6	<200*	Sharma et al., 1985
India, Kerala State	Trivandrum	1697*	31.0*	23.8*	27.3*	<200*	Sharma et al., 1985
Minimum value		438	23.6	13	17.7	1	
Maximum value		5217	32.5	24.3	27.6	1100	

1. All values from New et al. (1999, 2000), except those indicated by * are from references as listed.
2. All values from GTOPO30 global digital elevation model, except those indicated by * are from references as listed. Elevation was not considered when the specific location was not known.
3. Reported by M.J. Wingfield.

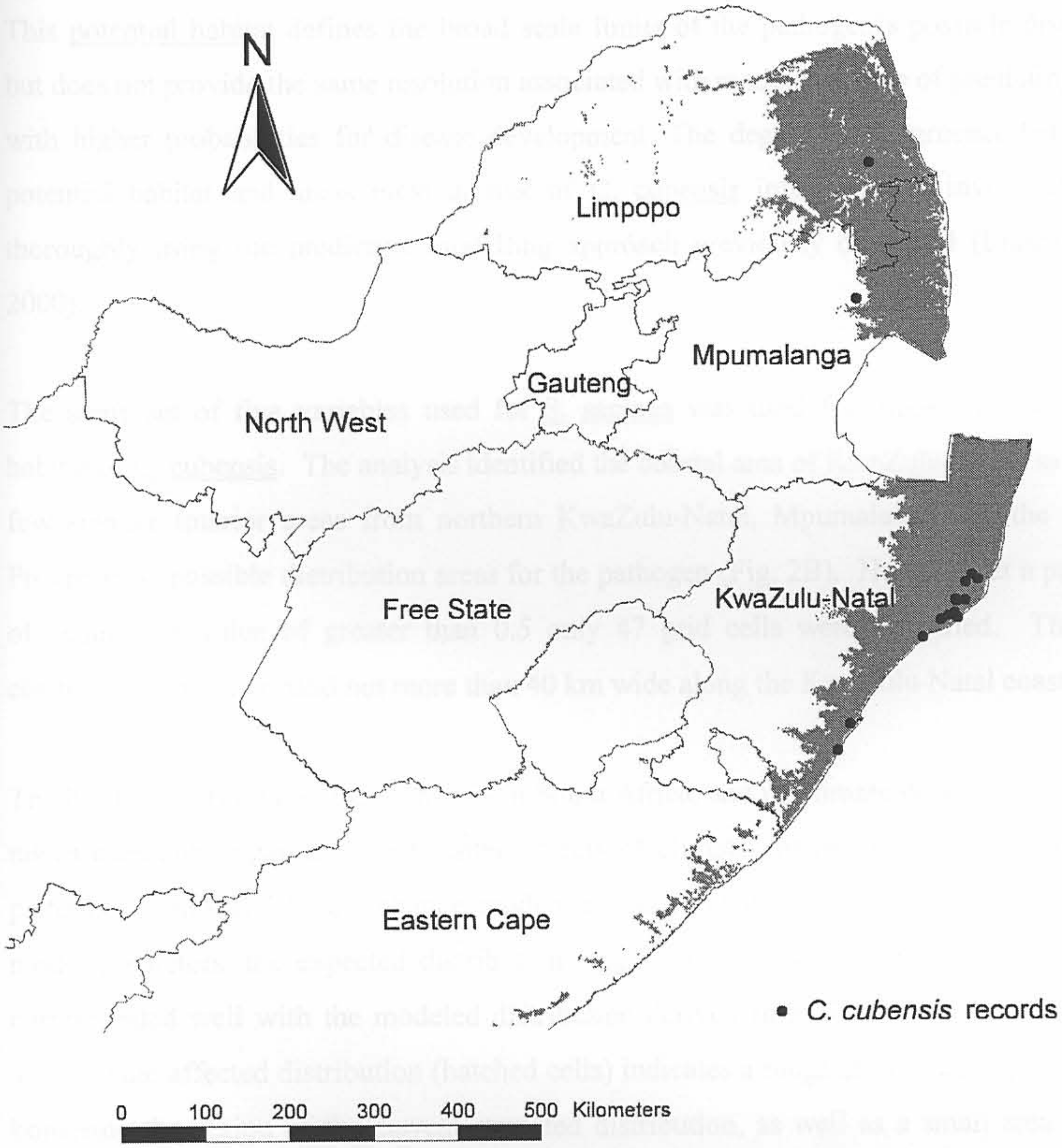

Fig. 2(A) Risk areas for Cryphonectria cubensis infection in South Africa. Black dots indicate known distribution records for this species. The shaded area represents a region predicted as suitable habitat for C. cubensis based on matching of climatic conditions from other locations. This area has an elevation between 1 and 1100 m, mean annual precipitation between 438 and 5217 mm, minimum annual temperature between 13 and 24.3°C, maximum annual temperature between 23.6 and 32.5°C, and mean annual temperature between 17.7 and 27.6°C. Names of provinces of South Africa are indicated.

This potential habitat defines the broad scale limits of the pathogen's possible distribution, but does not provide the same resolution associated with models capable of predicting regions with higher probabilities for disease development. The degree of congruence between the potential habitat and areas most at risk of C. cubensis infection was investigated more thoroughly using the predictive modelling approach previously described (Erasmus et al., 2000).

The same set of five variables used for S. sapinea was used for modelling the predicted habitat of C. cubensis. The analysis identified the coastal area of KwaZulu-Natal, as well as a few smaller interior areas from northern KwaZulu-Natal, Mpumalanga and the Limpopo Province, as possible distribution areas for the pathogen (Fig. 2B). However, at a probability of occurrence value of greater than 0.5 only 47 grid cells were identified. These were clustered mainly in a band not more than 40 km wide along the KwaZulu-Natal coast.

The limited distribution of C. cubensis in South Africa, and its climate-dependent occurrence, raises questions regarding the possible effects of climate change on its future distribution patterns. Although climate change modeling was conducted using only three variables as model predictors, the expected distribution (Fig. 3) from historic climate data (solid cells) corresponded well with the modeled distribution derived from five variables (see Fig. 2B). The climate affected distribution (hatched cells) indicates a range shift to the region west and bordering the region of the current expected distribution, as well as a small area in the far north of the country. Grid cells selected, represented areas with a predicted probability of disease occurrence greater than 0.5. Most of the distribution areas predicted under climate change conditions (Fig. 3) also border, but do not overlap, the areas identified in Fig. 2A. This confirms that these areas would only become a potential habitat for the pathogen once temperature and rainfall patterns have altered.

DISCUSSION

Indigenous tree species suitable for short rotation plantations in support of timber and pulp production are extremely scarce in South Africa. Thus the local commercial forestry industry

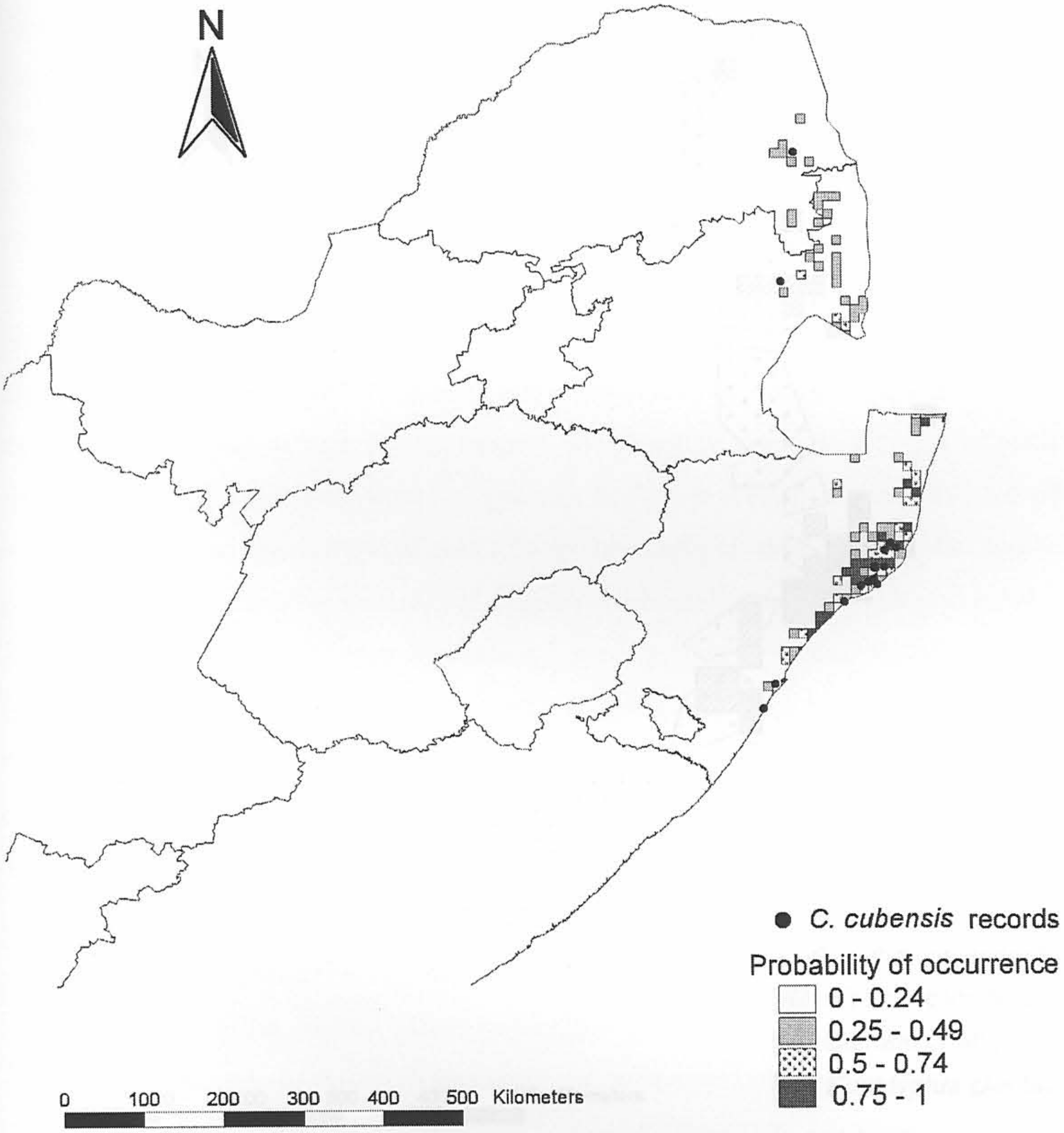

Fig. 2(B) Risk areas for <u>Cryphonectria</u> <u>cubensis</u> infection in South Africa. Black dots indicate known distribution records for this species. The bioclimatically modelled probability of occurrence surface for <u>C.</u> <u>cubensis</u> distribution

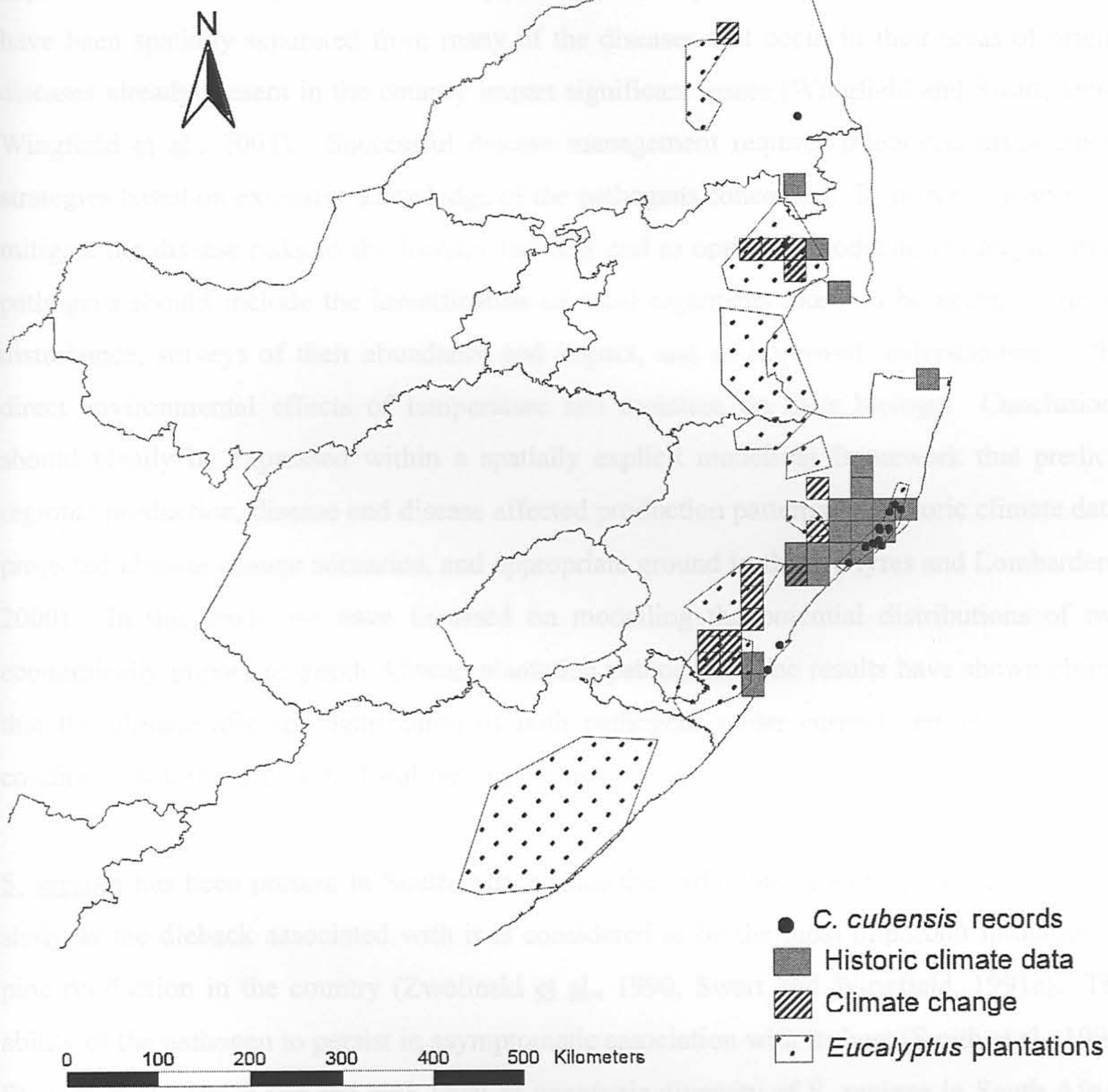

Fig. 3 The modelled distribution for <u>Cryphonectria</u> <u>cubensis</u> derived from mean annual precipitation, minimum monthly temperature and maximum monthly temperature from historic climate data (solid cells) or under a climate change scenario (hatched cells). Black dots indicate known distribution records for this species. Perimeters of regions which encompass approximately 90% of commercial eucalyptus plantations are indicated

depends almost entirely on exotic tree species, grown in plantations. Although these exotics have been spatially separated from many of the diseases that occur in their areas of origin, diseases already present in the country impart significant losses (Wingfield and Swart, 1994; Wingfield et al., 2001). Successful disease management requires integrated management strategies based on extensive knowledge of the pathogens concerned. Research to assess and mitigate the disease risks to the forestry industry and to optimize production strategies from pathogens should include the identification of focal organisms likely to be agents of future disturbance, surveys of their abundance and impact, and an improved understanding of the direct environmental effects of temperature and moisture on their biology. Conclusions should ideally be expressed within a spatially explicit modelling framework that predicts regional production, disease and disease affected production patterns for historic climate data, projected climate change scenarios, and appropriate ground truthing (Ayres and Lombardero, 2000). In this study we have focussed on modelling the potential distributions of two economically important South African plantation pathogens. The results have shown clearly that the climate affected distribution of both pathogens under current and future climate conditions will impact on the local forestry industry.

S. sapinea has been present in South Africa since the early 1900's, and was selected for this study as the dieback associated with it is considered to be the most important limitation to pine production in the country (Zwolinski et al., 1990; Swart and Wingfield, 1991a). The ability of the pathogen to persist in asymptomatic association with its host (Smith et al., 1996; Stanosz et al., 1997) and the high level of genotypic diversity of S. sapinea in South Africa (Smith et al., 2000), complicates disease management strategies (McDonald and McDermott, 1993). Although factors governing Sphaeropsis disease manifestation are clearly complex, we attempted to correlate the range of this pathogen with climate at a regional scale. Based on a suite of five environmental variables, an area stretching from the Limpopo Province, through Mpumalanga, KwaZulu-Natal, Eastern Cape and Western Cape Provinces was identified as potential risk areas for Sphaeropsis disease. This area closely corresponds to the regions utilised for commercial forestry in South Africa, confirming the potential threat of Sphaeropsis dieback in all susceptible pine plantations.

The use of a statistical re-sampling technique enabled the identification of a core risk region for Sphaeropsis occurrence with a consistently high probability of disease occurrence.

Isolated cases of extensive losses from Sphaeropsis have been reported from the Southern Cape, an all year rainfall region, following a single severe hail storm and infestation of trees by cambiophagous insects (Zwolinski et al., 1990; Zwolinski et al., 1995). The core risk region, however, falls in the summer rainfall region of South Africa, which regularly experiences thunderstorms and hail. When the expected annual hail occurrences are viewed together with the Sphaeropsis risk area, it is clear that the production of susceptible pine species will necessarily be affected by Sphaeropsis dieback along the eastern Mpumalanga escarpment. Thus, in this region the emphasis should be on planting Pinus spp. which are not susceptible to S. sapinea infection.

Disease severity and distribution associated with C. cubensis infection appears to be much more directly related to climatic conditions than is the case for S. sapinea. We used two different approaches - through either homoclime matching, or modelling the predicted distribution - to identify general and high-risk areas for C. cubensis infection. Superimposing the results modelled from historic climate data (predicted distribution, Fig. 2B) onto the broad potential habitat (Fig. 2A) illustrated that the modelled distribution of C. cubensis only extends over less than a fifth of the suitable habitat identified through homoclime matching. The reason for this is that large parts of the area selected as potential habitat fall only marginally within the global climate parameter limits obtained from Table 1.

In the case of mean annual rainfall, the fungus has been reported from locations with rainfall figures ranging from less than 500 mm to more than 5000 mm per annum (see Table 1). However 72% of these locations record more than 1200 mm annually, and in Brazil the severity of the disease has been shown to be more intense in areas of high rainfall (Hodges et al., 1979). Although no attempt was made here to investigate the different contributions of temperature and rainfall on the fungus's biology, it has been shown that colonization of young Eucalyptus plants by C. cubensis following artificial inoculation under greenhouse conditions was inhibited by drought stress (Swart et al., 1992). South Africa is relatively dry, and only about 3% of the country receives more than 1000 mm per year. This includes the narrow strip along the eastern coast where most of the local occurrences of C. cubensis have been recorded. Therefore, the predicted distribution modelled from historic climate data (Fig. 2B), which represents a probability of occurrence based on a suite of relevant parameters, probably more accurately reflects the actual risk areas for Cryphonectria canker than the potential habitat area identified through the homoclime / climate matching approach (Fig. 2A). Although a much smaller area of South Africa is suitable for the occurrence of C. cubensis than for S. sapinea, these areas are also exactly within extant forestry areas.

Increases in atmospheric greenhouse gases are expected to have significant impacts on the world's future climate. There is evidence that the anomalous climate of the past century has already affected the physiology, distribution and phenology of some species in ways consistent with theoretical predictions (Hughes, 2000). Projected climate change will obviously also impact on forest growth and composition (Lindner, 2000). An investigation of local forestry regions showed that climate changes could lead to substantial loss of production in the core areas presently used by the forestry industry (Fairbanks and Scholes, 1999). Climate will however also impact indirectly on forests by altering disturbance patterns from pathogens (Loehle and LeBlanc, 1996; Ayres and Lombardero, 2000). For C. cubensis in South Africa, the distribution predicted under the climate change scenario suggests that the fungus could in the future establish itself in areas inland of where it is currently considered a problem. Most of these areas already support eucalypt plantations. Of greatest concern here is that many of the areas that would become suitable for C. cubensis are currently planted with E. grandis seedlings or clones. E. grandis is especially susceptible to C. cubensis infection in other parts of the world and in South Africa (Hodges et al., 1979; Conradie et al.,1990) and losses could be severe.

This study aimed to investigate gradual, long-term distribution changes (Easterling et al., 2000). These changes are the sum of seasonal range expansions and contractions as determined by a complex interaction of climate and community level processes, with climate being more important at broader temporal scales. Theoretically our modelling technique would be equally suitable for use with short-term climate and distribution data; the calculations are blind to the source of the data. However, we feel that such short-term (intra-annual) modelling results based on weather data would not be robust. The reason for this concern lies with the nature of the short-term climate data needed for such an analysis. There has been significant improvements in the reliability of decadal scale climate change predictions (Zwiers, 2002; Knutti et al., 2002; Stott and Kettleborough, 2002) and such developments allow for insightful analyses of distribution shifts, either historically (Parmesan et al., 1999; Pounds et al., 1999) or predicted (Erasmus et al., 2000; Peterson et al., 2002).

It is true that many currently relevant ecological concerns operate at finer temporal scales (Walther et al., 2002). However, at increasingly finer scales (i.e. seasonal or intra-annual), the paucity of data on the relative importance of physiological processes (Chown and Gaston, 1999), community processes and climate on population dynamics (Stenseth et al., 2002), renders model outputs extremely uncertain. In addition, an increase in the frequency of extreme climate events is predicted to co-occur with climate change (Easterling et al., 2000). Such extreme events would have a large negative impact on the reliability of a fine temporal scale model, and as such provides additional support for avoiding intra-annual distribution shift predictions.

Forestry management decisions are based on information pertaining to current and future resource conditions, and many forest simulation models have been widely used to provide information for sound decision making. Different applications require different types of models and varying modelling approaches (Peng, 2000). We have investigated the use of a bioclimatic model to predict the distribution of two important South African forestry pathogens. This provides the first such study, and provides valuable information to the South African Forestry Industry. The results can be integrated into other existing decision support systems to meet the demands of forest management and pathogen control under uncertain future environmental conditions. Further refinement, and the use of more detailed and systematically collected data for diseases will make it possible to improve systematic plantation risk assessment for management and planning purposes.

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REFERENCES

Anonymous, 2001. Forest Facts. Forest Owners Association. Rivonia, South Africa

Ayres, M.P., Lombardero, M.J., 2000. Assessing the consequences of global change for forest disturbance from herbivores and pathogens. Science Total Environment 262, 263-286.

Boerboom, J.H.A., Maas, P.W.T., 1970. Canker of Eucalyptus grandis and *E. saligna* in Surinam caused by *Endothia havanensis*. Turrialba 20, 94-99.

Bruner, S.C., 1916. A new species of *Endothia*. Mycologia 8, 239-242.

Chown, S.L., Gaston, K.J., 1999. Exploring links between physiology and ecology at macro-scales: the role of respiratory metabolism in insects. Biological Review 74, 87-120.

Conradie, E., Swart, W.J., Wingfield, M.J., 1990. Cryphonectria canker of Eucalyptus, an important disease in plantation forestry in South Africa. S. Afr. For. J. 152, 43-49.

Denison, N.P., Kietzka, J.E., 1993. The use and importance of hybrid intensive forestry in South Africa. S. Afr. For. J. 165, 55-60.

Easterling, D.R., Meehl, G.A., Parmesan, C., Changnon, S.A., Karl, T.R., Mearns, L.O., 2000. Climate extremes: observations, modeling and impacts. Science 289, 2068-2074.

Erasmus, B.F.N., Kshatriya, M., Mansell, M.W., Chown, S.L., van Jaarsveld, A.S. 2000. A modelling approach to antlion (Neuroptera: Myrmeleontidae) distribution patterns. African Entomol. 8, 157-168.

Erasmus, B.F.N., van Jaarsveld, A.S., Chown S.L., Kshatriya, M., Wessels, K.J. 2002. Vulnerability of South African animal taxa to climate change. Global Change Biology 8, 678-693.

Fairbanks, D.H.K., Scholes, R.J., 1999. South African country study on climate change: Vulnerability and adaptation assessment for plantation forestry. CSIR Environmentek Report ENV/C/99, National Research Facility, Sustainable Development Program, Pretoria, South Africa

Fielding, A.H., Bell, J.F., 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environ. Conserv. 24(1), 38-49.

Florence, E.J.M., Sharma, J.K., Mohanan, C., 1986. A stem canker disease of Eucalyptus caused by Cryphonectria cubensis in Kerala. Kerala Forest Research Institute Scientific Paper 66, 384-387.

Guisan, A., Zimmermann, N.E., 2000. Predictive habitat distribution models in ecology. Ecol. Model. 135, 147-186.

Hassan, R.M., 1999. Correcting measures of national income for environmental values: The case of water abstractions and carbon sink externalities of industrial plantations in South Africa. S. Afr. For. J. 184, 1-11.

Hodges, C.S., 1980. The taxonomy of Diaporthe cubensis. Mycol. 72, 542-548.

Hodges, C.S., Reis, M.S., 1974. Identificacao do fungo causador do cancro de Eucalyptus spp. no Brasil. Brasil Florest. 5, 19.

Hodges, C.S., Geary, T.F., Cordell, C.E., 1979. The occurrence of Diaporthe cubensis on Eucalyptus in Florida, Hawaii, and Puerto Rica. Plant Dis. Rep. 63, 216-220.

Hodges, C.S., Alfenas, A.C., Ferreira, F.A., 1986. The conspecificity of Cryphonectria cubensis and Endothia eugeniae. Mycologia 78, 343-350.

Hughes, L., 2000. Biological consequences of global warming: is the signal already apparent? Tree 15(2), 56-61.

Jeffree, E.P., Jeffree, C.E., 1994. Temperature and the biogeographical distribution of species. Functional Ecology 8, 640-650.

Jeffree, E.P., Jeffree, C.E., 1996. Redistribution of the potential geographical ranges of mistletoe and Colorado beetle in Europe in response to the temperature component of climate change. Functional Ecology 10, 562-577.

Knutti, R., Stocker, T.F., Joos, F., Plattner, G-K., 2002. Constraints on radiative forcing and future climate change from observations and climate model ensembles. Nature 416, 719-723.

Laughton, E.M., 1937. The incidence of fungal disease on timber trees in South Africa. S. Afr. J. Sci. 33, 377-382.

Le Roux, N.J., Olivier, J., 1996. Modelling hail frequency using a generalized additive interactive technique. S. Afr. Geogr. J. 78, 7-12.

Lindenmayer, D.B., Nix, H.A., McMahon, J.P., Hutchinson, M.F., Tanton, M.T., 1991. The conservation of Leadbeater's possum, Gymnobelideus leadbeateri (McCoy): a case study of the use of bioclimatic modelling. J. Biogeogr. 18, 371-383.

Lindner, M., 2000. Developing adaptive forest management strategies to cope with climate. Tree Physiology 20, 299-307.

Loehle, C., LeBlanc, D., 1996. Model-based assessments of climate change effects on forests: a critical review. Ecol. Model. 90, 1-31.

McDonald, B.A., McDermott, J.M., 1993. Population genetics of plant pathogenic fungi. BioScience 43(5), 311-319.

New, M., Hulme, M., Jones, P., 1999. Representing twentieth-century space-time climate variability. Part I: Development of a 1961-90 mean monthly terrestrial climatology. J. Climate 12, 829-856.

New, M., Hulme, M., Jones, P., 2000. Representing twentieth-century space-time climate variability. Part II: Development of 1901-96 monthly grids of terrestrial surface climate. J. Climate 13, 2217-2238.

Peng, C., 2000. Understanding the role of forest simulation models in sustainable forest management. Environmental Impact Assessment Review 20, 481-501.

Roux, J., Wingfield, M.J., Coutinho, T.A., Bouillett, J.P., Leigh, P., 2000. Diseases of plantation Eucalyptus in the Republic of Congo. S. Afr. J. Sci. 96, 454-456.

Sharma, J.K., Mohanan, C., Florence, E.J.M., 1985. Occurrence of Cryphonectria canker disease of E*ucalyptus* in Kerala, India. Ann. appl. Biol. 106, 265-276.

Smith, H., Wingfield, M.J., Crous, P.W., Coutinho, T.A., 1996. Sphaeropsis sapinea and *Botryosphaeria dothidea* endophytic in Pinus Spp and Eucalyptus Spp in South Africa. S. Afr. J. Bot. 62, 86-88.Smith, H., Wingfield, M.J., de Wet, J., Coutinho, T.A., 2000. Genotypic diversity *of* Sphaeropsis sapinea from South Africa and Northern Sumatra. Plant Dis. 84, 139-142.

Stanosz, G.R., Smith, D.R., Guthmiller, M.A., Stanosz, J.C., 1997. Persistence of Sphaeropsis sapinea on or in asymptomatic shoots of red and jack pines. Mycol. 89, 525-530.

Stenseth, N., Mysterud, A., Ottersen, G., Hurrel, J.W., Chan, K-S., Lima, M., 2002. Ecological effects of climate fluctuations. Science 297, 1292-1296.

Stott, P.A., Kettleborough, J.A., 2002. Origins and estimates of uncertainty in predictions of twenty-first century temperature rise. Nature 416, 723-726.

Swart, W.J., Wingfield, M.J., 1991a. Biology and control of Sphaeropsis sapinea on Pinus species in South Africa. Plant Dis. 75, 761-766.

Swart, W.J., Wingfield, M.J., 1991b. Seasonal response of Pinus radiata in South Africa to artificial inoculation with Sphaeropsis sapinea. Plant Dis. 75, 1031-1033.

Swart, W.J., Knox-Davies, P.S., Wingfield, M.J., 1985. Sphaeropsis sapinea, with special reference to its occurrence on Pinus spp. in South Africa. S. Afr. For. J. 35, 1-8.

Swart, W.J., Wingfield, M.J., Knox-Davies, P.S., 1987a. Conidial dispersal of Sphaeropsis sapinea in three climatic regions of South Africa. Plant Dis. 71, 1038-1040.

Swart, W.J., Wingfield, M.J., Knox-Davies, P.S., 1987b. Factors associated with Sphaeropsis sapinea infection of pine trees in South Africa. Phytophylactica 19, 505-510.

Swart, W.J., Conradie, E., Wingfield, M.J., Venter, W.B., 1992. Effects of water stress on the development of cambial lesions caused by Cryphonectria cubensis on Eucalyptus grandis. Plant Dis. 76, 744-746.

Van Heerden, S.W., Wingfield, M.J., 2001. Genetic diversity of Cryphonectria cubensis isolates in South Africa. Mycol. Res. 105, 94-99.

Van Zyl, L.M., Wingfield, M.J., 1998. Ethylene production by Eucalyptus clones in response to infection by hypovirulent and virulent isolates of Cryphonectria cubensis. S. Afr. J. Sci. 94, 193-194.

Van Zyl, L.M., Wingfield, M.J., 1999. Wound response of Eucalyptus clones after inoculation with Cryphonectria cubensis. Eur. J. For. Pathol. 29, 161-167.

Walther, G-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J,C., Fromentin, J-M., Hoegh-Guldberg, O., Bairlein, F., 2002. Ecological responses to recent climate change. Nature 416, 389-395.

Wingfield, M.J., Swart, W.J., 1994. Integrated management of forest tree diseases in South Africa. For. Ecol. Manage. 65, 11-16.

Wingfield, M.J., Swart, W.J., Abear, B., 1989. First record of Cryphonectria canker on Eucalyptus in South Africa. Phytophylactica 21, 311-313.

Wingfield, M.J., Roux, J., Coutinho, T.A., Govender, P., Wingfield, B.D., 2001. Plantation disease and pest management in the next century. S. Afr. For. J. 190, 67-72.

Zwiers, F.W., 2002. The 20-year forecast. Nature 416, 690-691.

Zwolinski, J.B., Swart, W.J., Wingfield, M.J., 1990. Economic impact of a post-hail outbreak of dieback induced by Sphaeropsis sapinea. Eur. J. For. Pathol. 20, 405-411.

Zwolinski, J.B., Swart, W.J., Wingfield, M.J., 1995. Association of Sphaeropsis sapinea with insect infestation following hail damage of Pinus radiata. For. Ecol. Manage. 72, 293-298.

CHAPTER 5

The effects of climate change on the farm sector in the Western Cape

THE EFFECTS OF CLIMATE CHANGE ON THE FARM SECTOR IN THE WESTERN CAPE

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Abstract

This paper links two different methodologies to determine the effects of climate change on the Western Cape farm sector. First, it uses a general circulation model (GCM) to model future climate change in the Western Cape, particularly with respect to precipitation. Second, a sector mathematical programming model of the Western Cape farm sector is used to incorporate the predicted climate change, specifically rainfall, from the GCM to determine the effects on key variables of the regional farm economy. In summary, results indicate that future climate change will lead to lower precipitation, which implies that less water will be available to agriculture in the Western Cape. This will have a negative overall effect on the Western Cape farm economy. Both producer welfare and consumer welfare will decrease. Total employment in the farm sector will also decrease as producers switch to a more extensive production pattern. The direct economic impacts, therefore, will fall disproportionately on the poor.

1.1 Introduction

At any one location, year-to-year variations in weather can be large, but analyses of meteorological and other data over large areas and over period of decades or more have provided evidence for some important systematic changes in weather over the past century (IPCC, 1995a). For example, global mean surface air temperature has increased by between 0,3 and 0,6 degrees centigrade, with some regional variations, since the late 19th century.

Considerable progress has been made in the 1990s in the modelling of climatic change. Three advances are of particular interest. First, in order to distinguish between natural and anthropogenic influences on climate, the inclusion of effects of sulphate aerosols in addition to greenhouse gases has led to more realistic estimates of human-induced radiative forcing. Second, simulations with coupled atmosphere-ocean models have provided important information about decade to century time-scale natural internal climate variability. Third, there has been a shift of focus from studies of global-mean changes to comparisons of modelled and observed spatial and temporal patterns of climate change (IPPC, 1995a). Two results from these models are important: The balance of evidence suggests that there is a discernible human influence on global climate, and climate is expected to continue to change in the future.

A range of future scenarios, incorporating future greenhouse gas and aerosol precursor emissions based on assumptions concerning population and economic growth, land-use, technological changes, energy availability and fuel mix during the period 1990-2100, has been developed. General circulation models (GCMs) use these emissions to develop projections of future climate by linking the global carbon cycle and atmospheric chemistry (IPCC, 1995b). However, the limitations of these GCM results should be recognised when quantifying effects of climate change. Due to the complex nature of atmospheric conditions giving rise to precipitation, there is more confidence in temperature predictions than in hydrological predictions. Confidence is also presently higher in broad scale (global and hemispheric) climate predictions than in regional predictions. In spite of these limitations, these results remain important, as they provide the only indication of the potential effects of climate change, particularly precipitation, on regions that are to a large degree dependent on favourable climatic conditions for securing livelihoods for the inhabitants. One such region is the Western Cape, where agricultural production, based largely on irrigation, provides the backbone of the regional economy.

Against this background, the objectives of this paper are twofold. First, it uses a general circulation model (GCM) to model future climate change in the Western Cape, particularly with respect to precipitation. Second, a sector mathematical programming model of the Western Cape farm sector is used to incorporate the predicted climate change, specifically rainfall, from the GCM to determine the effects on key variables of the regional economy. Ideally, each farm in a region should be modelled independently, with its own unique set of production conditions. However, this is hardly feasible and not necessary when production conditions are broadly homogeneous over an area. For both the GCM and sector mathematical programming model, the Western Cape has been divided into ten relatively homogeneous regions. This demarcation follows the Statistical Regions constituting the former Development Region A of South Africa, but includes a new Region 10 and leaves out the districts which were incorporated into the new Northern Cape Province. The Western Cape region modelled here thus closely approximates the Western Cape Province as defined in the 1997 Constitution.

The paper is organised as follows: The modelling of climate change in the Western Cape, using a GCM, is discussed next (Section 2). This is followed by a description of the regional mathematical programming model of the Western Cape farm economy in Section 3. The modelling of the effects of future climate change on the Western Cape farm economy is done in Section 4. Some conclusions follow in Section 5.

2. Modelling climate change in the Western Cape

2.1 General

There are a host of GCM models developed by various metereological offices world-wide. The model used to predict climate changes for the Western Cape region was developed by the Hadley Centre for Climate Prediction and Research of the United Kingdom Metereological Office. The model gives pessimistic but robust predictions and is generally accepted as reliable. It is currently being employed in the South African Country Studies Programme on Climate Change.

There are two options when implementing this model: with and without the potential mitigating effects of sulphate aerosols. Climate change values for this paper were derived by implementing the Hadley Centre Unified Model with no sulphates (http://www.meto.govt.uk/sec5/NWP/NWP_sys.html). The model was implemented by the Computing Centre for Water Research (CCWR) and the resultant values represent a worst case scenario for South Africa (Hewitson, 1998). This GCM predicts a temperature rise of 2,5-3,0 degrees centigrade for South Africa by the time that atmospheric CO_2 levels have doubled from their pre-industrial levels. Erring on the side of caution, this means that significant climate change can be expected at latest by the year 2050 (and quite possibly earlier) (Hewitson, 1998).

Historical precipitation data consisted of annual and monthly means from the past 30 years. These data at 1 minute resolution were re-sampled to a quarter degree resolution since predictions at the 1 minute resolution were considered unreliable because of modelling limitations (CCWR). Predicted changes in monthly precipitation were provided for each quarter degree grid square by the CCWR. The annual change for every quarter degree grid square was derived by adding up the changes for each of the 12 months. These precipitation data were then spatially intersected with the ten homogenous regions of the Western Cape (derived from 50 magisterial districts) to arrive at a map where every region is assigned a mean precipitation value based on the values of all the quarter degree grid squares intersecting that specific region.

Previous experience with analyses of these data (Erasmus *et al.*, in review) has shown that temporal variability is a dominant feature. Annual means therefore tend to disguise seasonal effects of climate change. In order to account for this, seasonal data were represented by values for February and August. These months were chosen because a factor analysis (Statsoft Inc, 1995) of the 12 monthly rainfall shows that February rainfall contributed most to Factor 1, explaining 56% of the variance in rainfall data, and August rainfall contributed most to Factor 2, which explained 37% of the variance in the data.

2.2 Results

Table 1 contains a summary of the future changes in precipitation that can be expected in the Western Cape. All the sub-regions have lower predicted precipitation values in February and August, as well as mean annual precipitation, compared to present values. There is a relatively wide range in the predicted decrease in mean annual precipitation from just over 3 per cent in

Table 1: Summary of present and predicted future mean precipitation for the Western Cape sub-regions.

Sub-region	Present mean PPT February (mm)	Predicted Future PPT February (mm)	% Change (%)	Present mean PPT August (mm)	Predicted Future PPT August (mm)	% Change (%)	Mean Annual PPT (mm)	Predicted Future Mean PPT (mm)	% Change (%)
1	9.800	9.522	2.8	81.000	75.020	7.4	632.400	602.142	4.8
2	14.111	13.688	3.0	117.889	112.485	4.6	831.187	801.741	3.5
3	14.871	13.654	8.2	52.516	46.351	11.7	514.499	477.792	7.1
4	32.048	29.363	8.4	38.857	33.227	14.5	531.023	486.128	8.5
5	32.385	28.033	13.4	32.462	28.707	11.6	501.820	448.008	10.7
6	17.731	13.953	21.3	22.962	18.750	18.3	351.138	302.068	14.0
7	6.750	5.461	19.1	47.021	43.617	7.2	421.029	391.111	7.1
8	4.227	3.976	5.9	61.773	60.071	2.8	417.708	399.470	4.4
9	1.213	0.922	24.0	27.574	27.273	1.1	219.157	203.190	7.3
10	16.551	10.015	39.5	7.562	6.703	11.4	225.812	164.932	27.0

Sub-region 2 to 27 per cent in Sub-region 10. The relationship between mean annual precipitation and percentage change in precipitation was further investigated by using these values for the original 50 magisterial districts from which the above-mentioned 10 regions were constructed, A linear least-squares regression of percentage change in precipitation on current mean annual precipitation shows a significant negative relationship that accounts for 42% of observed variation ($y = -0.0242x + 22.3317$; $F = 36{,}09$, df(49), $p<0.0001$). Further evidence for this trend becomes clear when the mean annual precipitation data set is divided in half to represent drier and wetter conditions; there is a significant difference in the percentage precipitation change that is expected to occur between these two groups (Kruskal Wallis chi square = 17.4981, $p<0.000001$). It is clear that drier areas will be more affected.

3. Modelling the farm sector in the Western Cape[1]

3.1 *Basic considerations*

The theory for the construction of sector mathematical programming models has been applied to South African agriculture on a number of occasions[2]. In this paper, these procedures are used to model the Western Cape farm sector to determine the effects of climatic change, particularly the effects of rainfall. Due to time and other constraints, Western Cape agriculture is modelled using 1988 census reports (CSS, 1993), which appeared in June 1993, as a basis. A number of more recent features of the economy are, however, modelled onto this base.

The construction of the model was done in three phases. First, the basic model with costs and fixed prices only was assembled. Next, risk was included by the mean absolute deviation method (MOTAD). Finally, variable product and input prices were modelled by using stepped demand functions.

In this model the Western Cape has been divided into ten relatively homogeneous regions, as described above. Two import and export 'regions' were also included, namely Cape Town for international imports and exports and Beaufort West for domestic trade with the rest of South Africa. Farm commodities can be produced in any of the ten resource regions, or imported from

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[1] This section describes a model of the Western Cape farm sector developed by Vink and Van Zyl (1998).

[2] The model construction is described in a report to the Development Bank of Southern Africa by Van Zyl (1995) which summarises much of the relevant theoretical literature. South African applications include Ortmann, 1985; Frank, 1986; Van Zyl, 1987; 1989a; 1989b; Howcroft, 1991; Van Zyl *et al*, 1991; Meyer and Van Zyl, 1992; Vink

the international market or the rest of South Africa. Similarly, commodities are either consumed in the region (on the consumption side no differentiation is made between the regions), or exported to the international market or to the rest of South Africa.

It is important to identify those commodities that compete for land and other resources so that the alternative production possibilities that face the farmer are also specified in the computer model. In this way, substitution in supply is included in the analysis. The 20 major agricultural commodities produced in the Western Cape were selected as production alternatives in this particular application. These commodities were selected on the basis of their contribution to gross farm income, as well as the land allocated to them. The selected commodities account for more than 90 per cent of the total agricultural land used in the region, and more than 85 per cent of the gross value of agricultural production.

Because there is a constraint for land in each area the model generates shadow prices for land if all the land is used. It is assumed that farmers employ a resource until its marginal revenue equals its price within a given set of physical, financial and institutional constraints. Therefore, the shadow price of land serves as a check on the model, because these shadow prices can be compared with the rental value of land. Labour and credit were assumed to be freely available, albeit at an increased cost for increasing amounts. Supply elasticities of 5 and 6, respectively, were assumed.

Water is included as a conventional input into irrigation farming at existing price levels, while the total availability of irrigation water is set as the outer limit to irrigation use. This allows manipulation of both the price of water (the tariff) as well as the total availability of irrigation stocks. In the former case a change in water tariffs will affect net farm income, and therefore the objective function of the model. In the latter case the model optimises using a different total availability of water as a binding constraint.

Since Freund's (1956) article on the inclusion of risk in a programming model, rapid developments have occurred in techniques for incorporating risk, particularly in single-period optimisation models (Hazell, 1982). Evidence suggests that farmers behave in a risk-averse manner (Young, 1979:1065). Neglect of risk can lead to considerable overstatement of the size

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et al, 1996.

of risky enterprises. Risk can be considered as a cost, namely the additional expected return that farmers want as compensation for taking risk (Barry & Fraser, 1976:288). Risk associated with various enterprises may be taken as the deviations of gross income per hectare from the mean or from the trend line over time (at least six years) as the enterprise price elasticities relate price and yield variability to income variability. The mean absolute deviation method (MOTAD), first proposed by Hazell (1971) and later developed by Hazell & Scandizzo (1974), was used in this application. Income variations during the six year period 1982 to 1988 were used to model the production risk associated with production of each of the commodities in each of the ten regions.

Transport opportunities/activities link the supply and demand sections of the model. Each of the thirteen resource regions or two import 'harbours' can supply any of the three consumption points, namely the Western Cape as a whole, and the two export 'harbours' (Cape Town and Beaufort West). Supply and demand for each region is treated as if it is coming from a specific point rather than from all over a region. This is done to make the representation of transport costs between and within resource regions easier. Consumption and production points were subsequently developed to facilitate this treatment. This is in line with the assumption that production practices, yields, risk and prices are the same within each of the regions.

The final model has 200 production activities (20 commodities in 10 regions); 24 import activities (12 commodities with two import points); 624 transport activities (200 production activities transported to 3 consumption areas, and 24 import activities); 42 demand schedules (of which 24 consist of 10 steps each), and 6 years of risk data for each commodity in each region. In addition, the model was structured to allow for the easy measurement of producer, consumer and total welfare, which form part of the different objective functions, depending on the scenario followed.

3.2 Model validation

Validation of the model is a process that leads to: (1) a numerical report of the model's fidelity to the historical data set; (2) improvements to the model in the case of imperfect validation; (3) a qualitative judgement on the reliability of the model in terms of its stated purposes; and (4) a conclusion (preferably explicit) concerning the kinds of applications for which it should not be used (Hazell and Norton, 1986). Validation begins with a series of comparisons of model results with the reported actual values of the variables.

Production is the variable most commonly used in validation tests, and for a number of agricultural models there are reported validation results that can be used for comparative purposes. Typically, there is considerable variation in the closeness of the fit to the historical data across different products, and the model builder may be willing to accept greater deviations in minor products if the predictions are good for the major products. There is no consensus on the statistic to be used in evaluating the fit, but in most cases a simple measure such as the mean absolute deviation (MAD) or the percentage absolute deviation (PAD) have been used.

The testing of the model was done by imposing all of the relevant policies which were current in 1988, specifically the marketing and pricing regime for each product, credit policy and other on-farm policies, in order to see how well it simulated the existing (1988) situation. The better the current situation is represented by the model, the more reliable the model. The values generated by the model correspond fairly well with the actual values for the Western Cape as a whole, although this is not necessarily true for the 10 sub-regions.[3] If a deviation of 15 per cent is deemed acceptable as a general rule of thumb (as suggested by Hazell and Norton, 1986), all the generated production quantities for the Western Cape are within this limit. A PAD of 8.19 per cent across all commodities for the Western Cape (as a whole) is obtained, which is adequate for this type of model.

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[3] In some of the individual sub-regions, relatively small quantities of some specific commodities are produced. In these areas, the model predicts a relatively large deviation (increase or decrease) of up to 75 per cent of the actual production, but in absolute terms these variations are small and insignificant. Where a specific commodity is important in a region, the model predicts both the relative and absolute production levels fairly accurately.

4. Modelling the effects of future climate change on the Western Cape farm economy

4.1 General

Different scenarios were modelled to demonstrate the effects of climate change, particularly as it impacts on water availability, on selected key variables to determine the effects of such change. These variables include the physical change in output (area under production for each of the commodities and livestock numbers); commodity prices; employment; and changes in producer welfare, consumer welfare and total (social) welfare. The information provided by the base scenario simulation depicting the 'before scenario' was subsequently used to compare the different climate scenarios (indicated by different amounts of water availability). It is important to emphasise that all other variables, for example transport costs, exchange rates, international prices and interest rates, stay the same for each scenario.[4]

The results obtained with the different simulations are often a function of the set of assumptions that underpin the analysis. Therefore, it is necessary to explicitly state some of the most important assumptions, which impact on the subsequent results.[5] Also, the direction of change is often much more important than the actual magnitude of the results obtained. For this reason less emphasis should be placed on the actual results than on the direction of change, while the assumptions which underpin the analysis should be considered together with the analysis of the results.

4.2 Results

Two different types of scenarios are used. First, the total availability of water to the each of the ten sub-regions comprising the Western Cape farm sector is limited by 10 and 30 per cent of current use, respectively. Second, the changes in rainfall generated by the GCM (Table 1) are used to model water availability for each of the sub-regions. New crop budgets had to be developed for each scenario. These scenarios allow for the full complementarity and

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[4] This restrictive *ceteris paribus* assumption allows for evaluation of the effects of the specific scenario in relative isolation.

[5] The most limiting factors in the analysis are as follows: (1) only the farm sector is modelled, with no attention given to changes in the farm input sector (credit aside); (2) there is no scope for changing input mixes of commodities in reaction to changes in output prices -- the assumed underlying technologies and market demand guide the whole system; (3) income changes and its effects on demand are not taken into account; (4) specific transport costs, exchange rates and international prices underlie the analysis; and (5) changes are not shown in a dynamic manner, but as final results.

supplementarity that exists with respect to water use between the different commodities within the different production sub-sectors. The production of the different commodities will be affected in different ways when water availability becomes increasingly limited, and the available water is transferred to the most profitable commodities. It was assumed that water could not be transferred between the ten relatively homogeneous sub-regions within the model. Table 2 provides a summary of the results.

From the table it is clear that the production of field crops and extensive livestock products will increase with lower water availability, while vegetable, fruit and intensive livestock production will decrease. The direction of change stays the same regardless of the level of the constraint on water availability, but as expected, the magnitude of change increases the less water is available. This seemingly counter-intuitive result has important consequences for total welfare and for the level of employment in Western Cape agriculture.

The sequence of the argument starts with the availability of water. In the first example, the stock of water is decreased by 10 per cent. The first reaction of the model is to reallocate water to its highest and best use. However, because water is less available, some amounts of other resources such as land are left idle. So, for example, one would expect that water would be reallocated from wheat under irrigation to higher value fruit. The land that was being used for the less valued irrigation crops will be left idle, as there is not enough water for it to be kept under irrigation. It is then reallocated to uses that do not require water, such as dryland field crop production and extensive livestock production.

Table 2 also shows the details of this result. All the sectors that are water-intensive (vegetables, fruit, dairy, angoras, pigs and chickens) experience a drop in output as water is allocated away from their use. The freed resources are allocated to wheat, barley, oats, beef cattle, and wool and non-wool sheep. These increases and decreases are reflected in the changes in commodity prices in the lower half of the table. So, for example, an increase in field crop production is reflected in a lower price, while a decrease in fruit production results in a higher price. It is important to note, as stated previously, that these changes in the physical volume of production and in prices are the net result of a chain of shifts in supply and demand that take place as a result of the changing availability of water.

Table 2: Effects of different scenarios of decreased water availability to the farm sector

Measure	Item	Deviation of simulation results from base values (%)		
		10% less water in all sub-regions	30% less water in all sub-regions	Water availability determined from GCM
Production	Production of crops (ton):			
	Field crops:	+	+	+
	Vegetables:	-	-	-
	Fruit:	-	-	-
	Number of livestock:			
	-Extensive	-	-	-
	-Intensive	+	+	+
Prices	Field crops:	-	-	-
	Vegetables:	+	+	+
	Fruit:	+	+	+
	Livestock:			
	- Extensive	-	-	-
	- Intensive	+	+	+
Welfare	Producers	-4.72	-21.54	-3.61
	Consumers	-2.48	-8.49	-1.86
	Total	-2.64	-10.25	-1.98
Employment	Farm employment	-3.56	-13.40	-2.74

The effect on welfare and employment are fairly predictable, and disastrous. Producers as a group lose, because production shifts away from high value crops and livestock products to extensive field and livestock sectors. Consumers (as a group) lose, even though they are paying less for basic foodstuffs. The total welfare of the Western Cape, which is the sum of the producer and the consumer surplus, therefore also decreases. Finally, as production shifts from intensive to extensive industries, the labour intensity of agriculture also declines, as can be seen by the decline in employment. This discriminates against the poor, so the conclusion can be drawn that the net effect of the changes is regressive in terms of income distribution.

5. Conclusions

This paper links two different methodologies to determine the effects of climate change on the Western Cape farm sector. First, it uses a general circulation model (GCM) to model future climate change in the Western Cape, particularly with respect to precipitation. Second, a sector mathematical programming model of the Western Cape farm sector is used to incorporate the predicted climate change, specifically rainfall, from the GCM to determine the effects on key variables of the regional economy.

In summary, results indicate that future climate change will lead to lower precipitation, which implies that less water will be available to agriculture in the Western Cape. This will have a negative overall effect on the Western Cape farm economy. Climate change will lead to a relative shift away from intensive production sectors in agriculture towards more extensive sectors. Both producer welfare and consumer welfare decrease. Total employment in the farm sector decreases as producers switch to a more extensive production pattern. The total decline in welfare, therefore, falls disproportionately on the poor in the province. These consequences could, of course be mitigated if the restriction on available water were to be matched by reactions such as a more efficient use of available water.

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References

BARRY, P.J. & FRASER, D.R., 1976. Risk management in primary agricultural production: Methods, distribution, rewards, and structural implications. American Journal of Agricultural Economics, Vol. 58 : 186-295.

CSS, 1993. Report No. 11-02-02 (1988). Pretoria, Central Statistical Services.

ERASMUS, B.F.N., KSHATRIYA, M., MANSELL, M.W., CHOWN, S.L. & VAN JAARSVELD, A.S. In review. The response of antlion (Neuroptera: Myrmeleontidae) distribution patterns to climate change: a modelling approach. African Entomology.

FRANK, D.B., 1986. An economic analysis of various policy options for the South African maize industry. Unpublished MSc(Agric) thesis, University of Natal, Pietermaritzburg.

FREUND, R.J., 1956. The introduction of risk into a programming model. Econometrica, Vol 24: 253-263.

HAZELL, P.B.R., 1971. A linear alternative to quadratic and semi-variance programming for farm planning under uncertainty. American Journal of Agricultural Economics. Vol 53: 53-62.

HAZELL, P.B.R., 1982. Application of risk preference estimates in firm-household and agricultural sector models. American Journal of Agricultural Economics. Vol 64: 384-390.

HAZELL, P.B.R. & NORTON, R.D., 1986. Mathematical Programming for Economic Analysis in Agriculture. Macmillan Publishing Company, New York.

HAZELL, P.B.R. & SCANDIZZO, P.L., 1974. Competitive demand structures under risk in agricultural linear programming models. American Journal of Agricultural Economics, Vol 56: 235-244.

HEWITSON, B.C., 1998. South African National Assessment for the Framework Convention for Climate Change: Climate Change Scenarios. Http://tie.egs.uct.ac.za/fcc/hadcm2.html.

HOWCROFT, P., 1991. An economic analysis of different policies in the wheat industry. Unpublished MSc(Agric) dissertation, Department of Agricultural Economics, University of Natal, Pietermaritzburg.

IPCC, 1995a. Summary for Policymakers: The Science of Climate Change – IPCC Working Group I. Http://www.ipccc.ch/pub/sarsum1.html.

IPCC, 1995b. 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.

MEYER, N.G. & VAN ZYL, J., 1992. Comparative advantages in Development Region G: An application of a sectoral linear programming model. Agrekon. Vol. 31(4).

ORTMANN, G.F., 1985. The Economic Feasibility of Producing Ethanol from Sugar-Cane in South Africa. Unpublished Ph.D. Thesis, Department of Agricultural Economics, University of Natal, Pietermaritzburg.

Statsoft Inc., 1995. STATISTICA for Windows [Computer Program Manual]. Tulsa, OK. Http:/www.statsoft.com

VAN ZYL, J. 1987. Interrelationships in the South African maize market. Unpublished research report, Development Bank of South Africa. 129 pp.

VAN ZYL, J. 1989a. Interrelationships in the maize industry I: Production and price aspects. Development Southern Africa, Vol. 6(2).

VAN ZYL, J. 1989b. Interrelationships in the maize industry II: Welfare aspects. Development Southern Africa, Vol. 6(3).

VAN ZYL, J. 1995. Theoretical Considerations in the Development of a Sectoral Mathematical Programming Model. Midrand, Development Bank of Southern Africa, Unpublished report.

VAN ZYL, J., VINK, N. & FéNYES, T.I., 1991. Market liberalization in the South African maize industry. Journal of Agricultural Economics.

VINK, N. & VAN ZYL, J., 1998. Effects of water restrictions on the Western Cape farm sector. Agrekon, 37(4):

VINK, N, J VAN ZYL, D VAN SEVENTER AND J B ECKERT. 1996. The macroeconomics of rural livelihoods creation in the Western Cape province. In Lipton M, De Klerk M, Lipton Merle (Eds.) Land, labour and livelihoods in rural South Africa. Volume 1: Western Cape. Indicator Press, 1996: 51-70

YOUNG, D.L., 1979. Risk preferences of agricultural producers : Their use in extension and research. American Journal of Agricultural Economics, Vol 61: 1063-1069.

CHAPTER 6

Improving species' distribution model outputs using jackknife procedures

Improving species' distribution model outputs using jackknife procedures

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ABSTRACT

Bioclimatic envelope modeling of species' distributions can be misleading if no measure of uncertainty is associated with the predicted probability of occurrence values. Here we demonstrate how jackknife procedures can be used to generate such measures of uncertainty in the case of the distribution of a carpenter bee (*Xylocopa senior*) in South Africa. The modelled probability of occurrence surface for *Xylocopa senior* is more meaningful when interpreted in the context of the variation underlying these predictions, i.e., when more confidence/weight is ascribed to predictions with limited variation. This procedure is potentially of considerable value for any approach based on interpolated species distributions, including survey planning, area selection, modelling of climate change effects and biogeography. Resampling techniques can also be used as a means to provide insights into model performance and for crossvalidation, without the need for data partitioning or the acquisition of additional data.

INTRODUCTION

Bioclimatic models are routinely used to predict and define the broad scale limits of species distributions (Lindenmayer *et al*. 1991). Thus, where the spatial distribution of a taxon is not fully defined, bioclimatic analyses allow researchers to describe the probable limits of distribution. (Lindenmayer *et al*. 1991; Brzeziecki *et al.* 1995; Lindsay *et al.* 1998). Moreover, such models can be used to evaluate the risks and benefits likely to arise for species under future climatic scenarios (Lindenmayer *et al*. 1991; Jeffree & Jeffree 1994; Huntley *et al*. 1995; Sykes & Prentice 1995; Jeffree & Jeffree 1996; Sykes *et al.* 1996; Hill *et al.* 1999). The underlying principle of bioclimatic modelling is to determine whether there is any relationship between the known distribution of a species and some climatic variable or variables. Popular modelling approaches that have been employed include generalised linear regression (e.g. logistic regression) (Margules & Stein 1989; Austin *et al.* 1990; Walker 1990; Osborne & Tigar 1992; Cary & Ullyett 1993; Hill *et al.* 1999), classification trees (Walker 1990) and discriminant function analysis (Caughley *et al*. 1987) (see Guisan & Zimmerman (2000) for a comprehensive review of predictive habitat distribution models).

The product of such modelling is usually a map with grid coverage that is used to present the model's prediction of the probable distribution of a species. The model makes an individual prediction for every grid cell. The predicted distribution maps can be either *binary maps* or *probability of occurrence surface maps*, depending on the model used (see Osborne & Tigar (1992) for a combination). In the binary map, each grid cell is assigned either a presence or an absence rating (e.g. Huntley *et al*. 1995; Lindsay *et al.* 1998; Hill *et al.* 1999). A limitation of these maps is that they do not distinguish between areas that are most suitable and those that are only marginally suitable. Probability surface maps overcome this problem by assigning a probability of occurrence to each grid cell (see for example Walker 1990; Beerling *et al.* 1995; Erasmus *et al.* 2000, Erasmus *et al.* 2002). The probability assigned to a specific cell is an indication of the suitability of climate (i.e. the predictors in the model) in that grid cell for the species (Robertson *et al.* 2001). Since a continuum of suitability values is generated, the relative suitability of areas (with regard to the variables included as predictors in the model) can be compared. Because probability surface maps communicate more information than binary maps, we focus on the former approach.

Irrespective of the modelling approach used for predicting the probability surface of a species, the result is a single predicted probability value for each grid cell. These probabilities could also be called *best estimates,* because the models base their calculations on all the available data. The predicted distribution is therefore presented as a geographical area divided into grid cells with a single probability (best estimate) of the suitability of that locality for a specific species (as determined by the selected predictor variables) (e.g. Fig. 1). Although the best estimate gives an indication of the probability of a grid cell being climatically suitable, the best estimate is still a value of a stochastic variable (new data will necessarily lead to a new best estimate) and it can be misleading if no indication of the *uncertainty* associated with that value is provided. In their review, Guisan & Zimmerman (2000) identify the lack of spatially explicit uncertainty measurements of predicted probabilities as a key area requiring further development. One way of attributing a useful uncertainty measurement is to estimate the variation underlying each stochastic best estimate. All else being equal, more confidence can be placed in a best estimate associated with less variation than a best estimate associated with substantial variation. However, probabilities of climate suitability are usually not presented together with estimates of uncertainty since probability surface models predict only a single probability of occurrence for each grid cell, using all the relevant data available.

Using a case study, the present paper makes a start at addressing Guissan & Zimmerman's (2000) concerns regarding the lack of a spatially explicit uncertainty measure for interpolated distributions and shows how jackknife re-sampling procedures can be used to estimate the variation around each probability of occurrence value. The manner in which such estimates of variation can improve the interpretation of a probability surface map generated by a bioclimatic model is shown, and the implications of this approach are outlined.

MATERIAL AND METHODS

Xylocopa senior Vachal distribution records

Collection records from the Plant Protection Research Institute of South Africa and the South African Museum were combined into a data set containing 27 records of a carpenter bee, *Xylocopa senior* (Fig. 1). The data set of *Xylocopa senior* was chosen because 27 records do

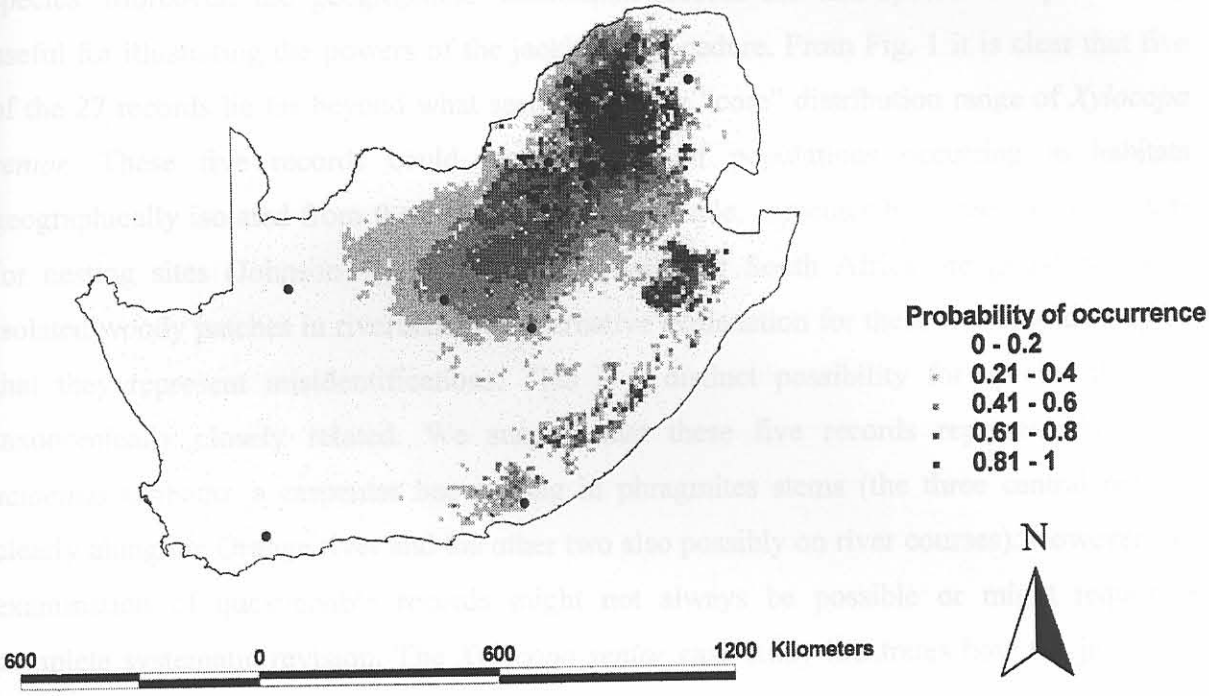

Fig. 1: Known distribution records (•) of *Xylopa senior* and the bioclimatically modelled probability of occurrence surface

not represent a comprehensive data set, and this is often a reality for poorly surveyed species, especially invertebrates (Koch *et al.* 2000). This example illustrates how limited distribution data can be used to provide useful information with regard to the probable distribution of a species. Moreover, the geographical distribution records for this species are particularly useful for illustrating the powers of the jackknife procedure. From Fig. 1 it is clear that five of the 27 records lie far beyond what seems to be the "core" distribution range of *Xylocopa senior*. These five records could be indicative of populations occurring in habitats geographically isolated from the core range. For example, carpenter bees need woody plants for nesting sites (Johnson 1997). The central parts of South Africa are grasslands with isolated woody patches in riverbeds. An alternative explanation for these five records may be that they represent misidentifications. This is a distinct possibility for species that are taxonomically closely related. We suspect that these five records represent *Xylocopa scioensis* Gribodo, a carpenter bee nesting in phragmites stems (the three central records clearly along the Orange river and the other two also possibly on river courses). However, re-examination of questionable records might not always be possible or might require a complete systematic revision. The *Xylocopa senior* case study illustrates how the jackknife procedure provides a way to further understand questionable or outlying distribution records.

Climate data

The Computing Centre for Water Research (CCWR) provided the historic climate data (thirty-year means; 1960-1990). These data comprise interpolated climate surfaces at a minute by minute resolution. These climate surfaces were resampled to a 10km x 10km grid cell size. Grid cell size was dictated by the total number of cells that can realistically be analysed given the available computer time without sacrificing output resolution too much. Bee point occurrence records were also generalised to this 10 km gridcell resolution.

The objective of this paper is not to make any concrete conclusions about the distribution of *Xylocopa senior* or the factors controlling its distribution, but rather to illustrate how the interpretation of a probability of occurrence surface of a species can be improved by employing jackknife procedures. Consequently, we did not strive to optimise the model by using the minimum number of significant variables, nor have we interpreted the model outcomes fully. The complexity of the model and the modeling approach is therefore considered relatively unimportant in this paper. Six climatic variables (mean temperature, minimum temperature, maximum temperature, mean annual rainfall, mean rainfall for the driest month and mean rainfall for the wettest month) were selected as the climatic predictors. These variables were selected because they represent a suite of climatic variables likely to control the distribution of insects, either directly or indirectly (see Chown & Gaston 1999).

Model

The model we used here is a multivariate generalisation of the bivariate model described by Jeffree & Jeffree (1994). Briefly, using this method the grid cells where a particular species is recorded are referred to as *known* records. A scatter plot of the climate values of all grid cells for any two chosen climate variables is defined as the climate space. The climate values at points in the climate space that represent known records are used to construct the principle axes of an elliptical confidence region by using the sums of squares of the distance from the major and minor principal axis. The elliptical confidence region is superimposed on the climate space and can be interpreted as a climate envelope containing localities climatically similar to known records. All points falling within this climate envelope are then mapped back into geographical space to form an interpolated distribution of climatically similar areas where this species might potentially be found (see Jeffree & Jeffree (1994) for additional information). This approach by Jeffree & Jeffree (1994) is similar to the technique described by Sokal & Rohlf (1981) and relies heavily on the graphical interpretation of a two-dimensional scatter plot. In consequence, it has very limited application in scenarios where the climate space has to be multidimensional if three or more climate variables are needed to explain observed distribution patterns satisfactorily. Thus, we have adapted the original model to incorporate m climatic predictor variables. Not only is this a significant improvement on the original model, but it also allows the production of a probability surface of suitability for each species (Erasmus *et al.* 2000), rather than a more simplistic presence-absence distribution model. In the multivariate generalisation of the bivariate model the values of selected climate variables for each known record cell are plotted on an m-dimensional scatter plot (for the m climate variables), and mean climate values are subtracted to centre values around the origin of the multidimensional scatter plot. An $m \times m$ covariance matrix is calculated and this matrix is used as an input to calculate eigen values and eigen vectors for the covariance matrix. These eigen vectors from the orthogonal principle axis of an m-dimensional hyperspace with the origin representing the theoretical core of the species' distribution, as defined by the predictor climate variables (see Robertson *et al.* 2001 for a detailed description of a similar, PCA-based model). The climate variable values of all grid cells are then transformed into this eigen vector space. These transformed climate variables are subsequently divided by the eigen values. In the resulting *m*-dimensional hyperspace, the distance of any particular unsampled grid cell from the origin represents a measure of the suitability of that locality for the specific species (Robertson *et al* 2001). The entire calculation for this multivariate technique is relatively straightforward and does not require considerable computing power. The outcome of this analysis is a probability surface map of suitability, as determined by the set of predictor variables, for a species. Hereafter, this probability surface of climate suitability will be referred to as the probability of occurrence.

Estimating variation using the jackknife procedure

By using jackknife procedures, *n* probability of occurrence values (*n* = size of data set) can be generated for each grid cell instead of a single value. This method re-calculates the statistic of interest, in this case a probability of occurrence, *n* times, each time using a different combination of *n-1* of the data set records. The jackknife principle uses these *n* pseudovalues to estimate the variation associated with the statistic.

In the Erasmus *et al.* (2000) modelling procedure, the whole data set (*n* = 27) is used to calculate a single probability of occurrence for each grid cell (the best estimate, Fig. 1). The jackknife procedure re-calculates the probability of occurrence for each grid cell 27 (*n*) times using the same model with a different combination of 26 (*n-1*) records each time. These re-calculated estimates are referred to as the *jackknife pseudovalues.*

The jackknife pseudovalues can be used to calculate the standard error of the best estimate, which is an estimate of the variation associated with that best estimate, using the following formula (Efron & Tibshirani 1993; Shao & Tu 1995):

$$se_{jack} = \sqrt{n/(n-1) \times (\sum_{i=1}^{n} \hat{\theta}_i^2 - (\sum_{i=1}^{n} \hat{\theta}_i)^2 / n)} \qquad \text{(eqn 1)}$$

where se_{jack} = estimated standard error of the best estimate;

$\hat{\theta}_i$ = i th jackknife pseudovalue;

n = size of data set.

se_{jack} is an estimate of the standard error of the best estimate and does not merely represent the standard deviation of the n jackknife pseudovalues.

The se_{jack} and the coefficient of variation ($\frac{se_{jack}}{best\ estimate}$) are therefore measures of variation associated with the best estimate. The se_{jack} is a measure of *absolute* variation while the coefficient of variation is a measure of *relative* variation (variation relative to the best estimate) (see results section). In reality, by assessing the best estimate's variation, the jackknife procedure has generated additional information from the original data set. These variance estimates are likely to improve the interpretation of the generated probability surfaces considerably.

RESULTS

Best estimate probability surface (model prediction)

The probability of occurrence surface (best estimates) for *Xylocopa senior* in South Africa, using a suite of six climatic variables as predictors in the model (Erasmus *et al.* 2000), is illustrated in Fig. 1. The model's prediction seems to provide a reasonably good fit for the data records, except for the distortion caused by five influential records which "pull" the probability surface well into the central parts and down towards the eastern shores of the country.

Estimated variance

The se_{jack} and coefficient of variation associated with the best estimate for each grid cell are illustrated in Figs. 2a and 2b respectively.

The best estimate communicates a lot more information when interpreted in the context of its estimated variance. For example, cell A (Fig. 2b) has a probability of occurrence (best estimate) of 0.72 and a se_{jack} of 0.42. This large variation suggests that the best estimate is

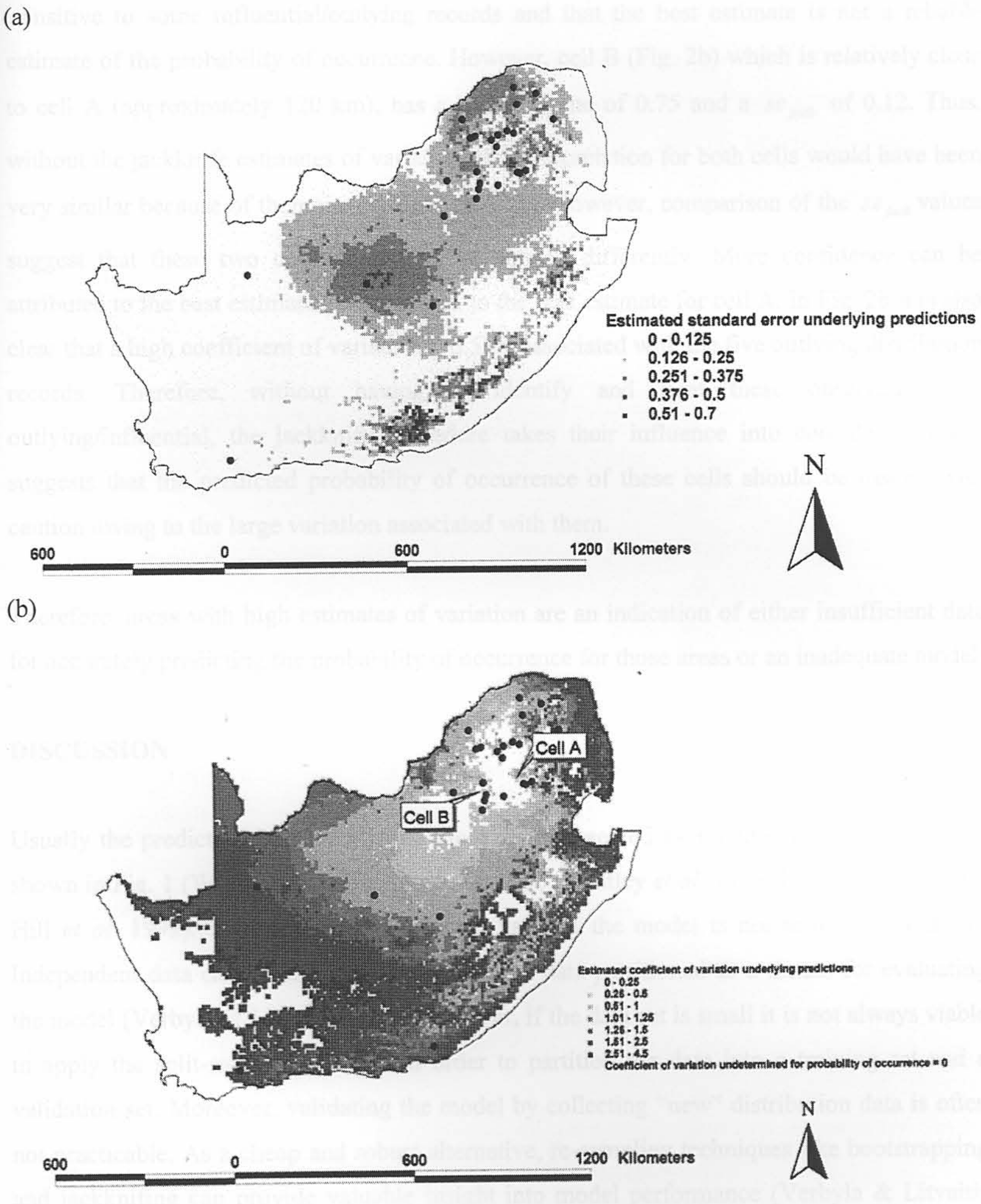

Fig. 2: Known distribution records (•) of *Xylopa senior* and (a) the estimated standard error (se_{jack}), and (b) coefficient of variation underlying the predicted probability of occurrence surface for the species. The modelled probability of occurrence values for cell A and B are 0.72 and 0.75. The estimated standard error underlying each prediction is 0.42 and 0.12 for cells A and B respectively.

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sensitive to some influential/outlying records and that the best estimate is not a reliable estimate of the probability of occurrence. However, cell B (Fig. 2b) which is relatively close to cell A (approximately 120 km), has a best estimate of 0.75 and a se_{jack} of 0.12. Thus, without the jackknife estimates of variation, the interpretation for both cells would have been very similar because of their similar best estimates. However, comparison of the se_{jack} values suggest that these two cells should be interpreted differently. More confidence can be attributed to the best estimate of cell B than to the best estimate for cell A. In Fig. 2b it is also clear that a high coefficient of variation (>0.5) is associated with the five outlying distribution records. Therefore, without having to identify and treat these observations as outlying/influential, the jackknife procedure takes their influence into consideration and suggests that the predicted probability of occurrence of these cells should be treated with caution owing to the large variation associated with them.

Therefore, areas with high estimates of variation are an indication of either insufficient data for accurately predicting the probability of occurrence for those areas or an inadequate model.

DISCUSSION

Usually the prediction of a bioclimatic model is represented as a single distribution map as shown in Fig. 1 (Walker 1990; Beerling *et al.* 1995; Huntley *et al.* 1995; Lindsay *et al.* 1998; Hill *et al.* 1999). Such maps are of limited value if the model is not tested or validated. Independent data can be collected or the original data partitioned as a means for evaluating the model (Verbyla & Litvaitis 1989). However, if the data set is small it is not always viable to apply the split-sample approach in order to partition the data into a training set and a validation set. Moreover, validating the model by collecting "new" distribution data is often not practicable. As a cheap and robust alternative, re-sampling techniques like bootstrapping and jackknifing can provide valuable insight into model performance (Verbyla & Litvaitis 1989; Osborne & Tigar 1992; Fielding & Bell 1997; Manel *et al.* 1999, Guisan & Zimmerman 2000). For example, when modelling techniques using presence/absence data instead of presence only data are used (e.g. logistic regression), real values can be compared to values predicted by the jackknife procedure, using the prediction from the model without the observation considered..The overall predictive ability of the model can then be evaluated by applying, for instance, the ROC-plot approach (Fielding & Bell 1997). Moreover, although the value of re-sampling techniques for validating or testing distribution models has been recognised, they are still not routinely used. Here we have shown how re-sampling can be used effectively to provide a measure of confidence in model predictions, and how, in consequence, the interpretation of predicted distributions can be improved. Arguably, insights can be gained from a careful, expert-based scrutiny of the data; the main advantage of this jackknife procedure is that it provides quantitative support for such expert opinions, and where expert opnion is not readily available, it provides a method with which to assess to data of unknown quality.

Jackknifing may also to some extent be used to detect misclassifications of species, especially for species that are taxonomically closely related. For example, in the *Xylocopa senior* case study presented in this paper we suspected that five of the observations were misclassifications due to their geographical location. However, without having to treat these observations as misclassification or re-examining these records, the jackknife technique supported our suspicion by attributing high variation to the predicted probability of occurrence values at these sites and the surrounding areas (Fig. 2b).

It has to be borne in mind that there might be computational limitations when applying this jackknife approach to large datasets. There are more small data sets than larger ones, and the potential limitation of computing power on large data sets do not invalidate the usefulness of the approach on smaller data sets, where there are no computing limitations. The analyses in this paper was conducted on what can now be considered an entry level Pentium 3 workstation, and analysis on other data sets of up to 1000 records have been achieved within reasonable time limits

Arbitrary thresholds are sometimes placed on probability surfaces to identify "core" distribution areas of species (Walker 1990; Buckland & Elston 1993; Huntley *et al*. 1995). Fig. 3. illustrates all the grid cells with a probability of occurrence ≥ 0.5. We arbitrarily used this threshold value for illustration purposes, but methods for optimising this value can be found in the literature (e.g. Huntley *et al*. 1995, Zweig & Campbell 1993). The variation underlying predictions can be used as an additional condition to identify core distribution areas. In Fig. 3, all the filled cells have a probability of occurrence ≥ 0.5, but the dark grey

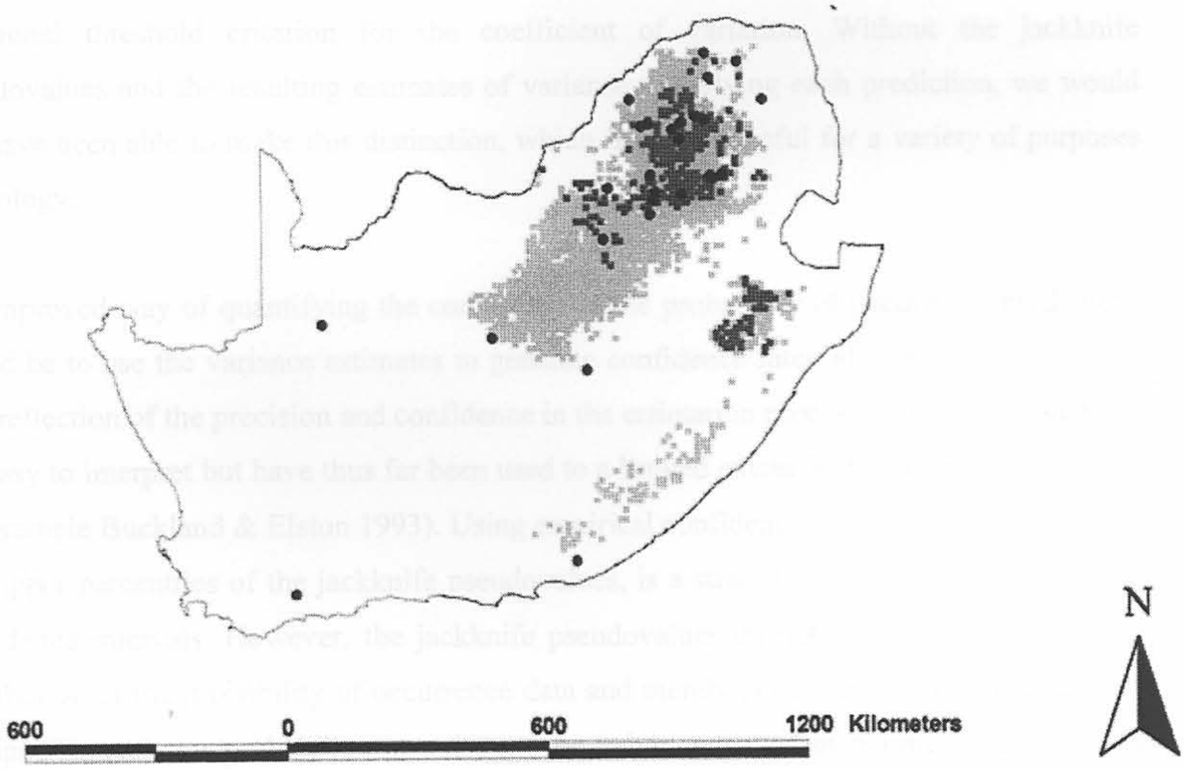

Fig. 3: Known distribution records (•) of *Xylocopa senior*. All the filled cells have predicted probability of occurrence values of ≥ 0.5. Dark grey cells satisfy the additional condition that the coefficient of variation underlying the predicted probability of occurrence is ≤ 0.15

cells satisfy the additional condition that the coefficient of variation is ≤ 0.15 (also arbitrary). Therefore, the dark grey cells are a filtered subset of the light grey cells, satisfying the additional threshold criterion for the coefficient of variation. Without the jackknife pseudovalues and the resulting estimates of variance underlying each prediction, we would not have been able to make this distinction, which is clearly useful for a variety of purposes in ecology.

An improved way of quantifying the confidence in the probability of occurrence predictions would be to use the variance estimates to generate confidence intervals. These intervals will be a reflection of the precision and confidence in the estimation process. Confidence intervals are easy to interpret but have thus far been used to a limited extent in distribution studies (see for example Buckland & Elston 1993). Using empirical confidence limits, based on the lower and upper percentiles of the jackknife pseudovalues, is a straightforward way of calculating confidence intervals. However, the jackknife pseudovalues do not simulate the underlying distribution of the probability of occurrence data and merely generates pseudovalues closely clumped around the probability as only one record is removed at a time. The empirical confidence intervals will therefore consistently underestimate the real interval length. The purpose of these jackknife pseudovalues is to estimate the variation (using equation 1) and they should not be used for calculating empirical confidence limits. Empirical confidence limits can only be used with bootstrapping, another re-sampling method, which simulates the underlying distribution of the statistic under consideration (this approach was followed by Buckland & Elston 1993). Since empirical confidence limits cannot be used for jackknifing, the normal approximation is sometimes used. Equation 2 gives the upper and lower confidence limits of a jackknife confidence interval if it can be assumed that $\hat{\theta}_{best\ estimate}$ is normally distributed:

$$\hat{\theta}_{best\ estimate} \pm \{z_{\alpha/2} \times se_{jack}\} \qquad \text{(eqn 2)}$$

where: $\hat{\theta}_{best\ estimate}$ = best estimate;

$z_{\alpha/2} = (1-\alpha/2)$th percentile of the standard normal distribution;

se_{jack} = standard error of the best estimate (from equation 1)

One of the assumptions of equation 2 is that the underlying distribution of the statistic under consideration is approximately normal (Efron & Tibshirani 1993). This condition is not true for a statistic that is bounded, like the probability of occurrence values generated in the present study ($0 \leq \theta_{best\ estimate} \leq 1$). Where a statistic is bounded, transformations can be used to normalise the data. For example, Efron & Tibshirani (1993) used the Fisher transformation to normalise jackknife pseudovalues before confidence limits were calculated for correlation coefficients (a correlation coefficient, ρ, is bounded: $-1 \leq \rho \leq 1$). We tested a range of transformations, inter alia the probit (Cox 1970) and logit (Williamson & Gaston 1999) transformations that are suitable for probability values that are bounded between zero and one. After transforming the raw data, histograms for jackknife pseudovalues for each grid cell were drawn and a Kolmogorov-Smirnov normality test employed to test whether the data were adequately transformed to an approximate normal distribution. However, all of the transformations we employed failed to normalise the data adequately. Further work is needed in this regard since confidence intervals, as a function of the estimated variation, will be easier to present and interpret.

The predicted probabilities of occurrence and their variance estimates can have important implications for ecological surveys, conservation and management. The jackknife procedure presents a quantitative way to identify outliers in known distribution records. Such outliers might be real and truly peripheral to the core distribution, or they may indicate some error in data collection. Either way, further attention to these specific records is warranted.. The same argument can be applied to the planning of productive sampling sites, conservation hotspot identification (Meyers *et al.* 2000*)* and reserve selection (Margules & Pressey 2000). Therefore, without having to conduct extensive surveys, probabilities of occurrence together with their variance estimates can be used as a source of reference, as a decision-making tool in planning and for development proposals (Buckland & Elston 1993).

Another potential application of bioclimatic models is to predict possible distribution changes that may result from changing climates (Lindenmayer *et al.* 1991; Jeffree & Jeffree 1994; Huntley *et al*. 1995; Jeffree & Jeffree 1996; Sykes & Prentice 1995; Sykes *et al.* 1996; Hill *et al.* 1999). The interpretation of the predicted distributions under various climatic scenarios can be considerably improved by supplementing this information with indications of the variance underlying such predictions. Data sets with few known records may give rise to a probability of occurrence surface associated with large variance parameters, especially when the climate predictors for the different records are dissimilar.

Although the advantages of jackknifing is illustrated in this paper using a specific modelling approach, it is important to note that this re-sampling technique can readily be applied to most existing modelling techniques (e.g. GLM, GAM, CART, etc.). This makes jackknifing an important tool for estimating the variation underlying the predictions of various bioclimatic modelling techniques.

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REFERENCES

Austin, M.P. & Meyers, J.A. (1996) Current approaches to modelling the environmental niche of eucalypts: implications for management of forest biodiversity. *Forest Ecol. Manag.*, 85, 95-106.

Austin M.P., Nicholls A.O. & Margules C.R. (1990) Measurement of the realized qualitative niche: environmental niches of five *Eucalyptus* species. *Ecol. Monogr.*, 60(2), 161-177.

Beerling D.J., Huntley B. & Bailey J.P. (1995) Climate and the distribution of *Fallopia japonica*: use of an introduced species to test the predictive capacity of response surfaces. *J. Veg. Sci.*, 6, 269-282.

Brzeziecki B., Kienast F. & Wildi O. (1995) Modelling potential impacts of climate change on the spatial distribution of zonal forest communities in Switzerland. *J. Veg. Sci.*, 6, 257-268.

Buckland S.T. & Elston D.A. (1993) Empirical models for the spatial distribution of wildlife. *J. Appl. Ecol.*, 30, 478-495.

Carey P. & Ullyett J. (1993) Modelling the effects of climate change of species' distribution. *NERC News*, 24-25.

Caughley G., Short J., Grigg G.C. & Nix H. (1987) Kangaroos and climate: an analysis of distribution. *J. Anim. Ecol.*, 56, 751-761.

Chown S.L & Gaston K.J. (1999) Exploring links between physiology and ecology at macro-scales: the role of respiratory metabolism in insects. *Biol. Rev.*, 74, 87-102.

Cox D.R. (1970) *The analysis of binary data*. Chapman & Hall, New York.

Efron B & Tibshirani R.J. (1993) *An introduction to the Bootstrap*. Chapman and Hall, New York.

Erasmus B.F.N., Kshatriya M., Mansell M.W., Chown S.L. & Van Jaarsveld A.S. (2000) A modelling approach to antlion (Neuroptera: Myrmeleontidae) distribution patterns. *Afr. Entomol.*, 8, 157-168.

Erasmus, B.F.N., Van Jaarsveld, A.S., Chown, S.L., Kshatriya, M. & Wessels, K.J. (2002). Vulnerability of South African animal taxa to climate change. *Glob. Change Biol.*, 8, 679-693.

Fielding A.H. & Bell J.F. (1997) A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environ. Conserv.*, 24, 38-49.

Guisan A. & Zimmerman N.E. (2000) Predictive habitat distribution models in ecology. *Ecol. Model.*, 135, 147-186.

Hill J.K., Thomas C.D. & Huntley B. (1999) Climate and habitat availability determine 20th century changes in a butterfly's range margin. *P. Roy. Soc. Lond. B Bio.*, 266, 1197-1206.

Huntley B., Berry P.M., Cramer W. & McDonald A.P. (1995) Modelling present and potential future ranges of some European higher plants using climate response surfaces. *J. Biogeogr.*, 22, 967-1001.

Jeffree C.E. & Jeffree E.P. (1996) Redistribution of the potential geographical ranges of Mistletoe and Colorado Beetle in Europe in response to the temperature component of climate. *Funct. Ecol.*, 10, 562-577.

Jeffree E.P. & Jeffree C.E. (1994) Temperature and the biogeographical distribution of species. *Funct. Ecol.*, 8, 640-650.

Johnson S.D. (1997) Pollination ecotypes of *Satyrium hallackii* (Orchidaceae) in South Africa. *Bot. J. Linn. Soc.*, 123, 225-235.

Koch S.O., Chown S.L., Davis A.L.V., Endrödy-Younga S. & van Jaarsveld A.S. (2000) Conservation strategies for poorly surveyed taxa: a dung beetle (Coleoptera, Scarabaeidae) case study from southern Africa. *J. Insect Conser.*, 4, 45-56.

Lindsay S.W., Parson L. & Thomas C.J. (1998) Mapping the ranges and relative abundance of the two principal African malaria vectors, *Anopheles gambiae sensu stricto* and *An. arabiensis*, using climate data. *P. Roy. Soc. Lond. B Bio.*, 265, 847-854.

Lindenmayer P.B., Nix H.A., McMahon J.P., Hutchinson M.F. & Tanton M.T. (1991) The conservation of Leadbeater's possum, *Gymnobelideus leadbeateri* (McCoy): a case study of the use of bioclimatic modelling. *J. Biogeogr.*, 18, 371-383.

Manel S., Dias J.M., Buckton S.T. & Ormerod S.J. (1999) Alternative methods for predicting species distribution: an illustration with Himalayan river birds. *J. Appl. Ecol.*, 36, 734-747.

Margules C.R. & Pressey R.L. (2000). Systematic conservation planning. *Nature*, 405, 243-253.

Margules C.R. & Stein J.L. (1989) Patterns in the distribution of species and the selection of nature reserves: an example from *Eucalyptus* forests in South-eastern New South Wales. *Biol. Conserv.*, 50, 219-238.

Meyers N. , Mittermeier R.A., Mittermeier C.G., Fonseca G.A.B. & Kent J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, 403, 853 – 858.

Osborne P.E. & Tigar B.J. (1992) Interpreting bird atlas data using logistic models: an example from Lesotho, Southern Africa. *J. Appl. Ecol.*, 29, 55-62.

Robertson, M.P., Caithness, N. & Villet, M.H. (2001) A PCA-based modelling technique for predicting environmental suitability for organisms from presence records. *Divers. Distrib.*, 7, 15-27.

Shao J. & Tu D. (1995) *The Jackknife and Bootstrap*. Springer-Verlag, New York.

Sokal R.R. & Rohlf F.J. (1981) *Biometry. The Principles and Practice of Statistics in Biological Research.* 2nd edn. W.H. Freeman, San Francisco.

Sykes M.T. & Prentice I.C. (1995) Boreal forest futures: modelling the controls on tree species range limits and transient responses to climate change. *Water Air Soil Poll.*, 82, 415-428.

Sykes M.T., Prentice I.C. & Cramer W. (1996) A bioclimatic model for the potential distributions of north European tree species under present and future climates. *J. Biogeogr.*, 23, 203-233.

Verbyla D.L. & Litvaitis J.A. (1989) Resampling methods for evaluating classification accuracy of wildlife habitat models. *Environ. Manage.*, 13, 783-787.

Walker P.A. (1990) Modelling wildlife distributions using a geographic information system: kangaroos in relation to climate. *J. Biogeogr.*, 17, 279-289.

Williamson M. & Gaston, K.J. (1999) A simple transformation for sets of range sizes. *Ecography*, 22, 674-80.

Zweig, M.H. & Campbell, G. (1993) Receiver operating characteristic (ROC) plots: a fundamental evaluation tool in clinical medicine. *Clin. Chem.*, 39(4), 561-577.

CHAPTER 7

Predictive species distribution models disagree in ecological and environmental transition zones

Predictive species distribution models disagree in ecological and environmental transition zones

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Abstract

As predictive distribution modelling has become more common in response to a need to understand potential effects of environmental change, there has been a concomitant increase in the diversity of models used for such predictive modelling. This study contributes to this body of work by comparing 3 different predictive distribution models: a climate envelope model, BIOCLIM and GARP. Comparisons were done by using a standard set of climatic predictor variables for a set selection of species. Receiver operating characteristic analysis showed good overall model accuracy and little difference in the mean output between models. However, by mapping the distributions of individual species for which models disagree, it was found that although the models perform adequately, they disagreed on the predicted distributions of individual species in the same geographically distinct region. This region was shown to be an area of significant environmental heterogeneity, with climate, vegetation and avian community transitions occurring here. Identifying such areas prior to a distribution modelling exercise and explicitly accounting for this source of model disagreement, will improve the accuracy of model predictions. The methods followed in this study present a simple analysis to identify such transition zones.

Introduction

The number of investigations using predictive species distribution modelling is increasing rapidly, largely because these models are of considerable value for understanding the likely impacts of environmental change. The models can be used to understand biogeographic patterns (Jeffree and Jeffree 1994, Cowling and Lombard 2002), ascertain the potential distributions of economically important pest species (Bylund 1999, Robertson et al. 2001, Todd et al. 2002, Watt and McFarlane 2002), determine changes in threats associated with infectious and vector-borne diseases (Daszak et al. 2000, Rogers and Randolph 2000, Harvell et al. 2002), predict potential species invasions (Peterson and Vieglais 2001), and understand the ecological and conservation implications of global environmental change (Pounds et al. 1997, Petchey et al. 1999, Rutherford et al. 1999, Beaumont and Hughes 2002, Feria and Peterson 2002, Hannah et al. 2002, Peterson et al. 2000, 2001, 2002).

By definition, all models, including predictive species distribution models, constitute an incomplete abstraction of reality (see Samways 2003). In consequence, they will fail to capture all sources of variation, whether these are a result of predictor variable or model characteristics. The extent to which this abstraction of reality is useful for understanding natural phenomena is determined by the model's ability to describe variation in the observed data, using predictor variables selected *a priori* by the modeller (Sutherst 2003). Different types of models differ in their ability to describe this variation.

Climate envelope models have their roots in the concept of "envirograms" first put forward by Andrewartha and Birch (1954, 1986). Since the first generation climate envelope models were developed as specific software applications (Sutherst and Maywald 1985), the approach has found wide application (Walker and Cocks 1991, Carpenter et al. 1993, Jeffree and Jeffree 1994, 1996, Robertson et al. 2001, Erasmus et al. 2000, 2002, Van Staden et al. in press). Standardising the approach into readily available software packages (BIOCLIM[1] and CLIMEX[2]) has made it more accessible and fostered a wider user base, not only for these packages (Busby 1986, 1988, 1991, Nix 1986, Lindenmayer et al. 1991, Beaumont and

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[1] http://cres.anu.edu.au/outputs/anuclim.html
[2] http://www.ento.csiro.au/climex/climex.htm

Hughes 2002)[3], but also for climate envelope models in general. On the other hand, the increase in computing power in standard desktop computers has made it practical to utilise computing-intensive machine learning type models for distribution predictions (Guegan et al. 1998, Kobler and Adamic 2000). Until fairly recently, this complicated methodology was not readily accessible to biologists. A genetic algorithm-based model developed specifically for species distribution prediction from incomplete data (GARP, Stockwell and Peters (1999)) was made available first as a web application[4] and then later as a stand-alone Windows application[5]. An increase in the number of GARP applications (Feria and Peterson 2002, Peterson and Cohoon 1999, Peterson et al. 2000, 2001, 2002, Peterson and Vieglais 2001,) can be expected, given the fact that it is user friendly, easily accessible, well supported, and places a powerful, well-documented computational technique at the disposal of biologists. Consequently, a comparison between the more established climate envelope models that already have a broad user base, represented by BIOCLIM and the simple PCA-based model developed by Jeffries (Jeffree and Jeffree 1994, 1996), and modified by Erasmus (Erasmus et al. 2000), and GARP, which is likely to become more widely used in future, would be useful to ascertain the extent to which these approaches are comparable. Given that these kinds of modelling approaches provide only a broad-brush view of the likely responses of species to climate, strong model disagreement would strengthen the case against them (see Davis et al. 1998, Gaston 2003, Sutherst 2003 for additional discussion). On the other hand, agreement between models would provide additional support for their continued use. Moreover, explicit investigation of lack of congruence between models would improve confidence in the utility of modelling exercises. The aims of this study are therefore to compare the ability of different predictive distribution models to describe observed variation given a fixed set of predictor variables for a selected number of species, and to investigate the spatial attributes of predictor variables that cause between-model disagreement of predicted species distributions. In so doing, this work contributes to the useful and growing body of model evaluations (Fielding and Bell 1997, Manel et al. 2001) and model comparisons (Brito et al. 1999, Manel et al. 1999, Guisan and Zimmermann 2000).

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[3] See http://www.ento.csiro.au/climex/bibliography.htm for a list of 148 references on the implementation of the original climate envelope model called CLIMEX by Sutherst and Maywald (1985)

[4] http://biodi.sdsc.edu/bsw_home.html

[5] http://www.lifemapper.org/desktopgarp/

Methods

Data

Distribution data for birds were obtained from the Avian Demography Unit, University of Cape Town[6] (Southern African Bird Atlas Project (SABAP, Harrison et al. (1997)). These data are the result of a directed sampling effort to map the birds of southern Africa (1987-1992), and unlike data for other taxa from the region (Scholtz and Chown 1995; van Jaarsveld et al.1998a,b, Koch et al. 2000), constitute a close approximation of true presence-absence data. From the total data set for southern African birds, a data subset for grid cells with reliable climate data for South Africa was extracted. This subset consisted of 294816 unique records for 748 bird species occurring in 1858 grid cells (~625km^2 per grid cell), encompassing South Africa and Lesotho, but excluding the other countries included in the SABAP. For a previous predictive distribution modelling study (see Erasmus et al. 2002 for a species list), 34 species were selected from this South African data subset based on (a) accurate but not necessarily complete distribution data, (b) representative geographic range types (e.g. species restricted to winter or to summer rainfall regions), (c) robust, well-resolved taxonomy and (d) species known from a reasonable number of records. We used the same 34 species in this study. These 34 species have 23047 records in total, and their summed distributions encompass all 1858 grid cells. The number of records for each of these 34 species varies from 49 to 1574, with half the species having distributions of less than a third of the region's total area.

Van Rensburg et al. (2002) showed that mean annual precipitation (mm.yr^{-1}) and mean absolute monthly minimum temperature (^{0}C) averaged over the year are significant positive correlates of avian species richness in South Africa (see also Dean 2000). These results for South Africa are supported by similar findings for other taxa in North America (Currie and Paquin 1987, Boone and Krohn 2000a), New Zealand (Leathwick et al. 1998), Costa Rica (Enquist 2002) and sub-Saharan Africa (Jetz and Rahbek 2002). Based on these known relationships between richness, temperature and precipitation at broad scales, we made use of the same mean annual precipitation and mean absolute monthly minimum and maximum temperature data used by Van Rensburg et al. (2002) as predictor variables in this study. South African climate data were provided by the Computing Centre for Water Research

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[6] http://www.uct.ac.za/depts/stats/adu/index.html

(CCWR, University of Natal, Pietermaritzburg, metadata published in Schulze and Maharaj (1997)). The historic data (30 year monthly and annual means: 1960 – 1990) were re-sampled to 15' x 15' grid cells from interpolated climate surfaces available at a minute by minute resolution to conform to the resolution of the bird data.

Modelling procedure

Using these bird distribution and climate data, we implemented three different species distribution prediction models that have been exposed to peer review: Jeffree's multivariate climate envelope model (Jeffree and Jeffree 1994, 1996, Erasmus et al. 2000, 2002, Olwoch et al. in press, Van Staden et al. in press, also see Robertson et al. 2001 for a similar PCA-based model), the BIOCLIM envelope model (Busby 1986, 1988, 1991, Nix 1986, Lindenmayer et al. 1991, Beaumont and Hughes 2002) and GARP, an inferential genetic algorithm-based model (Peterson et al. 2000, 2001, 2002, Peterson and Cohoon 1999, Peterson and Vieglais 2001, Feria and Peterson 2002). GARP has different output options; we used the probability surface output option to enable comparisons with the probability surfaces generated by the other two envelope models.

Model output was evaluated (Oreskes et al. 1994, Guisan and Zimmerman 2000) by comparing predicted distributions with known records. However, model output consists of a probability of occurrence value and to compare this continuous variable with a binary presence-absence value presents a methodological problem. Although the predicted probability output can be dichotomised to predicted presence-absence by applying a threshold probability, this procedure results in a significant loss of information (Deleo 1993, Fielding and Bell 1997). For example, if a threshold probability of 0.5 is chosen, this means that species having a predicted probability of occurrence of 0.51 will be regarded as present together with species that have a much higher predicted probability of occurrence. However, receiver operating characteristic (ROC) analysis enables the use of the actual predicted probabilities, and is threshold-independent. 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 the evaluation of clinical medical tests (Fielding and Bell 1997) and here it is used to measure the performance of a predictive species distribution model. 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 and Bell 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. An AUC value of 0.5 corresponds to a random test with no discriminatory ability. AccuROC® software (Vida 1993) was used to determine the statistical significance of the difference between any two or three AUC values according to the nonparametric method of Delong et al. (1988). The confidence interval for the AUC was calculated using the asymptotic method (Obuchowski and Lieber 1998).

The chosen model evaluation criteria should be prevalence (frequency of occurrence) independent across models (Manel et al. 2001). Following suggestions from previous model comparisons (Manel et al. 1999, 2001, Guisan and Zimmerman 2000), we tested ROC analysis (Fielding and Bell 1997, Deleo 1993, Obuchowski and Lieber 1998) for prevalence independence by performing a linear least squares regression of AUC values on prevalence.

Kraemer's (1988) critique of the use of ROC in biology is limited to medical and behavioural contexts where a human observer applies a procedure under evaluation to detect the presence of a signal. This signal is typically the presence of a disease or a particular animal behaviour. Kraemer (1988) regarded such a human observer as subjective and prone to be influenced by preconceived ideas. In the classical engineering application of ROC analysis, such a bias does not exist for a mechanical or electronic detector (Kraemer 1988). Likewise, in predictive distribution modelling, the predicted probability of occurrence is a value determined by a statistical model that is not subject to observer bias. Indeed, the output value of this model is analogous to the reading an electronic detector would record for a particular electronic signal. Although the model can have biases in terms of predictor variables and modelling assumptions, these are explicit, constant and objective. Erroneous species identification may also lead to a false evaluation of model performance, but the bird data set has been subjected to extensive expert vouching procedures and as such presents as close an approximation of objective observations and accurate identifications as can realistically be expected (Harrison et al. 1997, Van Jaarsveld et al. 1998a). In summary, the specific application of ROC analysis to predictive distribution modelling evaluation is much closer to the original engineering application than Kraemer's (1988) "biobehavioural context", and therefore we regard classical ROC analyses as suitable for our purposes of model comparison.

Model comparisons proceeded in three phases. In the first phase, we compared the output of each model for each species to a random model with no discriminatory ability. Phase two consisted of obtaining a mean AUC value for all 34 species, for each model, and comparing these three values using a nonparametric Kruskal-Wallis test. Phase three compared models on a species-by-species basis and as such provides more detail on which models disagree for which species. The procedure followed in phase three is summarised in Figure 1, and consists of the following steps:

Step 1: Three species-by-species pairwise between-model comparisons were undertaken (e.g. Jeffree-BIOCLIM (J-B), Jeffree-GARP (J-G), GARP-BIOCLIM (G-B)), as well as a species-by-species three-way between-model comparison (Jeffree-GARP-BIOCLIM (JGB)), resulting in a total of four model comparisons. Each of these four comparisons was done for every species, summarised in the table shown for step 1 in Figure 1. Each comparison resulted in a list of species for which that particular comparison showed significant differences between the models that were compared.
Steps 2 to 4 were subsequently repeated for each of these species lists.

Step 2: The original presence-absence distribution data for every species on the lists (i.e. those species for which model outputs differed) generated in Step 1 were drawn from the database, and all individual presence-absence maps for species were overlaid in a GIS.

Step 3: Every grid cell was queried for the presence or absence of a species, and the number of species from the lists that occurred in each of the grid cells was recorded.
The end result of this process was a map where each grid cell represented the number of species for which the models in question gave significantly different model outputs ($p < 0.05$). Grid cells that contained a large number of species for which model outputs disagreed, were referred to as cells rich in model disagreement species.

Step 4: Homogenous spatial clusters of grid cells that contain similar numbers of model disagreement species are identified by calculating Moran's I values as a local indicator of spatial association (LISA) (Anselin 1995). These values were calculated using the SPLUS® for ArcView extension to ArcView® GIS. The module calculates generalised LISA values

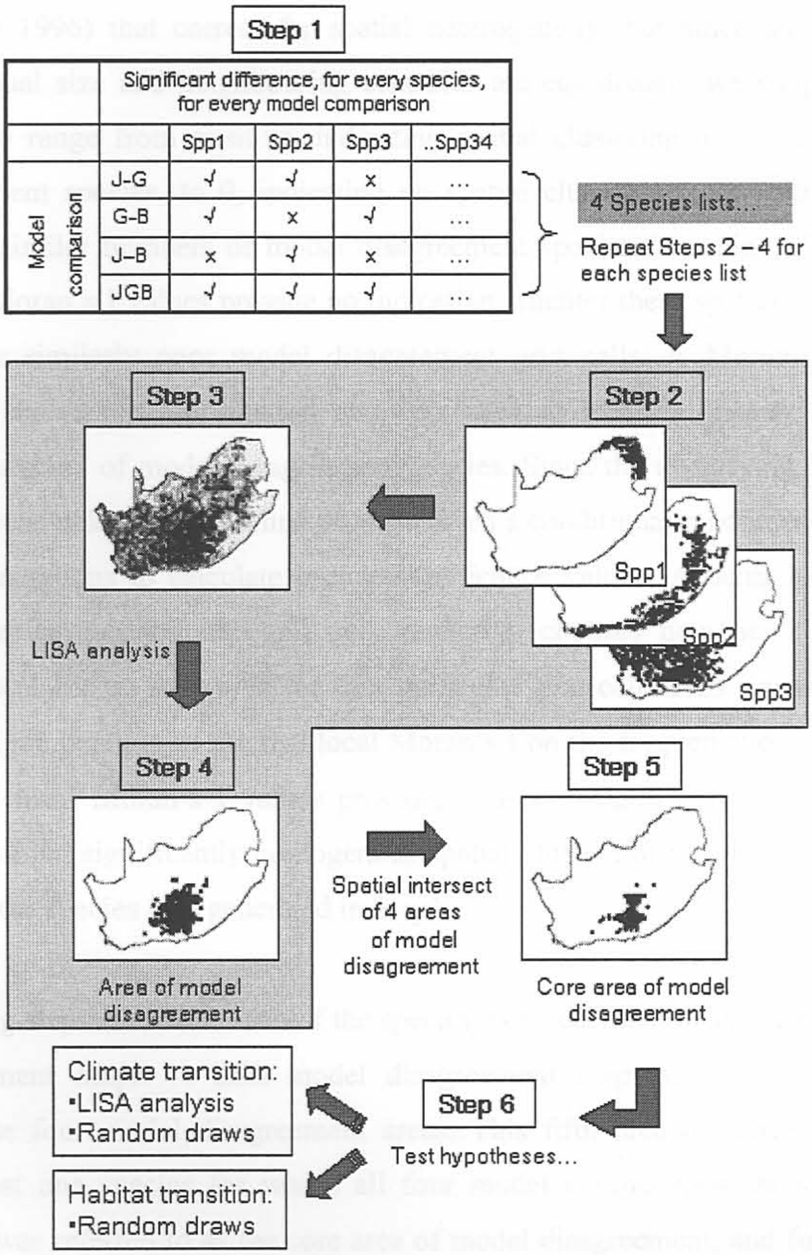

Fig 1: Flow chart of the methods followed. Significant disagreement between the predictive distribution models for a particular species is shown in the table under step 1. For example, species 1 and 2, but not 3, would be members of the species list for model comparison J-G in figure 1. These four generated lists contained the species for which model outputs differed significantly. Each of these lists are used as input to first generate species richness maps, where richness refers to the number of model disagreement species occurring in each grid cell (steps 2 and 3). Step 4 calculates significantly homogenous areas of model disagreement by LISA analysis, and then a spatial intersect between the 4 LISA maps from step 4 creates the map of the core area of model disagreement in step 5. Two hypotheses about this core area of model disagreement are tested in step 6.

(Bao and Henry 1996) that correct for spatial heterogeneity, but since all grid cells are effectively of equal size and neighbouring centroids are equidistant, we simply use LISA. Moran's I values range from positive, indicating spatial clustering of similar numbers of model disagreement species, to 0, indicating no spatial clustering, to negative, indicating clustering of dissimilar numbers of model disagreement species (Anselin 1995). However, highly positive Moran's I values provide no indication whether these spatial clusters contain similarly rich or similarly poor model disagreement grid cells. A Moran's I scatterplot (Anselin 1998) shows this information and was used to identify clusters of cells with similarly high numbers of model disagreement species. Since the underlying distribution of this LISA statistic is unknown (Anselin 1995), we used a conditional randomisation approach with 10000 permutations to calculate pseudo-significance values (Anselin 1995). In short, this approach selects a particular grid cell, randomly chooses new neighbours and re-calculates the local Moran's I value for that particular grid cell. This process is repeated 10000 times and the position of the real local Moran's I on the frequency distribution of the 10000 permuted local Moran's I values provides a pseudo-significance value. Using this method, we identified significantly homogenous spatial clusters of rich model disagreement cells for each of the species lists generated in Step1.

Step 5: Repeating steps 2 to 4 for each of the species lists generated in step 1 resulted in four model disagreement maps. A fifth model disagreement map was created by spatially intersecting these four model disagreement areas. This fifth area of model disagreement contained at least one species for which all four model comparisons showed significant differences and was referred to as the core area of model disagreement, and further analyses were focussed on this particular area.

Step 6: We tested two hypotheses relating to this core area of model disagreement: first, that it is an area of climate transition, and secondly, that it is an area of habitat transition.

For the climate transition hypothesis, spatial variation of the climatic variables across the entire study area as well as in the core area of model disagreement was investigated. Mean annual precipitation is a measure of the expected quantity of water available to a catchment in a decadal to centennial time scale (Schulze et al. 2001). Potential evapotranspiration provides a measure of how easily water could potentially be lost to the atmosphere through evaporation and transpiration (Currie 1991, Hulme 1996). Therefore, the relationship between precipitation and potential evapotranspiration gives a broad indication of whether a system is run-off or evaporation dominated, and as such summarises the water balance in a system (Knapp and Smith 2001). We used this single climate variable, the precipitation/evapotranspiration ratio (PPT/PET), as a descriptor of the general environmental constraints on water availability, and indirectly, species distributions. Calculating LISA values and corresponding pseudo-significance values for the PPT/PET ratio, we identified areas with high and low local spatial autocorrelation of their PPT/PET ratios. The geographic positions of homogenous spatial clusters of PPT/PET ratios indicate areas that are subject to similar water balance conditions. The boundaries between these homogeneous clusters provide an indication of areas that can be interpreted as transitional zones between low and high PPT/PET ratios.

The climate transition hypothesis was further tested by determining whether the core area of model disagreement showed greater values of the PPT/PET ratio and local Moran's I of the PPT/PET ratio than expected by chance. The mean values for the PPT/PET ratio and local Moran's I of the PPT/PET ratio in the core area of model disagreement were compared to the mean PPT/PET ratio and mean local Moran's I of the PPT/PET ratio for 10 000 sets of randomly selected grid cells from across the study region. The number of randomly selected grid cells was equivalent to the number of grid cells in the core area of model disagreement.

The habitat transition zone hypothesis was tested using 10 000 random draws in a similar fashion, using biome heterogeneity as a variable. Low and Rebelo's (1996) classification of the study area into seven biome types was used to calculate the percentage of each biome type per quarter-degree cell. These were the forest, thicket, savanna, grassland, Nama karoo, succulent karoo, and fynbos biomes. Each of these is characterised by several vegetation types, giving a total of 68 different vegetation types for the study area (see Low and Rebelo, 1996 for further information). Following Gaston et al. (2001), biome heterogeneity was obtained using Simpson's index of diversity (Krebs 1989):

$$1 - \mathrm{Sum}\,(p_i)^2$$

where p_i is the fraction of the grid cell's area occupied by biome i. This index ranges from zero (only one biome present in a cell) to 0.86 (all seven biomes present in the same proportions) and is expected to reach high values in areas of transition between biomes. The values recorded ranged between 0 and 0.76.

Results

In contrast to Manel et al.'s (2001) study, we found a significant ($p<0.001$), but weak negative relationship for the linear regressions of AUC on prevalence for each of the three models that we employed. (Jeffree model: adjusted $R^2=0.28587591$, $F(1,32)=14.210$ $p<0.00067$; GARP: adjusted $R^2=0.28261882$, $F(1,32)=14.001$ $p<0.00072$; BIOCLIM: adjusted $R^2=0.17839935$, $F(1,32)=8.1655$ $p<0.00745$) This relationship between prevalence and AUC values was constant across all three models – there was no significant difference between the intercepts or slopes of each of the regression lines of AUC on prevalence across the predictive models (ANCOVA, Zar 1986) (Intercept: $F(2,98)=1.06$; $p<.3509$, slope: $F(2,96) = 0.007$; $p<.9932$).

The first phase of model comparison showed that all three models performed significantly better than a random model. In the second phase of model comparison, the mean AUC value across species for each of the three models was not significantly different from the mean AUC value for any of the other models (AUC values Jeffree: 0.843± 0.084, GARP: 0.834±0.082, BIOCLIM: 0.816±0.105).

Results from the third phase of model comparison, which was conducted on a species-by-species basis, showed that there were several significant differences in model outputs ($p < 0.05$) for a number of species. In total , 28 (82%) of the species produced modelled outputs that differed significantly across all three models. Fourteen (41%) species were common to all four lists of species for which model outputs differed significantly. From this it appears that there are more species from this sample for which the comparative model outputs disagree than ones about which they agree.

The core area of model disagreement derived in step 5 of Figure 1 is presented as the hatched area in Figure 2. This core area of model disagreement showed a proportional overlap (Prendergast et al. 1993) with the other four areas of model disagreement ranging from 44% to 59%.

Testing the climate transition zone hypothesis, LISA analyses of PPT/PET ratios across the study area showed two highly significant ($p<0.001$) spatial clusters: a cluster of low PPT/PET

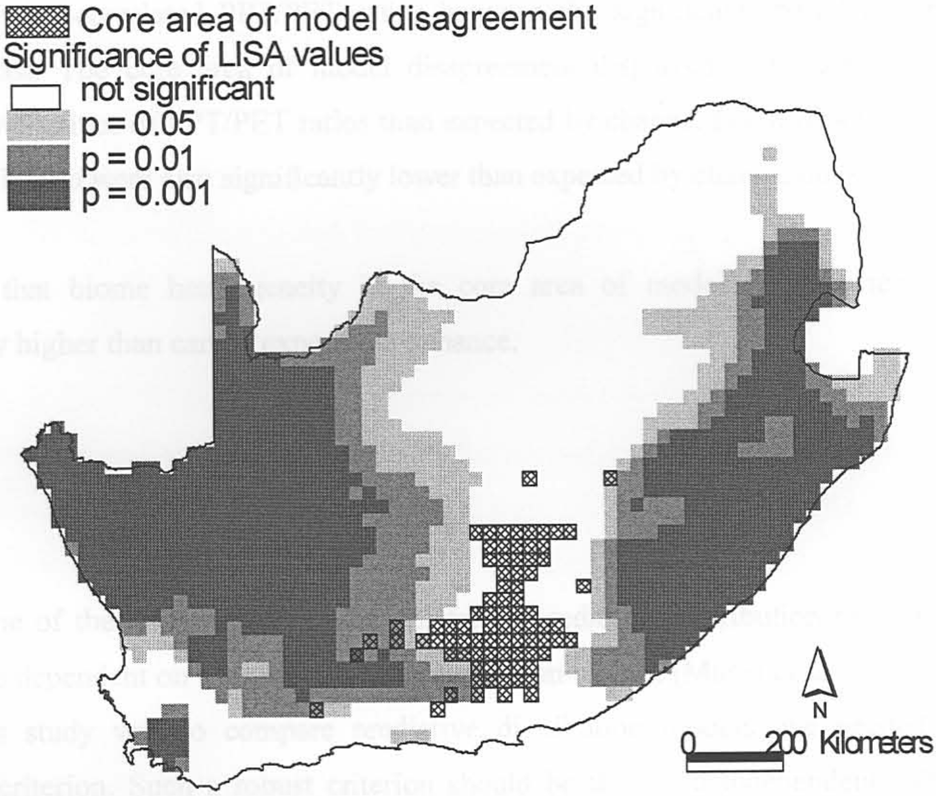

Fig 2: Significant LISA values for the PPT/PET ratio over the study area. Hatched cells represent the core area of model disagreement.

values in the west and a cluster of high PPT/PET values in the east (Fig. 2). Figure 2 also shows the geographical position of the core area of model disagreement relative to these two PPT/PET spatial clusters. The core area of model disagreement is spatially congruent (proportional overlap value of 83% - Prendergast et al. 1993) with a narrow strip of non-significantly autocorrelated PPT/PET ratios between the significant spatial clusters in the west and east. The core area of model disagreement displayed significantly (two-tailed $p<0.05$) lower values of PPT/PET ratios than expected by chance. Local Moran's I values of the PPT/PET ratio were also significantly lower than expected by chance, but still positive.

We found that biome heterogeneity in the core area of model disagreement was also significantly higher than can be expected by chance.

Discussion

The outcome of the comparison between different predictive distribution models has been shown to be dependent on the chosen model evaluation criteria (Manel et al. 2001). Since the aim of this study was to compare predictive distribution models, we needed a robust evaluation criterion. Such a robust criterion should be threshold independent, which ROC analysis is by definition, and prevalence independent (Manel et al. 2001). The literature shows two approaches to assess prevalence independence: a regression of the AUC values from ROC analysis on the prevalences for each species in the dataset, so that the number of data points is equal to the number of species in the data set (the approach followed here, and by Manel et al. 2001); or using random subsets of different sizes of the data for an individual species and regressing those AUC values on the prevalences determined by the size of the subsets.

The AUC values in the first approach are derived from different known species distributions with different climate envelopes. These known species distributions have different prevalences and different spatial configurations. Therefore, differences in AUC values derived in this fashion reflect not only the effects of prevalence, but also the model's ability to predict species distributions for these different climate envelopes. This approach is well-suited to evaluate model performance over a range of different types of distributions and get an overall view of model performance. Manel et al. (2001) used ROC analysis to identify optimal probability thresholds, and therefore this approach was well suited to that study. No regression diagnostics were provided with which to compare the regression results from the current study and we can only conclude that for our study, the relationship between AUC and prevalence is weak when using data from all species. However, the main aim of the current study was not to provide an overall view of model performance, but to compare model outputs for individual species. Such comparisons were done with a fixed set of predictor variables applied by different models to the distribution of a specific species. Therefore, even though there is a relationship between prevalence and AUC values, this relationship is weak and constant for all three models and therefore its influence, if any, will be constant across model comparisons.

Further support for ROC analysis as an appropriate model evaluation criterion for this study comes from other studies that have followed the second approach to assess the prevalence independence of AUC values. Cumming (2000) used different sized subsets of known data for a tick species to derive an AUC-prevalence graph and found that the AUC values were prevalence independent, all be it without regression diagnostics. Since our study focuses on model comparisons for individual species, rather than overall model performance for an assemblage of species, it is closer in scope to Cumming (2000) than Manel et al. (2001). Cumming (2000) also investigated the effects of hypothetically small prevalences on AUC values and found that AUC values are more prevalence dependent at low prevalences. Using the same data as the current study, Erasmus et al. (2002) investigated model performance for individual species at low prevalences and found that, for the majority of species studied, there was no significant difference between models based on a 20% random subsample of the known distribution and models based on 100% of the known distribution. In short, we maintain that ROC analysis is an appropriate model evaluation criterion for our purposes of comparing different predictive distribution models, not only for the reasons provided above, but also because of its broad support in the literature (Fielding and Bell 1997).

The first two phases of model comparison showed little differences between models, irrespective of whether the comparison was with a random model or with another model. Using other model evaluation criteria, Manel et al. (1999) compared a discriminant analysis, a neural network and a logistic regression model and also found little differences in model performance. These similar results for studies using different models with different predictor variables, suggest that, despite the differences in the underlying assumptions of the various models, all of the models have an ability to extract at least partial environmental dependencies of species distributions and facilitate meaningful predictions. Therefore, these results suggest that model performance is more strongly influenced by predictor variable selection than by model selection.

The core area of model disagreement identified in phase three of the model comparison process showed the geographic location of an area with a high number of model disagreement species, i.e. the three model outputs, although reasonably accurate by themselves, differed from each other for a high number of species. The fact that this area was a discrete homogenous spatial cluster, and not a large extensive area, raises a question about the cause of such model disagreement in an area that comprises only 4% of the country's total surface area. Although the different models use predictor variables in different ways to arrive at a predicted distribution, the common factor between all models remains their use of climatic predictor variables. If model disagreement shows a common spatial clustering, it stands to reason that some climate-related process drives this pattern.

LISA analysis of PPT/PET values identified a transition zone of environmental water surplus, i.e. an area with no significant local spatial autocorrelation in PPT/PET ratios. This narrow strip where significant spatial autocorrelation of the PPT/PET ratio is absent, represents a transition zone from areas where evaporation plays a more important role, such as the drier western regions of the country, to areas where run-off is more prevalent, e.g. the moister eastern regions. The interpretation of PPT/PET ratio is relative. Knapp and Smith (2001) showed grasslands to have PPT/PET ratios of around unity, with deserts closer to zero and forests larger than unity in North America. For South Africa, some 93% of grid cells experience a PPT/PET ratio of smaller than 0.5, therefore South Africa generally experiences an evaporation-dominated water balance, and that the transition zone identified by the LISA analysis is a relative one with run-off only dominating evapotranspiration for short and strictly seasonal periods across the eastern half of the country. Note that it is only where there is a steep transition gradient that model predictions disagree; the core area of model disagreement does not extend to the north where the PPT/PET ratio transition is diluted over a larger area. Therefore, by virtue of the spatial congruence between the core area of model disagreement and the steep PPT/PET transition zone, this study suggests that the distribution prediction models implemented here differed in their predictions of species that are found in this climate transition zone. Figure 3 shows the PPT/PET values for the

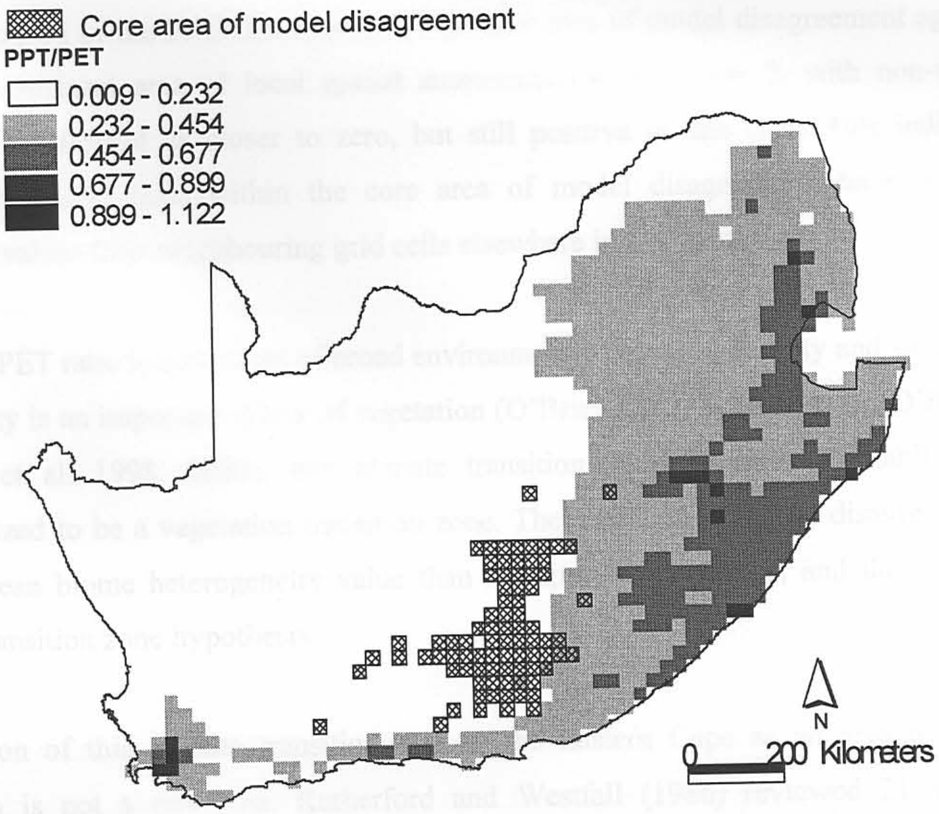

Fig 3: Map of PPT/PET values for South Africa. Legend classes are of equal interval, so areas with similar shading indicate the frequency of values in that class interval.

study area with equal interval classes. The core area of disagreement coincided almost totally with an area that has low values of PPT/PET. This area was also the largest (white area in Figure 3) and therefore it is to be expected that PPT/PET ratios will be lower than can be expected by chance in the core area of model disagreement. The significantly lower mean local Moran's I of the PPT/PET values for the core area of model disagreement agreed with the non-significant area of local spatial autocorrelation in Figure 2, with non-significant values being defined as closer to zero, but still positive in this case. This indicates that neighbouring grid cells within the core area of model disagreement have less similar PPT/PET values than neighbouring grid cells elsewhere in the country.

The PPT/PET ratio is a measure of broad environmental water availability and since moisture availability is an important driver of vegetation (O'Brien 1993, Schulze 1997, O'Brien 1998, O'Brien et al. 1998, 2000), this climate transition zone of water availability can be hypothesized to be a vegetation transition zone. The core area of model disagreement has a higher mean biome heterogeneity value than is expected by chance, and this supports the habitat transition zone hypothesis.

The notion of this climate transition area in the Eastern Cape as an area of vegetation transition is not a new one. Rutherford and Westfall (1986) reviewed 21 studies that identified "major natural biotic divisions" (Rutherford and Westfall 1986) between 1936 and 1986. These classifications were by no means transparent and used combinations of edaphic factors, plant life forms, climate and expert opinion to do the classification. In spite of these differences in methods, the area that we identified as the core area of model disagreement coincides with boundaries between four biomes in almost half of these old classifications. An earlier review of phytogeographical studies (Werger 1978) found a similar result of agreement between 9 studies dating from between 1886 and 1971. A more rigorous definition (Rutherford and Westfall 1986) of South African biomes, primarily based on climate and plant life forms, lends further support for the core area of model disagreement as a vegetation, and habitat, transition zone. The climate component of this classification was based on a Summer Aridity Index (SAI), calculated from precipitation for the four hottest months of the year, and winter concentration of precipitation, calculated from winter precipitation as a proportion of mean annual precipitation. SAI gives an indication of moisture stress during growing periods of peak physiological water demand (Rutherford and Westfall 1986) and winter precipitation concentration provide an indication of the importance of seasonal rainfall. Together, these precipitation-derived indices give a similar, but more detailed picture of environmental water availability than the PPT/PET ratio used in our study. On a scatterplot of winter precipitation concentration against SAI, Rutherford and Westfall (1986) identified biomes and biome boundaries. Using Acocks' veldtypes, (Acocks 1975), we found that four veld types dominated in the core area of model disagreement, accounting for 74% of this area. These veld types were located along the common boundaries of the nama karoo, grassland, fynbos, forest and savanna biomes on the scatterplot of SAI against winter precipitation concentration. These principles that aided in the identification of Rutherford and Westfall's (1986) biomes provide further evidence that the core area of model disagreement is an area of climate, and subsequently, habitat transition.

An important feature of Rutherford and Westfall's (1986) classification is the role the inclusion of a measure of rainfall seasonality plays in delineating biomes. Low and Rebelo (1996) identified a thicket biome as intermediary between forest and savanna biomes (Vlok and Euston-Brown 2002). This thicket biome, which is present in 28% of the core area of model disagreement's grid cells, is maintained by the balance between winter and summer rainfall. Winter rainfall is more dominant in the west, and here the thicket becomes fragmented and is replaced by fynbos, whereas more summer-dominated rainfall fragments the thicket in the north and east. It is clear then, that the vegetation transition in the core area of model disagreement is not only influenced by the amount of precipitation but also the seasonality. This balance between winter and summer rainfall also explains to some extent the more gradual vegetation transition that takes place north of the core area of model disagreement. Winter rainfall is limited to the coastal area, and therefore the climate gradient further north is only a gradient of the amount of precipitation, and not seasonality too, as is the case along the coastal area. The complex vegetation patterns in this core area of model disagreement also have some roots in the distant past. Van Zinderen Bakker (1978) found that Quaternary glacial cycles enabled repeated intrusion and retreat of fynbos into temperate grassland and forest areas, resulting in a mosaic of fynbos remnants in altitudinal refugia during unfavourable periods.

So far we have shown that the areas in which the models disagreed were areas of climate and habitat transition. However, it has been demonstrated elsewhere that habitat heterogeneity is an important driver for bird species richness not only in sub-Saharan Africa (Jetz and Rahbek 2002), but also for South Africa (Van Rensburg et al. 2002). Spatial congruence between avian species range limits and areas with high vegetation heterogeneity have also been found for other regions (e.g. see Boone and Krohn 2000b). More importantly, in the same study area, Gaston et al. (2001) have shown that biome edges experience a significantly higher degree of avian beta diversity than expected by chance. Therefore it is clear that the areas in which the three predictive distribution models disagree are not only areas of climate and habitat transition, but also very likely form areas of avian community transition. At broader scales, using 1437 Afrotropical endemic bird species, De Klerk et al. (2002) showed that 4 biogeographical districts share boundaries in the area that we have identified as the core area of model disagreement.

Due to the unique biodiversity elements, i.e. the thicket biome, in this ecological transition zone, considerable effort has been directed at integrated conservation planning in this region (Cowling et al. 2003, Kerley et al. 1999). An integral part of this conservation plan is the integration of process that drive biodiversity patterns in this area; macroclimatic gradients has been explicitly identified as important drivers for maintaining biodiversity in the thicket biome (Cowling et al. 2003).

In summary, we have shown that there is little difference in model output for the three different predictive distribution models employed here. We have also shown that these models fail in the same ecological transition zone by having different predicted distributions for species occurring here. Although this disagreement seems to point to differences between models, the fact that there is agreement about where the disagreement occurs is noteworthy and supports the usefulness of a modelling approach to species distributions. We suggest that such general ecological transition zones should be sought in environmentally complex landscapes before blanket analyses (i.e. Erasmus et al. 2002, Van Jaarsveld and Chown 2001) are applied. Understanding the potential effects of these areas, and how to deal with them explicitly is likely to be important in efforts to improve model performance. Given the rate of environmental change and the need for up-to-date conservation planning, the use of predictive distribution models is likely to increase. It is in the interests of climate-change integrated conservation planning that such modelling exercises are as accurate and transparent as possible and therefore, procedures that identify sources of model error are important. Further research is needed not only into how existing conventional equilibrium (Guisan and Zimmerman 2000) models treat such transition zones, but also how these transition zones should be treated to ensure geographically homogenous model performance.

Such a model performance might only be attained if the model allows for predictor variables to make a spatially variable contribution to prediction accuracy. Models that have a spatially explicit component (i.e. spatial regression, cellular automata) might perform better in areas where predictor variables undergo transitions.

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References

Acocks, J.P.H. 1975. Veld types of South Africa. Memoirs of the Botanical Survey of South Africa 54.

Andrewartha, H.G., and Birch, L.C. 1954. The distribution and abundance of animals. University of Chicago Press, Chicago, 782 p.

Andrewartha, H.G. and Birch, L.C. 1986. The ecological web: more on the distribution and abundance of animals. University of Chicago Press, Chicago, 506 p.

Anselin, L. 1998. Exploratory spatial data analysis in a geocomputational environment. In: Longley, P. A., Brooks, S., MacMillan, B., McDonnel, R. (Eds). Geocomputation: a primer. John Wiley, New York, pp. 77-94.

Anselin, L. 1995. Local indicators of spatial association - LISA. Geographical Analysis 27, 93-115

Bao, S., Henry, M. 1996. Heterogeneity isues in local measurements of spatial association. Geographical Systems 3: 1-13.

Beaumont, L. J., Hughes, L. 2002. Potential changes in the distributions of latitudinally restricted Australian butterfly species in response to climate change. Global Change Biology 8, 954-971.

Boone, R. B., Krohn, W. B. 2000a. Partitioning sources of variation in vertebrate species richness. Journal of Biogeography 27, 457-470.

Boone, R. B., Krohn, W. B. 2000b. Relationship between avian range limits and plant transition zones in Maine. Journal of Biogeography 27, 471-482.

Brito, J. C., Crespo, E. G., Paulo, O. S. 1999. Modelling wildlife distributions: logistic multiple regression vs overlap analysis. Ecography 22, 251-260.

Busby, J. R. 1986. A biogeoclimatic analysis of Nothofagus cunninghamii (Hook.) Oerst. in southeast Australia. Australian Journal of Ecology 11, 1-7.

Busby, J. R. 1988. Potential impacts of climate change on Australia's flora and fauna. In: Pearman, G. I. (Ed). Greenhouse: planning for climate change. CSIRO, Melbourne, pp. 387-396.

Busby, J. R. 1991. BIOCLIM - a bioclimate analysis and prediction system. In: Margules, C. R.,Austin, M. P. (Eds). Nature conservation: cost effective biological surveys and data analysis. CSIRO, Australia pp. 64-68.

Bylund, H. 1999. Climate and the population dynamics of two insect outbreak species in the north. Ecological Bulletins 47, 54-62.

Carpenter, G., Gillison, A. N., Winter, J. 1993. DOMAIN: a flexible modelling procedure for mapping potential distributions of plants and animals. Biodiversity and Conservation 2, 667-680.

Cowling, R. M., Lombard, A.T. 2002. Heterogeneity, speciation/extinction history and climate: explaining regional plant diversity patterns in the Cape Floristic Region. Diversity and Distributions 8, 163-179.

Cowling, R.M., Lombard, A.T., Rouget, M., Kerley, G.I.H., Wolf, T., Simms-Castley, R., Knight, A., Vlok, J.H.J., Pierce, S.M., Boshoff, A.F. Wilson, S.L. 2003. A conservation assessment of the subtropical thicket biome. TERU Report 43, Terrestrial Ecology Research Unit, University of Port Elizabeth, pp. 112. http://zoo.upe.ac.za/step

Cumming, G.S. 2002. Using between model-comparisons to fine-tune linear models of species' ranges. 27, 441-455.

Currie, D. J. 1991. Energy and large-scale patterns of animal- and plant-species richness. American Naturalist 137,27-49.

Currie, D. J., Paquin, V. 1987. Large-scale biogeographical patterns of species richness of trees. Nature 329, 326-327.

Daszak, P., Cunningham, A. A., Hyatt, A. D. 2000. Emerging infectious diseases of wildlife - threats to biodiversity and human health. Science 287, 443-449.

Davis, A. J., Lawton, J. H., Shorrocks, B., Jenkinson, L. S. 1998. Individualistic species responses invalidate simple physiological models of community dynamics under global environmental change. Journal of Animal Ecology 67: 600-612.

Dean, W. R. J. 2000. Factors affecting bird diversity patterns in the Karoo. South Africa. South African Journal of Science 96, 609-616.

De Klerk, H.M., Crowe, T.M., Fjeldså, J.,Burgess, N.D. 2002. Biogeographical patterns of endemic terrestrial Afrotropical birds. Diversity and Distributions 8,147-162.

Deleo, J. M.1993. Receiver operating characteristic laboratory (ROCLAB): software for developing decision strategies that account for uncertainty. Proceedings of the Second International Symposium on Uncertainty Modelling and Analysis, IEEE Computer Society Press, Ottawa.

Delong, E. R., Delong, D. M., Clarke-Pearson, D. L. 1988. Comparing areas under two or more correlated receiver operating characteristic curves: a nonparametric approach. Biometrics 44, 837-845.

Enquist, C.A.F. 2002. Predicted regional impacts of climate change on the geographical distribution and diversity of tropical forests in Costa Rica. Journal of Biogeography 29, 519-534.

Erasmus, B. F. N., Kshatriya, M., Mansell, M. W., Chown, S. L., Van Jaarsveld, A. S. 2000. A modelling approach to antlion (Neuroptera: Myrmeleontidae) distribution patterns. African Entomology 8, 157-168.

Erasmus, B. F. N., Van Jaarsveld, A. S., Chown, S. L., Kshatriya, M.,Wessels, K. J. 2002. Vulnerability of South African animal taxa to climate change. Global Change Biology 8, 678-693.

Feria A., T. P., Peterson, A. T. 2002. Prediction of bird community composition based on point-occurrence data and inferential algorithms: a valuable tool in biodiversity assessments. Diversity and Distributions 8, 49-56.

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

Gaston, K.J. 2003. The Structure and Dynamics of Geographic Ranges. Oxford University Press, Oxford.

Gaston, K. J., Rodrigues, A. S. L., van Rensburg, B. J., Koleff, P., Chown, S. L. 2001 Complementary representation and zones of ecological transition. Ecology Letters 4, 4-9.

Guegan J-F., Lek, S.,Oberdorff, T. 1998. Energy availability and habitat heterogeneity predict global riverine fish diversity. Nature 391, 382-384.

Guisan, A., Zimmerman, N. E. 2000. Predictive habitat distribution models in ecology. Ecological Modelling 135, 147-186.

Hannah, L., Midgley, G. F., Lovejoy, T., Bond, W. J., Bush, M., Lovett, J. C., Scott, D., Woodward, F. I. 2002. Conservation of biodiversity in a changing climate. Conservation Biology 16, 264-268.

Harrison, J.A., Allan, D.G., Underhill, L.G., Herremans, M., Tree, A.J., Parker, V., Brown, C.J. 1997. The atlas of southern African birds. Birdlife South Africa, Johannesburg, vol I 732 pp., vol II 785 pp.

Harvell, C. D., Mitchell, C. E., Ward, J. R., Altizar, S., Dobson, A. P., Ostfeld, R. S., Samuel, M. D. 2002. Climate warming and disease risks for terrestrial and marine biota. Science 296, 2158-2162.

Hulme, M., Conway, D., Joyce, A., Mulenga, H. 1996. A 1961-90 climatology for Africa south of the Equator and a composition of potential evapotranspiration estimates. South African Journal of Science 92, 334-343.

Jeffree, C. E., Jeffree, E. P. 1996. Redistribution of the potential geographical ranges of Mistletoe and Colorado beetle in Europe in response to the temperature component of climate change. Functional Ecology 10, 562-577.

Jeffree, E. P., Jeffree, C. E. 1994. Temperature and the biogeographical distributions of species. Functional Ecology 8, 640-650.

Jetz, W., Rahbek, C. 2002. Geographic range size and determinants of avian species richness. Science 297, 1548-1551.

Kerley, G.I.H., Boshoff, A.F., Knight, M.H. 1999. Ecosystem integrity and sustainable land-use in the thicket biome South Africa. Ecosystem Health, 5(2):104-109.

Knapp, A. K., Smith, M. D. 2001. Variation among biomes in temporal dynamics of aboveground primary production. Science 291, 481-484.

Kobler, A., Adamic, M. 2000. Identifying brown bear habitat by a combined GIS and machine learning method. Ecological Modelling 135, 291-300.

Koch, S.O. *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, H. C. 1988. Assessment of 2x2 associations: generalization of signal-detection methodology. The American Statistician 42, 37-49.

Krebs, C. J. 1989. Ecological methodology, 2nd edition. Harper Collins, New York, pp. 654.

Leathwick, J. R., Burns, B. R.,Clarkson, B. D. 1998. Environmental correlates of tree alpha-diversity in New Zealand primary forests. Ecography 21, 235-246.

Lindenmayer, D. B., Nix, H. A., McMahon, J. P., Hutchinson, M. F., Tanton, M. T. 1991. The conservation of Leadbeater's possum, *Gymnobelideus leadbeateri* (McCoy): a case study of the use of bio climatic modelling. Journal of Biogeography 18, 371-383.

Low, A.B., Rebelo, A.G. 1996. Vegetation of South Africa, Lesotho, and Swaziland. Department of Environmental Affairs and Tourism, Pretoria, South Africa.

Manel, S., Dias, J-M., Ormerod, S. 1999. Comparing discriminant analysis, neural networks and logistic regression for predicting species distributions: a case study with a Himalayan river bird. Ecological Modelling 120, 337-347.

Manel, S., Williams, H. C., Ormerod, S. J. 2001. Evaluating presence-absence models in ecology: the need to account for prevalence. Journal of Applied Ecology 38, 921-931.

McLaughlin, J. F., Hellman, J. J., Boggs, C. L.,Ehrlich, P. R. 2002. Climate change hastens population extinctions. Proceedings of the National Academy of Sciences of the United States of America 99, 6070-3074.

Nix, H. 1986. A biogeographic analysis of Australian elapid snakes. In: Longmore, R. (Ed). Atlas of elapid snakes of Australia. Bureau of Flora and Fauna, Canberra. Pp. 4-15.

O'Brien, E. M. 1993. Climate gradients in woody plant species richness: towards an explanation based on an analysis of southern Africa's woody flora. Journal of Biogeography 20,181-198.

O'Brien, E. 1998. Water-energy dynamics, climate, and prediction of woody plant species richness: an interim general model. Journal of Biogeography 25,379-398.

O'Brien, E. M.,Whittaker, R. J.,Field, R. 1998. Climate and woody plant diversity in southern Africa: relationships at species, genus and family levels. Ecography 21, 495-509.

O'Brien, E. M., Field, R.,Whittaker, R.J. 2000. Climatic gradients in woody plant (tree and shrub) diversity: water-energy dynamics, residual variation, and topography. Oikos 89, 588-600.

Obuchowski, N. A., Lieber, M. L. 1998. Confidence intervals for the receiver operating characteristic area in studies with small samples. Academic Radiology 5, 561-571.

Olwoch, J.M, Rautenbach, C.J.de W., Erasmus, B.F.N., Engelbrecht, F.A., Van Jaarsveld, A.S. In press. Simulating ticks distributions over sub-Saharan Africa: the use of observed and simulated climate surfaces. Journal of Biogeography.

Oreskes, N., Shrader-Frechette, K.,Belitz, K. 1994. Verification, validation and confirmation of numerical models in the earth sciences. Science 263, 641-644.

Petchey, O.L., McPhearson, P.T., Casey, T.M., Morin, P. J. 1999. Environmental warming alters food-web structure and ecosystem function. Nature 402, 69-72.

Peterson, A.T.,Cohoon, K. P. 1999. Sensitivity of distributional prediction algorithms to geographic data completeness. Ecological Modelling 117, 159-164.

Peterson, A.T., Egbert, S. L., Sánchez-Cordero, V., and Price, K. P. 2000. Geographic analysis of conservation priority: endemic birds and mammals in Veracruz, Mexico. Biological Conservation 93, 85-94.

Peterson, A.T., Sanchez-Cordero, V., Soberon, J., Bartley, J., Buddemeier, R.H., Navarro-Siguenza, A. G. 2001. Effects of global climate change on geographic distributions of Mexican Cracidae. Ecological Modelling 144, 21-30.

Peterson, A.T., Vieglais, D. A. 2001. Predicting species invasions using ecological niche modelling: new approaches from bioinformatics attack a pressing problem. BioScience 51, 363-371.

Peterson, A.T., Ortega-Huerta, M. A., Bartley, J., Sanchez-Cordero, V., Soberon, J., Buddemeier, R. H., Stockwell, D. R. B. 2002. Future projections for Mexican faunas under global climate change scenarios. Nature 416, 626-628.

Pounds, J. A., Fogden, M. P., Savage, J. M., and Gorman, G. C. 1997. Tests of null models for amphibian declines on a tropical mountain. Conservation Biology 11, 1307-1322.

Prendergast, J.R., Quinn, R.M., Lawton, J.H., Eversham, B.C., Gibbons, D.W. 1993. Rare species, the coincidence of diversity hotspots and conservation strategies. Nature 356, 335-337.

Robertson, M. P., Caithness, N.,Villet, M. H. 2001. A PCA-based modellingtechnique for predicting environmental suitability for organisms from presence records. Diversity and Distributions 7, 15-27.

Rogers, D. J.,Randolph, S. E. 2000. The global spread of malaria in a future warmer, warmer world. Science 289, 1763-1766.

Rutherford, M. C., Powrie, L. W., Schulze, R. E. 1999. Climate change in conservation areas of South Africa and its potential impact on floristic composition: a first assessment. Diversity and Distributions 5, 253-262.

Rutherford, M.C., Westfall, R.H. 1986. Biomes of southern Africa – an objective categorization. Memoirs of the Botanical Survey of South Africa 54.

Samways, M.J. 2003. Critical response from Professor Michael J. Samways. Journal of Biogeography, 30:817.

Scholtz, C.H., Chown, S.L. 1995. Insects in southern Africa: How many species are there? South African Journal of Science, 91, 124-126.

Schulze, R. 1997. Climate. In: Cowling, R.M., Richardson, D.M. Pierce, S.M. (eds.) Vegetation of Southern Africa, Cambridge University Press, Cambridge, pp613.

Schulze, R., Maharaj, M. 1997. South African Atlas of Agrohydrology and Climatology.Water Research Commission report TT82/96, Pretoria, 276 pp.

Schulze, R., Meigh, J., Horan, M. 2001. Present and potential future vulnerability of eastern and southern Africa's hydrology and water resources. South African Journal of Science 97, 150-160.

Stockwell, D.,Peters, D. 1999. The GARP modelling system: problems and solutions to automated spatial prediction. International Journal of Geographical Information Science 13,143-158.

Sutherst, R.W. 2003. Prediction of species geographical ranges. Journal of Biogeography, 30: 805–816

Sutherst, R. W., Maywald, G. F. 1985. A computerised system for matching climates in ecology. Agriculture, Ecosystems and Environment 13, 281-299.

Todd, M. C., Washington, R., Cheke, R. A., Kniveton, D. 2002. Brown locust outbreaks and climate variability in southern Africa. Journal of Applied Ecology 39, 31-42.

Van Jaarsveld, A. S., Gaston, K. J., Chown, S. L., Freitag, S. 1998a. Throwing biodiversity out with the binary data? South African Journal of Science 94, 210-214.

Van Jaarsveld, A. S., Freitag, S., Chown, S. L., Muller, C., Koch, S., Hull, H., Bellamy, C., Kruger, M., Endrody-Younga, S., Mansell, M. W.,Scholtz, C. H. 1998b. Biodiversity assessment and conservation strategies. Science 279, 2106-2108.

Van Jaarsveld, A.S., Chown, S.L. 2001. Climate change and its impacts in South Africa. Trends in Ecology and Evolution 16, 13-14

Van Rensburg, B. J., Chown, S. L.,Gaston, K. J. 2002. Species richness, environmental correlates, and spatial scale: a test using South African birds. The American Naturalist 159(5), 566-577.

Van Staden, V., Erasmus, B.F.N., Roux, J., Wingfield, M.J., Van Jaarsveld, A.S. In press. Modelling the spatial distribution of two important South African plantation forestry pathogens. Forest Ecology and Management.

Van Zinderen Bakker Sr, E.M. 1978. Quaternary vegetation changes in southern Africa. In: Werger, M.J.A. (ed) Biogeography and Ecology of Southern Africa. W.Junk Publishers, The Hague, pp 131 – 143.

Vida, S. 1993. A computer program for non-parametric receiver operating characteristic analysis. Computer Methods and Programs in Biomedicine 40, 95-101.

Vlok, J.H., Euston-Brown, D. 2002. Subtropical thicket ecosystem planning: biological survey report. Unpublished report. Terrestrial Ecology Research Unit, University of Port Elizabeth, pp. 165. (http://zoo.upe.ac.za/step)

Walker, P. A., Cocks, K. D. 1991. HABITAT: a procedure for modelling a disjoint environmental envelope for a plant or animal species. Global Ecology and Biogeography Letters 1, 108-118.

Watt, A. D., McFarlane, A. M. 2002. Will climate change have a different impact on different trophic levels? Phenological development of winter moth *Operophtera brumata* and its host plants. Ecological Entomology 27, 254-256.

Werger, M. J. A. 1978. Biogeographical division of southern Africa. In: M. J. A. Werger (ed) Biogeography and Ecology of Southern Africa, W. Junk, The Hague, pp. 145-170.

Zar J.H. (1996). Biostatistical analysis, 3rd edition. Prentice-Hall, Upper Saddle River, NJ, pp. 121.

CHAPTER 8

Summary and conclusion

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The case studies presented have a common thread – all evidence, modeled solutions as well as observed shifts in the literature, points to the fact that species distributions are expected to show substantial changes in response to a changing climate. These changes, whether they are range shifts, range contractions or complete range dislocations, are expected to be severe enough that long term land-use planning can no longer afford not to incorporate a climate change contingency plan (Hannah et al. 2002)

Conservation, where conservation goals are often measured by the presence of vulnerable species or communities, faces a particular challenge. Not only will the reserve network need considerable redundancy in the off-reserve matrix for anticipated range shifts, but it will also have to deal with range contraction, and associated potential local population declines (Gaston et al. 1996, Gaston 1998). Range contraction is a common predicted outcome (Erasmus et al. 2002). Even without any climate change, species with contracted ranges would already be at greater risk through simple area-abundance relationships (Gaston et al. 1996). However, given the degree of stress that most populations are already subjected to in their present ranges due to unsustainable land-use practices (Lande 1998), the additional stress of climate change may make local extinctions a more likely outcome. This finding from this South African assessment concurs with sentiments expressed by the IPCC Regional Assessment (IPCC 1997) on the vulnerability of African ecosystems to climate change due to unsustainable land-uses. It is a significant step forward to be able to confirm findings from broad regional assessments at a national scale where conservation planning decisions are taken (Erasmus et al. 1999).

Eastward range shifts are another typical feature of predicted future species distributions in South Africa. This predicted shift tracks the predicted decrease in precipitation across the east-west aridity gradient in South Africa. This predicted shift confirms the IPCC report (IPCC 1997) that deserts in Africa are particularly at risk; the arid western parts of South Africa are expected to lose species as arid regions become too arid for even arid-adapted species which might be close to physiological tolerance limits. This report (IPCC 1997) also identifies the grasslands of southern and eastern Africa as biomes vulnerable to climate change. Erasmus et al. (2002) show that the predicted eastward shifts will result in new species entering this biome, with novel species interactions as a result. The outcomes of these novel interactions are difficult to predict, but it is likely that some species will be out-competed (Lande 1998). Microcosm experiments with novel communities might provide insight into potential outcomes of species interactions.

The likelihood of successful range shifts will be decreased by habitat fragmentation, the presence or absence of suitable habitat in intermediate areas and the degree of land transformation encountered. Climate change and habitat fragmentation are likely to be opposing shifting forces, with climate change forcing a distribution a shift and habitat fragmentation preventing that shift through absence of suitable habitat (Warren et al. 2001). In South Africa, conflict is expected as areas of significant land transformation straddle potential range displacement routes (Erasmus et al. 2002). A distribution shift consists of one edge of the distribution experiencing a net mortality, and the other edge a net colonization. Honnay et al. (2002) have shown that habitat fragmentation inhibits net colonization at the edge of a shifting distribution, resulting in a severely reduced ability to shift. Apart form the caveats associated with the availability of suitable habitat for a successful shift, the required rate of shift is a further complicating factor. In his review, Huntley (1998) shows that the time frame within which climate change is expected to induce shifts, may be too short; and that few species have the ability to shift at the required rates. Once again, the net result is likely to be local extirpation of the population, rather than a shifted population.

The pattern of range contraction and range shift predicted for South Africa confirms assessments at broader scales. Vulnerable areas (e.g. arid areas and grasslands) identified at a continental scale (IPCC 1997) were confirmed, and quantified, by a more detailed fine scale analysis (Erasmus et al. 2002). At the outset of this study a main aim was to fulfill the need identified by the IPCC for more detailed level studies. This has been done, and in doing so, confirmed that the broader scale assessments of the IPCC (IPCC 1997, 2002) are generally applicable to South Africa.

Range shifts and the resulting novel species interactions also have indirect implications for conservation, agriculture and forestry through a change in risk profile to potential pathogens. This change in risk profile will happen through shifting distributions of pathogens (Van Staden et al in press) as well as through pathogens encountering novel hosts. The same principles governing the outcome of novel species assemblages will determine the survival of the pathogen in the presence of a new host. In South Africa susceptible eucalypt plantations are currently planted in areas to which a pathogen is expected to shift. This result is consistent with changes in disease risk due to climate change reported elsewhere (Daszak et al. 2000, Rogers & Randolph 2000, Harvell et al. 2002).

The other main focus of this thesis was a methodological one, and some valuable insights were gained. Climate envelope modelling is by definition a static equilibrium approach (Guisan & Zimmerman 2000) that relies on a snapshot of climate and distribution data to make predictions. This approach has three main shortcomings:

1. The nature of the climate data is such that there is limited scope to incorporate an explicit temporal component into a single variable. Long-term mean monthly values can be used to describe the "normal" onset of a particular season in a particular month. However, inter-annual variation in the onset of such a "normal" season is easily lost with long term mean data and processes dependent on particular climate cycles, i.e. seasonal reproductive events, of which the timing can be critical for population persistence, cannot easily be described. Climates of the future are expected to exhibit increased levels of inter-annual variability (Easterling et al. 2000, also see Schulze et al. 2001 for a South African perspective). Climate fluctuations have well-documented effects on ecosystems (Stenseth et al. 2002). These effects might be amplified in future climates that are more variable. Currently, effects of such changes in variability, i.e. more flash floods, can be estimated but the events themselves cannot be predicted. Even if climate science progresses to the point where such events can be predicted, an equilibrium model will still struggle to incorporate this dynamic-orientated data. A solution at this stage is to use derived variables such as precipitation seasonality (see Erasmus et al. 2000) that describe intra-annual variability.
2. The equilibrium nature of the model also pertains to population processes; dynamic interactions between populations as well as sub-populations of a metapopulation cannot be captured with this approach.
3. Analogous to the climate envelope model's inability to capture interactions between populations, it cannot capture interactions between species either. Such interactions have been shown to enforce range limitations (Hochberg & Ives 1999; Samways 2003).

In spite of these seemingly gross oversimplifications, the climate envelope model implemented throughout this study performed well using a standard model evaluation technique. Further support for the climate envelope model came from its agreement with other more complex models that were specifically developed for distribution prediction. Not only is there agreement in the mean outputs of these models, but there is also agreement about the areas in which the models perform poorly. Robertson et al. (2003) have shown that an equilibrium type envelope model can perform at least as well, if not better, than a mechanistic model that is based on explicit and known ecophysiological constraints. Such a mechanistic model effectively uses the fundamental niche (Hutchinson 1957) to determine the bioclimatic envelope of a species; however, if the fundamental niche is not realized at present then it is unlikely to be realized in future. Bioclimatic envelopes based on observed distributions effectively capture the realized niche, and are likely to be more adept at predicting future distributions (Pearson & Dawson 2003), since some measure of the factors determining the realized niche is implicitly included. It seems as if all the models tested here have at least some useful ability to extract a climate-related distribution dependency from the climate data. Although this finding needs to be tested with a wider selection of models, it may be that predictor variable selection are more important than model selection to improve predictive model outputs.

Although we identified the inability of a climate envelope model to incorporate detail information on species- and population interactions as a weakness, there are in fact very few communities, or even populations, for which this sort of detailed information exists. Typically, detail data on species' habitat preferences at the individual scale lends itself to a different modelling approach (e.g. Gurnell et al. 2002), but these more detailed approaches, very seldom lend themselves to extrapolating to scales at which integrated conservation planning is conducted.

Therefore, although the broad scale climate envelope approach does have its limitations, at present it is one of the only techniques with which a quick and useful assessment of potential climate change vulnerabilities can be made. The technique can be applied in such a way as to limit the effects of its shortcomings. For example, although it is tempting to interpret predicted distributions as actual ranges, in fact, they only represent potential climatic areas of occupancy. The re-sampling technique developed by Smit et al. (in prep) provides an additional tool with which to interpret the reliability of the envelope model output.

Identifying and partitioning sources of variation in the data (including spatial variation) *a priori*, and treating these data explicitly to ensure geographically homogenous model performance (Erasmus et al. in prep), will improve the quality of envelope model output.

In spite of all the caveats of the envelope modelling approach, I hold that the results from such modeling exercises are useful for showing potential effects of climate change and the magnitudes of these effects. Despite criticism (Davis et al. 1998, Samways 2003) of the envelope approach, it has been shown that some species have moved (Parmesan 1996, Parmesan & Yohe 2003, Root et al. 2003) and ecosystem changes have occurred in response to climate. The often-cited critique of climate envelope models being "invalidated" by species interactions (Davis et al.1998) was only performed at fine scale in a laboratory. This is not the scale at which bioclimatic envelopes have proven their usefulness as a tool for conservation practitioners. In a recent review, Pearson & Dawson (2003) concluded that the usefulness of bioclimatic envelope modelling is dependent on the scale at which it is applied. They argue that at broad scales climate is the most important factor that shapes distribution patterns and therefore this is a sensible scale at which to apply this technique. At increasing finer scales, other limiting factors such as land use, soil type, and biotic interactions become more important, and results from bioclimatic envelope modelling at these finer scales should be interpreted with informed caution (Pearson & Dawson 2003). The studies presented in this thesis was conducted at the interface of what Pearson & Dawson (2003) calls regional and landscape scales, where climate and topography are important factors, and these (or their covariates) are the variables which were used.

Therefore, the notion that all climate envelope approaches are irrelevant is not true. Species interactions may be important but so is climate, and if a model using the latter gives useful answers, then conservation practitioners cannot afford to discard any of these approaches at present. Conservation has become a time-critical discipline and we cannot afford to wait until ideal data and methods are developed before taking mitigating action (Van Jaarsveld et al 1998).

Consequently, by exploring a series of case studies about the application of climate change modeling on biodiversity features I identify a number of procedures that need to be incorporated into a national level study on the biodiversity consequences of climate change:

1. The study should have a long-term view to collect time series data.

2. This longer-term study should include different taxa at different scales.
3. The study should incorporate an effort to improve information on animal diversity and distribution in South Africa. Current databases present a historic snapshot, and are becoming increasingly irrelevant as land-uses change.
4. There should be an effort to identify systems especially vulnerable to climate change, and conduct detailed investigations, but not exclusively so. Fynbos, succulent karoo, isolated pockets of afromontane forest, highveld grassland and extreme arid areas have been identified by the IPCC as vulnerable (IPCC 2002). This procedure should include the identification of potential climate change indicator species *a priori*.
5. Methodologies should be standardized to facilitate between-site comparisons, but also follow IPCC guidelines for climate change assessment (Benioff et al. 1996, IPCC 1994). Following these guidelines would ensure comparability with studies elsewhere and as such make a contribution to climate change impact studies at a global level. Modelling procedures should be well established in the scientific literature.
6. The study should be designed with a view to inform non-scientific decision makers and politicians. A shortcoming of the latest IPCC report (IPCC 2001a,b,c,d) is that it is based on studies that were not intended to inform policy makers as an end-result (Viner 2003).
7. The study should have a dual approach by modelling broad scale patterns and at the same time, conduct detail investigations into the causal links between climate and animal distributions. The latter takes place at the level of individual species, and it is envisaged that as the nature of climate dependence becomes known for a larger number of species and systems, this information will be used to feed back into the broader scale models, and thus improve their predictions.
8. As an outcome, the study should have a mechanism to feed recommendations into an integrated land-use planning exercise. Part of this integrated planning should be a representative conservation area network for South Africa that incorporates considerable redundancy in order to buffer effects of climate change.

Mitigation of the impacts of climate change is ultimately a function of political will to confront difficult issues such as climate change-integrated land-use planning. Climate change presents a significant threat to the South African national biodiversity estate, and our ability to manage it, and should be considered as of the utmost importance. Implementing the steps outlined above would go a long way towards improving our ability to meet this challenge successfully.

References

Benioff, R., Guill, S. & Lee, J. (1996) Vulnerability and adaptation assessment – an international handbook. Kluwer Academic Publishers, Dordrecht.

Daszak, P., Cunningham, A.A. & Hyatt, A.D. (2000) Emerging infectious diseases of wildlife - threats to biodiversity and human health. *Science* 287: 443-449.

Davis, A.J. *et al.* (1998) Individualistic species responses invalidate simple physiological models of community dynamics under global environmental change. *Journal of Animal Ecology* 67: 600-612.

Easterling, D.R., Meehl, G.A., Parmesan, C., Changnon, S.A., Karl, T.R. & Mearns, L.O. (2000) Climate extremes: observations, modelling, and impacts. *Science* 289: 2068-2074.

Erasmus, B.F.N., Freitag, S., Gaston, K.J., Erasmus, B.H., & Van Jaarsveld, A.S. (1999) Scale and conservation planning in the real world. *Proceedings of the Royal Society of London Series B* 266:315-319.

Erasmus, B.F.N., Kshatriya, M., Mansell, M.W., Chown, S.L. & Van Jaarsveld, A.S. (2000) A modelling approach to antlion (Neuroptera: Myrmeleontidae) distribution patterns. *African Entomology* 8(2):157-168.

Erasmus, B.F.N., Van Jaarsveld, A.S., Chown, S.L., Kshatriya, M., & Wessels, K.J. (2002) Vulnerability of South African animal taxa to climate change. *Global Change Biology* 8:679-693.

Erasmus, B.F.N., Van Rensburg, B.J., Van Jaarsveld, A.S., Sutton, T., Turner, A., Stockwell, D. & Chown, S.L. (in prep) Predictive species distribution models disagree in ecological and environmental transition zones. *Ecological Modelling.*

Midgley, G.F., Hannah, L., Millar, D., Rutherford, M.C., & Powrie, L.C. (2002) Assessing the vulnerability of species richness to anthropogenic climate change in a biodiversity hotspot. *Global Ecology & Biogeography* 11:445-451.

Gaston, K.J. (1998) Rarity as double jeopardy. *Nature* 394: 229-230.

Gaston, K.J., Blackburn, T.M. & Lawton, J.H. (1996) Interspecific range-size abundance relationships: an appraisal of mechanisms. *Journal of Animal Ecology* 66: 579-601.

Guisan, A. & Zimmerman, N.E. (2000) Predictive habitat distribution models in ecology. *Ecological Modelling* 135: 147-186.

Gurnell, J., Clark, M.J., Lurz, P.W.W., Shirley, M.D.F. & Rushton, S.P. (2002) Conserving red squirrels (Sciurus vulgaris): mapping and forecasting habitat suitability using a Geographic Information System. *Biological Conservation* 105: 53-64.

Hannah, L., Midgley, G.F. & Millar, D. (2002) Climate change-integrated conservation strategies. *Global Ecology & Biogeography* 11:485-495.

Harvell, C.D., Mitchell, C.E., Ward, J.R., Altizar, S., Dobson, A.P., Ostfeld, R.S. & Samuel, M.D. (2002) Climate warming and disease risks for terrestrial and marine biota. *Science* 296: 2158-2162.

Hochberg, M.E. & Ives, A.R. (1999) Can natural enemies enforce geographical range limits? *Ecography* 22: 268-276.

Honnay, O., Verheyen, K., Butaye, J., Jacquemyn, H., Bossuyt, B. & Hermy, M. (2002) Possible effects of habitat fragmentation and climate change on the range of forest plants. *Ecology Letters* 5: 525-530.

Huntley B. (1998) The dynamic response of plants to environmental change and the resulting risks of extinction. In: *Conservation in a changing world*, Mace, G.M., Balmford, A. & Ginsberg, J.R. (Eds) Cambridge University Press, UK, pp 69-88.

Hutchinson, G.E. (1957) Concluding remarks. *Cold Spring Harbour Symposium on Quantitative Biology* 22:415-457.

Lande R. (1998) Anthropogenic, ecological and genetic factors in extinction. In: *Conservation in a changing world*, Mace, G.M., Balmford, A. & Ginsberg, J.R. (Eds) Cambridge University Press, UK, pp 29-51.

IPCC (1994) IPCC Technical Guidelines for Assessing Climate Change Impacts and Adaptations with a Summary for Policy Makers and a Technical Summary (Eds) Carter, T.R., Parry, M.L., Harasawa, H. & Nishioka, S. Department of Geography, University College London, UK and the Center for Global Environmental Research, National Institute for Environmental Studies, Japan, pp 59.

IPCC (1997) The Regional Impacts of Climate Change: An Assessment of Vulnerability. (Eds) Watson, R.T., Zinyowera, M.C. & Moss, R.H. Cambridge University Press, UK, pp 517.

IPCC (2001a) Climate Change 2001: Synthesis Report. (Eds) Watson, R.T. and the Core Writing Team. Cambridge University Press, UK, pp 398.

IPCC (2001b) Climate Change 2001: The Scientific Basis. (Eds) Houghton, J.T., Ding, Y., Briggs, D.J., Noguer, M., van der Linden, P.J. & Xiaosu, D. Cambridge University Press, UK, pp 944.

IPCC (2001c) Climate Change 2001: Impacts, Adaptation & Vulnerability (Eds) McCarthy, J.J., Canziani, O.F., Leary, N.A., Dokken, D.J. & White, K.S. Cambridge University Press, UK, pp 1000.

IPCC (2001d) Climate Change 2001: Mitigation. (Eds) Metz, B., Davidson, O., Swart, R. & Pan, J. Cambridge University Press, UK, pp 700.

IPCC (2002) Climate Change and Biodiversity: IPCC Technical Paper V. (Eds) Gitay, H., Suarez, A., Watson, R.T. & Dokken, D.J. IPCC Secretariat, Geneva, pp.86.

Parmesan, C. (1996) Climate and species' range. *Nature* 382: 765-766.

Parmesan, C. & Yohe, G. (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421:37-42.

Pearson, R.Q. & Dawson, T.P. (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography* 12:361-371.

Robertson, M.P., Peter, C.I., Villet, M. & Ripley, B.C. (2003). Comparing models for predicting species' potential distributions: a case study using correlative and mechanistic predictive modelling techniques. *Ecological Modelling* 164:153-167.

Rogers, D.J. and Randolph, S.E. (2000) The global spread of malaria in a future warmer, warmer world. *Science* 289: 1763-1766.

Root, T., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweig, C. & Pounds, J.A. (2003) Fingerprints of global warming on wild animals and plants *Nature*, 421-57-60.

Samways, M.J. (2003) Critical response from Professor Michael J. Samways. *Journal of Biogeography,* 30:817.

Stenseth, N. Chr., Mysterud, A., Ottersen, G., Hurrell, J.W., Chan, K-S., and Lima, M. (2002) Ecological effects of climate fluctuations. *Science* 297: 1292-1296.

Schulze, R., Meigh, J. & Horan, M. (2001) Present and potential future vulnerability of eastern and southern Africa's hydrology and water resources. *South African Journal of Science* 97, 150-160.

Van Jaarsveld, A.S., Gaston, K.J., Chown, S.L., and Freitag, S. (1998) Throwing biodiversity out with the binary data? *South African Journal of Science* 94: 210-214.

Viner, D. (2003). Climate change impact assessments. *Global Ecology and Biogeography* 12:87-88.

Warren, M.S., Hill, J.K., Thomas, J.A., Asher, J., Fox, R., Huntley, B., Roy, D.B., Telfer, M.G., Jeffcoate, S., Harding, P., Jeffcoate, G., Willis, S.G., Greatorex-Davies, J.N., Moss, D. & Thomas, C.D. (2001) Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature* 414:65-69.