Journal of Biogeography, **26**, 595–617

The influence of climate change on the distribution of indigenous forest in KwaZulu-Natal, South Africa

Harriet A. C. Eeley, Michael J. Lawes* and Steven E. Piper *The Forest Biodiversity Programme, School of Botany and Zoology, University of Natal, Pietermaritzburg, Private Bag X01, Scottsville 3209, South Africa email: lawes@zoology.unp.ac.za*

Abstract

Aims (1) To define the physical correlates of indigenous forest in KwaZulu-Natal province and develop a model, based on climatic parameters, to predict the potential distribution of forest subtypes in the province. (2) To explore the impact of palaeoclimatic change on forest distribution, providing an insight into the regional-scale/historical forces shaping the pattern and composition of present-day forest communities. (3) To investigate potential future shifts in forest distribution associated with projected climate change.

Location KwaZulu-Natal province, South Africa.

Methods A BIOCLIM-type approach is adopted. Bioclimatic 'profiles' for eight different forest subtypes are defined from a series of grid overlays of current forest distribution against nineteen climatic and geographical variables, using ArcInfo GIS grid-based processing. A principal components analysis is performed on a selection of individual forests to identify those variables most significant in distinguishing different forest subtypes. Five models are developed to predict the distribution of forest subtypes from their bioclimatic profiles. Maps of the potential distribution of forest subtypes predicted by these models under current climatic conditions are produced, and model accuracy assessed. One model is applied to two palaeoclimatic scenarios, the Last Glacial Maximum (LGM) ($\approx$18,000 BP) and the Holocene altithermal ($\approx$7000 BP), and to projected future climate under a doubling in global atmospheric carbon dioxide.

Results Seven variables; altitude, mean annual temperature, annual rainfall range, potential evaporation, annual temperature range, mean annual precipitation and mean winter rainfall, are most important in distinguishing different forest subtypes. Under the most accurate model, the potential present-day distribution of all forest subtypes is more extensive than is actually observed, but is supported by recent historical evidence. During the LGM, Afromontane forest occupied a much reduced and highly fragmented area in the mid-altitude region currently occupied by scarp forest. During the Holocene altithermal, forest expanded in area, with a mixing of Afromontane and Indian Ocean coastal belt forest elements along the present-day scarp forest belt. Under projected climatic conditions, forest shifts in altitude and latitude and occupies an area similar to its current potential and more extensive than its actual current distribution.

Main conclusions Biogeographical history and present physical diversity play a major role in the evolution and persistence of the diversity of forest in KwaZulu-Natal. It is important to adopt a long-term and regional perspective to forest ecology, biogeography, conservation and management. The area and altitudinal and latitudinal distribution of forest subtypes show considerable sensitivity to climate change. The isolation of forest by anthropogenic landscape change has limited its radiation potential and ability to track environmental change. Long-term forest preservation requires reserves in climatically stable areas, or spanning altitudinal or latitudinal gradients allowing for forest migration, along with innovative matrix management strategies. Dune, sand, swamp, riverine and lowland forest subtypes are most at risk. Scarp forests are highlighted as former refugia and important for the future conservation of forest biodiversity.

Keywords
Indigenous forest, distribution, climate change, bioclimatic models, South Africa.

INTRODUCTION

Indigenous forest is the smallest biome represented in South Africa (Cooper, 1985; Geldenhuys, 1989; Rutherford & Westfall, 1994), recently estimated to cover 7177 km^2, or 0.56% of the total land area of the country (Low & Rebelo, 1996). The distribution of forest is highly fragmented, most occurring in patches of less than 1 km^2 (Cooper, 1985; Geldenhuys, 1989; Low & Rebello, 1996). Anthropogenic changes have severely affected the extent of the biome, with the clearance of large areas of forest in particular along the eastern coastal region (Fourcade, 1889; Bews, 1912, 1913, 1920; King, 1941; Cooper, 1985; Geldenhuys, 1989). However, in spite of its small area, fragmented nature, and continued degradation by agro-commercial enterprise and rural communities, the indigenous forest biome in South Africa supports a high proportion of the country's floral and faunal diversity (Geldenhuys, 1989). For example, it is estimated that both forest mammals and forest birds represent over 14% of the total terrestrial component of these taxa in southern Africa (Geldenhuys & MacDevette, 1989).

Approximately one sixth of South Africa's remaining indigenous forest is found within the province of KwaZulu-Natal (1185 km^2, or 16.5%: Low & Rebello, 1996). The province is, however, unique in that it supports both the major forest types of the southern African subcontinent, Afromontane forest and Indian Ocean coastal belt forest, and the eight different forest subtypes into which these may be divided (Moll & White, 1978; White, 1978, 1981; Cooper, 1985; MacDevette *et al.*, 1989). KwaZulu-Natal thus plays a critical role in supporting and maintaining indigenous forest diversity in South Africa. The province is also one of marked climatic and physical diversity and, in our opinion, this has played a fundamental role in the evolution and persistence of the diversity of forest types in the province. Afromontane forest is known to have been present in the southern African subcontinent at least prior to the Last Glacial Maximum (LGM) ($\approx$18,000 BP), and Indian Ocean coastal belt forests from around 8000 BP (Moreau, 1963; White, 1978, 1981; MacDevette *et al.*, 1989; Lawes, 1990). Both the diversity of forest types in KwaZulu-Natal, and the distribution of forest fauna, imply a complex biogeographical history for forest in the region (Lawes, 1990).

At the regional (to global) level it is climate that sets the broad limits to the distribution of plant taxa (Box, 1981; Woodward, 1987; Prentice, 1992; Taylor & Hamilton, 1994), although fire too plays an important role in limiting the extent of forest patches both locally and regionally (Grainger, 1984; Meadows & Linder, 1993; Geldenhuys, 1994; Bond, 1997; Midgley *et al.*, 1997). Consequently, bioclimatic analyses and spatial modelling have been used extensively to define the factors which govern the distribution of species and entities (such as vegetation types or biomes), and to predict where and under what conditions particular taxa (or entities) might be expected to occur (see for example, Box, 1981; Busby, 1986; Woodward & Williams, 1987; Woodward, 1987; Hill, Read & Busby, 1988; Prentice *et al.*, 1992; Rutherford & Westfall, 1994). Recognizing the dynamic nature of species' distribution (Woodward, 1987; Hengeveld, 1995), an understanding of the present-day climatic limits of species, or entities, also allows for the exploration of how distributional patterns might change in response to climatic change (for example, Busby, 1988; Graham *et al.*, 1990; Prentice *et al.*, 1992; Prentice, 1992; Gates, 1993; Dale & Rauscher, 1994; Taylor & Hamilton, 1994; Huntley, 1995).

The objectives of this study are the following.

1. To define the physical correlates of indigenous forest in KwaZulu-Natal, and to develop a model based on climatic parameters to predict the potential present-day distribution of different forest subtypes in the province.
2. Using this model, to explore the impact of palaeoclimatic change on forest distribution in order to gain insight into the regional-scale/historical forces that have shaped the pattern and composition of present-day forest communities. Thus, we attempt to identify those present-day and historical factors that have contributed to the development and persistence of the diversity of forest types in the region.
3. To investigate the potential shifts in the pattern of forest distribution in KwaZulu-Natal that may be associated with projected climate change consequent to increasing levels of global atmospheric carbon dioxide. Developing such an understanding is important if we are to develop effective strategies for the long-term management and conservation of indigenous forest in the region (Taylor & Hamilton, 1994; Hulme *et al.*, 1995; Hulme, 1996).

KWAZULU-NATAL: FOREST AND CLIMATE

Indigenous forest diversity

Closed canopy, multistrata communities of evergreen indigenous trees make up two broad classes of indigenous forest in the southern African subcontinent; Afromontane forests and

* Correspondence: Michael J. Lawes, The Forest Biodiversity Programme, School of Botany and Zoology, University of Natal, Pietermaritzburg, Private Bag X01, Scottsville 3209, South Africa.

Indian Ocean coastal belt forests (Moll & White, 1978; White, 1978; Huntley, 1984; Cooper, 1985; Rutherford & Westfall, 1994). These differ in their species composition, recruitment dynamics and regeneration patterns, as well as their evolutionary history and status, with the Afromontane forests being the older and more persistent forest type in the region (Moll & White, 1978; White, 1978; Lawes, 1990). Both Afromontane forests and Indian Ocean coastal belt forests are represented in KwaZulu-Natal and, in turn, these may be divided into eight different forest subtypes, primarily on the basis of their floristics and faunal composition (Cooper, 1985; MacDevette *et al*., 1989). Following Cooper (1985: after Edwards, 1967; Moll & White, 1978; White, 1978), two subtypes are recognized within the Afromontane forests: montane *Podocarpus* forest (montane) and mist belt mixed *Podocarpus* forest (mist belt), while the Indian Ocean coastal belt forests comprise dune forest, swamp forest, sand forest, riverine forest, coast lowland forest (lowland), and coast scarp forest (scarp). The variety of forest subtypes occurring in KwaZulu-Natal is noteworthy; the province is unique in the country, and indeed in the subcontinent, for the diversity of forest communities it supports.

Physical geography

KwaZulu-Natal covers an area of 92,285 km^2 (Schulze, 1997), lying between 26°50′ and 31°10′ South and 28°50′ and 32°50′ East, in eastern South Africa. The geology, topography and climate of the province are remarkably varied (King, 1978; Schulze, 1982). The land rises from the relatively flat coastal plain in the east, over a series of plateaux, to the Drakensberg mountains which reach over 3000 m in places and form the western boundary of the province, running in a predominantly north–south direction 150–280 km from the coast. The whole province lies in the summer rainfall belt, but while the mountainous western region experiences large annual variation in both rainfall and temperature, the climate of the eastern coast is ameliorated by the offshore Mozambique current and receives year round rain (Schulze & McGee, 1978; Schulze, 1982, 1997).

Indigenous forest occurs throughout the higher rainfall areas of KwaZulu-Natal (Fig. 1). Afromontane (montane and mist belt) forests occur in the western half of the province, and are associated with south and south-eastern facing slopes of the hills and mountains of this area. Indian Ocean coastal belt forests occupy the relatively flat coastal plain, with swamp, sand and riverine forests being confined to the north, while dune and lowland forests form a belt along the coast to just south of Durban. Scarp forests occur on the south and south-eastern facing slopes of the hills, ridges and gorges of the first plateau escarpment, ≈15–20 km from the coast in the south of the province and up to 70 km inland in the north.

Palaeoclimatic change – a review

Over the past two million years, southern Africa has experienced some 20 climatic cycles, each lasting ≈100,000 years and mirroring periods of expansion and contraction of the glacial ice sheets at higher latitudes (Deacon, 1983; Tyson, 1986; Deacon & Lancaster, 1988). Hyperthermal periods have been characterized in general by warmer, wetter conditions and the expansion of the forest biome, while hypothermal periods experienced cooler drier climates and a reduction in the extent of forest (Deacon, 1983; Tyson, 1986; Deacon & Lancaster, 1988). Evidence for climatic change in southern Africa during the Quaternary comes from a variety of sources but remains both temporally and geographically patchy. The evidence is reviewed in detail elsewhere (see for example, Tyson, 1986; Deacon & Lancaster, 1988; Partridge *et al*., 1990; Partridge, 1997; and, in relation to forests, Lawes, 1990). Here we outline only the main climatic changes from the last interglacial (≈130,000–40,000 BP), from which time there was a decline in temperature to the LGM (≈18,000 BP) when temperatures reached their lowest limits in 125,000 years and conditions were significantly more dry than at present (Deacon, 1983; Deacon *et al*., 1984; Tyson, 1986). In South Africa, estimates of temperature at the LGM vary from 8 to 5.5 °C lower than at present (Heaton *et al*., 1986; Tyson, 1986; Deacon & Lancaster, 1988; Talma & Vogel, 1992), and for the southern African subcontinent in general a temperature decrease of 5–6 °C is likely and consistent with generally accepted conditions world wide (Partridge *et al*., 1990; Tyson, 1990; Stute & Talma, 1997).

Over most of southern Africa precipitation at the LGM varied from ≈40–70% of the present mean (Partridge, 1997). An intensification of circulation patterns is likely to have brought increased winter rainfall to the western part of the country and a greater penetration into the interior of the country (Van Zinderen Bakker, 1982; Deacon, 1983; Deacon & Lancaster, 1988; Partridge, 1997). However, westerly winds are unlikely to have had any major effect on patterns of rainfall in the more easterly regions (and KwaZulu-Natal). Here, generally cold, dry conditions prevailed during the winter, with strong winds and cold air drainage off the Drakensberg mountains exacerbating the drying effect, particularly in the southern part of the province where the high mountains (altitude 1750 m) lie closer to the coast. Sea surface temperatures were ≈4 °C lower than during the interglacial periods (Van Zinderen Bakker, 1982 and references therein), and the Agulhas current off the east coast was cooler, weaker and shallower than at present (Prell *et al*., 1980), contributing to lower temperatures and increased aridity in eastern coastal regions. Summer was marked by strong, high pressure easterly winds. The Agulhas return current strengthened resulting in lowered surface water temperature off the south Mozambique channel and dry summer conditions on the coast as rain development was inhibited by cold inshore waters (Deacon & Lancaster, 1988; Lawes, 1990).

There was a fairly rapid amelioration of climatic conditions following LGM (Deacon, 1983; Deacon *et al*., 1984), with wetter conditions becoming re-established over much of the area between 17,000 and 15,000 BP (Tyson, 1986, 1990; Partridge, 1997). The period since has experienced a general increase in temperature, with temperatures rising after 8000 BP to up to 3 °C warmer than at present during the Holocene altithermal (≈7000 BP) (Tyson, 1986; Deacon & Lancaster,

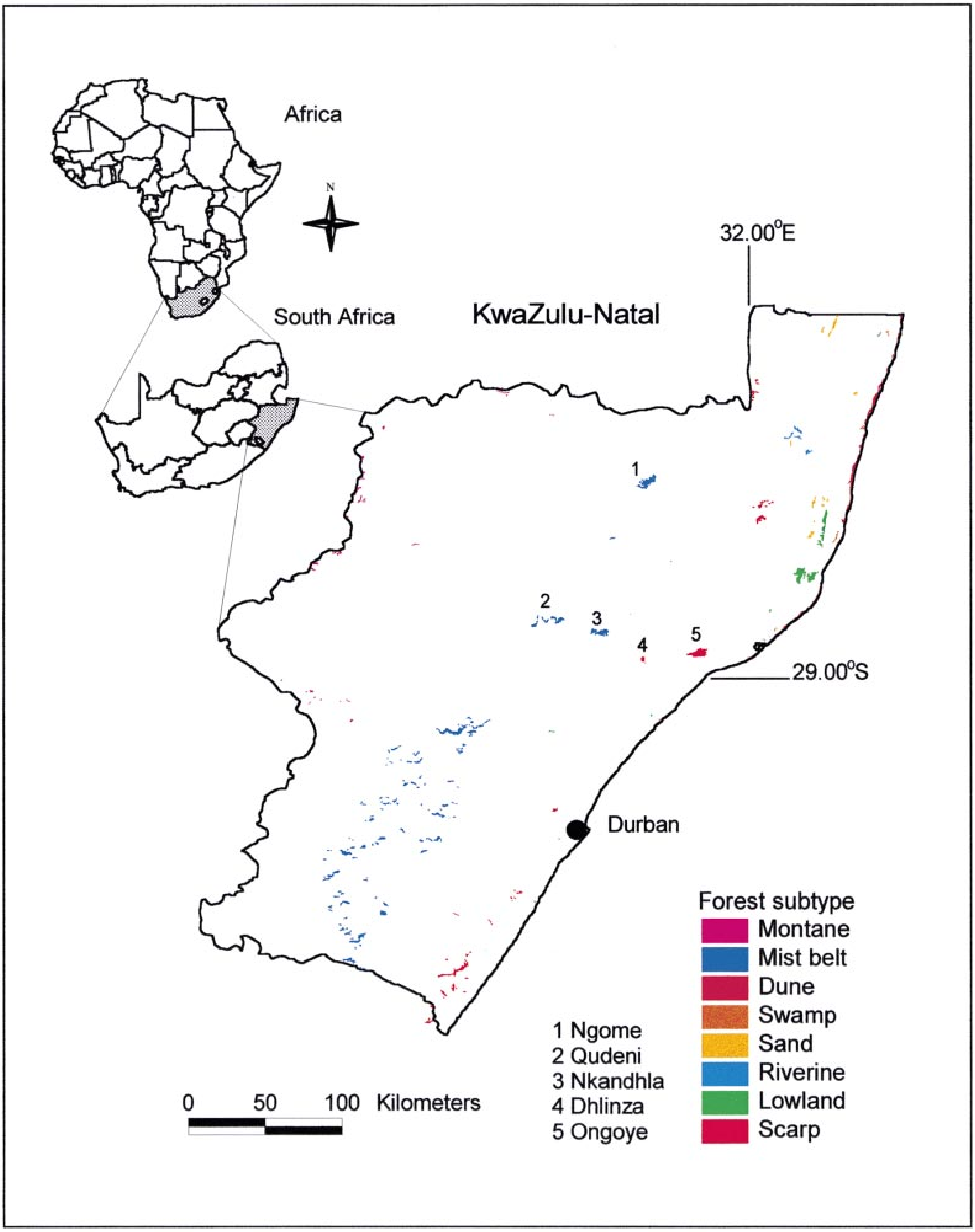

Figure 1 The distribution of indigenous forest in KwaZulu-Natal province, South Africa, showing the eight different forest subtypes. Forests over 50 ha in area are mapped, and localities mentioned in the text are identified.

1988; du Pisani & Partridge, 1990; Partridge *et al*., 1990). At this time there appears to have been considerable regional variation in precipitation, with the Karoo and southern Cape regions being drier than at present and the Kalahari, the mountains of the western Cape and the eastern region (including KwaZulu-Natal) being considerably wetter (Partridge *et al*., 1990; Partridge, 1997). In summary, while conditions in KwaZulu-Natal during the LGM were considerably colder and drier than at present, leading to a contraction in forest extent in the province, during the Holocene altithermal conditions were warmer and wetter and conducive to forest growth and expansion.

Global warming and projected climate change

Anthropogenic emissions of greenhouse gasses have already produced a 'discernible human influence on global climate' (IPCC, 1996). Global mean surface air temperature has increased by between 0.3 and 0.6 °C since the late nineteenth century, with seven of the ten warmest years on record occurring since 1980 (Gates, 1993; IPCC, 1996). Similar figures have been recorded for southern Africa (Hulme, 1996). With the current levels of increase, global atmospheric carbon dioxide is expected to reach double preindustrial concentrations by the end of the twenty-first century (IPCC, 1996). Similar increases in other greenhouse gasses, such as methane, ozone, chlorofluro-carbons and nitrous oxide, may further contribute to rising global temperatures through enhanced radiative forcing (IPCC, 1991, 1996; Gates, 1993). The overall result is a predicted increase in global mean surface air temperatures of 2 °C relative to 1990 levels by 2100 (with estimates ranging from 0.9 to 3.5 °C) (IPCC, 1991, 1996). Along with this, global average sea level is projected to rise by 50 cm, and an increase in the intensity of the hydrological cycle is anticipated, entailing an increased frequency of both severe floods and drought (IPCC, 1996).

General circulation models (GCMs) are used extensively to model climate and climate change at the global level (Gates, 1993; Harrison & Foley, 1995; IPCC, 1996). Substantial regional variation in patterns of temperature and precipitation is projected, but the resolution of current GCMs makes their application at this scale difficult (Tyson, 1990; Harrison & Foley, 1995; IPCC, 1996). For southern Africa, estimates of change vary, but an increase in summer and winter temperatures of around 2 °C (1.5–2.5 °C) is likely, and up to 4 °C possible, by 2100 with a doubling in levels of atmospheric carbon dioxide (Tyson, 1990; Hulme, 1996; Joubert & Hewitson, 1997). Minimum temperatures may increase more than maximum temperatures and winter warming may be greater than summer warming (Tyson, 1990). Greater increases are also anticipated inland than in coastal regions (Hulme *et al*., 1995; Hulme, 1996). Predicted changes in regional precipitation also vary considerably between models. Empirical downscaling techniques suggest a decrease in summer rainfall of 10–15% in the summer rainfall region of eastern South Africa but minimal changes elsewhere (Joubert & Hewitson, 1997). Relatively small changes in mean conditions may however, be accompanied by much larger changes in the frequency and intensity of extreme conditions; floods and droughts (Joubert & Hewitson, 1997).

METHODS

The modelling approach

As a first step in developing a model to predict the distribution of forest, a BIOCLIM-type approach was adopted. BIOCLIM is a bioclimate analysis and prediction system used to predict the distribution of entities such as species or vegetation types (Nix, 1986; Busby, 1988, 1991). BIOCLIM generates a set of variables (climatic indices) considered to have biological significance and to describe the range, extremes and seasonality of climatic conditions (Nix, 1986; Busby, 1988). These variables are interpolated across the geographical surface (at various scales) on the basis of longitude, latitude and elevation. By geocoding and matching the known distribution of a taxon or entity (for example from survey data or museum specimen localities) to these geographical surfaces of variables, a statistical summary of the values of the climatic indices for that taxon or entity is produced. This summary, or bioclimatic 'profile', provides a quantitative description of the climatic environment occupied by the entity (Nix, 1986). Points on the surfaces of variables that match the bioclimatic profile of the entity can then be identified to delimit its potential distribution (i.e. the area of suitable climatic conditions). This "homoclime" matching can be performed at any level of the bioclimatic profile, for example minimum to maximum values, 10–90 percentile range, or 25–75 percentile range, to provide different levels of prediction (Busby, 1991; Lindenmayer *et al*., 1991). The primary assumption of BIOCLIM is that entities can only colonize and survive in areas with climates fitting their *current* climatic profile (Nix, 1986; Busby, 1988). The model does not take any account of the potential interaction between climatic variables (Nix, 1986).

Although there has been some criticism of BIOCLIM (see for example Walker & Cocks, 1991; Carpenter *et al*., 1993), the approach was adopted here as a generic method and a baseline for the model development. It is, however, a broad-based approach that generally incorporates a large number of variables. A principal components analysis (PCA) was therefore carried out to identify those variables of the initial suite that were most significant in defining the distribution of different forest subtypes. This procedure enabled a more refined model to be developed, based only on those variables identified by the PCA. These variables may also be regarded as those whose present-day variability is most crucial to the persistence of the diversity of forest subtypes in the province.

Model assumptions

1. All species have different climatic tolerances and will respond independently to change (Hamilton, 1981; Hamilton & Taylor, 1991; Prentice, 1992; Dale & Rauscher, 1994; Hengeveld, 1995; Huntley, 1995). However, for the purpose of this analysis we are interested in the distribution of forest subtypes, and thus the community level organization, and while we recognize that present-day communities may represent temporally transient associations, we model

different forest subtypes as separate biotypes (i.e. individual entities).
2. We model only climatic parameters and physical geography, and assume that these are the most important factors controlling the distribution of vegetation types at the regional level. We do not, for example, take any account of anthropogenic factors or fire, although we recognize the importance of both in determining the present day distribution of indigenous forest at regional and local levels.
3. The model is an equilibrium model. We do not consider the process of change, only explicit end points: present-day climatic conditions, two palaeoclimatic scenarios, and one future climatic scenario.
4. With regard to modelling the potential future distribution of forest, we do not take any account of the potential feedback to the environment that changes in forest distribution may have.
5. Models are developed on the basis of present-day climatic correlates of forest, but we recognize that forests comprise communities of relatively long-lived species for which a time lag effect may operate, and the present distribution of forest may more accurately reflect the climate of the recent past than that of the present-day.

Datasets and maps

A digital map (coverage) of the distribution of indigenous forest in South Africa was obtained from Forestek (CSIR, 1995). Indigenous forest cover (minimum area 50 ha) had been digitized from the 1:250,000 scale national forestry maps (van der Zel, 1988). The indigenous forest represented on these in turn had been transferred manually from original 1:50,000 map sheets compiled as part of the Wildlife Society of South Africa's indigenous forest surveys (Cooper, 1985; Cooper & Swart, 1992). The coverage of forest distribution was verified against Cooper's original 1:50,000 map sheets in order to classify the subtype of each forest patch, and this information was added to the coverage.

The forest coverage was converted to cell-based raster format (or grid) for analysis. A grid-cell size of $15'' \times 15''$ of arc ($\approx 0.1858\ km^2$, or 18.5 ha, on the ground) was selected as appropriate to the resolution of the original forest coverage, but not so small as to be impracticable. Forest was given a priority weighting (Arc/Info, 1996) in the vector to raster conversion so that any cell crossed by a forest boundary, and therefore including both forest and nonforest, was weighted so that it was recorded as a 'forest' grid-cell, ensuring that all forest was represented where it occurs. The eight different forest subtypes were identified as separate zones in the forest grid.

Nineteen climatic and physical variables were selected, representative of average conditions, as well as climatic seasonality and extremes (Table 1). Rainfall and temperature data were obtained as $1' \times 1'$ of arc grid coverages for the province (from the Computer Centre for Water Research, and R. Schulze, Department of Agricultural Engineering, University of Natal Pietermaritzburg, respectively), having been previously modelled at this scale for the whole of South Africa, Swaziland and Lesotho (Dent *et al*., 1989; Schulze, 1997). These data grids were re-sampled for this analysis to $15'' \times 15''$ of arc, using a cubic convolution re-sampling algorithm (Arc/Info, 1996). Digital maps of the categoric variables (geology and soil type) were obtained in a vector format and converted to cell-based grids (cell size $15'' \times 15''$ of arc) using a majority weighting algorithm (Arc/Info, 1996).

BIOCLIM-type analysis

To describe the bioclimatic profile of the eight forest subtypes: (a) the forest grid was overlain in turn on each of the nineteen grids of variables, and the minimum, maximum, mean and standard deviation of each continuous variable and the majority type of the two categoric variables were determined for each forest subtype using zonal statistics (Arc/Info, 1996). (b) Eight individual grids were created, representing separately each of the forest subtypes, in which forest presence/absence was represented in binary format. The seventeen grids of continuous variables were multiplied in turn by each of these eight binary grids to obtain, for each forest subtype, the complete range of values of each continuous variable and a count of the number of cells of each value. The soil and geology grids were also multiplied by each binary forest grid to obtain the full variety of each categoric variable covered by each forest subtype. (c) For each forest subtype, the 5, 25, 75 and 95 percentile limits of each continuous variable were determined from the results of (b) which were output in a tabular format.

Two models of potential forest distribution were developed, based on these bioclimatic profiles.

Model 1: based on the 25–75 percentile limits of all continuous variables and the majority geology and soil types.

Model 2: based on the 5–95 percentile limits of all continuous variables and the full variety of geology and soil types.

All nineteen variables were included in both Models 1 and 2, and each forest subtype was predicted to occur only where all conditions were satisfied. Thus, for example, under Model 1 montane forest was predicted to occur in any grid-cell for which altitude fell between 1583 and 1795 m, and Jan. max. temp. between 24 and 26 °C, and July min. temp. between 1 and 3 °C, and so on (see Appendix 1), and geology = type 531, and soil type = 55. Under the same model, mist belt forest was predicted to occur in any grid-cell for which altitude fell between 1172 and 1473 m, and Jan. max. temp. between 24 and 25 °C, and July min. temp. between 3 and 5 °C, and so on, and geology = type 3991, and soil = type 29.

Maximum and minimum values of the bioclimatic profiles were not used to model forest distribution as these included extreme and/or unusual values and in a preliminary analysis were found to overestimate the distribution of the forest subtypes. Maximum and minimum values are generally used to predict marginal areas (Nix, 1986; Busby, 1988, 1991).

Principal components analysis

A PCA was carried out on a sample of individual forests. Sixty-nine forests were selected from the original map: ten each of montane, mist belt, dune, sand, lowland (later reduced to nine

Table 1 Climatic and physical variables investigated.

Variable		Unit	Source*
1	Altitude	m	1
2	January maximum temperature	°C	2
3	July minimum temperature	°C	2
4	Mean maximum temperature hottest quarter (December–February)	°C	0
5	Mean minimum temperature coolest quarter (June–August)	°C	0
6	Mean annual temperature	°C	2
7	Annual temperature range (i.e. 2–3)	°C	0
8	Mean annual precipitation	mm	2
9	Median annual precipitation	mm	1
10	January median rainfall	mm	1
11	July median rainfall	mm	0
12	Mean median rainfall wettest quarter (November–January)	mm	0
13	Mean median rainfall driest quarter (June–August)	mm	0
14	Mean median summer rainfall (October–March)	mm	0
15	Mean median winter rainfall (April–September)	mm	1
16	Annual rainfall range (i.e. 10–11)	mm	1
17	Annual potential evaporation	mm	2
18	Geology	Categoric	3
19	Soil type	Categoric	3

* Source
0, Created for this analysis from coverages obtained from sources below using ArcInfo grid-based modelling (Arc/Info, 1996).
1, The Computing Centre for Water Research (University of Natal, Pietermaritzburg).
2, Professor R. Schulze (Department of Agricultural Engineering, University of Natal, Pietermaritzburg).
3, The Institute for Commercial Forestry Research (University of Natal, Pietermaritzburg).

as one forest was found to be misclassified on verification of the forest coverage against Cooper's original 1:50,000 map sheets) and scarp forest, and five each of swamp and riverine forest (as there were, in total, only five forests of these two subtypes). The sixty-nine forests were identified individually as separate zones on a new grid. This was overlain on each of the seventeen grids of continuous variables, and the mean value of each variable determined for each individual forest using zonal statistics (Arc/Info, 1996). The resulting variables were checked for normality and several found to be non-normally distributed, but as these could not be transformed to a normal distribution, and across the whole province these data are normally distributed, they were retained in their un-transformed form. All variables were standardized prior to principal components analysis.

A refined model was developed, incorporating only those variables identified by the principal components analysis:

Model 3: based on the 5–95 percentile limits of the subset of continuous variables selected as a result of the PCA and the full variety of geology and soil types.

Additional changes were made to Model 3 as a result of qualitative model validation and to provide the flexibility necessary when modelling under scenarios of past and future change. Models 4 and 5 were produced as a result of these alterations (see below).

Model validation

All models were assessed quantitatively and qualitatively. Grid-based maps of the predicted distribution of forest subtypes resulting from each model under current climatic conditions were produced by matching the model conditions against the original grids of continuous and categoric variables. These predicted distribution maps were then overlain in turn on the actual present-day distribution of forest in the province as represented by the original forest grid (the surface reference data). In each case, for each forest subtype, the number of cells predicted but not actually present (commissions, or false positive), actually present but not predicted (omissions, or false negative), and the extent of congruence between the actual and predicted distribution (the number of cells in common) were determined. The coefficients of Jaccard and Dice were calculated for each forest subtype to assess the fit of each model (Sokal & Sneath, 1963).

$$\text{Jaccard} = \frac{\text{common}}{(\text{common} + \text{omissions} + \text{commissions})}$$

$$\text{Dice} = \frac{(2 \times \text{common})}{((2 \times \text{common}) + \text{omissions} + \text{commissions})}$$

A low coefficient indicates a poor fit, little congruence between the actual and predicted distributions, many omissions and/or many commissions, while a high coefficient indicates that the congruence is high and few cells are either omitted or committed. The congruence between the actual and the predicted distribution of each forest subtype was also expressed as a proportion of total number of cells in the surface reference data. A qualitative assessment of each model was performed on the basis of current knowledge and recent historical information.

It should be pointed out that throughout these analyses the maximum expected Jaccard and Dice coefficients were estimated to be around 5–10% and 15–20%, respectively, for the following reason. Given that, if the surface reference data are perfectly represented by the model (i.e. if omissions = 0), and if the total number of cells = n, and the number of cells in common = p, then the number of commissions = n-p and the Jaccard and Dice coefficients are $p/(p+0+n\text{-}p) = p/n$ and $2p/(2p+0+n\text{-}p) = 2p/(n+p)$, respectively. In a detailed study of the Karkloof region of the KwaZulu-Natal midlands, Lawes, Mealin and Piper (submitted) mapped in detail 199 forests. Of these, twelve forests were over 50 ha in size and thus represented by our surface reference data. The total area of these twelve forests was 4619 ha (= n) and the total study area was 62,982.92 ha (= p). Therefore, taking this well studied area as representative of the province, the Jaccard coefficient would be 0.0733 and the Dice coefficient 0.1367.

RESULTS AND DISCUSSION

BIOCLIM-type models and the predicted present-day distribution of forest

The full bioclimatic profile of the forest subtypes is given in Appendices 1 and 2.

Model 1: based on the 25–75 percentile limits of all continuous variables and the majority geology and soil types

Model 1 is a poor predictor of the present-day distribution of forest, with only four forest subtypes predicted to occur (Fig. 2a), and little or no congruence between their actual distribution (as represented by the original forest grid) and that predicted (Table 2). Three forest types (swamp, riverine and lowland) are not predicted at all, and dune forest is barely represented. The very small predicted areas are, however, unsurprising considering that the model selects, for each forest subtype, only the proportion of the area lying simultaneously within the central 50% of each of the seventeen continuous variables (as well as the majority geology and soil types). Assuming independence of variables, this is only 0.5^{17}, or 0.00076%, of the feasible region of each forest subtype (i.e. the area lying within the maximum and minimum values of each variable for that forest subtype). In other words, if the proportion of each variable in the model is r and if there are n variables then r^n of the grid cells will be selected.

Model 1 effectively highlights the core areas of montane, mist belt, scarp and sand forest (Nix, 1986; Busby, 1988, 1991). In the case of sand forest, this suggests that conditions favourable to this specialized forest subtype are more widespread than its actual present-day distribution. Either sand forest has never reached its full potential in the province or, more probably, its area has been drastically reduced in the recent past (Reitz, 1938; King, 1941; Moll, 1978). Interestingly, the core area predicted for sand forest does not overlap with its actual distribution, which lies slightly to the west. A closer examination reveals that a combination of annual temperature range, mean annual precipitation, and mean winter rainfall limits the westward extension of sand forest, suggesting that for all three variables this forest subtype currently exists at or near its absolute limits.

A core area of scarp forest is predicted in the extreme south-east of the province, an area of sandstone outcrops that has long been recognized as important for this forest subtype (Van Wyk, 1989). Core areas of mist belt forest are found in the KwaZulu-Natal midlands, and core areas of montane forest in patches along the foothills of the Drakensberg mountains. Both these predictions typify the present distribution of these forest subtypes (White, 1978; Cooper, 1985). Core areas of the older Afromontane forest subtypes are better defined by the model than are the younger Indian Ocean coastal belt forests. The latter extend down the eastern seaboard of southern Africa, and reach their southernmost limit in KwaZulu-Natal. We suggest that little (or no) core area is predicted for these forest subtypes because they are already existing in the area at their limit under current climatic conditions, and extend into the region under the influence of the warm offshore currents. Any core areas for these forest types, under the conditions of this model, are thus likely to lie to the north of the province.

Model 2: based on the 5–95 percentile limits of all continuous variables and the full variety of geology and soil types

A greater distribution of all forest subtypes was predicted by Model 2, as would be expected given that the proportion of the area lying simultaneously within the central 90% range of seventeen continuous variables (assuming independence of variables) is 0.9^{17}, or 16.68%. The congruence between the predicted and the actual distribution increased in comparison with Model 1 for all but lowland forest, and the coefficients of Jaccard and Dice, increased in six cases (Table 2). Jaccard and Dice coefficients decreased for montane forest due to an increase in the number of commissions. For montane, mist belt, riverine and scarp forest, over 50% of the surface reference data was represented by the predicted distributions.

Model 2 provides a more accurate prediction of the present-day distribution of all forest subtypes than Model 1 (Fig. 2b). However, dune, swamp and lowland forest remain poorly predicted. Forest areas show a naturally fragmented pattern, particularly among the Afromontane forests (Meadows & Linder, 1993). Montane, mist belt, sand, riverine and scarp forest are predicted over a much greater area than these forest subtypes actually occupy at present, indicating that their potential distribution under suitable climatic conditions as represented by this model, is more extensive. Indigenous forest throughout the province is indeed known to have been more widespread in the recent past, prior to anthropogenic influence (Fourcade, 1889; Bews, 1913, 1920; King, 1941; Cooper, 1985), but to quite what extent remains unknown. Furthermore, the surface reference data represents only forests of 50 ha or more, and much of the forest in the province exists in smaller fragments (Cooper, 1985). Local climatic variation at a scale below that of this model will also contribute to the actual pattern seen, and all of these factors may help account for the

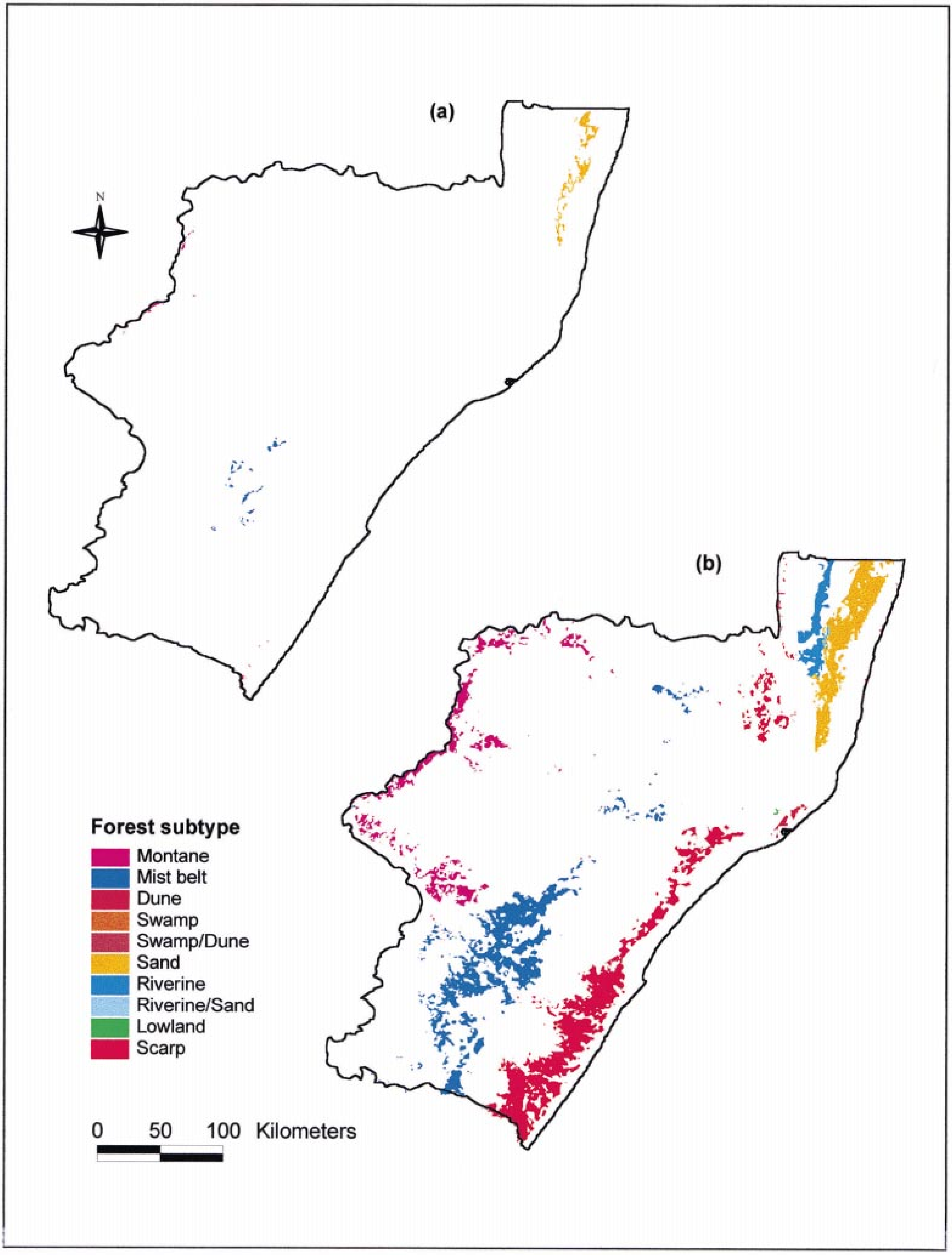

Figure 2 The predicted distribution of indigenous forest in KwaZulu-Natal under (a) Model 1, and (b) Model 2 (see text for model details).

Table 2 Validation of Models 1–5: comparison of predicted distribution of forest subtypes and their present-day distribution as represented by the surface reference data (SRD). SRD, Model, Common[1], Omissions[2] and Commissions[3] are expressed as number of grid cells. The total number of $15' \times 15'$ cells in the province is 500 008. See text for equations for coefficients of Jaccard and Dice.

Forest subtype	SRD	Model	Common	Omissions	Commissions	Jaccard percentage	Dice percentage	Common/SRD percentage
Model 1								
Montane	570	196	28	542	168	3.79	7.31	4.91
Mist belt	3432	486	90	3342	396	2.35	4.59	2.62
Dune	1100	2	2	1098	0	0.18	0.36	0.18
Swamp	117	0	0	117	0	0.00	0.00	0.00
Sand	403	1636	0	403	1636	0.00	0.00	0.00
Riverine	214	0	0	214	0	0.00	0.00	0.00
Lowland	723	0	0	723	0	0.00	0.00	0.00
Scarp	1292	40	27	1265	13	2.07	4.05	2.09
Model 2								
Montane	570	8243	304	266	7939	3.57	6.90	53.33
Mist belt	3432	18613	1960	1472	16653	9.76	17.78	57.11
Dune	1100	438	25	1075	413	1.65	3.25	2.27
Swamp	117	21	1	116	20	0.73	1.45	0.85
Sand	403	10505	34	369	10471	0.31	0.62	8.44
Riverine	214	3779	137	77	3642	3.55	6.86	64.02
Lowland	723	38	0	723	38	0.00	0.00	0.00
Scarp	1292	23176	679	613	22497	2.85	5.55	52.55
Model 3								
Montane	570	12941	377	193	12564	2.87	5.58	66.14
Mist belt	3432	23880	2300	1132	21580	9.20	16.84	67.02
Dune	1100	859	25	1075	834	1.29	2.55	2.27
Swamp	117	1451	72	45	1379	4.81	9.18	61.54
Sand	403	18814	287	116	18527	1.52	2.99	71.22
Riverine	214	4525	164	50	4361	3.58	6.92	76.64
Lowland	723	67	0	723	67	0.00	0.00	0.00
Scarp	1292	24826	716	576	24110	2.82	5.48	55.42
Model 4								
Dune	1100	4391	440	660	3951	8.71	16.03	40.00
Lowland	723	10761	585	138	10176	5.37	10.19	80.91
Model 5								
Montane	570	53379	422	148	52957	0.79	1.56	74.04
Mist belt	3432	42926	2644	788	40282	6.05	11.41	77.04
Dune	1100	6468	850	250	5618	12.65	22.46	77.27
Swamp	117	4374	97	20	4277	2.21	4.32	82.91
Sand	403	21141	334	69	20807	1.57	3.10	82.88
Riverine	214	7743	177	37	7566	2.28	4.45	82.71
Lowland	723	45850	644	79	45206	1.40	2.77	89.07
Scarp	1292	61789	846	446	60943	1.36	2.68	65.48

[1] Common = cells shared by SRD and the model.
[2] Omissions = cells present in the SRD but not predicted by the model.
[3] Commissions = cells predicted by the model but not actually present in the SRD.

high level of commissions and the low overall values of the coefficients of Jaccard and Dice.

PCA analysis and derived models

The seventeen climatic variables were entered in an initial PCA analysis, and the first two principal components were found to account for 91.19% of the variance in the sixty-nine forests. Five variables (median annual rainfall, mean temperature of the coldest quarter, mean temperature of the hottest quarter, mean rainfall of the driest quarter and mean rainfall of the wettest quarter) were removed from the analysis as these were highly correlated with other variables. The PCA was repeated on the remaining twelve variables, with only a slight reduction in the amount of variance accounted for by the first two principal components (89.98%). When plotted against the first two principal components, the forests show a clear clustering into different forest subtypes (Fig. 3a).

Afromontane forests separate from the Indian Ocean coastal belt forests along the first principal component (PC_1), which

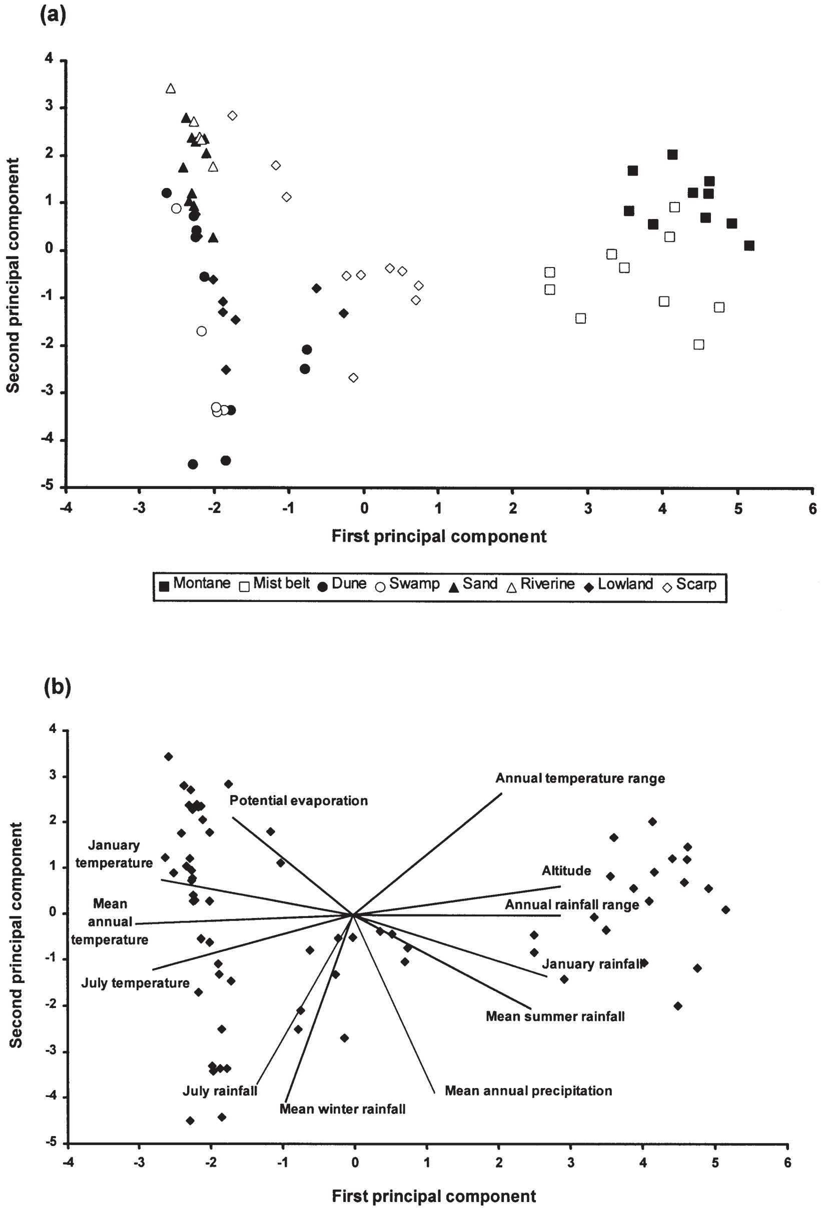

Figure 3 Principal components analysis of twelve climatic variables for sixty-nine individual forests showing (a) the separation of different forest subtypes, and (b) the relationship between climate variables and the first two principal components.

primarily comprises an altitudinal gradient and associated gradients in mean annual temperature and annual range in rainfall (Figs 3b and 4a). Afromontane forests (montane and mist belt) are characterized by high PC_1 scores, indicating high altitude, low temperature and a large difference between summer and winter rainfall, while Indian Ocean coastal belt forests (dune, swamp, sand, riverine and coast lowland) have low PC_1 scores, indicating lower altitude, higher temperatures and a lower annual rainfall range. The scarp forests fall in a belt between the two groups, but towards the coastal belt forests. The second principal component (PC_2) partially separates montane from mist belt forests, and sand and riverine forests from dune, swamp and lowland forests, although the latter three, as well as scarp forests, show a considerable range along this axis. PC_2 comprises four main gradients: potential evaporation, annual temperature range, mean annual precipitation and mean winter rainfall (Fig. 3b). High PC_2 scores indicate high potential evaporation and annual temperature range, and low mean annual precipitation and mean winter rainfall. PC_2 is likely related to both latitude and the distance from the coast (Fig. 4b,c).

That the forest subtypes separate primarily along an altitudinal gradient is unsurprising given that most of the climatic variables described here, and which affect fundamental plant processes, and ultimately growth, reproduction and survival, are a consequence of altitude. The separation of high altitude Afromontane forests from the lowland tropical forests to which the Indian Ocean coastal belt forests owe their affinity

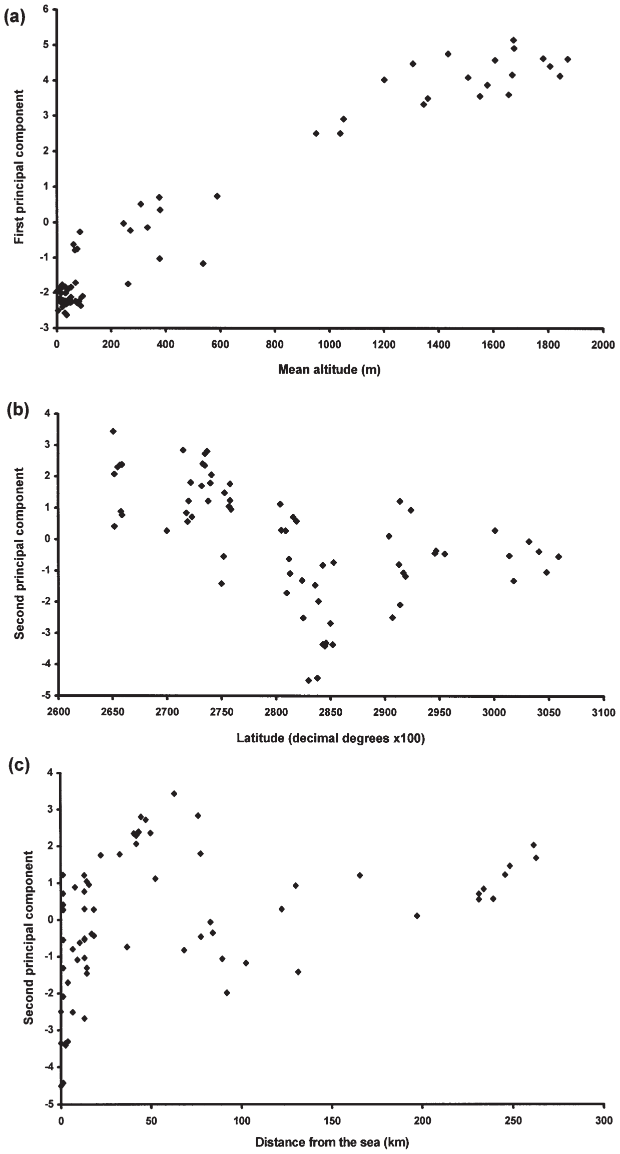

Figure 4 The relationship between (a) the first principal component and altitude (b) the second principal component and latitude, and (c) the second principal component and the distance from the sea.

has long been recognized (e.g. Moll & White, 1978; White, 1978). Along the coast of KwaZulu-Natal the climate is conducive to year round plant growth; rainfall is high, and both temperature and rainfall fluctuate little throughout the year. As altitude increases, oreographic rainfall increases but it is less evenly distributed, falling almost entirely in the summer months. At higher altitudes plants may experience physiological drought as a result of lower temperatures and seasonal water stress. Temperatures also fluctuate, with frequent winter frosts in more exposed areas. Forests of higher altitudes are dominated by *Podocarpus* species and are restricted to the wetter and more shaded south and south-east facing slopes (Low & Rebello, 1996). Scarp forests lie between the two extremes, where climatic conditions may allow for elements of both Afromontane and Indian Ocean coastal belt forests to survive. In the Transkei region, south of KwaZulu-Natal, the distribution of different forest types also appears to be related to rainfall regimes (Cawe, 1994).

Model 3: based on the 5–95 percentile limits of the subset of continuous variables selected as a result of the PCA and the full variety of geology and soil types

Model 3 included seven climatic variables: altitude, mean annual temperature, annual temperature range, mean annual precipitation, mean winter rainfall, annual rainfall range, and annual potential evaporation. The remaining variables were excluded as they did not show a major influence on either PC_1 or PC_2.

The predicted area of all forest subtypes by Model 3 under current climate conditions was greater than that of Model 2 (Fig. 5a, Table 2). Again this is anticipated on the basis that the number of continuous variables in Model 3 was reduced, and the proportion of area lying simultaneously within the central 90% of seven variables is $0.9^7 = 47.82\%$. There was an increase in the congruence between the actual forest distribution and that predicted for six forest subtypes, and for all but dune and lowland forest over 55% of the surface reference data lay within the predicted distribution (Table 2). However, an increase in the number of commissions led to a reduction in the coefficients of Jaccard and Dice in four cases. Model 3 provides a reasonable prediction of montane, mist belt, swamp, sand, riverine and scarp forests with reference to recent historical information (Fourcade, 1889; Bews, 1912, 1913, 1917, 1920; King, 1941). However, given that dune forest currently extends in a belt along the coast from the extreme north of the province to Durban, and that, prior to the conversion of much of this area to sugarcane, lowland forest extended in a relatively continuous band from this dune cordon to the first escarpment inland (Fourcade, 1889; Bews, 1912, 1920; Reitz, 1938; King, 1941; Moll, 1978; Cooper, 1985), these two forest subtypes remain poorly predicted.

Model 4: adjusted for lowland and dune forest

For dune and lowland forest, continuous variables were removed one at a time from Model 3. The predicted distribution of the two forest subtypes was mapped and assessed subjectively on the removal of each variable from the model. The new model was accepted when the predicted distribution of each forest subtype covered the area it is known to actually occupy at present, the only condition being that as many variables as possible were retained in the model. For dune forest Model 4 comprised the 5–95 percentile limits of altitude, annual rainfall range, annual potential evaporation, annual temperature range, mean annual precipitation, and mean winter rainfall. For lowland forest Model 4 comprised the 5–95 percentile limits of altitude, mean annual rainfall, and mean winter rainfall. For both forest subtypes Model 4 also included the full range of geology and soil types. For all other forest subtypes Model 4 remained the same as Model 3.

For both dune and lowland forest there was an increase in the area predicted, in the congruence between the surface

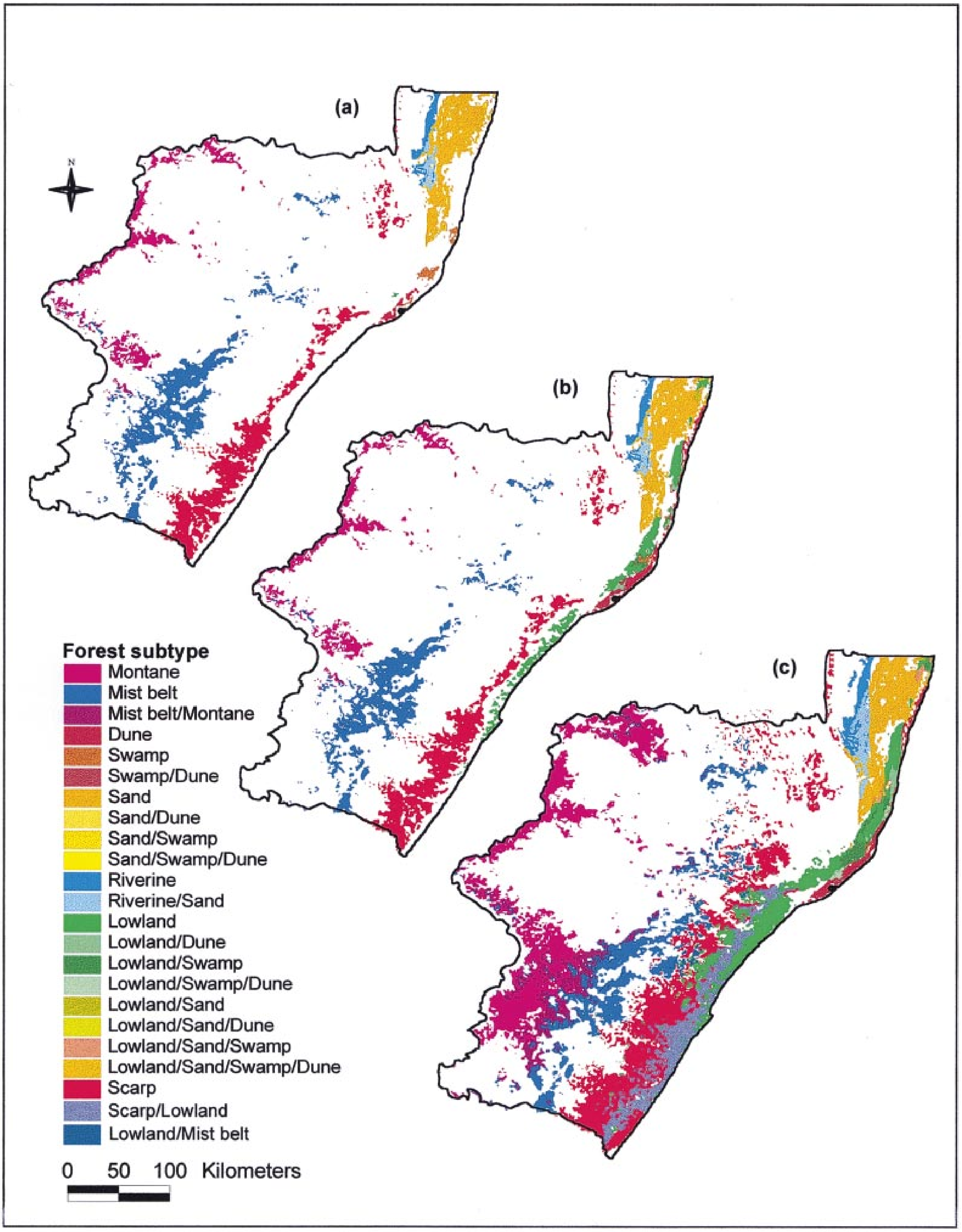

Figure 5 The predicted distribution of indigenous forest in KwaZulu-Natal under (a) Model 3 (b) Model 4, and (c) Model 5 (see text for model details).

reference data and the predicted distribution, and in the coefficients of Jaccard and Dice under Model 4 (Table 2). In our opinion Model 4 provides the best prediction of the distribution of forest subtypes in the province (Fig. 5b).

Model 5: to predict forest distribution under climate change
A number of changes were made to Model 4 in order to assess the potential distribution of forest under scenarios of past and future climate change. First, altitude was removed from the model to allow for altitudinal flexibility in response to climate change. Second, as potential evaporation is a complex variable difficult to estimate under palaeoclimatic and future climatic scenarios this too was removed. Geology and soil were removed from the model for those forest subtypes that occupied a variety of different substrate types; montane, mist belt, lowland and scarp forest (Appendices 1 and 2), as these variables will also restrict the potential movement of forest in response to climate change. However, geology and soil were retained in the model for dune, swamp, sand and riverine forest, which are more tightly constrained by their substrate.

Under Model 5 there was a considerable increase in both the area of each forest subtype predicted under current climate conditions and the degree of overlap between different forest subtypes (Fig. 5c). The congruence between the predicted and the actual distribution increased in all cases, with between 65 and 90% of the surface reference data being represented (Table 2). However, as a consequence of an increase also in the number commissions, the coefficients of Jaccard and Dice decreased for all but dune and sand forest. While we recognize that Model 5 is not as good a predictor of the present-day pattern of forest distribution as Model 4, we are constrained by the above considerations to use this model to predict past and future forest distribution.

Climate change and forest distribution

The application of the model
Forest distribution was modelled under two palaeoclimatic scenarios: the LGM (≈18,000 BP), which represents the most extreme conditions the forest biome has experienced in KwaZulu-Natal, and the Holocene altithermal (≈7000 BP), representing a period of warmer and wetter conditions than at present, and which may also be used (imperfectly) as a simulation of conditions under future global warming (Partridge *et al*., 1990; T. Partridge, pers. comm.). While there have been several good reviews of palaeoclimatic change in southern Africa, obtaining specific values to input the model proved difficult. The scenarios adopted were chosen as the best estimates available at this time, based on recent reviews (Partridge, 1997; T. Partridge, pers. comm.). The grids of present climate were adjusted according to these scenarios (Table 3), and Model 5 was run on the adjusted grids.

The United Kingdom Meteorological Office (UKMO) model of projected climate change with a doubling in atmospheric greenhouse gasses was adopted as this provides an appropriate model for Africa south of the equator (Tyson, 1990). These data exist in 3.75° grid format and comprise by month the average, minimum and maximum temperatures, and daily precipitation. The five land-based grid points lying within and around KwaZulu-Natal were selected, and the following variables calculated both for the present-day and for the future.

1. Mean annual temperature: the mean of the average monthly temperature for each month (approximated as mid-point of minimum and maximum values).
2. Annual temperature range: maximum January temperature – minimum July temperature.
3. Mean annual precipitation: the sum of monthly precipitation (from the daily average per month).
4. Mean winter rainfall: average monthly precipitation April to September.
5. Annual rainfall range: January precipitation – July precipitation.

The difference between the present and future values was determined, and for each variable the median of the five points was selected. The variable grids of present climate were then scaled up or down by this difference (Table 3), and Model 5 run on the adjusted grids.

Palaeoclimatic change and forest distribution
The distribution of indigenous forest in KwaZulu-Natal shows a much reduced area and highly fragmented pattern at the height of the LGM (Fig. 6a). Montane and mist belt forests both show an altitudinal shift in response to the general lowering of temperature and reduction in precipitation, and are found in areas occupied at present primarily by mist belt or scarp forest. The large degree of overlap in their distribution highlights the essential similarity and shared evolutionary history of the Afromontane forests, as well as the Afromontane origin of the present-day scarp forests. Areas of potential importance for forest at this time include the plateau region at present occupied by the Ngome forest, the highland region that parallels the Tugela River and is now home to an archipelago of forests including Dhlinza, Nkandhla and Qudeni.

There is a considerable expansion in the area of forest predicted under the climatic conditions of the Holocene altithermal (Fig. 6b). Afromontane forests extend through the midlands of KwaZulu-Natal and along the Drakensberg mountains, and there is again a fairly high level of overlap between the montane and mist belt forest subtypes. Conditions suitable for Indian Ocean coastal belt forests extend all along the coast, with large areas occupied by lowland and dune forest. Scarp forests occupy a belt between the two main forest types, with both mist belt and lowland forest subtypes interdigitating. Under the climatic conditions modelled during the Holocene altithermal, there is thus the potential for a mixing of Afromontane and Indian Ocean coastal belt forest subtypes along the scarp forest belt. This may explain, at least in part, the relatively high species diversity of modern scarp forests such as Ongoye (Geldenhuys, 1989; MacDevette *et al*., 1989; Oatley, 1989; Lawes, 1990), and the presence within these forests of both Afromontane and Indian Ocean coastal belt elements.

The changing pattern of forest distribution in response to

Table 3 Alterations made to current climate grids under scenarios of past and future climate change.

Variable	18,000 BP*	7000 BP*	Double atmospheric CO_2†
Mean annual temperature	Present −5.5 °C	Present +2 °C	Present +2.99 °C
Annual temperature range	(Jan tmp. −5 °C)–(July tmp. −6 °C)	Same as present	Present +0.28 °C
Mean annual precipitation	70% of present	Present +7.5%	Present −3.83 mm
Mean winter rainfall	70% of present	Present +7.5%	Present +0.60 mm
Annual rainfall range	Same as present	Same as present	Present −26.97 mm

* Based on Partridge (1997) and T. Partridge personal communication.
† Based on the United Kingdom Meteorological Office model for projected climate change.

palaeoclimatic change illustrates the underlying dynamism of vegetation communities. The changes in KwaZulu-Natal reflect those throughout tropical Africa, where the extent of forest has expanded and contracted in response to the changing environmental conditions associated with glacial and interglacial cycles (for example, Van Zinderen Bakker, 1978, 1982; Hamilton, 1976, 1981; White, 1981; Hamilton & Taylor, 1991; Maley, 1991; Taylor & Hamilton, 1994). More locally, palaeobiological evidence reviewed by Deacon & Lancaster (1988) indicates a reduction in forest area in both southern and north-eastern South Africa during the LGM and a re-expansion in the more recent Holocene. Palynological evidence from Wonderkrater in the Northern Transvaal, for example, shows a decline in the proportion of arboreal pollen between 35,000 BP and 20,000–16,000 BP. From a landscape dominated by grassland and montane *Podocarpus* forest, forests became increasingly restricted and were replaced during the LGM by open grassland and ericaceous vegetation. This gave way to a Kalahari-type savanna, and restricted montane forest reappeared around 4000–2000 BP with the return to subhumid conditions (Scott, 1982, 1984; Deacon & Lancaster, 1988). Micromammalian fossils from Border Cave in the Lebombo mountains of northern KwaZulu-Natal also indicate a reduction in forest and an increase in open grassland from around 30,000–13,000 BP (Avery, in Deacon & Lancaster, 1988), while pollen from the Port Durnford region in coastal KwaZulu-Natal indicates a succession from open marshland to *Podocarpus* dominated forest during the LGM (Oschadleus *et al*., 1996) supporting a decrease in altitude among forests at this time.

Predicted future distribution of forest

A greater area of forest is predicted under future projected climatic conditions than exists at present (Fig. 7). The extent of cover is, however, similar both to that predicted under modern climatic conditions by Model 4 and that predicted under the climatic conditions of the Holocene altithermal, although the pattern of distribution of the different forest subtypes differs. Afromontane forests show an overall reduction in area, increased fragmentation and an increase in altitude. Scarp forests also show an increase in altitude, along with a northward expansion, and occupy a position similar to that predicted during the Holocene altithermal although in the south-east of the province the pattern is more fragmented than during the latter period. Lowland forest extends the full length of the coastal belt, again occupying a position similar to that during the Holocene altithermal. In contrast, the area of dune forest predicted is much reduced, and sand, swamp and riverine forests are absent.

To date there has been little study of the potential impact of global warming on the distribution of natural vegetation in South Africa. Using the BIOME model (Prentice *et al*., 1992), Hulme (1996) predicts an increase in both seasonal and dry forest biomes in southern Africa under increased temperatures and 'wet', 'dry' and 'core' (intermediate) scenarios of changing precipitation, and an increase in tropical forest under 'wet' scenarios, all three forest types being recognized at present in KwaZulu-Natal. In South Africa, CSIR (1993) explored the potential impact of future climate change on plantation forestry in the country. Their findings depend on the timber species considered, however most show an increase in optimum growing area with increased temperature provided there is a concomitant increase in rainfall. In a review of the impact of climate change on tropical forests in Africa, Taylor & Hamilton (1994) also stress the importance of changes in precipitation patterns, and that the response of forest to global climate change will be difficult to predict until these are better known. They suggest that forests may shift in altitude in response to temperature increases, as they have in the past, but that potential increasing aridity may mean that the pattern observed has no historical analogue.

Conservation implications

1. With the potential migration of Afromontane forests to higher latitudes, the forests of the southern Drakensberg mountains and KwaZulu-Natal midlands could provide an important refuge in the future.
2. The scarp forests have a high biodiversity and contain a unique mixture of Afromontane and Indian Ocean coastal belt elements. These, in particular Ongoye forest, and the more northerly mist belt forests (Ngome, Nkandhla, and Qudeni), have provided important refuges in the past, and remain foci for forest into the future; their protection should be given a high priority (see also Lawes, 1990).
3. Large areas remain climatically suitable for lowland forest along the coast, but this forest subtype remains a cause of

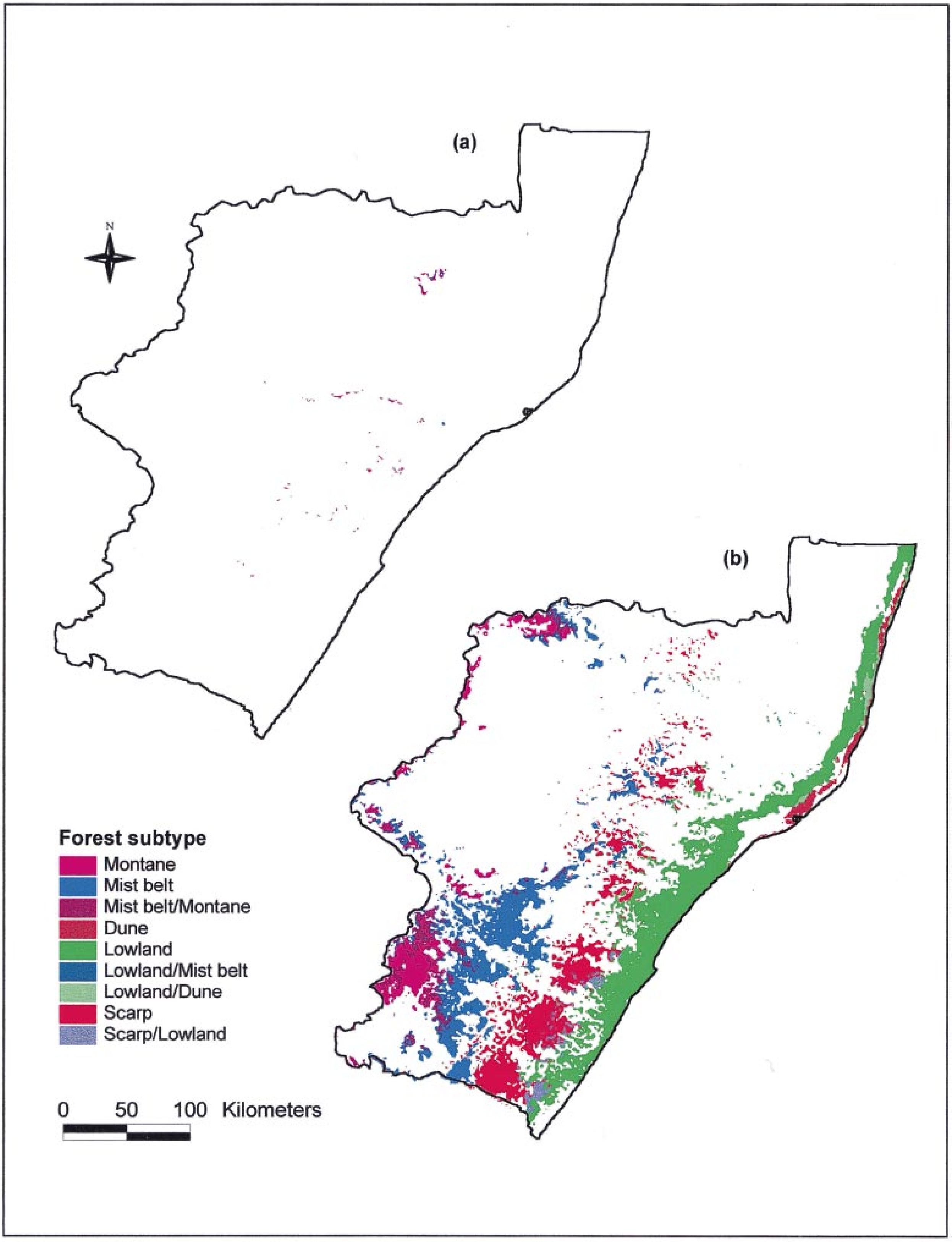

Figure 6 The predicted distribution of indigenous forest in KwaZulu-Natal under (a) the climatic conditions of the Last Glacial Maximum (LGM) ($\approx$18,000 BP), and (b) the climatic conditions of the Holocene altithermal ($\approx$7000 BP).

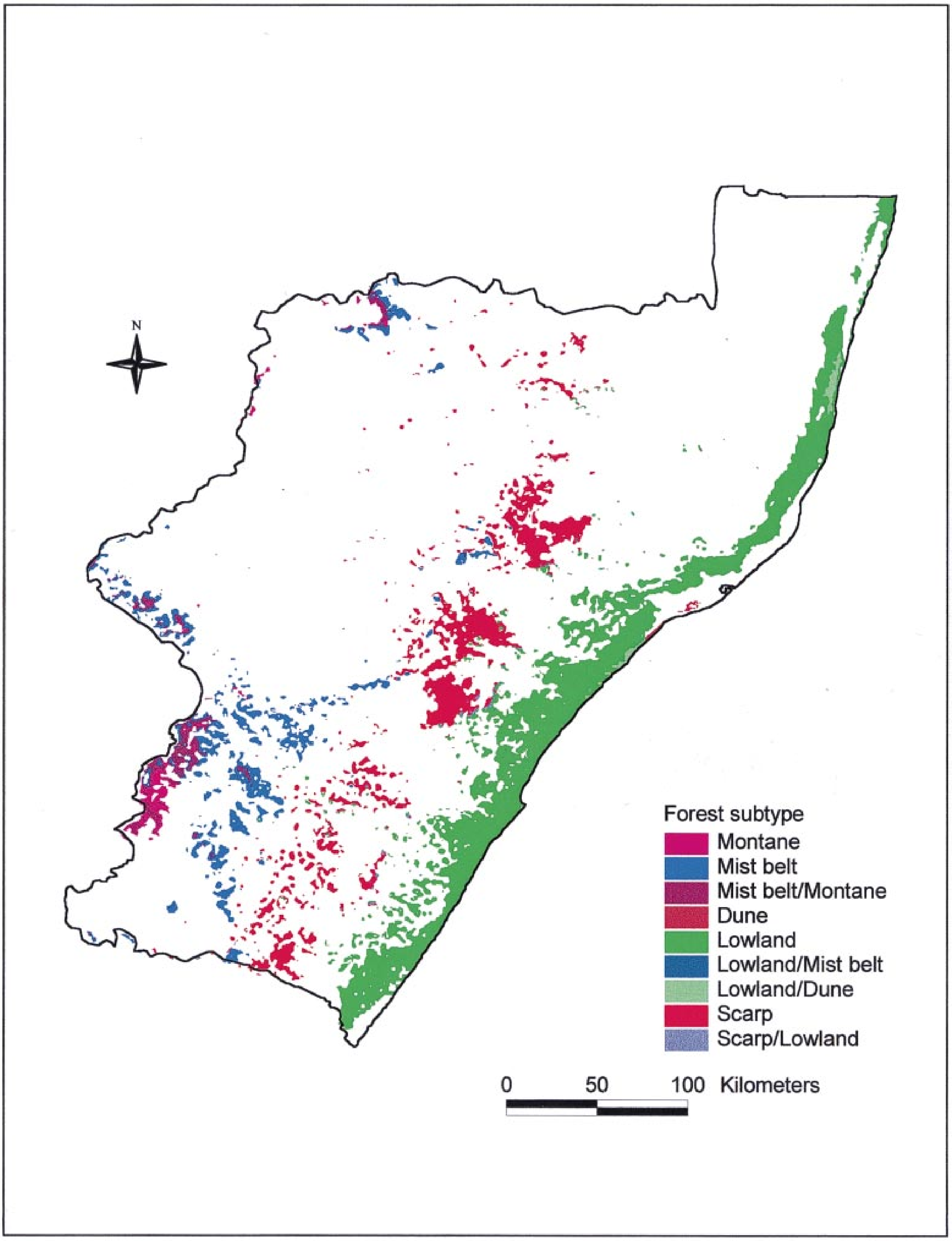

Figure 7 The predicted distribution of indigenous forest in KwaZulu-Natal under the United Kingdom Meteorological Office projected climatic conditions associated with a doubling of atmospheric carbon dioxide.

concern because insufficient area is currently protected (most has already been converted to sugar cane production).

4. In comparison to other forest subtypes, dune, sand, riverine and swamp forest are more tightly constrained by their substrate. The potential of these forests to respond to climate change by migration is therefore limited, and their survival in the province more doubtful.
5. With regard to forest conservation in tropical Africa Taylor & Hamilton (1994) stress the importance both of protected areas in climatically relatively stable areas, and of the need for protected areas to be of adequate area to span substantial climatic (temperature/rainfall) gradients, and to be linked by corridors of natural/seminatural habitat. These recommendations apply equally at the regional level to KwaZulu-Natal. Altitudinal shifts are seen in most of the forest subtypes, and reserves that take in a wide altitudinal range should be considered. The flexibility of forest is the key, and strategies for the management of matrix may be increasingly important. In KwaZulu-Natal, we would stress in this regard the consideration of longitudinal corridors, as forest types are primarily aligned along this axis.

However, a number of additional factors should be considered. First, although migration is the primary response to climatic change, and the distribution of forest has shown considerable geographical movement in the past, the rapidity and direction of projected future climate change is unprecedented at least since the Pleistocene (Huntley, 1995). Maximum rates of migration by species in response to past environmental change have been in the region of 10^2–10^3 m per year (Huntley, 1995), and it remains questionable whether forests have the potential to respond quickly enough to future change (Graham *et al*., 1990; Taylor & Hamilton, 1994; Huntley, 1995). Second, the extent of anthropogenic pressure on forest ecosystems and the way in which the potential migration of forest may be restricted, will be of fundamental importance (Graham *et al*., 1990; Taylor & Hamilton, 1994). The human population of KwaZulu-Natal has expanded dramatically in the last 100–200 years, and the land converted to agriculture and forestry. With such areas acting as barriers to the potential future movement of species, effective conservation will need to give more consideration to the matrix within which natural vegetation is to be preserved. Furthermore, KwaZulu-Natal has a rural population of approximately five million (Human Sciences Research Council, Durban) and, with a current population growth of 2.5% for the province as a whole (1991–93, Bureau of Market Research, Durban), the integration of forest conservation with community development is an important consideration (Dale & Rauscher, 1994; Hulme, 1996). Third, the distribution of commercial forestry at present closely mirrors that of indigenous forest. Areas which show increasing importance for indigenous forest are likely also to become the focus of commercial forestry in the region. It is all the more important therefore that flexible conservation strategies are developed for the conservation of forest into the future.

CONCLUDING REMARKS

The biogeographical history and present-day physical diversity of the province has, we believe, played a major a role in the evolution and persistence of the diversity of forest types in KwaZulu-Natal. Different forest types in KwaZulu-Natal can be delimited by a few physiologically important climatic controls; altitude, mean annual temperature, annual temperature range, mean annual precipitation, mean winter rainfall, annual rainfall range, and annual potential evaporation. The distribution of forest in the province has shown large-scale migrations under palaeoclimatic change, and may respond similarly to future climate change.

It is important that we begin to adopt a long-term and regional perspective to forest ecology, biogeography and conservation. It is clear that forest ecosystems are spatially and temporally dynamic and that they respond relatively rapidly to climatic change. Some areas and forest types may be more resilient under different regimes of change, and may be important both in the past and in the future as refugia and evolutionary centres (Lawes, 1990). Understanding how forest distribution is governed in the present, how it has changed in the past, and how it may change in the future, will enable us to make more enlightened management decisions and to develop flexible conservation strategies to accommodate the fluctuating pattern of indigenous forest distribution, to protect this biome and the biodiversity it comprises.

ACKNOWLEDGMENTS

We thank Roland Schulze, The Computer Centre for Water Research (CCWR), University of Natal, Pietermaritzburg, Richard Kunz and Bruce Hewitson for present-day climatological and physical data, and UKMO projected future climates for KwaZulu-Natal, and Tim Partridge and A. S. Talma for discussion on palaeoclimates, as well as two anonymous reviewers. The staff of CCWR, especially Brad Howe, provided support with ArcInfo GIS. During this research, H.A.C.E. was funded by the Foundation for Research Development, South Africa, and the Phyllis and Eileen Gibbs Travelling Research Fellowship, Newnham College, Cambridge.

REFERENCES

Arc/Info. (1996) *Cell-based modelling with GRID*. Environmental Systems Research Institute, Inc., Redlands, U.S.A.

Bews, J. W. (1912) The vegetation of Natal. *Ann. Natal Mus*, **2,** 253–331.

Bews, J. W. (1913) An oecological survey of the Midlands of Natal, with special reference to the Pietermaritzburg district. *Ann. Natal Mus*, **2,** 485–543.

Bews, J. W. (1917) The plant ecology of the Drakensberg range. *Ann. Natal Mus*, **3,** 511–565.

Bews, J. W. (1920) Plant ecology of the coast belt of Natal. *Ann. Natal Mus*, **4,** 367–470.

Bond, W. J. (1997) Fire. *Vegetation of southern Africa* (ed. by R. M. Cowling, D. M. Richardson and S. M. Pierce), pp. 421–446. Cambridge University Press, Cambridge.

Box, E. O. (1981) *Macroclimate and plant forms: an introduction to predictive modelling in phytogeography*, 258 pp. Junk, The Hague.

Busby, J. R. (1986) A biogeoclimatic analysis of *Northofagus cunninghamii* (Hook.) Oerst. in southeastern Australia. *Aust. J. Ecol*, **11,** 1–7.

Busby, J. R. (1988) Potential impacts of climate change on Australia's flora and fauna. *Greenhouse: planning for climate change* (ed. by G. I. Pearman), pp. 387–398. CSIRO, Melbourne.
Busby, J. R. (1991) BIOCLIM: A bioclimatic analysis and prediction system. *Nature conservation: cost effective biological surveys and data analysis* (ed. by C. R. Margules and M. P. Austin), pp. 64–68. CSIRO, Australia.
Carpenter, G., Gillison, A. N. & Winter J. (1993) DOMAIN: a flexible modelling procedure for mapping potential distributions of plants and animals. *Biodiv. Conserv*, **2,** 667–680.
Cawe, S. G. (1994) Rainfall and vegetation patterns in Transkei and environs. *S. Afr. J. Sci*, **90,** 79–85.
Cooper, K. H. (1985) *The conservation status of indigenous forests in Transvaal, Natal and O.F.S., South Africa*, 108 pp. Wildlife Society of South Africa, Durban.
Cooper, K. H. & Swart, W. (1992) *Transkei Forest Survey*, 96 pp. Wildlife Society of South Africa, Durban.
CSIR. (1993) *The effect of global change on forestry in South Africa*, 26 pp. CSIR, Pretoria.
CSIR. (1995) *Update of National forestry coverage map*, 14 pp. CSIR, Pretoria.
Dale, V. H. & Rauscher, H. M. (1994) Assessing impacts of climate change on forests: the state of biological modelling. *Clim. Change* **28,** 65–90.
Deacon, H. J. (1983) Another look at the Pleistocene climates of South Africa. *S. Afr. J. Sci*, **79,** 325–328.
Deacon, J. & Lancaster, N. (1988) *Late Quaternary palaeoenvironments of southern Africa*, 225 pp. Clarendon Press, Oxford.
Deacon, J., Lancaster, N. & Scott L. (1984) Evidence for Late Quaternary climatic change in southern Africa: summary of the proceedings of the SASQUA workshop held in Johannesburg, September 1983. *Late Cainozoic palaeoclimates of the southern Hemisphere* (ed. by J. C. Vogel), pp. 391–404. Balkema, Rotterdam.
Dent, M. C., Lynch, S. D. & Schulze R. E. (1989) *Mapping mean annual and other rainfall statistics over southern Africa*, 230 pp. WRC Report 109/1/89. Water Research Council, Pretoria.
Edwards, D. (1967) A plant ecological survey of the Tugela River Basin. *Mem. Bot. Surv. S. Afr*, **36,** 1–285.
Fourcade, H. G. (1889) *Report on the Natal forests*, 197 pp. W. Watson, Pietermaritzburg.
Gates, D. M. (1993) *Climate change and its biological consequences*, 280 pp. Sinauer Associates, Inc., Sunderland.
Geldenhuys, C. J. ed. (1989) *Biogeography of the mixed evergreen forests of southern Africa*. Ecosystems Programmes Occasional Report no. 45. FRD, Pretoria.
Geldenhuys, C. J. (1994) Bergwind fires and the location of forest patches in the southern Cape landscape, South Africa. *J. Biogeogr*, **21,** 49–62.
Geldenhuys, C. J. & MacDevette, D. R. (1989) Conservation status of coastal and montane evergreen forest. *Biotic diversity in southern Africa: concepts and conservation* (ed. by B. J. Huntley), pp. 224–238. Oxford University Press, Cape Town.
Graham, R. L., Turner, M. G. & Dale V. H. (1990) How increasing CO_2 and climate change affect forests. *Bioscience*, **40,** 575–587.
Grainger, J. E. de (1984) Fire in forest. *Ecological effects of fire in South African ecosystems* (ed. by P. V. Booysen and N. M. Tainton), pp. 177–197. Springer-Verlag, Berlin.
Hamilton, A. C. (1976) The significance of patterns of distribution shown by forest plants and animals in tropical Africa for the reconstruction of upper Pleistocene palaeoenvironments, a review. *Palaeoecol. Afr*, **9,** 63–97.
Hamilton, A. C. (1981) The Quaternary history of African forests: its relevance to conservation. *Afr. J. Ecol*, **19,** 1–6.
Hamilton, A. C. & Taylor, D. (1991) History of climate and forests in tropical Africa during the last 8 million years. *Clim. Change*, **19,** 65–78.
Harrison, S. P. & Foley, J. A. (1995) General circulation models, climate change and ecological impact studies. *Impacts of climate change on ecosystems and species: environmental context* (ed. by J. C. Pernetta, R. Leemans, D. Endler and S. Humphrey), pp. 9–25. IUCN, Gland.
Heaton, T. H. E., Talma, A. S. & Vogel J. C. (1986) Dissolved gas palaeotemperatures and ^{18}O variations derived from groundwater near Uitenhage, South Africa. *Quat. Res*, **25,** 79–88.
Hengeveld, R. (1995) Species response to climate change. *Impacts of climate change on ecosystems and species: environmental context* (ed. by J. C. Pernetta, R. Leemans, D. Endler and S. Humphrey), pp. 27–42. IUCN, Gland.
Hill, R. S., Read, J. & Busby J. R. (1988) The temperature-dependence of photosynthesis of some Australian temperate rainforest trees and its biogeographical significance. *J. Biogeogr*, **15,** 431–449.
Hulme, M., (ed.) (1996) *Climate change and southern Africa: an exploration of some potential impacts and implications in the SADC region*. Climatic Research Unit, University of East Anglia, Norwich.
Hulme, M., Conway, D., Kelly, P. M., Subak, S. & Down, T. E. (1995) *The impacts of climate change on Africa*, 46 pp. Stockholm Environment Institute, Stockholm.
Huntley, B. J. (1984) Characteristics of South African biomes. *Ecological effects of fires in South African ecosystems* (ed. by P. V. Boosen and N. M. Tainton), pp. 1–17. Springer-Verlag, Berlin.
Huntley, B. J. (1995) How vegetation responds to climate change: evidence from palaeovegetation studies. *Impacts of climate change on ecosystems and species: environmental context* (ed. by J. C. Pernetta, R. Leemans, D. Endler and S. Humphrey), pp. 43–63. IUCN, Gland.
IPCC. (1991) *Climate change. The IPCC response strategies*, 272 pp. Island Press, Washington, D.C.
IPCC. (1996) *Climate change 1995. The science of climate change,* 572 pp. Cambridge University Press, Cambridge.
Joubert, A. M. & Hewitson, B. C. (1997) Simulating present and future climates of southern Africa using general circulation models. *Prog. Phys. Geogr*, **21,** 51–78.
King, N. L. (1941) The exploitation of the indigenous forests of South Africa. *Jl S. Afr. For. Ass*, **6,** 26–48.
King, L. (1978) A geomorphology of central and southern Africa. *Biogeography and ecology of southern Africa. Monographiae Biologicae 31* (ed. by M. J. A. Werger), pp. 1–17. Junk, The Hague.
Lawes, M. J. (1990) The distribution of the samango monkey (*Cercopithecus mitis erythrarchus* Peters, 1852 and *Cercopithecus mitis labiatus* I. Geoffroy, 1843) and forest history in southern Africa. *J. Biogeogr*, **17,** 669–680.
Lawes, M. J., Mealin, P. E. & Piper, S. E. (submitted) Patch occupancy and potential metapopulation dynamics of three rare forest mammals in fragmented Afromontane mist-belt *Podocarpus* forest in South Africa. *Conserv. Biol.*
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.
Low, A. B. & Rebelo, A. G. (eds) (1996) *Vegetation of South Africa, Lesotho and Swaziland*, 84 pp. Department of Environmental Affairs and Tourism, Pretoria.
MacDevette, D. R., MacDevette, D. K., Gordon, I. G. & Bartholomew, R. L. C. (1989) Floristics of the Natal indigenous forests. *Biogeography of the mixed evergreen forests of southern Africa* (ed. by C. J. Geldenhuys), pp. 124–145. Ecosystems Programmes Occasional Report no. 45. FRD, Pretoria.

Maley, J. (1991) The African rain forest vegetation and palaeoenvironments during the late Quaternary. *Clim. Change*, **19**, 79–98.

Meadows, M. E. & Linder, H. P. (1993) A palaeoecological perspective on the origin of Afromontane grasslands. *J. Biogeogr*, **20**, 345–355.

Midgley, J. J., Cowling, R. M. & Seydack A. H. W. (1997) Forest. *Vegetation of southern Africa* (ed. by R. M. Cowling, D. M. Richardson and S. M. Pierce), pp. 278–299. Cambridge University Press, Cambridge.

Moll, E. J. (1978) The vegetation of Maputaland. A preliminary report of the plant communities and their present and future conservation status. *Trees S. Afr*, **29**, 31–58.

Moll, E. J. & White, F. (1978) The Indian Ocean coastal belt. *Biogeography and ecology of southern Africa. Monographiae Biologicae 31* (ed. by M. J. A. Werger), pp. 561–598. Junk, The Hague.

Moreau, R. E. (1963) Vicissitudes of the African biomes in the late Pleistocene. *Proc. Zool. Soc. Lond*, **141**, 395–421.

Nix, H. (1986) A biogeographic analysis of Australian elapid snakes. *Snakes. Atlas of elapid snakes of Australia* (ed. by R. Longmore), pp. 4–15. Bureau of Flora and Fauna, Canberra.

Oatley, T. B. (1989) Biogeography of the forest avifauna in South Africa. *Biogeography of the mixed evergreen forests of southern Africa*, (ed. by C. J. Geldenhuys), pp. 48–59. Ecosystems Programmes Occasional Report no. 45. FRD, Pretoria.

Oschadleus, H. D., Vogel, J. C. & Scott L. (1996) Radiometric date for the Port Durnford peat and development of yellow-wood forest along the South African east coast. *S. Afr. J. Sci*, **92**, 43–45.

Partridge, T. C. (1997) Cainozoic environmental change in southern Africa, with special reference on the last 200,000 years. *Prog. Phys. Geogr*, **21**, 3–22.

Partridge, T. C., Avery, D. M., Botha, G. A., Brink, J. S., Deacon, J., Herbert, R. S., Maud, R. R., Scholtz, A., Scott, L., Talma, A. S. & Vogel, J. C. (1990) Late Pleistocene and Holocene climatic change in southern Africa. *S. Afr. J. Sci*, **86**, 302–306.

du Pisani, A. L. & Partridge, T. C. (1990) Effects of global warming on crop production in South Africa. *S. Afr. J. Sci*, **86**, 306–311.

Prell, W. L., Hutson, W. H., Williams, D. F., Bé, A. W. H., Geitzenauer, K. & Molfino, B. (1980) Surface circulation of the Indian Ocean during the last glacial maximum, approximately 18,000 yr. B.P. *Quat. Res*, **14**, 309–336.

Prentice, I. C. (1992) Climate change and long-term vegetation dynamics. *Plant succession: theory and prediction* (ed. by D. C. Glenn-Lewin, R. K. Peet and T. T. Veblen), pp. 293–339. Chapman & Hall, London.

Prentice, I. C., Cramer, W., Harrison, S. P., Leeman, R., Monserud, R. A. & Soloman, A. M. (1992) A global biome model based on plant physiology and dominance, soil properties and climate. *J. Biogeogr*, **19**, 117–134.

Reitz, D. (1938) The forests of northern Zululand. *Jl. S. Afr. For. Ass*, **1**, 28–29.

Rutherford, M. C. & Westfall, R. H. (1994) Biomes of Southern Africa: an objective categorization. *Mem. Bot. Surv. S. Afr*, **63**, 1–94.

Schulze, R. E. (1982) *Agrohydrology and climatology of Natal*, 136 pp. Water Research Commission, Pretoria.

Schulze, R. E. (1997) *South African atlas of agrohydrology and climatology*, 276 pp. Water Research Commission, Pretoria.

Schulze, R. E. & McGee, O. S. (1978) Climatic indices and classifications in relation to the biogeography of southern Africa. *Biogeography and ecology of southern Africa. Monographiae Biologicae 31* (ed. by M. J. A. Werger), pp. 19–52. Junk, The Hague.

Scott, L. (1982) Pollen analysis of late Cainozoic deposits in the Transvaal, South Africa, and their bearing on palaeoenvironments. *Palaeoecology, 15*, 101–107.

Scott, L. (1984) Palynological evidence for Quaternary palaeoenvironments in southern Africa. *Southern African prehistory and palaeoenvironments* (ed. by R. G. Klein), pp. 65–80. Balkema, Rotterdam.

Sokal, R. R. & Sneath, P. H. (1963) *Principals of numerical taxonomy*, 359 pp. W.H. Freeman, San Francisco.

Stute, M. & Talma, A. S. 1997) Glacial temperatures and moisture transport regimes reconstructed from noble gases and ^{18}O, Stampriet aquifer, Namibia. *Proceedings of International Symposium on Isotope Techniques in the Study of Past and Current Environmental Changes in the Hydrosphere and the Atmosphere*, International Atomic Energy Agency, Vienna.

Talma, A. S. & Vogel, J. C. (1992) Late Quaternary palaeotemperatures derived from a speleotherm from Cango Caves, Cape Province, South Africa. *Quat. Res*, **37**, 203–213.

Taylor, D. & Hamilton, A. (1994) Impact of climate change on tropical forests in Africa: implications for protected area planning and management. *Impacts of climate change on ecosystems and species: implications for protected areas* (ed. by J. C. Pernetta, R. Leemans, D. Endler and S. Humphrey), pp. 77–94. IUCN, Gland.

Tyson, P. D. (1986) *Climatic change and variability in southern Africa*, 220 pp. Oxford University Press, Cape Town.

Tyson, P. D. (1990) Modelling climatic change in southern Africa: a review of available methods. *S. Afr. J. Sci*, **86**, 318–330.

Van Wyk, A. E. (1989) Floristics of the Natal/Pondoland sandstone forests. *Biogeography of the mixed evergreen forests of southern Africa* (ed. by C. J. Geldenhuys), pp. 145–157. Ecosystems Programmes Occasional Report no. 45. FRD, Pretoria.

Van Zinderen Bakker, E. M. (1978) Quaternary vegetation changes in southern Africa. *Biogeography and ecology of southern Africa. Monographiae Biologicae 31* (ed. by M. J. A. Werger). Junk, The Hague.

Van Zinderen Bakker, E. M. (1982) African Palaeoenvironments 18,000 yrs BP. *Palaeoecol. Afr*, **15**, 77–99.

Walker, P. A. & Cocks, K. D. (1991) HABITAT: a procedure for modelling a disjoint environmental envelope for a plant or animal species. *Global Ecol. Biogeogr. Letts*, **1**, 108–118.

White, F. (1978) The Afromontane region. *Biogeography and ecology of southern Africa. Monographiae Biologicae 31* (ed. by M. J. A. Werger), pp. 463–560. Junk, The Hague.

White, F. (1981) The history of the Afromontane archipelago and the scientific need for its conservation. *Afr. J. Ecol*, **19**, 33–54.

Woodward, F. I. (1987) *Climate and plant distribution*, 174 pp. Cambridge University Press, Cambridge.

Woodward, F. I. & Williams, B. G. (1987) Climate and plant distribution at global and local scales. *Vegetatio*, **69**, 189–197.

van der Zel, D. W. (1988) *A forest map of southern Africa with the aid of LANDSAT imagery*, 78 pp. CSIR, Pretoria.

BIOSKETCHES

Harriet Eeley is a postdoctoral researcher with the Forest Biodiversity Programme. Prior to this she worked at the Natural History Museum, London, on the UNEP Global Biodiversity Assessment. Research interests include landscape ecology, forest biodiversity, and macroecology.

Michael Lawes is the founder and director of the Forest Biodiversity Programme and an associate professor at the School of Botany and Zoology, University of Natal, Pietermaritzburg. For 10 years he has been researching forest ecology and the behavioural ecology of *Cercopithecus* monkeys and Ploceiid birds in KwaZulu-Natal. Current research interests include forest biodiversity, community and population ecology, conservation, primatology and behavioural ecology.

Professor Steven Piper is an engineer, statistician and mathematician by training, with an interest in the application of mathematical methods (e.g. GIS and remote sensing) to problems in natural history. He has studied the Cape griffon (vulture) and the long tailed wagtail for over 20 years.

Appendix 1. The bioclimatic profiles of the indigenous forest subtypes of KwaZulu-Natal province, South Africa

Forest subtype	Altitude										January maximum temperature										July minimum temperature									
	Min	5%	25%	75%	95%	Max	Mean	Median	SD	CV	Min	5%	25%	75%	95%	Max	Mean	Median	SD	CV	Min	5%	25%	75%	95%	Max	Mean	Median	SD	CV
Montane	1229	1443	1583	1795	1949	2216	1691.241	1695	163.868	9.69	22.386	23	24	26	27	29.001	25.325	25	1.376	5.43	-0.312	1	1	3	5	6.932	2.263	2	1.384	61.16
Mist belt	538	900	1172	1473	1653	1925	1314.501	1339	230.167	17.51	21.68	23	24	25	26	31.305	25.399	25	1.363	5.37	0.48	1	3	5	7	9.671	4.396	4	1.716	39.04
Dune	0	4	18	66	100	160	47.416	40	34.294	72.33	27.9	28	29	29	29	29.9	29.355	29	0.337	1.15	10.9	11	12	13	13	13.4	12.589	12	0.533	4.23
Swamp	0	2	5	10	26	39	7.949	6	7.687	96.70	29.1	29	29	29	29	29.9	29.615	29	0.282	0.95	11.62	11	12	12	12	12.8	12.345	12	0.409	3.31
Sand	0	6	19	82	101	129	51.792	47	34.792	67.18	29.906	29	30	31	31	31.221	30.669	30	0.359	1.17	9.737	9	9	11	11	12.037	10.885	11	0.869	7.98
Riverine	25	30	31	56	87	108	48.152	45	17.919	37.21	30.792	30	31	31	32	32.1	31.213	31	0.33	1.06	9.3	9	10	10	10	10.716	10.274	10	0.372	3.62
Coast lowland	0	10	23	47	67	102	35.407	34	17.831	50.36	27.3	29	29	30	30	30.384	29.926	30	0.407	1.36	9.9	11	12	12	12	12.406	12.061	12	0.348	2.89
Coast scarp	6	177	282	466	626	1022	383.153	372	144.865	37.81	24.67	25	26	28	29	31.679	27.389	27	1.284	4.69	5.92	8	9	10	11	12.215	9.652	9	0.934	9.68

Forest subtype	Mean maximum temperature hottest quarter										Mean minimum temperature coolest quarter										Mean annual temperature									
	Min	5%	25%	75%	95%	Max	Mean	Median	SD	CV	Min	5%	25%	75%	95%	Max	Mean	Median	SD	CV	Min	5%	25%	75%	95%	Max	Mean	Median	SD	CV
Montane	22.01	22	23	26	26	28.678	25	25	1.394	5.58	0.465	1	2	3	5	7.372	2.949	2	1.303	44.18	12.675	13	14	15	16	18.385	15.093	15	1.156	7.66
Mist belt	20.97	23	24	25	27	30.98	25.222	25	1.433	5.68	1.294	2	3	5	8	9.868	5.003	4	1.651	33.00	12.429	13	15	16	18	20.548	16.133	15	1.386	8.59
Dune	27.73	28	28	29	29	29.53	29.019	29	0.303	1.04	11.47	12	12	13	13	13.8	13.08	13	0.488	3.73	20.73	21	21	21	21	22.04	21.727	21	0.231	1.06
Swamp	28.767	28	28	29	29	29.59	29.275	29	0.272	0.93	12.219	12	12	13	13	13.3	12.863	13	0.358	2.78	21.479	21	21	21	22	22.061	21.826	21	0.183	0.84
Sand	29.54	29	30	30	30	30.879	30.311	30	0.368	1.21	10.482	10	10	12	12	12.593	11.521	11	0.797	6.92	21.808	21	21	22	22	22.257	22.028	22	0	0.00
Riverine	30.445	30	30	30	31	31.7	30.838	30	0.327	1.06	10.133	10	10	11	11	11.356	10.962	11	0.337	3.07	21.899	22	22	22	22	22.487	22.151	22	0.133	0.60
Coast lowland	27.133	29	29	29	29	29.977	29.567	29	0.369	1.25	10.533	12	12	12	12	12.931	12.588	12	0.325	2.58	20.175	21	21	21	21	22.088	21.801	21	0.245	1.12
Coast scarp	24.698	25	26	28	29	31.315	27.247	27	1.208	4.43	6.581	8	9	10	11	12.488	10.184	10	0.9	8.84	16.985	18	19	20	20	21.953	19.713	19	0.824	4.18

Forest subtype	Annual temperature range										Mean annual precipitation										Median annual precipitation									
	Min	5%	25%	75%	95%	Max	Mean	Median	SD	CV	Min	5%	25%	75%	95%	Max	Mean	Median	SD	CV	Min	5%	25%	75%	95%	Max	Mean	Median	SD	CV
Montane	17.338	19	22	24	25	26.754	23.062	23	1.765	7.65	738	831	951	1147	1280	1531	1055.682	1064	130.381	12.35	743	829	942	1127	1247	1494	1041.266	1052	124.375	11.94
Mist belt	14.889	18	20	22	23	24.662	21.003	20	1.552	7.39	744	909	1005	1240	1522	1787	1141.045	1103	184.926	16.21	742	899	986	1215	1493	1777	1119.214	1082	179.158	16.01
Dune	15.9	15	16	17	17	18	16.766	16	0.477	2.85	653	763	859	1210	1439	1495	1045.929	991	218.538	20.89	635	740	829	1177	1390	1444	1013.895	967	213.967	21.10
Swamp	16.4	16	16	17	18	18.258	17.27	17	0.622	3.60	699	798	1001	1245	1272	1320	1090.726	1117	163.102	14.95	651	743	973	1187	1227	1278	1046.564	1088	166.477	15.91
Sand	18.11	18	18	21	21	21.465	19.784	19	1.203	6.08	538	605	723	814	920	953	769.624	763	84.811	11.02	532	597	686	791	889	921	737.803	716	83.106	11.26
Riverine	20.091	20	20	21	21	22.8	20.939	20	0.695	3.32	547	558	602	699	775	793	658.374	659	65.791	9.99	508	518	595	687	760	777	644.274	647	68.996	10.71
Coast lowland	17.293	17	17	18	18	18.497	17.866	17	0.261	1.46	759	797	926	1124	1233	1275	1033.548	1053	134.135	12.98	739	773	898	1094	1201	1250	1004.826	1030	132.439	13.18
Coast scarp	15.598	16	16	18	20	22.584	17.737	17	1.252	7.06	562	637	800	1066	1338	1396	948.065	923	211.848	22.35	546	621	780	1039	1302	1356	923.696	901	205.416	22.24

Forest subtype	January median rainfall										July median rainfall										Mean median rainfall wettest quarter									
	Min	5%	25%	75%	95%	Max	Mean	Median	SD	CV	Min	5%	25%	75%	95%	Max	Mean	Median	SD	CV	Min	5%	25%	75%	95%	Max	Mean	Median	SD	CV
Montane	129	141	161	192	211	256	177.243	179	21.879	12.34	0	1	1	2	3	3	1.543	2	0.739	47.89	108.424	121	139	167	180	214.362	154.276	156	17.948	11.63
Mist belt	103	131	151	186	224	256	169.943	165	27.123	15.96	3	4	6	8	11	18	7.186	7	2.115	29.43	95.312	123	138	170	210	243.998	156.405	151	25.926	16.58
Dune	67	78	87	114	126	132	99.242	94	16.425	16.55	11	12	14	41	63	87	28.296	20	18.004	63.63	62.222	71	80	104	115	126.94	92.315	90	14.343	15.54
Swamp	66	76	87	111	116	119	97.299	96	13.308	13.68	12	14	26	45	47	48	32.368	32	11.498	35.52	63.498	72	86	101	105	109.266	92.83	95	10.745	11.57
Sand	62	65	74	82	87	90	77.376	78	6.277	8.11	4	5	7	11	16	17	8.954	8	3.272	36.54	60.006	63	68	77	84	86.6	73.193	71	6.22	8.50
Riverine	63	64	69	78	84	85	73.983	74	5.975	8.08	3	3	5	6	8	9	5.678	5	1.418	24.97	57	57	67	75	81	82.252	71.245	72	6.582	9.24
Coast lowland	73	76	89	106	114	117	98.041	101	11.509	11.74	11	12	17	33	42	46	26.524	27	9.925	37.42	70.768	74	83	97	104	111.441	91.026	92	9.499	10.44
Coast scarp	72	77	91	125	142	148	108.145	106	20.204	18.68	1	2	8	13	34	38	13.336	11	9.435	70.75	67.722	72	86	118	136	142.96	103.723	103	19.839	19.13

Forest subtype	Mean median rainfall driest quarter										Mean median summer rainfall										Mean median winter rainfall									
	Min	5%	25%	75%	95%	Max	Mean	Median	SD	CV	Min	5%	25%	75%	95%	Max	Mean	Median	SD	CV	Min	5%	25%	75%	95%	Max	Mean	Median	SD	CV
Montane	1.204	1	2	4	6	8.928	3.52	3	1.703	48.38	94.708	107	122	147	162	194.303	135.113	136	16.649	12.32	11.06	12	15	19	24	29.292	17.756	17	3.521	19.83
Mist belt	5.138	7	8	11	15	22.191	10.598	10	2.464	23.25	90.132	114	126	154	188	215.934	141.919	137	22.156	15.61	17.171	20	23	29	37	48.161	27.054	26	5.021	18.56
Dune	10.646	12	13	44	59	75.667	29.543	22	17.174	58.13	60.68	71	80	105	118	123.873	91.804	88	15.126	16.48	19.397	22	25	55	70	84.023	40.969	34	17.215	42.02
Swamp	13.67	15	33	47	49	52.519	37.051	39	12.224	32.99	63.919	73	86	104	109	112.282	93.963	95	11.457	12.19	22.805	26	30	60	63	66.316	48.151	49	12.883	26.76
Sand	4.831	5	7	13	20	22.54	10.998	9	4.739	43.09	55.988	61	67	76	84	86.148	71.331	70	6.8	9.53	12.48	14	19	23	31	33.822	22.288	21	4.663	20.92
Riverine	3.333	3	5	6	8	9.508	6.184	5	1.532	24.77	53	53	62	71	77	78.301	66.696	67	6.555	9.83	12.667	13	13	17	19	20.407	15.852	15	2.119	13.37
Coast lowland	13.991	16	23	35	43	46.644	30.004	30	8.441	28.13	69.605	73	84	99	105	107.286	91.515	94	9.996	10.92	24.49	26	34	45	54	57.801	40.896	41	8.695	21.26
Coast scarp	2.155	2	11	19	37	40.233	17.503	15	9.691	55.37	61.008	68	83	113	130	136.155	98.6	99	19.391	19.67	11.059	12	22	32	52	54.331	29.392	27	11.167	37.99

Forest subtype	Annual rainfall range										Annual potential evaporation										Geology		Soil type	
	Min	5%	25%	75%	95%	Max	Mean	Median	SD	CV	Min	5%	25%	75%	95%	Max	Mean	Median	SD	CV	Majority	Variety	Majority	Variety
Montane	128	140	159	191	208	253	175.7	178	21.559	12.27	1551.082	1674	1718	1803	1860	1924.938	1758.517	1746	61.236	3.48	531	7	55	6
Mist belt	99	125	145	178	214	245	162.757	159	25.934	15.93	1220.292	1478	1573	1704	1790	1940.013	1639.349	1641	100.09	6.11	391	13	29	6
Dune	37	57	66	75	89	97	70.946	70	9.183	12.94	1718.7	1748.00	1790	1947	2015	2053.1	1875.419	1878	84.257	4.49	537	2	16	2
Swamp	54	58	62	68	70	72	64.932	65	3.734	5.75	1759.8	1759	1768	1805	2037	2039.175	1846.384	1802	107.638	5.83	537	1	16	1
Sand	58	60	65	72	74	76	68.422	70	4.293	6.27	1826.16	1831	1865	2072	2083	2090.2	1956.952	1923	100.439	5.13	537	2	12	3
Riverine	60	61	64	72	76	76	68.304	69	4.746	6.95	1900.569	1905	1924	1962	2062	2064.7	1952.137	1938	46.113	2.36	537	2	81	1
Coast lowland	61	64	69	73	76	99	71.517	71	5.49	7.68	1577.4	1778	1789	1828	1854	2040.946	1814.612	1807	55.676	3.07	537	9	16	2
Coast scarp	67	74	85	104	115	133	94.81	95	13.367	14.10	1474.416	1506	1564	1771	1865	2003.469	1673.908	1639	126.867	7.58	657	11	34	8

Appendix 2. The geology and soil types characterising the indigenous forest subtypes of KwaZulu-Natal province, South Africa

Soil	Montane		Mist belt		Dune		Swamp		Sand		Riverine		Coast lowland		Coast scarp	
Code	no. cells	%	no. cells	%	no. cells	%	no. cells	%	no. cells	%	no. cells	%	no. cells	%	no. cells	%
12	-	-	-	-	-	-	-	-	173	42.93	-	-	-	-	-	-
16	-	-	-	-	1102	98.22	117	100	150	37.22	-	-	702	97.10	3	0.22
18	-	-	-	-	20	1.78	-	-	-	-	-	-	21	2.90	161	11.83
19	99	16.05	-	-	-	-	-	-	-	-	-	-	-	-	131	9.63
26	52	8.43	-	-	-	-	-	-	-	-	-	-	-	-	-	-
29	19	3.08	1819	53.00	-	-	-	-	-	-	-	-	-	-	22	1.62
34	98	15.88	1040	30.30	-	-	-	-	-	-	-	-	-	-	477	35.05
40	-	-	48	1.40	-	-	-	-	-	-	-	-	-	-	40	2.94
41	22	3.57	-	-	-	-	-	-	-	-	-	-	-	-	-	-
46	-	-	196	5.71	-	-	-	-	-	-	-	-	-	-	309	22.70
47	-	-	34	0.99	-	-	-	-	-	-	-	-	-	-	-	-
50	-	-	295	8.60	-	-	-	-	-	-	-	-	-	-	-	-
55	327	53.00	-	-	-	-	-	-	-	-	-	-	-	-	-	-
81	-	-	-	-	-	-	-	-	80	19.85	210	100	-	-	218	16.02

Geology	Montane		Mist belt		Dune		Swamp		Sand		Riverine		Coast lowland		Coast scarp	
Code	no. cells	%	no. cells	%	no. cells	%	no. cells	%	no. cells	%	no. cells	%	no. cells	%	no. cells	%
153	-	-	91	2.65	-	-	-	-	-	-	-	-	-	-	-	-
157	-	-	8	0.23	-	-	-	-	-	-	-	-	-	-	-	-
192	-	-	52	1.51	-	-	-	-	-	-	-	-	-	-	-	-
196	-	-	-	-	-	-	-	-	-	-	-	-	-	-	149	10.95
201	-	-	-	-	-	-	-	-	-	-	-	-	8	1.11	32	2.35
303	-	-	-	-	-	-	-	-	-	-	-	-	-	-	149	10.95
389	-	-	-	-	-	-	-	-	-	-	-	-	-	-	88	6.47
391	144	23.34	1551	45.15	-	-	-	-	-	-	-	-	-	-	105	7.71
403	-	-	-	-	-	-	-	-	-	-	-	-	-	-	131	9.63
506	16	2.59	-	-	-	-	-	-	-	-	-	-	-	-	-	-
531	283	45.87	1066	31.03	-	-	-	-	-	-	-	-	-	-	-	-
535	-	-	-	-	-	-	-	-	60	14.89	46	21.90	-	-	-	-
537	-	-	-	-	1171	99.15	117	100	343	85.11	164	78.10	702	97.10	-	-
543	27	4.38	-	-	-	-	-	-	-	-	-	-	-	-	-	-
555	22	3.57	-	-	-	-	-	-	-	-	-	-	-	-	-	-
557	72	11.67	89	2.59	-	-	-	-	-	-	-	-	-	-	-	-
560	-	-	126	3.67	-	-	-	-	-	-	-	-	-	-	-	-
569	-	-	28	0.82	-	-	-	-	-	-	-	-	-	-	-	-
570	53	8.59	-	-	-	-	-	-	-	-	-	-	-	-	-	-
580	-	-	-	-	-	-	-	-	-	-	-	-	-	-	131	9.63
597	-	-	38	1.11	-	-	-	-	-	-	-	-	-	-	-	-
606	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
607	-	-	59	1.72	-	-	-	-	-	-	-	-	-	-	-	-
617	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
626	-	-	-	-	-	-	-	-	-	-	-	-	13	1.80	-	-
628	-	-	-	-	10	0.85	-	-	-	-	-	-	*	-	-	-
634	-	-	110	3.20	-	-	-	-	-	-	-	-	-	-	-	-
647	-	-	131	3.81	-	-	-	-	-	-	-	-	-	-	-	-
649	-	-	-	-	-	-	-	-	-	-	-	-	-	-	80	5.88
655	-	-	86	2.50	-	-	-	-	-	-	-	-	-	-	-	-
657	-	-	-	-	-	-	-	-	-	-	-	-	-	-	369	27.11
765	-	-	-	-	-	-	-	-	-	-	-	-	*	-	10	0.73
771	-	-	-	-	-	-	-	-	-	-	-	-	-	-	117	8.60

* Coast lowland forest known to occur also on these geology types, and types 177, 600, 623, 764 (not shown).