

Do geographic distribution, niche property and life form explain plants' vulnerability to global change?

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Abstract

We modelled the future distribution in 2050 of 975 endemic plant species in southern Africa distributed among seven life forms, including new methodological insights improving the accuracy and ecological realism of predictions of global changes studies by: (i) using only endemic species as a way to capture the full realized niche of species, (ii) considering the direct impact of human pressure on landscape and biodiversity jointly with climate, and (iii) taking species' migration into account. Our analysis shows important promises for predicting the impacts of climate change in conjunction with land transformation. We have shown that the endemic flora of Southern Africa on average decreases with 41% in species richness among habitats and with 39% on species distribution range for the most optimistic scenario. We also compared the patterns of species' sensitivity with global change across life forms, using ecological and geographic characteristics of species. We demonstrate here that species and life form vulnerability to global changes can be partly explained according to species' (i) geographical distribution along climatic and biogeographic gradients, like climate anomalies, (ii) niche breadth or (iii) proximity to barrier preventing migration. Our results confirm that the sensitivity of a given species to global environmental changes depends upon its geographical distribution and ecological properties, and makes it possible to estimate *a priori* its potential sensitivity to these changes.

Keywords: biodiversity, biogeographic gradients, Cape floristic region, climate change scenarios, land transformation, Succulent Karoo

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Introduction

Ecologists commonly agree that biodiversity is already facing the effects of climate change at various scales, revealed for instance in modifications of the phenology and physiology of species, or in induced displacements of species distributions that may ultimately lead to increased extinction rates (Walther *et al.*, 2002; Parmesan & Yohe, 2003; Root *et al.*, 2003). Another major threat to biodiversity is habitat destruction and fragmentation caused by the intensification of human land use practices. Both have been recognized as a major threat to

biodiversity (Wilcove *et al.*, 1998; Hughes *et al.*, 2002). There is now substantial evidence that these global changes are increasingly affecting ecosystems.

In order to anticipate threats and prioritize conservation actions, ecologists have developed various modelling tools to predict species and diversity distribution in the future, in order to help develop planning responses to the impacts of global environmental change on biodiversity (Schroter *et al.*, 2005). One such tool is to apply species distribution models (SDMs; see Guisan & Zimmermann, 2000; Austin, 2002; Guisan & Thuiller, 2005) to assess the potential responses of individual species to climate change. These models relate present-day distributions to current climate, and then project the fitted climatic envelopes under future scenarios to

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identify how and where spatial shifts could occur (e.g. Huntley *et al.*, 1995; Iversen & Prasad, 1998; Bakkenes *et al.*, 2002; Peterson *et al.*, 2002; Thomas *et al.*, 2004; Thuiller *et al.*, 2005b). Species turnover – the net change in number of species that could persist in, disappear from, or colonize a particular area – has been used as a measure of the community composition change (Erasmus *et al.*, 2002; Peterson *et al.*, 2002). Accordingly, it has been widely used to assess the potential impact of climate change from regional to continental scales (e.g. Peterson *et al.*, 2002; Thuiller, 2004).

Species' vulnerability to global change can result from both ecological and geographical characteristics. Emphasis has been placed on the assumption that marginal species – (i.e. species with requirements which do not correspond to the mean climate conditions prevailing in the study area) – should be more sensitive to climate change than species that have their optimum close to or coinciding with the centroid of the realized environmental space (Swihart *et al.*, 2003). Furthermore, generalist species (e.g. species with a large niche breadth) should have broader tolerances to climate changes than specialist species (Brown *et al.*, 1995). Thuiller *et al.* (2004) demonstrated that such a relationship between the ecological and distributional properties of species could be successfully drawn from modelling studies. Moreover, because climate changes are not predicted to be uniform over landmasses, particular patterns of change in future distributions of species could also result from the geographical coincidences between species' range and spatial patterns of climate change anomalies. Disentangling these physiological and geographical effects on the future distribution of species would greatly improve our ability to predict patterns of change.

Several shortcomings are associated with most studies predicting climate change ecological impact conducted so far (Loehle & LeBlanc, 1996; Davis *et al.*, 1998; Pearson & Dawson, 2003; Hampe, 2004; Guisan & Thuiller, 2005). Firstly, modellers often have to model species inside arbitrary boundaries (e.g. political borders). Hence, resulting response curves are often incomplete descriptions of species' responses to environmental predictors. As a result, difficulties in projecting species' distributions in different areas or times than those used to calibrate the models may arise (Van Horn, 2002; Thuiller *et al.*, 2004b). Using species restricted to the area under study, like endemics, should allow capturing their full realized niche and prevent biased projections at range limits, in both geographic and environmental space.

Secondly, land transformation is rarely included in climate change impact scenarios (but see Dirnbock *et al.*, 2003; Thuiller *et al.*, 2006a), although it is a major cause

of biodiversity loss (Sala *et al.*, 2000; Lavergne *et al.*, 2005). There are at least two reasons for this: (i) reliable land use data do not exist for key regions; and (ii) climate change studies are hampered by a lack of fine-scale species and climate data, and as such are often conducted at such large extent and coarse resolution that accounting for land use is difficult (Pearson & Dawson, 2004; Thuiller *et al.*, 2004a). At the continental scale, climate can be considered the prevailing factor, whereas factors including topography and land-cover type become increasingly important toward more local scales (Guisan & Thuiller, 2005). A simple approach is to use aggregated land use data to weight or filter predictions of species' occurrence (e.g. Guisan *et al.*, 1998; Thuiller *et al.*, 2006a), rather than including them within the statistical component of models.

Thirdly, dispersal ability is usually not taken explicitly into account when projecting species distribution in the future (Pearson, 2006, but see Iversen *et al.*, 1999; Williams *et al.*, 2005). Instead, either dispersal is assumed to be fully effective, so that ranges that have become newly suitable are invariably colonized ('unlimited dispersal' hypothesis), or dispersal is assumed to be zero, so that all individuals of the study are unable to shift to their new ranges ('no dispersal' hypothesis; e.g. Thomas *et al.*, 2004; Thuiller *et al.*, 2005b). These two extremes encompass the range of possible migration rates, but neither of these approximations is satisfactory because migration rate depends to a large extent on the capacity of each individual species to migrate, which itself is a composite of individual's various abilities. The first hypothesis would be a realistic approximation only if the climate was changing slowly enough to allow the species to track changes, and the second would only be realistic if the migration rate was negligible compared with the extent of the study area. The extent to which plants will be able to track climate change by migration is still largely debated (Ronce, 2001; Pearson, 2006; for a review, Pitelka *et al.*, 1997). Fossil evidence of plant migrations following climatic upheavals in the Holocene, shows a wide range of migration rates among trees (Clark, 1998). Today, anthropogenic habitat loss and fragmentation are likely to substantially constrain migrations compared with those measured in the past (Schwartz, 1993; Dyer, 1994, 1995; Malanson & Cairns, 1997; Peters & Thackway, 1998; Iversen *et al.*, 1999; Collingham & Huntley, 2000). According to some authors, long-distance dispersal events might also play a crucial role for some species (Clark *et al.*, 1998; Cain *et al.*, 2003), but whether this is a general or a marginal phenomenon among plants is still under debate. For some taxa, lags in their response to past climate change tend rather to indicate that no long-distance event occurred that helped them to keep pace with the chan-

ging climate (Huntley, 1991). Hence, including even an unspecific and overestimated migration rate would greatly refine predicted species distributions under climate change.

Finally, comparisons between groups of species or systems should thus provide a powerful approach for examining hypotheses on species' distribution (Parmesan *et al.*, 2005). In this way, assessing effects of climate changes by life form or plant functional types (PFTs) should allow the identification of future trends in ecosystem structure (Dawson & Chapin, 1993; Lavorel *et al.*, 1997). Although individual species are expected to respond idiosyncratically to climate change, some species that share the same ecological properties (e.g. life-history traits, life forms, history) might respond in the same way (Thuiller *et al.*, 2005a). Although this approach is central in the conceptual and theoretical framework of dynamic global vegetation models (DGVM, Daly *et al.*, 2000; Sitch *et al.*, 2003; Woodward & Lomas, 2004), it has been rarely tested in climate change impact studies involving SDMs (but Thuiller *et al.*, 2006b). To date, SDMs have concentrated on quantifying species' range changes, with few efforts to explain the predicted ecological patterns (but see Guisan & Theurillat, 2000; Peterson & Holt, 2003; Thuiller *et al.*, 2005a). Identifying which particular species or group of species might be at greater risk is a major issue that remains to be investigated.

Here, we derive projections for a large set of 975 endemic plant species in southern Africa belonging to seven different life forms. This region exhibits high levels of endemism and harbours two of the five African hotspots: the Cape floristic region (CFR) and the Succulent Karoo hotspots (Myers *et al.*, 2000) which were identified as candidate areas of prime importance to become a world floristic heritage (www.conservation.org). Some studies in southern Africa have concentrated on the global change impacts on plant species of the Proteaceae family (Midgley *et al.*, 2002, 2003; Bomhard *et al.*, 2005; however, few studies have dealt with other taxa in this region (Erasmus *et al.*, 2002; Simmons *et al.*, 2004; Thuiller *et al.*, 2006a). Focusing on endemics is a priority task for conservation in its own right, but it also avoids one frequent shortcoming in modelling, which is to fit only a part of a species' niche, as the entire geographic range of a species can be modelled (Guisan & Thuiller, 2005). Biodiversity hotspots are the biologically richest yet among the most threatened places on Earth (Howlett, 2000; but see Orme *et al.*, 2005), where exceptional concentrations of endemic species are undergoing exceptional loss of habitat. As much as 44% of all species of vascular plants and 35% of all species in four vertebrate groups are confined to 25 hotspots that only cover 1.4% of the Earth's land surface

(Myers *et al.*, 2000). If all threatened species cannot be conserved, focusing on hotspots is one way to protect a maximum of species at a minimum cost (Myers *et al.*, 2000).

Our main objectives are:

- (1) to assess the relative sensitivity of endemic species of Namibia and South Africa to both climate change and land transformation by 2050;
- (2) to compare the predicted patterns of species sensitivity with global change across life forms, using ecological and geographic characteristics of the species in the study area. We ask particularly whether some species or specific groups are constrained in their migration toward cooler seacoasts or areas at higher elevation;
- (3) to propose an improved modelling approach that considers the three limitations previously discussed: (i) use of endemic species only to capture the full realized niche of species, (ii) impose constraints by land transformation types, and (iii) impose constraints related to species' ability to migrate.

Material

Study area

The study area encompasses four southern African countries namely Namibia, South Africa, Lesotho and Swaziland. It harbours two of the five African biodiversity hotspots, namely the CFR of South Africa and the Succulent Karoo of South Africa and Namibia. The CFR, located at the southwestern tip of Africa, is one of five Mediterranean-type systems included in nearly all assessments of global conservation priorities. As the smallest floral kingdom, it occupies only 90 000 km², yet contains nearly 3% of the world's plant species on 0.05% of the land area. The Succulent Karoo covers an area of approximately 116 000 km², stretching from South Africa's Little Karoo along the arid western side of the country into southern Namibia. It is the richest arid region in the world to be declared as a biodiversity hotspot and includes a spectacular array of 6356 species, of which over 40% are endemic.

Species data

We used a subset of the PRECIS Database (National Herbarium Pretoria Computerised Information Service; Germishuizen & Meyer, 2003), which contains records for more than 736 000 specimens in 24 500 taxa (species and infraspecies) from southern African countries. Species endemic to the region including Namibia and South

Africa were selected, and those with less than 20 records in the dataset were excluded from analysis to reduce errors associated with excessively small sample sizes (Stockwell & Peters, 1999). The 975 remaining species were distributed among life forms as follows: 59 trees, 278 shrubs, 168 perennial herbs, 100 annual herbs, 62 grasses, 230 geophytes and 68 succulent plants. The classification of species into life forms was achieved by sorting the PRECIS specimen database and by retaining the 'higher' life form presented by the species (for example, when a plant was found either as a tree or a shrub, it was classified as a tree). In ambiguous cases, we used expert knowledge (M. Rutherford, personal communication). This PRECIS locality data were recorded by quarter degree grid (QDS) cells ($\sim 25 \times 25 \text{ km}^2$ at this latitude).

Climate data

We used the CRU CL 2.0 dataset (New *et al.*, 2000) to represent current climate and to derive six climatic variables considered critical to plant physiological function and survival (Bartlein *et al.*, 1986; Woodward, 1987). In order to produce consistent datasets, all subsequent data layers were developed at a spatial resolution of 10' and resampled at QDS scale for model calibration. Climate data were averaged for the period 1961–1990 and included mean annual potential evapotranspiration, mean annual growing degree days ($> 10^\circ\text{C}$), mean annual temperature, mean temperature of the coldest month of the year, mean temperature of the warmest month of the year and mean annual precipitation sum. Potential evapotranspiration estimates were obtained using the FAO 56 Penman Monteith combination equation (Allen *et al.*, 1998). These variables were already used successfully elsewhere to predict species distribution (e.g. Huntley *et al.*, 1995; Thuiller *et al.*, 2005a).

Future climate predictions by 2050 were produced by perturbing the current climatic data with anomalies derived from climatic simulations produced by the HadCM3 general circulation model (GCM) using the A1, A2, B1 and B2 IPCC SRES scenarios (Nakicenovic & Swart, 2000). The A1 storyline describes a future world of very rapid economic growth, global population that peaks by mid-century and then declines, and the rapid introduction of new and more efficient technologies. The A2 storyline describes a very heterogeneous world, preserving local identities. Economic development is primarily regionally oriented and *per capita* economic growth and technological changes are more fragmented and slower than in the other storylines. The B1 storyline describes a convergent world that peaks by mid-century and declines thereafter, but with rapid change in economic structures towards a service and information

economy, with the introduction of clean and resource-efficient technologies. The B2 storyline describes a world in which the emphasis is on local solutions to economic, social and environment sustainability (Nakicenovic & Swart, 2000).

Land transformation data

The 'human footprint' (Sanderson *et al.*, 2002) is a regionally consistent way to represent land transformation on a global scale. It represents the sum of the ecological footprints of the human population as a continuum of human influence stretched across the land surface. This dataset use four types of data as surrogates for human influence: population density, land transformation, accessibility and electrical power infrastructure. The footprint index ranges from 0 to 1, from natural to completely transformed habitat. The original GIS layer at a resolution of 1 km was resampled to a 10' resolution.

Methods

Current potential distributions

Statistical modelling. SDMs were fitted to climatic data using the BIOMOD package in SPLUS (Thuiller, 2003). For each species, generalized linear model (GLM), generalized additive model (GAM), classification tree analysis (CTA) and artificial neural networks (ANN) were fitted on a random sample (70%) of the initial data. Then for every species the accuracy of each model was assessed using the area under the curve (AUC) of a receiver operating characteristic (ROC) curve on the remaining 30% of the initial data (test set for independent evaluation; Guisan & Zimmermann, 2000; Pearce & Ferrier, 2000; Liu *et al.*, 2005).

Land use filters. We used the 'human footprint' dataset to filter the resulting climatic potential distributions. We applied this filter by weighting the probability of occurrence by the 'human footprint' index. We assumed that completely transformed pixels corresponded to unsuitable habitat for wildlife, and their probability of occurrence was set to 0. Finally, the probabilities of occurrence from the filtered models were converted to presence/absence using a threshold maximizing the percentage of presence and absence correctly predicted.

Future potential distributions

Statistical modelling. Models calibrated under current conditions were then used to generate projections of future climatically suitable habitat under the scenarios

HadCM3 A1, A2, B1 and B2 for 2050. Only the best model for each species according to the ROC curve criterion was used to project future potential climatic suitable habitats (Thuiller, 2004).

Land use filters. As no dataset of future land transformation was available for each IPCC scenario, we assumed future land transformation to be best described by the current land transformation dataset, as this represents a conservative prognosis of the future (i.e. a 'best case' scenario) and limits additional uncertainty owing to future land transformation projections. Accounting for current land transformation in this way was expected to be better than ignoring it, as it is very unlikely that currently transformed areas will revert to 'untransformed' areas in the future (although there may be few exceptions). The future potential distribution maps were filtered following the same procedure as the current distribution maps. Finally, the probabilities of occurrence from the filtered models were converted to presence/absence using a threshold maximizing the percentage of presence and absence correctly predicted.

Migration limits. In order to avoid unreliable future potential distributions, we constrained the migration of any species to no more than $\sim 1 \text{ km yr}^{-1}$ (based on data by Clark *et al.*, 1998), even if the climate becomes suitable at larger distances. This has the effect to restrict species movement to maximum 0.5° for the 50-year period until 2050. For every species, if any pixels geographically more distant than 0.5° from the source pixel became suitable under climate change, its probability value was set to 0.

Climate change impact measurements

Spatial patterns. For each pixel, we calculated the number of species predicted both under present and future climatic conditions. From these values, we assessed the number and percentage of species predicted to no longer be present in the pixel in the future (*species loss*) as well as the number and percentage of species predicted to newly arrive (*species gain*). The difference between species loss and species gain allowed us to quantify the intensity of species reshuffling (*species turnover*):

$$\text{species turnover} = 100 \times (\text{species gain} + \text{species loss}) / (\text{initial species richness} + \text{species gain}). \quad (1)$$

A turnover value of 0 indicates that the assemblage of species is predicted to remain the same in the future

(i.e. no loss or gain of species), whereas a value of 100 indicates that the assemblage of species is completely different (i.e. the species loss equals the initial species richness; e.g. Thuiller *et al.*, 2005b).

Sensitivity of species. For each species, we calculated the percentage of pixels that remain suitable for the species under both present and future climatic conditions. The remaining grid cells, predicted to become unsuitable, were used to calculate the percent of lost habitat (*habitat loss*). We also calculated the percent of new suitable habitats (*habitat gain*), defined as the pixels unsuitable at present but predicted to become suitable after climate change, according to the assumption of constrained dispersal. Finally, for each species the percentage of range expansion or contraction (*species range change*) was calculated as the relative difference between habitat loss and habitat gain.

Ecological and geographical drivers of vulnerability

To investigate the spatial patterns of species vulnerability (expressed as species range changes), we derived a set of factors summarizing the ecological and geographic properties of the species expected to respond to climate change.

Niche breadth. The ecological niche of a species can be described by its mean position and breadth along various environmental axes (Schoener, 1989). Here, niche breadth along climatic axes was described using the multivariate coinertia analysis outlying mean index (OMI: Doledec *et al.*, 2000), which makes no assumption about the shape of species response curves to the environment, and gives equal weights to species-rich and species-poor pixels (for more details see Thuiller *et al.*, 2004c).

Spatial patterns of climate change. We derived maps of mean temperature and precipitation anomalies (differences between present and future values) over the study area, and related these to the present distributions of species. Only temperature and precipitation anomalies were used as a surrogate of global climate changes, because these two variables explain the major variation in future climate (Hulme *et al.*, 2001), and allow straightforward interpretations.

Change in proximity to seacoast. For each species, we calculated the centroid of the current and future distribution, and calculated the distance of both centroids to the seacoast. This allowed calculating how much closer the centroid of the distribution moved toward seacoast. This estimate highlighted if a

species would move toward or in the opposite direction to the coast, and if these movements could explain the species' sensitivity to climate change. The scale of the *change in proximity to seacoasts* axis represents the percent change of the proximity of the range centroid to seacoast after climate change.

Altitudinal rise. We calculated the centroid of present and future distributions of each species, and used it to calculate the expected altitudinal rise of species in the future. The scale of the *altitudinal rise* axis represents the absolute elevation change (in meters) of the centre of the distribution after climate change.

The influence of these factors on the vulnerability of species to climate change was then assessed by identifying the statistically supported relationships between these factors and predicted species' range changes using a linear regression fitted for each different life form. Note that some factors may act directly on the sensitivity of species to climate change (*niche breadth*, *temperature anomalies* and *precipitation anomalies*), whereas some others may act indirectly by constraining the response of the species (*change in proximity to seacoast* and *altitudinal rise*). The relationships between response and these explanatory variables were assumed to be linear, and no interaction term was allowed in the models to facilitate interpretation. An iterative stepwise analysis was performed to remove variables that did not significantly contribute to the explained deviance. This analysis was only carried out for the scenario A2 HadCM3, because this socio-economic scenario was understood as being reasonably credible in the future and showed important impacts on species, allowing a detailed investigation of the relationships between climate changes and species traits (including characteristics of species' range change). To facilitate the interpretation of the resulting trends, we further examined the mean position of each species along the ecoclimatic and biogeographic gradients.

Results

Modelling current and future species distribution

Model accuracy. The average AUC calculated from the evaluation dataset is 0.95 ± 0.04 (Fig. 1). This reflects an excellent predictive accuracy ($AUC > 0.9$; Swets, 1988). Only three species show a poor predictive accuracy ($AUC < 0.7$; Swets, 1988). Although AUC is high for every life form, the model accuracy of annuals and succulents is slightly lower than for others. By contrast, geophytes are in average almost perfectly modelled (mean $AUC = 0.97$). An example of a species

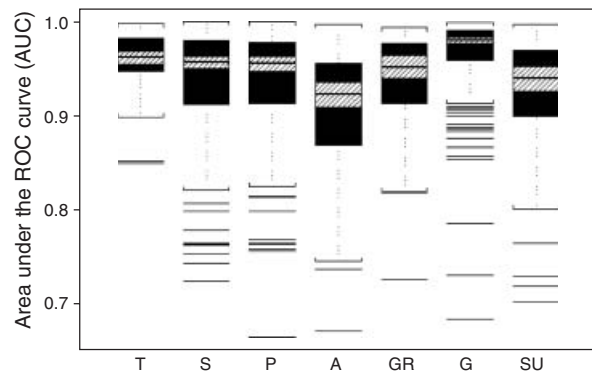


Fig. 1 Summary of the area under the curve (AUC) generating from the models using the evaluation dataset (30% of the total dataset). AUC 0.90–1, excellent; 0.80–0.90, good; 0.70–0.80, fair; 0.60–0.70, poor; 0.50–0.60, fail (). The boxplots indicate the accuracy of models for T, trees; S, shrubs; P, perennials; A, annuals; GR, grasses; G, geophytes; SU, succulents. The medians of range changes are shown (black horizontal lines) with their respective 95% confidence interval (hatched boxes). The core boxes of boxplots indicate the interquartile range of data whereas the whisker lines symbolize the centiles 5 and 95. Single horizontal bars represent outliers of the relationships.

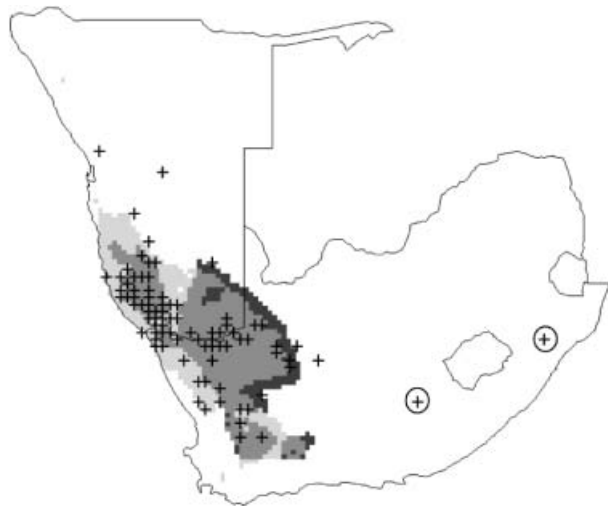


Fig. 2 Examples of species model (*Heliophila deserticola*) for the scenario HadCm3 A22050. Areas in light grey correspond to habitat predicted to be lost in the future, in mid grey those predicted to be stable habitat and in dark grey those predicted to be potentially colonized according to the dispersal assumptions used in this study. Crosses point out observation presences used to calibrate the model. Crosses surrounded by circles indicate erroneous outlier observations outside the relevant biomes.

model is shown for *Heliophila deserticola* (Fig. 2) for scenario A2-HadCM3 by 2050, with potentially stable, lost and gained habitat in the future, as well as presence data used to calibrate the model. A predicted southeast distributional shift of the species in the future is

denoted for this rare and endemic annual herb, characteristic of the Succulent Karoo and Nama Karoo Biomes. The obviously erroneous outlier observations outside the relevant biomes (crosses surrounded by circles, Fig. 2) illustrate the difficulty of using herbarium data. These observations may reflect errors in determination, database handling or the presence of specimens in botanical gardens. However, the resulting predicted distributions correspond globally well to the known distribution of the species, highlighting the fact that the model is not particularly sensitive to such outliers.

Spatial patterns. Consequences of climate change for the species richness of endemic plants are predicted to be fairly severe (Table 1, Fig. 3). By 2050, each pixel of the study area is predicted to lose, on average, 41–51% of its current endemic species richness, whereas only gaining 30–33% of new species. This is predicted to result in a high species turnover (54–62%).

Some biomes are predicted to be more severely affected than others (Table 1). The Namib Desert and Fynbos are the less affected biomes with 30–40% of species turnover predicted by 2050. By contrast, Albany Thicket, Grassland and Savanna are predicted to undergo 60–70% turnover.

In term of absolute number of species however, the results are quite different, because of the high disparity of species richness among biomes. The CFR in the southwestern part of South Africa in particular is predicted to suffer a massive loss of endemic species, with up to 273 species lost in areas at the transitions

zones between Fynbos and Succulent Karoo and between Fynbos and Nama-Karoo.

Sensitivity of species. Consequences of climate change and land transformation on selected endemic plant distributions are first analysed globally (all life forms together) and then by life form, namely: *trees, shrubs, perennials, annuals, grasses, geophytes* and *succulents*. Effects on selected endemic plants are predicted to be fairly severe, broadly the same order of magnitude as found on *species richness* (Fig. 4). By 2050, plants of this study would lose on average 39–49% of their current suitable habitat, whereas mean percentage of gained habitat ranges from 16% to 21%. This results in mean species range changes between –21% and –29%.

Extremes percentages of stable suitable habitats range from 0% (e.g. *Baphia massaiensis*) to 100% (e.g. *Agapanthus campanulatus*), highlighting the idiosyncratic response of species. By contrast, median range changes by life forms reveal more consistent patterns (Fig. 4), with a variance among life forms higher than that among the different climate change scenarios by 2050 (GLM: species range change ~ scenarios + life forms; life forms: $F = 52.59$, $P < 0.00001$; scenarios: $F = 7.77$, $P = 0.00003$). Annual herbs in particular show a very different pattern than all other life forms. It is the only life form not predicted to undergo a globally significant decrease in species ranges (–4% to 2%) by 2050. By contrast, geophytes are predicted to consistently suffer higher decreases in species ranges (–36% to –45%). Other life forms share more similar patterns, with a decrease of species range of about 20% for the less extreme scenarios and of about 30% for the most extreme scenarios (trees: –18% to –27%; perennials –23% to –31%; shrubs: –19% to –28%; grasses: –19% to –27% and succulents: –23% to –31% of decrease in species range).

Table 1 Average percent of species losses, gains and turnover

Biome	Endemic species richness	% of species loss	% of species gain	% of turnover
Global	94	41–51	30–33	54–62
Namib Desert	151	20–28	14–18	30–39
Succulent Karoo	203	36–49	14–21	45–56
Nama Karoo	90	35–43	33–38	51–57
Fynbos	415	24–35	7–12	30–41
Albany Thicket	200	56–67	10–16	60–72
Grassland	67	51–64	27–28	62–73
Savanna	57	45–57	36–40	59–67
Forest (1 pixel)	176	24–34	15–21	33–45

The range of average values across scenarios is presented here for time slice 2050. Values are calculated for the biomes occurring in the study area. The mean species richness by biome is also indicated.

Ecological and geographical explanation of spatial patterns of vulnerability

For the variable *niche breadth*, we estimated the variability of habitat conditions used by each species by calculating the variance of the positions of each occurrence on the first axis of the OMI analysis (Fig. 5c). This axis captures a continental gradient (Table 2) running from the seacoast to the centre of the African continent. We only used the first OMI axis, because it explained most of the variance among data (70.28%), and because there was no distinct hierarchy between the contributions of other axis.

Multivariate GLMs identifying statistically supported relationships between biogeographical variables and species range changes are presented in Table 3. When

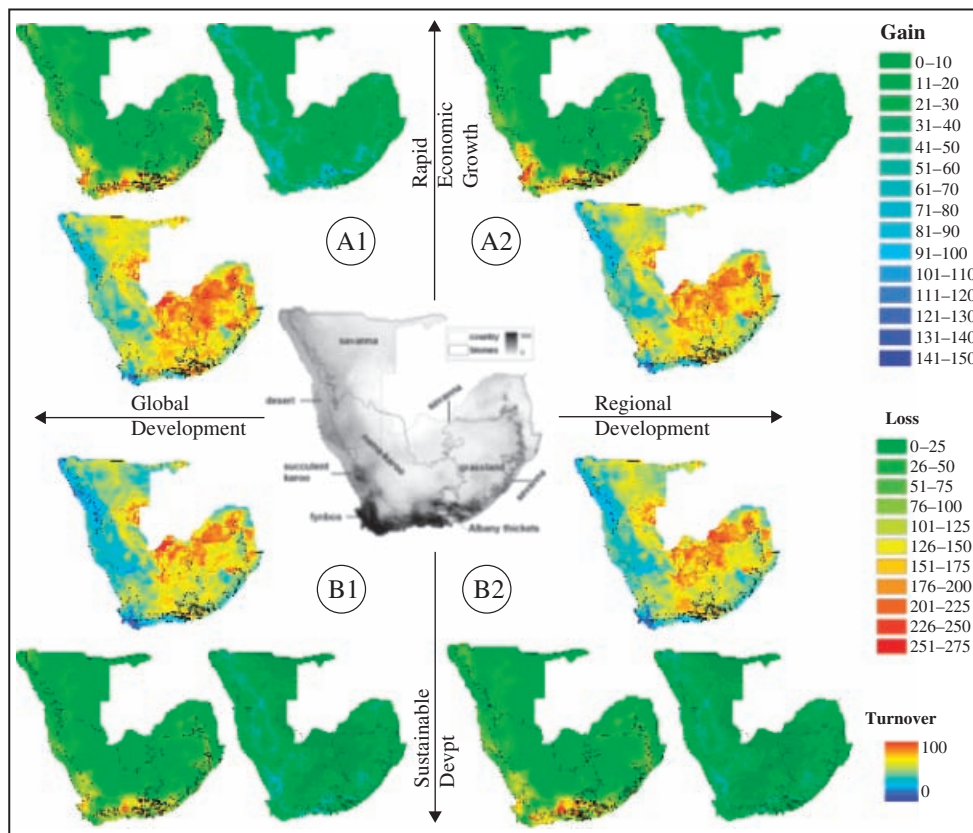


Fig. 3 Species loss, species gain and percentage of turnover in 2050. The absolute number of species predicted to be lost (species loss; green to red scale), the absolute number of species predicted to be gained (species gain; green to blue scale) and the percentage of species turnover are shown for scenarios HadCm3 A1 (upper left corner), HadCm3 A2 (upper right corner), HadCM3 B1 (lower left) corner and HadCM3 B2 (lower right corner) by 2050. For each scenario, species loss is on the left and species gain is on the right. Predicted endemic species richness at present time is shown in the centre of the figure.

considering the pool of species globally, *temperature anomalies* are positively correlated with species range changes, which indicate that in our study area, higher temperature anomalies tend to be associated with an expansion of species ranges. *Niche breadth* is also positively correlated with species range change, which indicates that species having a broad *niche breadth* tend to be less affected by climate change in the future. On the contrary, *change in proximity to seacoasts* and *altitudinal rise* are negatively correlated with species range change, meaning that species predicted to shift toward seacoasts and higher elevations are the most affected by climate changes. Precipitation anomalies do have a significant relationship with species range change when considering all species together.

The response of some life forms seems to depend upon specific geoclimatic and biogeographic patterns. *Temperature anomalies*, *change in proximity to seacoasts* and *altitudinal rise* have a stronger influence on the vulnerability of species and act similarly on the majority of life forms, whereas others – *precipitation*

anomalies and *niche breadth* – only affect particular life forms.

The range changes for trees, shrubs, annuals and succulents' are best explained by the same factors (*temperature anomalies*, *change in proximity to seacoasts* and *altitudinal rise*), while the response of perennial species are additionally influenced by their *niche breadth*. Grasses and geophytes exhibit distinct patterns. Grasses seem affected by *precipitation anomalies* and *niche breadth* whereas geophytes are influenced by all variables except *temperature anomalies*. Note, however, that the influence of such geographic factors, even significant, do not always explain a large part of the deviance of the models. Models for annuals and grasses, for instance, have a particularly low explained deviance ($D^2 = 0.49$ and 0.40 , respectively; Table 3).

The mean value of species along geoclimatic and biogeographic gradients (Fig. 5) allows further investigation of the statistically supported relationships. Not all results are described here (see Fig. 5), but some life forms show interesting patterns. For instance, annuals

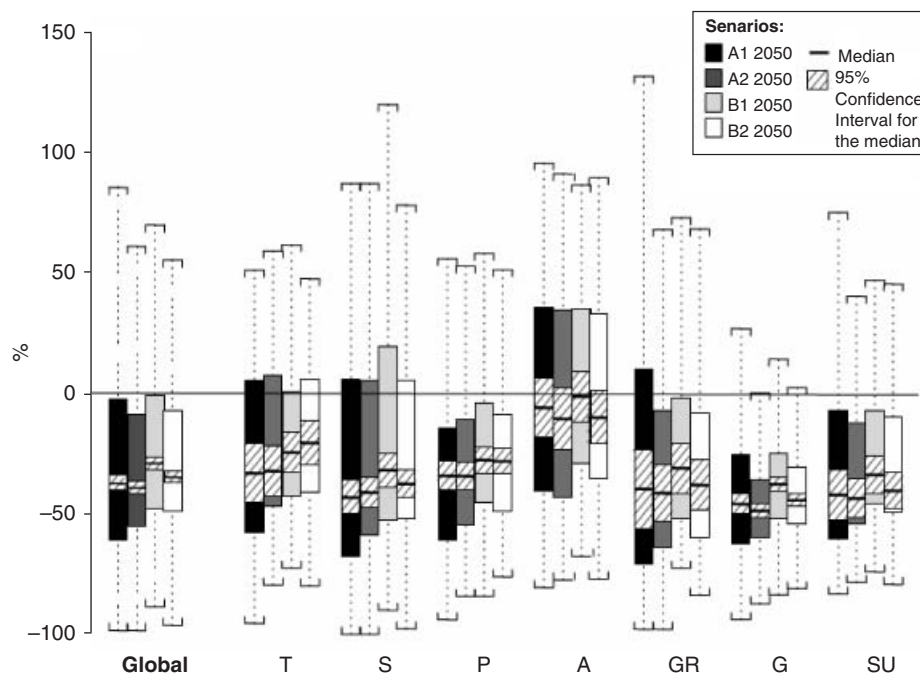


Fig. 4 Percentage of species' range change between present and 2050. Global, whole dataset; T, trees (69 sp); S, shrubs (278 sp); P, perennial herbs (168 sp); A, annual herbs (100 sp); GR, grasses (62 sp); G, geophytes (230 sp); SU, succulents (68 sp). Boxplots in black, dark grey, light grey and white represent results for scenario HadCM32.050 A1, A2, B1 and B2, respectively. The medians of range changes are shown (black horizontal lines) with their respective 95% confidence interval (hatched boxes). The core boxes of boxplots indicate the interquartile range of data whereas the whisker lines symbolize the centiles 5 and 95.

is the only life form which does not overall move seawards (-1.25% proximity, whereas the entire set of species will experience an average change in proximity of $+9.13\%$). By contrast, geophytes have more restricted niche breadths compared with other life forms (1.32, whereas 1.56 for the entire set of species), and will undergo stronger precipitation reduction in the future (-50.93 mm, whereas -47.07 mm for the entire set of species).

Discussion

Vulnerability of South African and Namibian endemic flora to global change

In this study, we modelled 975 endemic plant species in southern Africa distributed among seven life forms. Our results predict that impacts of climate change and current land transformation on endemic plant species in the study area are likely to be fairly severe, both at a geographic scale and a systematic level, with a 41% average decrease in species richness among habitats and a 39% average decrease of species distribution range for even the most optimistic scenario. The analysis of contraction or expansion of species distributions revealed highly idiosyncratic responses across species.

However, two life forms – annuals and geophytes – revealed particular and consistent patterns of changes. The annual life form is the only one not predicted to undergo a global significant decrease in species ranges, whereas by contrast, geophytes are consistently predicted to suffer high decreases in species range.

Interpreting habitat exposure to climate change – i.e. losses, gains and resulting turnovers – requires careful consideration of both absolute and relative numbers of species. Pinpointing regions with high absolute numbers of species lost or gained is of prime importance for conservation planning, whereas regions with high percentage turnover may experience a high reshuffling of biological assemblages, which may further lead to some ecosystem disruptions (Bakkenes *et al.*, 2002; Erasmus *et al.*, 2002; Peterson *et al.*, 2002). For instance, the CFR is predicted to suffer particularly massive losses of endemic species. These high absolute losses compared with other regions can be partly explained by the fact that this region shelters the majority of species present in the study area. However, losses in certain part of the CFR cannot be explained by initial species richness. Regions in the west and at the northern edge with the Nama Karoo are predicted to face the highest percentage of species loss. This echoes the results of Midgley *et al.* (2003), who showed that these regions were

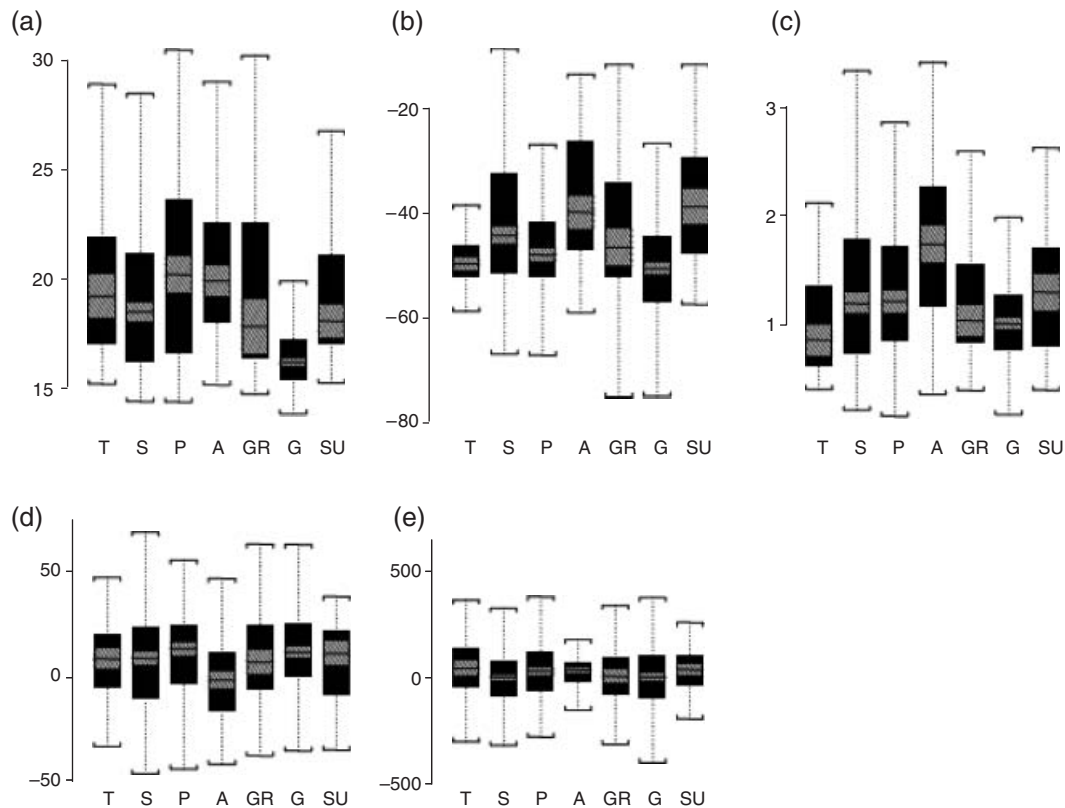


Fig. 5 Mean position of species along geoclimatic and biogeographic gradients. The boxplots indicate the mean position of modelled species on the geoclimatic and biogeographic gradients, namely: (a) temperature anomalies, (b) precipitation anomalies, (c) niche breadth, (d) closure to seacoast and (e) altitudinal rise. For each ecogeographic variable, each life form is analysed separately (T, tree; S, Shrubs; P, perennials; A, annuals; GR, grasses; G, geophytes; SU, succulents). The medians of range changes are shown (black horizontal lines) with their respective 95% confidence interval (hatched boxes). The core boxes of boxplots indicate the interquartile range of data whereas the whisker lines symbolize the centiles 5 and 95.

Table 2 OMI analyse

Climate variable	Niche breadth
mean annual potential evapotranspiration	-0.7973645
mean annual growing degree days (> 10°C)	-0.6644312
mean temperature of the coldest month	0.2398013
mean temperature of the warmest month	-0.7044085
mean annual precipitation sum	0.6725009
mean annual temperature	-0.6239156

The respective importance of climate variables in the first axis of the co-inertia analysis outlying mean index (OMI; Doledec *et al.*, 2000) is presented

particularly vulnerable to climate changes. On the contrary, the central parts of CFR that constitute the core of the Fynbos biome are predicted to face attenuated losses.

Our analysis concerns only a portion of the total Namibian and South African plant diversity, and cannot be extrapolated to the whole plant diversity of the area.

Nevertheless, the geographical patterns in percentage of species turnover probably depict fairly well the general trends of changes expected in this region, because our species dataset comprises a fair representation of life forms. Moreover, our predictions concern only endemic species, and thus the most sensitive part of the biodiversity. Predicted trends of extinction should therefore be considered as a very serious threat to this world floristic heritage.

Species vulnerability as a function of geographic properties and niche traits

The basic idea suggested by our analyses is that the sensitivity to climate change of a given species depends on its geographical distribution and ecological niche properties. The most vulnerable species are those with a restricted niche breadth (and thus often a restricted distribution) distributed within regions most exposed to climate change (i.e. high anomalies), or which direction of range change hits barriers to migration like

Table 3 Ecological and geographical variables determining species range changes

Life form	D2	Temperature anomalies	Precipitation anomalies	Niche breadth	Proximity to seacoasts	Altitudinal rise
Trees	0.71	Positive*	ns	ns	Negative*	Negative*
Shrubs	0.56	Positive****	ns	ns	Negative****	Negative****
Perennials	0.56	Positive*	ns	Positive****	Negative***	Negative**
Annuals	0.49	Positive***	ns	ns	Negative****	Negative**
Grasses	0.40	Positive*	Positive***	Positive***	ns	ns
Geophytes	0.75	ns	Negative**	Positive**	Negative**	Negative**
Succulents	0.59	Positive**	ns	ns	Negative**	Negative**
Global	0.59	Positive****	ns	Positive****	Negative****	Negative****

Results of the stepwise GLM between species range change (with scenario HadCM3 A2 2050) vs. temperature and precipitation anomalies, niche breadth, proximity to seacoasts and altitudinal rise for each life form are shown. Details provide explained deviance (D2) as well as the shape of the partial relationship between response and explicative variables with their relative statistical significance.

* $0.05 < P < 1 \times 10^{-4}$; ** $1 \times 10^{-5} < P < 1 \times 10^{-7}$; *** $1 \times 10^{-8} < P < 1 \times 10^{-10}$; **** $P < 1 \times 10^{-11}$.

seacoasts or mountains. This suggests that the potential sensitivity of species to climate change can be – at least partly – estimated *a priori* from their distribution along these gradients and from their niche characteristics.

Indeed, the linear analyses by life forms of the relationships between species' range change and species' position along geoclimatic and biogeographic gradients allowed us to identify variables that can significantly explain species vulnerability to climate changes in our study area. Species are likely to suffer less of a range decrease in the future when their geographic distribution is predicted to move away from seacoasts, hence providing species with larger areas to colonize. For instance, in our study, annuals is the only life form that does not get overall closer to seacoasts, which can explain why it does not show high susceptibility to climate change. All other life forms are predicted to undergo serious distributional shrinkage. Similarly, in agreement with ecological niche theory (Brown *et al.*, 1995), we assume the high vulnerability of geophytes to be related to their restricted niches, which results in a lower probability of establishment elsewhere. Also for geophytes, their high vulnerability seems to result from the greater reduction in rainfall in their distribution range. This is not surprising, because precipitation is considered to be the most critical factor to plant physiological function and survival (Bartlein *et al.*, 1986; Woodward, 1987).

Curiously, species occurring at places of greater climatic anomalies are not predicted to lose more of their range than other species. A likely explanation is that when considered alone, *temperature anomalies* may be positively correlated to species range change, but once other variables are included in the linear model, the

correlation becomes negative because of geographic patterns and correlations with other variables.

Improvements to previous projections and remaining limitations

Our modelling was improved as much as possible over three usual shortcomings of SDMs (Guisan & Thuiller, 2005), by: (i) using endemic species as a way to capture the full realized niche of species, (ii) considering the impact of human pressure on landscape and biodiversity jointly with climate, and (iii) taking species' dispersal into account.

Considering endemics prevents the risk of fitting truncated response curves of species to the main environmental gradients, which can result in limited transferability of models to new environmental conditions (Thuiller *et al.*, 2004b; Guisan & Thuiller, 2005).

By using the human footprint dataset (Sanderson *et al.*, 2002) to weight probability of presence in areas with high human pressure, we accounted for human influence on the landscape. We assumed species to be absent from areas heavily influenced by human, either because habitats are not suitable or because they are suitable but not valuable for conservation purposes. Unfortunately, there was no available dataset on future land transformation for the study area. It was thus assumed that future land transformation is best conservatively described by the current land transformation dataset, as this represents a conservative prognosis of the future and limits additional uncertainty owing to future land transformation projections. As our way of taking land use into account is not species specific, the influence of land use might have been exaggerated for some species and underestimated for others. One way

to take species specificity into account in future work would be to include land use variables directly in the models, taking care not to overfit models. But this would require specific knowledge about the susceptibility of every modeled species to land use impact. Hence, we advocate that such a method using land use variables separately is a reasonable compromise for incorporating such variables in global studies, because land use variables are distal predictors that do not act as direct factors constraining plant physiology or providing energetic resource (Austin, 2002). To avoid overfitting and provide better generality, proximal variables should be included preferentially in models (Guisan & Zimmermann, 2000).

Restricting migration of species to 1 km yr^{-1} was considered a more realistic approach than considering the two extreme hypothesis – ‘no dispersal’ and ‘unlimited dispersal’ – that are usually considered in this type of studies (e.g. Thomas *et al.*, 2004; Thuiller *et al.*, 2005b). This extent of migration, corresponding to the maximum rates observed in ancient climate changes in the Holocene (Clark *et al.*, 1998), allows avoidance of spurious distribution areas that would appear when modelling future species distribution with no dispersal limit. This approach is not species specific, but it has the potential to be implemented meaningfully with large species datasets. Specific implementation of migration requires specific knowledge on the dispersal ability, which is impractical in many studies, as necessary data are lacking for most species even in well-studied areas. One possible – although still crude – approach to overcome this limitation would be to consider groups of species with particular dispersal syndromes and to allow each group to migrate with a particular rate (e.g. entomochory vs. zoochory vs. wind dispersal; G. F. Midgley *et al.*, unpublished).

Notwithstanding our effort to account for possible bias in the models, some weaknesses still remain to be investigated. For example, fire regime – type of fire, intensity, frequency, season, duration – is known to be an important ecosystem regulator in southern Africa (Bond *et al.*, 2003), but is not available as a coherent dataset over the whole study area and could thus not be incorporated in our modelling framework. Nor did we account for species persistence and inertia of ecological systems. Niche base modelling techniques predict the habitat suitability of species at a given time and not, *per se*, the presence of the species. For instance, a long-lived plant can persist several decades even if its habitat has become unsuitable. But as no more suitable habitat will be available in the neighbourhood, the population will experience a decrease in offspring recruitment, becoming a sink population (Pulliam, 2000). It will survive only until the youngest individuals, born before

the habitat became unsuitable, die. When predicting extinctions, we include the possible persistence of individuals in unsuitable habitat even after decades or centuries, depending on species lifespan.

Conclusion

Our analysis shows important promise concerning the impact of climate changes on the endemic flora of southern Africa. A better understanding of the likely impacts will allow the prediction and prioritization of global conservation strategies to prevent massive loss of biodiversity. In particular, we demonstrated that:

1. CFR and the Succulent Karoo hotspot are predicted to undergo a minimum of 41% loss of species richness and 39% species range reduction by 2050. However, species with core distributions in Fynbos and the Namib Desert biomes, as well as species belonging to particular life forms, like annuals, may suffer attenuated – but yet considerable – consequences of future global changes. Because CFR and the Succulent Karoo constitute a world floristic heritage of prime global and regional importance, our results underline the necessity to take political decisions in order to circumvent major biodiversity impacts in that region.
2. Species and life form vulnerability to climate change can be partly explained according to (i) the position of their geographical distribution along geoclimatic and biogeographic gradients, like climate anomalies, (ii) their niche breadth or (iii) their proximity to barriers preventing migration and expansion. Our results confirm that the sensitivity of a given species to climate change depends upon its geographical distribution and ecological properties, which can be used for predictive purposes.
3. New methodological insights can be implemented for improving the accuracy and ecological realism of predictions, avoiding three usual limitations inherent to many global or continental climate changes studies. These are: (i) using endemic species only as a way to capture the full realized niche of species, (ii) considering the impact of human pressure on landscape and biodiversity jointly with climate, and (iii) taking species' migration into account.

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