

https://dspace.org/

Gazing into the future The potential impact of climate change on habitat suitability of the Sungazer Smaug giganteus

Wade Stanton-Jones; Graham Alexander

WILEY-BLACKWELL
https://hdl.handle.net/10539/42511
WOS

Downloaded from a DSpace repository. https://dspace.org/

Received: 25 January 2024 | Revised: 15 July 2024 | Accepted: 5 August 2024

DOI: 10.1111/aec.13577

RESEARCH ARTICLE

Gazing into the future: The potential impact of climate change on habitat suitability of the Sungazer (*Smaug giganteus*)

Wade K. Stanton-Jones[1,2] | **Graham J. Alexander**[1]

[1]School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Johannesburg, South Africa

[2]Kirstenbosch Research Centre, South African National Biodiversity Institute, Cape Town, South Africa

Correspondence
Wade K. Stanton-Jones, School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Johannesburg, P.O. Wits, 2050, South Africa.
Email: wadesj13@gmail.com

Funding information
Rufford Foundation, Grant/Award Number: 29137-1

Abstract

The sungazer (*Smaug giganteus*) is a strict grassland specialist lizard endemic to South Africa's highveld grasslands. It is currently listed as Vulnerable (IUCN) and is primarily threatened by anthropogenic activities. Because sungazers are habitat specialists, climate change may be detrimental to the species, considering their life-history traits, and the area of available suitable habitat. We assessed how climate change may impact the sungazers' geographic range by first producing an ecological niche model (ENM) for the species within a buffered region of its extent of occurrence (buffered EOO). The ENM was then projected to 2040, 2060, 2080 and 2100 under two climate change scenarios using Shared Socioeconomic Pathways (SSP); SSP245 (moderate-case) and SSP585 (worst-case). A mean ensemble of three global circulation models for each time period and scenario was used to create habitat suitability maps which were refined using a natural grassland variable overlay. Resulting maps were clipped to the sungazers' EOO and interpreted distribution. Within the interpreted distribution, models predicted an area of 10 198 km^2 of current suitable habitat. At this scale, future habitat suitability is predicted to remain relatively stable (area: 9910 km^2; 3% decline) under SSP245 by 2100. However, a 24% decline (area: 7705 km^2) in habitat suitability was predicted under SSP585. Within the buffered EOO, habitat suitability increased in south-western regions, which was more prominent under SSP585. Although this finding suggests that sungazers could track favourable conditions, their life history and low dispersal ability makes climate tracking unlikely. Because sungazers only occur in primary grasslands, regions dominated by agricultural activities, further land use developments are likely to affect the species survival. Thus, careful conservation management is essential, and we recommend the establishment of protected areas with cognizance of our predictions for current and future suitable habitat within the sungazers' interpreted distribution.

KEYWORDS
climate change, ecological niche model, habitat specialist, habitat suitability, *Smaug giganteus*

INTRODUCTION

The expansion of the human population and associated anthropogenic activities in recent decades has caused greenhouse gases to rise

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.
© 2024 The Author(s). *Austral Ecology* published by John Wiley & Sons Australia, Ltd on behalf of Ecological Society of Australia.

significantly (IPCC, 2022). Consequently, the effects of climate change on global biodiversity are being exacerbated. Since climate is an important factor that influences organismal biology, it is not surprising that the effects of climate change have imposed challenges to the survival of many species (Parmesan, 2006; Sinervo et al., 2010). Some species, such as many reptiles, whose life-history traits and geographic ranges are highly dependent on climate (Böhm et al., 2016; Moreno-Rueda et al., 2012; Perold et al., 2021), may be more vulnerable to climate change than others (Parmesan, 2006). More than 80% of reptile species are predicted to be highly sensitive to climate change, and nearly half may not be able to adapt to changing conditions effectively (Böhm et al., 2016). Predictions indicate the local extinctions of nearly 40% of lizard populations, and total extinction of approximately 20% of lizard species (Sinervo et al., 2010). These predictions highlight the importance of climate change mitigation measures, as species that are unable to respond to climate change fast enough will likely face an increased risk of extinction (Román-Palacios & Wiens, 2020).

Reptiles may respond to climate change by shifting their geographic ranges to track suitable conditions (Araújo et al., 2006; Petford & Alexander, 2021). During most historical changes in climate, reptiles probably simply tracked suitable conditions, so that eco-physiological processes could continue to function without change. However, physical barriers such as mountains or water bodies may limit dispersal into future climatically suitable areas, but these areas may also be compromised by habitat loss and fragmentation due to anthropogenic land use (Albaladejo-Robles et al., 2023; Gouveia et al., 2016). Species biological traits may also hinder their ability to track suitable conditions (Böhm et al., 2016; Bradshaw & Holzapfel, 2006). This is particularly true for habitat specialists, species with low dispersal rates and species with restricted geographic ranges (Böhm et al., 2016; Parmesan, 2006; Petford & Alexander, 2021). In such cases, this may cause geographic range contraction under future climates (Parmesan, 2006; Petford & Alexander, 2021). Nevertheless, knowing how the geographic distribution of a species could change in future climates provides valuable information for conservation management plans (Carroll et al., 2010), which may be particularly important for high-risk species.

The sungazer (*Smaug giganteus*; Smith, 1844) is a threatened (Vulnerable; Alexander et al., 2022) habitat specialist lizard restricted to the Highveld grasslands of South Africa. Its geographic range is restricted to the northern Free State and southernmost parts of the Mpumalanga provinces (De Waal, 1978; Jacobsen, 1989; Parusnath et al., 2017). These regions are heavily impacted by agricultural activity (DEAT, 2005). Consequently, approximately only half of sungazer habitat remains in a natural state (Parusnath et al., 2017). Even though the rate of natural grassland decline has slowed significantly in recent decades (Parusnath et al., 2017), the species may still be exposed to other anthropogenic pressures such as poaching and mining (e.g. McIntyre, 2006). These pressures, along with an already small geographic range, are likely to increase the sungazer's vulnerability to climate change.

Sungazer life history does not appear to be conducive to responding to changing climates. Sungazers are large-bodied, long-lived ambush foragers that can spend their entire life taking refuge in a single self-constructed burrow (Bates et al., 2014; Parusnath, 2014; Van Wyk, 1992). Because of this, sungazers have strict habitat requirements at both the macro and micro scale, and changes in their environment are expected to be detrimental to the long-term survival of the species. Sungazers are mostly active within a 2-m radius of their burrow entrances (Ruddock, 2000; Van

Wyk, 1992), and dispersal appears to be limited, with an average dispersal distance of 126.3-m over a 12 to 16-year period (Stanton-Jones et al., 2023). Since litter size is relatively small (maximum of three young per litter), and live birth is generally biennial, reproductive rate in sungazers is low (Van Wyk, 1992). This not only reduces the chances of adaptation to climate change through evolutionary mechanisms but also limits dispersal into suitable habitats in future climates. Even though the life-history traits of sungazers may increase the species risk of extinction under climate change, predicting potential changes of their geographic distribution in future climates is vital for conservation planning (Carroll et al., 2010; McShea, 2014).

In this study, we used two climate change scenarios under the Coupled Model Intercomparison Project Phase 6 (CMIP6) and assessed the potential impact that each scenario would have on the geographic range of *S. giganteus*. Although Stanton-Jones et al. (2018) predicted that sungazers could possibly adjust to climate change through behavioural adjustment, the species life-history traits, relatively low target body temperature, and the anthropogenic pressures to which subpopulations are exposed, increases their vulnerability to climate change, and the species may be more at risk of extinction than previously assessed. Because the moderate-case climate change scenario assumes that conditions do not deviate dramatically from current climate, we predicted that in the near future, the current geographic range of sungazers would remain stable, but that changes would become apparent in distant futures. We also hypothesized that the worst-case climate change scenario would result in a substantial contraction of the species current suitable habitat, particularly in distant futures. We contend that the approach used in this study can be widely applied for predicting the conservation needs of reptiles into the future.

METHODS

Sungazer occurrence records

Presence-only records of *Smaug giganteus* were gathered from our own field work (2015–2022), Parusnath (2014, 2020) and from the Endangered Wildlife Trust. The resulting combined dataset included 1957 locality records. Given that sungazers are restricted to a relatively small geographic range (Parusnath et al., 2017), and because the dataset used in this study is the most comprehensive available, it is possible for spatial sampling bias to exist when constructing and running an ecological niche model (ENM). Thus, to minimize any potential effects of spatial autocorrelation, the dataset was cleaned, and spatially filtered with a 5-km radius (filtering using a 1-km and 3-km radius, respectively, resulted in overfitting) using the *spThin* package (Aiello-Lammens et al., 2015) in *R* 4.1.1 (R Core Team, 2021). This resulted in the number of locality records being reduced to 171. Importantly, because the sungazer is a threatened species, and as recommended by the South African National Biodiversity Institute (http://nssl.sanbi.org.za/), we have not presented exact localities of the species.

Environmental variables

Bioclimatic variables for current and future conditions were downloaded from the WorldClim database (Version 2.1; www.worldclim.org; Fick & Hijmans, 2017). For current conditions, we used the standard 19 bioclimatic

variables at a resolution of 30 arc-seconds (arcsec; ~1 km). Because sungazers construct their own burrows which are often used as permanent refuge sites (Van Wyk, 1992), we also included soil composition (% sand, % silt and % clay) and the cation exchange capacity (CEC) of soils (Batjes, 2004) when constructing the ENMs. Geology type (categorical data; scale = 1: 1000000; Council for Geosciences, 2018) and elevation (30 arcsec resolution; Fick & Hijmans, 2017) were also downloaded and included as predictor variables in the models. Vegetation type was excluded as a variable since it is likely that patterns of vegetation type will also change with changing climate. All bioclimatic and environmental variables were cropped to a rectangular-shaped buffer (buffered extent) in QGIS (Version 3.26.0), with a perimeter delimited to within a half a degree square outside of the minimum convex hull (Extent of Occurrence; EOO) for sungazers (Figure 1). We tested for correlations among the 19 bioclimatic variables using a Pearson's correlation coefficient in *R* 4.1.1 (R Core Team, 2021). Careful consideration was made to highly correlated ($|r| \geq 0.75$) variable pairs (Table S1), and the variables considered to be the most ecologically important for sungazer distribution were retained and included in the ENM for sungazers (Table 1).

For projections into the future, we used two Shared Socioeconomic Pathways (SSPs) under the Coupled Model Intercomparison Project Phase 6 (CMIP6); SSP245 (moderate-case) and SSP585 (worst-case). These scenarios offer different realistic predictions for future climate based on socioeconomic and technological trends. SSP245 ('Middle of the Road'; Riahi et al., 2017) predicts that trends in socioeconomic and technological sectors, as well as carbon dioxide emissions, do not deviate significantly from current conditions. By the end of the 21st century, SSP245 predicts

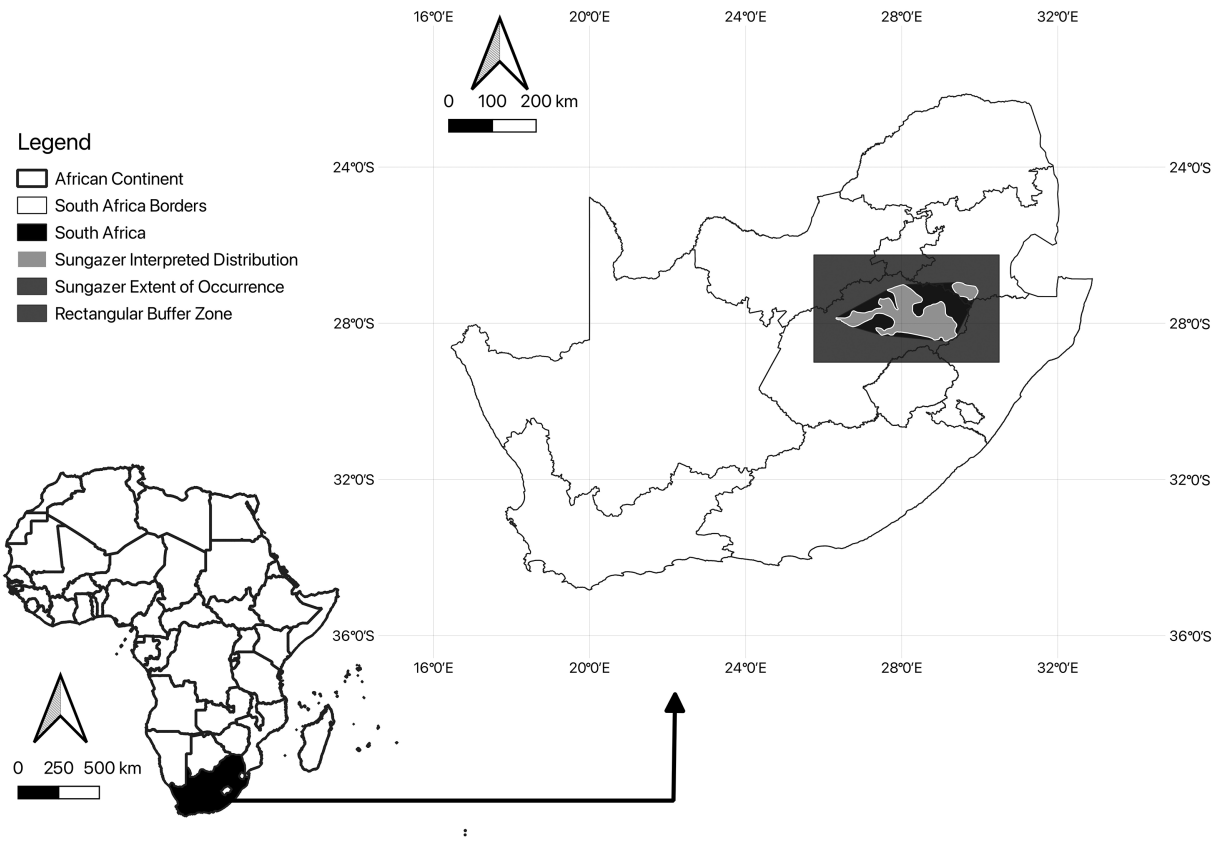


FIGURE 1 Map of Africa zoomed into South Africa that shows the different scales used to predict habitat suitability for sungazers. Dark grey represents the rectangular buffer zone (142 884 km^2) from which current and future sungazer distributions were modelled. Inside the buffer zone is the EOO (black; 40 573 km^2) and the interpreted distribution (light grey; 21 985 km^2) for sungazers.

TABLE 1 Bioclimatic and environmental variables that were retained after highly correlated variable pairs were inspected and variables removed accordingly.

Code	Description	References
Bio 1	Annual mean temperature	Fick and Hijmans (2017)
Bio 3	Isothermality	Fick and Hijmans (2017)
Bio 6	Minimum temperature of the coldest month	Fick and Hijmans (2017)
Bio 12	Annual precipitation	Fick and Hijmans (2017)
Bio 15	Precipitation seasonality	Fick and Hijmans (2017)
Bio 17	Precipitation of the driest quarter	Fick and Hijmans (2017)
Soilcec	Cation exchange capacity of soils	Batjes (2004)
Clayperc	Percentage of clay content in soils	Batjes (2004)
Sandperc	Percentage of sand content in soils	Batjes (2004)
Siltperc	Percentage of silt content in soils	Batjes (2004)
Elevation	Elevation	Fick and Hijmans (2017)
Sggeol	Geology	Council for Geosciences (2018)

Note: The variables listed below were used to construct the sungazer species distribution model.

that annual surface temperature will likely be warmer by 2.1–3.5°C compared to the 1850–1900 period (IPCC, 2021). In contrast, the worst-case scenario, SSP585 ('Taking the Highway'; Riahi et al., 2017), predicts very little mitigation measures for climate change, and a fossil-fuel dominant future where, compared to 1850–1900, annual surface temperature will likely be 3.3–5.7°C warmer by 2081–2100.

GCMeval (gcmeval.met.no; Parding et al., 2020) was used to identify the best ranked models for southern Africa. Three global circulation models (GCMs) existing within the top 15 ranked models for southern Africa were selected to create an ensemble for projections up to 2100: (1) First Institute of Oceanography Earth System Model version 2.0 (FIO-ESM-2-0); (2) Max Planck Institute for Meteorology Earth System Model using the high-resolution protocol (MPI-ESM1-2-HR); and (3) Meteorological Research Institute Earth System Model version 2.0 (MRI-ESM2-0). Using GCMeval, the ensemble for the selected models was inspected to ensure that the models were normally distributed. Bioclimatic variables for each GCM and SSP scenario were downloaded, and only the relevant bioclimatic variables that were also identified for current conditions (Table 1) were processed for modelling into near (2021–2040), medium (2041–2060 and 2061–2080) and distant (2081–2100) futures.

Ecological niche model

Sungazer distribution models were constructed following the maximum entropy (Maxent) approach. Maxent has a proven track record for dealing with presence-only records when modelling species distributions (Elith et al., 2006; Phillips et al., 2006). However, species-specific tuning is necessary for optimal predictive power, and results in models that perform as efficiently to other ensemble approaches (Hao et al., 2020; Kaky et al., 2020; Valavi et al., 2022).

To maximize the predictive ability, 4187 occurrence records of all reptiles (Tolley et al., 2023) within the buffered extent were used to create a bias file for background point sampling. The bias file was created in *R* 4.1.1 (R Core Team, 2021) and was used to randomly sample 10 000 background points, within the buffered extent, through different model iterations. The *R*

package, ENMeval 2.0 (Kass et al., 2021), was used to construct a variety of models with different levels of complexity, all within the buffered extent. To construct these models, we implemented the Maxnet algorithm (Version 0.1.4) which employs an infinitely weighted logistic regression to fit Maxent models (Phillips, 2021; Phillips et al., 2017). The algorithm places strong emphasis on background points compared to presence points and uses the same feature classes (FC: linear (L), quadratic (Q), hinge (H), product (P) and threshold (T)), and regularization multipliers (RM) as the traditional *Maxent.jar* algorithm (Phillips et al., 2017). Thus, we constructed models with varying combinations of FCs (L; LQ; H; LQH; LQH; LQHP; LQHPT), and RMs (0.5–4.5, increments of 0.5).

Because this study investigated cross-time projections, the spatial block method (a variant of *k*-fold cross-validation) was used for data partitioning (Muscarella et al., 2014). Here, occurrence and background data are partitioned equally into four bins based on longitude and latitude; one testing bin and three training bins (Muscarella et al., 2014). The above resulted in 54 model runs, each with a different combination of FCs and RMs. The model with the lowest delta Akaike information criterion corrected for small sample sizes (AIC_c) was considered to provide the optimal settings for generating the sungazer ENM (Warren & Seifert, 2011). We evaluated this model and ensured that it prevented overfitting by inspecting the following metrics: the threshold-independent metric (area under the curve; AUC), the 10th-percentile omission rate (OR_{10}) and the minimum training presence omission rate (OR_{mtp}; Anderson & Gonzalez, 2011). These model settings were used to predict the current distribution of sungazers. The model was then projected into the near, medium and distant futures using the three different GCMs under SSP245 and SSP585, resulting in 24 model runs across different temporal scales and scenarios. For projections into the future, only the bioclimatic variables from current conditions were replaced with those from each GCM under each climate change scenario, but the environmental variables (e.g. soil composition, geology and elevation) used for current conditions remained constant when making the future predictions for each GCM and scenario.

Habitat suitability assessment

Models from the three GCMs under the SSP245 and SSP585 scenarios were combined using the 'Raster Calculator' function in QGIS (Version 3.26.0) to create a simple mean ensemble for each scenario and time period (Palm & Zellner, 1992; Petford & Alexander, 2021). To assess habitat suitability, we used the 'Raster Calculator' function in QGIS (Version 3.26.0) to convert the predicted distribution maps from the ensembles and current conditions into binary maps (suitable/unsuitable habitat), with the 10th-percentile training presence value used as the threshold for conversion (Liu et al., 2005). Because sungazers occur only in natural grassland within their distribution (Parusnath et al., 2017), we used the most recent land cover map of South Africa (DFFE, 2020) to extract this land cover type, resulting in a binary land cover map distinguishing natural grasslands from the other land cover types. Since no future land cover types exist for our study region, and because Parusnath et al. (2017) reported stability among natural grassland, we overlaid the binary natural grassland layer onto our binary maps for current and future distributions of sungazers. This additive approach resulted in maps with values of zero (not suitable for sungazers nor is natural grassland), one (is natural grassland only), 10 (predicted sungazer habitat) and 11 (suitable sungazer habitat after accounting for natural grassland, i.e. a more realistic interpretation of suitable habitat).

The resulting maps not only show areas of suitable sungazer habitat but also show the importance of taking ecological factors into account when running species distribution models. These maps were then clipped to the EOO and interpreted distribution for *S. giganteus* to identify potential fine scale differences in habitat suitability.

The GRASS *r.report* function in QGIS (Version 3.26.0) was used to calculate the predicted area of suitable habitat for current and future climate scenarios under the three scales (buffered extent, EOO, interpreted distribution). For an estimate of the total area considered suitable for sungazers, area measures were calculated as a percentage of the area of each scale. This was also done for all future predictions. The percentage of habitat change (+/–) between current and future conditions was also calculated, and Schoener's D statistic from the *nicheOverlap* function of the *dismo* package (Hijmans et al., 2017) in *R* 4.1.1 (R Core Team, 2021) was used to quantify niche overlap between current and future predictions.

RESULTS

Sungazer ENM

The sungazer distribution model showed no obvious signs of overfitting and performed well under the tuning parameters (FC = LQHP; RM = 1.5; $\Delta AIC_c = 0.00$; $OR_{10} = 0.14$; $OR_{mtp} = 0.02$). The average test AUC was 0.905 ± 0.022, indicating very good model performance (Swets, 1988). Habitat conditions appear to be more suitable for sungazers at higher elevations (>1500 m.a.s.l.) and under increasing values of annual mean temperature, minimum temperature of the coldest month, annual precipitation and precipitation seasonality (Figure 2). Conversely, when isothermality and precipitation of the driest quarter increases, habitat conditions become

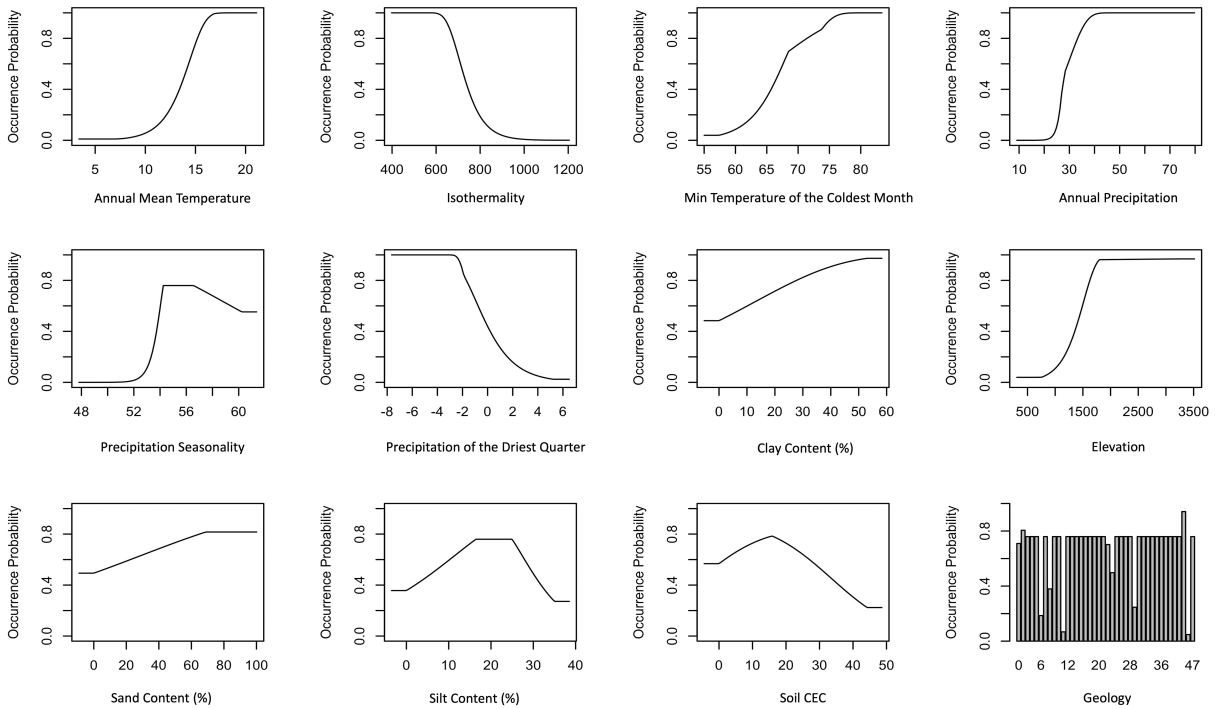


FIGURE 2 Response curves of the bioclimatic and environmental variables for the sungazer ENM. The x-axis of each graph represents each variable, and the y-axis indicates the probability of occurrence (cloglog output) for sungazers. The Geology plot is indicative of geology type (categorical data).

less suitable for the species (Figure 2). At the soil level, higher percentages of clay and sand content increases the probability of occurrence of sungazers, but soils composed of more than 25% silt have reduced habitat suitability (Figure 2). Soils with a cation exchange capacity (CEC) of 5–20 meq/100 g appear to increase the probability of sungazer occurrence. Although most geology types were considered suitable for sungazers, the Ecca group appeared to be the most suitable while the Clarens, Elliot and Molteno (Stormberg group) have reduced habitat suitability for sungazers (Figure 2).

Current predictions

The proportion of suitable habitat varied depending on the scale. At the broad-scale level (buffered extent), approximately 25 000 km^2 was predicted suitable for sungazers under current climatic conditions, accounting for 18% of the total area of the buffered extent (Table 2). At smaller scales, the EOO and interpreted distribution, the areas of suitable habitat predicted for sungazers were approximately 19 400 km^2 (48% of the total area) and 10 200 km^2 (46% of the total area), respectively. Although the percentages of the area were higher than the percentage at the scale of the buffered extent, they are still relatively low considering that proportion of suitable habitat at these finer scales was less than 50% (Figure 3; Table 2).

Future predictions

Interpreted distribution

In the near- and medium-term futures, and under moderate climatic conditions (SSP245), the proportion of suitable habitat within the interpreted distribution of sungazers was similar to the prediction for current conditions (46%; approximately 10 200 km^2), and niche overlap was also high in these periods (Table 2). However, an eastward shrinking trend in habitat suitability was observed in distant futures under SSP245 (Figure 4b). Approximately, 9900 km^2 (a decrease of 3% from current conditions) of suitable habitat was predicted to remain by 2100 under moderate conditions (Table 2). By comparison, decreasing trends in habitat suitability were more noticeable under SSP585 (Figure 4c). Suitable habitat was predicted to decrease marginally (3%) in near- and medium-term futures, a similar trend to distant futures under SSP245. In distant futures, however, suitable habitat within the interpreted distribution for sungazers decreased substantially (24%) under SSP585, with only 7700 km^2 of suitable habitat predicted to remain by 2100 (Table 2). Loss of suitable habitat predominantly occurred from the east and west edges of current sungazer distribution, with the shrinking trends more prominent compared to the SSP245 scenario (Figure 4). Niche overlap was also lower by 2100 under SSP585.

Extent of occurrence

At the scale of the EOO of sungazers, habitat suitability was predicted to marginally increase (2%) under SSP245 in near- and medium-term futures (Table 2). Although habitat suitability during these periods partially reduced around the east and west edges of the EOO, suitable habitat

TABLE 2 Changes in the predicted suitable habitat of sungazers from current conditions to future climates under different scales.

Scenario	Time	Scale	Area (km^2)	Suitable habitat (km^2)	Proportion suitable (%)	Habitat change (± %)	Schoener's D statistic
Current	Current	Buffered Extent	142884	25028	18	–	–
		EOO	40573	19342	48	–	–
		ID	21985	10198	46	–	–
SSP245	2040	Buffered Extent	142884	27192	19	+9	0.888
		EOO	40573	19555	48	+1	0.978
		ID	21985	10149	46	0	0.992
	2060	Buffered Extent	142884	30612	21	+22	0.799
		EOO	40573	19709	49	+2	0.974
		ID	21985	10149	46	0	0.991
	2080	Buffered Extent	142884	26213	18	+5	0.840
		EOO	40573	17755	44	−8	0.915
		ID	21985	9594	44	−6	0.940
	2100	Buffered Extent	142884	28315	20	+13	0.830
		EOO	40573	18608	46	−4	0.955
		ID	21985	9910	45	−3	0.970
SSP585	2040	Buffered Extent	142884	27225	19	+9	0.893
		EOO	40573	19567	48	+1	0.978
		ID	21985	10103	46	−1	0.988
	2060	Buffered Extent	142884	29865	21	+19	0.826
		EOO	40573	18787	46	−3	0.964
		ID	21985	9879	45	−3	0.967
	2080	Buffered Extent	142884	25656	18	+3	0.817
		EOO	40573	16627	41	−14	0.855
		ID	21985	9213	42	−10	0.902
	2100	Buffered Extent	142884	20499	14	−18	0.631
		EOO	40573	12541	31	−35	0.646
		ID	21985	7705	35	−24	0.755

Note: Measures for two climate change scenarios (SSP245 and SSP585), at 20-year intervals are shown. Area represents the total area of each scale. Suitable habitat and proportion suitable depict the area and the proportion (%) of which that area is predicted to be suitable within each scale. Habitat change (%) shows net gain or loss of habitat. Schoener's D statistic is an estimate of niche overlap between current and future conditions.

Abbreviations: EOO, extent of occurrence; ID, interpreted distribution; SSP, shared socioeconomic pathways.

began to shift south-westerly (Figure 5b). In distant futures under SSP245, habitat suitability is predicted to decrease by 4% from current predictions by 2100 but niche overlap with current predictions remains high (Table 2). Conversely, under the SSP585 scenario, suitable habitat within sungazer EOO shrank more rapidly compared to SSP245 (Figure 5), with approximately 12500 km^2 (down 35% from current predictions) predicted to remain by 2100. Niche overlap in distant futures was also lower than in near- and medium-term futures (Table 2). Under SSP585, prominent declines in east, west and north-east edges of the EOO were observed with central and south-westerly regions remaining suitable (Figure 5c).

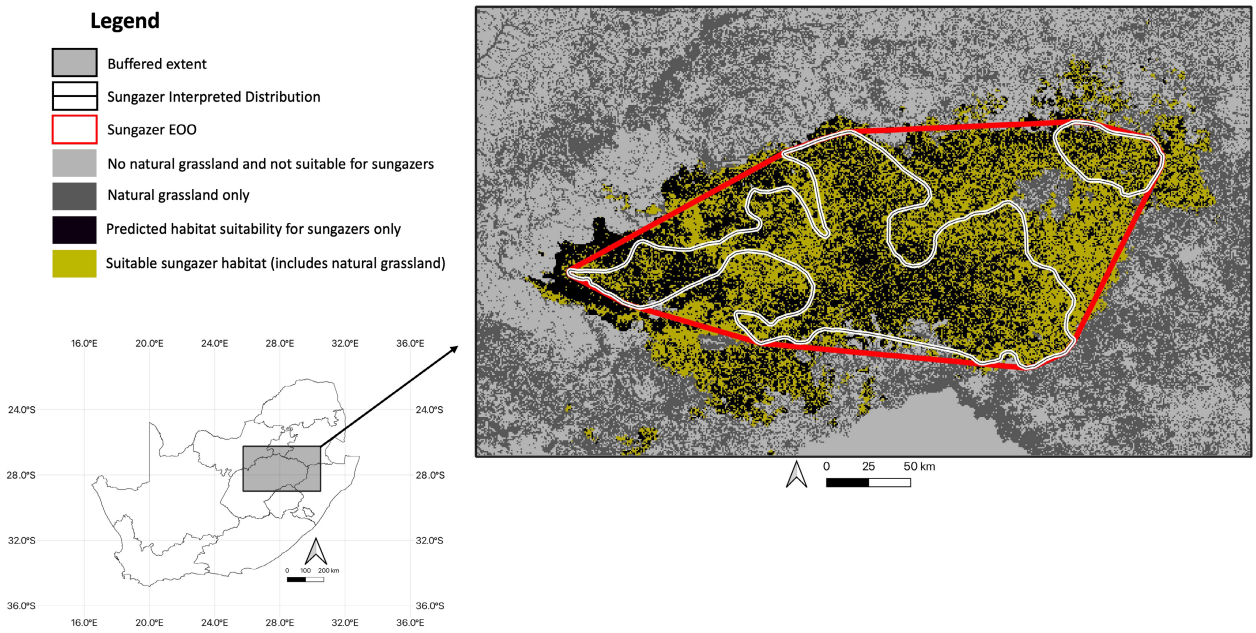


FIGURE 3 Predicted habitat suitability map for sungazers under current conditions. The buffered extent overlaid with the current EOO (red boundary) and interpreted distribution (white boundary) for sungazers are shown. The map shows South Africa zoomed into an overlay of the binary output (suitable/unsuitable) of predicted sungazer occurrence with natural grassland only. The intersection (yellow) between natural grassland and predicted sungazer occurrence is considered suitable sungazer habitat. The 10th-percentile training presence value was used as a threshold for conversion to binary format.

Buffered extent

At the broad-scale level, trends in habitat reduction in the buffered extent were similar to the other scales under the SSP245 climatic scenario (Table 2). Despite the apparent decreases in those regions, the predicted area of suitable habitat increased by 22% to approximately 30 600 km^2 in the medium-term future (2060) before reducing again in distant futures (Table 2). By 2100, the area of suitable habitat predicted for sungazers was approximately 28 300 km^2, representing a 13% increase from current predictions (Table 2). However, it is important to note that progression through the different futures resulted in a noticeable shift of suitable habitat in a south-west direction, which accounts for the observed increase in suitable habitat in distant futures (Figure 6). Consequently, north-east regions of suitable habitat in current predictions decreased as habitat suitability in south-west regions increased (Figure 6). Under SSP585, reductions in suitable habitat in east, west, south-east and north-east regions were greater than the reductions observed under SSP245 as progression through the different futures occurred (Figure 6). Even though suitable habitat also shifted south-westerly under SSP585, the area of predicted suitable habitat reduced to approximately 20 500 km^2, 18% lower compared to current estimates. Niche overlap was also lower in the buffered extent under both climatic scenarios compared to smaller scales (EOO and interpreted distribution) but reduced through the different futures (Table 2). The reduction in niche overlap was also supported by the south-west shift of suitable habitat.

DISCUSSION

We assessed the potential impact of climate change on habitat suitability of *S. giganteus* under two climate change scenarios at 20-year intervals

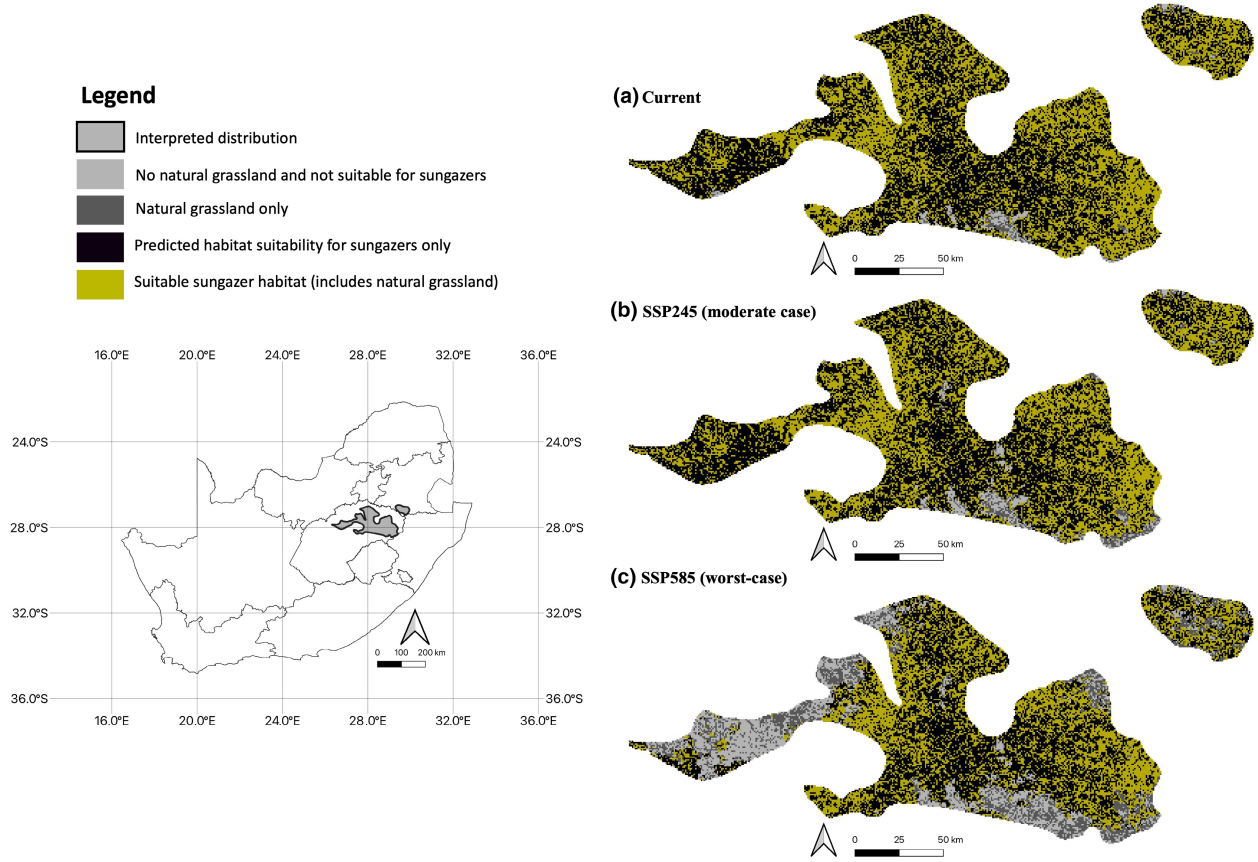


FIGURE 4 Habitat suitability maps showing the predicted distribution of sungazers within their current interpreted distribution. The map shows South Africa zoomed into an overlay of the binary output (suitable/unsuitable) of predicted sungazer occurrence with natural grassland only. The intersection (yellow) between natural grassland and predicted sungazer occurrence is considered suitable sungazer habitat. Maps shown represent current (a), and future 2100 (SSP245 (b) and SSP585 (c)) predictions. SSP, shared socioeconomic pathways.

up to 2100. In general, sungazers do not appear to be particularly vulnerable under SSP245 (moderate-case), but vulnerability increases under the SSP585 (worst-case) scenario. The models predicted that by 2100 the sungazer could lose approximately a quarter of its suitable habitat within the current interpreted distribution. At broader scales, models reveal a south-west shift of suitable habitat suggesting that the species could climate tack in this direction. However, given the life history and low dispersal ability of the species (Van Wyk, 1992), it is unlikely that climate tracking would be a realistic outcome. The results of our study support the hypothesis that under worst-case climatic scenarios, the predicted loss of suitable habitat could result in local extinctions of many sungazer subpopulations. Although modelling the future distribution of a species may identify potential changes, results must be interpreted with caution. Thus, the combined effect of climate change and land use could threaten the survival of sungazers, highlighting the need for careful conservation management, particularly in central regions of their current distribution.

Under the moderate-case scenario, observable range contraction was predicted in the south-eastern parts of the sungazer's interpreted distribution. The same is predicted under the worst-case scenario but not only are contractions amplified in this scenario, they are also predicted to occur in the western parts of their range. Although the predicted loss of suitable habitat within the interpreted distribution of the species was minimal in medium-term futures, the loss of suitable habitat appears to accelerate in longer term futures with sungazers predicted to lose a quarter of their

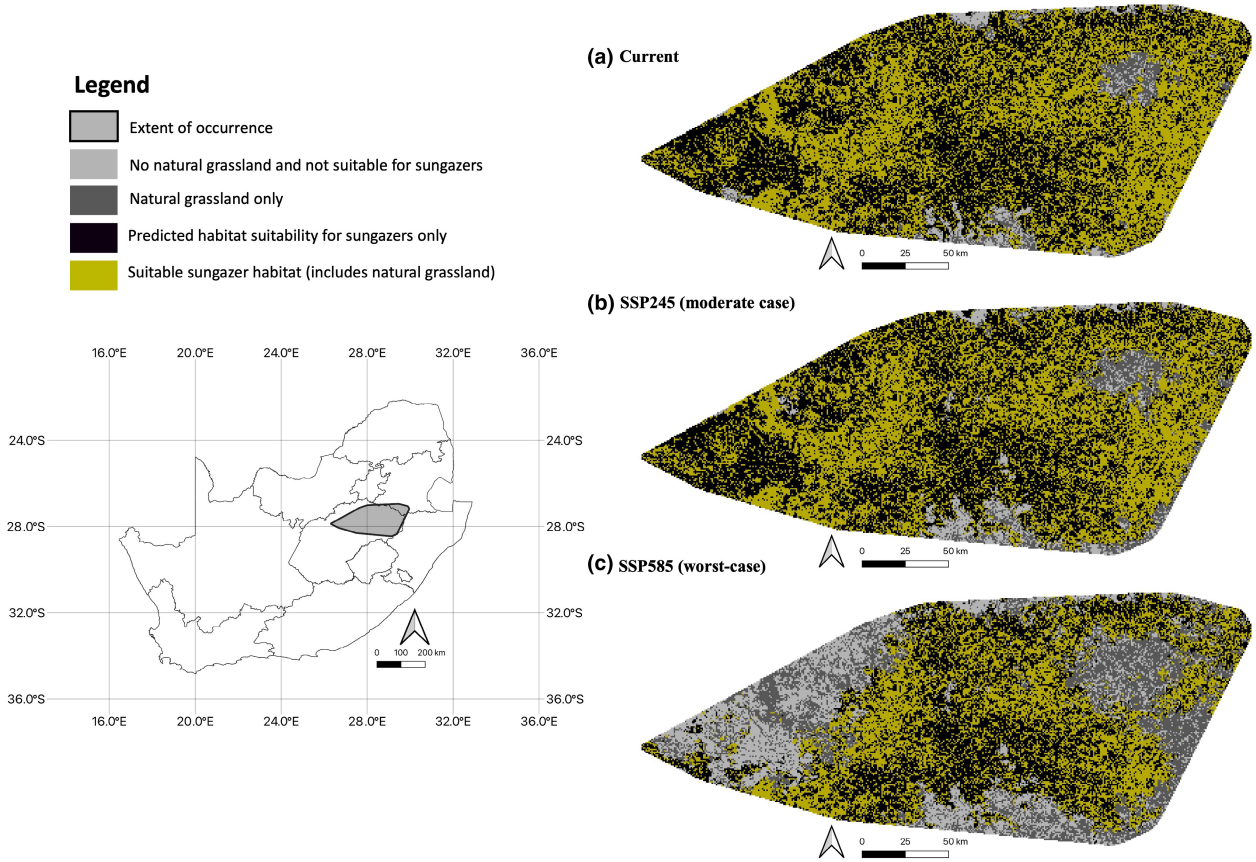


FIGURE 5 Habitat suitability maps showing the predicted distribution of sungazers within their current extent of occurrence (EOO). The map shows South Africa zoomed into an overlay of the binary output (suitable/unsuitable) of predicted sungazer occurrence with natural grassland only. The intersection (yellow) between natural grassland and predicted sungazer occurrence is considered suitable sungazer habitat. Maps shown represent current (a), and future 2100 (SSP245 (b) and SSP585 (c)) predictions. SSP, shared socioeconomic pathways.

suitable habitat by 2100, especially if mitigation measures to reduce the effects of climate change are limited. This suggests that subpopulations of sungazers in the south-eastern and western regions of their distribution may be at risk of becoming locally extinct. It is important to note that these predictions are only based on climatic factors and do not account for potential transformation of habitat due to agricultural activity and mining, both of which are prominent within the species distribution (DEAT, 2005; McIntyre, 2006). Thus, while our predictions under the moderate-case scenario suggest a relatively low-impact outcome for sungazers, worse scenarios could be detrimental to the species, especially when coupled with existing anthropogenic pressures that sungazers face (Jacobsen, 1989; Mouton, 2014; Parusnath et al., 2017).

The scale used in our modelling did not have a marked impact on our predictions although modelling at the broadest scale was most informative. Despite observable range contractions, habitat suitability within medium-term futures was predicted to increase. This is because the loss of suitable habitat was countered by a gain in suitable habitat in the south-west regions, most noticeable within the buffered extent. Although the net area of suitable habitat was predicted to decrease again in further futures, gains were still prevalent within the south-west regions of the EOO and buffered extent. If habitat suitability was only examined at the scale of the interpreted distribution, evidence for potential climate tracking would not be revealed. Thus, by modelling the distribution of sungazers at a buffered extent, and then overlaying finer extents onto the predictions not only allows

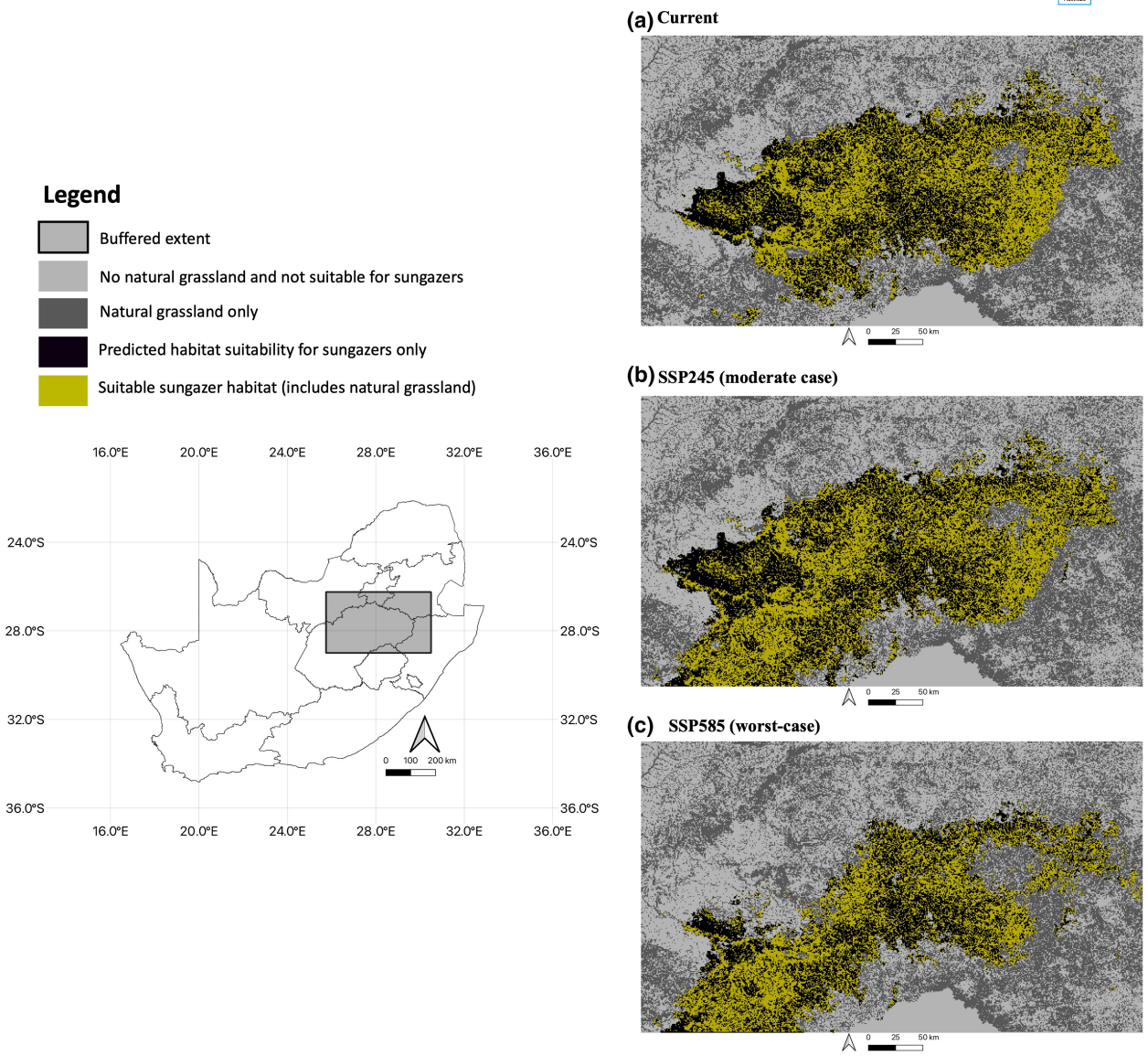


FIGURE 6 Habitat suitability maps showing the predicted distribution of sungazers within the buffered extent of the EOO. The map shows South Africa zoomed into an overlay of the binary output (suitable/unsuitable) of predicted sungazer occurrence with natural grassland only. The intersection (yellow) between natural grassland and predicted sungazer occurrence is considered suitable sungazer habitat. Maps shown represent current (a), and future 2100 (SSP245 (b) and SSP585 (c)) predictions. SSP, shared socioeconomic pathways.

for interpretation at multiple scales but also demonstrates the importance of selecting an appropriate scale to model the distribution of a species, especially if predictions about a species future distribution are to be made. However, the degree to which scale affects predictions of habitat suitability goes beyond the scope of this study.

Our study is the first to model the potential impact of climate change on habitat suitability of *S. giganteus*. However, it should be noted that the modelling procedure is complex and multifaceted and can lead to uncertainty when interpreting predictions (Gould et al., 2014; Tang et al., 2018). Thus, species-specific tuning of correlative ENMs is critical (Anderson & Gonzalez, 2011; Kaky et al., 2020). By spatially filtering occurrence records of sungazers (Aiello-Lammens et al., 2015), and incorporating ecologically relevant predictor variables (Anderson & Gonzalez, 2011; Guevara et al., 2018; Radosavljevic & Anderson, 2013), our models had a strong predictive performance. It is also important to note that, although arbitrary,

careful selection of the extent to which a species distribution is modelled must be made (Anderson & Raza, 2010). While this study has shown the significance of modelling from a buffered extent (from the EOO) to provide insights into range expansion, choosing an extent that is too large, and which includes areas where dispersal may be limited (because of geographic barriers or biotic interactions), may result in reduced performance of correlative ENMs (Anderson & Raza, 2010). Given the good performance of the models in this study, the buffered extent used appeared to be reasonable, and provided valuable insights into how sungazers might respond to climate change. Overlaying natural grassland onto the predictions also showed the importance of careful interpretation and evaluation of species distribution models. This is evident in the apparent reduction of suitable sungazer habitat after accounting for natural grasslands. The results provided important information regarding areas that are suitable for sungazers, which may be important in future conservation planning.

When assessing a species vulnerability to climate change, the use of hybrid-ENMs (correlative and mechanistic models, e.g. Gamliel et al., 2020; Meineri et al., 2015; Mi et al., 2022) can provide a more informative assessment of a species vulnerability to climate change. However, as in this study and many others (e.g. Guo et al., 2021; Houniet et al., 2009; Petford & Alexander, 2021), a lack of behavioural and physiological data of a species may limit the use of hybrid-ENMs. Nevertheless, even though correlative models may not be definitive, when fine-tuned, they do provide an indication of what the future distribution of a species could be under climate change, and may enhance conservation efforts (Guisan & Thuiller, 2005; Petford & Alexander, 2021; Raxworthy et al., 2003).

Despite the use of a correlative model in this study, by examining known life-history traits of sungazers, inferences about their ability to respond to climate change can be made. Sungazers are habitat specialists that display high burrow fidelity, rarely stray far from their home burrows (Ruddock, 2000; Stanton-Jones, 2018; Van Wyk, 1992), and individuals have been found occupying the same burrow for at least 16 years (Stanton-Jones et al., 2023). This philopatric nature suggests that the species has low vagility and because of this, may not be able to track suitable conditions. In addition, because a significant portion of sungazer habitat has been fragmented due to habitat transformation through anthropogenic activity (Branch, 1988; Parusnath et al., 2017), dispersal capacity may further be reduced (Honnay et al., 2002; Opdam & Wascher, 2004; Robillard et al., 2015; Saunders et al., 1991). Even if the effects of anthropogenic habitat transformation are ignored, geographic barriers such as wetlands, dams, rivers and mountain ranges may also prevent dispersal into suitable areas (Parusnath et al., 2017). Therefore, it is unlikely that sungazers will be able to respond to climate change by shifting their geographic range.

Species living in fragmented habitats are more vulnerable to the effects of climate change (Travis, 2003). Dispersal limitations because of fragmented habitats not only affects the ability of a species to track suitable conditions, but the associated reduction of gene flow among populations, and a loss of genetic diversity within populations (Frankham, 2006; Parusnath, 2020), may compromise a species ability to evolve adaptations in response to climate change. In addition, evolving adaptations would require a long time. Since sungazers are long-lived, have low fecundity, long generation lengths and limited dispersal capacity (Van Wyk, 1992), keeping pace with rapid climate change through genetic adaptation appears unlikely (Dunham & Overall, 1994; Sinervo et al., 2010), especially considering that the effects of historical habitat fragmentation have not yet manifested in the genetics of sungazers (Parusnath, 2020). Given that reduced genetic diversity in sungazers, as a result of habitat fragmentation, may

only be observed within the next ~120 years (Parusnath, 2020), it seems unlikely that they will evolve adaptations in response to changing climates within the next century.

Range contractions and distribution shifts are common predicted responses to climate change among reptiles (e.g. Araújo et al., 2006; Houniet et al., 2009; Moreno-Rueda et al., 2012; Petford & Alexander, 2021). However, as with the predictions of this study, the ability to track suitable climates may be compromised in habitat specialists. In such cases, behavioural plasticity may be an appropriate response to shifting climate. Sungazers are efficient thermoregulators and can achieve target body temperature over a wide range of environmental conditions through simple behavioural adjustments (Stanton-Jones et al., 2018). This suggests that behavioural plasticity may assist the species in coping with changing climates, particularly if basking opportunities become limited (see Caldwell et al., 2017). However, changes in behaviour and activity patterns to compensate for a warmer environment may have eco-physiological implications (Sinervo et al., 2010): (i) reduced activity outside of burrows may restrict foraging time, (ii) prey abundance may be limited during foraging periods, (iii) growth rates may be reduced and (iv) aspects of reproduction such as mate acquisition and embryonic development could be compromised. However, more studies relating sungazer behaviour to warming temperatures are required to enhance current predictions of their vulnerability to climate change.

The predicted range contractions under both climate change scenarios, and the unlikelihood that sungazers will track suitable conditions, suggest that conservation management for the species is critical. Although the current suitable habitat for sungazers remains severely fragmented, Parusnath et al. (2017) reported a significant reduction in the rate of transformation of natural grassland within the current distribution of sungazers. However, there are still some important considerations: (i) there is much uncertainty as to how landowners will modify agricultural practices under changing climates, (ii) sungazers occur in an area where mining activities are prevalent and thus the amount of suitable habitat for sungazers may be reduced even further in the future, particularly while alternative energy solutions are being explored and (iii) sungazer distribution falls within parts of South Africa where rates of incoming solar radiation are relatively high (Fluri, 2009; Singh, 2016), and could support developments of solar power plants. While renewable energy resources are important to mitigate the effects of climate change, their implementation may fragment suitable habitat for sungazers even further. Thus, careful selection of areas to develop renewable energy systems is required to mitigate any associated threats to remaining sungazer subpopulations.

The Endangered Wildlife Trust (EWT) has begun conservation efforts through their ‘Sungazer Custodianship Programme’ whereby landowners sign a 5-year renewable agreement to protect the habitat on their properties where sungazers occur (Gibbons, 2022). It is, however, important to note that this programme may only offer short-term protection for the species. Because of this, EWT are also working to establish protected areas within sungazer distribution through biodiversity stewardship programmes (Gibbons, 2022). The predictions in our study suggest that stewardship programmes should be concentrated within the central and southern parts of sungazer distribution – areas predicted to remain stable under climate change. Although the eastern and western regions of sungazer distribution may become unsuitable in the future, we recommend that monitoring programmes of existing sungazer subpopulations within those regions are implemented to ensure early detection of changes in population dynamics, such that swift conservation action can be taken (Parusnath et al., 2017).

This study has provided the first indication as to how sungazers could respond to climate change. Although there is much uncertainty associated with modelling the future distribution of a species, examining the life-history traits can enhance interpretations of the models. Despite the prediction that sungazer distribution may shift in the future, the species life-history traits, and low dispersal capacity suggests that climate tracking may not be possible. When the detrimental effects of habitat fragmentation are considered, sungazers may be more vulnerable to effects of changing climates than what the models predict. Nevertheless, the modelling techniques in this study have provided sufficient evidence to inform conservation planning. We suggest that this approach should be widely applied to reptile species as part of conservation planning.

AUTHOR CONTRIBUTIONS

Wade K. Stanton-Jones: Conceptualization (equal); data curation (equal); formal analysis (lead); funding acquisition (lead); investigation (lead); methodology (equal); visualization (equal); writing – original draft (lead). **Graham J. Alexander:** Conceptualization (equal); data curation (equal); formal analysis (supporting); investigation (supporting); resources (equal); supervision (lead); visualization (equal); writing – review and editing (lead).

ACKNOWLEDGEMENTS

This research was financially supported by the Rufford Foundation (grant number: 29137-1) and the Alexander Herp Lab. We would like to thank Shivan Parusnath and the Endangered Wildlife Trust for providing additional occurrence records of *Smaug giganteus*, and the South African National Biodiversity Institute for supplying reptile occurrence records within our modelling region. Melissa Petford and Jody Taft provided guidance on the modelling procedure. Permission to conduct field work was received by the Department of Economic, Small Business Development, Tourism and Environmental Affairs (permit numbers: 01/3474, JM938/2017, JM5067/2019 and 202112000008380), and ethical clearance was received by the University of the Witwatersrand's Animal Ethics Screening Committee (ethics numbers: 2014/56/B, 2016/06/30B and 2019/04/29B).

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ORCID

Wade K. Stanton-Jones https://orcid.org/0000-0003-1149-3667
Graham J. Alexander https://orcid.org/0000-0003-3991-4099

REFERENCES

Aiello-Lammens, M.E., Boria, R.A., Radosavljevic, A., Vilela, B. & Anderson, R.P. (2015) *spThin*: an R package for spatial thinning of species occurrence records for use in ecological niche models. *Ecography*, 38, 541–545. Available from: https://doi.org/10.1111/ecog.01132

Albaladejo-Robles, G., Böhm, M. & Newbold, T. (2023) Species life-history strategies affect population responses to temperature and land-cover changes. *Global Change Biology*, 29(1), 97–109. Available from: https://doi.org/10.1111/gcb.16454

Alexander, G.J., Tolley, K.A., Bates, M.F. & Mouton, P.L.F.N. (2022) *Smaug giganteus*. The IUCN Red List of Threatened Species 2022: e.T5336A197397987. https://doi.org/10.2305/IUCN.UK.2022-1.RLTS.T5336A197397987.en

Anderson, R.P. & Gonzalez, I. (2011) Species-specific tuning increases robustness to sampling bias in models of species distributions: an implementation with Maxent. *Ecological*

Modelling, 222, 2796–2811. Available from: https://doi.org/10.1016/j.ecolmodel.2011.04.011

Anderson, R.P. & Raza, A. (2010) The effect of the extent of the study region on GIS models of species geographic distributions and estimates of niche evolution: preliminary tests with montane rodents (genus *Nephelomys*) in Venezuela. *Journal of Biogeography*, 37(7), 1378–1393. Available from: https://doi.org/10.1111/j.1365-2699.2010.02290.x

Araújo, M.B., Thuiller, W. & Pearson, R.G. (2006) Climate warming and the decline of amphibians and reptiles in Europe. *Journal of Biogeography*, 33(10), 1712–1728. Available from: https://doi.org/10.1111/j.1365-2699.2006.01482.x

Bates, M.F., Branch, W.R., Bauer, A.M., Burger, M., Marais, J., Alexander, G.J. et al. (Eds.). (2014) *Atlas and red list of the reptiles of South Africa, Lesotho and Swaziland. Suricata 1*. Pretoria: South African National Biodiversity Institute.

Batjes, N.H. (2004) *SOTER-based soil parameter estimates for southern Africa*. Report 2004/04. Wageningen: ISRIC – World Soil Information.

Böhm, M., Cook, D., Ma, H., Davidson, A.D., García, A., Tapley, B. et al. (2016) Hot and bothered: using trait-based approaches to assess climate change vulnerability in reptiles. *Biological Conservation*, 204, 32–41. Available from: https://doi.org/10.1016/j.biocon.2016.06.002

Bradshaw, W.E. & Holzapfel, C.M. (2006) Evolutionary response to rapid climate change. *Science*, 312(5779), 1477–1478. Available from: https://doi.org/10.1126/science.1127000

Branch, W.R. (1988) Threats. In: Branch, W.R. (Ed.) *South African red data book – reptiles and amphibians*. Pretoria, South Africa: South African National Scientific Programmes Report No. 151. Committee for Nature Conservation National Programme for ecosystem research, pp. 14–19.

Caldwell, A.J., While, G.M. & Wapstra, E. (2017) Plasticity of thermoregulatory behaviour in response to the thermal environment by widespread and alpine reptile species. *Animal Behaviour*, 132, 217–227. Available from: https://doi.org/10.1016/j.anbehav.2017.07.025

Carroll, C., Dunk, J.R. & Moilanen, A. (2010) Optimizing resiliency of reserve networks to climate change: multispecies conservation planning in the Pacific northwest, USA. *Global Change Biology*, 16(3), 891–904. Available from: https://doi.org/10.1111/j.1365-2486.2009.01965.x

Council for Geoscience. (2018) *Downloadable material* [www document]. Available from: https://www.geoscience.org.za/index.php/publication/downloadablematerial [Accessed 18th July 2022].

De Waal, S.W.P. (1978) *The squamata (Reptilia) of the Orange Free State, South Africa*. Bloemfontein, South Africa: Memoirs of the National Museum, 11.

DEAT (Department: Environmental Affairs and Tourism). (2005) *South Africa's National Biodiversity Strategy*. South Africa: Pretoria.

DFFE (Department of Forestry, Fisheries, and the Environment). (2020) *South African National Land Cover (SANLC) 2020 (TIFF) [Raster]*. Available from: https://egis.environment.gov.za/data_egis/data_download/current [Accessed 10th August 2022].

Dunham, A.E. & Overall, K.L. (1994) Population responses to environmental change: life history variation, individual-based models, and the population dynamics of short-lived organisms. *American Zoologist*, 34, 382–396. Available from: https://doi.org/10.1093/icb/34.3.382

Elith, J.H., Graham, C.H., Anderson, R.P., Dudík, M., Ferrier, S., Guisan, A. et al. (2006) Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, 29(2), 129–151. Available from: https://doi.org/10.1111/j.2006.0906-7590.04596.x

Fick, S.E. & Hijmans, R.J. (2017) WorldClim 2: new 1km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, 37(12), 4302–4315. Available from: https://doi.org/10.1002/joc.5086

Fluri, T.P. (2009) The potential of concentrating solar power in South Africa. *Energy Policy*, 37(12), 5075–5080. Available from: https://doi.org/10.1016/j.enpol.2009.07.017

Frankham, R. (2006) Genetics and landscape connectivity. In: Crooks, K.R. & Sanjayan, M. (Eds.) *Connectivity conservation*. Cambridge, UK: Cambridge University Press, pp. 72–96.

Gamliel, I., Buba, Y., Guy-Haim, T., Garval, T., Willette, D., Rilov, G. et al. (2020) Incorporating physiology into species distribution models moderates the projected impact of warming on selected Mediterranean marine species. *Ecography*, 43, 1090–1106. Available from: https://doi.org/10.1111/ecog.04423

Gibbons, B. (2022) *Sungazer custodians*. Endangered Wildlife Trust. Available from: https://ewt.org.za/sp-march-2022-sungazer-custodians/ [Accessed 17th February 2023].

Gould, S., Beeton, N., Harris, R., Hutchinson, M.F., Lechner, A.M., Porfirio, L.L. et al. (2014) A tool for simulating and communicating uncertainty when modelling species distributions under future climates. *Ecology and Evolution*, 4, 4798–4811. Available from: https://doi.org/10.1002/ece3.1319

Gouveia, S.F., Souza-Alves, J.P., Rattis, L., Dobrovolski, R., Jerusalinsky, L., Beltrão-Mendes, R. et al. (2016) Climate and land use changes will degrade the configuration of

the landscape for titi monkeys in eastern Brazil. *Global Change Biology*, 22(6), 2003–2012. Available from: https://doi.org/10.1111/gcb.13162

Guevara, L., Gerstner, B.E., Kass, J.M. & Anderson, R.P. (2018) Toward ecologically realistic predictions of species distributions: a cross-time example from tropical montane cloud forests. *Global Change Biology*, 24(4), 1511–1522. Available from: https://doi.org/10.1111/gcb.13992

Guisan, A. & Thuiller, W. (2005) Predicting species distribution: offering more than simple habitat models. *Ecology Letters*, 8(9), 993–1009. Available from: https://doi.org/10.1111/j.1461-0248.2005.00792.x

Guo, K., Yuan, S., Wang, H., Zhong, J., Wu, Y., Chen, W. et al. (2021) Species distribution models for predicting the habitat suitability of Chinese fire-bellied newt *Cynops orientalis* under climate change. *Ecology and Evolution*, 11(15), 10147–10154. Available from: https://doi.org/10.1002/ece3.7822

Hao, T., Elith, J., Lahoz-Monfort, J.J. & Guillera-Arroita, G. (2020) Testing whether ensemble modelling is advantageous for maximising predictive performance of species distribution models. *Ecography*, 43, 549–558. Available from: https://doi.org/10.1111/ecog.04890

Hijmans, R.J., Phillips, S., Leathwick, J., Elith, J. & Hijmans, M.R.J. (2017) Package '*dismo*'. *Circles*, 9, 1–68.

Honnay, O., Verheyen, K., Butaye, J., Jacquemyn, H., Bossuyt, B. & Hermy, M. (2002) Possible effects of habitat fragmentation and climate change on the range of forest plant species. *Ecology Letters*, 5(4), 525–530. Available from: https://doi.org/10.1046/j.1461-0248.2002.00346.x

Houniet, D.T., Thuiller, W. & Tolley, K.A. (2009) Potential effects of predicted climate change on the endemic south African dwarf chameleons, *Bradypodion. African Journal of Herpetology*, 58(1), 28–35. Available from: https://doi.org/10.1080/21564574.2009.9635577

IPCC. (2021) Summary for policymakers. In: Masson-Delmotte, V., Zhai, P., Pirani, A., Connors, S.L., Péan, C., Berger, S. et al. (Eds.) *Climate change 2021: the physical science basis. Contribution of working group I to the sixth assessment report of the intergovernmental panel on climate change*. Cambridge, United Kingdom and New York, NY, USA: Cambridge University Press, pp. 3–32. Available from: https://doi.org/10.1017/9781009157896.001

IPCC. (2022) In: Shukla, P.R., Skea, J., Slade, R., Al Khourdajie, A., van Diemen, R., McCollum, D. et al. (Eds.) *Climate change 2022: mitigation of climate change. Contribution of working group III to the sixth assessment report of the intergovernmental panel on climate change*. Cambridge, UK and New York, NY, USA: Cambridge University Press. Available from: https://doi.org/10.1017/9781009157926

Jacobsen, N.H.G. (1989) *A herpetological survey of the Transvaal [Doctoral thesis]*. Pietermaritzburg, Kwazulu-Natal, South Africa: University of Natal.

Kaky, E., Nolan, V., Alatawi, A. & Gilbert, F. (2020) A comparison between ensemble and MaxEnt species distribution modelling approaches for conservation: a case study with Egyptian medicinal plants. *Ecological Informatics*, 60, 101150. Available from: https://doi.org/10.1016/j.ecoinf.2020.101150

Kass, J.M., Muscarella, R., Galante, P.J., Bohl, C.L., Pinilla-Buitrago, G.E., Boria, R.A. et al. (2021) ENMeval 2.0: redesigned for customizable and reproducible modeling of species' niches and distributions. *Methods in Ecology and Evolution*, 12(9), 1602–1608. Available from: https://doi.org/10.1111/2041-210X.13628

Liu, C., Berry, P.M., Dawson, T.P. & Pearson, R.G. (2005) Selecting thresholds of occurrence in the prediction of species distributions. *Ecography*, 28(3), 385–393. Available from: https://doi.org/10.1111/j.0906-7590.2005.03957.x

McIntyre, T. (2006) *Impact of gold mining on Cordylus giganteus and recommendations for conservation and management* [Master's dissertation]. Johannesburg, South Africa: University of the Witwatersrand.

McShea, W.J. (2014) What are the roles of species distribution models in conservation planning? *Environmental Conservation*, 41(2), 93–96. Available from: https://doi.org/10.1017/S0376892913000581

Meineri, E., Deville, A.S., Grémillet, D., Gauthier-Clerc, M. & Béchet, A. (2015) Combining correlative and mechanistic habitat suitability models to improve ecological compensation. *Biological Reviews*, 90(1), 314–329. Available from: https://doi.org/10.1111/brv.12111

Mi, C., Ma, L., Wang, Y., Wu, D., Du, W. & Sun, B. (2022) Temperate and tropical lizards are vulnerable to climate warming due to increased water loss and heat stress. *Proceedings of the Royal Society B: Biological Sciences*, 289, 20221074. Available from: https://doi.org/10.1098/rspb.2022.1074

Moreno-Rueda, G., Pleguezuelos, J.M., Pizarro, M. & Montori, A. (2012) Northward shifts of the distributions of Spanish reptiles in association with climate change. *Conservation Biology*, 26(2), 278–283. Available from: https://doi.org/10.1111/j.1523-1739.2011.01793.x

Mouton, P.L.F.N. (2014) *Smaug giganteus* (smith, 1844). In: Bates, M.F., Branch, W.R., Bauer, A.M., Burger, M., Marais, J., Alexander, G.J. et al. (Eds.) *Atlas and red list of*

the reptiles of South Africa, Lesotho and Swaziland. Suricata 1. Pretoria: South African National Biodiversity Institute, 209.
Muscarella, R., Galante, P.J., Soley-Guardia, M., Boria, R.A., Kass, J.M., Uriarte, M. et al. (2014) ENMeval: an R package for conducting spatially independent evaluations and estimating optimal model complexity for Maxent ecological niche models. *Methods in Ecology and Evolution*, 5(11), 1198–1205. Available from: https://doi.org/10.1111/2041-210X.12261
Opdam, P. & Wascher, D. (2004) Climate change meets habitat fragmentation: linking landscape and biogeographical scale levels in research and conservation. *Biological Conservation*, 117, 285–297. Available from: https://doi.org/10.1016/j.biocon.2003.12.008
Palm, F.C. & Zellner, A. (1992) To combine or not to combine? Issues of combining forecasts. *Journal of Forecasting*, 11(8), 687–701. Available from: https://doi.org/10.1002/for.3980110806
Parding, K.M., Dobler, A., McSweeney, C.F., Landgren, O.A., Benestad, R., Erlandsen, H.B. et al. (2020) GCMeval–an interactive tool for evaluation and selection of climate model ensembles. *Climate Services*, 18, 100167. Available from: https://doi.org/10.1016/j.cliser.2020.100167
Parmesan, C. (2006) Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics*, 37(1), 637–669. Available from: https://doi.org/10.1146/annurev.ecolsys.37.091305.110100
Parusnath, S. (2014) *A conservation assessment of the sungazer (Smaug giganteus) [Master's dissertation]*. Johannesburg, South Africa: University of the Witwatersrand.
Parusnath, S. (2020) *Population genetics and sociality in the Sungazer (Smaug giganteus) [Doctoral thesis]*. Johannesburg, South Africa: University of the Witwatersrand.
Parusnath, S., Little, I.T., Cunningham, M.J., Jansen, R. & Alexander, G.J. (2017) The desolation of Smaug: the human-driven decline of the Sungazer lizard (*Smaug giganteus*). *Journal for Nature Conservation*, 36, 48–57. Available from: https://doi.org/10.1016/j.jnc.2017.02.002
Perold, V., Ferguson, J.W.H., Verburgt, L. & Malherbe, J.B. (2021) Are high elevation crag lizards sensitive to climate change? *Austral Ecology*, 46(3), 359–373. Available from: https://doi.org/10.1111/aec.12991
Petford, M.A. & Alexander, G.J. (2021) Potential range shifts and climatic refugia of rupicolous reptiles in a biodiversity hotspot of South Africa. *Environmental Conservation*, 48(4), 264–273. Available from: https://doi.org/10.1017/S0376892921000370
Phillips, S. (2021) Maxnet: fitting 'Maxent' species distribution models with 'glmnet'. R package version 0.1.4. Available from: https://CRAN.R-project.org/package=maxnet [Accessed 19th February 2023].
Phillips, S.J., Anderson, R.P., Dudík, M., Schapire, R.E. & Blair, M.E. (2017) Opening the black box: an open-source release of Maxent. *Ecography*, 40(7), 887–893. Available from: https://doi.org/10.1111/ecog.03049
Phillips, S.J., Anderson, R.P. & Schapire, R.E. (2006) Maximum entropy modelling of species geographic distributions. *Ecological Modelling*, 190, 231–259. Available from: https://doi.org/10.1016/j.ecolmodel.2005.03.026
R Core Team. (2021) R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. Available from: https://www.R-project.org/ [Accessed 11th August 2021].
Radosavljevic, A. & Anderson, R.P. (2013) Making better Maxent models of species distributions: complexity, overfitting and evaluation. *Journal of Biogeography*, 15, 629–643. Available from: https://doi.org/10.1111/jbi.12227
Raxworthy, C.J., Martinez-Meyer, E., Horning, N., Nussbaum, R.A., Schneider, G.E., Ortega-Huerta, M.A. et al. (2003) Predicting distributions of known and unknown reptile species in Madagascar. *Nature*, 426(6968), 837–841. Available from: https://doi.org/10.1038/nature02205
Riahi, K., van Vuuren, D.P., Kriegler, E., Edmonds, J., O'Neill, B.C., Fujimori, S. et al. (2017) The shared socioeconomic pathways and their energy, land use, and greenhouse gas emissions implications: an overview. *Global Environmental Change*, 42, 153–168. Available from: https://doi.org/10.1016/j.gloenvcha.2016.05.009
Robillard, C.M., Coristine, L.E., Soares, R.N. & Kerr, J.T. (2015) Facilitating climate-change-induced range shifts across continental land-use barriers. *Conservation Biology*, 29(6), 1586–1595. Available from: https://doi.org/10.1111/cobi.12556
Román-Palacios, C. & Wiens, J.J. (2020) Recent responses to climate change reveal the drivers of species extinction and survival. *Proceedings of the National Academy of Sciences*, 117(8), 4211–4217. Available from: https://doi.org/10.1073/pnas.1913007117
Ruddock, L. (2000) *Social structure of the lizard, Cordylus giganteus [Masters dissertation]*. Stellenbosch, Western Cape, South Africa: Stellenbosch University.
Saunders, D.A., Hobbs, R.J. & Margules, C.R. (1991) Biological consequences of ecosystem fragmentation-a review. *Conservation Biology*, 5, 18–32. Available from: https://doi.org/10.1111/j.1523-1739.1991.tb00384.x

Sinervo, B., Mendez-de-la-Cruz, F., Miles, D.B., Heulin, B., Bastiaans, E., Villagran-Santa Cruz, M. et al. (2010) Erosion of lizard diversity by climate change and altered thermal niches. *Science*, 328(5980), 894–899. Available from: https://doi.org/10.1126/science.1184695

Singh, J. (2016) Ranking south African provinces on the basis of MERRA 2D surface incident shortwave flux. *Journal of Energy in Southern Africa*, 27(3), 50. Available from: https://doi.org/10.17159/2413-3051/2016/v27i3a1555

Stanton-Jones, W.K. (2018) *The development and use of an automated cellular PIT tag reader system for assessing the activity patterns of the Sungazer (Smaug giganteus) [Master's dissertation]*. Johannesburg, South Africa: University of the Witwatersrand.

Stanton-Jones, W.K., McIntyre, T. & Alexander, G.J. (2023) Habitat transformation correlates with the decline of sungazer (*Smaug giganteus*) subpopulations. *African Journal of Wildlife Research*, 53(1), 135–146. Available from: https://doi.org/10.3957/056.053.0135

Stanton-Jones, W.K., Parusnath, S. & Alexander, G.J. (2018) The impact of posture and basking orientation on thermoregulation in the Sungazer (*Smaug giganteus*). *Journal of Thermal Biology*, 75, 45–53. Available from: https://doi.org/10.1016/j.jtherbio.2018.05.005

Swets, J.A. (1988) Measuring the accuracy of diagnostic systems. *Science*, 240(4857), 1285–1293. Available from: https://doi.org/10.1126/science.3287615

Tang, Y., Winkler, J.A., Viña, A., Liu, J., Zhang, Y., Zhang, X. et al. (2018) Uncertainty of future projections of species distributions in mountainous regions. *PLoS One*, 13(1), e0189496. Available from: https://doi.org/10.1371/journal.pone.0189496

Tolley, K.A., Conradie, W., Pietersen, D.W., Weeber, J., Burger, M. & Alexander, G.J. (Eds.). (2023) *Conservation status of the reptile of South Africa, Eswatini and Lesotho. Suricata 10*. Pretoria: South African National Biodiversity Institute.

Travis, J.M.J. (2003) Climate change and habitat destruction: a deadly anthropogenic cocktail. *Proceedings of the Royal Society B: Biological Sciences*, 270(1514), 467–473. Available from: https://doi.org/10.1098/rspb.2002.2246

Valavi, R., Guillera-Arroita, G., Lahoz-Monfort, J.J. & Elith, J. (2022) Predictive performance of presence-only species distribution models: a benchmark study with reproducible code. *Ecological Monographs*, 92(1), e01486. Available from: https://doi.org/10.1002/ecm.1486

Van Wyk, J.H. (1992) *Life history and physiological ecology of the lizard, Cordylus giganteus [Doctoral thesis]*. Cape Town, South Africa: University of Cape Town.

Warren, D.L. & Seifert, S.N. (2011) Ecological niche modelling in Maxent: the importance of model complexity and the performance of model selection criteria. *Ecological Applications*, 21(2), 335–342. Available from: https://doi.org/10.1890/10-1171.1

How to cite this article:
Stanton-Jones, W.K. & Alexander, G.J. (2024) Gazing into the future: The potential impact of climate change on habitat suitability of the Sungazer (*Smaug giganteus*). *Austral Ecology*, 49, e13577. Available from: https://doi.org/10.1111/aec.13577

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.