

South African mouse shrews (*Myosorex*) feel the heat: using species distribution models (SDMs) and IUCN Red List criteria to flag extinction risks due to climate change

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Abstract Five species of mouse or forest shrews (*Myosorex*) are endemic to South Africa, Lesotho and Swaziland, four of which (*Myosorex varius*, *Myosorex cafer*, *Myosorex longicaudatus* and *Myosorex* cf. *tenuis*) are associated with montane or temperate grassland, fynbos and/or forest habitats while a fifth (*Myosorex sclateri*) is associated with lowland subtropical forests. Due to their small size, specialised habitat, low dispersal capacity, high metabolism and sensitivity to temperature extremes, we predicted that, particularly for montane species, future climate change should have a negative impact on area of occupancy (AOO) and ultimately extinction risks. Species distribution models (SDMs) indicated general declines in AOO of three species by 2050 under the A1b and A2 climate change scenarios (*M. cafer*, *M. varius*, *M. longicaudatus*) while two species (*M. sclateri* and *M. cf. tenuis*) remained unchanged (assuming no dispersal) or

increased their AOO (assuming dispersal). While temperate species such as *M. varius* appear to be limited by temperature maxima (preferring cooler temperatures), the subtropical species *M. sclateri* appears to be limited by temperature minima (preferring warmer temperatures). Evidence for declines in AOO informed the uplisting (to a higher category of threat) of the Red List status of four *Myosorex* species to either vulnerable or endangered as part of a separate regional International Union for Conservation of Nature (IUCN) Red List assessment.

Keywords Maxent · *Myosorex* · Shrews · South Africa · Climate change

Introduction

Anthropogenic climate warming is a major potential threat to biodiversity, affecting phenology, distribution, extinction risk and the morphology of species (Coetsee et al. 2009; Eastman et al. 2012; García-Domínguez et al. 2014; Hughes 2000; Monadjem et al. 2012; Parmesan 2006; Thomas et al. 2004). Historical data examining recent ecological responses to climate change closely corroborate estimates of extinction risk based only on predictions and suggest that globally some 10 % of plant and animal species may be extinct by 2100 due to climate change (Maclean and Wilson 2011).

High rates of local extinction due to climate change have been predicted especially for populations of montane vertebrates (McCain and Colwell 2011) because of their narrow and often discontinuous ranges and their inability to disperse. Although few data are available for montane species in Africa, Taylor et al. (2015) predicted alarming range contractions due to climate change by 2050 in two species of

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vlei rats (*Otomys*) from montane regions of South Africa. Historical data corroborated this trend, documenting virtual local extinction of one of these species (*Otomys auratus*) over part of its former range in the Soutpansberg Mountains (Taylor et al. 2015). Recent studies have revealed cryptic speciation and interesting patterns of microendemism among Afromontane vertebrates (e.g. Blackburn et al. 2010; Bowie et al. 2005; Lawson et al. 2015; Taylor et al. 2009, 2011, 2012, 2014), including shrews of the genus *Myosorex* (Stanley and Hutterer 2000; Stanley and Esselsteyn 2010; Taylor et al. 2013). Given the preponderance of range-restricted taxa having low dispersal capability and high sensitivity to ambient climate changes, we might expect high rates of local extinction among Afromontane vertebrates as predicted globally for montane vertebrates (McCain and Colwell 2011).

Global surface temperature has been reported to have increased by 0.08–0.14 °C per decade between 1950 and 2012, and it is predicted in many scenarios to rise by 2 °C by 2100 (IPCC 2014). In southern Africa over the last century, annual minimum and maximum temperatures have increased by an average of 0.057 and 0.046 °C respectively per decade (Davis 2011). Rising temperatures have also been reported in South Africa (Kruger and Shongwe 2004), particularly in Limpopo Province (Tshiala et al. 2011).

Because of their high metabolism and small body size, shrews are highly sensitive to adverse climatic conditions due to their thermal inertia and reduced resistance to starvation (Genoud 1988; Brown et al. 1997; Churchfield 2013). For these reasons and because of their limited dispersal capacity (home range size varies from <100 to 2800 m²; Churchfield 2013), they should be highly sensitive to future predicted changes in temperature and/or precipitation that may exceed their current physiological tolerances, leading to range shifts, contractions or local extinctions (McCain and Colwell 2011).

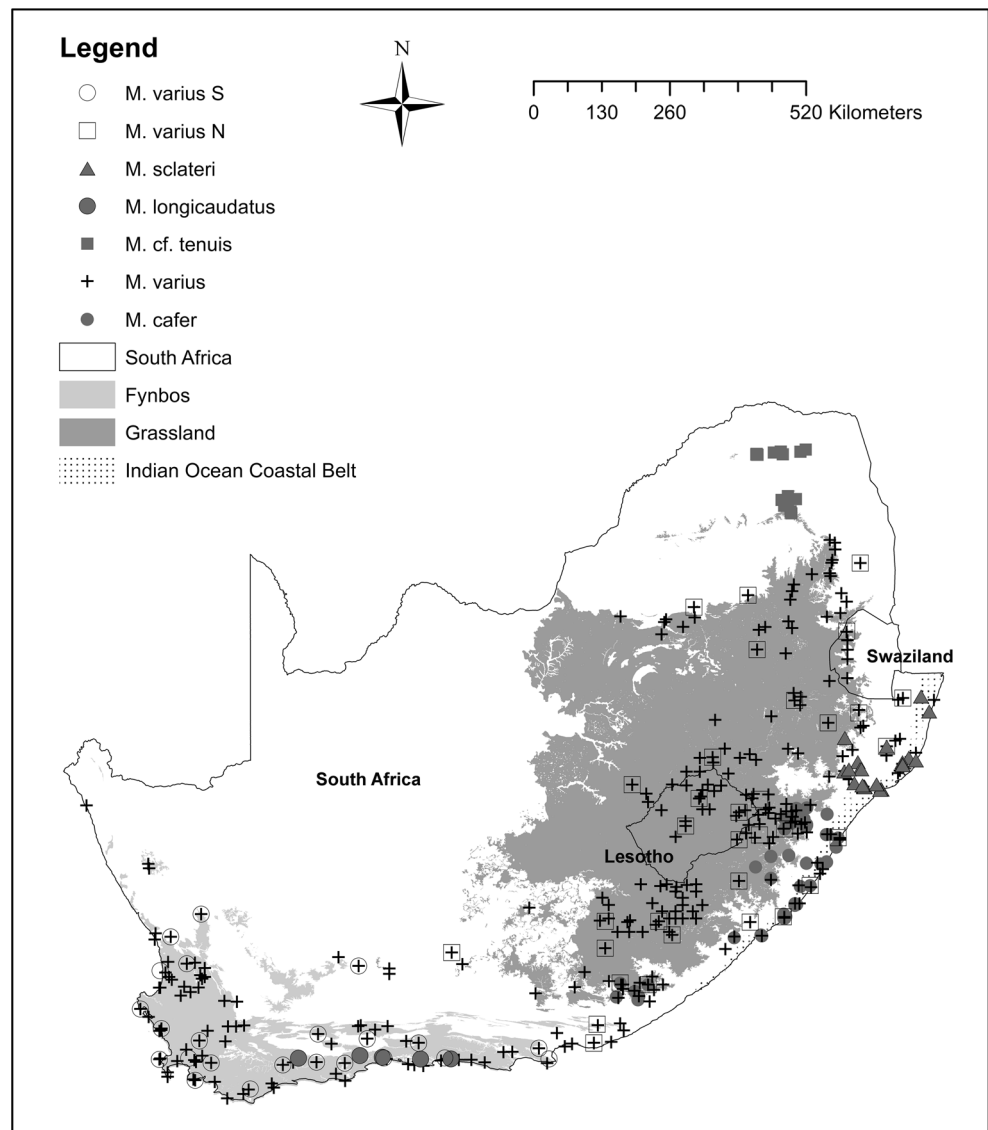
Mice shrews or forest shrews (*Myosorex*) comprise 14 species that are distributed mostly in isolated Afromontane forests, heathlands and grasslands in western, central, eastern and southeastern Africa (Hutterer 2013). The present study focused on seven species and subspecific lineages of *Myosorex* from South Africa. Two South African-endemic species are listed globally by the International Union for Conservation of Nature (IUCN) as least concern (*Myosorex cafer* and *Myosorex varius*; Baxter 2008a,b); one is listed as near threatened (*Myosorex sclateri*; Baxter 2008c), and one is listed as vulnerable (*Myosorex longicaudatus*; Baxter 2008d; Dippenaar 1995; Dippenaar and Baxter 2013). Recent molecular and morphological evidence argued for specific recognition of populations from the northern escarpment of South Africa and the Soutpansberg Mountains of Limpopo Province, termed *Myosorex* cf. *tenuis* (pending

formal description; Taylor et al. 2013; Fig. 1). A recent regional IUCN Red List assessment of South African mammals (Child et al. 2016) has reassessed the above species, and these results are discussed later under the **Discussion** in the light of new data contributed by the current study.

M. varius is widely distributed throughout montane grassland and fynbos (Mediterranean-climate heathlands and shrublands of the Western Cape of South Africa) habitats in South Africa (Fig. 1). *M. cf. tenuis* also occurs in montane (grassland and forest) habitats, while *M. cafer* and *M. longicaudatus* are associated with montane and temperate forests, and *M. sclateri* is associated with lowland coastal and scarp forests falling mostly under the Indian Ocean Coastal Belt biome (Mucina and Rutherford 2006) of northeastern South Africa (Baxter and Dippenaar 2013a,b; Dippenaar and Baxter 2013; Jenkins and Churchfield 2013a,b) (Fig. 1). Based on molecular evidence, Willows-Munro and Mathee (2011) described distinct northern and southern mitochondrial DNA lineages within *M. varius*, whose distributions coincide closely with the grassland and fynbos biomes of South Africa respectively (Fig. 1).

Since all South African *Myosorex* species apart from *M. sclateri* (which occupies lowland forests) have predominantly montane or submontane distributions (see above), and following from McCain and Colwell's (2011) results, we postulated that all South African species of *Myosorex* except for *M. sclateri* should be adversely affected by global warming. We further hypothesised that generalist and widely distributed shrew species such as *M. varius* should be less susceptible to future climate change (suffer lower predicted range losses) than narrow-range and specialist species such as *M. longicaudatus*, *M. cf. tenuis*, *M. cafer* and *M. sclateri*. We used species distribution models (SDMs), specifically generalised linear models (GLMs) and Maxent (Elith et al. 2006; Phillips et al. 2006) to test the above hypotheses using bioclimatic variables to compare models based on the “present” conditions (based on historical weather data from a range of dates centred around 1975) with those predicted by two future (A1b and A2) emission scenarios for 2050. To obtain estimates of area of occupancy (AOO) for each species range (current and future), we used a recent high-resolution (30 × 30 m) land cover map of South Africa to subtract transformed habitats (i.e. anthropogenic habitats unsuitable for shrews, where natural vegetation cover has been removed) from predicted current and future ranges obtained from the SDMs, under the two assumptions of full dispersal and no dispersal. Based on these results, we make recommendations for the conservation of mouse (forest) shrews in South Africa, using IUCN Red List criteria pertaining to predicted range (AOO) changes. Details of the criteria and categories used by the IUCN are described by IUCN Standards and Petitions Subcommittee (2014).

Fig. 1 Map showing the distribution of five *Myosorex* species and of southern and northern genetic lineages of *M. varius* and the distributions of three major vegetation biomes, grassland, fynbos and Indian Ocean Coastal Belt (Mucina and Rutherford 2006), associated with them



Materials and methods

Occurrence data

Unpublished records from RMB together with museum specimen records from the Ditsong National Museum of Natural History, formerly the Transvaal Museum (TM), and the Durban Natural Science Museum (DNSM), and field records from the Soutpansberg Mts of Limpopo Province, resulted in 578 unique *Myosorex* locality records from South Africa, Swaziland and Lesotho. These were used to create occurrence datasets for five *Myosorex* species, *M. cafer* ($n = 50$), *M. varius* ($n = 478$), *M. cf. tenuis* ($n = 21$), *M. sclateri* ($n = 24$) and *M. longicaudatus* ($n = 5$), as well as genetically defined northern ($n = 34$) and southern ($n = 18$) lineages of *M. varius* (based on Willows-Munro and Matthee 2011) that were used for model creation (Fig. 1). Species identification of

museum and field-collected specimens was checked by PJT (DNSM) and LO (TM) using existing keys (Meester et al. 1986), and those that could not be correctly identified were excluded from model building. The oldest natural history collection records corresponded closely with the earliest period of weather station records used to estimate the present environmental (bioclimatic) variables used for SDM. Locality coordinates were extracted directly from museum specimen labels or from official gazetteers. Records from unknown localities were not included in the model, and the remaining records were plotted on maps and inspected visually to detect obvious errors. Duplicates (records from the same pixel) were removed during the SDM analyses to reduce bias caused by spatial autocorrelation.

Standard small mammal live trapping (with Sherman traps) and specimen preparation procedures were used to collect *Myosorex* during ongoing small mammal surveys in the

Soutpansberg Mountains (Nemakhavhani 2014; Nengovhela et al. 2015; Taylor et al. 2014, 2015) under a collecting permit from the Limpopo Department of Economic Development, Environment and Tourism (LEDET) (Permit No. 001-CPM403-00010). Capture and handling followed the guidelines prescribed by the American Society of Mammalogists (Sikes et al. 2011). These records were added to those obtained from unpublished and museum records.

Species distribution models of current and future distribution

To test the robustness of SDMs to correctly predict present and future species distributions, we used two different modelling approaches, namely regression-based (GLM) and machine learning-based (maximum entropy or Maxent; Phillips et al. 2006). Analyses were conducted using R version 3.0.3 (downloaded from <https://cran.r-project.org> on 6 March 2014) within RStudio Version 0.98.501 (downloaded from www.rstudio.com on 6 March 2014) and the following packages: raster, dismo, rgdal, rjava and maptools. Maxent analyses were computed both within the dismo package of R for initial comparisons with GLM models as well as using the program Maxent version 3.3.3.k for final validation and predictions of models and calculations of areas of occupancy. GLM and Maxent are both widely used approaches for SDMs. Maxent works well with small sample sizes and outperforms profile-based SDM programs like GARP and BIOCLIM (Elith et al. 2006; Elith and Leathwick 2009; Elith et al. 2011; Phillips et al. 2006; Phillips and Dudík 2008).

For present and future (2050) climate scenarios, eight continuous climatic variables (Bioclim) were used as predictors in the SDMs: Bio 01 (annual mean temperature (AMT)), Bio 04 (temperature seasonality, Tseason, determined from the standard deviation of monthly values), Bio 05 (maximum temperature of warmest month, Tmax), Bio 06 (minimum temperature of coldest month, Tmin), Bio 12 (annual precipitation (AP)), Bio 13 (precipitation of wettest month, Pmax), Bio 14 (precipitation of driest month, Pmin) and Bio 15 (precipitation seasonality, Pseason, determined from the standard deviation of monthly values). These variables were extracted from the CliMond website (<https://www.climond.org>) (Kriticos et al. 2012) at a grid resolution of 30" (16.6 × 16.6 km for our study region in Albers equal area projection for Africa). Since animals may respond to either mean or extreme climatic conditions in addition to seasonal changes (e.g. hibernation in small mammals induced by cold winters), we selected variables to represent both extreme and mean temperature and rainfall parameters in addition to indices of seasonality. Correlation coefficients were calculated for all pairs of bioclimatic variables using the SDM toolbox, with the tool "Universal tools: Explore climate data" within ArcMap 10.2 (Brown 2014). Variables were generally poorly correlated with each other ($r < 0.7$) with few

exceptions (AMT and Tseason $r = 0.84$; Tseason and Tmin $r = 0.79$; AP and Pmax $r = 0.93$; Pmin and Pseason $r = 0.71$).

ArcMap version 10.2 (www.esri.com) was used to project the bioclimatic variables to Albers equal area for Africa and to crop them to the required background (see below) in the same projection. ArcMap was also used to compute AOO for each species model (present and future) obtained from Maxent and to subtract transformed habitats (based on the South African national land cover map created in 2008) after resampling the raster grids for each model from 30" (16.6 × 16.6 km) to the same resolution (30 × 30 m) as the South African national land cover map (<http://bgis.sanbi.org/landcover/project.asp>; Driver et al. 2012) and summing the two grids.

Future climate variables (for 2050) were based on the CSIRO-MK3.0 general circulation model (GCM) under both the A1b and A2 emission scenarios (IPCC 2007). The A1b scenario is more optimistic and assumes a human population that will peak and decline after mid-century in addition to the rapid update of efficient and clean energy sources, while the A2 scenario assumes a growing human population and continued reliance on fossil fuels. There is strong evidence that alternative less "extreme" scenarios (such as the B-family scenarios) may no longer be relevant under current greenhouse gas emission rates (Beaumont et al. 2008).

The analysis was conducted in two stages. In the first stage, except for *M. longicaudatus* where small sample size ($n = 5$) precluded this, the occurrence dataset for each species and lineage was randomly split into 30 % testing and 70 % training datasets. All species models for GLM and Maxent and both future scenarios were trained and evaluated with the same environmental predictors and background (2000 background points; see below for discussion of the background used). Predictions were made for present (1975) and future (2050: A1b and A2) environmental predictor datasets, and these were evaluated using two criteria: the percent of correct predictions and the area under the curve (AUC) of receiver operating curves (ROCs). Based on the "equal training sensitivity and specificity" threshold, binary maps were plotted for each species, modelling approach, time period and scenario. This threshold maximises the accuracy of correctly predicting both presence and absence records and is widely used in SDMs (Freeman and Moisen 2008; Monadjem et al. 2012). Values below the threshold indicate areas that are unsuitable for the species, whereas values above the threshold represent those that are suitable. In the second stage, since Maxent models outperformed those using GLM (Table 1), in order to calculate mean AOO for each species, time frame and scenario, Maxent models were rerun with and without clamping (restricting environmental variables to the range of values encountered during model training) and five replicates were run for each model using the cross-validate setting. The regularisation multiplier was set to 1; maximum number of background points was set to 10,000; maximum iterations were set to 500, and the

Table 1 Model fit (AUC and % correct prediction) and important predictor variables (defined as variables having model parameters with $P < 0.01$ in GLM or variables having the highest % contribution in Maxent) for species distribution models (SDMs) for two model-building approaches (GLM and Maxent) for five species of mice shrews (*Myosorex*) and two genetic lineages of *M. varius*

Species	Maxent				GLM (binomial distribution)			
	N^a	AUC	% Correct prediction	Important variables (% contribution >10 %)	N^a	AUC	% Correct prediction	Important variables ($P < 0.01$)
<i>M. cafer</i>	34	0.941	89.4	Annual precipitation (57 %), minimum precipitation (27 %)	34	0.917	80.2	Temperature seasonality, annual precipitation
<i>M. varius</i>	287	0.74	66.6	Maximum temperature (36 %), annual precipitation (14 %), precipitation seasonality (13 %)	287	0.664	62.6	Mean annual temperature
<i>M. sclateri</i>	13	0.975	94.2	Minimum temperature (73 %), temperature seasonality (14 %)	13	0.967	94.8	Annual precipitation, maximum temperature, maximum precipitation
<i>M. cf. tenuis</i>	11	0.99	97.3	Precipitation seasonality (82 %), maximum precipitation (16 %)	11	0.992	98.8	–
<i>M. longicaudatus</i>	5	0.983	96.3	Precipitation seasonality (99 %)	5	0.993	98.3	–
<i>M. varius</i> S lineage	22	0.937	84.4	Precipitation seasonality (40 %), maximum precipitation (24 %), minimum temperature (19 %)	22	0.836	66.6	Minimum temperature, mean annual temperature
<i>M. varius</i> N lineage	33	0.859	70.0	Annual precipitation (49 %), maximum precipitation (17 %)	33	0.629	56.0	–

The background comprised a raster mask based on the combined distribution of *M. varius* and *M. cf. tenuis*, with a 50-km buffer surrounding all occurrences of these two species

^a Sample size after removal of duplicate records from the same cell

convergence threshold was set to 0.00001. As before, binary maps were created using the equal training sensitivity and specificity threshold. Finally, calculation of the area of occupancy (number of pixels multiplied by the area of each pixel which was $16.6 \times 16.6 \text{ km} = 275.56 \text{ km}^2$) in each model was calculated in ArcMap 10.2 from the layer property of the corresponding model raster layers. Using the “Plus” tool in the Spatial Analysis toolbox of ArcMap 10.2, raster layers for the current and future models for each species were summed in order to detect dispersal events in the A1b and A2 projections (i.e. grid cells occurring outside the range of occupancy of the current climate models). AOOs were calculated with and without dispersal, and transformed areas were subtracted as described above. Since land cover predictions are not available for the future, we assumed conservatively that the proportion of transformed land in the present map (based on calculations made in 2008) will be similar in 2050.

Study regions (backgrounds) that are defined too broadly may include large areas of unsuitable habitat that may bias model results, whereas study regions that are too limited in extent may result in “truncated responses” due to environmental values outside the study region being assigned to species (Anderson and Raza 2010; Van Der Wal et al. 2009). To accommodate such potential biases, we constructed a mask based on all occurrence records of *M. varius* and *M. cf. tenuis* combined. *M. varius* has a broad range which encompasses that of

all of the other species but excludes Limpopo Province where only *M. cf. tenuis* occurs. Combining occurrence records of these two species, with a 50-km buffer around each point, therefore defines potentially suitable mesic and/or montane habitats for the genus of mouse shrews as a whole and excludes unsuitable drier habitats in the west and central regions of South Africa.

Biases may also be introduced by not considering the important factor of dispersal (Midgley et al. 2006). In our study, we analysed model results with respect to two distinct scenarios of “no dispersal” and “full dispersal”. In the case of no dispersal, pixels predicted by the models to occur in new areas (relative to the current distribution model) were not considered to be suitable for the survival of the species. In the case of full dispersal, we assumed no limit to the dispersal capacity of the species and pixels were retained as part of the future distribution even when they were not part of the current predicted range, irrespective of the number of intervening pixels.

Results

Maxent models generally performed better than GLM (higher AUC and % correct prediction values; Table 1), and the resulting maps of the former were more biologically meaningful as explained below. Predicted current and future (A1b and A2) binary maps (with equal sensitivity and specificity

threshold) of all species and lineages are shown for both GLM (Fig. 2) and Maxent (Fig. 3) models. In general, maps based on GLM models had larger predicted ranges than those based on Maxent, often considerably exceeding the geographical scope of occurrence points (i.e. see *M. cafer*, *M. varius* and *M. sclateri* and both lineages of *M. varius* [cf. Figs. 2 and 3]). However, for species having small sample sizes, like *M. tenuis* and *M. longicaudatus*, the opposite was true and GLM-derived ranges (Fig. 2) were smaller than Maxent-derived ranges (Fig. 3). Some GLM models showed very large and unlikely range differences between the present and future models. The model for the southern lineage of *M. varius* showed an apparent massive range increase under the A2 scenario which covered most of South Africa including arid regions such as the Kalahari and Karoo semi-deserts. In three of the GLM models (*M. cf. tenuis*, *M. longicaudatus* and the northern lineage of *M. varius*), none of the bioclimatic variables were significant. Variables identified as significant in GLM models tended to be different from those identified as important (from their % contributions) from Maxent models (Table 1). For the above reasons, future consideration of range changes due to climate change and land transformation were based on Maxent models which have been shown to perform best particularly when sample sizes are small (Phillips et al. 2006).

Subtracting transformed land cover from the raster files for the different Maxent models for present climate (at 30×30 m grid size) using the national land cover coverage (<http://bgis.sanbi.org/landcover/project.asp>) resulted in decreases in AOO of between 28 and 44 % for different species (Table 2).

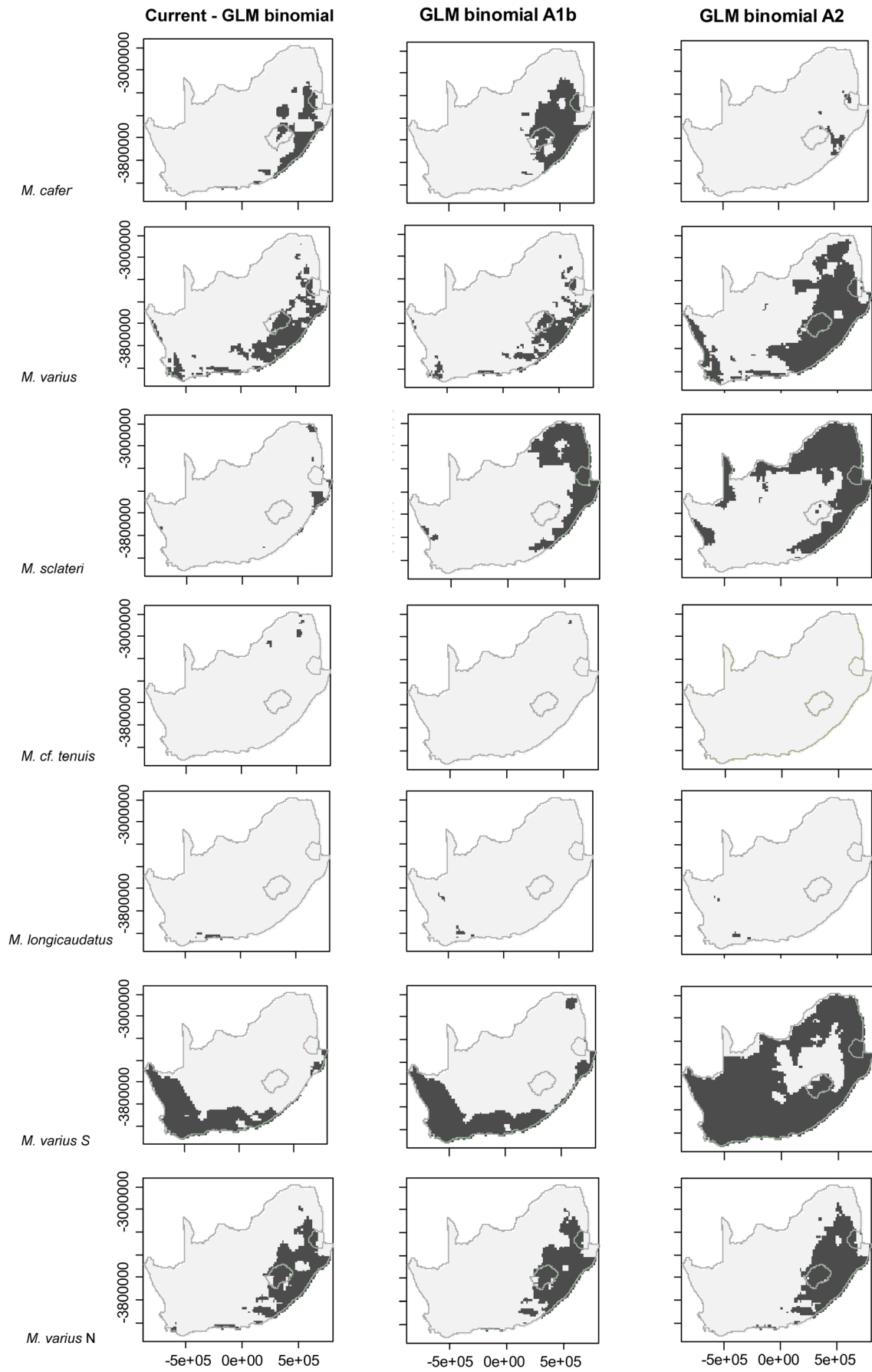
Just considering the Maxent results, the probability of occurrence (habitat suitability) of most *Myosorex* species increased at higher precipitations (AP, Pmax or Pmin: *M. cafer*, *M. tenuis*, *M. varius* and S and N lineages of *M. varius*), colder maximum temperatures (Tmax: *M. varius*) and reduced seasonal differences in precipitation (Pseason: *M. varius*, *M. cf. tenuis*, *M. longicaudatus*), reflecting cool, wet, seasonally stable temperate niches. On the other hand, probability of *M. sclateri* responded positively to warmer extreme minimum temperatures (Tmin) (Table 1).

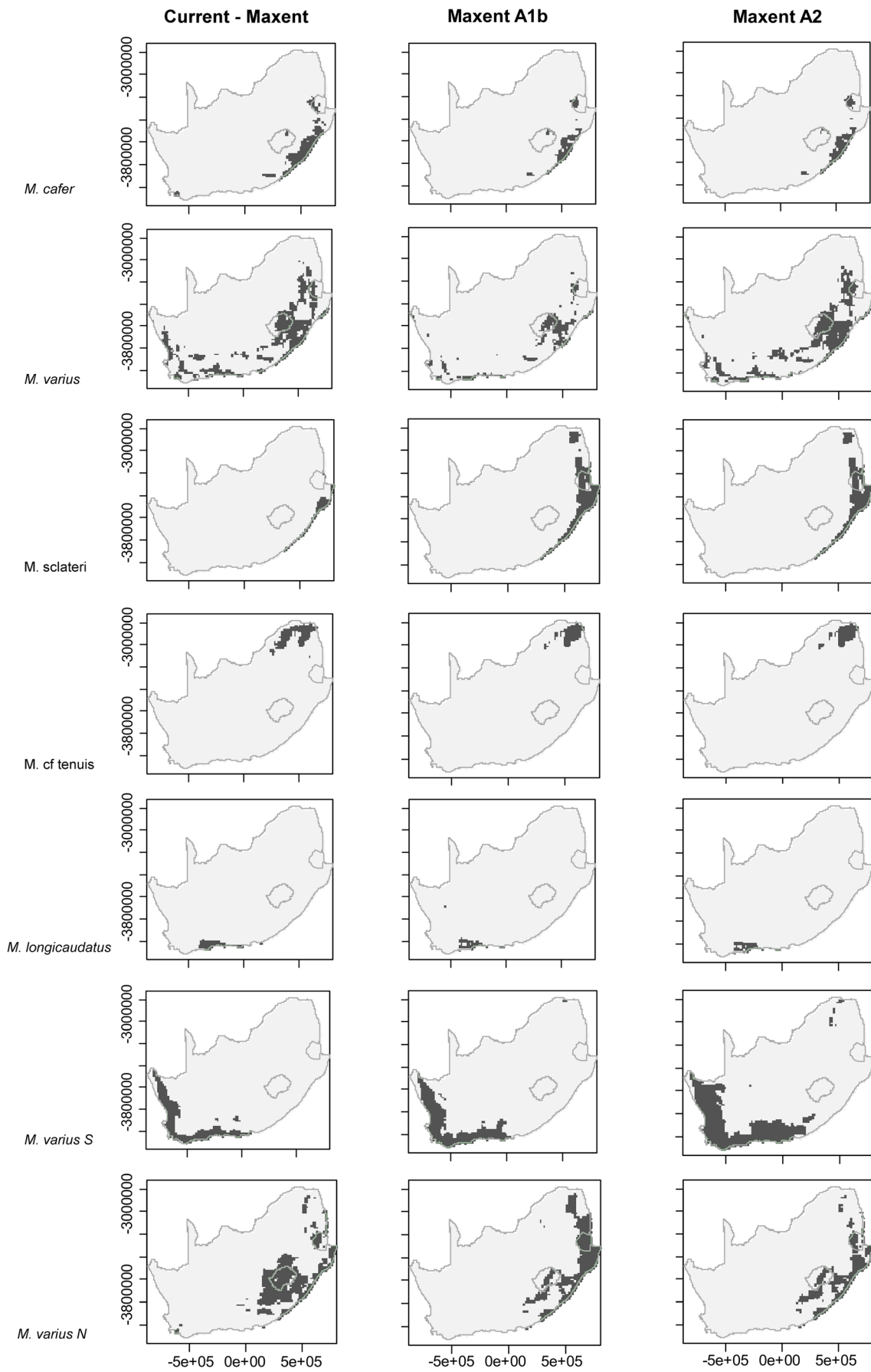
Considering Maxent models only and assuming full dispersal, most species showed range contractions and fragmentation in future models compared to the present (Fig. 3; Table 2). In *M. cafer*, for both future scenarios, the ranges tended to contract towards the coast and outlying populations from the Eastern Cape in the south. Moreover, in both future scenarios, *M. cafer* in the Swaziland highlands in the north become increasingly isolated and disconnected from the stronghold of the species range in KwaZulu-Natal province. In *M. varius*, the A1b model predicted general fragmentation of the present range and a retreat towards higher elevations along the Cape Fold Belt and Natal Drakensberg of the Great Escarpment. However, in the A2 scenario, the range of

M. varius remained similar to the present and even expanded slightly (Table 2). In both future scenarios, the predicted future range of *M. sclateri* expanded considerably northwards and southwards along the eastern foothills of the Drakensberg Range. The present model for *M. cf. tenuis* suggests that suitable habitat for the species currently occurs just outside its known range in the Soutpansberg Mountains and northern Drakensberg, extending westwards to the Waterberg Mountains. However, both future models show a retreat of suitable habitats for the species to their currently described range, with potential small isolated populations occurring further south along the Drakensberg Escarpment. Under both scenarios, the future predicted range of *M. longicaudatus* was more fragmented compared with the present. The models for the southern (fynbos) and northern (grassland) genetic lineages of *M. varius* revealed distinct patterns compared with the combined species, but this might have been in part due to the much smaller sample sizes of genetically determined specimens ($n = 22\text{--}33$) compared with the combined species dataset ($n = 287$). The southern fynbos lineage showed small changes or an increase in range in the future, while the northern grassland lineage showed a future contraction in the region of the central highveld plateau of South Africa. One commonality found in the models for *M. varius* and its two lineages (but not in other models) concerned the observation that range reductions in the A2 scenario were much less severe than in the case of A1b (Fig. 4).

Figure 4 summarises the declines for each species based on the assumption of no dispersal and adjusted for land transformation. For *M. varius* and its lineages, and to a lesser extent for *M. cafer* and *M. longicaudatus*, declines under the more pessimistic A2 model scenario tended to be less extreme than for the more optimistic A1b scenario (Fig. 4). Depending on assumptions of dispersal (no dispersal versus full dispersal), future climate models predicted range declines in four species, *M. cafer* (42–48 and 37–41 % for A1b and A2 respectively), *M. varius* (63–66 % decline for A1b and 36 % increase to 10 % decline for A2), *M. cf. tenuis* (34–41 and 35–40 % for A1b and A2 respectively) and *M. longicaudatus* (57–61 and 18–33 % for A1b and A2 respectively), and range expansions in *M. sclateri* (0–188 and 0–180 % increases for A1b and A2 respectively) (Table 2). The northern lineage of *M. varius* showed moderate declines (38–43 % for A1b and 23–25 % for A2), while the southern lineage showed a decline under A1b (29–33 %) but an increase under A2 (0–44 %).

Fig. 2 Maps showing GLM-modelled current and future (2050; A1b and A2 scenario) distributions of all seven *Myosorex* species and subspecific lineages, assuming unrestricted dispersal capability. The coordinates indicated on the map axes represent metres in the Albers equal area projection for Africa





◀ **Fig. 3** Maps showing Maxent-modelled current and future (2050; A1b and A2 scenario) distributions of all seven *Myosorex* species and subspecific lineages, assuming unrestricted dispersal capability. The coordinates indicated on the map axes represent metres in the Albers equal area projection for Africa

Discussion

Implications for climate change

Our hypothesis that the habitat generalist, widespread species (*M. varius*) would be more adaptable and less susceptible to climate change than its more habitat specialist congeners was not supported by our results since the A1b scenario predicted a large AOO decline of 63–66 %. On the other hand, the A2 scenario predicted a slight increase in range, but this result is contested due to the extreme under-prediction of the model (see below). Conclusions about impacts of climate change can therefore be influenced by technical aspects of SDMs as emphasised below, requiring caution and careful analysis when making interpretations from these results.

The Maxent model for *M. varius* performed more poorly than all other models (AUC 0.74, 67 % correct predictions). This is largely because many of the peripheral and outlying records occur in marginally suitable riparian or restricted higher elevation habitats surrounded by unsuitable habitats (Fig. 1, R. M. Baxter personal communication) and hence were not included in the range predicted by the model. Indeed, the present habitat suitability model for *M. varius* excludes many of the outlying known occurrence points (cf. Figs. 1 and 3). Thus, the apparent increase in potential habitat in the A2 model is

not a real increase but rather a decline since the predicted A2 range falls well within the polygon of known occurrence points for the species (Figs. 1 and 3). This under-prediction of the present habitat suitability map may also have arisen due to the mask (background) chosen for this study being possibly too restrictive for this widespread species, leading to “truncated responses” (Anderson and Raza 2010; Van Der Wal et al. 2009).

Another reason for the poor performance of the *M. varius* model could be that this species comprises at least two distinct lineages occupying diverse fynbos and grassland biomes (Willows-Munro and Matthee 2011). If these lineages constitute good evolutionary and ecological species having distinct niches, then it may not make sense to model these diverse lineages together, and this may explain the poor model evaluation success and discrepancy between different scenarios. Indeed, when the two lineages are modelled differently (using a much smaller subset of occurrence points based on genetically identified voucher specimens and hence avoiding many of the outlying localities included in the species dataset), model fit is much improved (AUC 0.86–0.94) and contrasting patterns are obtained for the southern fynbos lineage, which shows either a small decline or a range increase, and for the northern grassland lineage which shows consistent declines (23–44 %) in range size across different scenarios, similar to those predicted for the A2 scenario for a grassland-associated Afrotropical rodent (*O. auratus*) having a very similar range (Taylor et al. 2015).

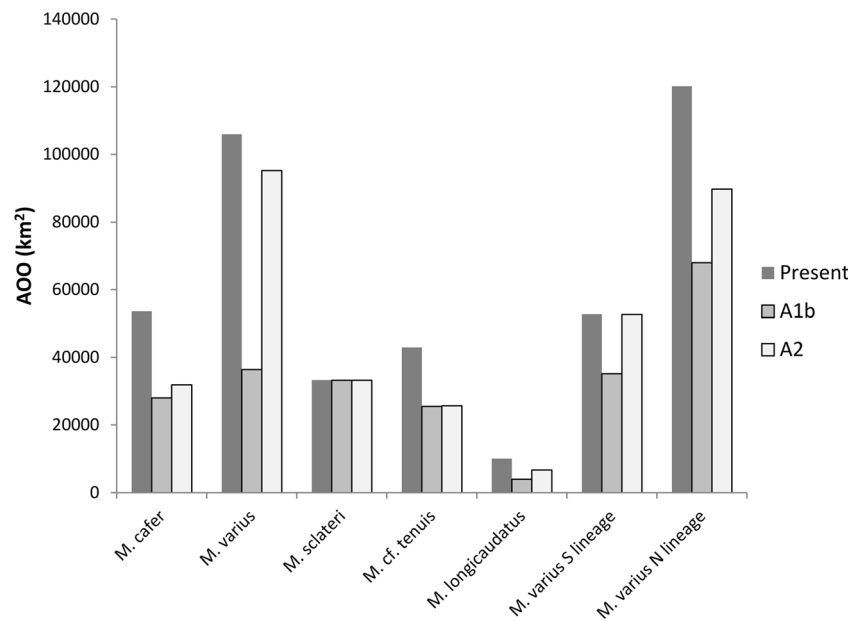
As elaborated below, temperature maxima rather than minima limit the distribution of *M. varius*. The most influential variable in the SDM for *M. varius* was the mean maximum temperature of the warmest month (36 % contribution) (Table 1). The current distribution

Table 2 Area of occupancy (AOO; km²) estimated for fivefold cross-validation Maxent models of current (1975) and future (2050) distribution for five mice shrew species, using two different IPCC climate scenarios (A1b and A2), assuming either no dispersal or full dispersal

Species	Present		A1b		A2		A2		A2	
	Not adjusted for land cover transformation AOO (km ²)	Adjusted for land cover transformation AOO (km ²)	Full dispersal AOO (km ²)	% Change	No dispersal AOO (km ²)	% Change	Full dispersal AOO (km ²)	% Change	No dispersal AOO (km ²)	% Change
<i>M. cafer</i>	91,319	53,604 (–41 %)	30,895	–42	27,983	–48	33,968	–37	31,865	–41
<i>M. varius</i>	174,849	105,958 (–39 %)	38,742	–63	36,403	–66	144,445	+36	95,184	–10
<i>M. sclateri</i>	59,316	33,276 (–44 %)	95,845	+188	33,236	0	93,062	+180	33,236	0
<i>M. cf. tenuis</i>	59,038	42,967 (–28 %)	28,084	–35	25,477	–41	28,084	–35	25,678	–40
<i>M. longicaudatus</i>	14,070	10,120 (–28 %)	4359	–57	3962	–61	8321	–18	6736	–33
<i>M. varius</i> S lineage	74,762	52,719 (–30 %)	37,494	–29	35,162	–33	107,432	+104	52,647	0
<i>M. varius</i> N lineage	192,010	120,187 (–37 %)	74,865	–38	67,965	–43	92,288	–23	89,700	–25

In all models except where indicated, transformed land cover was subtracted using the national land cover coverage (<http://bgis.sanbi.org/landcover/project.asp>). For the present model, percentages in parentheses indicate declines in AOO after adjusting for land cover transformation. Elsewhere, % changes indicate declines or increases for future climate models relative to the present model (with both present and future models adjusted for transformed land cover)

Fig. 4 Present and future (2050; based on A1b and A2 climate change scenarios) predicted areas of occupancy (AOO) for seven species and genetic lineages of *Myosorex* shrews from Maxent models. All AOO values reflect habitat untransformed by humans (see text for details)



of the species in South Africa coincides largely with areas having mean maximum monthly temperatures lower than 28 °C (Supp. Fig. 1; see also Brown et al. 1997). Under both the A1b and A2 scenarios, peripheral parts of the species range currently experiencing monthly maxima less than 28 °C are replaced in 2050 with grids having maximum temperatures of 28–30 °C (Supp. Fig. 1). Thus, the predicted decline in the species AOO by 2050 can be largely explained by projected increases in monthly maximum temperatures. Due to their small body size and high metabolic rate, shrews have a high heat load resulting in high metabolic costs of evaporative cooling at high ambient temperatures, as well as reduced starvation resistance. While tropical or arid-adapted shrews may adapt to higher ambient temperatures by having higher body temperatures or a lower basal metabolic rate (BMR), such adaptations are not found in temperate shrews (Brown et al. 1997; Sparti 1990). For a temperate-montane species like *M. varius*, ambient temperatures above 28 °C appear to exceed the physiological tolerance of the species, possibly due to excessive water losses required for evaporative cooling. However, laboratory studies indicate a thermoneutral zone for *M. varius* of 29–35 °C (Brown et al. 1997) that does not support the idea of increased metabolic costs at temperatures higher than 28 °C.

Further studies are required to determine the physiological or other mechanisms that appear to limit the species to maximum monthly temperatures of 28 °C. *M. varius* would therefore be an ideal model species to explore mechanistic models for predicting climate change impacts. Mechanistic models that depend on responses of physiological traits to temperature (performance curves) in order to predict distribution changes in response to

climate change have begun to receive increased attention as an alternative to correlative models such as Maxent (Chown et al. 2010).

At the same time, we need to stress the importance of microhabitat refuges which allow individual shrews to occupy environments buffered from ambient climate to some extent, at least when they are resting and not foraging, e.g. *Myosorex* have sharp claws allowing them to burrow (Hutterer 2013).

This leads to the second hypothesis that temperate-montane species should be more susceptible to climate change than the non-montane (lowland forest), subtropically distributed species, *M. sclateri*. This hypothesis is supported by the results since, as expected, the temperate-montane species, *M. varius*, *M. cf. tenuis*, *M. cafer* and *M. longicaudatus*, all experienced moderate to severe range contractions, while *M. sclateri* showed either no change in the area of occupancy (assuming no dispersal) or a potential range expansion of 180 % (under the improbable assumption of full dispersal). Range expansion is improbable since *M. sclateri* is a coastal forest specialist and most of the areas included in the expanded range include unsuitable habitat which would not support populations of the species.

As expected from differences in the responses of montane-temperate and lowland subtropical species, while montane-temperate species such as *M. varius* seem to be limited by intolerance for higher ambient temperatures (see above), the SDM for *M. sclateri* is strongly influenced (73 % contribution) by the mean minimum temperature of the coldest month (Tmin) where optimal habitats occur at minimum temperatures exceeding 12 °C, suggesting that low temperatures limit physiologically the distribution of this subtropical species.

The biogeographical affinity (temperate or tropical) of *M. cf. tenuis* is somewhat unclear. Although populations of this

species occupy montane grassland and forest habitats (Taylor et al. 2013), they occur mostly north of the Tropic of Capricorn (in the Soutpansberg Mountains) and at lower altitudes (up to 1750 m in the Soutpansberg, 2050 m in the Wolkberg), leading to moderate temperatures, e.g. mean monthly temperatures measured at 1750 m in the Soutpansberg varied from -0.4 to 29.6 °C (Taylor et al. 2014). The SDM for *M. cf. tenuis* is most strongly influenced (82 % contribution) by seasonality of precipitation (P_{season}) as well as precipitation of the wettest month (P_{max}; 16 %), rather than by temperature. The SDM predicts the current range to include additional areas of the Waterberg Range of Limpopo Province, west of the Soutpansberg, where no known occurrence records exist. The SDM for 2050 indicates minimal change in the area of occupancy except for the loss of apparently suitable present habitats in the Waterberg. Thus, although recorded as future declines when compared to the (overpredicted) present model (Table 2), in fact the future models correspond with the current range based on known occurrence records. Commensurate with this, both the current and projected (2050) maps for P_{max} (Supp. Fig. 2) revealed stable areas of maximum (>50 mm) precipitation of the wettest month that coincided geographically with the optimal current and future habitats for *M. cf. tenuis*.

Conservation implications

Few studies have attempted to evaluate the extinction risk of species due to projected future climate change and land transformation changes using the IUCN (2012) Red List criteria. Bomhard et al. (2005), for example, used the A (population size reduction) and B (geographic range) Red List criteria to reclassify threat categories of Proteaceae in the Cape Floristic Region based on future climate change and land transformation projections. Up to one third of all 227 taxa considered were uplisted (became more threatened) when future climate change threats projected for 2020 were included (Bomhard et al. 2005). Similarly, assuming no dispersal and using the A3(c) Red List criterion (population reduction projected, inferred or suspected to be met in the future (up to a maximum of 100 years) based on a decline in AOO, extent of occurrence (EOO) and/or habitat quality), Thuiller et al. (2006) showed that 10–15 % of 277 species of large and medium-sized African mammals could fall into critical endangered or extinct categories by 2050 due to the combined effects of climate change and land transformation (where future land transformation was conservatively taken to correspond to current levels).

In species having small or very small areas of occurrence or occupancy (according to prescribed thresholds), and either fluctuating populations or highly fragmented habitats, projected continuing declines (of unspecified magnitude) due to climate change can be used to formally justify

threatened categories (vulnerable, endangered or critically endangered) under the B1 (EOO) and B2 (AOO) criteria of the IUCN (2012). In the present study, although we corrected for transformed habitats, calculated AOOs were still overestimated given the fact that most of the *Myosorex* species are habitat specialists, occurring in Afromontane grasslands (*M. varius* and *M. cf. tenuis*) and forests (*M. cafer*), fynbos (*M. varius* and *M. longicaudatus*) and coastal and scarp forests (*M. sclateri*). Thus, based on our conservative calculations of untransformed habitats, no species AOO fell below the threshold value of 2000 km² to qualify for the vulnerable category (Table 2). However, based on actual calculations of respective remaining habitats (vegetation types) within the extent of occurrence of different *Myosorex* species in an independent study, Child et al. (2016) obtained AOO estimates that qualified *M. cf. tenuis* and *M. longicaudatus* as endangered and *M. cafer* and *M. sclateri* as vulnerable. These data could not be incorporated into the present study due to different approaches and databases used.

Given both the small estimated AOOs (from Child et al. 2016) as well as the fragmented nature of habitats, the evidence presented herein for ongoing projected declines in AOO due to climate change (assuming no dispersal) contributed to listing *M. cafer* under the B2 criteria as vulnerable (Taylor et al. 2016a) and *M. longicaudatus* as endangered (Baxter et al. 2016) in a recent Mammal Red List of South Africa, Swaziland and Lesotho (Child et al. 2016). In the case of *M. sclateri* and *M. cf. tenuis*, although climate models predicted little or no reduction in area of occupancy by 2050, accelerated land cover transformation in KwaZulu-Natal and Limpopo provinces respectively (Driver et al. 2012) provides strong evidence for continuing declines of these two species, allowing them to be listed as vulnerable (Taylor et al. 2016b) and endangered (Taylor et al. 2016c) respectively. These new IUCN assignments represent uplistings of previous categories (Baxter 2008a,c,d): *M. cafer* from least concern to vulnerable, *M. sclateri* from near threatened to vulnerable and *M. longicaudatus* from vulnerable to endangered. *M. cf. tenuis* was not assessed previously as it was formerly assigned to *M. cafer* (Taylor et al. 2013). Since all *Myosorex* taxa in “greater South Africa” (including Swaziland and Lesotho) are endemic to this region, the revised assessments from the recent regional assessment will also apply globally (Child et al. 2016).

The results of this study confirm those of Taylor et al. (2015) that climate change can be expected to have significant negative impacts on the diversity of small mammals occupying montane regions of Africa. These results also agree generally with other modelling studies which predict considerable losses of plant and animal biodiversity due to climate change in southern Africa (Coetzee et al. 2009; Erasmus et al. 2002; Hannah et al. 2005; Hughes et al. 2008; Midgley et al. 2006; Pio et al. 2014; Simmons et al. 2004; Thomas et al. 2004;

Thuiller et al. 2006) and eastern Africa (Monadjem et al. 2012). Such losses will be further compounded by accelerated rates of habitat loss in South Africa (Driver et al. 2012), making it extremely important to increase the extent of protected area networks particularly in mountainous areas which could function as climate change refugia for threatened montane taxa by allowing safe migration along elevational “corridors”.

Methodological caveats

The better performance (AUC and % correct prediction) and improved biological interpretation of Maxent over GLM in our study confirmed previous studies which have endorsed the former for SDMs, particularly where sample sizes are small (Elith et al. 2006). Although we expected very similar results from the two future scenarios used (A1b and A2) or at least increased range losses in the more pessimistic A2 scenario which predicts higher global temperatures, our results revealed some surprising departures from expectation, most notable decreased range losses (or even apparent range gains) in the A2 scenario, particularly in the case of *M. varius* and its two lineages. Since precipitation variables were important in these models, more so than temperature in the case of the *M. varius* lineages, responses to climate change may be mediated by both precipitation and temperature and precipitation may respond in complex and unpredictable ways to climate change.

Apparent future range gains in some temperate species and lineages were misleading and due to under-prediction of the current models for *M. varius* and its two lineages. Under-prediction may be due to the background being too small. Since the background was designed largely based on the range of *M. varius*, this could explain the under-prediction in the current model for this species. When Maxent models were repeated using South Africa, Lesotho and Swaziland as the background, under-prediction for the current range was reduced and consistent range declines (not increases) were reported for both A1b and A2 scenarios (results not shown but available from PJT). On the other hand, the current model for *M. cf. tenuis* was overpredicted, leading to apparent range declines which were not realised since future modelled ranges coincided closely with extent of known occurrence points.

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