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Susceptibility of dwarf chameleons to climate and land use change: a vulnerability framework for conservation planning

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Climate and land use changes are eroding biodiversity globally, and reptiles are highlighted as being particularly susceptible. In South Africa, global changes threaten the persistence of an assemblage of dwarf chameleons (*Bradypodion*) located in a biodiversity hotspot. We used ecological niche modelling to assess the combined effect of climate change and habitat transformation on these species and assessed their susceptibility in a vulnerability framework under optimistic and pessimistic change scenarios. Although our models showed a gain in suitable climatic space for all coastal species in some scenarios, considerable losses were predicted for most species under the most pessimistic change scenarios. *Bradypodion ngomeense*, for example is predicted to incur a complete loss of climatic suitability by 2050. The vulnerability framework predicts inland species to be more adversely affected by climate change than coastal species. However, no species show resilience to the combined effects of climate change and habitat transformation. Our models predicted a loss of climatically suitable habitat for most species in protected areas. These findings highlight the importance of a protected area network design to remain a step ahead of these anticipated changes.

Keywords: Africa, biodiversity declines, *Bradypodion*, conservation planning, global change, niche modelling, reptiles, species distribution modelling, vulnerability

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Introduction

Climate and land use change are the two most significant direct threats to global biodiversity and are known to affect the geographic distributions of some species (Sala et al. 2000; Parmesan and Yohe 2003; Hockey et al. 2011; Jenkins et al. 2013; Oliver and Morecroft 2014; Botts et al. 2015). These threats have the potential to be particularly disastrous when operating in tandem, but the severity of impacts is predicted to vary depending on the taxon and location (Travis 2003). Reptiles and amphibians are forecast to undergo substantial declines in species richness (Newbold 2018; Sinervo et al. 2010; Warren et al. 2013; Petford and Alexander 2021), and as a consequence of these changes more than 20% of reptiles are threatened with extinction (Cox et al. 2022). The threat of biodiversity loss is particularly pressing in areas of high species richness and endemism and in areas of high levels of habitat transformation (Myers et al. 2000).

Threats to biodiversity relate primarily to the rapid degradation and fragmentation of natural habitat due to the conversion of natural land through agriculture, urban and industrial sprawl and afforestation (see Tolley et al. 2016; 2019; Cox et al. 2022). The rate and extent of habitat loss is linked to human population growth (Herrmann et al. 2020) although some areas of the globe are not expected to have further substantial population increases (UN DESA 2022). In contrast, Africa with a present-day human population of approximately 1.5 billion is expected to reach nearly 4 billion

humans by the end of the century (UN DESA 2022). The already stressed African landscape can be expected to fare poorly as the human population increases (Biggs et al. 2008). These impacts are compounded by climate change, with Africa anticipated to be disproportionately affected (Engelbrecht et al. 2015). For example, temperatures in South Africa are expected to rise by 1–2.3 °C on the coast and 3–4.6 °C inland by the year 2100 (DEA 2013; Ziervogel et al. 2014). Thus, it is conceivable that biotic assemblages in southern Africa will be disproportionately subjected to impacts from climate change. This provides strong motivation to regionalise analyses of both climate and habitat changes when predicting outcomes for biodiversity. Thus, our focus needs to be on identifying conservation priorities for species groups that are disproportionately threatened and occur in regions that are under high pressure for land conversion, particularly those which correspond with biodiversity hotspots.

South Africa is home to a rich faunal biodiversity (Mittermeier 1997) and the country is known to have at least three major biodiversity hotspots (Myers et al. 2000). Nevertheless, there is a notable decline in natural habitat quality and extent, with a concomitant trend for species declines (Skowno et al. 2019; Skowno et al. 2021). Habitat loss is essentially concentrated in areas with high human population density, and in many instances, biodiversity hotspots (Myers et al. 2000). A case in point is the

Maputaland–Pondoland–Albany biodiversity hotspot located in the eastern part of South Africa, largely in KwaZulu-Natal Province (KZN). The province alone supports as much as 40% of South Africa's reptile species, some of which are endemic to the province (see Tolley et al. 2023). However, being one of the most populous provinces in South Africa (SSA 2016), KZN is experiencing exceptionally high rates of land transformation at a rate of 1.2% per annum (Jewitt et al. 2015). This is higher than the national average of natural habitat loss of 2% over a four-year period (2010–2014) (Skowno et al. 2019; Skowno et al. 2021). Currently, less than 54% of the land area in KZN is in a wild natural state. However, this land area is expected to decrease to 45% by 2050 (Jewitt et al. 2015). Therefore, there is a strong correlation between biodiversity declines and habitat loss.

Although all vertebrate groups appear to be in decline in South Africa (Skowno et al. 2019; Raimondo et al. 2023), of particular concern for conservation are the dwarf chameleons (*Bradypodion*), a genus of 20 described species (plus several undescribed species) of small-bodied, viviparous lizards that are near-endemic to South Africa (Tolley and Burger 2007; Tolley et al. 2023). Of these, approximately 25% are threatened with extinction due to habitat loss (Tolley et al. 2023), which far exceeds the threat level compared to the global average (~20%) for reptiles (Cox et al. 2022). In addition, another 20% of *Bradypodion* are considered Near Threatened. Moreover, nearly half of the dwarf chameleon taxa (i.e. seven described plus two undescribed species) occur in KZN, and of these, seven are endemic to the province. All have small, non-overlapping geographic distributions in different areas of the province (Tolley and Burger 2007) and therefore face different levels of threat. Most are of concern for conservation, with two listed as Endangered (*Bradypodion caeruleogula* and *Bradypodion thamnobates*), two Vulnerable (*Bradypodion nemorale* and *Bradypodion ngomeense*) and three Near Threatened (*Bradypodion dracomontanum*, *Bradypodion melanocephalum*, *Bradypodion setaroi* (Tolley et al. 2023)). The two undescribed taxa have not yet been assessed for their IUCN threat status. Overall, half of the globally threatened *Bradypodion* occur in a single province, KZN, with the acute habitat loss in the province as the greatest threat for *Bradypodion*. However, illegal export for pet trade may also be a threat (Tolley 2022a).

Given the disproportionate threats to *Bradypodion* together with the extent and projected rate of landcover change and risk of climatic change in the province, we applied a regional vulnerability assessment for this local group of species. This included species distribution modelling to assess which areas of the province are climatically suitable for each of these species and projected model forecasts using various climate change scenarios. We then evaluated the modelled climate spaces together with current and predicted land cover change to estimate risk from the combined effects of habitat loss and climate change. A vulnerability framework was constructed to account for these factors and to provide a means for assessing the effects of both drivers on dwarf chameleons. Climate change outlooks (Naidu et al. 2006; Ziervogel et al. 2014) predict increases in annual temperature and

precipitation throughout the province but with greater rainfall periodicity and intensity inland. In contrast, anthropogenic land transformation rates are known to be higher along the coast (Jewitt et al. 2015; Skowno et al. 2019). Dwarf chameleon occurrence in the province appears to be negatively associated with increasing aridity and land transformation. We thus predict that inland species are more likely to be adversely impacted by climate change than the coastal species, whereas the coastal species are more likely to be adversely impacted by land transformation. Nevertheless, we anticipate that all KZN dwarf chameleon species are likely to be susceptible to the combined effects of both change drivers.

Materials and methods

Locality data and spatial layers

Point locality data for *Bradypodion* were sourced from four databases: ReptileMap (<http://vmus.adu.org.za>); the South African National Biodiversity Institute; iSpot (Open University, <https://www.ispotnature.org/>) and iNaturalist (<https://www.inaturalist.org/>). In addition, we carried out two field surveys in KwaZulu-Natal (KZN), South Africa, from 24 November to 17 December 2016 and from 12 to 31 March 2017 to collect additional locality records. The appropriate provincial research permits and ethical clearances for research on live vertebrates were sought and approved by the authorising bodies responsible for such permits and ethical clearance certificates (further details in Acknowledgements section).

For species distribution modelling, 19 bioclimatic and two topographic raster layers were used as predictor variables. The bioclimatic variables were sourced from the WorldClim online repository (<http://www.worldclim.org>). This dataset is at 30 arc-second resolution and constitutes monthly temperature and rainfall values that include annual trends, seasonality, and extreme or limiting environmental factors from 1950 to 2000 (Hijmans et al. 2005). The two topographic variables, slope and aspect, were derived from high resolution (7 arc-second) United States Geological Survey (USGS) digital elevation model (DEM) data (Danielson and Gesch 2010) using ArcMap 10.2.2 software.

Land cover estimates were based on the 2011 KwaZulu-Natal Land Cover 2011 V1 GIS Coverage (Ezemvelo KZN Wildlife 2013). This coverage represents the latest in a time-series set of high resolution (6 arc-seconds), remotely derived layers for KZN and was derived from SPOT 5 multi-spectral and panchromatic satellite imagery (GeoTerraImage 2010; Ezemvelo KZN Wildlife 2013).

We used current geographic range estimates from the interpreted distribution maps available on the IUCN (<https://www.iucnredlist.org>; see also Tolley et al. 2019) as of January 2022. The exceptions to this were for the two undescribed species (*B. sp.* 'Karkloof' and *B. sp.* 'Emerald') (Tolley and Burger 2007), which have not yet been assessed for the IUCN, and *B. dracomontanum* for which new records were collected during this study. For *B. sp.* 'Emerald' sufficient locality data allowed us to produce a convex hull polygon to represent the interpreted range. However, there were few records for *B. sp.* 'Karkloof' making it difficult to interpret the geographic range

with confidence. Thus, the convex hull polygon for this species encompassed only the known records, which we acknowledge is likely to be an underestimate of the actual range. Regarding *B. dracomontanum*, the existing IUCN distribution map was updated to incorporate new localities. Although the model outputs would ultimately be clipped to KZN Province, the locality data used to train the models included additional records of two species that extend marginally into Mozambique and the Free State Province of South Africa (Supplemental Material Figure S1) to cover the full distribution of the study species.

Climate niche modelling

The climate niche models were run using Maxent (Phillips et al. 2009), with the sourced locality data input as presences. Locality data were first visualised in ArcMap 10.2.2 and vetted to allow for the removal of questionable outliers, misidentifications or georeferencing errors. Presence-only algorithms such as Maxent rely on the generation of a set of artificial absence points or pseudo-absences to accompany the known presence localities used for model building. However, the selection of pseudo-absences from the background of environmental variables (otherwise known as the area of calibration) has the potential to strongly affect model performance due to false absences (Van Der Wal et al. 2009; Phillips et al. 2009). To minimise the incidence of false absences, pseudo-absences were drawn from the localities of all reptile taxa recorded in KZN, sourced from the same data sources (except for iNaturalist) as the presence data but excluded all *Bradypodion* records. These user-defined pseudo-absence data were incorporated into Maxent in the form of a bias file generated in ArcGIS by creating a binary raster with the same cell size as the predictor variables used for the modelling. Raster cells where a reptile was recorded (but not a dwarf chameleon) were assigned a value of 1.

This file was then converted from raster to ASCII file format and inputted into Maxent under the advanced settings tab as the bias file. This approach, referred to as target-group background selection, is said to improve model performance (Phillips and Dudík 2008, Phillips et al. 2009; Searcy and Shaffer 2014). Pseudo-absence data are taken from localities where species with similar life histories have been documented or where species that require similar survey methods have been found, but where observers have failed to record the target species. The model benefits from being more discriminatory in areas of higher sampling effort and more generous in under-sampled areas, thereby more closely representing the true potential distribution of the species (Searcy and Shaffer 2014).

The refined set of georeferenced pseudo-absence points ($n = 9\,641$) was first converted into a binary raster with the same cell size as the predictor variables using ArcMap 10.2.2 before importation into Maxent as a bias file. Six of the most biologically meaningful and least correlated variables that best explained the distribution of given species were selected for the final models. Pairwise correlation coefficients were used to identify highly correlated variables, and in each case, one of the two variables was removed from the dataset. This data matrix was calculated in ArcMap 10.2.2 following the methods of Measey et al. (2012). To explain the modelled distribution of each species (Table 1), a jack-knife analysis in Maxent was used to identify the variables with the best response curve and thus the highest percentage contribution.

Model evaluation

Model performance in Maxent was evaluated by dividing occurrence records into 70% training and 30% testing datasets and re-running the model over 10 replicates with bootstrapping through 2 000 iterations. Model output format was set to logistic; default prevalence was set to 0.5 and

Table 1: Model performance, bioclimatic and topographic variable importance, and global circulation model (GCM) with respective representative concentration pathways (RCPs) selected from the ensemble to represent the most optimistic and pessimistic future scenarios for *Bradypodion* found in KwaZulu-Natal Province, South Africa. Variables in bold font are those which contributed most to the current model output

Species	Variables	Current	Future Optimistic		Future Pessimistic			
		AUC	GCM	RCP	AUC	GCM	RCP	AUC
Coastal								
<i>B. caeruleogula</i>	2,3,9,12,17, asp	0.99	NorESM1-M	85	0.99	MIROC5	45	0.99
<i>B. melanocephalum</i>	5,6,11,12,14,15	0.97	MIROC5	45	0.96	MPI-ESM-LR	45	0.97
<i>B. setaroi</i>	4,5,6,14,15, slo	0.93	MPI-ESM-LR	45	0.94	MPI-ESM-LR	85	0.94
Inland								
<i>B. dracomontanum</i>	4,6,14,15,18, slo	0.97	MIROC5	45	0.98	HadGEM2-ES	85	0.99
<i>B. nemorale</i>	3,4,7,10,14, slo	0.99	NorESM1-M	85	0.99	MPI-ESM-LR	45	0.99
<i>B. ngomeense</i>	3,4,6,8,12,13	0.99	MIROC5	45	0.99	CNRM-CM5	85	0.99
<i>B. sp. 'Karkloof'</i>	3,6,7,11,12,17	0.99	CNRM-CM5	85	0.99	HadGEM2-ES	85	0.99
<i>B. sp. 'Emerald'</i>	4,11,15,18,slo,19	0.99	HadGEM2-ES	85	0.99	NorESM1-M	45	0.99
<i>B. thamnobates</i>	1,3,6,7,14,15	0.98	MPI-ESM-LR	45	0.98	NorESM1-M	45	0.98

Variable abbreviations: slo, slope; asp, aspect; 1, annual mean temperature; 2, mean diurnal temperature range; 3, isothermality; 4, temperature seasonality; 5, mean temperature of warmest month; 6, minimum temperature of coldest month; 7, temperature annual range; 8, mean temperature of wettest quarter; 9, mean temperature of driest quarter; 10, mean temperature of warmest quarter; 11, mean temperature of coldest quarter; 12, annual precipitation; 13, precipitation of wettest month; 14, precipitation of driest month; 15, precipitation seasonality; 16, precipitation of wettest quarter; 17, precipitation of driest quarter; 18, precipitation of warmest quarter; 19, precipitation of coldest quarter.

the minimum training presence logistic threshold was used. Area under curve (AUC) statistics were used to evaluate model fit (Phillips et al. 2006). The AUC values were interpreted in terms of model fit as: <0.5 random; 0.5–0.69 poor; 0.7–0.89 useful and ≥ 0.9 excellent (Swets 1988). Model reliability due to sample size (n = number of locality records) was inferred from the findings of Wisz et al. (2008) and van Proosdij et al. (2015) which suggest low reliability with sample sizes smaller than 30.

Modelling future climatically suitable natural habitat

The effects of climate and land cover change were estimated by first modelling and then overlaying predicted future climate and land cover conditions by the year 2050. Areas of current and future climatically suitable remaining natural habitat are, hereafter, referred to as 'climatically suitable natural habitat'. To model the effects of predicted climate change, five global circulation models (GCMs) were used for two representative concentration pathways (RCPs) for each of the nine species (Table 1). This resulted in a total of one current and 10 future models for each species. For each species a final subset of three models that included the current projection, as well as the best- and worst-case scenarios for each, were selected. The same set of bioclimatic variables used to create the current models was substituted with future datasets representing two scenarios of climate change. The variables were based on the latest climate change trajectories described by two RCPs of the International Panel of Climate Change's (IPCC) fifth assessment report (AR5), sourced from the WorldClim online repository. Representative concentration pathways are estimates of future greenhouse gas concentrations based on changes in atmospheric energy levels from anthropogenic and other causes (van Vuuren et al. 2011). This study utilised RCPs 4.5 and 8.5. These represent the most realistic range of possible energy levels denoted as radiative forcing values (in Watts m^{-2}) predicted for year 2050 relative to pre-industrial values. Final climate model outputs for each species were divided into areas of low, moderate and high climatic suitability based on data reclassification by equal intervals.

As no future land use scenarios exist for KZN, following Gouveia et al. (2016), a habitat conversion rule was applied to the 2011 KZN Land Cover layer to produce a map depicting natural and transformed habitat by 2050. To do this, we reclassified all 45 land cover classes in the 2011 land cover dataset into a binary map depicting natural and transformed landscapes in accordance with the 2008 KwaZulu-Natal Conventional Transformation Coverage (Ezemvelo KZN Wildlife 2011). This binary output was then clipped to exclude the KZN protected areas network on the assumption that there would be no appreciable transformation in these protected areas. The extent of habitat transformation was based on a study (Jewitt et al. 2015) in which extrapolated estimates, in a business-as-usual model, suggests that 45% of KZN is likely to remain natural by 2050. Pixels were converted using focal statistics on a 9×9 cell neighbourhood in ArcMap 10.2.2 with the premise that non-protected, natural pixels that were closest to transformed pixels would presumably be transformed in future.

All subsequent analyses were based on a final subset of three models per species which depicted the extent of climatically suitable natural habitat both at present and by 2050 in the most optimistic ($\sim 1^\circ C$) and pessimistic ($\sim 2^\circ C$) scenarios (see Baek et al. 2013). Models were selected on a species-specific basis. To facilitate a more biologically meaningful interpretation of the data, three dispersal scenarios were applied. Under dispersal Assumption 1, individuals have unlimited dispersal and therefore a population could expand to reach any forecasted climatically suitable natural habitat. Under dispersal Assumption 2, individuals could not disperse beyond the polygon of climatically suitable natural habitat modelled under current conditions. Under dispersal Assumption 3, individuals could not disperse beyond the polygon currently defined as the known range (the interpreted distribution).

Model outputs were then used in conjunction with the Ezemvelo KZN Wildlife (EKZNW) protected areas network spatial dataset (EKZNW 2015) to estimate the proportion of climatically suitable natural habitat for each species that overlaps with gazetted protected areas.

To represent the susceptibility of each species to the combined effects of climate and land use change, we constructed a vulnerability framework using a bubble plot in three dimensions. The first two dimensions represented the proportion of climatically suitable natural habitat predicted to remain by 2050 (in their current extent of climatically suitable natural habitat or dispersal Assumption 1, for each species under the most pessimistic climate scenarios (x and y axis respectively)). The third dimension was added to account for changes in the intensity of climatic suitability (bubble size). Change in climatic suitability was defined as the proportional difference in climatic suitability values between the present and the year 2050. Suitability values were calculated by multiplying the area (km^2) of each suitability class by its respective suitability score (1 = low; 2 = moderate and 3 = high). The resulting plot was then divided into four quadrants to classify their degree of vulnerability as either climate constrained, (natural) habitat constrained, resilient (neither), or vulnerable (both). A constraint threshold was set at $< 50\%$ remaining natural habitat, given that the capacity of landscapes to support viable populations rapidly declines beyond this level (see Flather and Bevers 2002).

Results

Variables that contributed most to the models (Table 1) in the current climate scenario included isothermality (*B. caeruleogula* and *B. nemorale*), maximum temperature of warmest month (*B. melanocephalum*), minimum temperature of coldest month (*B. dracomontanum* and *B. thamnobates*), mean temperature of wettest quarter (*B. ngomeense*), mean temperature of coldest quarter (*B. sp.* 'Karkloof' and *B. sp.* 'Emerald'), precipitation of driest month (*B. setaroi*).

The current extent of modelled climatically suitable natural habitat in KZN varied considerably among species (Tables 2 and 3, Supplemental Material Table S1). *Bradypodion melanocephalum* has the largest area of climatically suitable natural habitat at present (20 751 km^2), whereas all other

KZN dwarf chameleons are considerably more limited in their extent of climatically suitable natural habitat, ranging from 6 264 km² for *B. setaroi* to 297 km² for *B. ngomeense*. Note that for all species, the modelled climatic envelope is an overprediction compared to the known distribution, as the model's forecast areas of climatically suitable habitat does not account for other potentially limiting factors.

Assuming unlimited dispersal ability (dispersal Assumption 1), in both optimistic and pessimistic future climate scenarios, the extent of climatically suitable natural habitat was predicted to expand for species that occur nearer the coast (Figure 1, Table 2). On the other hand, inland species showed losses of climatically suitable natural habitat in both optimistic and pessimistic future climate scenarios (Figure 1, Table 2). Some inland species (*B. dracomontanum*, *B. nemorale*, *B. thamnobates*) showed gains in climatically suitable habitat in the most optimistic scenarios and losses in the most pessimistic scenarios.

The relative contribution of climate and land use change (Figure 2, Supplemental Material Table S1) varied among the species in future climatic and dispersal scenarios. For dispersal Assumption 2, where individuals were

assumed not to be able to disperse beyond the polygon of climatically suitable natural habitat modelled under current conditions, Table 3 predicted losses were primarily attributed to climate change for inland species. Land transformation was predicted to be the predominant loss driver for coastal species in both optimistic and pessimistic climate scenarios (Figure 2a). However, for *B. sp. 'Karkloof'* and *B. nemorale* (inland species) land transformation was identified as the primary driver in the optimistic future climate scenario but with climate change becoming proportionally more impactful than land transformation in the pessimistic future climate scenario (Figure 2a). In contrast, the predicted losses for *B. ngomeense* in both climatic scenarios were attributed almost entirely to climate change. The loss of natural habitat predicted for *B. caeruleogula* was entirely attributed to land transformation in areas outside its protected forest patches.

When considering models in which chameleons are assumed not to be able to disperse beyond their current range (dispersal Assumption 3, Supplemental Material Table S1), all the study species showed substantial losses (Table 3). Of particular concern were *B. ngomeense*,

Table 2: A comparison of known range sizes of *Bradypodion* found in KwaZulu-Natal Province, South Africa. Areas of modelled climatically suitable natural habitat both predicted current range and as predicted for optimistic and pessimistic future climate change scenarios under Assumption 1 (assuming individuals can disperse beyond their current extent of climatically suitable natural habitat)

Species	Known range (km ²)	Climatically suitable natural habitat				
		Current	Optimistic (2050)		Pessimistic (2050)	
		Extent (km ²)	Extent (km ²)	Change (%)	Extent (km ²)	Change (%)
Coastal						
<i>B. caeruleogula</i>	44	746	31 205	+4 082	4 651	+523
<i>B. melanocephalum</i>	8 957	20 751	35 519	+71	34 536	+66
<i>B. setaroi</i>	5 303	6 264	59 999	+858	50 583	+708
Inland						
<i>B. dracomontanum</i>	2 975	5 397	6 574	+22	3 212	-40
<i>B. nemorale</i>	39	3 034	11 797	+289	1 350	-56
<i>B. ngomeense</i>	26	297	0	-100	0	-100
<i>B. sp. 'Emerald'</i>	1 376	3 995	1 664	-58	374	-91
<i>B. sp. 'Karkloof'</i>	-	440	286	-35	250	-43
<i>B. thamnobates</i>	3 295	4 591	5 322	+16	4 484	-2

Table 3: Comparison of known range sizes of *Bradypodion* found in KwaZulu-Natal Province, South Africa, with areas of modelled climatically suitable natural habitat for both the present and predicted optimistic and pessimistic future climate change scenarios under Assumption 2 (assuming individuals cannot disperse beyond their current extent of climatically suitable natural habitat)

Species	Known range (km ²)	Climatically suitable natural habitat				
		Current	Optimistic (2050)		Pessimistic (2050)	
		Extent (km ²)	Extent (km ²)	Change (%)	Extent (km ²)	Change (%)
Coastal						
<i>B. caeruleogula</i>	44	746	419	-44	419	-44
<i>B. melanocephalum</i>	8 957	20 751	10 162	-51	8 469	-59
<i>B. setaroi</i>	5 303	6 264	4 274	-32	4 090	-35
Inland						
<i>B. dracomontanum</i>	2 975	5 397	3 593	-33	1 474	-73
<i>B. nemorale</i>	39	3 034	2 052	-32	575	-81
<i>B. ngomeense</i>	26	297	0	-100	0	-100
<i>B. sp. 'Emerald'</i>	1 376	3 995	1 355	-66	341	-92
<i>B. sp. 'Karkloof'</i>	-	440	44	-90	1	-100
<i>B. thamnobates</i>	3 295	4 591	2 312	-50	1 276	-73

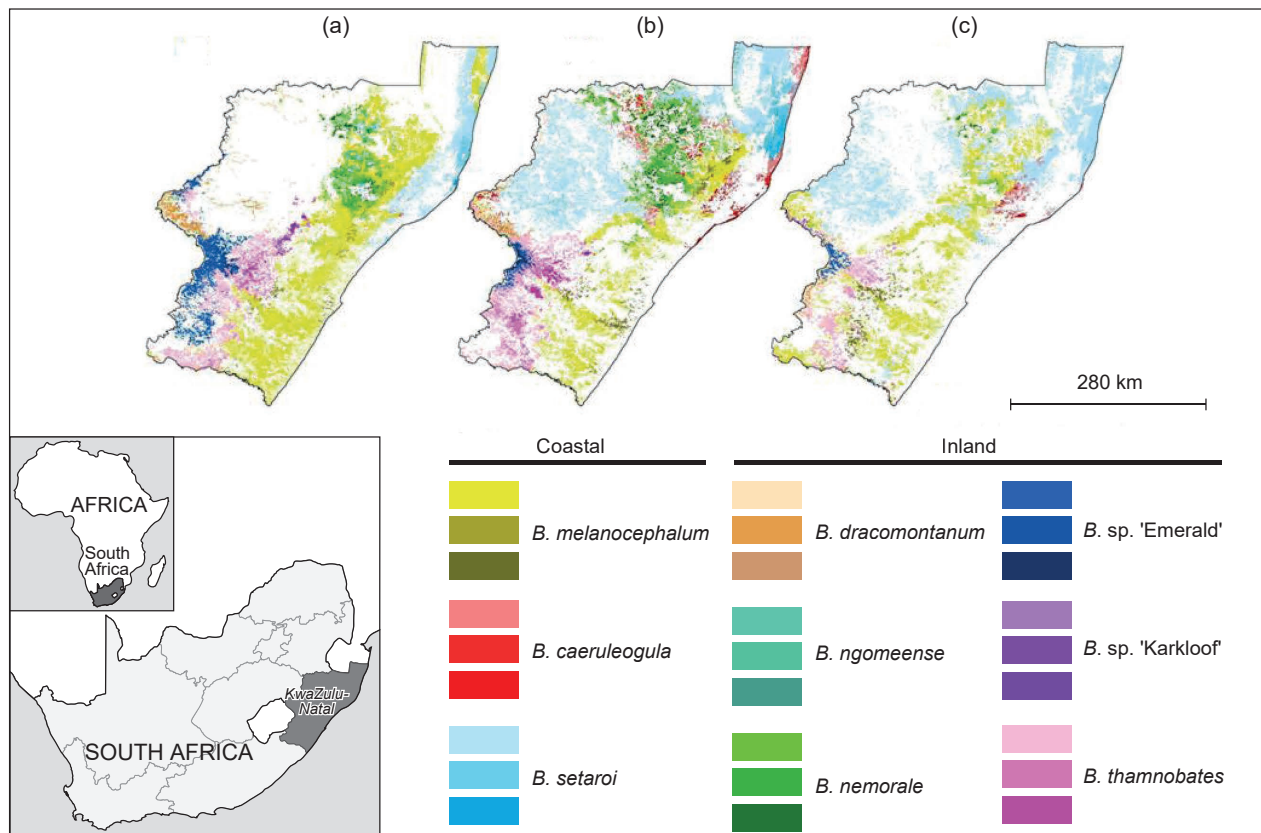


Figure 1: Extent of climatically suitable natural habitat for all *Bradypodion* species found in KwaZulu-Natal for model scenarios from L–R (a) optimistic scenario (b) pessimistic scenario (c) scenarios selected from the ensemble of 10 models (per species) that were generated using five GCMs and two RCPs. Climatically suitable natural habitat is colour coded by species, representing low, medium and high climatic suitability (colour ramp from light to dark shades) based on equal intervals classification of probability values (from 0–1)

B. nemorale, *B. sp. 'Emerald'*, *B. sp. 'Karkloof'* and to some degree, *B. thamnobates*. Under these dispersal assumptions the models predicted losses for even the most climatically resilient species, such as *B. melanocephalum*, *B. caeruleogula* and *B. setaroi* (Table 3). Under this Assumption, the combined effects of climate and land use change were idiosyncratic with respect to species, although most of the species are predicted to be more gravely impacted by the combined effects of both change drivers (Figure 2b).

The extent to which climatically suitable natural habitat for each species overlaps with the protected areas network in KZN (for current, optimistic, and pessimistic future climate scenarios) under the three dispersal assumptions was estimated (Figure 3, Supplemental Material Table S2), except for *B. sp. 'Karkloof'* given the uncertainty of its distribution. From this figure it is apparent that, at present, *B. caeruleogula* (63 km²), *B. sp. 'Karkloof'* (36 km²) and *B. ngomeense* 16 (km²) have by far the lowest extent of formally protected climatically suitable natural habitat. In contrast to absolute area, the protected proportion of climatically suitable natural habitat in the known ranges of each species (Assumption 3) is far lower for *B. melanocephalum*, *B. thamnobates* and *B. 'Karkloof'* (all < 11%) than it is for the remaining species (all > 43%). Table

4 shows that by 2050 the extent of protected climatically suitable natural habitat (dispersal Assumption 3) is predicted to decrease for *B. sp. 'Emerald'* (68%), *B. melanocephalum* (14%), *B. nemorale* (82%), *B. ngomeense* (100%), *B. setaroi* (3%) and *B. thamnobates* (53%). Conversely, the statutory protection of suitable habitat is modelled to increase for the species *B. caeruleogula* (by 3%) and *B. dracomontanum* (by 22%).

The vulnerability framework (Figure 4) predicted that all species except for two high elevation species, *B. dracomontanum* and *B. sp. 'Emerald'* would become more habitat constrained by the year 2050. Species predicted to be constrained by both climate change and habitat transformation (vulnerable quadrant) include *B. sp. 'Karkloof'* (entirely constrained by climate) and *B. nemorale*, *B. ngomeense* and *B. thamnobates*. Species predicted to be less constrained by climate include *B. melanocephalum*, *B. setaroi* and *B. caeruleogula*. Analysis of the intensity of climate suitability (as indicated by the bubble sizes in Figure 4) reveals subtle differences in vulnerability among species. *Bradypodion setaroi*, for example, is expected to be more impacted by climate change than *B. caeruleogula*. Likewise, the effects of climate change are more impactful for *B. nemorale* than for *B. dracomontanum* and *B. thamnobates*.

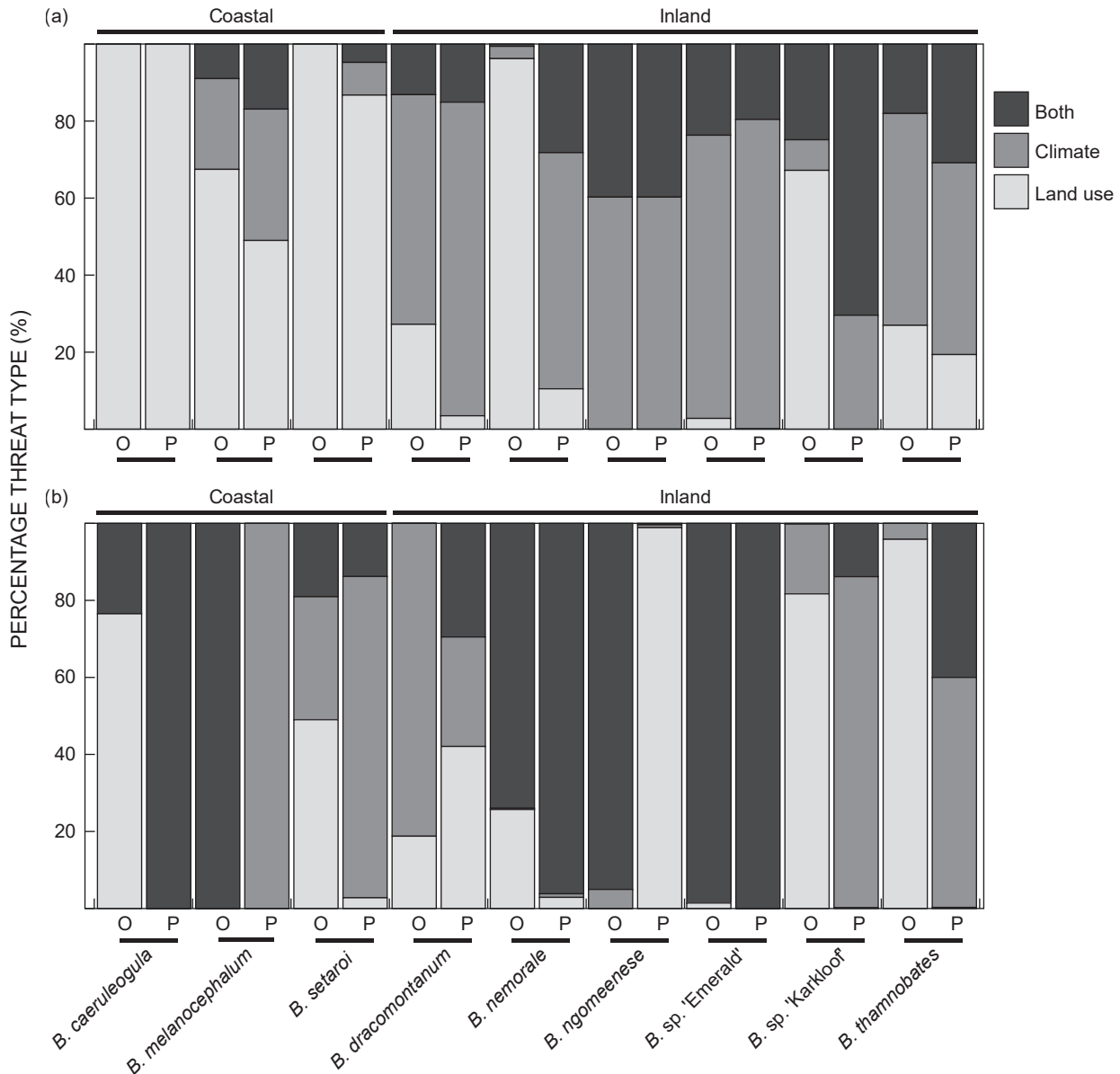


Figure 2: Proportional contribution of threat type – climate change, land cover change, and areas to be impacted simultaneously by both threats for *Bradypodion* species found in KwaZulu-Natal under (a) both* Dispersal Assumption 1 (unlimited dispersal) and Dispersal Assumption 2 (dispersal limited to currently climatically suitable natural habitat) and (b) Assumption 3 (dispersal limited to known range), denoted for the two climate change scenarios (O, optimistic; P, pessimistic). Colour codes for bars are denoted in the key. *Note: Assumptions 1 and 2 resulted in the same outcomes

Discussion

Modelling of dwarf chameleon distributions into the future showed dissimilar responses for the two species groupings (coastal and inland). In a climate-change-only scenario, models predicted an increase in climatic suitability for coastal species but a decrease for inland species. However, when considering the presumed low dispersal abilities of chameleons, even the most climatically resilient species faced notable contractions in climatic suitability available to them by 2050. When considering the combined effects of both climate and land use change, however,

there were negative responses for all the species, ranging from complete loss of range size for one species to very significant losses for others. In addition, models predicted a considerable loss of climatic suitability in the protected areas network for most of the species. The vulnerability framework allowed for both threats to be considered concurrently and highlighted species that are most likely to be at risk of extinction (e.g., *B. ngomeense*, *B. nemorale*, *B. thamnobates*, *B. sp. 'Karkloof'* and *B. sp. 'Emerald'*) due to a combination of climate and land use change.

While some generalisations could be made about coastal and inland species, the relative impact depended on the

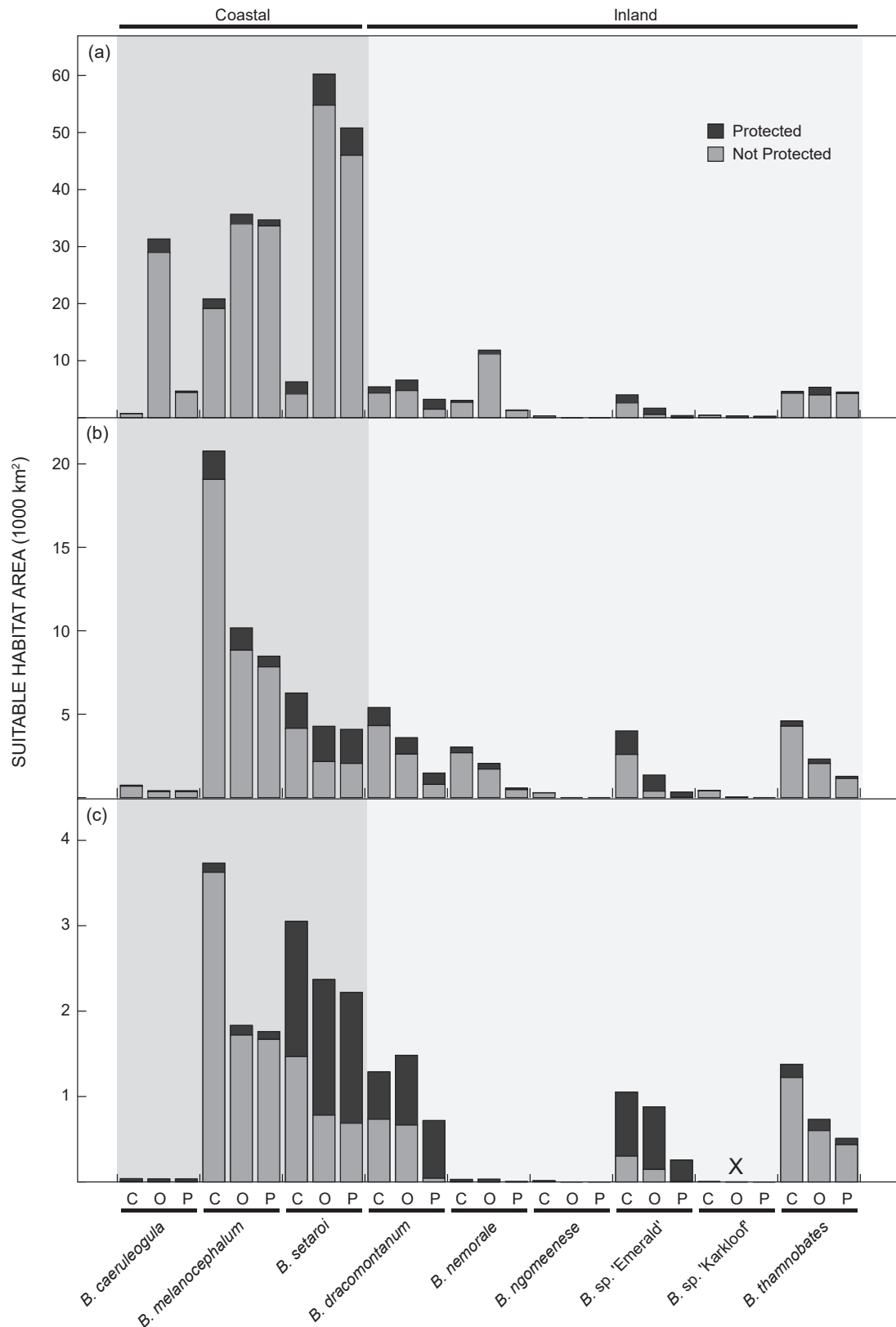


Figure 3: The area (1 000 km²) of climatically suitable natural habitat in protected areas (dark grey shading) or outside protected areas (light grey shading) for *Bradypodion* species found in KwaZulu-Natal. (a) Dispersal Assumption 1 (unlimited dispersal) (b) Dispersal Assumption 2 (dispersal limited to currently climatically suitable natural habitat) and (c) Assumption 3 (dispersal limited to known range). C, current; O, optimistic; P, pessimistic climate scenarios. Species names for panels (a) and (b) are abbreviated on the x-axis. Note: The y-axes are not scaled to the same range of area values. *Bradypodion* sp. 'Karkloof' not included in Assumption 3 due to uncertainty of its range (denoted by X)

Table 4: The extent to which the natural habitat of *Bradypodion* in KwaZulu-Natal Province, South Africa is found in the protected areas network at present contrasted with predictions for how this may change according to three climate scenarios (current, optimistic, and pessimistic future). Assumptions of unlimited dispersal (Assumption 1) were compared to the assumption where dispersal was limited to their currently known range (Assumption 3). The last column shows the percentage change in modelled climatically suitable habitat in protected areas when the models (current, optimistic and pessimistic scenarios) are constrained to the species' known distribution. Assumptions 1 and 2 reflected the same outcomes

Species	Climate scenario	Assumption 1 & 2	Assumption 3	
		Area (km ²)	Area (km ²)	% Change
Coastal				
<i>B. caeruleogula</i>	Current	63	33	
	Optimistic	2 351	34	+3
	Pessimistic	270	34	+3
<i>B. melanocephalum</i>	Current	1 702	107	
	Optimistic	1 683	111	+4
	Pessimistic	1 060	91	-15
<i>B. setaroi</i>	Current	2 114	1 579	
	Optimistic	5 440	1 581	+0.1
	Pessimistic	4 777	1 525	-3
Inland				
<i>B. dracomontanum</i>	Current	1 088	552	
	Optimistic	1 830	812	+47
	Pessimistic	1 735	673	+22
<i>B. nemorale</i>	Current	348	28	
	Optimistic	663	31	+11
	Pessimistic	105	5	-82
<i>B. ngomeense</i>	Current	16	11	
	Optimistic	0	0	-100
	Pessimistic	0	0	-100
<i>B. sp. 'Karkloof'</i> *	Current	36	-	-
	Optimistic	37	-	-
	Pessimistic	53	-	-
<i>B. sp. 'Emerald'</i>	Current	1 410	747	
	Optimistic	1 113	729	-2
	Pessimistic	359	252	-68
<i>B. thamnobates</i>	Current	316	154	
	Optimistic	1 355	129	-16
	Pessimistic	274	72	-53

*Assumption 3 for *B. sp. 'Karkloof'* was excluded due to uncertainties about its distribution.

climatic change scenario and the modelled dispersal assumption. Some inland species are estimated to be at greater risk to climate change (*B. thamnobates*, *B. sp. 'Emerald'* and *B. dracomontanum*) than to land transformation whereas all others are at risk from both. In contrast, land transformation was predicted to be the predominant driver of range reduction for all coastal species. Coastal species appear to be more resilient to climate change than inland species, but large portions of their ranges fall within rapidly transforming coastal areas (Armstrong 2009). Overall, four of the nine species (*B. thamnobates*, *B. nemorale*, *B. ngomeense* and *B. sp. 'Karkloof'*) were considered vulnerable to both threat types, and none of the species in the framework was deemed to be resilient.

Of particular concern are *B. nemorale* and *B. sp. 'Karkloof'* which are highly range restricted species due to past habitat losses from afforestation and rural development. In most scenarios, climate change is predicted to become more of an important driver of loss for these species. At present, *B. nemorale* is considered Vulnerable under the IUCN D2 category (Tolley 2022b)

given the future plausible threat of habitat loss in an already small range (39 km²). Should future habitat loss be realised, with climate change compounding the threat level, this species could easily become Critically Endangered in a short period of time. In addition, *B. sp. 'Karkloof'* has not yet undergone an extinction risk assessment, but with an unknown range size (due to lack of sufficient records) and the compounded risk of climate change and habitat loss, it is likely that this species would be listed in a threatened category. The extent of Karkloof forest is not likely to be greater than 25 km², which suggests that this chameleon would have a similar range size (being endemic to the forest). Should the future threats be plausible, then this would place the chameleon at the Critically Endangered threshold.

A unique case is that of *B. ngomeense* which is predicted to incur a complete loss of suitable climatic space. Although the risk associated with future land transformation was not considered noteworthy, its forest habitat falls within a national "Forest Reserve" which is not a protected area. Instead, the area is gazetted for potential

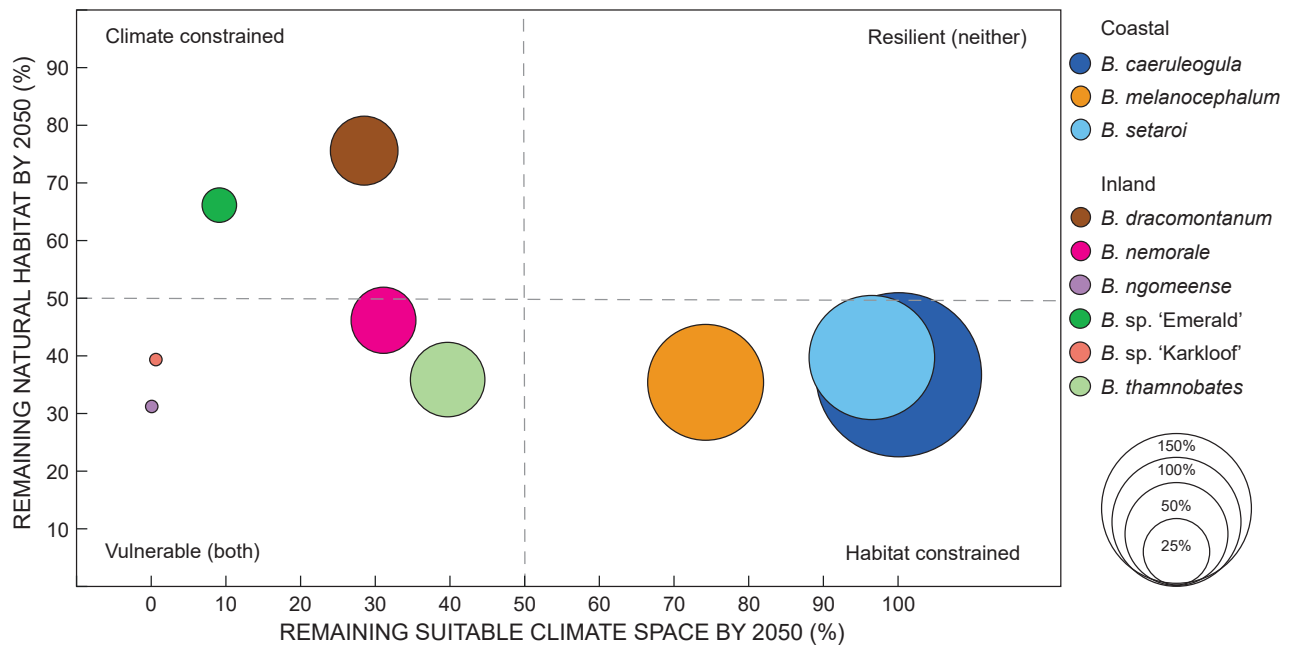


Figure 4: Vulnerability framework incorporating both climatic space and land use predictions for the *Bradypodion* species found in KwaZulu-Natal. Each species is represented by a circle of different colours - located on the x-axis given the proportion of the current climatic niche predicted to be suitable and, on the y-axis given the proportion of habitat predicted to be suitable by the year 2050. The size of the circles is relative for each species, calculated as the total suitable climate space (km²) for the 2050 pessimistic model as a percentage of the current suitable climate space (km²). Thus, species predicted to have a larger climate space in the future have circles larger than 100%, whereas those predicted to have a smaller climate space are represented by circles smaller than 100% (compare to legend showing circle sizes). The percentages for two species (*B. ngomeense* and *B. sp. 'Karkloof'*) were close to zero and were therefore scaled up to 1.0 to be visible on the figure

commercial development by the Management of State Forests Act 128 of 1992 managed by the Department of Forestry, Fisheries and the Environment (<https://www.gov.za/about-sa/forestry>; Government Gazette for the Republic of South Africa 1992). Thus, the species *B. ngomeense* may be at much higher risk given the lack of genuine protection of its habitat as a conservation area. There is a plausible threat of unanticipated changes in land use practice should government shift current practices in Forest Reserve management (Tolley 2022c). This species is currently considered Vulnerable under the IUCN D2 criterion (Tolley 2022c) and has a range size of only 44 km². As with *B. nemorale*, should this threat become active and compounded by climate change, the species could easily become Critically Endangered in a short period of time.

Although most species are likely to become habitat constrained in the future, more positive examples are that of *B. dracomontanum* and *B. sp. 'Emerald'* which both occur in the Ukhahlamba-Drakensberg protected area that forms a considerable buffer for these species against land use change. However, these species are considered climate constrained and therefore not entirely resilient to risk. Despite *B. dracomontanum* being categorised as Least Concern given its large range (2975 km²) and low level of threat (Tolley 2022d), and the likelihood of *B. sp. 'Emerald'* (not currently assessed) also being classified as such for similar reasons, they are both projected to have massive range reductions (73% and 92%, respectively), potentially

forcing these species into an IUCN threat category as high as Endangered and Critically Endangered, respectively.

The proportion of protected climatically suitable natural habitat is predicted to decrease for the most vulnerable inland species (*B. nemorale*, *B. ngomeense*, *B. sp. 'Emerald'* and *B. thamnobates*) with only small changes or increases predicted (i.e. range shifts into protected areas) for the remaining species. Considering these predictions, the protected areas network appears to be inadequate for safeguarding some of the species already at high extinction risk. Ultimately though, the long-term value of any remaining climatically suitable natural habitat depends not only on the current extent of protection but also on how well it aligns with the protected areas network in the future. Our predictions suggest that the extent of protected climatically suitable natural habitat (considering a pessimistic scenario under Assumption 3 of no dispersal beyond current known range) may decrease for all but two (*B. caeruleogula* and *B. dracomontanum*) KZN dwarf chameleon species. This highlights the potentially disastrous effects of climate change if proactive conservation planning is not implemented. Moreover, even some of the most climatically resilient species, such as *B. melanocephalum* and *B. setaroi*, may soon surpass critical threshold levels of natural habitat, should transformation continue at the forecasted rates.

Although our study makes important steps towards evaluating the vulnerability for biodiversity, the actual responses will depend on how effectively each species is

able to climate track. This is dependent on, *inter alia*, the vagility of the species, the characteristics of habitat change, the potential to adapt to new conditions, and a host of shifting biotic interactions (Urban et al. 2013; Petford and Alexander 2021). For dwarf chameleons, data on dispersal ability has been limited, although short-term telemetry work suggests that the congener, *Bradypodion pumilum*, is capable of directional movement to nearby habitat patches (a few hundred metres over weeks) when suitable corridors are present (Rebello et al. 2022). However, daily displacement distances appear to be low (tens of metres), even for a large-bodied chameleon (*Trioceros jacksoni*) that showed low vagility both in its native ranges (Toxopeus et al. 1998) and non-native ranges (Chiaverano et al. 2014). It is thus unlikely that populations of dwarf chameleons will climate track quickly, especially given that they are habitat specialists and need their specific habitats to remain intact (Hopkins and Tolley 2011; da Silva and Tolley 2013; da Silva et al. 2014).

On an evolutionary timescale, the *Bradypodion* species appear to have a propensity for adapting to novel habitats (Tolley et al. 2008; da Silva et al. 2014). However, whether any or all species can do this on a short timescale has not been established and is likely to be idiosyncratic. Moreover, species would need to adapt to both the novel land cover and new climate conditions. Should these species' adaptation in terms of both phenotype and thermal physiology, not occur in time, then changing climate is likely to bring about a reduction in the area suitable for their occurrence. Regardless of the primary driver, none of the species appear to be resilient to the combined effects of both drivers when considered simultaneously.

Conclusions

Niche models such as Maxent are subject to several types of uncertainty. For example, model predictions are based almost entirely on climatic suitability, which comprises just one of many aspects that limit species to realised geographic distributions. Other factors such as biotic interactions, barriers to dispersal and anthropogenic disturbances may exclude a species from an area that is otherwise environmentally suitable (Jiménez-Valverde et al., 2011), or even allow a species to extend occurrence into an area that it would otherwise not be able to persist (Rebello et al. 2019). Also, the modelling protocol assumes that current observed distributions are at equilibrium with the environment (Guisan and Thuiller, 2005), which may not always be the case. Modelling species distributions into the future also comes with the uncertainties inherent in climate models. These limitations may result in inaccuracies in the estimation of the fundamental niche and responses to novel climate in the future. Thus, outputs and predictions made in studies such as ours should always be evaluated with a level of caution. Actual species' responses will most certainly be stochastic as many other abiotic and biotic factors, not captured in our analyses, will contribute to their realised distribution. In addition, we have not incorporated the possibility of potential adaption, phenotypic or behavioural plasticity nor the possibility of flexible thermal physiology which requires further investigation.

Ultimately, the fate of these chameleons will lie not only in their ability to cope with and track global change but also in their ability to utilise habitat that is no longer natural. Despite model uncertainty, our study provides valuable insights into the future risk to *Bradypodion*, many of which are already considered threatened. By simultaneously incorporating the threats of habitat loss and climate change into our vulnerability framework we have an indication of the species at greatest risk and the most likely drivers of that risk. We assert that the IUCN extinction risk status of most of these species may require uplisting in the absence of proactive conservation. A large part of the solution lies in our ability to use forecasting studies such as this to inform conservation planning that advocates the safeguarding of core habitats and refugia through proactive planning and effectively incorporating these concepts into protected areas expansion strategies.

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References

- Armstrong AJ. 2009. Distribution and conservation of the coastal population of the black-headed dwarf chameleon *Bradypodion melanocephalum* in KwaZulu-Natal. *African Journal of Herpetology* 58: 85–97. <https://doi.org/10.1080/21564574.2009.9650028>
- Baek HJ, Lee J, Lee HS, Hyun YK, Cho C, Kwon WT, Marzin C, Gan S-Y, Kim M-J, Choi D-H, et al. 2013. Climate change in the 21st century simulated by HadGEM2-AO under representative concentration pathways. *Asia-Pacific Journal of Atmospheric Sciences* 49: 603–618. <https://doi.org/10.1007/s13143-013-0053-7>
- Biggs R, Simons H, Bakkenes M, Scholes RJ, Eickhout B, van Vuuren D, Alkemade R. 2008. Scenarios of biodiversity loss in southern Africa in the 21st century. *Global Environmental Change* 18: 296–309. <https://doi.org/10.1016/j.gloenvcha.2008.02.001>
- Botts EA, Erasmus BFN, Alexander GJ. 2015. Observed range dynamics of South African amphibians under conditions of global change. *Austral Ecology* 40: 309–317. <https://doi.org/10.1111/aec.12215>
- Cox N, Young BE, Bowles P, Fernandez M, Marin J, Rapacciuolo G, Böhm M, Brooks TM, Hedges SB, Hilton-Taylor C, et al. 2022. A global reptile assessment highlights shared

- conservation needs of tetrapods. *Nature* 605: 285–290. <https://doi.org/10.1038/s41586-022-04664-7>
- da Silva JM, Herrel A, Measey GJ, Vanhooydonck B, Tolley KA. 2014. Linking microhabitat structure, morphology and locomotor performance traits in a recent radiation of dwarf chameleons. *Functional Ecology* 28: 702–713. <https://doi.org/10.1111/1365-2435.12210>
- da Silva JM, Tolley KA. 2013. Ecomorphological variation and sexual dimorphism in a recent radiation of dwarf chameleons (*Bradypodion*). *Biological Journal of the Linnean Society* 109: 113–130. <https://doi.org/10.1111/bij.12045>
- Danielson JJ, Gesch DB. 2011. Global multi-resolution terrain elevation data 2010 (GMTED2010): US Geological Survey Open-File Report 2011–1073, 26 p. <https://doi.org/10.3133/ofr20111073>
- Department of Environmental Affairs (DEA). 2013. Long-Term Adaptation Scenarios Flagship Research Programme (LTAS) for South Africa. Pretoria, South Africa.
- Engelbrecht F, Adegoke J, Bopape MJ, Naidoo M, Garland R, Thatcher M, et al. 2015. Projections of rapidly rising surface temperatures over Africa under low mitigation. *Environmental Research Letters* 10: 85004. <https://doi.org/10.1088/1748-9326/10/8/085004>
- Ezemvelo KZN Wildlife (EKZNW). 2011. KwaZulu-Natal land cover 2005 v3.1 (clp_KZN_2005_LC_v3_1_grid_w31.zip) [GIS coverage]. Pietermaritzburg: Biodiversity Conservation Planning Division, Ezemvelo KZN Wildlife.
- Ezemvelo KZN Wildlife (EKZNW). 2013. KwaZulu-Natal land cover 2011 v1 (clp_KZN_2011_LC_v1_grid_w31.zip) [GIS coverage]. Pietermaritzburg: Biodiversity Research and Assessment, Ezemvelo KZN Wildlife.
- Ezemvelo KZN Wildlife (EKZNW). 2015. Ezemvelo KZN Wildlife Proclaimed Protected Area boundary (2015). Unpublished GIS Coverage [ekznw_pabnd_2015_wdd.zip], Pietermaritzburg: Biodiversity Conservation Planning Division, Ezemvelo KZN Wildlife.
- GeoTerralimage. 2010. 2008 KZN Province land-cover mapping (from SPOT5 satellite imagery circa 2008): Data users report and metadata (version 1). Pietermaritzburg: Ezemvelo KZN Wildlife.
- Gouveia SF, Souza-Alves JP, Rattis L, Dobrovolski R, Jerusalinsky L, Beltrão-Mendes R, Ferrari SF. 2016. Climate and land use changes will degrade the configuration of the landscape for titi monkeys in eastern Brazil. *Global Change Biology* 22: 2003–2012. <https://doi.org/10.1111/gcb.13162>
- Government Gazette for the Republic of South Africa. 1992. Management of State Forests Act. Act No. 128. Government Gazette 10 July 1992, No. 14132. https://www.gov.za/sites/default/files/gcis_document/201409/act128of1992.pdf (accessed 2 April 2024).
- Guisan A, Thuiller W. 2005. Predicting species distribution: offering more than simple habitat models. *Ecology Letters* 8: 993–1009. <https://doi.org/10.1111/j.1461-0248.2005.00792.x>
- Herrmann SM, Brandt M, Rasmussen K, Fensholt R. 2020. Accelerating land cover change in West Africa over four decades as population pressure increased. *Communications Earth & Environment* 1: 53. <https://doi.org/10.1038/s43247-020-00053-y>
- Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A. 2005. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* 25: 1965–1978. <https://doi.org/10.1002/joc.1276>
- Hockey PAR, Sirami C, Ridley AR, Midgley GF, Babiker HA. 2011. Interrogating recent range changes in South African birds: confounding signals from land use and climate change present a challenge for attribution. *Diversity and Distributions* 17: 254–261. <https://doi.org/10.1111/j.1472-4642.2010.00741.x>
- Hopkins KP, Tolley KA. 2011. Morphological variation in the Cape Dwarf Chameleon (*Bradypodion pumilum*) as a consequence of spatially explicit habitat structure differences. *Biological Journal of the Linnean Society* 102: 878–888. <https://doi.org/10.1111/j.1095-8312.2011.01618.x>
- Jenkins C, Pimm S, Joppa L. 2013. Global patterns of terrestrial vertebrate diversity and conservation. *Proceedings of the National Academy of Sciences of the USA* 110: E2602–E2610. <https://doi.org/10.1073/pnas.1302251110>
- Jewitt D, Goodman PS, Erasmus BFN, O'Connor TG, Witkowski ETF. 2015. Systematic land-cover change in KwaZulu-Natal, South Africa: Implications for biodiversity. *South African Journal of Science* 111: 9. <https://doi.org/10.17159/sajs.2015/20150019>
- Jiménez-Valverde A, Peterson AT, Soberon J, Overton J, Aragon P, Lobo JM. 2011. Use of niche models in invasive species risk assessments. *Biological Invasions* 13: 2785–2797. <https://doi.org/10.1007/s10530-011-9963-4>
- Measey GJ, Rödder D, Green SL, Kobayashi RK, Lillo F, Lobos G, et al. 2012. Ongoing invasions of the African Clawed Frog, *Xenopus laevis*: A global review. *Biological Invasions* 14: 2255–2270. <https://doi.org/10.1007/s10530-012-0227-8>
- Mittermeier RA, Robles GP, Mittermeier CJ. 1997. Megadiversity: earth's biologically wealthiest nations. México: CEMEX.
- Myers N, Mittermeier RA, Mittermeier CG, Da Fonseca GAB, Kent J. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403: 853–858. <https://doi.org/10.1038/35002501>
- Naidu S, Hounsborne R, Iyer K. 2006. Climatic Future for Durban: Revised Report. Durban: CSIR Environmentek and eThekweni Municipality.
- Newbold T. 2018. Future effects of climate and land-use change on terrestrial vertebrate community diversity under different scenarios. *Proceedings of the Royal Society, Series B* 285: 20180792. <https://doi.org/10.1098/rspb.2018.0792>
- Oliver TH, Morecroft MD. 2014. Interactions between climate change and land use change on biodiversity: Attribution problems, risks, and opportunities. *Wiley Interdisciplinary Reviews: Climate Change* 5: 317–335. <https://doi.org/10.1002/wcc.271>
- Parmesan C, Yohe G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421: 37–42. <https://doi.org/10.1038/nature01286>
- Petford MA, Alexander GJ. 2021. Potential range shifts and climatic refugia of rupicolous reptiles in a biodiversity hotspot of South Africa. *Environmental Conservation* 48: 264–273. <https://doi.org/10.1017/S0376892921000370>
- Phillips SJ, Anderson RP, Schapire RE. 2006. Maximum entropy modelling of species geographic distributions. *Ecological Modelling* 190: 231–259. <https://doi.org/10.1016/j.ecolmodel.2005.03.026>
- Phillips SJ, Dudik M, Elith J, Graham CH, Lehmann A, Leathwick J, Ferrier S. 2009. Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. *Ecological Applications* 19: 181–197. <https://doi.org/10.1890/07-2153.1>
- Raimondo D, Young BE, Brooks T, Cardoso P, Van Der Colff D, Dias B, et al. 2023. Using Red List Indices to monitor extinction risk at national scales. *Conservation Science and Practice* 5: e12854. <https://doi.org/10.1111/csp2.12854>
- Rebelo AD, Altwegg R, Katz EM, Tolley KA. 2022. Out on a limb: female chameleons (*Bradypodion pumilum*) position themselves to minimise detection, whereas males maximise mating opportunity. *African Journal of Herpetology* 71: 39–50. <https://doi.org/10.1080/21564574.2021.1998233>
- Rebelo AD, Bates MF, Burger M, Branch WR, Conradie W. 2019. Range expansion of the Common Dwarf Gecko, *Lygodactylus capensis*: South Africa's most successful reptile invader. *Herpetological Notes* 12: 643–650.
- Sala OE, Stuart Chapin F, Iii, Armesto JJ, Berlow E, Bloomfield J, Dirzo R, Huber-Sanwald E, Huenneke LF, Jackson RB, et al. 2000. Global biodiversity scenarios for the year 2100. *Science* 287: 1770–1774. <https://doi.org/10.1126/science.287.5459.1770>

- Searcy CA, Shaffer HB. 2014. Field validation supports novel niche modeling strategies in a cryptic endangered amphibian. *Ecography* 37: 983–992. <https://doi.org/10.1111/ecog.00733>
- Sinervo B, Méndez-de-la-Cruz F, Miles DB, Heulin B, Bastiaans E, Villagrán-Santa Cruz M, Lara-Resendiz R, Martínez-Méndez N, Calderón-Espinosa ML, Meza-Lázaro RN, et al. 2010. Erosion of lizard diversity by climate change and altered thermal niches. *Science* 328: 894–899. <https://doi.org/10.1126/science.1184695>
- Skowno A, Poole CJ, Raimondo D, Sink KJ, Van Deventer H, Van Niekerk L, et al. 2019. National Biodiversity Assessment 2018: The status of South Africa's ecosystems and biodiversity. Synthesis Report. Pretoria: South African National Biodiversity Institute, an entity of the Department of Environment, Forestry and Fisheries. pp. 1–214.
- Skowno A L, Jewitt D, Slingsby JA. 2021. Rates and patterns of habitat loss across South Africa's vegetation biomes. *South African Journal of Science* 117: 1–5. <https://doi.org/10.17159/sajs.2021/8182>
- Statistics South Africa (SSA). 2016. Provincial Profile: KwaZulu-Natal Community Survey 2016. Retrieved from http://www.statssa.gov.za/?page_id=964
- Swets KA. 1988. Measuring the accuracy of diagnostic systems. *Science* 240: 1285–1293. <https://doi.org/10.1126/science.3287615>
- Tolley KA. 2022a. *Bradypodion thamnobates*. The IUCN Red List of Threatened Species 2022: e.T3017A197397461. <https://dx.doi.org/10.2305/IUCN.UK.2022-1.RLTS.T3017A197397461.en>. (accessed 8 December 2023).
- Tolley KA. 2022b. *Bradypodion nemorale*. The IUCN Red List of Threatened Species 2022: e.T3009A197397165. <https://doi.org/10.2305/IUCN.UK.2022-1.RLTS.T3009A197397165.en>. (accessed 20 December 2023).
- Tolley KA. 2022c. *Bradypodion ngomeense*. The IUCN Red List of Threatened Species 2022: e.T42683297A197416110. <https://doi.org/10.2305/IUCN.UK.2022-1.RLTS.T42683297A197416110.en>. (accessed 20 December 2023).
- Tolley KA. 2022d. *Bradypodion dracomontanum*. The IUCN Red List of Threatened Species 2022: e.T176291A197407014. <https://doi.org/10.2305/IUCN.UK.2022-1.RLTS.T176291A197407014.en>. (accessed 20 December 2023).
- Tolley KA, Alexander GJ, Branch WR, Bowles P, Maritz B. 2016. Conservation status and threats for African reptiles. *Biological Conservation* 204: 63–71. <https://doi.org/10.1016/j.biocon.2016.04.006>
- Tolley KA, Burger M. 2007. Chameleons of Southern Africa. Cape Town: Struik.
- Tolley KA, Chase B, Forest F. 2008. Speciation and radiations track climate transitions since the Miocene Climatic Optimum: a case study of southern African chameleons. *Journal of Biogeography* 35: 1402–1414. <https://doi.org/10.1111/j.1365-2699.2008.01889.x>
- Tolley KA, Conradie W, Pietersen DW, Weeber J, Burger M, Alexander GJ. 2023. Conservation status of the reptiles of South Africa, Eswatini and Lesotho. Suricata 10. Pretoria: South African National Biodiversity Institute.
- Tolley KA, Weeber J, Maritz B, Verburgt L, Bates MF, Conradie W, Hofmeyr MD, Turner AA, da Silva JM, Alexander GJ. 2019. No safe haven: Protection levels show imperilled South African reptiles not sufficiently safe-guarded despite low average extinction risk. *Biological Conservation* 233: 61–72. <https://doi.org/10.1016/j.biocon.2019.02.006>
- Travis MJJ. 2003. Climate change and habitat destruction: a deadly anthropogenic cocktail. *Proceedings of the Royal Society of London, Series B* 270: 467–473. <https://doi.org/10.1098/rspb.2002.2246>
- United Nations Department of Economic and Social Affairs, Population Division. 2022. World Population Prospects 2022: Summary of Results. UN DESA/POP/2022/TR/NO. 3.
- Van Der Wal J, Shoo LP, Graham C, William SE. 2009. Selecting pseudo-absence data for presence-only distribution modeling: how far should you stray from what you know? *Ecological Modelling* 220: 589–594. <https://doi.org/10.1016/j.ecolmodel.2008.11.010>
- van Proosdij ASJ, Sosef MSM, Wieringa JJ, Raes N. 2016. Minimum required number of specimen records to develop accurate species distribution models. *Ecography* 39: 542–552. <https://doi.org/10.1111/ecog.01509>
- Van Vuuren DP, Edmonds J, Kainuma M, Riahi K, Thomson A, Hibbard K, Hurtt GC, Kram T, Krey V, Lamarque J-F, et al. 2011. The representative concentration pathways: an overview. *Climatic Change* 109: 5–31. <https://doi.org/10.1007/s10584-011-0148-z>
- Warren R, VanDerWal J, Price J, Welbergen JA, Atkinson I, Ramirez-Villegas J, Osborn TJ, Jarvis A, Shoo LP, Williams SE, et al. 2013. Quantifying the benefit of early climate change mitigation in avoiding biodiversity loss. *Nature Climate Change* 3: 678–682. <https://doi.org/10.1038/nclimate1887>
- Ziervogel G, New M, Archer van Garderen E, Midgley G, Taylor A, Hamann R, Stuart-Hill S, Myers J, Warburton M. 2014. *Wiley Interdisciplinary Reviews: Climate Change* 5: 605–620. <https://doi.org/10.1002/wcc.295>