Endemic species and ecosystem sensitivity to climate change in Namibia

WILFRIED THUILLER*†, GUY F. MIDGLEY*‡, GREG O. HUGHES*§, BASTIAN BOMHARD*, GILL DREW*, MICHAEL C. RUTHERFORD* and F. IAN WOODWARD¶

*Climate Change Research Group, Kirstenbosch Research Centre, South African National Biodiversity Institute, P/Bag x7, Claremont 7735, Cape Town, South Africa, †Laboratoire d'Ecologie Alpine, CNRS, Université Joseph Fourier, BP 53, 38041 Grenoble Cedex 9, France, ‡Center for Applied Biodiversity Science, Conservation International, 1919 M St Suite 600, Washington, DC, USA, §Environment Systems, ADAS, Woodthorne, Wergs Road, Wolverhampton, WV6 8TQ, UK, ¶Department of Animal & Plant Sciences, University of Sheffield, Sheffield S10 2TN, UK

Abstract

We present a first assessment of the potential impacts of anthropogenic climate change on the endemic flora of Namibia, and on its vegetation structure and function, for a projected climate in $\sim$ 2050 and $\sim$ 2080. We used both niche-based models (NBM) to evaluate the sensitivity of 159 endemic species to climate change (of an original 1020 plant species modeled) and a dynamic global vegetation model (DGVM) to assess the impacts of climate change on vegetation structure and ecosystem functioning.

Endemic species modeled by NBM are moderately sensitive to projected climate change. Fewer than 5% are predicted to experience complete range loss by 2080, although more than 47% of the species are expected to be vulnerable (range reduction $>$ 30%) by 2080 if they are assumed unable to migrate. Disaggregation of results by life-form showed distinct patterns. Endemic species of perennial herb, geophyte and tree life-formsare predicted to be negatively impacted in Namibia, whereas annual herb and succulent endemic species remain relatively stable by 2050 and 2080. Endemic annual herb species are even predicted to extend their range north-eastward into the tree and shrub savanna with migration, and tolerance of novel substrates. The current protected area network is predicted to meet its mandate by protecting most of the current endemicity in Namibia into the future. Vegetation simulated by DGVM is projected to experience a reduction in cover, net primary productivity and leaf area index throughout much of the country by 2050, with important implications for the faunal component of Namibia's ecosystems, and the agricultural sector. The plant functional type (PFT) composition of the major biomes may be substantially affected by climate change and rising atmospheric CO_2 – currently widespread deciduous broad leaved trees and C_4 PFTs decline, with the C_4 PFT particularly negatively affected by rising atmospheric CO_2 impacts by $\sim$ 2080 and deciduous broad leaved trees more likely directly impacted by drying and warming. The C_3 PFT may increase in prominence in the northwestern quadrant of the country by $\sim$ 2080 as CO_2 concentrations increase. These results suggest that substantial changes in species diversity, vegetation structure and ecosystem functioning can be expected in Namibia with anticipated climate change, although endemic plant richness may persist in the topographically diverse central escarpment region.

Keywords: climate change, dynamic global vegetation model (DGVM), ecosystem functioning, Namibia, niche-based model (NBM), protected areas, species' range shift

Received 1 November 2004; revised version received 5 November 2005 and accepted 30 December 2005

Correspondence: Wilfried Thuiller, Laboratoire d'Ecologie Alpine, UMR-CNRS 5553, Université Joseph Fourier, BP 53, 38041 Grenoble Cedex 9, France, e-mail: Wilfried.thuiller@ujf-grenoble.fr

Introduction

Rapid anthropogenic climate change has already begun to displace species in nature, and repercussions for

ecosystems have now been recorded (Walther *et al.*, 2002; Parmesan & Yohe, 2003). With expected increases in temperature and precipitation change, such impacts are likely be exacerbated into the future (Peterson *et al.*, 2002; Thomas *et al.*, 2004; Thuiller *et al.*, 2005b). Future distributions of plant species in particular will not only be influenced by changing climate, but also by the on-going increase of atmospheric CO_2, which influences plant physiological responses (Ainsworth & Long, 2005) and may fundamentally alter species ecological success and even ecosystem structure (Bond *et al.*, 2003). Positive responses to increased atmospheric CO_2, the potential for CO_2 fertilization, or changes to water use efficiency (Cowling, 1999; Cowling & Sykes, 1999), may be particularly relevant for plants of drier climates such as occur in Namibia.

Niche-based models (NBM) have been used extensively to predict species distributions for a wide range of biota, using bioclimatic variables to project the likely impacts of future climate change for different time slices (Bakkenes *et al.*, 2002; Iverson & Prasad, 2002; Thuiller *et al.*, 2004b, 2005a). The advantage of such an approach is that it allows a substantial number of both plant and animal species to be modeled using simple occurrence data. The strong caveat is that through their static equilibrium assumptions (Guisan & Zimmermann, 2000; Guisan & Thuiller, 2005), they are conceptually unable to cope with nonequilibrium situations, as they do not distinguish between the transient and equilibrium response of species to a stochastically and dynamically changing environment, and therefore have uncertain powers of extrapolation to no-analog climate and atmospheric CO_2 conditions. In complement to this 'equilibrium snapshot' (Bachelet *et al.*, 2003) provided by NBM, alternative mechanistically based models have been designed to simulate dynamic changes in the vegetation type and its associated biogeochemical cycle in response to transient climate and atmospheric compositional change. LPJ (Sitch *et al.*, 2003), Sheffield dynamic global vegetation model (SDGVM) (Woodward & Lomas, 2004b) and MC1 (Daly *et al.*, 2000) are three examples of dynamic global vegetation models (DGVM). Vegetation in a grid cell is described in terms of the fractional coverage of populations of different plant functional types (PFTs). PFTs are central to DGVMs because, on the one hand, they are assigned different parameterizations with respect to ecosystem processes (e.g. phenology, leaf thickness, minimum stomatal conductance, photosynthetic pathway, allocation, rooting depth), whereas on the other, the proportional representation of different PFTs at any point in time and space defines the structural characteristics of the vegetation (Woodward & Cramer, 1996). DGVMs

have been shown to capture successfully vegetation distributions, biomass and primary production at the resolution required for continental to global-scale studies (Cramer *et al.*, 2001). This mechanistic approach also allows the study of the direct impact of rising atmospheric CO_2 on vegetation structure and ecosystem functioning, which is currently not possible using correlation-based NBM. However, through the fact that they generally deal with vegetation in terms of its structure and function, DGVMs are of little use in addressing conservation strategies of species of concern or to predict the response of large numbers of species to both climate and land-use change (although some applications of DGVM at species level have been published, e.g. Smith *et al.*, 2001).

Our objectives are to assess the potential impact of climate change in Namibia on endemic species diversity, vegetation structure and ecosystem functioning using two contrasting approaches (NBM and DGVM) to determine firstly whether particular vulnerabilities can be identified using either approach, and secondly, whether their complementary use provides additional insights into the potential response and vulnerabilities of ecosystems and species. Using the BIOMOD framework (Thuiller, 2003), we predict the current distribution for 159 endemic plant species and project them into the future for two time slices ~ 2050 and ~ 2080 (IPCC-TGCIA, 1999; IPCC, 2001) under one middle-range climate change scenario, namely HadCM3 A2 (Ruosteenoja *et al.*, 2003) and two extreme assumptions about species' migration (null migration and full migration). Secondly, using the Sheffield DGVM (SDGVM, Woodward *et al.*, 1998; Woodward & Lomas, 2004b) we also assess the change in PFT distribution, biomass and ecosystem functioning for ~ 2050 and ~ 2080 under the HadCM3 A2 climate change scenario, with and without direct CO_2 fertilization effects on plant physiology.

We address the following questions that might begin to inform Namibian policy makers and conservation authorities of the potential vulnerabilities of indigenous species and ecosystems to climate change:

1 How vulnerable are endemic plant species in Namibia to reductions in range size and exceedance of climatic tolerance limits under climate change scenarios of ~ 2050 and ~ 2080?
2 What extent of endemic species turnover and community change may occur in the 12 Namibian protected areas under climate change?
3 Will climate change and rising CO_2 concentrations alter Namibian vegetation structure and function with implications for ecosystem management strategies?

Material and methods

Study area

This region is under the strong aridifying influence of the cold Benguela current and is positioned in the latitudinal zone of stable descending air of the Hadley Cell, limiting convectional rainfall throughout much of the country's interior. Namibian climate ranges from arid and semiarid in the west, with a temperate, regionally fog-bound coastal desert, to more subtropical summer-rainfall conditions in the northeast. The central, southern and coastal areas are among the most arid landscapes south of the Sahara. In relation to the rest of southern Africa, Namibia represents a low rainfall extreme and experiences intermediate to warm temperatures and high potential evapotranspiration. Regardless of these climatic constraints, Namibia is home to a remarkable biodiversity, notably among its plant species. Within its borders, more than 4500 plant taxa have been recorded, almost 700 of which are endemic to the country, and a further 275 of which are Namib desert endemics shared with southern Angola (Maggs *et al.*, 1998). Plant species endemism is concentrated in five centers, the Kaokoveld in the north, the Otavi highland in the Kalahari basin in the east, the Okavango region in the northeast, the Auas mountains on the western edge of the central plateau and the succulent-rich southern Namib desert (Maggs *et al.*, 1994). This variety of plant species in Namibia makes up a broad range of ecosystem types ranging from desert landscapes with sparse plant cover on the western coastal belt with high succulent dominance in the southwest, through arid shrubland and sparse woodland with C_4 photosynthetic pathway species along the escarpment, to tree-shrub mixed savanna and woodland vegetation in areas of higher rainfall in the northeastern Kalahari basin. Various categorizations of Namibian vegetation types have been proposed. These can be summarized most simply as a set of four biomes based on plant life-form dominance (Irish, 1994), namely the ephemeral therophyte-dominated desert, succulent-shrub-dominated Succulent Karoo, C_4 grass and shrub codominated Nama Karoo, and tree and shrub codominated savanna.

Species-specific model

Plant species. Plant species distribution data were extracted from the Namibian National Botanical Research Institute herbarium database (WIND, 2004), which forms part of the Southern African Botanical Diversity Network (SABONET), digitized at quarter degree scale (QDS, around $25 \, \text{km} \times 25 \, \text{km}$ at this latitude). The database contains records detailing 213 families, 1196 genera and more than 4500 species and subspecies covering 95% of the country. These records were checked to ensure they reflected current taxonomic nomenclature (C. Mannheimer, personal communication). A subset of 1020 species, each with more than 20 unique QDS occurrences, was selected for modeling. We attributed each species to a specific life-form (succulent, geophyte, grass, annual herb, perennial herb, shrub and tree) in order to derive an index of species range change by life-forms (Germishuizen & Meyer, 2003, C. Mannheimer, personal communication). The type of model used in this study (NBM) relies on the definition of the ecological niche of the selected species (Pulliam, 2000). To be reliable, the model needs to capture the full-realized niche of the selected species. Indeed, if only part of an important environmental gradient is sampled (e.g. when using political boundaries), the model can lead to an incorrect interpretation (Van Horn, 2002) and spurious projections (Thuiller *et al.*, 2004c). For instance, the resulting response curves of a species might appear truncated – possibly expressing a negative (e.g. on the colder part of the temperature gradient), a positive (e.g. on the warmer part of the temperature gradient) or nearly no relationship (e.g. on the intermediate part of the temperature gradient) – when the full response should be unimodal (Van Horn, 2002; Guisan & Thuiller, 2005). To avoid such problems, we restricted the analysis only to endemic species of Namibia (159 species of the original 1020).

Climate datasets. The CRU CL 2.0 dataset (New *et al.*, 2000) at a resolution of $16 \times 16 \, \text{km}^2$ was chosen to represent current climate (average from 1961 to 1990). Future (~ 2050 and ~ 2080) climate predictions were produced by perturbing the current climatic data with anomalies derived from climatic simulations produced by the HADCM3 general circulation model using the IPCC SRES A2 scenario (Nakicenovic & Swart, 2000). The time slices have been chosen in accordance with the guidelines on the use of scenario data for climate impact and adaptation assessment made available by the IPCC (IPCC-TGCIA, 1999). Fifteen variables were first selected based on their known effects on plant survival and growth (Midgley *et al.*, 2002, 2003): Annual and seasonal sum of precipitation (four seasons of 3 months), annual and seasonal mean temperature (four seasons of 3 months) and annual and seasonal mean evapotranspiration (four seasons of 3 months). Potential evapotranspiration estimates were calculated using the FAO 56 Penman Monteith combination equation (Allen *et al.*, 1998). Because some of the variables were obviously correlated and will thus lead to multicolinearity (Guisan & Thuiller, 2005), we

then ran a principal component analysis to identify only the least-correlated variables. We finally selected annual and winter temperature, annual, winter and summer precipitation, and annual and winter potential evapotranspiration. Winter temperature is likely to discriminate between species based on their ability to assimilate soil water and nutrients, and continue cell division, differentiation and tissue growth at low temperatures (lower limit), and chilling requirement for processes such as bud break and seed germination (upper limit). Potential evaporation discriminates through processes related to transpiration-driven water flow through the plant, and xylem vulnerability to cavitation and water transport efficiency.

We did not assess the impacts of land-use change, even though this factor will potentially compound the effects of climate change on species distributions (Travis, 2003). However, given the spatial extent and resolution of our data and the magnitude of climate change in most projections, at this scale the effect of land use would be most likely overridden by climate (Pearson *et al.*, 2004; Thuiller *et al.*, 2004a).

Red List status. To communicate our findings through a common conservation tool, we assigned each endemic species to a threat category (IUCN, 2001), or classified it as lower risk (LR), depending on the projected reduction in range size from present to 2050 or 2080. Present and future range size (area of occupancy) was estimated from the number of pixels ($\sim 320\,km^2$) where a species occurs. Loss in range size was calculated by subtracting future range size from present range size. In line with IUCN Red List criterion A3(c), the following thresholds were then used to assign a species to a threat category (IUCN, 2001):

- *Extinct (EX)*: species with a projected range loss of 100%.
- *Critically endangered (CR)*: projected range loss of >80%.
- *Endangered (EN)*: projected range loss of >50%.
- *Vulnerable (VU)*: projected range loss of >30%.

It is important to note that our Red Listing approach is simplistic, generalist and considers only the future effects of rapid anthropogenic climate change.

NBM. Models relating species distributions to the seven bioclimatic variables were fitted using the BIOMOD framework (see details in Thuiller, 2003) on a random sample of the initial data (70%). For each species, generalized linear model (GLM), generalized additive model (GAM), classification tree analysis (CTA) and artificial neural networks (ANN) were calibrated.

Then each model for each species was evaluated on the remaining 30% of the initial dataset using the values obtained for the area under the curve (AUC) of a receiver operating characteristic (ROC) plot of sensitivity against (1-specificity) (Swets, 1988). Sensitivity is defined as the proportion of true positives correctly predicted, whereas specificity is the proportion of true negatives correctly predicted. For each species, the model with the highest AUC was retained to project future distributions (Thuiller, 2003). We transformed the probability of occurrence from models using a threshold maximizing the percentage of presence and absence correctly predicted (Pearce & Ferrier, 2000).

To evaluate potential extinction rates, we summed the number of species lost (*L*) by pixel and related this to current species richness by pixel ($10' \times 10'$, $\sim 320\,km^2$). The same procedure was used to assess the percentage of species gained (*G*) by pixel (under assumptions that species could reach new location, full migration ability hereafter). Percentage of species turnover by pixel under the assumption of migration was estimated by $T = 100 \times (L + G)/(SR + G)$; where SR is the current species richness.

PFT and ecosystem model

Climate datasets. The observed time series of climate for the period 1901–2000 was derived from the CRU TS 2.0 dataset (New *et al.*, 2000; Mitchell *et al.*, 2004) at a resolution of 30 min. These data were resampled to $10'$ using a technique described by Hewitson (2003) and used to force SDGVM for the period 1971–2000. The Hadley Centre HadCM3 global climate change modeled data were used as the climate input data using the A2 IPCC SRES scenario (Nakicenovic & Swart, 2000) for the two future periods, namely 2040–2069 (called 2050 hereafter) and 2070–2099 (called 2080 hereafter). The sensitivity of HadCM3 to a doubling of CO_2 falls within the range of sensitivities of other GCMs of this generation (Ruosteenoja *et al.*, 2003). Thus, we consider this climate change scenario representative of current attempts to model the climate response to emission scenarios. Furthermore, to adjust for climate model bias, all climate model outputs were taken as anomalies relative to the 1971–2000 simulated mean climate, and applied to the observed climatology for the same period. This procedure preserved interannual variability and sensitivity of the model, while simultaneously forcing the spatial pattern to be in agreement with recent observations.

The atmospheric CO_2 input data are also provided by the Hadley Centre, and consists of an average for each year from 1830 to 2100, given as a partial pressure.

SDGVM description. The vegetation model used for these simulations is the SDGVM (Woodward *et al.*, 1998, Woodward & Lomas, 2004b). The basic processes and assumptions in the model are also outlined in Cramer *et al.* (2001). The SDGVM requires input data of climate, atmospheric carbon dioxide concentration and soil texture. The climate variables required are the monthly mean temperature, precipitation and relative humidity. These are used to calculate the minimum temperature and the number of wet days. The physiology and biophysical module simulates carbon and water fluxes from vegetation (Woodward *et al.*, 1995) with water and nutrient supply defined by the water and nutrient flux module. The soil module incorporates the century soil model of carbon and nitrogen dynamics (Parton *et al.*, 1993), with a model of plant water uptake.

Water fluxes are modeled within the SDGVM using a 'bucket' model (Woodward & Lomas, 2004b). This is a layered model, which simulates the moisture profile through the depth of the soil, without modeling it as a continuous medium. The model is composed of four buckets: one thin (5 cm) layer at the surface and three buckets of equal depth, which make up the remainder of the soil layer. The depth of the total soil layer is currently set to 1 m everywhere, but the facility to alter the soil depth is built into the SDGVM. The effects of bare soil evaporation, sublimation, transpiration and interception (each of which represents a loss of water available to the vegetation system) are incorporated into the model. The primary productivity model simulates canopy CO_2 and water vapor exchange, as well as nitrogen uptake and partitioning within the canopy. Nitrogen uptake is linked directly with the century soil model, which simulates the turnover of carbon and nitrogen in plant litter, of differing ages and depths within the soil, in addition to soil water status.

The primary productivity model determines the assimilated carbon available for the growth of plant leaves, stems and roots. The plant structure and phenology module defines the vegetation leaf area index (LAI) and the vegetation phenology. Leaf phenology is defined by temperature thresholds for cold deciduous vegetation and by drought duration for drought deciduous vegetation (Cramer *et al.*, 2001).

The vegetation dynamics module (Cramer *et al.*, 2001; Woodward *et al.*, 2001) simulates the establishment, growth, competition and mortality of PFTs (evergreen and deciduous broad leaved trees, grasses with the C_4 photosynthetic metabolisms and C_3 grasses and shrubs). Needle-leaved trees are not modeled as they do not occur naturally in southern Africa. In the vegetation dynamics module, functional types compete for light and soil water, and all undergo random mortality that increases with age. The densities (plants per unit area), heights and ages of all the functional types, except grasses, are simulated at the finest spatial resolution (pixel) of the model. A fire module, based on temperature and precipitation, simulates disturbance by burning a fraction of the smallest pixel of the study area (Woodward *et al.*, 2001). It is assumed that 80% of aboveground carbon and nitrogen are lost as a consequence of the fire. Fire only occurs when, in effect, leaf litter reaches a critical point of dryness, at which point fire will occur at a random time and for a random subset of the pixel (Woodward *et al.*, 2001).

The simulations of the individual models and the SDGVM as a whole compare well with a range of contemporary independent measurements (Woodward *et al.*, 1995, 2001; Cramer *et al.*, 2001; Woodward & Lomas, 2004a). The vegetation modeled by SDGVM is the potential natural vegetation based on the conditions provided as inputs and does not take into account processes such as anthropogenic modifications of the land surface.

SDGVM simulations. At the start of a SDGVM simulation, the model is given only soil data (defined by texture and depth), the climate variables and atmospheric CO_2 concentration. There is therefore a necessary initialization stage in which the soil carbon and nitrogen storage are determined, followed by the appropriate vegetation for the start of the simulated climate period. The model initialization is undertaken with a repeated and random selection of annual climates from 1901 to 1920 thereby ensuring data independent of the simulation periods and minimally influenced by climate change is utilized. The soil carbon and nitrogen values are first determined by solving the century model analytically. The full dynamic model is then run until the vegetation structure is at equilibrium, typically after 200 years. When initialization is completed, the SDGVM is then used to simulate vegetation for specific time periods and CO_2 conditions.

Five model integrations were performed and are identified by the time period they represent, these being:

(1) *2000*: A control run representing current condition (1971–2000);
(2) *2050clm*: Medium-range (2040–2069) forecast with no change in CO_2;
(3) *2050CO_2*: Medium-range (2040–2069) forecast with a change in CO_2;
(4) *2080clm*: Long-range (2070–2099) forecast with no change in CO_2;

(5) *2080CO2*: Long-range (2070–2099) forecast with a change in CO_2.

Experiments 2 and 4 simulate vegetation and ecosystem functioning under current (1971–2000) CO_2 atmospheric rates, whereas 3 and 5, simulate vegetation and ecosystem functioning under elevated CO_2 as predicted by the A2 scenario.

All other parameters were set to the default, and the model was run with annual results recorded for each simulation. The control experiment was used as a baseline for comparing responses with the climatic perturbations.

The SDGVM provides a wide range of outputs, but only a small subset has been extracted for this simulation; namely the vegetation structure (future potential cover and biomass of all the simulated PFTs) and some key ecosystem functions (net primary productivity and LAI).

SDGVM validation. Model validation is a key step in assessing the fidelity of simulation results, especially because credible simulation under a wide range of current climatic conditions improves confidence in model simulation of future changes (Giorgi *et al.*, 2001). The SDGVM has been extensively tested at a global scale (Woodward *et al.*, 1995, 2001; Beerling & Woodward, 2001; Cramer *et al.*, 2001) and subcontinental scale (Drew, 2004). Recently, Woodward & Lomas (2004a) validated SDGVM at a finer scale along the Kalahari transect experiment between latitudes of 15.251°S and 24.251°S in Botswana. Botswana borders Namibia and indeed shares much of its flora (Cowling *et al.*, 1997), encouraging confidence in its performance in this region.

Because of the broad definition of PFT's in SDGVM, the validation of the potential distribution of the PFTs with observed land cover was not straightforward. However, if SDGVM simulates potential vegetation structure credibly using bare ground, C_3 and C_4 pathway PFTs and deciduous broad-leaved trees, those PFTs should predict and explain the observed pattern of land cover. To validate the SDGVM simulation, we related the observed land cover (explained by four biomes) to the PFTs defined and simulated by SDGVM using CTA, and then measured the strength of the relationship using a multivariate Cohen's κ statistic. As much of Namibia is sparsely vegetated, we predicted the occurrence of the four Namibian biomes (namely Nama Karoo, Namib desert, Tree and shrub savanna, and Succulent Karoo) using the biomass of each PFT simulated by SDGVM, and not cover. To be as parsimonious as possible, we used a 50-fold cross-validation CTA using the library

rpart under the R-CRAN software (Ihaca & Gentleman, 1996).

Results

Regional climate and climate anomalies

The geographic variation of current mean annual and winter temperature showed a south–north gradient, where northern Namibia experiences highest temperatures (Fig. 1a). Precipitation varies markedly with season. Winter is generally very dry (less than 40 mm) though the extreme southwest of Namibia is wetter (Fig. 1b). By contrast, summer is generally wet, though exhibiting a strong southwest–northeast gradient. Annual evapotranspiration is low along the Atlantic coast, and shows a north–south gradient inland (Fig. 1c). The same trend along the coast was observed for winter evapotranspiration, whereas the inland gradient was reversed (south-northward).

Future anomalies for the selected bioclimatic variables, averaged by biome, showed that some biomes might be more exposed to climate change than others. In general, temperature and evapotranspiration rise from the coast to the interior and from south to north. Therefore, the coastal and southerly Succulent Karoo biome was projected to experience smaller annual temperature increases (1.6 °C and 2.7 °C for 2050 and 2080, respectively) than the other biomes. The northern inland savanna biome was predicted to undergo a temperature increase almost double that of the Succulent Karoo (2.8 °C for 2050 and 4.7 °C for 2080), with a relative doubling of potential evapotranspiration (Table 1). Rainfall in summer and winter was projected to decrease for all biomes, but summer rainfall changes were projected to be rather small for all biomes. Winter rainfall changes were significant for savanna (−49.4% for 2050 and −64.1% for 2080), Nama Karoo (−32.2% for 2050 and −37.6% for 2080), and coastal Namib desert biome (−31.7% for 2050 and −38.9% for 2080).

Vulnerability of endemic species, using niche-based modeling

Validation. The average accuracy for the 159 endemic species' distribution models assessed using the AUC approach showed a mean AUC = 0.91 for all species (0.81 < AUC < 1) which suggests very good general model predictivity. We were able to capture the full climatic range of every species, and can therefore project their future potential climatic habitats with confidence based on climate alone (but ignoring species-specific CO_2 fertilization effects).
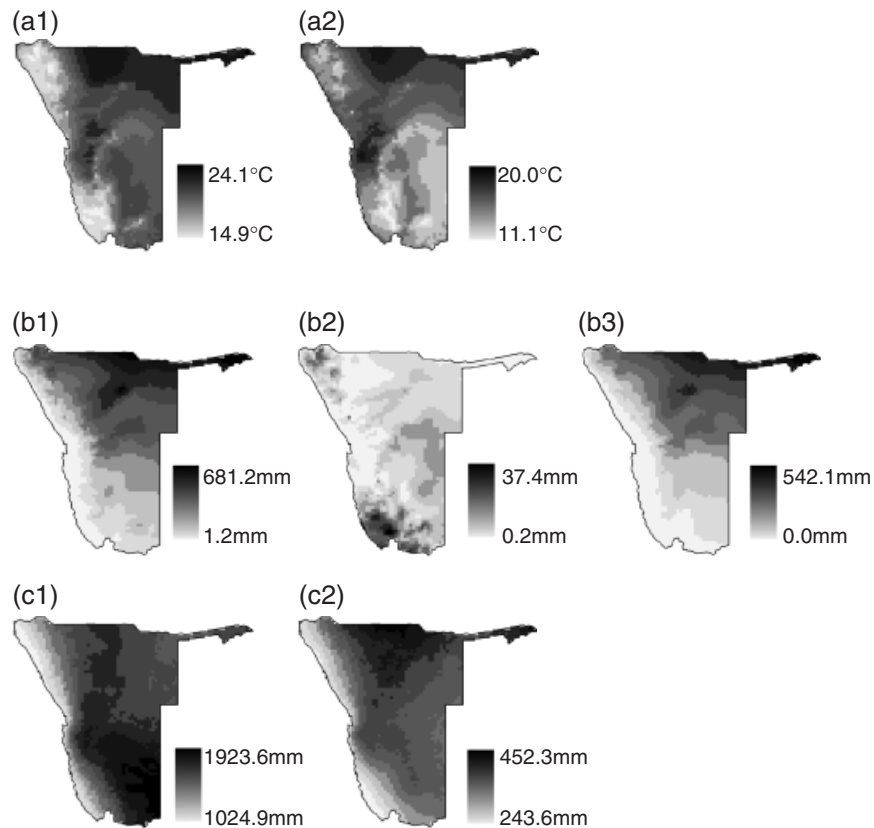
Fig. 1 Geographic variation of the bioclimatic variables used to model species distributions: (a1) mean annual temperature; (a2) mean winter temperature; (b1) annual sum of precipitation; (b2) winter sum of precipitation; (b3) summer sum of precipitation; (c1) mean annual potential evapotranspiration; (c2) mean winter potential evapotranspiration.

Table 1 Mean regional climate anomalies for each biome for the two slices considered (2050 and 2080)

	Temperature (°C)		Precipitation (%)			Potential evapo. (%)	
	Annual	Winter	Annual	Winter	Summer	Annual	Winter
2050							
Nama Karoo	2.2	2.3	−16.4	−32.2	−10.8	12.7	22.1
Namib desert	1.9	1.9	−18.2	−31.7	−14.0	10.1	14.7
Savanna	2.8	3.0	−14.5	−49.4	−12.6	15.6	21.9
Succulent Karoo	1.6	1.6	−14.8	−16.1	−3.8	7.0	11.6
2080							
Nama Karoo	3.8	4.0	−23.0	−37.6	−31.3	21.4	33.3
Namib desert	3.2	3.3	−22.2	−38.9	−34.2	17.5	21.5
Savanna	4.7	4.7	−20.7	−64.1	−27.3	26.0	31.2
Succulent Karoo	2.7	2.8	−15.7	−16.9	−20.0	26.0	31.2

Evapo., evapotranspiration. On the map, Nama Karoo, Namib desert, savanna and Succulent Karoo are, respectively, represented by (1), (2), (3) and (4). Anomalies for temperature are absolute mean difference between future and current temperature (°C), whereas anomalies for precipitation and evapotranspiration variables are relative mean difference between future and current (% of change).

Impacts on plant life forms. Life-forms respond differentially to climate change (Fig. 2). Annual herbs were the least affected with the smallest range loss (8.5% for 2050 and 10.1% for 2080) and with gains in range for both time slices assuming full migration (100.7% for 2050 and 117.2% for 2080). Conversely, geophytes (64.3% and 81.6%), trees (45.2% and 63.1%) and perennial herbs (27.6% and 44.7%) are projected to
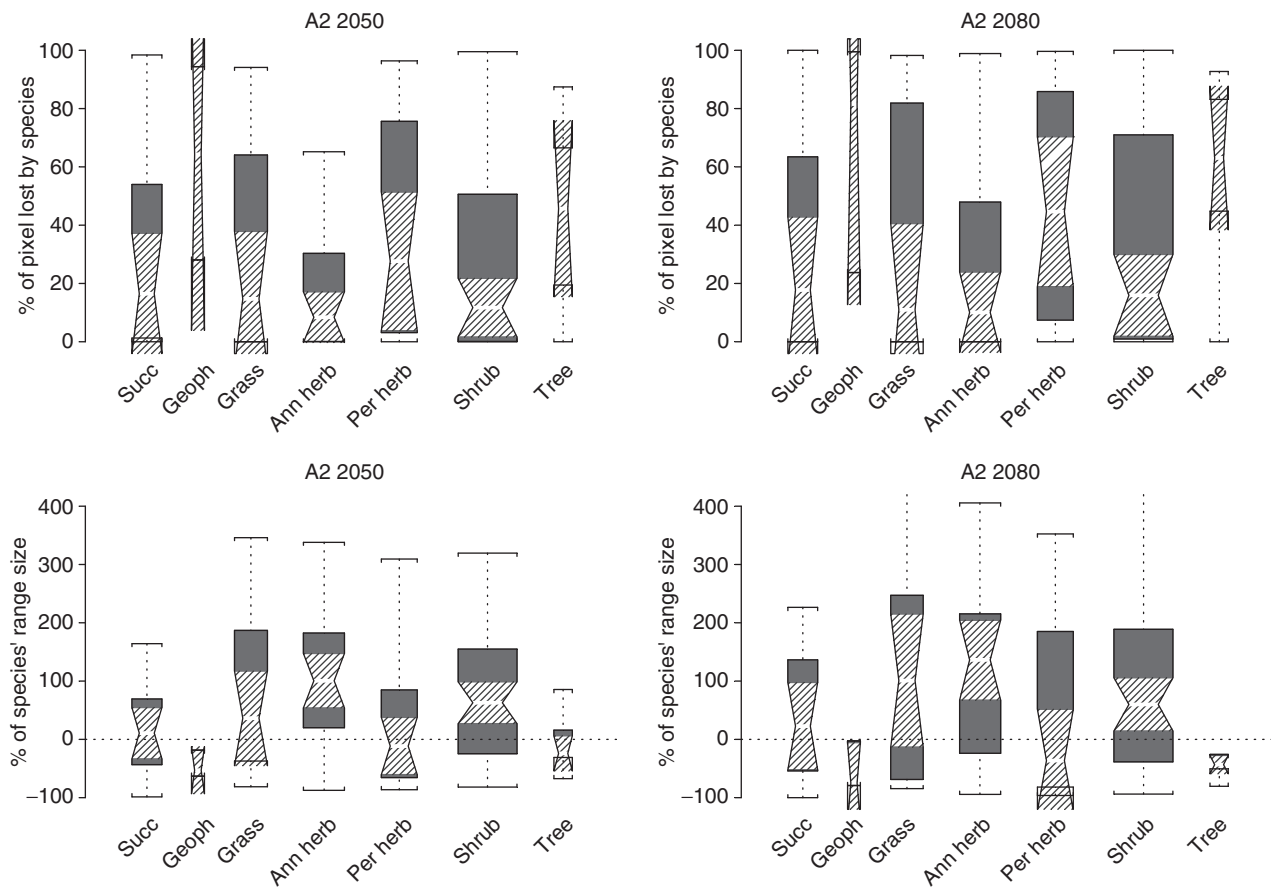
Fig. 2 Boxplots representing the percentage of range loss and range change by endemic plant life form. Upper extreme, upper quartile, median, lower quartile and lower extreme are represented on each box. Hatched section corresponds to the confidence limits at 95% around the mean. The width of each box is proportional to the number of species inside the life form. Succ is succulent life form. Geoph is geophyte, Ann herb is annual herb and Per herb is perennial herb life form.

lose large parts of their range size for both 2050 and 2080. Strong to moderate negative range reductions are projected with full migration, −53.0% and −74.9% for geophytes, −24.2% and −43.3% for trees and −11.3% and −35.9% for perennial herbs, by 2050 and 2080, respectively. The three other life forms, succulents, grasses and shrubs showed intermediate patterns. However, shrubs and grasses were projected to increase their range with migration. It is also worth noting that under the assumption of full migration, some grasses and shrubs species were also predicted to increase their range by more than 400%. In general, these results showed the strong differential sensitivity of endemic plant life-formsin Namibia to climate change, and the high level of uncertainty because of species migration assumptions.

Impacts on Red List status. Our simple application of a single IUCN Red List criterion highlighted that many Namibian endemic plant species might be threatened

by future climate change alone (Fig. 3). More than 47% of the species were expected to be threatened with or committed to extinction in 2080 with no migration (Fig. 3). For both time slices, climate change affected species less under the full migration assumption because of the possibility for species to move across landscapes. Under the null migration assumption for 2050, 8% of the species were classified as critically endangered (CR, >80% range loss) but none as extinct (EX). These numbers increased for 2080 to 18% CR and 1% EX, respectively.

As an example of the above pattern, an endemic herb species in the northeastern part of the country, *Ruelliopsis damarensis* (Acanthaceae), was expected to lose 96% of its current range in Namibia by 2050, and to gain few new areas (13% increase) assuming full migration. This species was consequently classified as potentially critically endangered in Namibia in the future, under both migration ability assumptions. Conversely, *Manuleopsis dinteri* (Scrophulariaceae), a

shrub species in the western highlands, was expected to be very stable (0% range loss) and to gain substantial areas assuming full migration (180% increase). This species was thus classified as LR.
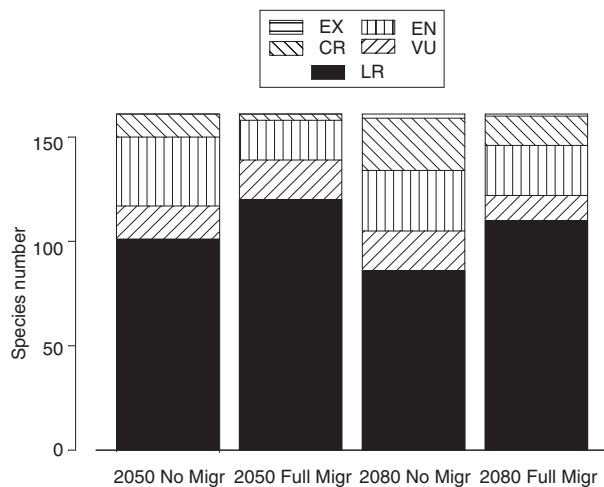

Fig. 3 Barplots representing the number of endemic plant species classified according to our IUCN Red List assessment for each time slice and under both assumptions on species' migration. Full Migr and no Migr represent, respectively, full migration ability and null migration ability. EX, Extinct; CR, critically endangered; EN, endangered; VU, vulnerable; LR, lower risk.

Impacts on endemic species diversity. Two life forms, annual herb and shrub, were predicted to increase their prominence substantially in the Namibian landscape (Figs 4 and 5), given favorable rates of spread and suitable substrates for establishment. These two life-formswere projected to experience a decrease in species richness only in the central western part of Namibia, but gain substantially in the eastern part of the country (tree and shrub savanna biome, Fig. 5). The succulent, grass and perennial herb life-formsshowed similar geographic patterns, with a decrease in one specific area and an increase in the rest of the country. The richness of species belonging to the succulent life-form was thus predicted to fall dramatically in the southwestern part of Namibia (Succulent Karoo biome, Fig. 5) even with migration, but to increase further north and east across the tree and shrub savanna biome (Fig. 5). The number of grass species was predicted to decrease in the highlands of Namibia (Fig. 4) but increase in most of the country and especially southward in the Succulent Karoo biome (Fig. 5), whereas the number of perennial herb species decreases along the northwest to southeast transect and increases north-eastward (Figs 4 and 5). The number of geophyte and tree species is projected to decline almost everywhere they currently occur assuming both null and full migration of species, excepted in some specific, small areas along the Atlantic coast. Endemic tree
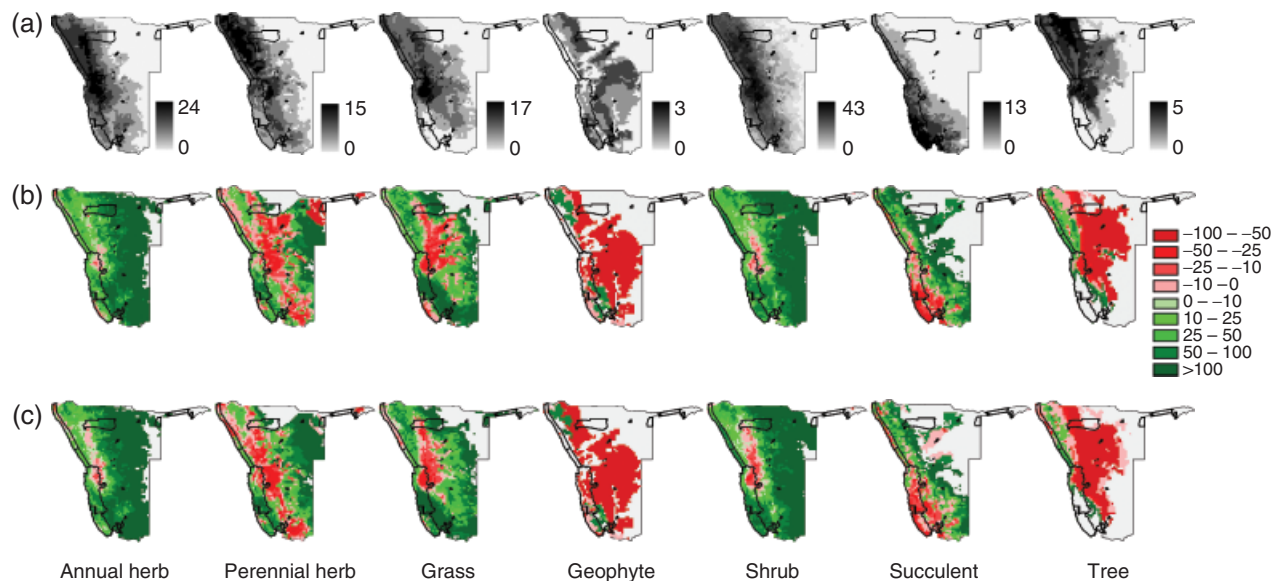

Fig. 4 Relative change in geographic endemic species richness distribution according to the different life-formsanalyzed: (a) current endemic species richness, (b) changes under the A2 2050 scenario and (c) changes under the A2 2080 scenario. The gray scale for (a) represents an increase in species richness. The color scale for (a) and (b) represent the percentage of change in species richness. Red color scale represents a decrease in species richness whereas green represents an increase in species richness. The Namibian protected areas are also highlighted.
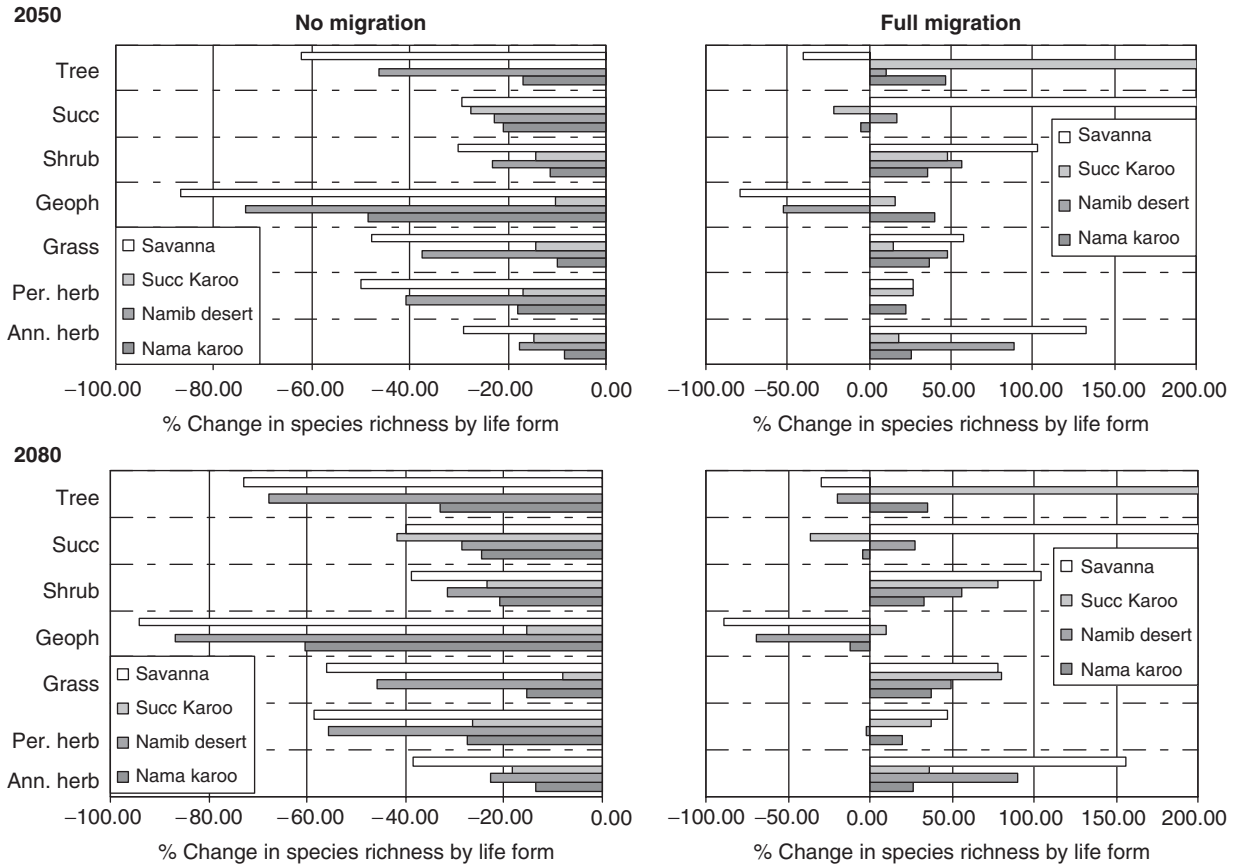
Fig. 5 Relative change in species richness for each studied life-form as projected by niche-based models , expressed for each Namibian biome, assuming both null and full migration and according to the time slices considered (2050 and 2080).

Table 2. Current modeled endemic plant species richness found in Namibian protected areas and projected species losses, gains and net turnover under the A2 climate change scenario and the two time-slices

Protected areas	Current SR	A2 2050			A2 2080		
		Loss	Gain	Turnover	Loss	Gain	Turnover
Ai-Ais Hot Springs	78	6	49	43	9	59	50
Caprivi	2	2	12	10	2	18	16
Etosha	100	9	23	14	20	22	2
Hardap	28	10	47	37	11	51	40
Khaudum	4	3	19	16	3	28	25
Mahango Game Reserve	2	2	8	6	2	19	17
Mamili	0	0	8	8	0	13	13
Mudumu	0	0	7	7	0	13	13
Nonemib-Noneukluft Park	151	4	4	0	8	4	−4
NonetioNonel West Coast Recreation Area	90	7	20	13	10	24	14
Skeleton Coast Park	124	10	11	1	12	7	−5
Waterberg Plateau Park	40	29	32	3	31	49	18

SR means species richness, Loss, Gain represent, respectively, the number of species expected to be lost or gained by the protected area. Turnover calculated as species gained minus species lost independently of current species richness. Gain and turnover are estimated under the assumption of unlimited migration across the landscape.

richness, for example, was predicted to increase in the Succulent Karoo biome (Fig. 5).

Effectiveness of Namibian protected areas. Our basic assessment of the effectiveness of the current protected areas showed that they are well-positioned to meet their mandate, at least for the selected species analyzed in this study (Table 2). For instance, the Namib Desert National Park (Nonemib-Noneukluft Park), the richest park in plant endemic species in Namibia (151 species of 159 analyzed in this study), was projected to experience a loss of only eight species by 2080 and a potential gain of four species, resulting in a small turnover. Most of the other Namibian parks were projected to increase in plant endemic species richness with migration. The renowned Etosha National Park may expect substantial losses (20 spp.) and gains of species (22 spp.), and may ultimately realize a substantial shift in endemic plant species composition (Table 2). This pattern may also be observed for the Waterberg Plateau Park (Table 2).

Vulnerability of vegetation structure and ecosystem functioning, using dynamic vegetation modeling

Validation. A simple classification tree, based on the biomass of the PFTs simulated by SDGVM, allowed the categorization and spatial projection of the current distribution of the biomes in Namibia (Fig. 6). The primary discriminatory variable selected was biomass of deciduous broad-leaved trees, which differentiated between the tree and shrub savanna biome and the

others. Nodes were further discriminated based on the biomass of C_3 and C_4 photosynthetic pathway PFTs, as follows:

- The tree and shrub savanna biome is defined when the biomass of deciduous broad-leaved trees is higher than $0.94\,t\,ha^{-1}$, or when the biomass of the C_4 pathway PFTs is higher than $49.5\,t\,ha^{-1}$.
- The Nama Karoo is defined when the biomass of deciduous broad-leaved trees is lower than $0.94\,t\,ha^{-1}$, and when either the biomass of the C_3 pathway PFTs is higher than $7.35\,t\,ha^{-1}$ (for biomass in C_4 pathway <1.18) or the biomass in the C_4 pathway PFTs is between 1.12 and $49.5\,t\,ha^{-1}$.
- The Namib desert occurs where the biomass of deciduous broad-leaved trees was lower than $0.94\,t\,ha^{-1}$, and where the biomass of C_4 and C_3 pathway PFTs were respectively lower than 1.18 and $7.35\,tons\,ha^{-1}$.

Only one biome, the Succulent Karoo, was not defined by the potential biomass of PFTs simulated by SDGVM. The vegetation of this biome is dominated by dwarf-succulent shrubs, of which the Mesembs (Mesembryanthemaceae) and Stonecrops (Crassulaceae) are particularly prominent. Grasses are rare, except in some sandy areas, and are of the C_3 type. Species richness (mostly succulents with CAM or C_3/CAM photosynthetic pathway) is very high and unparalleled elsewhere in the world for an arid area of this size. Unfortunately, SDGVM does not simulate succulent or
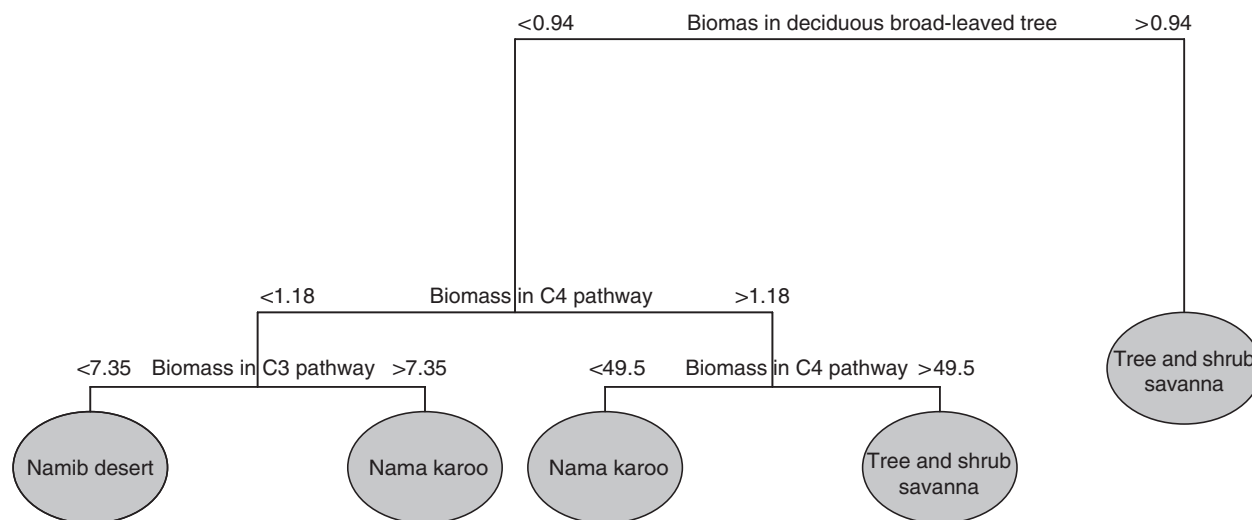

Fig. 6 Classification tree representing the occurrence of Namibian biomes based on the definition of Sheffield dynamic global vegetation model (SDGVM) plant functional type biomass (tons ha^{-1}). The length of each leave of the tree is proportional to the explained deviance.

CAM pathway PFTs, explaining why this biome was not predicted based on SDGVM simulated biomass.

The SDGVM simulations are tested against the observed distributions of Namibian biomes with the modeled biomass distribution (based on the CTA) (Fig. 6) using a multi-Cohen's κstatistic (Monserud & Leemans, 1992). A κstatistic of 0.85 indicated that the SDGVM made credible predictions of Namibian vegetation structure, despite the absence of a succulent or CAM pathway PFT.

Impacts on vegetation structure. The future climate scenarios (under assumption of zero CO_2 fertilization) caused significant changes in PFT distribution (Fig. 7) and PFT success throughout the country, especially in the central escarpment and southern central regions. The C_3 PFT, predicted to be a minor component of Namibian vegetation under current climatic conditions, showed a strong decrease in cover by 2050 under both scenarios of CO_2 levels (Fig. 7). This decrease was much more pronounced in the
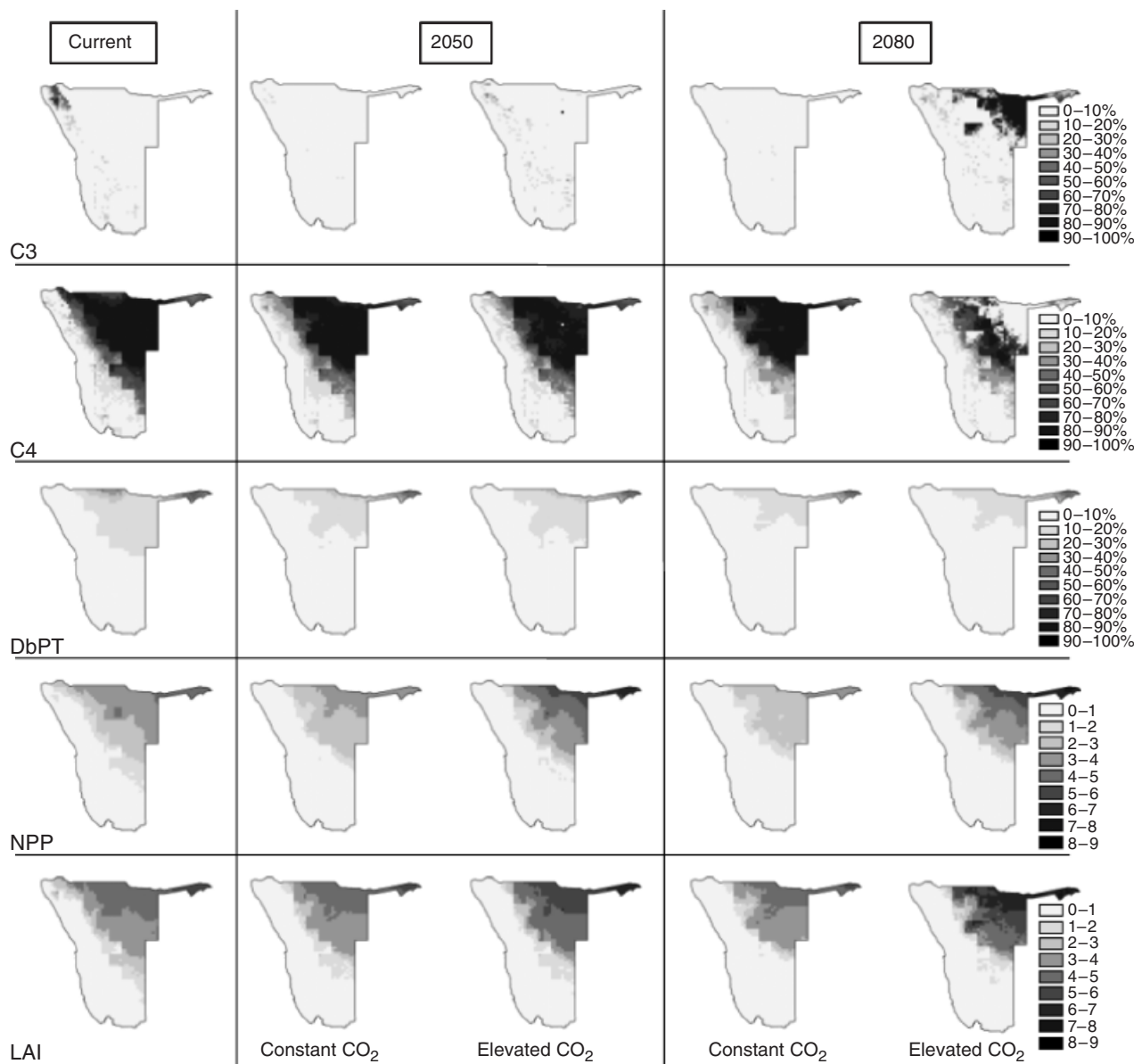

Fig. 7 Potential vegetation cover and ecosystem processes simulated by Sheffield dynamic global vegetation model (SDGVM) for current and future conditions (with constant and elevated atmospheric CO_2 concentration for 2050 and 2080). C_3, C_4 and DblT labels represent, respectively, the percentage of cover by C_3, C_4 and deciduous broad-leaved tree plant functional types. NPP, LAI labels represent, respectively, the annual net primary productivity ($t\,ha^{-1}$) and leaf area index (no unit).
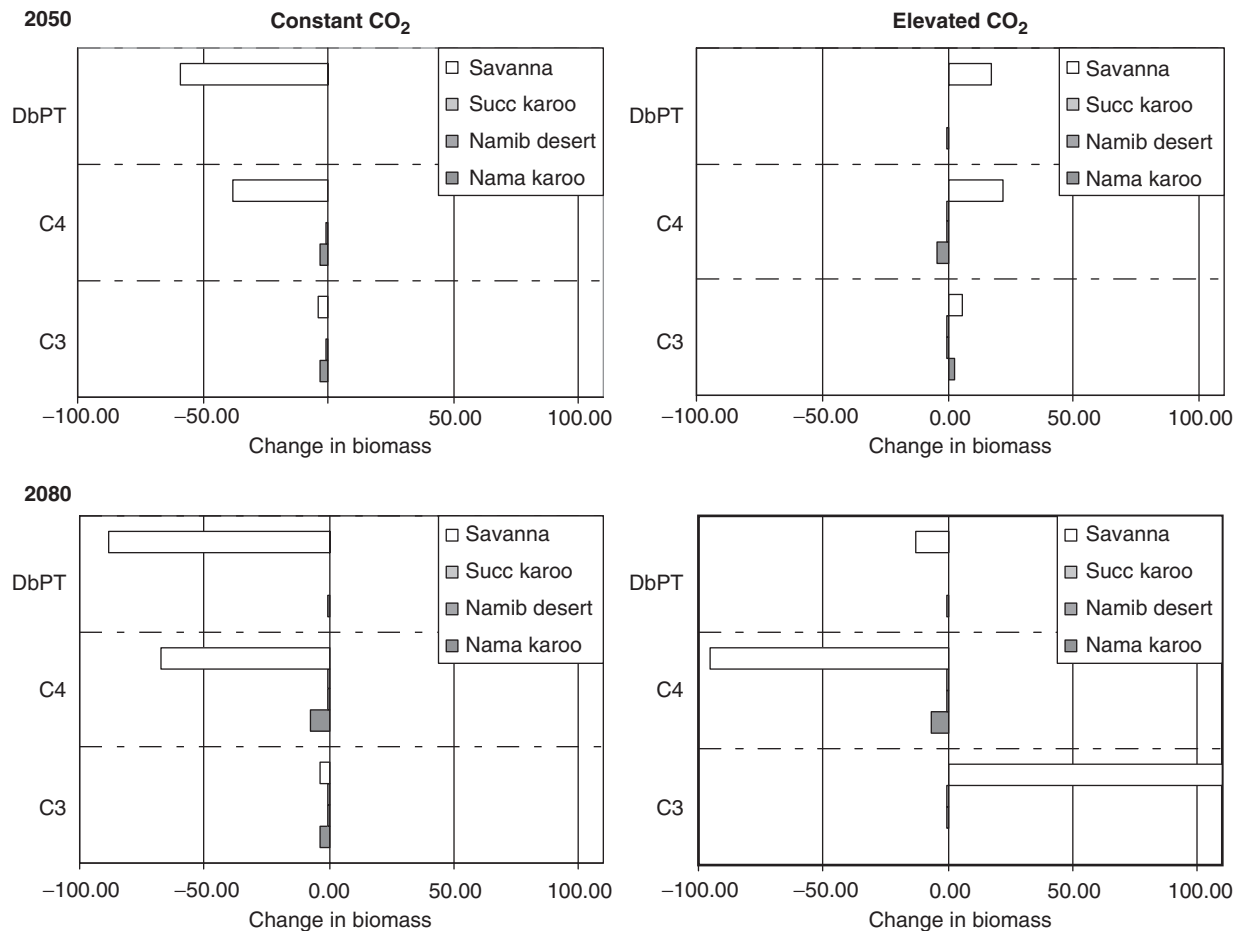
Fig. 8 Percentage change in biomass of the plant functional types as simulated by Sheffield dynamic global vegetation model simulated under both average climates 2050 and 2080, and according to the two atmospheric CO_2 scenarios (constant and elevated).

northwestern part of Namibia, where this PFT was currently projected (Namib desert biome). The decrease in cover was also accompanied by a small decrease in biomass (Fig. 8). Under constant CO_2 concentration, SDGVM simulated an almost complete extinction of this PFT by 2080, probably because of the decrease in precipitation. However, when the direct effects of rising CO_2 concentration are explicitly simulated, this PFT showed a strong increase in cover (Fig. 7) and biomass (Fig. 8) in the northeastern part of Namibia (tree and shrub savanna biome), with some areas completely dominated by C_3 vegetation and with an increase in biomass higher than 100% (Fig. 8).

The cover of C_4 vegetation under current climatic conditions was projected to be quite stable by 2050 (Fig. 7), with a slight decrease throughout Namibia (Fig. 8) under constant CO_2 concentrations. Although the cover of C_4 was also projected to be stable by 2080 under a constant CO_2 concentration, the direct effect of elevated CO_2 on plant gas exchange was projected to dramatically increase the negative impacts in 2080

with the virtual elimination of this PFT in the northeastern plain, replaced by a C_3 vegetation (see above) and a 90% drop in C_4 cover (Fig. 8).

Cover and biomass of the deciduous broad-leaved trees, the second-most dominant PFT, was also slightly reduced in extent by climate change under both constant and elevated CO_2 simulations (Figs 7 and 8). This PFT showed a reduction in cover throughout its current range under all simulations, showing a general retreat toward the northeast, where it was predicted to gain in biomass under elevated CO_2 by 2050 but not by 2080 (Fig. 8). Elevated CO_2 reduced substantially the reduction in biomass of this PFT by 2080, shown under constant CO_2 concentration.

Impacts on ecosystem functioning. LAI and net primary production (NPP) changes showed similar trends independently of CO_2 concentration (Fig. 7). Under constant CO_2, both NPP and LAI decreased throughout Namibia by both 2050 and 2080, and particularly in the central-northwestern region, but

remained relatively high in northeastern areas, where C$_4$ vegetation and deciduous broad-leaved trees were dominant. When CO$_2$ increased, both NPP and LAI showed significant increases in northeastern Namibia, more markedly by 2080 than 2050. In this case, C$_3$ vegetation expanded drastically and deciduous broad-leaved trees increased in biomass despite a reduction in cover.

Discussion

Endemic species and conservation issues

Under both time slices, results showed large variations in species responses, with range reductions expected for some species and range expansion for others. Geophytes, perennial herbs and trees are predicted to be negatively affected by climate change with consistent range reduction. Geophytes are found in a wide variety of habitats, and it is difficult to impute a particular sensitivity of these life-forms to climate change, given their stress-avoidance capabilities and water storage capacity. Clearly, this life-form demonstrates the weakness of simple correlative techniques that lack a mechanistic underpinning in projecting climate change impacts, as their ability to persist under stressful conditions may be underestimated by the correlative approach. The strong sensitivity of endemic trees is not surprising considering the strong temperature increase and reduction in rainfall. Even if these endemic trees have adapted to dry environments in evolutionary time, they would probably experience significantly greater stress from reduced water availability in the near future.

By contrast, the annual herb and succulent life-forms are relatively stable under the projected climate change scenarios. This might be expected because succulent species are thought to be tolerant of arid conditions, and represent a significant portion of the endemic flora of Namibia. However, it is also important to note that annual herb and succulent species occur mainly in the coastal and escarpment regions where climate change is projected to be the least severe in Namibia, especially the rainfall decrease (Table 1). Topographic refuges may also have facilitated the persistence of biodiversity here during periods of significant climate change during the Pleistocene (Midgley *et al.*, 2001), a repeating pattern that may also help explain high plant endemism in the mountainous Cape Floristic Region to the south, and even the Eastern Arc Mountains in Tanzania (Lovett *et al.*, 2000). This underscores the importance of including such landscape types in reserve networks designed to be robust to uncertain climate changes.

Coastal fog conditions are widely thought to support high levels of succulent plant endemism in Namibia and western South Africa, and therefore, some negative effects of climate change on the succulent life form, as well as the annual and perennial herbs, might be ameliorated by coastal fog where most species are concentrated. However, as fog is not simulated by current climate models, this explanation cannot be invoked to explain their modeled persistence with anthropogenic climate change. This shortcoming does indicate a potential uncertainty in coastal species' vulnerability to reductions in fog into the future, and deserves urgent attention.

Surprisingly, Namibian endemic species show an overall response to climate change which is distinct from the main body of nonendemic species modeled (data not shown). Endemics appear remarkably less affected than the nonendemic species both in term of species range change and extinction risk assessment. Three simple and possible interactive explanations could be advanced to explain this. First, NBM on nonendemic species could provide truncated response curves, as the species full climate space is not described, thereby biasing future projections (Van Horn, 2002). Second, endemic species, situated mainly in the coastal desert regions, are heat-stress tolerant and could even be favored by climate warming. Thirdly, this coastal desert region is predicted to experience less extreme climate change than any other part in Namibia.

Adaptive capacity by conservation is limited by the extensive spatial extent of these impacts, and the high cost of active adaptive interventions such as *ex situ* conservation or species translocation. On the other hand, the relatively low risk found for endemic species suggests that well-positioned protected areas will continue to contribute to conservation aims for some time to come, whereas threatened nonendemics are likely to be less at risk of climate change impacts in less marginal areas of their ranges outside Namibia. Further analyses to identify additional protected areas to complement reserve networks (Araújo *et al.*, 2004; Williams *et al.*, 2005) would be an appropriate and effective strategy to counter climate change threats to endemic species. Most of the existing protected areas are situated along the coast, where the species loss and turnover should be less severe and where most of the endemic species occur, but some are also in the northeastern part of the country, where the expected species loss and turnover could be particularly severe (Scholes & Walker, 1993). Under the assumption of full migration across the landscape, some current protected areas were even predicted to increase in endemic species richness. However, because many endemic species of arid southern Africa appear to have short distance dispersal

syndromes (anti-telechory; Rheede van Oudtshoorn & van Rooyen, 1999), and because of the probable need for unusually favorable conditions to allow new populations to establish and grow, it seems that a conservative estimate of migration rate is advised, tending more closely toward a 'null' rather than 'full migration' scenario.

Vegetation structure and ecosystem functioning

It is notable that projections of ecosystem structure and function suggest a negative response of vegetation to the warming and drying trends generated by the climate scenarios. Reductions in vegetation cover, increases in proportion of bare ground, and overall reductions in NPP all point to reduced potential of vegetation to support rangeland activities, be they on a commercial or subsistence model. This finding is in general accordance with the findings of Scholes *et al.* (1999) for South African rangelands, in the sense that rising atmospheric CO2 appears to ameliorate the negative effects of drying and warming only in the more mesic northwestern Namibia. This is almost certainly because the CO_2 effect on stomatal control of evapotranspiration is not effective where low vegetation cover and LAI imply low control of soil water by canopy transpiration (Bonan, 2002). Our modeling results show that this could be the case in the arid regions of the western and especially southwestern regions of Namibia. Where LAI is high, in woodland vegetation types of the northeast quadrant, rising atmospheric CO_2 may cause significant changes in ecosystem structure and function, through increasing success by woody elements, and potential increases in NPP.

It is interesting that elevated CO_2 particularly results in C_3 PFT encroachment in the northeast, and not in greater tree success. The impact of a simulated increase in soil nitrogen availability (data not shown) may be the underlying cause for this, as greater tree success was expected because of accelerated shoot growth and increased ability to tolerate grass fire regimes (Bond *et al.*, 2003). The model in fact simulates a decrease in both grass and tree success and increased representation of C_3 forms, which are simulated as flammable, as fire increases in significance with elevated CO_2. The relationship of this change with increased soil nitrogen availability is interesting, especially in the light of experimental results that suggest decreased nitrogen mineralization rates with rising atmospheric CO_2 in arid grassland (Gill *et al.*, 2002), through direct impacts on leaf litter quality. However, other ecosystem feedbacks incorporated in the DGVM, including the switch in dominant growth form and likely changes in soil water availability through stomatal effects of elevated

CO_2, appear to negate the feedback through reduced mineralization in this case. The increased success of the C_3 PFT under these conditions may alternatively be due to increased water-use efficiency (Drake *et al.*, 1997) and a subsequent stimulation of growth by higher soil water availability, especially in this area of variable rainfall. Variable rainfall conditions likely limit the success of trees more than they limit C_3 PFTs of smaller stature, because of their higher carbon costs during frequent intermittent drought. This is an interesting and important area for more detailed study.

The direct effects of elevated CO_2 clearly introduce significant uncertainty into projections of ecosystem structure and function, with very important implications for land users, land managers and conservationists, and these complex ecosystem feedbacks require much more detailed attention before projections can be made with any confidence. It is important to note here that large-scale free-air CO_2 (FACE) experiments needed to supply key answers to these questions are sorely lacking in subtropical ecosystems. This is a vital uncertainty, as a recent review suggests that tree PFTs show the most significant positive response to elevated CO_2 of all PFTs investigated (Ainsworth & Long, 2005). The ability of FACE experiments to apply treatments to established trees with intact and developed rooting systems may provide the data needed to reassess the assumptions incorporated in DGVM algorithms.

Species vs. PFT results

Although a strict comparison between NBM and SDGVM was not straightforward, several interesting patterns emerge from this analysis, even though from a species-specific and conservation perspective, we analyzed only endemic plants that contribute to the extraordinary richness of these areas. For instance, most of the tree species studied here occurred in very arid zones (Namib desert and Nama Karoo), where they are a critical component of overall species diversity. However, as very rare and restricted, and probably very area-specific, they are not modeled by SDGVM which predicts bare-ground cover as dominant, and no tree cover. Therefore, according to the SDGVM projections, trees should be excluded from this area. This reveals some potential shortcomings of DGVM for regional assessments; they cannot currently take into account local variation in soil depth and hydrology without more complete global soil datasets, and they also ignore local evolutionary processes that may result in PFTs that have greater drought tolerance, for example, than a 'global average' PFT.

However, careful examination of the results from NBM and SDGVM show that they do provide similar

and complementary outputs in some respects. In the very arid biomes (Namib desert and Nama Karoo), SDGVM predicts a strong reduction in cover and biomass (mostly C_3 PFT) under both constant and rising CO_2 concentrations, whereas NBM also predicts a strong reduction in perennial herb, geophyte, grass, shrub and tree species richness. What SDGVM does not show, is the potential increase in migration of species toward the coast and cooler areas. This reveals how the approaches might complement one another, in addressing species and ecosystem responses at rather different scales and resolutions (Midgley & Thuiller, 2005).

The most surprising agreement between both approaches is observed in the northeastern quadrant of Namibia. According to the correlative NBMs, annual and perennial herbs, shrubs, and to a lesser extent, succulent species are predicted to expand north-eastward, which corroborates the SDGVM simulations, but only if the direct effect of rising CO_2 concentration is included. If this effect is ignored, SDGVM simulates a reduction in cover and biomass of most PFTs, which disagrees with NBM. It is very hard to find a simple explanation, because NBM are unable to incorporate CO_2 and nitrogen fertilization effects. A possible explanation may reside in the rooting depth assumptions of SDGVM, which adopt a limit of 1 m. Although the effective rooting depth of trees, shrubs and grasses is in all likelihood not significantly greater than this for nutrient uptake activity (Scholes & Walker, 1993), it is known that trees often extend 'sinker roots' to depths up to 2 m and deeper, and have been identified at depths of 50 m (Rutherford, 1978; Canadell et al., 1996). This shortcoming will almost certainly result in an over-estimation of plant mortality under variable rainfall conditions, regardless of CO_2 fertilization. On the other hand, the fertilizing effects of higher CO_2 would favor herbaceous and shrubby C_3 species under these conditions, thus more closely approximating the simulation of the NBM.

The strength of DGVM is to simulate accurately the transient dynamics of vegetation and ultimately ecosystem function at broad spatial scales. NBM are essentially static, but can be used to analyze the impact of climate change on vegetation structure at finer spatial scales, capturing potential impacts of species migration, for example, not simulated by DGVM. NBM might ultimately be used to infer changes in ecosystem functioning, for example, if detailed species distribution and abundance data, and fine-scale climate data were available, we might be able to predict all Namibian species' distributions and abundances (4500 plant taxa) and derive the vegetation structure based on simple life-history traits (Lavorel & Garnier, 2002) of dominant species (Grime, 1998). Basic rules to account for competition for above- and belowground resources would be necessary, but might be estimated. However, the significant computational requirements of such an approach shows the benefits of the mechanistic approach to simulating processes in SDGVM using abstract PFTs, and why these approaches currently appear conceptually far removed from one other.

References

Ainsworth EA, Long SP (2005) What have we learned from 15 years of free-air CO_2 enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO_2. New Phytologist, 165, 351–372.

Allen RG, Pereira LS, Raes D et al. (1998) Crop evapotranspiration guidelines for computing crop water requirements. Food and Agriculture Organization of the United Nations, Rome.

Araújo MB, Cabeza M, Thuiller W (2004) Would climate change drive species out of reserves? An assessment of existing reserve-selection methods. Global Change Biology, 10, 1618–1626.

Bachelet D, Neilson RP, Hickler T et al. (2003) Simulating past and future dynamics of natural ecosystems in the United States. Global Biogeochemical Cycles, 17, 14.11–14.21.

Bakkenes M, Alkemade RM, Ihle F et al. (2002) Assessing effects of forecasted climate change on the diversity and distribution of European higher plants for 2050. Global Change Biology, 8, 390–407.

Beerling DJ, Woodward FI (2001) Vegetation and the Terrestrial Carbon Cycle. Modelling the First 400 Million Years. Cambridge University Press, Cambridge.

Bonan GB (2002) Ecological Climatology: Concepts and Applications. Cambridge University Press, Cambridge.

Bond WJ, Midgley GF, Woodward FI (2003) The importance of low atmospheric CO_2 and fire in promoting the spread of grasslands and savannas. Global Change Biology, 9, 973–982.

Canadell J, Jackson RB, Ehleringer JR et al. (1996) Maximum rooting depth of vegetation types at the global scale. Oecologia, 108, 583–606.

Cowling SA (1999) Plants and temperature–CO_2 uncoupling. Science, 285, 1500–1501.

Cowling RM, Richardson DM, Pierce S (1997) Vegetation of Southern Africa. Cambridge University Press, Cambridge, UK.

Cowling SA, Sykes MT (1999) Physiological significance of low atmospheric CO_2 for plant–climate interactions. *Quaternary Research*, **52**, 237–242.

Cramer W, Bondeau A, Woodward FI et al. (2001) Global response of terrestrial ecosystem structure and function to CO_2 and climate change: results from six dynamic global vegetation models. *Global Change Biology*, **7**, 357–373.

Daly C, Bachelet D, Lenihan JM et al. (2000) Dynamic simulation of tree–grass interactions for global change studies. *Ecological applications*, **10**, 449–469.

Drake BG, Gonzalez-Meler MA, Long SP (1997) More efficient plants: a consequence of rising atmospheric CO_2? *Annual Review of Plant Physiology and Plant Molecular Biology*, **48**, 609–639.

Drew G (2004) *Modelling Vegetation Dynamics and their Feedbacks over Southern Africa in Response to Climate Change Forcing*. University of Cape Town South Africa.

Germishuizen G, Meyer NL (2003) Plants of southern Africa: an annotated checklist. *Strelitzia*, **14**, 1–1231.

Gill RA, Polley HW, Johnson HB et al. (2002) Nonlinear grassland responses to past and future atmospheric CO_2. *Nature*, **417**, 279–282.

Giorgi F, Hewitson BC, Christensen J et al. (2001) Regional climate information – evaluation and projections. In: *Climate Change 2001: The Scientific Basis* (eds Houghton JT, Ding Y, Nogouer M), pp. 583–638. Cambridge University Press, Cambridge.

Grime JP (1998) Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *Journal of Ecology*, **86**, 902–910.

Guisan A, Thuiller W (2005) Predicting species distribution: offering more than simple habitat models. *Ecology Letters*, **8**, 993–1009.

Guisan A, Zimmermann NE (2000) Predictive habitat distribution models in ecology. *Ecological Modelling*, **135**, 147–186.

Hewitson B (2003) Developing perturbations for climate change impact assessments. *EOS*, **84**, 337–339.

Ihaca R, Gentleman R (1996) R: a language for data analysis and graphics. *Journal of Computational and Graphical Statistics*, **5**, 299–314.

IPCC (2001). *Climate change 2001: impacts, adaptation, and vulnerability*. Contribution of Working Group II to the Third Asssessment Report of the IPCC. Cambridge University Press, United Kingdom and New York.

IPCC-TGCIA ed. (1999). *Guidelines on the Use of Scenario Data for Climate Impact and Adaptation Assessment. Intergovernmental Panel on Climate Change*. Task Group on Scenarios for Climate Impact Assessment.

Irish J (1994) Biomes of Namibia. *Navorsings van die Nasionale Museum*, **10**, 550–584.

IUCN, editor. (2001). *IUCN Red List Categories and Criteria: Version 3.1*. IUCN Species Survival Commission, IUCN, Gland and Cambridge.

Iverson LR, Prasad A (2002) Potential redistribution of tree species habitat under five climate change scenarios in the eastern US. *Forest Ecology and Management*, **155**, 205–222.

Lavorel S, Garnier E (2002) Predicting changes in community composition and ecosystem functioning from plant trait: revisiting the Holy Grail. *Functional Ecology*, **16**, 545–556.

Lovett JC, Rudd S, Taplin J et al. (2000) Patterns of plant diversity in Africa south of Sahara and their implications for conservation management. *Biodiversity and Conservation*, **9**, 37–46.

Maggs GL, Craven P, Kolberg HH (1998) Plant species richness, endemism, and genetic resources in Namibia. *Biodiversity and Conservation*, **7**, 435–446.

Maggs GL, Kolberg HH, Hines CJH (1994) Botanical diversity in Namibia – an overview. *Strelitzia*, **1**, 93–104.

Midgley GF, Hannah L, Millar D et al. (2002) Assessing the vulnerability of species richness to anthropogenic climate change in a biodiversity hotspot. *Global Ecology and Biogeography*, **11**, 445–451.

Midgley GF, Hannah L, Millar D et al. (2003) Developing regional and species-level assessments of climate change impacts on biodiversity: a preliminary study in the Cape Floristic Region. *Biological Conservation*, **112**, 87–97.

Midgley GF, Hannah L, Roberts R et al. (2001) Have Pleistocene climatic cycles influenced species richness patterns in the Greater Cape Mediterranean Region? *Journal of Mediterranean Ecology*, **2**, 137–144.

Midgley GF, Thuiller W (2005) Global environmental change and the uncertain fate of biodiversity. *New Phytologist*, **167**, 638–641.

Mitchell TD, Carter TR, Jones PD et al. 2004 *A comprehensive set of high-resolution grids of monthly climate for Europe and the globe: the observed record (1990-2000) and 16 scenarios (2001–2100)*. 55, Tyndall Centre Working Paper.

Monserud RA, Leemans R (1992) Comparing global vegetation maps with the Kappa statistic. *Ecological Modelling*, **62**, 275–293.

Nakicenovic N, Swart R), eds. (2000) *Emissions Scenarios: A Special Report of Working Group III of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge.

New M, Lister D, Hulme M et al. (2000) A high-resolution data set of surface climate over global land areas. *Climate Research*, **21**, 1–25.

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

Parton WJ, Scurlock JMO, Ojima DS et al. (1993) Observations and modeling of biomass and soil organic matter dynamics for the grassland biome worldwide. *Global Biogeochemical Cycles*, **7**, 785–809.

Pearce J, Ferrier S (2000) Evaluating the predictive performance of habitat models developed using logistic regression. *Ecological Modelling*, **133**, 225–245.

Pearson RG, Dawson TP, Liu C (2004) Modelling species distributions in Britain: a hierarchical integration of climate and land-cover data. *Ecography*, **27**, 285–298.

Peterson AT, Ortega-Huerta MA, Bartley J et al. (2002) Future projections for Mexican faunas under global climate change scenarios. *Nature*, **416**, 626–629.

Pulliam HR (2000) On the relationship between niche and distribution. *Ecology Letters*, **3**, 349–361.

Rheede van Oudtshoorn KV, van Rooyen MW (1999) *Dispersal Biology of Desert Plants*. Springer, New York.

Ruosteenoja K, Carter TR, Jylhä K *et al.* (2003) *Future Climate in World Regions: An Intercomparison of Model-Based Projections for the New IPCC Emissions Scenarios*. Finnish Environment Institute, Helsinki.

Rutherford MC (1978) Woody plant biomass distribution in *Burkea africana* Savannas. In: *Biogeography and Ecology of Southern Africa* (ed. Werger MJA), p. 659, Junk, The Hague.

Scholes RJ, Midgley GF, Wand SJE, eds. (1999) *Vulnerability and Adaptation of Rangelands*, South African Climate Change Country Studies Report CSIR Pretoria.

Scholes RJ, Walker BJ (1993) *An African Savanna: Synthesis of the Nylsvley Study*. Cambridge University Press, Cambridge.

Sitch S, Smith B, Prentice IC *et al.* (2003) Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model. *Global Change Biology*, 9, 161–185.

Smith B, Prentice IC, Sykes MT (2001) Representation of vegetation dynamics in modelling of European ecosystems: comparison of two contrasting approaches. *Global Ecology and Biogeography*, 10, 621–637.

Swets KA (1988) Measuring the accuracy of diagnostic systems. *Science*, 240, 1285–1293.

Thomas CD, Cameron A, Green RE *et al.* (2004) Extinction risk from climate change. *Nature*, 427, 145–148.

Thuiller W (2003) BIOMOD: optimising predictions of species distributions and projecting potential future shifts under global change. *Global Change Biology*, 9, 1353–1362.

Thuiller W, Araújo MB, Lavorel S (2004a) Do we need land-cover data to model species distributions in Europe? *Journal of Biogeography*, 31, 353–361.

Thuiller W, Araújo MB, Pearson RG *et al.* (2004b) Uncertainty in predictions of extinction risk. *Nature*, 430, 34.

Thuiller W, Brotons L, Araújo MB *et al.* (2004c) Effects of restricting environmental range of data to project current and future species distributions. *Ecography*, 27, 165–172.

Thuiller W, Lavorel S, Araújo MB (2005a) Niche properties and geographic extent as predictors of species sensitivity to climate change. *Global Ecology and Biogeography*, 14, 347–357.

Thuiller W, Lavorel S, Araújo MB *et al.* (2005b) Climate change threats to plant diversity in Europe. *Proceedings of the National Academy of Sciences, USA*, 102, 8245–8250.

Travis JMJ (2003) Climate change and habitat destruction: a deadly anthropogenic cocktail. *Proceedings of the Royal Society of London Series B*, 270, 467–473.

Van Horn B (2002) Approaches to habitat modelling: the tensions between pattern and process and between specificity and generality. In: *Predicting Species Occurrences: Issues of Accuracy and Scale* (eds Scott JM, Heglund PJ, Morrison ML *et al.*), pp.63–72. Island Press, Covelo, CA.

Walther G-R, Post E, Convey P *et al.* (2002) Ecological responses to recent climate change. *Nature*, 416, 389–395.

Williams PH, Hannah L, Andelman S *et al* (2005) Planning for climate change: identifying minimum-dispersal corridors for the Cape Proteaceae. *Conservation Biology*, 19, 1063–1074.

WIND, ed. (2004) *SPMNDB Database*. National Herbarium of Namibia, National Botanical Research Institute, MAWRD, Windhoek, Namibia.

Woodward FI, Cramer W (1996) Plant functional types and climate changes: introduction. *Journal of Vegetation Science*, 7, 306–308.

Woodward FI, Lomas MR (2004a) Simulating vegetation processes along the Kalahari transect. *Global Change Biology*, 10, 383–392.

Woodward FI, Lomas MR (2004b) Vegetation dynamics – simulating responses to climatic change. *Biological reviews*, 79, 643–670.

Woodward FI, Lomas MR, Betts RA (1998) Vegetation-climate feedbacks in a greenhouse world. *Philosophical Transactions of the Royal Society of London Series B*, 353, 29–38.

Woodward FI, Lomas MR, Lee SE (2001) Predicting the future productivity and distribution of global terrestrial vegetation. In: *Terrestrial Global Productivity* (eds Roy J, Saugier B, Mooney HA), pp. 521–541. Academic Press, New York.

Woodward FI, Smith TM, Emanuel WR (1995) A global land primary productivity and phytogeography model. *Global Biogeochemical Cycles*, 9, 471–490.