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Vulnerability of African mammals to anthropogenic climate change under conservative land transformation assumptions

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Abstract

Recent observations show that human-induced climate change (CC) and land transformation (LT) are threatening wildlife globally. Thus, there is a need to assess the sensitivity of wildlife on large spatial scales and evaluate whether national parks (NPs), a key conservation tools used to protect species, will meet their mandate under future CC and LT conditions. Here, we assess the sensitivity of 277 mammals at African scale to CC at 10′ resolution, using static LT assumptions in a 'first-cut' estimate, in the absence of credible future LT trends. We examine the relationship between species' current distribution and macroclimatic variables using generalized additive models, and include LT indirectly as a filter. Future projections are derived using two CC scenarios (for 2050 and 2080) to estimate the spatial patterns of loss and gain in species richness that might ultimately result. We then apply the IUCN Red List criteria A3(c) of potential range loss to evaluate species sensitivity. We finally estimate the sensitivity of 141 NPs in terms of both species richness and turnover. Assuming no spread of species, 10–15% of the species are projected to fall within the critically endangered or extinct categories by 2050 and between 25% and 40% by 2080. Assuming unlimited species spread, less extreme results show proportions dropping to approximately 10–20% by 2080. Spatial patterns of richness loss and gain show contrasting latitudinal patterns with a westward range shift of species around the species-rich equatorial zone in central Africa, and an eastward shift in southern Africa, mainly because of latitudinal aridity gradients across these ecological transition zones. Xeric shrubland NPs may face significant richness losses not compensated by species influxes. Other NPs might expect substantial losses and influxes of species. On balance, the NPs might ultimately realize a substantial shift in the mammalian species composition of a magnitude unprecedented in recent geological time. To conclude, the effects of global CC and LT on wildlife communities may be most noticeable not as a loss of species from their current ranges, but instead as a fundamental change in community composition.

Keywords: Africa, climate change, extinction risk, IPCC storylines, land transformation, mammals, national parks, species distribution models

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Introduction

Future changes in atmospheric CO_2 and climate will directly affect the distribution, abundance and life cycles of most species and ecosystems (Araújo *et al.*, 2005a; Schröter *et al*., 2005). Species are generally expected to respond individualistically to these changes, for example by shifting their distributions as they track moving climate zones (Prentice, 1986; Huntley, 1990; Graham, 1992). Hypothetically, the geographic ranges and/or coincidence of species that currently interact may therefore progressively move apart, while species that do not presently coexist may do so in the future (Araújo *et al*., 2005a). Thus, great potential exists for novel species combinations to occur, and for present-day relationships to become increasingly decoupled (Hughes, 2000). Recent metaanalyses have already shown species' range shifts because of climate change (CC) during the last century for both animal and plant taxa (Parmesan & Yohe, 2003; Root *et al*., 2003). Land transformation (LT) by humans restructures the landscape, enhancing or, more often, perturbing species range migrations that may be induced by CC. These synergistic human-induced global changes therefore threaten wildlife and vegetation around the globe (Sala *et al*., 2000), and decisions may have to be made to optimize the persistence of this biodiversity (Araújo *et al*., 2004).

In the past decade, several papers have related climate to the distribution of species (Huntley *et al*., 1995; Sykes, 2001; Bakkenes *et al*., 2002; Peterson *et al*., 2002; Thuiller *et al*., 2005a), plant functional types (Box, 1996; Smith *et al*., 2001; Sitch *et al*., 2003; Thuiller *et al*., 2006) or biomes (Malcolm *et al*., 2002), estimating the likely impacts of CC under a range of possible future scenarios. However, few studies have attempted to assess the impacts of global change on animal distributions, and especially mammals (but see Erasmus *et al*., 2002; Burns *et al*., 2003). Animals, as consumers at higher trophic levels, are influenced both by climate that potentially limits physiological processes, and by vegetation that determines resource availability and habitat. They are, therefore, likely colimited by vegetation and climate (Grayson, 2000). Evidence from palaeoecological studies suggests that mammals responded abruptly to Middle-Holocene CC, especially around the Great Basin of the western US (Grayson, 2000), by showing a decrease in species richness and evenness, driven largely by a series of local extinctions and near-extinctions coupled with a dramatic increase in the abundance of xerophytic taxa (Graham, 1992; Grayson, 2000). It is, therefore, likely that similar dynamics will occur in response to the projected CC for the 21st century, probably exacerbated by the increase of LT (Sanderson *et al*., 2002). National parks (NPs) and bioreserves are key conservation tools used to protect species and their habitats within the confines of fixed boundaries. With the distributional changes expected with CC comes a great uncertainty about the future ability of parks and protected areas to meet their conservation mandates (Burns *et al*., 2003).

In this paper, we assess the relative sensitivity of wild African mammals to CC taking into account the patterns of anthropogenic LT that have occurred on the continent in order to prevent an unrealistic assessment, and we evaluate the ability of African NPs to protect mammals into the future. Projections of future LT are not available for Africa, and are contingent on a plethora of socioeconomic drivers that may increase or decrease pressure on the expansion of land-use activities. Consequently, the use of current LT data provides a pragmatic first approximation of the future situation. We first relate the current distribution of 277 mammal species to present-day climate. Then, a LT map is used to filter the current potential distribution of every species by removing completely transformed climatically suitable habitats. We then project the future potential climatically suitable habitats of every species under two CC scenario extremes for 2050 and 2080. Finally, we address the following questions:

1. How sensitive are African mammals to CC, given current LT patterns?
2. What regions are most at risk to the impacts of CC on mammal ranges?
3. What level of species turnover may be experienced in the 141 selected African NPs under CC?

Materials

Species datasets

Distributions for 277 species, belonging to 12 orders and 28 families, were extracted from the African Mammals Databank, an atlas of medium to large mammals (AMD; IEA, 1998). Species included orders of Primates, Carnivora, Perissodactyla (except rhinoceros for security reasons), Hyracoidea, Tubulidentata, Artiodactyla, Pholidota, Lagomorpha, Macroscelidea and seven species of the Rodentia. The distributions from the AMD were extracted for each species in the form of extent of occurrence (EO), which defines the boundaries of a polygon in which observers have recorded occurrences of the species. The EO does not incorporate recorded absences inside the EO, and does not give any information about how abundance varies across the range. In order to match the resolution of environmental data, species' range polygons were rasterized to a $10' \times 10'$ grid.

Climate datasets

The CRU CL 2.0 dataset (New *et al*., 2000) at a resolution of $10' \times 10'$ was chosen to represent current climate.

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 A2 and B2 IPCC SRES scenarios (Nakicenovic & Swart, 2000) in accordance with globally accepted guidelines for climate impact assessment (IPCC-TGCIA, 1999).

We used six uncorrelated variables (selected after cross-correlation evaluation from principal component analysis) representing the major climatic gradients in Africa, namely: mean annual potential evapotranspiration, annual growing-degree days, minimum temperature of the coldest month, maximum temperature of the warmest month, mean annual temperature and annual sum of precipitation.

LT dataset

Data on LT at a resolution of $10' \times 10'$ were resampled from the $0.5'$ resolution 'Human Footprint' dataset (Sanderson *et al*., 2002). At present, this represents the most consistent source of LT on a global basis. The human footprint dataset is similar to the ecological footprint, a set of techniques for estimating the amount of land or sea necessary to support the consumption habits of one individual, population, product, activity or service (Wackernagel & Rees, 1996). The human footprint represents in some sense the total sum of ecological footprints of the human population. It expresses that sum not as a single number, however, but as a continuum of human influence stretched across the land surface, revealing through its variation the major patterns of human influence on nature. The Human Footprint uses four types of data as proxies for human influence: population density, LT, accessibility and electrical power infrastructure. It ranges from 0 to 1, proceeding from natural to completely transformed and inadequate habitat for wildlife.

Unfortunately, there is no available dataset for future LT in Africa. Because LT on the continent is driven by such a wide range of socioeconomic drivers, and is even subject to uncertainties as unpredictable as political instability, we concluded that simple estimates, such as extrapolations of past LT trends, are likely to be misleading. It was, thus, assumed that future LT is best conservatively described by the current LT dataset as this represents a conservative prognosis of the future and limits additional uncertainty owing to future LT projections.

Methods

Generalized additive models (GAM, Hastie & Tibshirani, 1990) implemented into the Splus-based BIOMOD application (Thuiller, 2003), relating the mammal species distributions to the six bioclimatic variables, were calibrated using a random sample of the initial data (70%) and a stepwise selection methodology, with the most parsimonious model being selected using the Akaike information criterion (AIC) (e.g. Thuiller *et al*., 2003, 2004a). The predictive power of each model 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 (one specificity) (Swets, 1988). Sensitivity was defined as the proportion of true positives correctly predicted, whereas specificity was the proportion of true negatives correctly predicted. We used the following conservative rough guide for AUC: <0.8, null model; $0.8<\text{AUC}<0.9$, fair model; $0.9<\text{AUC}<0.95$, good model and $0.95<\text{AUC}<1$, very good model. We only used the ROC curve procedure as it is does not require the estimation of an artificial threshold to transform probability of occurrence to binary data and it is not biased by prevalence like Cohen's κ index (Fielding & Bell, 1997; Pearce & Ferrier, 2000).

The probabilities of occurrence from the mammal models were then filtered by the LT information. We applied this filter by weighting the probability of occurrence by the human footprint following: $\text{FP}_i = \text{IP}_i \times \text{LT}_i$, where FP is the final probability of occurrence in the pixel i, IP is the initial probability of occurrence in the pixel i, and LT is the percentage of land untransformed in the pixel i.

For instance, if the probability of occurrence of a species based only on climate in a given pixel is 0.5, and the habitat is 90% transformed: $\text{FP} = 0.5 \times 0.1 = 0.05$.

Finally, the probabilities of occurrence from the filtered mammal models were converted into presence/absence using a threshold maximizing the percentage of presence and absence correctly predicted (Pearce & Ferrier, 2000).

The GAM models were then used to make projections into the future using the different CC scenarios for the two time slices considered, and weighting by the human footprint was applied to the future probabilities of occurrence. After transformation of the probabilities of occurrence into presence–absence values using the same threshold determined for current presence, we estimated indices of vulnerability. These indices have been estimated according two extreme assumptions concerning the ability of species to spread or colonize into new climatic suitable habitat. Either we assumed no spread ability of species (null spread), or unlimited spread (full spread). The full spread assumption assumes the spread to be instantaneous and fully effective, so that ranges that have become newly suitable are invariably colonized. Under the null spread assumption, spread is assumed to be totally limiting, and individuals are unable to occupy a new range. Neither of these approximations is satisfactory, as spread rates depend to a large extent on the characteristics of each individual species. However, based on current knowledge and modelling frameworks, they allow the expected impact on ranges to be bracketed.

Extinction risk

We assigned each 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 where a species was predicted to occur. 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% in 50 or 80 years; critically endangered (CR): projected range loss of $>80\%$; endangered (EN): projected range loss of $>50\%$; and vulnerable (VU): projected range loss

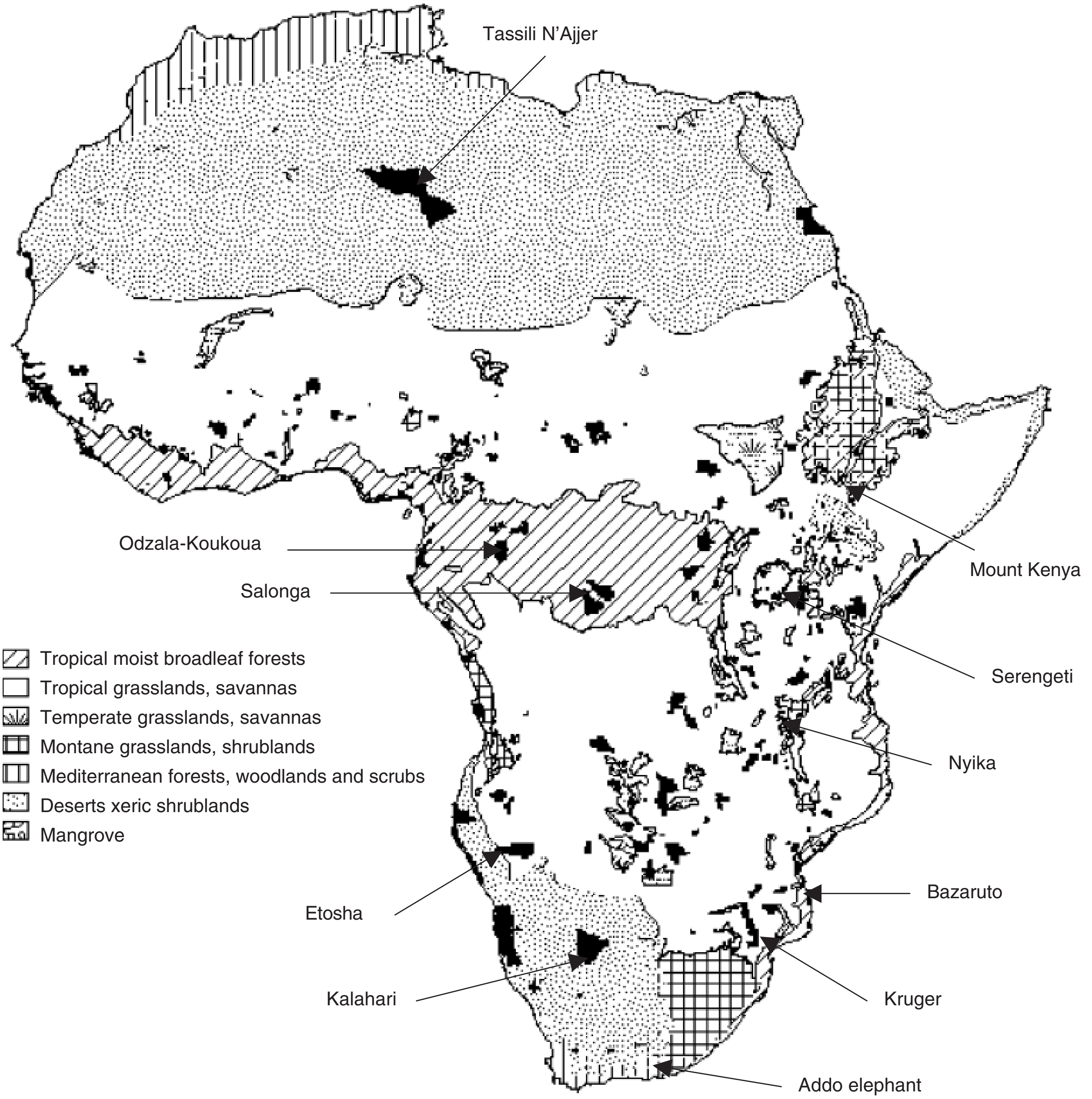


Fig. 1 Spatial distribution of African biomes and the representation of the national parks (NPs) in Africa. Named NPs correspond to those highlighted in Table 1.

of $>30\%$. It is important to note that our Red Listing approach is simplistic, general and considers only the future effects of rapid anthropogenic CC and static LT. More details and pro and con discussions on the use of Red Listing approach to derive extinction risks of species can be found in Bomhard *et al*. (2005).

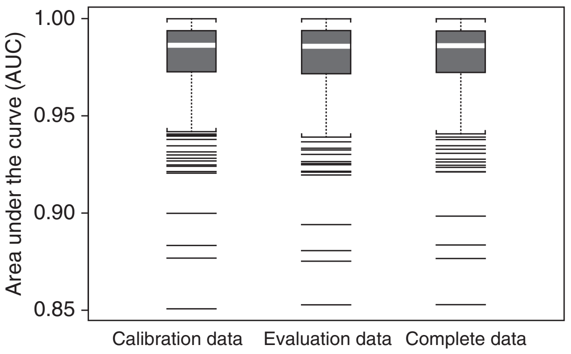


Fig. 2 Summary of the area under the curve (AUC) generated from the mammal models, using the calibration data used to calibrate the models (70% of the complete data), using the evaluation (the remaining 30%) and the complete dataset. Single horizontal bars represent outliers of the relationships.

Spatial index

To evaluate the percentage of extinction at pixel level, we summed the predicted number of species lost (L) by pixel and related it to the predicted current species richness (SR) by pixel. The procedure was also used to assess the percentage of species gained (G) by pixel (under full spread assumption).

Protected areas

The areas of African land especially dedicated to the protection and maintenance of biological diversity, and managed through legal or other effective means were extracted from the World Database on Protected Areas 2005 (WDPA, 2005). The WPDA is the most comprehensive global catalogue of protected areas, and includes data on size, locations and Word Conservation Union (IUCN) classifications of management designation. Protected areas in categories I–IV were explicitly designed for biodiversity protection while those in categories V and VI were designed with multiple-management objectives in mind (IUCN, 2001). At the African continental scale, we only focused on the NPs (category II; Fig. 1) (category II), representing natural area of land designated to (a) protect the ecological integrity of ecosystems for present and future generations, (b) exclude exploitation inimical to the purposes of designation of the area and (c) provide a environmentally and culturally compatible foundation for spiritual, scientific, educational, recreational and visitor opportunities (IUCN, 2001).

Finally, we assessed the sensitivity of each NP to CC estimating the predicted number of species lost, gained and the related turnover according to the different CC scenarios and time slices.

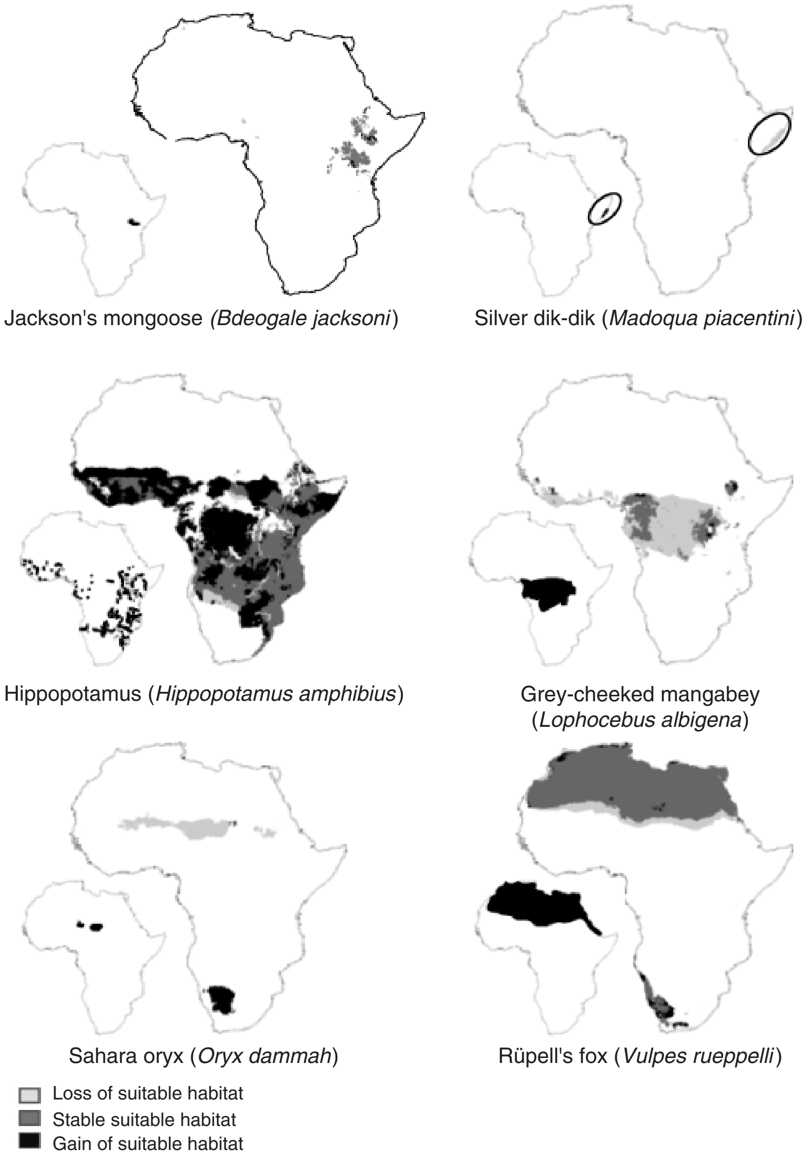
Results

Model evaluation

The mammal models filtered by the LT showed a good predictive power with a mean AUC of around 0.98 estimated on the evaluation data (Fig. 2). The minimum accuracy value was 0.85 recorded for the common hippopotamus (*Hippopotamus amphibious*) almost certainly because our analysis did not include wetland habitats. The maximum accuracy value was 1.0 recorded for the bovid Silver dik-dik (*Madoqua piacentini*), which showed perfect prediction (see Fig. 3). Such a high accuracy may be expected considering the spatial resolution of the analysis, as large-scale patterns are easier to predict than finer scale ones. For this reason, we consider an AUC of 0.85 as a weak model, although at a fine scale this would usually be considered a good model.

Species-specific sensitivity

Example results demonstrated the idiosyncratic response of species to potential CC and current LT (Fig. 3). The Jackson's mongoose (*Bdeogale jacksoni*), for instance, was predicted to be fairly stable and could potentially gain few suitable habitats closeby its current range. Inversely, the Silver dik-dik, a species currently classified as VU by the Red List, was predicted to experience an almost complete disappearance of its climatically suitable habitat. Our poor predictive ability for the hippopotamus was clearly apparent (Fig. 3). Nevertheless, the species was predicted to gain some potential climatically suitable habitat in the equatorial belt. The grey-cheeked mangabey (*Lophocebus albigena*), which was very well predicted under current conditions ($\mathrm{AUC} = 0.99$), was also predicted to lose a large amount of climatically suitable habitat, mainly in the middle of its current range, dividing its potential future range into two disjunct zones. The last two examples highlight the uncertainty provided by the two crude spread assumptions. The CR Sahara oryx (*Oryx dammah*) was predicted to lose almost all its current climatically suitable habitat in the Sahara desert, but to gain substantially in Namibia and Botswana, in a region to which it was unlikely to spread without human



Jackson's mongoose (*Bdeogale jacksoni*) Silver dik-dik (*Madoqua piacentini*)

Hippopotamus (*Hippopotamus amphibius*) Grey-cheeked mangabey (*Lophocebus albigena*)

Sahara oryx (*Oryx dammah*) Rüpell's fox (*Vulpes rueppelli*)

Fig. 3 Observed and predicted distribution under the HadCM3 A2 2050 scenario for six species. For each couple of maps, the small one is the observed distribution from the AMD, and the larger one is the predicted one. Clear grey indicates current climatic suitable habitats predicted to be unsuitable by 2050, moderate grey indicates the current climatic suitable habitats predicted to stay suitable by 2050 and dark grey indicates the current climatic nonsuitable habitats predicted to be suitable by 2050.

intervention. Similarly, while the current climatically suitable habitat of the Rüppell's fox (*Vulpes ruepelli*) was predicted to remain fairly stable in the future (Fig. 3), this species appeared to have current and future climatically suitable habitats in Namibia and South Africa although it had never been recorded in this region.

Our simple application of a single IUCN Red List A3(c) criterion highlighted that in the worst-case scenario, up to 4% of the African mammals species appeared severely threatened by future CC and current LT (Fig. 4). Under the assumption of null spread ability, between 40% and 50% of the species were classified at LR (respectively, for scenarios HadCM3-A2 and HadCM3-B2) for 2050 and 25% and 35% for 2080. Very few species were classified as EX under the null spread ability, but under the HadCM3-A2 storyline, 37.5% of the species were predicted to become CR after 2080. For both time slices, CC and LT affected species less under the full migration assumption because of the potential for species to move across landscapes and occupy new ranges. Under the full migration ability, between 56% and 62% of the species were classified as LR

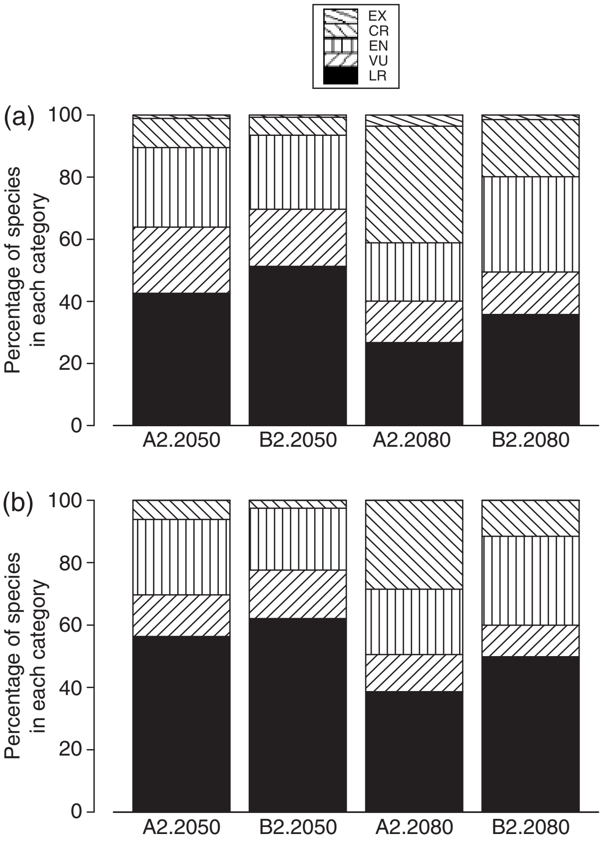


Fig. 4 Barplots representing the percentage of species classified according to our IUCN Red list assessment for each time slice and under both assumption on species' migration. (a) no migration ability, (b) full migration ability. EX, extinct; CR, critically endangered; EN, endangered; VU, vulnerable; LR, lower risk.

(respectively, for HadCM3-A2 and HadCM3-B2 storylines) for 2050 and between 39% and 50% for 2080.

The HadCM3-A2 storyline was more severe for wildlife distribution than the HadCM3-B2 storyline, reflecting economic vs. sustainable development strategies. As expected, projections for 2080 displayed more negative impacts than 2050 projections.

Spatial wildlife sensitivity

For both time slices and storylines, two regions of high species loss were discernible (Fig. 5). The first was situated in species-rich central Africa (mostly in the Congo Basin), which exhibited very high species losses (50–60% for A2 2050 and 60–75% for A2 2080) and extending patchily westwards along coastal regions. The second region was centred on the Kalahari region in arid Namibia, northern South Africa and Botswana, but extending patchily to the Mozambique coastline. The absolute numbers of species loss here were lower than for the central African region, but higher in relative terms (70–80% for A2 2050 and 80–100% for A2 2080). Similar to the species-specific projections, rates of species loss were exacerbated for 2080 under the storylines used in this study.

The rate of species gain was likely to be less reliable than rate of species loss, as we did not explicitly model spread across the landscape in our analysis. However, they provided insights into the directional trend of change. Interestingly, two regions of high species gains were detectible at the same latitude as the highest areas of species loss (Fig. 6). Nevertheless, there was a different longitudinal pattern. The northern region was situated around Gabon, western Zaire and northwestern Angola with an average of 40% gain for A2 2050 and 65% for A2 2080. The southern region occurred in northeastern South Africa and adjacent southern Mozambique with an increase in richness of 50% for A2 2050 and 80% for A2 2080.

Spatial patterns were quite clear and mostly related to the aridity gradients (Fig. 7): CC and land-use transformation could cause a substantial loss of species in the middle of the central Africa region and a substantial gain in the western region depending on the ability of mammals to move across the landscape. The Congo Basin was, for instance, projected to undergo a major reshuffling in species composition. The eastern part of the Congo Basin might experience a high rate of species loss while the western part might gain a substantial number of new species. There was a spatial shift of species towards cooler and moister areas (see east–west gradient on Fig. 7) causing major reshuffling in community composition.

In southern Africa, this latitudinal trend was reversed with a decrease of species richness in the western region and an increase in the eastern region. This inverse trend was mainly explained by west–east temperature and precipitation gradients, causing an eastward species shift towards cooler and moister areas (Fig. 7). These results suggested that the effects of CC on wildlife community may be most noticeable not only as a substantial loss of species from their current ranges but also as a fundamental change in community structure as species associations shift with influxes of new species.

The influence of LT on estimates of species sensitivity was not substantial for the relative predicted species lost per pixel (Fig. 8). If LT by 2050 was similar to the current situation, it would slightly increase the relative predicted species lost per pixel under CC alone. However, the impact of LT on the potential predicted species gained per pixel was more pronounced. It suggested that the current LT pattern would reduce (or preclude) the potential for species to spread to future climatically

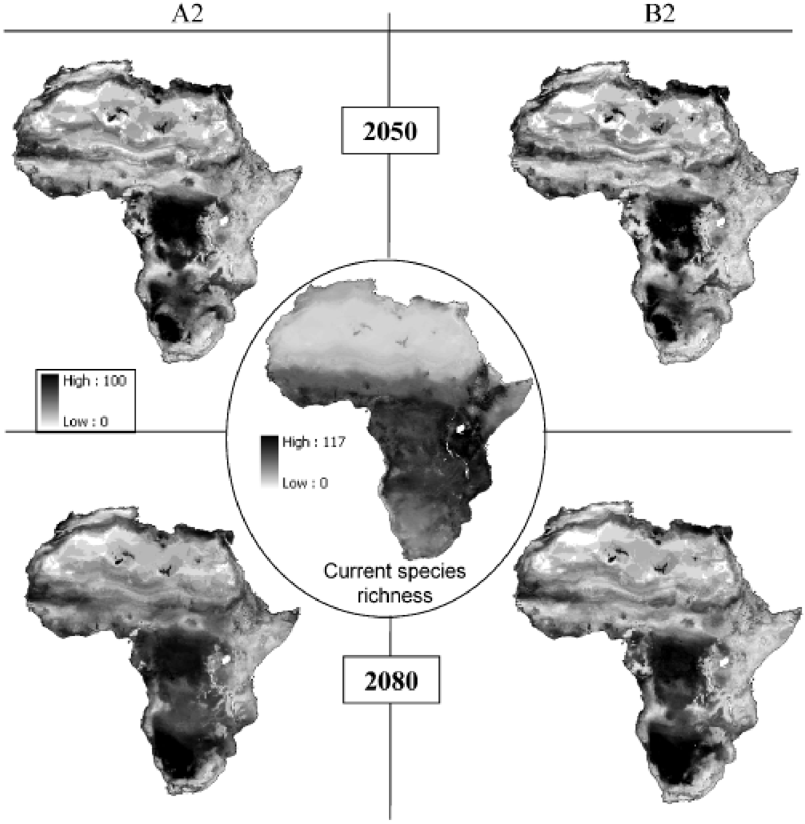


Fig. 5 Relative number of predicted species lost by pixel for the two time slices (2050 and 2080) and the two storylines (A2 and B2). Current species richness is displayed at the centre of the figure.

suitable habitats (Fig. 8). This analysis highlight the need for future LT scenarios, and stresses the critical need for assessments of 'corridor' approaches to facilitate species range shifts (e.g. Hannah *et al*., 2002).

Sensitivity of African NPs

We estimated the current and future species richness of the African NPs to highlight the degree to which they may be VU to CC (Fig. 9, see also Fig. 1). In order to provide a ranking, we grouped NPs by the dominant biome in which they are situated, using the classification and mapping of biomes by Olson *et al*. (2001). We present results only for A2 HadCM3. Results for B2 HadCM3 were spatially similar to A2 but with a lower impact, while results for 2080 were more extreme than for 2050.

NPs mostly situated in desert and xeric shrubland biomes were most sensitive to CC (Figs 9 and 1) as almost all these NPs here showed a marked decrease in species richness. These include mainly southwestern NPs (Kalahari Gemsbok), and the Algerian NP (Tassili N'Ajjer) where a very high number of species might be lost (~ 50%) with few immigrations (~ 10%) for all the scenarios and time slices (Table 1). The NPs situated in rare and patchy biomes (Mediterranean forest and mangroves) showed a neutral pattern where few losses and gains were projected. NPs situated in montane grassland biomes showed a positive response to CC (Figs 9 and 1) with a few neutral response exceptions. For instance, Mount Kenya and Nyika NPs were projected to gain a substantial number of species (i.e. Mt Kenya: 50% for A2 2050 and 80% of A2 2080), and retain most of their species currently found within their boundaries, suggesting that altitudinal species shifts towards currently cooler areas allow species persistence in the face of CC.

NPs situated mainly in tropical and subtropical montane grasslands, as well as tropical moist broadleaf forest did not exhibit unilateral patterns (Fig. 9), but the majority might experience an increase in species richness, enhancing a positive net turnover (Table 1).

Discussion

Limitations

Several recent papers discuss the broader theoretical limitations of the approach that we develop in this

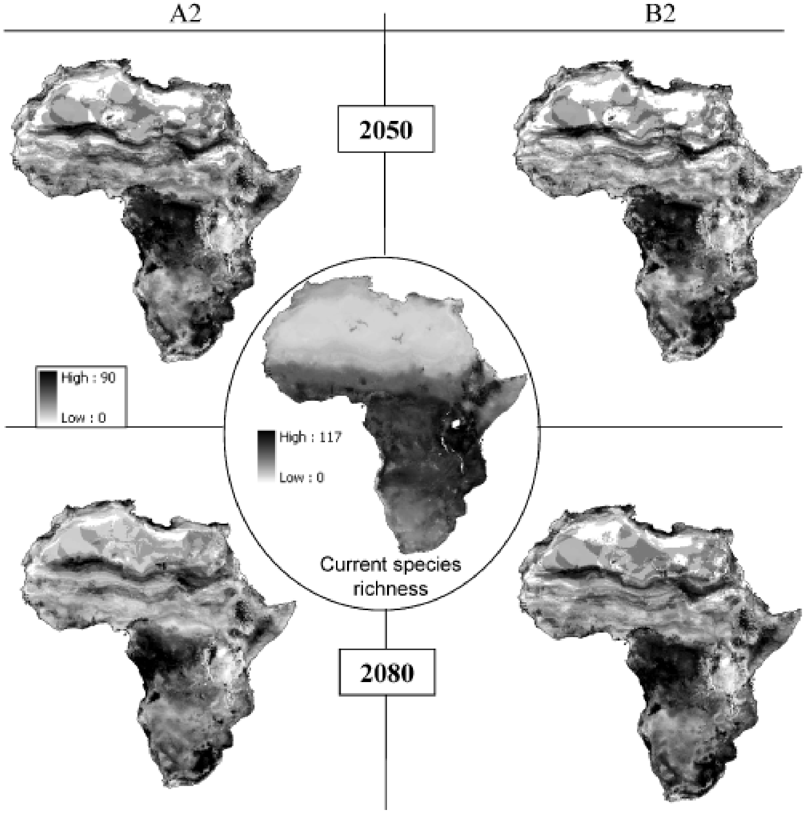


Fig. 6 Relative number of predicted species gained by pixel for the two time slices (2050 and 2080) and the two storylines (A2 and B2). Current species richness is displayed at the centre of the figure.

analysis (Pearson & Dawson, 2003; Hampe, 2004; Thuiller, 2004; Thuiller *et al.*, 2004b; Araújo *et al.*, 2005a; Guisan & Thuiller, 2005); hence, we focus this discussion to limitations and assumptions strictly relevant to this particular analysis.

A primary limitation is the lack of recorded absences inside the EO of the species. This is a common weakness of most of the animal atlases that only massive sampling efforts could remediate. However, it is the most reliable data available for mobile organisms, and GAM models have been shown to exhibit a relatively good performance even for highly mobile taxa (Brotons *et al.*, 2004; Huntley *et al.*, 2004; Araújo *et al.*, 2005a).

A further limitation is based on the relevance of the variables we used to assess the sensitivity of mammals. Here, we used climatic variables to produce climatically suitable habitat for every species and then weighted projected ranges by the LT variable. Our use of this approach does not mean that we are unaware that climate is only one of several determinants of species distribution (Araújo *et al.*, 2005b). Rather, we reason that while other factors, such as both competition and trophic interactions in ecosystems (Davis *et al.*, 1998a, b; Hochberg & Ives, 1999), and the phylogenetic history of taxa (Myers & Giller, 1988; Brown & Lomolino, 1998), are likely to influence species geographical distribution at a fine scale, mainly, geographical distributions at large spatial scale and resolution are likely to be determined to a large degree by climate (Root, 1988; Rogers & Williams, 1994; Chown & Gaston, 1999; Spicer & Gaston, 1999; Fischer *et al.*, 2001).

The influence of climate, especially rainfall conditions, on mammal distributions and abundances has been widely documented in Africa (Owen-Smith, 1990; Mills *et al.*, 1995; Owen-Smith & Ogutu, 2003). For instance, in the Kruger Park in South Africa, almost all of the ungulate species, except conspicuously the giraffe, seem extremely sensitive to lack of rainfall during the dry season, which is projected to be exacerbated into the future (Hulme *et al.*, 2001). Dry season rainfall may be directly important by influencing the retention of some green forage during this critical period when malnutrition takes hold (Owen-Smith & Ogutu, 2003).

Another concerns specific habitat, dietary or disturbance requirements of particular species. For instance, a number of mammal species (e.g. *H. amphibious*) strongly depend on fresh water availability (Sinibaldi *et al.*,

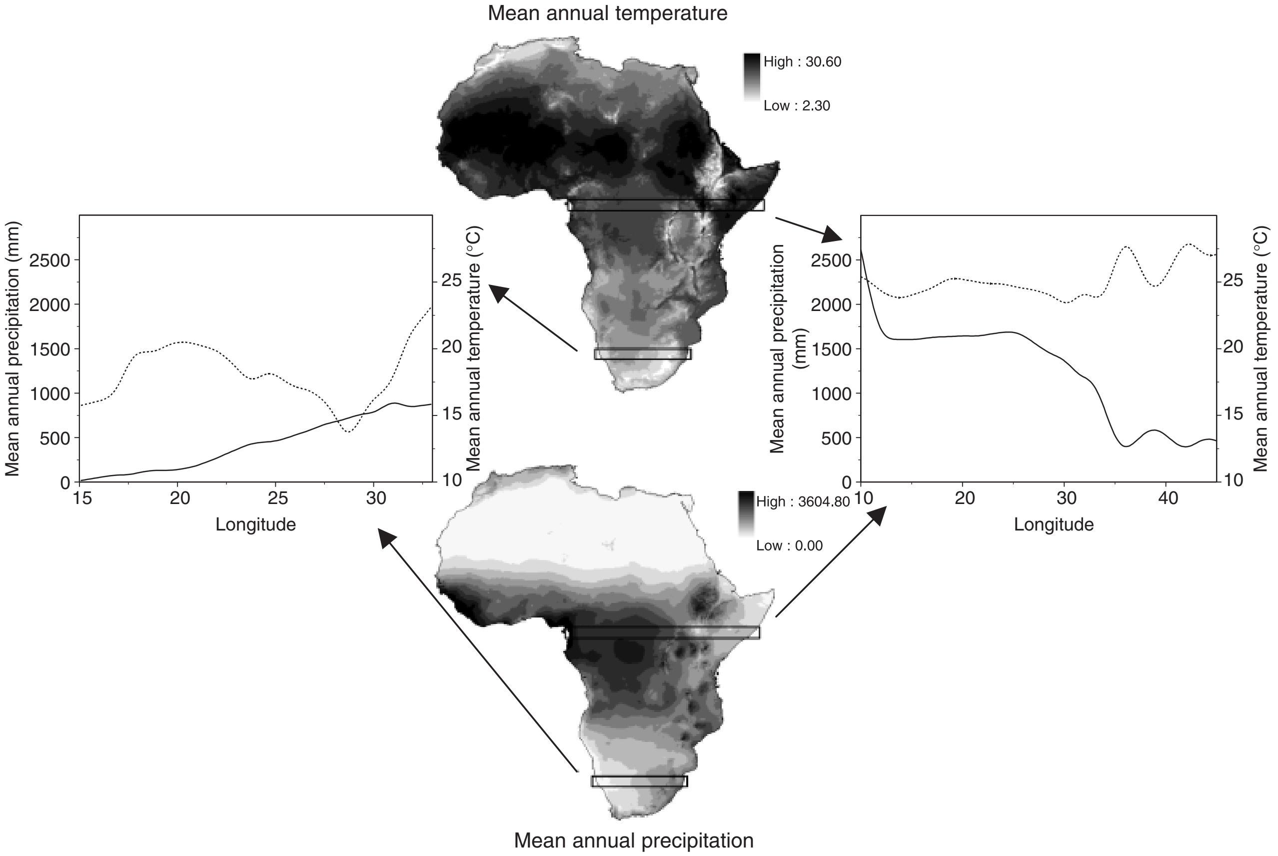


Fig. 7 Current mean annual temperature and mean annual precipitation along two east–west gradients. Dashed lines indicates temperature values along the transects while continuous lines indicates precipitation values along the transects.

2004), a parameter that was not included in our analysis. Thus, models on freshwater-dependent mammals exhibited the lowest predictive power in our analysis. While river coverages do exist at the African scale, these represent only primary rivers and lakes and we believe that at the resolution of the analysis (16 kmx16 km), they would only bias the results and not add useful information.

It is also clear that many animal species are dependent on habitat structure as well as climatic requirements for their persistence. Under future climate and atmospheric CO_2 change, habitat structure, such as the dominance of trees vs. grasses in savannas, may be altered through changes in fire regime (e.g. Bond *et al.*, 2003), with significant impacts on fauna.

A final problem is related to the crude assumptions about the potential spread of species, and their ability to track CC across transformed or untransformed landscapes. The consequence of such assumptions was highlighted in Fig. 3 for the Sahara oryx or the fox species. Clearly, it is very unlikely that these two species could reach these potential suitable habitats without human intervention. The spread of animals or migration of plants in the context of environmental change has raised great concern in the ecological community as they are likely to be unpredictable (Higgins *et al.*, 2003). Current knowledge on these issues is so poor that it is currently difficult to estimate even a maximum spread of the species we analysed in this study. This is a major weakness of the niche-based modelling approach and needs urgent attention in order to develop more reliable conservation plans (Williams *et al.*, 2005). The assumptions we used (no spread, universal spread) are debatable but this is currently the only way to deal with this issue.

An additional problem is the use of current LT as a conservative prognosis of future LT. We made this assumption because of the lack of reliable and sufficiently fine resolution projections of LT by 2050 or 2080. Moreover, the inclusion of LT would probably add a substantial amount of uncertainty, which combines with those from data, model, species biology and climate model uncertainty to increase overall uncertainty greatly. Case study evidence highlights the uncertainty and surprises inherent in the processes of land-use intensification and LT, as well as the importance of

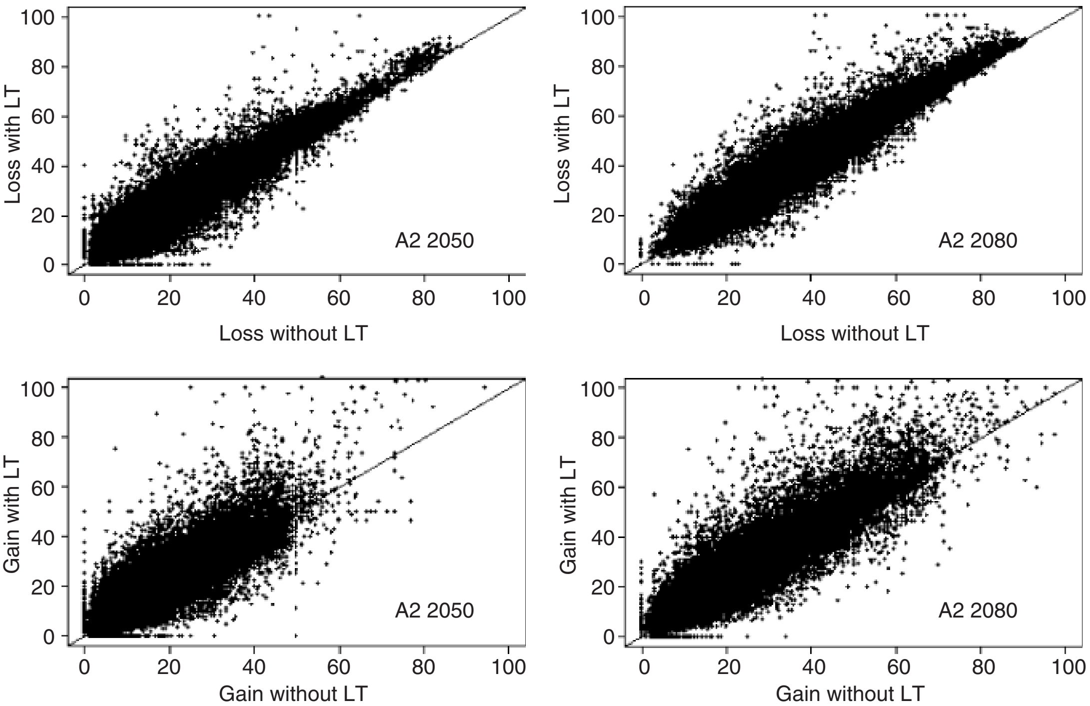


Fig. 8 Relationship between the relative numbers of predicted species lost/gained per pixel with climate change (loss and gain without LT) alone against the relative numbers of predicted species lost/gained per pixel accounting for current land transformation (loss and gain with LT). Only the results using the scenario A2 are represented here for both time slices (2050 and 2080).

decision making by land managers when facing a range of response options (Lambin *et al*., 2000), components that are currently poorly known at the African scale and relatively fine resolution.

Notwithstanding these weaknesses, the model used here represents a pragmatic estimate for a provisional estimate of the likely impacts of CC and LT on the mammals at the African scale.

Species extinction risks

Of the 277 species we examined, none were committed to extinction assuming full migration ability of species across the landscape, and a maximum of 10 species when assuming no migration under the A2 HadCM3 scenario for 2080. This number of expected extinctions corroborates a South African study on animal taxa using a similar approach (Erasmus *et al*., 2002), noting that 2.2% of the modelled species could be committed to extinction under a double CO_2 climate.

However, our extinction risk analysis highlights that a substantial number of African mammals species might be severely threatened by future CC and LT (Fig. 2). Indeed, assuming unlimited migration ability of species across the landscape, which is a likely overestimate, and under the extreme scenario (A2 HadCM3 2080), 30% of the species are classified as CR, while 40% are classified at LR. It is only when assuming that species are not able to migrate across the landscape that some species are predicted to lose 100% of their suitable habitats.

Because so many of the species we examined here show substantial range contraction (median = −49%, mean = −18% under A2 HadCM3 2080), it is this facet of range alterations that is of most concern. This concern is especially warranted because the range contractions we have predicted here may be underestimates and a conservative prognosis because of LT inhibiting the free migration of species across the landscape.

The major reason for concern regarding range contractions has to do with the negative relationship between range size and extinction probability (Gaston, 1994). A reduction in the absolute range of a species is likely to lead to an increased risk of local extinction (Thomas *et al*., 2004; Thuiller *et al*., 2005b). Indeed, a decrease in range size could mean that smaller stochastic events affect a larger proportion of the species' total population, especially in the context of fragmented landscapes. For instance, if a species becomes restricted to a few sites, then local catastrophic events (such as drought or disease outbreak) or an increase of LT by humans could easily cause the extinction of that species (Lawton & May, 1995). This is especially the case of mammals that directly threaten human lives, compete

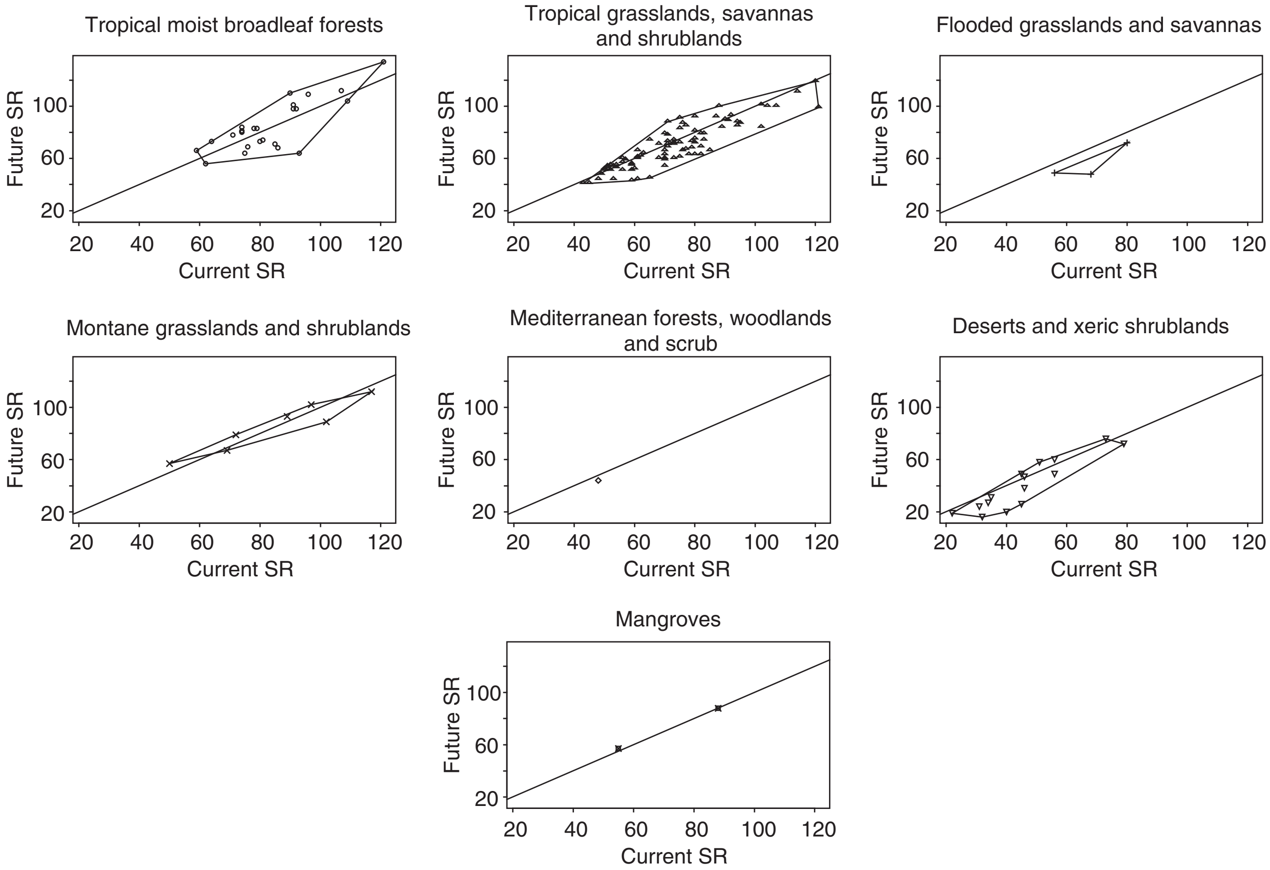


Fig. 9 Current and future species richness (under the A2 scenario for 2050) assuming full migration inside the African national parks ranked according to the biome where they occur. Lines indicate the steady-state situation (no species richness gain or loss).

with humans for resources and/or are restricted inside artificial boundaries.

Furthermore, additional drivers could enhance the risks of species extinctions because of CC and LTs. For instance, rainfall conditions can affect the susceptibility of animals to disease outbreaks, and particularly anthrax. The marked population decline by buffalo into the Kruger Park after 1990, and to some extent also that of kudu, was largely the result of an anthrax outbreak affecting these species resulting from unusually humid dry season. Life cycles of ticks or other parasites are also particularly influenced by climate variation and could exacerbate risks of extinctions. For instance, unusually warm winter in 1998 (1–2 °C warmer than the long-term average) allowed the tick *Boophilus decoloratus* larvae to peak twice in southern Kruger, once in June–July (unusual) and again in November–December (usual), implying that ticks had undergone an extra cycle that year (Bengis *et al*., 2003). Finally, competitive interactions may also influence some species according to the CC, especially waterbuck, which inhabit regions close to water likely to be most severely affected by other grazers during dry periods (Owen-Smith & Ogutu, 2003).

Spatial patterns

Spatial patterns of loss and gain show three contrasting patterns following the latitudinal position of the species. First, northern Africa does not exhibit a high number of loss and gain because of the very low number of mammals occurring in this area. The second pattern is a westward range shift of species in the Zaire and the Congo Basin. Given the pronounced west–east temperature and precipitation gradient across Africa (Fig. 7) at this latitude, the general decline in species richness in this direction, and replacements over this gradient of species that differ markedly in their physiological tolerances, these changes are undoubtedly a realistic reflection of the likely impacts of CC weighted by the substantial human pressure in these areas (Hulme *et al*., 2001; Sanderson *et al*., 2002).

The third pattern mirrors the second one but is situated in the Kalahari region of southern Africa and

Table 1. Current modelled species found in selected African national parks and projected species losses, gains and net turnover under different climate change scenarios and time slices

			2050						2080					
			A2			B2			A2			B2		
Park	Biome	Current SR	Sp lost	Sp gained	Turnover	Sp lost	Sp gained	Turnover	Sp lost	Sp gained	Turnover	Sp lost	Sp gained	Turnover
Kalahari	Desert an xeric shrublands	45	25	6	−19	23	7	−16	39	10	−29	39	8	−31
Tassili N'Ajjer	Desert an xeric shrublands	40	21	1	−20	21	1	−20	27	20	−25	25	1	−24
Etosha	Flooded grasslands and savanna	80	22	14	−8	18	13	−5	27	20	−7	27	16	−11
Bazaruto	Mangroves	88	12	12	0	7	10	3	29	18	−11	17	12	−5
Addo Elephant	Mediterranean forests	48	10	6	−4	7	3	−4	15	17	2	13	11	−2
Mount Kenya	Montane grasslands and savanna	50	18	25	7	12	26	14	18	39	21	16	35	19
Nyika	Montane grasslands and savanna	97	5	10	5	6	4	−2	10	10	0	12	7	−5
Kruger	Tropical grasslands and savanna	87	11	16	5	10	18	8	20	20	0	13	19	6
Serengeti	Tropical grasslands and savanna	120	7	6	−1	6	3	−3	15	14	−1	9	9	0
Odzala-Koukoua	Tropical moist broadleaf forests	74	16	23	7	12	19	7	42	37	−5	29	28	−1
Salonga	Tropical moist broadleaf forests	80	36	28	−7	20	25	5	53	34	−19	43	37	−6

SR represents species richness; Sp lost, Sp gained represent, respectively, the number of species expected to be lost or gained by the selected national parks. Turnover calculated as species gained minus species lost independent of current species richness.

centred on Namibia, Botswana, northern South Africa and Mozambique. In this area, there is an east–west aridity gradient (Fig. 7) across these countries (Rutherford & Westfall, 1986; Schulze, 1997), and this results in the same emerging relationships as around the equatorial transition zone (Freitag & Van Jaarsveld, 1995; Gelderblom *et al*., 1995). This pattern corroborates Erasmus *et al*.'s (2002) analysis carried out on a broad range of animals, highlighting the same eastward range shift towards the moister (cooler, higher altitude) end of the aridity gradient for most of the modelled species.

The extent to which predicted shifts in range and spatial modifications of species richness will translate into realized alterations in range position and species richness change will obviously also vary between taxa. If species are capable of adapting to local conditions by behavioural or physiological means, realized range shift may not be as pronounced as those projected. However, information on the relationships between species ranges and behavioural patterns and physiological tolerances, and the extent to which behavioural and physiological flexibility influence species ranges is very limited and inconsistent across the African mammals. However, we could argue that most of the predators, and especially cats, could be less susceptible to climate as they can easily supplement water availability with prey fluids (Kitchener, 1991; Bailey, 1993; Ogutu & Dublin, 2002). This fact would lead us to believe that predators would mainly follow their prey rather than explicitly tracking CC. Uncertainty also emerges with the complex response of large predators to long-term ecological change. For instance, Packer *et al*. (2005) showed that despite gradual changes in prey availability and vegetative cover, regional populations of Serengeti lions remained stable for 10–20-year periods and only shifted to new equilibria in sudden leaps (Packer *et al*., 2005; Ranta & Kaitala, 2005).

Landscape alteration in the central part of Africa as well as in the eastern and central portion of South Africa will also have a marked impact on the extent to which the predicted changes will be realized. We included LT in our assessment as a variable constraining the climatically suitable areas of species, but we did not consider migration of species across the transformed land. Extensive habitat alteration could create large gaps between suitable patches (Brown & Lomolino, 1998; Tokeshi, 1999) and, thus prevent free migration of species to keep pace with CC. If a species is unable to move into an area because of a lack of a suitable habitat, or because that area is too distant from the closest source population of that species, then area is effectively unavailable to the species and local extinction is the most likely outcome.

Sensitivity of NPs

The sensitivity of NPs to CC shows a very distinct pattern in accordance with the biomes in which the parks occur. NPs situated in xeric and desert shrublands are not expected to meet their mandate of protecting current mammalian species diversity within park boundaries. Indeed, these NPs are expected to face significant losses of species diversity that are not compensated by species influxes. The other NPs should expect both substantial losses of species and significant species influxes. On balance, the NPs will realize a substantial shift in mammalian species composition of a magnitude unprecedented in recent geological time. This conclusion is based on the assumptions that all species will reshuffle *en masse* in an orderly manner (Pimm, 2001), and that the rate of distribution change is commensurate with geographic shifts in habitat. These assumptions are debatable in general (Pimm, 2001), although comparatively rapid (20–50 years) range adjustments are not entirely out of the questions for mammals.

In addition, we must consider that, even when significant species losses are not anticipated, there may be repercussions because of indirect effects caused by the rearrangement of mammal communities and change in the patterns of interspecific interactions (see Stenseth *et al*., 2002 for a review). Indeed, as shifting species forge new ecological relationships with each other and with current park species, the character of species interactions and fundamental ecosystem processes stands to become transformed in unforeseen ways (Post *et al*., 1999; Walther *et al*., 2002; Schmitz *et al*., 2003). For instance, an influx of new species may alter existing competitive interactions and influence trophic dynamics with changes in predator–prey interactions. Further, climate warming is likely to result in phenological shifts, including changes in spring breeding dates, flowering and budburst (Walther *et al*., 2002; Parmesan & Yohe, 2003; Root *et al*., 2003), which can further disrupt current species associations. In some cases, it is possible that shifting species assemblages may lead to irreversible state changes, in which the relative abundance of species in different trophic levels can be radically altered (Schmitz *et al*., 2003). The outcome of these new species interactions may be particularity difficult to predict for nonlinearities that may emerge, for example.

Conclusion

Our results suggest that the effects of global CC and LT on wildlife communities may be most noticeable not as a drastic loss of species from their current range (even if some species could experience complete loss of suitable habitats), but instead as a fundamental change in community structure as species associations shift because of both species losses and influxes of new species. Our extinction risk assessment shows, however, that a substantial number of species could be CR because of CC and LT. Obtaining a clearer insight into these fine-scale effects rests squarely on developing more detailed models that better account for CC effects on species and the mosaic of habitat types within a geographic region, and on developing an understanding of ecosystem structural/functional change such as changes in tree/grass balance in savannas and fire frequency (Midgley & Thuiller, 2005). Better distribution data including true presence–absence or even abundance are urgently needed. Therefore, direct resources for animals should also be fully included to the process to provide more robust projections into the future, even though they are generally difficult to acquire for a large sample of species. Finally, the role of changes in habitat structure on faunal distribution, through the impacts of fire regime (e.g. Bond *et al*., 2003), should be incorporated in the future work of this nature.

Nevertheless, our prognosis for the extent and degree of change in Africa and specifically in park mammals can be viewed as a null hypothesis of distributional expectations (Peterson *et al*., 2002). Models that are more detailed will likely give a finer resolution, but the overall message is likely to be similar. In general, we should observe major changes in mammalian species composition in central Africa (tropical and subtropical areas) with a westward shift of diversity, and major losses of species in southern Africa with an eastward shift of mammal diversity. In addition, species interactions could increase the toll of species losses above and beyond what we find in this study (Pimm, 2001; Root *et al*., 2003).

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