Responses of Dwarf Chameleons to Global Change Drivers

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Declaration,

I, Tyron Clark declare that this dissertation and the information contained herein is the product of my own, unaided work unless otherwise acknowledged in text and accompanied by a citation. This dissertation is being submitted for the degree of Master of Science at the University of the Witwatersrand, Johannesburg on this the 15th day of March, 2019. It has not been previously submitted for any other degree or examination at any other institution of higher learning.

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Dedication

This dissertation is dedicated to my wife and life partner Cheri Clark, whose selfless and unwavering devotion made it all possible.

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Abstract

Habitat loss, driven by climate and land use change, poses one of the greatest threats to biodiversity worldwide. Together these global change drivers are expected to act not only additively but synergistically in their impacts on biodiversity. Despite this, few studies address both aspects simultaneously. Nowhere are these threats more pertinent than in areas of high species richness and endemicity where there are high levels of anthropogenic pressure. The dwarf chameleons (*Bradypodion*) of KwaZulu-Natal Province, South Africa (KZN), provide one such case. The province is rapidly developing and is subject to high rates of habitat loss, a threat which is likely to be exacerbated by climate change in the future. Such rapid rates of change are expected to challenge the persistence of the province's rich dwarf chameleon assemblage in the near future. Anticipating the responses of dwarf chameleons to these global change drivers and identifying traits which may infer higher vulnerability is critical to their effective protection especially as pressure mounts on conservationists to prioritise efforts and resources more discerningly. Recent advances in niche modelling techniques, global climatic change data and the production of a time series set of high resolution, directly comparable satellite derived land cover layers for KZN provided an opportunity to explore the potential effects of these global change drivers on this imperilled group of reptiles. Current ecological niche models (ENMs) were constructed for all nine *Bradypodion* species in KZN using a combination of fine-scale, bioclimatic variables and these land-cover datasets. These ENMs were then projected under scenarios of future climate (under five global circulation models for two atmospheric greenhouse gas concentrations) and land use change (using a simple yet intuitive habitat transformation rule based on published trends for the province). The findings suggest that KZN dwarf chameleon species are likely to respond individualistically to the effects of climate and land use change. Under an assumption of unlimited dispersal ability, a distinction can be made in the modelled responses of KZN dwarf chameleons to future climate change. Specifically, between inland species, whose responses are marked by contractions in climatically suitable natural habitat (CSNH), and more coastal species characterised by a maintenance or expansion in their extent of future CSNH. It was subsequently found that these groups and the gradient of susceptibility contained within them was better explained by niche preference and the future availability of a specific set of climatic conditions (variables) typically associated with a species' occurrence than it was by range size or niche breadth. However, under more restrictive (and perhaps more realistic) assumptions incorporating dispersal ability showed

notable contractions regardless of climatic resilience. Particularly concerning in this regard, is that most of the study species showed a reduction in the extent of CSNH predicted to coincide with the provinces protected area network in future. At present, the conservation status of KZN’s dwarf chameleons does not adequately reflect their anticipated susceptibility to these change drivers nor the extent of CSNH that is predicted to remain under statutory protection. These findings highlight the importance of upholding and pre-emptively expanding the provinces protected areas network to keep pace with the impending changes.

Chapter 1: Introduction and Literature Review

In a rapidly changing world, where conservationists struggle to keep pace with the unprecedented rates of habitat loss and species extinctions, prioritisation of conservation efforts is of utmost importance. What follows is an investigation of the potential responses of a group of dwarf chameleons to the pressing threats of climate and land use change in the rapidly transforming province of KwaZulu-Natal (KZN), South Africa.

Climate change as driver of biodiversity loss

The effects of climate change have received considerable attention lately, resulting in the publication of several seminal reviews (Araújo and Rahbek, 2006; Parmesan. 2006; Willis and Bhagwat, 2009; Bellard *et al*., 2012). The overwhelming consensus is that rising global surface temperatures have already had significant effects on the life cycles, distributions and community/population structures of a wide range of biota (Oliver and Morecroft, 2014). Consequently, climate change is considered to be one of the most serious and widespread threats to biodiversity, second only to habitat loss (IPCC, 2007; Leadley *et al*., 2010). In Africa, near surface temperatures have increased by more than 0.5 °C in the last 50 to 100 years. Southern Africa is no exception, having experienced much of this change within the last two decades (Niang *et al*. 2014). Observed changes in precipitation, however, have been less uniform across Africa with trends showing decreases in areas to the north and west of the continent and increases in the south and east. In southern Africa, an overall decrease in late summer precipitation in western South Africa and neighbouring countries has been observed and appears to be associated with increased Indian Ocean sea surface temperatures. Mean annual temperatures in South Africa are rising fast, having increased by more than 1.5 times the global average of 0.65 ºC over the past five decades (Niang *et al*., 2014; Ziervogel *et al*., 2014). Of concern is that this trend is set to continue, varying in intensity depending on the predicted trajectory of atmospheric CO_2 concentrations. Under optimistic trajectories, temperatures in South Africa are expected to rise by as much as 1-1.5 ºC on the coast and 3 ºC inland, while a more pessimistic outlook predicts rises of 2.3 ºC and 4.6 ºC respectively by the year 2100 (DEA, 2013; Ziervogel *et al*., 2014). Already there have been changes in the onset, duration and intensity of rainfall across southern Africa (Niang *et al*., 2014) and it is expected that climate change in the near future is going to intensify, accompanied not only by an increased frequency of extreme climatic events such as cyclones, droughts, floods and heat waves (Dash, 2011) but also by significant changes to everyday weather patterns such as diurnal temperature ranges, cloud cover and precipitation (Zhou *et al*., 2009). Such changes would undoubtedly challenge the persistence of many species.

Certainly, climate change is not a new phenomenon, neither to science nor biodiversity (Parmesan, 2006). In fact, it has long been suspected to be a primary driver of the speciation and extinction events that have shaped distribution and diversity of biota that we see today. A growing body of evidence supports this view, widely implicating the cyclic fragmentation and merging of distinct vegetation types as a result of paleoclimatic fluctuations as a primary cause of heightened biodiversity in certain parts of the world (Svenning *et al*., 2015). This pattern appears to hold true for chameleons, providing an explanation for their current distribution and extraordinary diversification in certain regions of the world (Tolley *et al*., 2006; 2008; 2011; Measey and Tolley, 2011). Climatic changes such as these, however, have occurred slowly, over an evolutionary time scale and any trends in extinction patterns drawn from such ancient evidence need to be interpreted in light of the unprecedented rates of current climate change if they are to usefully inform conservation strategies aimed at safeguarding species persistence (Brook *et al*. 2008; Oliver and Morecroft, 2014; Riordan and Rundel, 2014). Usually, species responses that allow for persistence in the face of climate change involve combinations of range changes, surviving in climatic refugia or developing a greater tolerance to climatic perturbations (Dawson *et al*., 2011).

The extent, intensity and direction of range change in response to changing climate varies greatly among taxa. Range contractions appear to be hardest felt by habitat specialists with low dispersal abilities and narrow physiological tolerance ranges that occupy temperate and mountainous regions of the world (Pounds *et al*., 1999, Raxworthy *et al*., 2008; Foden *et al*. 2013). In modern times, many species have undergone severe range contractions and even extinctions as a result of climate change (Parmesan, 2006). Most commonly, range contractions occur polewards and upslope along temperature and precipitation gradients (Parmesan *et al*., 1999; Parmesan and Yohe, 2003). Persistence in climatic refugia is particularly well represented by some forest chameleons which show a high degree of fidelity to their respective forests (Measey and Tolley, 2011). Studies from southern Africa provide evidence to suggest that relict patches of ancient Afrotemperate and mistbelt forest have provided climatically stable refugia for chameleons in contrast to more climatically volatile coastal forests (da Silva and Tolley, 2017).

Given that the current distribution and diversity of dwarf chameleons is largely a product of their evolutionary response to paleo-climatic induced habitat changes (Tolley *et al*. 2008), it is likely that climatic perturbations in the future will result in significant range changes. Indeed, the extent of climatically suitable habitat, at least for some South African dwarf chameleons, has been shown to vary considerably between species, with most predicated to show range contractions (Houniet *et al*., 2009). Ultimately, the effects of climate change on dwarf chameleons will be dependent on their ability to track changes in the distribution of suitable habitat, highlighting the importance of considering land use.

Land use change as a driver of biodiversity loss

Worldwide, extinctions at the hands of anthropogenic land use change are occurring at an alarming rate, with estimates in the order of one species for every thousand per decade (Pimm *et al*., 1995; Pimm and Raven 2000). The principal driving force behind this land conversion is the exploitation of earth's natural resources to meet the demands of a rapidly growing human population. The extent and intensity of land use change is not distributed evenly across the world. At present, land transformation is highest in the tropics and in developing countries, particularly in warmer areas with variable precipitation trends (Mantyka-Pringle *et al*., 2012). In more established countries land cover class conversion most typically involves from agriculture or arable land to infrastructure or rehabilitated natural land (Oliver and Morecroft, 2014).

Current estimates suggest that more than 50% of the earth's total ice-free land area has been directly modified by humans (Hooke *et al*., 2012). Global conservation area targets are failing to keep pace with the rate of transformation, indeed estimates suggest that as much as 3.3 million km^2 (or approximately 9.6%) of the world's remaining wilderness areas have been lost in the last two decades (Watson *et al*., 2016). With the human population having more than doubled in the past 40 years, and a similar increase expected in the next 40 years (Hooke *et al*., 2012), land use change currently is, and is likely to continue to be, the most significant cause of species extinctions (Vitousek 1992; Pimm and Raven, 2000; Vié *et al*., 2009). However, studies addressing the significant and potentially more immediate threats of land use change are scarce and underemphasised. One of the main reasons cited for this paucity of work on land use change is that unlike climate for which global-scale, high resolution and spatially explicit future change scenarios exist, a number of limitations hamper the production of comparable layers for future land use change (Riordan and Rundel, 2014).

Habitat loss as a result of anthropogenic land use has been identified as the most pervasive threat to conservation important reptiles in South Africa, Lesotho and Swaziland (Branch, 2014; Tolley *et al*., 2019), a trend that is reflected in the findings of conservation assessments for other vertebrate groups within this region (Friedman and Daly, 2004; Minter *et al*., 2004; Taylor *et al*., 2015). Bates *et al.*, (2014) cite agricultural (particularly afforestation) and infrastructural (particularly urban) development together with the cumulative effects of increased fragmentation, prevalence of soil aridity, fire and alien vegetation as affecting the highest number of conservation-important reptile taxa in coastal regions. This observation is largely in agreement with the findings of a study by Jewitt *et al.*, (2015b) that investigated systematic land use changes in KwaZulu-Natal Province, South Africa (KZN). The study highlights the province's exceptionally high rate of land transformation implicating agriculture as by far the most dominant driver of this change followed by the infrastructure and plantations.

Like climate change, land transformation has been widely implicated in causing species range changes that manifest in contractions, expansions or shifts. Typically, species with low dispersal abilities, restricted ranges and specialised niches that occupy fragmented landscapes that are subject to rapid rates of land transformation are most susceptible (Donald and Fuller, 1998; Sih *et al*., 2000; Warren *et al*., 2001; Parmesan and Yohe, 2003). A study by Myers *et al*. (2000) showed that species such as these are numerous and are concentrated in distinct regions of the world known as biodiversity hotspots which, together, account for as much 30-50% of the planet's vertebrate and plant species in less than 2% of its ice-free land area. Many of the species supported by these hotspots are of conservation concern due to the disproportionally high rates of land transformation within these areas (Myers *et al*., 2000). The biodiverse province of KZN falls within one such hotspot and is indeed subject to high rates of habitat transformation (Jewitt *et al*., 2015b).

Habitat loss, degradation and fragmentation affects many species through restricted gene flow, genetic bottlenecks and the typically non-linear relationship between habitat area and population size (Opdam and Wascher, 2004). Such effects are particularly pertinent for chameleons. A study by Shirk *et al*. (2014), for example, showed that habitat loss and fragmentation have greatly reduced the population sizes of at least three forest-dwelling chameleon species in the East Usambara Mountains of Tanzania. Indeed, habitat loss, degradation and fragmentation are among the most frequently cited and immediately significant threats to most of dwarf chameleons in KZN (Tolley, 2014) and warrant further investigation particularly in light of predicted climate change.

Status of dwarf chameleons in a rapidly changing landscape

Nowhere are the threats of land use and climate change more pressing than in areas of high species richness and endemicity facing correspondingly high levels of human pressure (Myers *et al*., 2000). A case in point are the dwarf chameleons (*Bradypodion*) of KZN, a tropical to sub-tropical province on South Africa’s eastern coast. Characterised by a deeply incised landscape, the province spans an altitudinal range of more than 3 000 m from the warm, humid coastal plains in the east to the cool, montane heaths of the Drakensburg escarpment in the west (DAEA & RD, 2010). The province is climatologically, geologically and floristically complex, supporting a rich and unique biodiversity accounting for as much as ca. 40% and 60% of the South Africa’s reptile and amphibian species respectively (adapted from data in Minter *et al*., 2004; Bates, *et al*., 2014; ADU, 2016). This represents a significant proportion considering that the province occupies less than 8% of the country by area. Indeed, KZN not only includes the Midlands, Maputaland, Pondoland and Drakensberg Alpine centres of endemism (Mucina and Rutherford, 2006), but also forms part of the Maputaland-Pondoland-Albany biodiversity hotspot (MPA) the second-most floristically diverse region in the subcontinent after the Cape Floristic Region (Cowling *et al*., 1997) and one of the top 32 most biodiverse regions globally (CEPF, 2010).

KwaZulu-Natal supports 10 chameleon species, more than any other province in South Africa (Tolley *et al*., 2008; Tolley and Burger, 2007). The majority are dwarf chameleons (seven described and two undescribed species) a group of small (45-150 mm total length), viviparous lizards that are endemic to southern Africa (Tolley and Burger, 2007; Tolley, 2014). Of these, seven species namely *Bradypodion caeruleogula*, *B. melanocephalum B. nemorale*, *B. ngomeense, B. thamnobates, B.* sp. 7 and *B.* sp. 8 (sensu, Tolley *et al*. 2008), are endemic to KZN while *B. dracomontanum* and *B. setaroi* extend marginally out of the province.

With one of highest human population densities in the country (SSA, 2016) KZN is facing exceptionally high rates of land transformation (1.2% per annum) such that more than 20% of its natural habitat has been lost since 1994 leaving less than 54% of the total land area in a natural state (Jewitt *et al*., 2015b). Of particular concern in this regard is that many of the province's dwarf chameleon species occupy particularly small ranges from 8957 km^2 (*B. melanocephalum*) for the most "widespread" species to as little as 26 km^2 (*B. ngomeense*) for the most restricted (Tolley *et al*., 2019). Consequently, all but one (*B. setaroi*) of the province's currently-described dwarf chameleons are of global conservation concern (*i.e*. an IUCN Red List status above Least Concern). These include two Endangered (*B. caeruleogula* and *B. thamnobates*) and four Near Threatened species (*B. dracomontanum*, *B. melanocephalum*, *B. nemorale* and *B. ngomeense*) species (Tolley *et al*., 2019). Although the conservation status of *B*. sp. 7 and *B*. sp. 8 are yet to be assessed it is worth noting that the current know range of *B*. sp. 7 is smaller than that of even *B. ngomeense* and the species may also warrant urgent conservation attention. By far the most pervasive threat to these species is the loss, degradation and fragmentation of suitable habitat as a result of the conversion of natural land through agriculture, rural and, particularly along the coast, urban/industrial sprawl, afforestation and alien and invasive vegetation (Armstrong, 2009; Tolley *et al*., 2019).

Land use and climate change in KZN are expected to act not only additively but synergistically, challenging the persistence of the province's rich dwarf chameleon assemblage in response to unparalleled rates of climate and land use change in the near future. Understanding interactions between these global change drivers is critical to effectively directing conservation efforts yet relatively few studies attempt to address both aspects simultaneously.

Aims and hypotheses

The objective of this study was to estimate the extent of climatically suitable natural habitat (CSNH) available to all nine of KZNs dwarf chameleons, both at present and in future (2050). This information was then used to address overall aims which were to investigate the susceptibility of each species to climate and land use change (Chapter 2) and identify the traits which may infer any observed vulnerabilities (Chapter 3). In Chapter 2 it is hypothesised that dwarf chameleons will respond individualistically to the change drivers and that inland species would be more adversely affected than ones closer to the coast. In Chapter 3, it is hypothesised that the direction of the response of a species is largely contingent on its climatic niche preference and its alignment with a set of key variables likely to become limiting under the forecasted conditions.

Chapter 2: The Susceptibility of Dwarf Chameleons to Climate and Land Use Change in KwaZulu-Natal, South Africa

Abstract

Biodiversity is being degraded at unprecedented rates due to human-induced climate and land use change, a situation which is set to accelerate in future. In particular, reptiles are predicted to experience some of the highest levels of species extinction in response to these changes. These impacts are most significant in areas of high species richness and endemicity where there is also high levels of anthropogenic pressure. Rapid rates of habitat transformation in KwaZulu-Natal Province, South Africa, and climate change threaten the persistence of its largely endemic dwarf chameleon assemblage. At present nine species are known to occur in the province and, of the seven which have been described, all but one have an IUCN Red List status above Least Concern. Here, I made use of recent advances in niche modelling techniques, the latest climatic change data and detailed, province-specific land cover data and published estimates on the rates of natural habitat loss to assess the vulnerability of these chameleons to the combined effects of climate and land use change. I hypothesised that KZN dwarf chameleons are likely to respond individualistically to these change drivers. The findings support this hypothesis revealing that inland species are more likely to be adversely affected than those that occur closer to the coast. The models also reveal that although a gain in climatically suitable natural habitat (CSNH) is predicted for three of the species, considerable losses are predicted for the others. Although species situated closer to the coast are more climatically resilient, none of the species appear immune to the combined effects of climate and habitat change when these impacts are considered in tandem. Of particular concern is not only the small proportion of CSNH that overlaps the protected areas network for three of the species at present, but the considerable loss of CSNH under protection for most species in future. These findings highlight the importance of maintaining and pre-emptively expanding the provinces protected areas network, a step ahead of these anticipated changes.

Introduction

Climate and land use change are among the most significant threats to global biodiversity, greatly impacting the distribution of many 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). In combination, they have the potential to be particularly disastrous depending on the taxa and locations concerned (Travis, 2003). Recent estimates suggest that over a third world's terrestrial vertebrates may be lost as a result of their cumulative effects by 2070 (Newbold, 2018). In particular, reptiles and amphibians are predicted to experience the greatest decreases in species richness in response to these changes (Newbold, 2018; Warren *et al*., 2013). Nowhere are these threats more pressing than in areas of high species richness and endemicity facing correspondingly high levels of human pressure (Myers *et al*., 2000).

One such area is KwaZulu-Natal Province, South Africa (KZN), a tropical to sub-tropical region on South Africa's eastern margin. The province supports a rich and unique biodiversity accounting for as much as 40% and 60% of the South Africa's reptile and amphibian species respectively, many of which are endemic (adapted from Minter *et al*., 2004; Bates, *et al*., 2014; ADU, 2016). This is significant considering that the province makes up less than 8% of South Africa by area. Such high levels of species richness and endemism are attributed to the province's high degree of topographical, climatic, edaphic and floral heterogeneity (Minter *et al*., 2004; Bourquin, 2004). Not only does it include the Midlands, Maputaland, Pondoland and Drakensberg Alpine centres of endemism (Mucina and Rutherford, 2006), it also forms part of the Maputaland-Pondoland Albany (MPA) hotspot (Cowling *et al*., 1997). Of all the vertebrate groups within the MPA, reptiles have the highest levels of endemism with 14.3% (Perera *et al*., 2011). However, with one of highest human population densities in the country (SSA, 2016), KZN is facing exceptionally high rates of land transformation at 1.2% per annum (Jewitt *et al*., 2015b). Currently, less than 54% of the total land area remains in a natural state and this expected to decrease to 45% by 2050 (Jewitt *et al*., 2015b).

Of particular conservation concern within the province are dwarf chameleons (*Bradypodion*), a group of small (< 150 mm total length), viviparous, South African endemic lizards. *Bradypodion* is the most diverse endemic reptile genus in KZN (Perera *et al*., 2011; Tolley and Burger; 2007; Tolley, 2014). Currently, KZN supports at least nine species (seven described and two undescribed), the most of all the provinces in South Africa (Tolley *et al*., 2008; Tolley and Burger, 2007; ADU, 2016). Of these, eight species namely *Bradypodion caeruleogula*, *B. melanocephalum*, *B. nemorale*, *B. ngomeense*, *B. thamnobates* and including the two undescribed species *B*. sp. 7 and *B*. sp. 8, are considered endemic to KZN while only, *B. dracomontanum* and *B. setaroi*, extend marginally out of the province into the Free State

Province and Mozambique respectively. None of these chameleons can be considered wide ranging with estimated range sizes (for the described species) varying from 8957 km^2 (*B. melanocephalum*) for the most "widespread" species to as little as 26 km^2 (*B. ngomeense*) for the most restricted (Tolley *et al*., 2019). Consequently, all but one of the province's currently-described dwarf chameleon species (*B. setario*) are of global conservation concern (i.e. an IUCN red listed status above Least Concern). These include two Endangered (*B. caeruleogula and B. thamnobates*), and four Near Threatened (*B. dracomontanum*, *B. melanocephalum*, *B. nemorale* and *B. ngomeense*) species (Tolley *et al*., 2019).

Common to all these species is the widespread and rapid degradation and fragmentation of suitable habitat as a result of the conversion of natural land through agriculture, urban and industrial sprawl, afforestation and alien vegetation infestation (Armstrong, 2009; Tolley, 2014). These pressures are likely to be compounded by climate change with mean annual temperatures in South Africa rising at more than 1.5 times the global average of 0.65 ºC over the past five decades (Niang *et al*., 2014; Ziervogel *et al*., 2014). Of particular concern is that this trend appears set to continue, varying in intensity depending on the predicted trajectory of atmospheric CO_2 concentrations. Under optimistic trajectories, temperatures in South Africa are expected to rise by as much as 1-1.5 ºC on the coast and 3 ºC inland, while a more pessimistic outlook predicts rises of 2.3 ºC and 4.6 ºC respectively by the year 2100 (DEA, 2013; Ziervogel *et al*., 2014).

The province's rich dwarf chameleon assemblage is thought to have been impacted to a large degree by their differing evolutionary responses to changes in vegetation driven by past climatic fluctuations (Tolley *et al*., 2006; 2008). However the rapid rates of land use and climate change in KZN are likely to challenge the persistence of the province's rich dwarf chameleon assemblage in the near future. Understanding interactions between these global change drivers is critical to effectively directing conservation efforts.

In this study, I made use of recent advances in niche modelling techniques, the latest climatic change data and detailed, province-specific land cover data and published estimates on the rates of natural habitat loss to assess the vulnerability of KZN dwarf chameleons to these major global change drivers. I hypothesised that KZN dwarf chameleons are likely to respond individualistically to these change drivers with some showing contractions and others expansions in their extent of in climatically suitable natural habitat. More specifically, I predicted that inland species which occupy cooler and more seasonal climates, particularly those whose distributions are centred in agricultural and communal areas, are most likely be adversely affected than those nearer the coast.

Methods

Locality data and layers

Point locality data were sourced from four databases including the South African Reptile Conservation Assessment SARCA and ReptileMap (http://vmus.adu.org.za), the Herpetological DNA bank at the South African National Biodiversity Institute and iSpot (Open University, https://www.ispotnature.org/). Together these databases represent an extensive collection of museum records, private and vetted citizen science contributions. In total, 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 includes 19 bioclimatic (Bioclim) variables at 30 arc-second resolution derived from 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) USGS digital elevation model (DEM) data (Danielson and Gesch, 2010) using ArcMap^{tm} 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; GeoTerraImage, 2013).

Modelling of current range

Sourced locality data were displayed in ArcGIS 10.2.2 and vetted to allow for the removal of any questionable outliers, potential misidentifications or obvious georeferencing errors. As presence-only algorithms such as Maxent rely on the generation of a set of artificial absence points or pseudo-absences for model building, 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 (Van Der Wal *et al*., 2009; Phillips *et al*., 2009). Ideally the degree of bias inherent in the presence data, arising from the ease of sampling in certain areas e.g. near roads, towns and reserves, should be reflected in the pseudo-absence data (Phillips *et al*., 2009). However, information on the degree of such bias is often lacking (Botts *et al*., 2011). Most studies therefore utilise a random set of background samples with the resulting models suffering from a lower predictive accuracy arising from the discrepancy between biased presence data and unbiased pseudo-absence data (Phillips *et al*., 2009). Bias within *Bradypodion* localities may be present given the accessibility issues associated with the extent of privately or commercially owned land in KZN as well as its topographical heterogeneity.

To account for such sampling bias, pseudo-absences were drawn from the localities of all reptilian taxa observed in KZN, sourced from the SARCA, ReptileMap and SANBI DNA Bank databases (ADU, unpublished data; SANBI, unpublished data). This approach, referred to as target-group background selection, is based on evidence that suggests using pseudo-absence data from localities where biologically similar species have been documented or where species that require similar survey methods have been found, but were samplers have failed to locate the target species, improves model performance (Phillips and Dudík 2005, Phillips *et al*., 2009; Searcy and Shaffer, 2014). The idea is that by drawing pseudo-absences from localities that reptile observers have actually sampled will more closely approach true presence - absence. By achieving a situation in which the spatial bias in pseudo-absence data is similar to that of the presence data the model is enabled to focus on any small difference between the presence and absence data rather than just focussing on areas with the most presence data (Phillips *et al*., 2009). The result is that 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 presence and pseudo-absence points (n = 9641) was tabulated and converted into the appropriate file format for importation into Maxent along with the various environmental predictor layers. Six of the most biologically meaningful and least correlated variables that best explained the distribution of given species were selected for the final models. To do this pairwise correlation coefficients were calculated in ArcMap^{tm} 10.2.2 to identify closely related variables (Measey *et al*., 2012) and reduce the effects of auto correlation. This was followed by a jack-knife analysis of variable importance, performed in Maxent, to assess the relative permutation importance and percent contribution of each variable to explaining the observed distribution of the species.

Model evaluation

Maxent settings were adjusted from default during model evaluation. Model performance was evaluated by dividing occurrence records into 70% training and 30% testing data sets and re-running the model over 10 replicates with bootstrapping through 2000 iterations. Model performance was evaluated using standard area under the receiver operating characteristics curve (AUC) statistics for evaluating how well a predictive model fitted the observed set of occurrence data (Phillips *et al*., 2006). The test AUC (Area Under Curve) value was interpreted as follows; < 0.5 model no better than random, 0.5-0.69 as poor, 0.7-0.89 as useful and values > 0.9 indicative of models with excellent predictive ability (Swets, 1988). Although some models such as Maxent perform consistently better than others with low sample sizes (Hernandez *et al*., 2006; Wisz *et al*., 2008), overall model performance increases with increasing sample size regardless of the algorithm used (Wisz *et al*., 2008). It is thus imperative to identify a lower limit to the number of locality records needed to create a robust model (van Proosdij *et al*., 2015). However, this value is often species specific and highly influenced by species prevalence, the fraction of the study area occupied by the species (McPherson *et al*., 2004) as well as the predictor variables used. Generally model performance for a given sample size increases with decreasing prevalence such that wide-ranging species often require a larger sample size than narrow ranging species. In this study, 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 at n < 30.

Modelling of future distributions

The effects of climate and land cover were estimated by first modelling and then overlaying predicted future climatic and land cover conditions by the year 2050 respectively. To model the effects of predicted climate change, five of the latest and most applicable global circulation models were used for two Representative Concentration Pathways (RCPs) for all nine study species. This resulted in a total of one current and 10 future models for each species. For each species a final subset of three models which 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. RCPs are four estimates of future greenhouse gas concentrations based on changes in atmospheric energy levels as a result of anthropogenic and other causes (van Vuuren *et al*., 2011). The four RCPs (2.6, 4.5, 6.0 and 8.5) represent a range of possible energy levels denoted radiative forcing values (in Watts/m2) predicted for year 2100 relative to pre-industrial values. Consistent with the current consensus on the rate of climate change based on observed global temperature and sea level trends (Rahmstorf *et al*., 2007) as well as post millennium CO_2 emission rates (Manning *et al*., 2010) the scenarios used in this study excluded unrealistically optimistic ones (e.g. RCP 2.6).

Limitations associated with future land use modelling are multifaceted due to the complex interaction of humans with their receiving environment which varies both spatially and temporally (Parker *et al*., 2008). An additional limiting factor is the general paucity of directly comparable land cover datasets collected over sufficiently long periods of time for many parts of the world. Consequently, unlike climate for which global-scale, high resolution and spatially explicit future change scenarios exist, these and other limitations hamper the production of comparable layers for future land use change. 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, I reclassified all 45 land cover classes within 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 within which conversion was assumed to not take place. The extent of habitat transformation was based on a study Jewitt *et al*., (2015b) in which extrapolated estimates, under a business as usual model, suggest that 45% of KZN is likely to remain natural by 2050. Pixels were converted using focal statistics on a 9 x 9 cell neighbourhood in ArcMap^{tm} 10.2.2 with the premise that non-protected, natural pixels that are closest to transformed pixels are most likely to 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 (CSNH) both at present and by 2050 under the most optimistic and pessimistic scenarios. To facilitate a more biologically meaningful interpretation of the data, three dispersal assumptions were applied. Under Assumption 1, species were assumed to be able to occupy habitats in future that lie beyond their current extent of CSNH. Under Assumption 2, species were not assumed to be able to disperse to novel habitats beyond their current extent of CSNH. Under Assumption 3, the species were not assumed to be able to disperse beyond their currently known range as estimated in Tolley *et al.*, 2019. These data were then used in conjunction with the Ezemvelo KZN Wildlife (EKZNW) protected areas network spatial dataset (EKZNW, 2015) to estimate the proportion of each species' climatically suitable natural habitat (CSNH) under protection. This dataset included Department of Agriculture, Forestry and Fisheries (DAFF) forest and wilderness areas, EKZNW protected areas (both proclaimed and yet to be proclaimed), KZN communal conservation areas, non EKZNW proclaimed protected areas, private nature reserves and stewardship areas.

Results

Model performance (**Table 1**) for all current future model outputs was considered excellent (AUC > 0.9) following Swets (1988). The variables which contributed most towards the ENMs (**Table 1**) under the current scenario included Isothermality (*B. caeruleogula, B. nemorale*), Max Temperature of Warmest Month (*B. melanocephalum*), Min Temperature of Coldest Month (*B. dracomontanum, B. thamnobates*), Mean Temperature of Wettest Quarter (*B. ngomeense*), Mean Temperature of Coldest Quarter (*B. sp*7, *B.* sp. 8), Precipitation of Driest Month (*B. setaroi*). Following Wisz *et al.*, (2008) the forest species *B. caeruleogula, B. nemorale* and *B.* sp. 7 are considered to have small sample sizes (n < 30) and their outputs, should be interpreted with caution.

Table 1. Results on model performance, variable importance as well as the GCM and respective RCP selected from the ensemble to represent the most optimistic and pessimistic future scenario for each species.

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

Variables in bold are those which contributed most to the current model output

Key to variables: 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 current extent of climatically suitable natural habitat (CSNH) in KZN (taking into account both climate and natural land cover) varied considerably among species (**Table 2**). With the exception of *B. melanocephalum*, which currently holds the largest extent of CSNH at 20751 km^2, all other KZN dwarf chameleons were found to be restricted in terms of CSNH ranging from 6264 km^2 for *B. setaroi* to 297 km^2 for *B. ngomeense*. Assuming unlimited dispersal ability, the extent of CSNH by the year 2050 was predicted to expand for species that occur nearer the coast such *B. caeruleogula*, *B. melanocephalum* and *B. setaroi* under both "optimistic" and "pessimistic" scenarios. In contrast, more inland species *B*. sp. 8 (58.4-90.63 %), *B*. sp. 7 (35.1-43.2 %) and *B. ngomeense* (100 %) showed losses of CSNH under both optimistic and pessimistic scenarios. The Extent of CSNH for all KZN dwarf chameleon species at present as well as predicted by the year 2050 under the most optimistic and pessimistic scenarios is shown in **Figure 1**.

Table 2. Area estimate comparisons between the current extent of CSNH and that predicted under the two climatic scenarios (optimistic and pessimistic). This is shown in relation to their currently known estimated distribution size). Range estimates are from Tolley *et al*., 2019 with the exception of *B*. spp. 7 and 8 (not assessed) and *B. dracomontanum* for which a range extension was required to include point localities from Lotheni in the southern Drakensberg.

		Modelled CSNH (km^2)		
Species	Known range (km^2)	Current	Optimistic (2050)	Pessimistic (2050)
B. caeruleogula	44	746	419	419
B. dracomontanum	2975	5397	3593	1474
B. melanocephalum	8957	20751	10162	8469
B. nemorale	39	3034	2052	575
B. ngomeense	26	297	0	0
B. setaroi	5303	6264	4274	4090
B. sp. 7	10	440	44	1
B. sp. 8	1376	3995	1355	341
B. thamnobates	3295	4591	2312	1276

Other inland species such as *B. dracomontanum*, *B. nemorale*, *B. thamnobates* showed gains in suitable climatic space under the most optimistic scenarios and losses under the most pessimistic of 40.5, 55.5 and 2.3% respectively (**Figure 4a**). However, when considering models in which chameleons are not assumed to disperse into novel habitats, all the study species showed substantial losses (**Figure 4b**). Particularly concerning were *B. ngomeense* (100%), *B*. sp. 7 (90-99.8%), *B*. sp. 8 (66.1-91.5%) as well as *B. nemorale* (32.4-81.1%), *B. dracomantanum* (33-4-72.7%) and *B. thamnobates* (49.7-72.2%). However, the models show notable losses even for the least climatically susceptible species, namely *B. melanocephalum* (51-59.2%), *B. caeruleogula* (43.9%) and *B. setaroi* (31.7-34.7%) as a result of habitat transformation in spite of their climatic resilience.

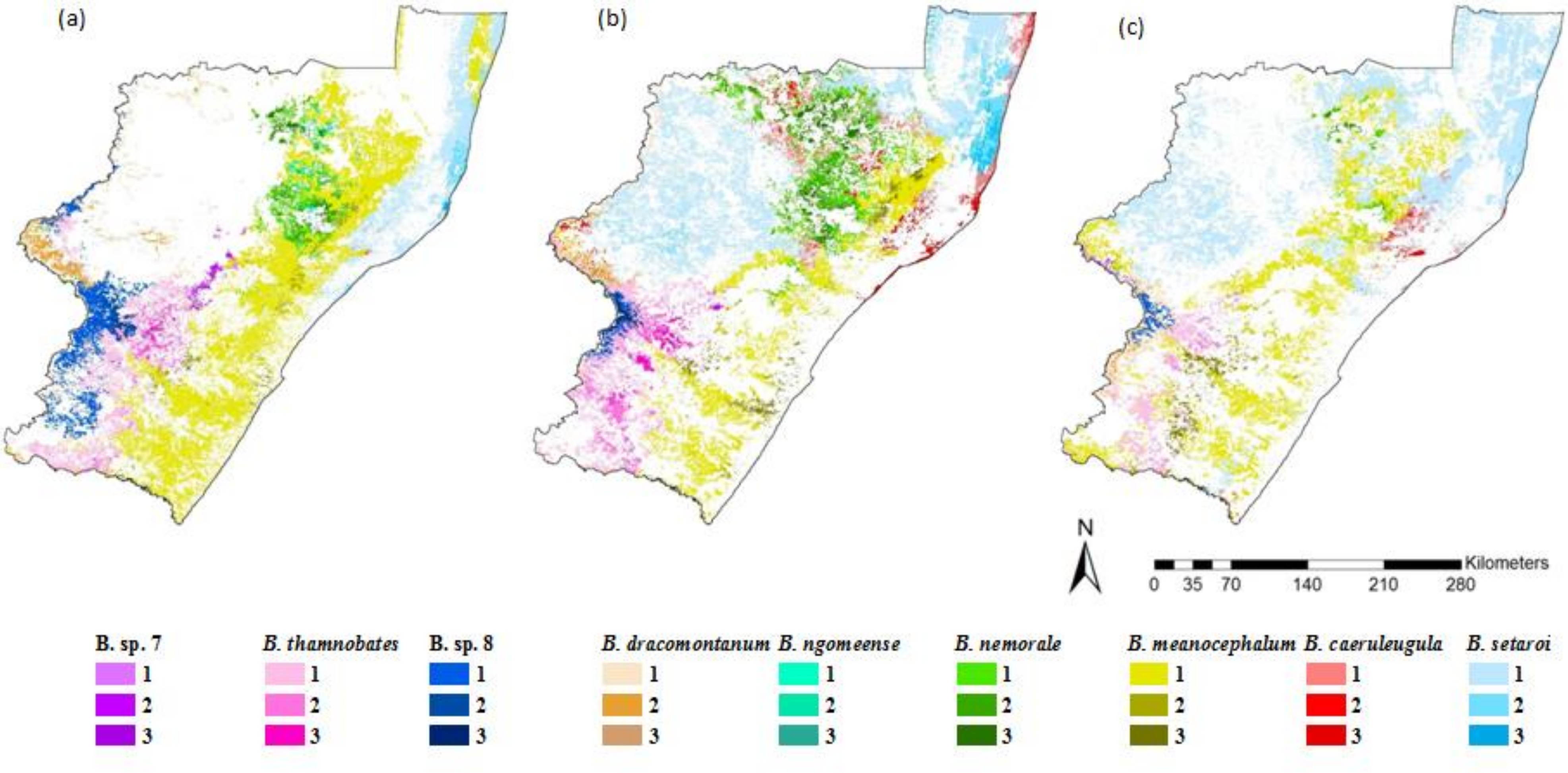

Figure 1. Extent of CSNH for all KZN dwarf chameleon species at (a) present as well as predicted by the year 2050 under the most optimistic (b) and pessimistic (c) scenarios selected from the ensemble of 10 models (per species) that were generated considering five GCMs and two RCPs. Species are colour coded with numbers (and corresponding shading) representing low (1), medium (2) and high climatic suitability (3).

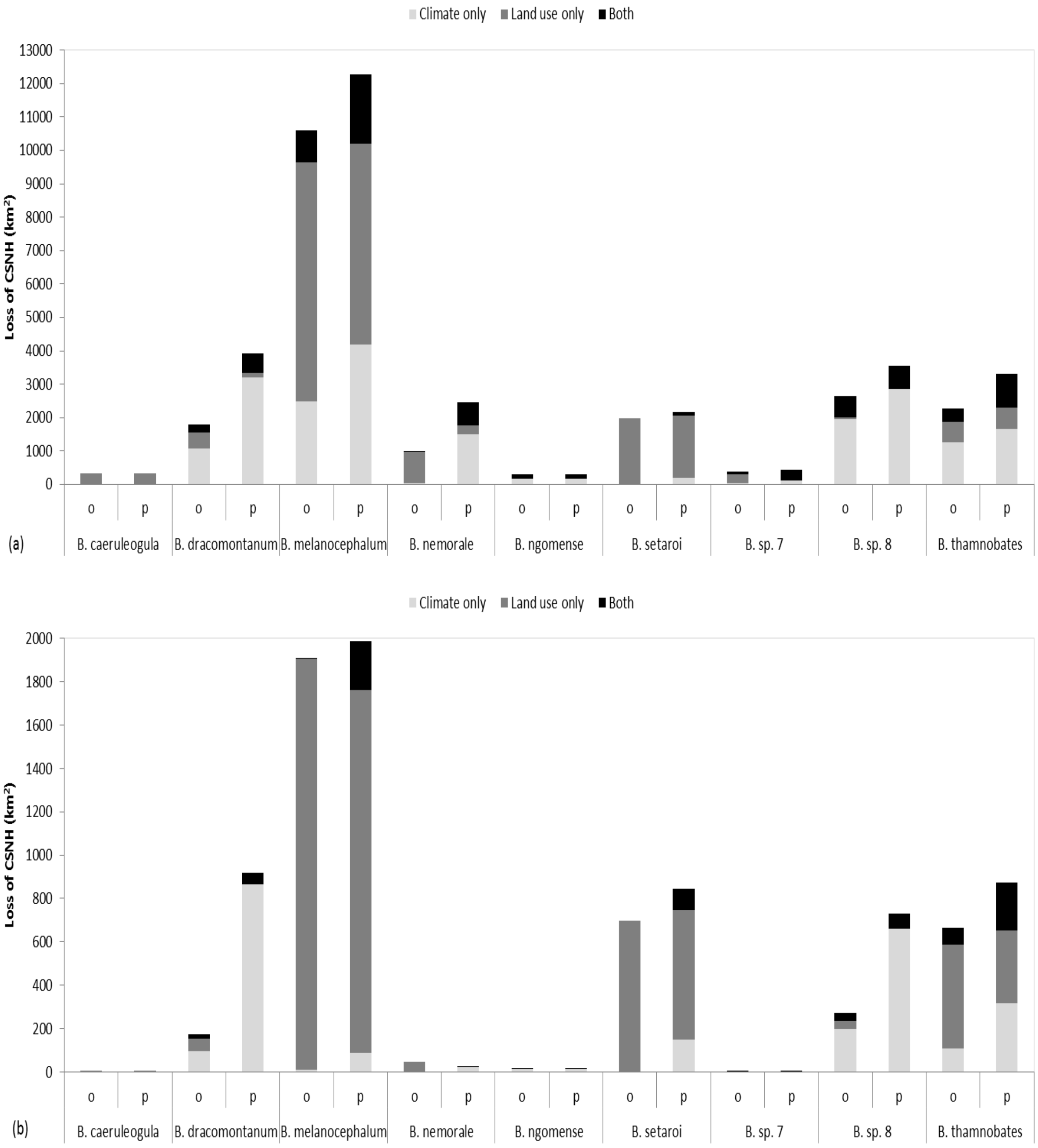

Figure 2: Relative contribution of climate and land use change to the loss of CSNH under two of the more "realistic" dispersal assumptions, (a) dispersal limited to within currently climatically suitable area (Assumption 2) and (b) dispersal limited to within known range (Assumption 3). Key to letters on "x" axis: o, optimistic; p, pessimistic climate scenario.

The relative contribution of climate and land use to the total loss of CSNH (**Figure 2**) varied among species, between climatic scenario and dispersal assumptions. Under Assumption 2 (**Figure 2a**) the predicted loss of CSNH is primarily attributed to climate change for the species *B. thamnobates*, *B.* sp. 8 and *B. dracomontanum* whereas land transformation is predicted to be the predominant loss driver for *B. melanocephalum* and *B. setaroi*. For *B.* sp. 7 and *B. nemorale*, land transformation is the primary driver under the optimistic scenario with climate becoming the dominant loss driver under the pessimistic scenario. The minor loss of CSNH predicted for *B. caeruleogula* is entirely attributed to land transformation in areas outside its protected forests. In contrast the considerable losses for *B. ngomeense* and *B. nemorale* anticipated under a worst-case climatic scenario are attributed primarily to climate loss. However, when considering Assumption 3 (**Figure 2b**), the most notable difference is the considerable increase in the contribution of land use to the losses predicted for *B. melanocephalum*.

Anthropogenic land use has already converted large proportions of climatically suitable habitat. Nevertheless, at present, all nine species still retain more than 50% of their total suitable climate within natural habitats. Most species currently range between 51.8 and 67.35% CSNH with the exception of *B.* sp. 8 and *B. dracomontamum* which support by far the highest amount of CSNH at 80.17% and 87.5% respectively. The vulnerability framework (**Figure 3**) revealed that regardless of the current extent of CSNH supported by a species or its climatic resilience, all species except *B. dracomontanum and B.* sp. 8, are predicted to become habitat constrained by the year 2050. Species predicted to be constrained by both climate and available natural habitat (vulnerable quadrat) include *B. ngomeense* and *B.* sp. 7 (entirely constrained by climate), as well as *B. thamnobates* and *B. nemorale*. Species anticipated to be less constrained by climate include *B. melanocephalum* followed by *B. setaroi* and *B. caeruleogula*. Analysis of the intensity of climatic suitability (as indicated by the bubble sizes in **Figure 3**) reveals subtle differences in vulnerability amongst species. *Bradypodion setaroi*, for example, is likely to maintain a lower intensity of climatic suitability than *B. caeruleogula* and as such is more susceptible. Likewise the effects of climate change are more intense for *B. nemorale* than *B. dracomontanum* and *B. thamnobates*.

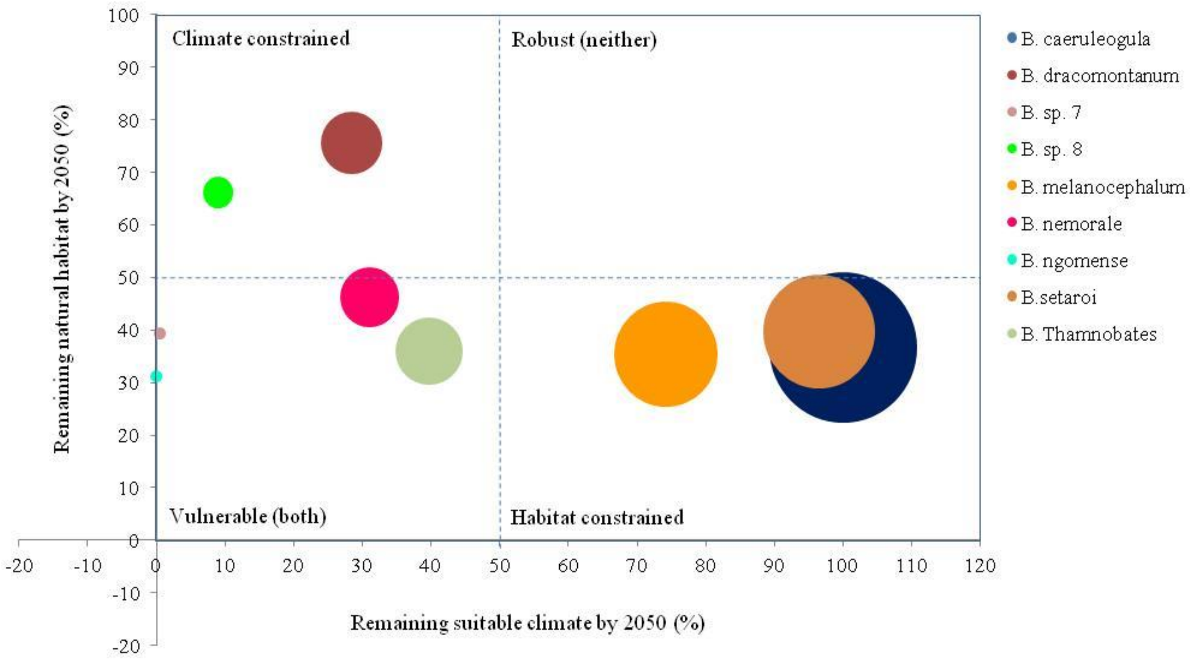

Figure 3. Vulnerability framework considering a pessimistic scenario for the nine currently recognised dwarf chameleon species from KwaZulu-Natal under climate and land use change. The "x" and "y" axes represent the proportion of the current climatic niche (in geographic space) which remains suitable and natural respectively by the year 2050. The size of the bubbles reflects the suitability of cells within the 2050 model prediction expressed as a percentage of the current suitability (scale 0-172%). Quadrat annotations adapted from Jewitt *et al*., 2015a.

The extent of climatic suitability expressed in terms protection status under assumption of limited and unlimited dispersal ability are shown in **Figure 4**. At present, the proportion of CSNH under statutory protection (**Table 3**) within the known ranges of the study species (Assumption 3) is far lower for *B. melanocephalum*, *B. thamnobates* and *B.* sp. 7 (all < 11%) than it is for the remaining species (all > 43%). By 2050 the extent of CSNH under protection (considering a worst-case scenario under Assumption 3) is predicted to decrease for *B. melanocephalum* (14%), *B. nemorale* (82%), *B. ngomeense* (100%), *B. setaroi* (3%), *B.* sp. 8 (68%), and *B. thamnobates* (53%). Conversely, statutory protection is expected to increase for the species *B. caeruleogula* (3%) and *B. dracomontanum* (22%). At present, the estimated range of *B.* sp. 7 (based on a convex hull around known localities) does not overlap any protected areas as listed by EKZNW. However, this may an artefact of low sample representation. Increased sampling may reveal its presence within nearby Karkloof, Gilboa and Mount Mabona reserves.

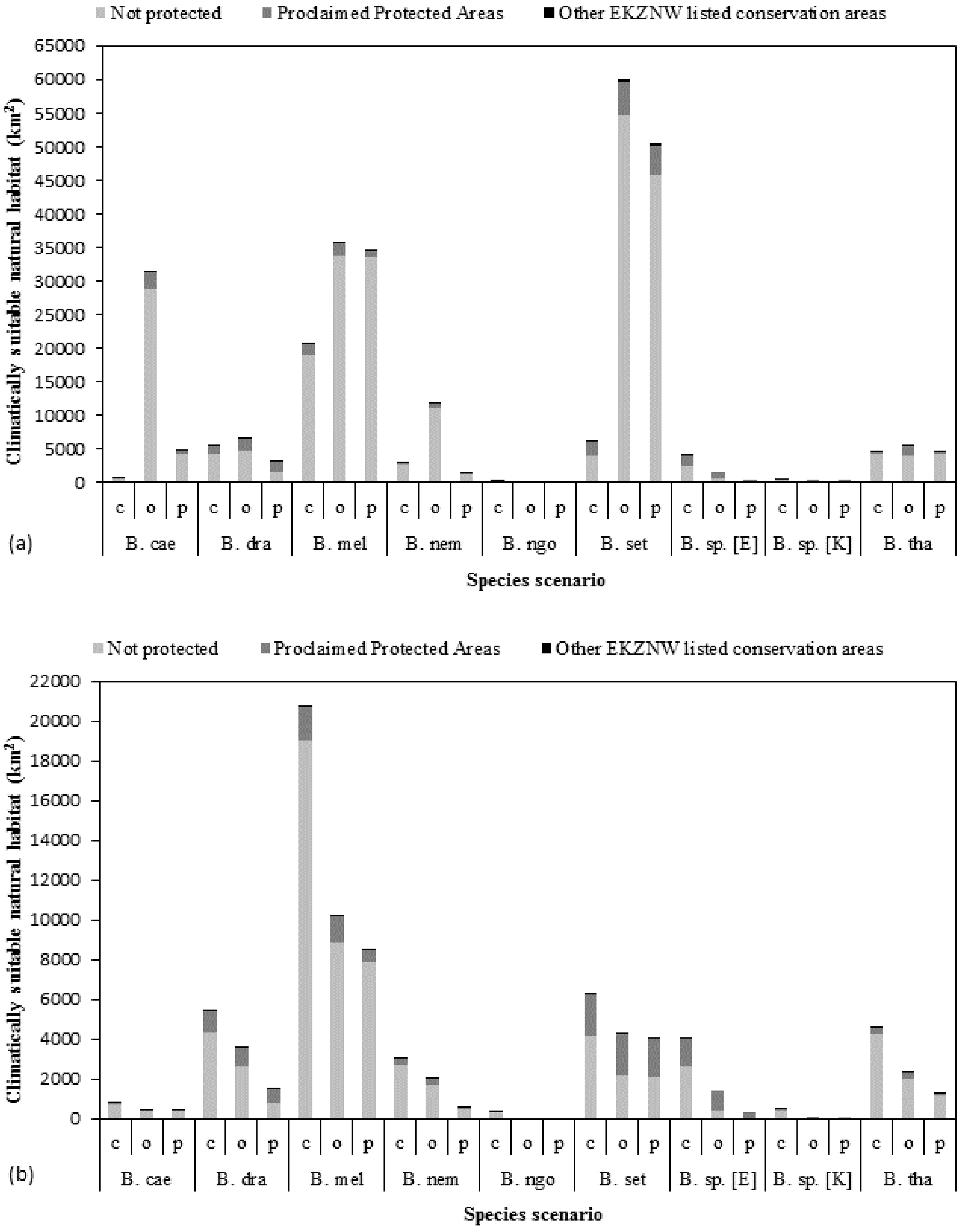

Figure 4: Graphical representation of the extent of climatic suitability expressed in terms protection status under the assumption of (a) unlimited dispersal ability (Assumption 1) and (b) that chameleons are not likely to occupy habitats within novel areas beyond the extent of current climatic suitability (Assumption 2). Key to letters on "x" axis: c, current; o, optimistic; p, pessimistic climate scenario.

Table 3. Comparison in the extent of CSNH that falls within the EKZNW protected areas network at present and as predicted for optimistic and pessimistic future scenarios under the three main dispersal assumptions for dwarf chameleons The last column shows the proportion of CSNH within a species' known range that currently falls within a protected area (in parenthesis) as well as the change predicted under each scenario.

Species	Scenario	Assumption 1	Assumption 2	Assumption 3	
		Area (km^2)	Area (km^2)	Area (km^2)	% Change
B. caeruleogula	a	63	63	33	0 (84)
	b	2351	63	34	+3
	c	270	63	34	+3
B. dracomontanum	a	1088	1088	552	0 (43)
	b	1830	988	812	+47
	c	1735	682	673	+22
B. melanocephalum	a	1702	1702	107	0 (3)
	b	1683	1335	111	+4
	c	1060	644	91	**-14**
B. nemorale	a	348	348	28	0 (93)
	b	663	343	31	+11
	c	105	100	5	**-82**
B. ngomeense	a	16	16	11	0 (71)
	b	0	0	0	-100
	c	0	0	0	**-100**
B. setaroi	a	2114	2114	1579	0 (52)
	b	5440	2113	1581	+0.1
	c	4777	2041	1525	**-3**
B. sp. 7	a	36	36	0	0 (0)
	b	37	14	0	0
	c	53	0	0	0
B. sp. 8	a	1410	1410	747	0 (71)
	b	1113	966	729	-2
	c	359	328	252	**-68**
B. thamnobates	a	316	316	154	0 (11)
	b	1355	271	129	-16
	c	274	130	72	**-53**

Discussion

These findings suggest that KZN dwarf chameleon species are likely to respond individualistically to climate and land use change. Although a gain in climatically suitable natural habitat (CSNH) was predicted for three of the species, considerable losses are predicted for the remainder, even under the assumption of unlimited dispersal ability. However, when considering a situation in which chameleons are not expected to be able to disperse into novel habitats outside of their current extent of CSNH, even the most climatically resilient species showed notable contractions. Although none of the species appear immune to the combined effects of both change drivers some are particularly vulnerable and warrant higher levels of conservation prioritisation. Concerning in this regard is the considerable loss of CSNH predicted for most species within protected areas.

The ecological niche models for the study species were found to align well with their known occurrences (based on model performance estimates), reflecting the small, fragmented and largely allopatric occurrence of the chameleons in the province (Tolley and Burger, 2007). At present, the models suggest that CSNH for each of the KZN dwarf chameleons, with the exception of *B. melanocephalum*, is restricted to less than 10 000 km^2. The findings of this study suggest that the individualistic responses of these chameleons to climate change will continue under the pressing and largely independent constraints of natural habitat loss from land use change.

Common to all six inland species which registered losses in CSNH under the assumption of unlimited dispersal ability is their occurrence at higher elevation, areas away from the coast. Here, the climate is cooler, drier and more seasonal than that experienced by the three species that occur closer to the coast. The global scale GCMs used in this study together with more local scale climate change outlooks (Naidu *et al.*, 2006; Ziervogel *et al.*, 2014) suggest a notably warmer and slightly wetter climate throughout the province, characterised by temperature regimes that are less seasonal and slightly less seasonal rainfall, albeit more erratic and intense. These conditions are less consistent with and fall on the outer edge of the observed climatic niche tolerances for the inland species prompting the modelling algorithm to project a reduction in CSNH, while the opposite is true for the coastal species. My findings are consistent with those of Houniet *et al.*, (2009) who found that a subset of *Bradypodion* from around South Africa are likely to respond individualistically. However, my results build on this important work by expanding it to all KZN dwarf chameleons as well as by more explicitly accounting for sampling bias and land use change.

In discerning which change driver was primarily responsible for predicted losses, I discovered that their relative contributions varied among species, climatic scenarios and dispersal assumptions. This finding makes sense considering their differing responses to climate change and the predicted spatial distribution of their climatic suitability in relation to natural habitat both now and in future. Climate change is predicted to be the dominant loss driver for *B. thamnobates*, *B.* sp. 8 and *B. dracomontanum*. These inland species although prone to the effects of climate change, still maintain a sizeable extent of climatically suitable habitat in natural areas. In contrast, land transformation was predicted to be the predominant loss driver for *B. melanocephalum* and *B. setaroi* that are relatively more robust to climate change but who have large proportions of their ranges within rapidly developing coastal areas (Armstrong, 2009). For species such as *B.* sp. 7 and *B. nemorale* which are currently heavily constrained in terms of available natural habitat (due to afforestation and rural development), yet are still somewhat vulnerable to climate change, a change is anticipated in the dominant loss driver from land transformation under optimistic climatic outlooks to climate under more pessimistic scenarios. As *B. caeruleuogula* is not predicted to lose any climatic suitability, the small losses that it is predicted to incur are exclusively attributed to land transformation in forest habitat on the periphery of Ngoye, Dlinza and Entumeni reserves. In contrast *B. ngomeense* is predicted to incur a complete loss of CSNH as a result of climate change in spite of also having a large proportion of its forest habitat under statutory protection within the Ntendeka Wilderness Area.

Using this information to construct a vulnerability framework (Jewitt *et al.*, 2015a) revealed a gradient in the degree of vulnerability and consequent need for conservation prioritisation among species (**Figure 3**). Considering land use driven habitat loss alone the framework revealed that with the exception of *B. dracomontanum* and *B.* sp. 8, dwarf chameleons in KZN are likely to become habitat constrained by the year 2050 due to the conversion of natural habitat to other land uses. This constraint threshold was considered to be < 50% remaining natural habitat based on a study Flather & Bevers (2002) who found that the capacity of landscapes to support viable populations rapidly declined beyond this point. However, when additionally taking into account potential losses due to climate change, the combined effect of these two drivers becomes apparent. For example, although the Ukhahlamba Drakensberg Park affords *B. dracomontanum* and *B.* sp. 8 considerable protection against land use driven losses in CSNH, the species are still predicted to incur considerable losses as a result of climate change. Overall this framework revealed that although some species (*B. caeruleogula*, *B. melanocephalum and B. setaroi*) show climatic resilience and others stability in natural habitat (*B. dracomontanum* and *B. sp 8*) none are resilient to the combined effects of both change drivers (**Figure 3**). Five species of these species are highlighted as being particularly vulnerable to the effects of both change drivers and warrant high conservation prioritisation.

At present the proportion of CSNH under statutory protection (**Table 3**) within the known ranges of the study species (Assumption 3) is far lower for *B. melanocephalum*, *B. thamnobates* and *B.* sp. 7 (all < 11%) than it is for the remaining species (all > 43%). By year 2050 the extent of CSNH under protection (considering a worst-case scenario under Assumption 3) is predicted to decrease for *B. melanocephalum* (14%), *B. nemorale* (82%), *B. ngomeense* (100%), *B. setaroi* (3%), *B.* sp. 8 (68%), and *B. thamnobates* (53%). Conversely statutory protection is expected to increase for the species *B. caeruleogula* (3%), *B. dracomontanum* (22%). At present the estimated range of *B.* sp. 7 (based on a convex hull around known localities) does not overlap any protected areas as listed by EKZNW, however, this may an artefact of low sample representation. Increased sampling may reveal its presence within nearby Karkloof, Gilboa and Mount Mabona reserves.

The importance of the EKZNW protected network in safeguarding habitat for the study species was highlighted by the finding that six of the nine species have more than 43% of their CSNH situated within EKZNW protected areas. However, *B. melanocephalum*, *B. thamnobates* and *B.* sp. 7 are considerably less well protected (< 11% CSNH within EKZN protected areas network) and would benefit from increased statutory protection. Ultimately though the long-term value of any remaining CSNH for these chameleons depends not only on its current extent of protection but also on how well it aligns with the protected areas network in the future. Here, it is anticipated that by the year 2050, the extent of CSNH under protection (considering a worst case scenario under Assumption 3) will decrease for all but two (*B. caeruleogula* and *B. dracomontanum*) of the province’s dwarf chameleon species, as the distribution of their CSNH contracts and / or shifts out of the current protected areas network. Most notable losses are anticipated for *B. ngomeense* (100%), *B. nemorale* (82), *B. sp*. 8 (68) and *B. thamnobates* (53). This drastic reversal in the extent of CSNH situated within protected areas in future alludes to the potentially deleterious effects that climate change may have if it is not proactively accounted for in conservation planning. Conversely, even some of the most climatically resilient species (e.g. *B. melanocephalum* and *B. setaroi*) may surpass critical natural habitat threshold levels in the near future, should development continue at the forecasted rates.

It is important to consider, however, that predictions made by correlative niche models such as this are based on currently available locality data and our understanding of the observed niche tolerances of the species associated with them. In doing so, we assume that their observed distribution is at equilibrium with the environment (Guisan and Thuiller, 2005) which, especially for species as cryptic and taxonomically intricate as these (Tolley *et al*., 2006), may not be the case. Additionally, climatic suitability comprises just one of many aspects influencing the realised distribution of a species and many other factors such as barriers to dispersal, biotic interactions, anthropogenic disturbances and population dynamics may preclude the presence of a species in an area that is otherwise environmentally suitable (Jiménez-Valverde *et al*., 2011). As such, we run the risk of underestimating their fundamental niche and consequently, their resilience to novel climate in the future. Additionally, the limitations associated with land use forecasting are multifaceted. However, this study is built on prior findings which suggest proximity of natural forest to disturbed areas may be the best predictor of its degradation (Souza & De Marco, 2014) and utilises an approach proven useful for the conservation of titi monkeys in Brazil (Gouveia *et al*., 2016).

Although this study takes important steps towards understanding how KZN's dwarf chameleons may respond to climate and land use change, their response is also likely to be reliant on how well they will be able to track suitable climate and/or persist in the face of the changing conditions. Tracking climatic suitability is dependent on dispersal ability and biotic interactions (Urban *et al*., 2013). Data on the dispersal abilities of dwarf chameleons is limited although short-term telemetry work suggests that a species from the Cape Peninsula (*B. pumilium*) is capable of rapid directional movement between nearby habitat patches provided a corridor of suitable vegetation is present. However, daily displacement distances were considered low compared to other lizards (Rebelo, 2014). Studies on the larger *Trioceros jacksoni* also reflect low vagility both in their native (Toxopeus *et al*., 1998) and non-native ranges (Chiaverano *et al*., 2014) where they are considered unlikely to inhabit habitat patches fragmented by more than a few hundred meters. As such, it is unlikely that dispersal into novel climates will be a viable option for these small-bodied lizards which are so often tied to distinct vegetation types.

Perhaps then, persistence in an area may be more contingent on adaptability and utilisation of climatic refugia (where available) than dispersal to novel climes. Pioneering studies have brought to the fore the potential role of genetic adaptability and phenotypic in rescuing species from the effects of climate change. Although this has been shown for some species, the body evidence, particularly with regards to genetic adaption, is not well supported and more research is required (Merila *et al*., 2014). Recent research on similarly small bodied arboreal lizards (*Anolis sagrei*) suggests, that heritability of traits considered important in dealing with conditions predicted under climate change may be low and, as such, that evolutionary change is unlikely to keep pace with the predicted rates of climate change (Logan *et al*., 2018). Although some dwarf chameleon species show considerable variation in phenotype between closed and open canopy habitats (da Silva *et al*., 2014), a study by Miller and Alexander (2009) did not find any evidence to suggest that this difference is driven by developmental plasticity but rather that it is hereditary. Ultimately, whether or not dwarf chameleons will be rescued by genetic adaptability, remains uncertain although it is possible that their capacity in this regard may be individualistic as well. For now, behavioural responses that allow for persistence in microhabitat refugia (e.g. sheltered gorges or movements up or down mountain slopes) not captured by the landscape-scale spatial data used in our study, remains a likely prospect. Another aspect of adaption worthy of investigation is the degree to which each chameleon species will tolerate man-made settings. A recent study by Winchell *et al*., 2018, for example, showed that two species of anoles from Puerto Rico responded very differently to the urbanisation of their habitat with one merely surviving while the other thrived.

Overall, the relative role of climate and land use change in driving habitat loss was found to be species dependant. For most, the changing climate is likely to bring about a contraction in the conditions they currently frequent while for some the opposite is true. Additionally while most species are situated in rapidly developing areas prone to habitat loss through land use change, a few are situated in more remote and well protected areas. Regardless of the dominant loss driver, none of the species were anticipated to be robustly resilient to the combined effects of both global change drivers when considered simultaneously. At present the conservation status of KZN’s dwarf chameleons does not adequately reflect their anticipated susceptibility to climate and land use change nor the extent of CSNH that is predicted to remain under statutory protection. In spite of the limitations, this study provides useful and urgently needed information which can be used to better guide conservation efforts for the provinces dwarf chameleon assemblage. More detailed information on the movement ecology and dispersal ability of dwarf chameleons, particularly across unfavourable habitats together with more accurate, population density estimates is required to estimate minimum patch sizes required to maintain viable populations. A deeper understanding of range size, niche breadth and preference will also help to unravel proximal causes behind the predicted responses. Ultimately, however, the fate of these chameleons will lie not only in their ability cope with and track changes to the distribution of climatically suitable habitat but also in their ability to persist in areas predicted to be unsuitable by means of adaption to new conditions, or persistence in refugia. Studies such as these will help to better understand whether the current extent of suitable habitat and its levels of protection are adequate to safeguard their long-term persistence. Undoubtedly, EKZNW protected areas have played a vital role in safeguarding the these species to date, yet, the importance of upholding and adaptively expanding this network using accurate pre-emptive information cannot be overemphasised in light of the rapid changes at hand.

Chapter 3: Patterns in the Modelled Responses of Dwarf Chameleons to Climate Change

Abstract

In the midst of rapid biodiversity loss brought on by a rapidly-changing climate, the need to identify patterns or traits that infer higher vulnerability of species has become increasingly more important as pressure mounts on conservationists to prioritise efforts and resources. A recent study (Chapter 2) on the effects of land use and climate change on dwarf chameleons from the eastern margin of South Africa has revealed that inland species are more likely to be adversely affected by impending climate change than those nearer the coast. Here, I make use of ordinal, multivariate and correlation analyses to investigate whether this susceptibility to climate change can be predicted by some of the more well established macro-ecological traits namely range size, niche breadth and niche preference. Findings suggest that although range size and niche breadth are correlated with one another, neither are appreciably correlated with susceptibility (as defined by proportional losses in climatically suitable natural habitat). Instead it appears that the future availability of a specific set of climatic conditions (variables) typically associated with species occurrence, or niche preference, better explained susceptibility. More specifically, species occupying climatically seasonal habitats where conditions are cooler and more desiccating during winter are more likely to contract as the future climate is predicted to become ever warmer and disproportionately drier inland.

Introduction

Biodiversity is being lost at unprecedented rates and climate change has been implicated as one of the main drivers (IPCC, 2007; Leadley *et al*. 2010). This has prompted a considerable body of important pre-emptive research aimed at forecasting habitat suitability under different scenarios of climate change. Most often, these have taken the form of correlative ecological niche models (Peterson *et al*. 2016) although, encouragingly, a growing number of studies are also incorporating empirical physiological data into their predictions (Gerick *et al*. 2014). In light of the magnitude of biodiversity loss, brought on by rapidly intensifying climate change, the need to characterise traits and identify macro-ecological patterns that infer higher vulnerability has become increasingly more important as pressure mounts on conservationists to prioritise efforts and resources. Far fewer studies, however, place emphasis on identifying the actual characteristics of a species' niche (breadth and preference) and geographic extent (range size) that may infer higher susceptibility to climate change (Thuiller *et al*. 2005). Furthermore, studies have traditionally tended to focus on temperature changes, while those highlighting the importance of precipitation (and its interaction with temperature) on limiting species distributions are comparatively scarce (McCain & Colwell, 2011). This is attributed to past uncertainties regarding model forecasts on precipitation, due to the multitude of factors associated with its occurrence and largely non linear relationship with altitude (Barry, 2008). Nevertheless, considerable advances have been made in the field of climate forecasting (Urich *et al*. 2014) and at least among the global circulation models (GCMs) used in this study there appears to be considerable consensus regarding the broad patterns of precipitation change in KwaZulu-Natal (KZN).

Although a number of traits have been suggested to confer high susceptibility to environmental change, range size (geographic extent), niche breadth (niche specificity) and preference (niche position) remain some of the most significant and consistently implicated predictors of vulnerability (Thuiller *et al*. 2005). Generally, species with smaller range sizes and niche breadths that also occupy a niche position along the environmental gradient that is more marginal compared to what is available tend to be more vulnerable (Broennimann *et al*. 2006; Botts *et al*. 2013; Williams *et al*. 2007). Species with these traits are generally less abundant, less mobile, poorer competitors and have lower reproductive success than species which tolerate a broader spectrum of conditions that is also more readily available in the area they occur, and as such are more susceptible to environmental change (Gaston, 1998; Thuiller *et al*., 2005; Williams *et al*. 2007). Common to most of these species, however, is that they tend to tolerate a narrower range of conditions suggesting that range size is, with some exceptions, a spatial representation of their degree of niche specialization (Botts *et al*. 2013; Devictor *et al*. 2010). However, vulnerability is also thought to be associated with niche preference (the position of the tolerance bracket along an environmental gradient). Generally, species whose set of tolerated conditions are more marginal compared to the prevailing conditions or are less aligned with those anticipated under environmental change are considered more susceptible to decline (Swihart *et al*. 2003).

Niche-based studies are made more insightful when they span climatic gradients (McCain *et al*. 2011). In this regard the dwarf chameleons of KwaZulu-Natal in South Africa are good study candidates. They are a group of mainly arboreal, small bodied, viviparous chameleons (Jackson, 2007) that are largely endemic to South Africa (Tolley, 2014). They reach a particularly high diversity in KZN where they are coincident with the Maputaland-Pondoland Albany (MPA) hotspot, one of two epicentres of their taxon's radiation along with the Cape Floristic Region (Tolley *et al*. 2008). In total, nine species occur in the province including seven described and two undescribed species (Tolley *et al*. 2008; Tolley & Burger, 2007). Here, their present-day diversity and distribution is understood to be linked to their past responses towards shifts in their ancestral forest habitat brought on by climatic changes since the Miocene Climatic Optimum (Tolley *et al*. 2008, da Silva and Tolley, 2017). Current consensus is that during the Pleistocene (which followed the Miocene), the forests of KZN, particularly the Mist Belt and Afromontane forests of the interior, receded into ever smaller and more fragmented pockets as the climate became cooler and drier (Lawes, 1990). Slightly warmer and wetter conditions during the Holocene Altithermal that followed saw the expansion of the comparatively younger coastal forests (Lawes, 1990). Today, the forest patches that remain have acted as refugia for a number of early diverging dwarf chameleon lineages. However, more recent lineages have emerged in response to the spread of open canopy habitats (Tolley *et al*. 2008). Despite their strong phenotypic differences, mitochondrial and microsatelltie markers show little or no divergence with incomplete lineage sorting suggesting that these species are still in the early stages of their move to more open habitats (da Silva and Tolley 2017, Tolley *et al*. 2008). Although it is clear these chameleons have endured considerable climatic changes in the past, these responses occurred slowly, over an evolutionary time scale. As with so many other species (Brook *et al*. 2008; Oliver and Morecroft, 2014; Riordan and Rundel, 2014) it is likely that current rates of climate change will pose challenges to conservation efforts aimed at safeguarding their persistence in future.

In the preceding study (Chapter 2) on the modelled responses of dwarf chameleons to climate and land use change in KwaZulu-Natal (South Africa) it was observed that inland species are more likely to be adversely affected by impending climate change than ones nearer the coast. Here, ordinal, multivariate and regression analyses are used to further investigate those findings, and search for commonalities among their macro-ecological traits namely range size, niche breadth and niche preference that infer a higher vulnerability to predicted climate change. It is hypothesised that the direction of the response of a species is largely contingent on its climatic niche preference and its alignment with a set of key variables likely to become limiting under the forecasted conditions.

Methods

Estimates of climatic suitability were based on ecological niche models (ENMs) produced in a previous study (see Chapter 2 for methodological details) for all nine dwarf chameleons modelled. In summary, this involved the production of models portraying the spatial extent of climatically suitable habitat (CSH) both at present and by the year 2050. To account for variability among the various climatic outlooks, future projections were based on two global CO_2 representative cost pathways (RCPs 4.5 and 8.5) for five GCMS (MIROC5, HadGEM2-ES, MPI-ESM-LR, CNRM-CM5 and NorESM1-M) yielding a total of 90 models. From these, a subset of models representing the most optimistic and pessimistic outlook for each species was drawn. Point locality data were sourced from the South African Reptile Conservation Assessment SARCA and ReptileMap (http://vmus.adu.org.za), the Herpetological DNA bank at the South African National Biodiversity Institute and iSpot (Open University, https://www.ispotnature.org/). Environmental data included 19 bioclimatic (Hijmans *et al*. 2005) and two topographic layers namely slope and aspect derived from USGS digital elevation models (Danielson and Gesch, 2010) at a spatial resolution of 30 and 7 arc seconds respectively. Models were generated using the presence-only modelling algorithm Maxent (Phillips *et al*. 2005). To better account for the effects of sampling bias and to more closely approximate true absences, a target background approach (Dudík, 2005; Phillips *et al*. 2009) was employed in which pseudo-absences (n = 9400) were drawn from the localities of other reptilian taxa observed in KZN. Models were initially run on all environmental variables using 70% training and 30% testing data sets and re-run over 10 replicates with bootstrapping through 2000 iterations. Final models were run on six of the most biologically meaningful and least correlated (correlation matrix generated in ArcMap^{tm} 10.2.2) variables that best explained the distribution of a given species.

These data were used to estimate the extent of remaining CSH predicted for each species by 2050 (assuming a pessimistic change scenario), expressed as a proportion of their current extent of CSH. Range size estimates were based on IUCN Red List assessment polygons (see Tolley *et al*. 2019) for the seven currently recognised species. For the two undescribed species (for which range polygons are not available) range size (km^2) was estimated by delineating a minimum convex hull polygon applied to point locality data using minimum bounding geometry in ArcMap^{tm} 10.2.2.

Principal components analysis (PCA) was used to visualise and evaluate dwarf chameleon niches in ordinal space. Input data included the range of conditions associated with recorded point localities for each species extracted from the environmental layers using spatial analyst in ArcMap^{tm} 10.2.2. To reduce the dimensionality of the data, and to ensure that all variables which made the greatest contribution to the ecological niche models for each species were included a covariance matrix was constructed using environmental data extracted from all raster cells within KZN. The final subset of 14 variables used in the PCA included only those that (a) contributed most towards the final ENMs for each species, (b) were considered most biologically relevant and (c) were the least correlated ($r^2<0.85$). These included slope; aspect; mean diurnal temperature range (bio2), isothermality (bio3), temperature seasonality (bio4), minimum temperature of coldest month (bio6), temperature annual range (bio7); mean temperature of wettest quarter (bio8), mean temperature of coldest quarter (bio 11), annual precipitation (bio12), precipitation of wettest month (bio 13), precipitation of driest month (bio14), precipitation seasonality (bio15), precipitation of warmest quarter (bio18).

From these data a PCA plot was generated in the R environment (RStudio Team, 2016) to examine niche breadth and preference as defined by the range of environmental conditions associated with the known point localities. Each species was colour coded and assigned a 95% CI ellipse to aid visualisation of its grouping in ordinal space. Communality estimates and the eigenvalues associated with each principal component were generated in SAS (SAS University Edition 9.4 software package (SAS Institute Inc., Cary, NC, USA). A varimax rotation was used, and principal components with an eigenvalue greater than one were retained for further analysis. To establish whether the PCs extracted showed significant differences between inland and more coastal species, an analysis of variance (ANOVA) was conducted on the PC scores for each species group. Inland species are those which are predicted to suffer a reduction in their extent of predicted climatically suitable natural habitat (CSNH) whereas the more coastal species are those that are predicted to experience either a maintenance or expansion in CSNH by 2050 (under an assumption of unlimited dispersal ability).

Niche breadth was defined in this study as the degree of spread of a species' PCA scores in ordinal space. To quantify differences in niche breadth among the species, following Anderson (2006), an ANOVA was conducted on the spread of the PCA scores for each species quantified as the mean Euclidian distance of each species' PCA score from its group centroid. Pairwise comparisons were made using Post-hoc Tukey-Kramer tests with least squares means adjustments for multiple comparisons to account for Type-1 errors.

To investigate differences in niche preference among species, ANOVAs were run on the subset of environmental variables associated with the principal component that was found to be most important in explaining the differences among inland and more coastal species groups (in this case PC1, see Results). Thereafter, a niche disparity test was conducted to detect differences in the positions of the species niches with respect to one another in ordinal space. To do this, a dissimilarity matrix was computed based on Euclidean distances between the PCA scores for each species. Following Anderson (2001), values within this dataset were then subject to a non-parametric (permutational) multivariate analysis of variance (MANOVA) similar to Fisher's F-ratio. Post-hoc, pairwise comparisons were made using Tukey's honestly significant difference test (Tukey's HSD) with Bonferroni corrections comparisons to account for Type-1 errors arising from multiple pairwise comparisons using the function Pairwise.adonis (Arbizu, 2019) in the R statistical environment (RStudio Team, 2016). To substantiate the distinction made between inland and more coastal species a proximity analysis on the distance of each locality record for each species to the nearest coastline was performed in ArcMap^{tm} 10.2.2 and subject to an ANOVA with post-hoc Tukey-Kramer pairwise comparisons. Tests on niche breadth, niche disparity and proximity to the nearest coastline were done using SAS University Edition 9.4 software package (SAS Institute Inc., Cary, NC, USA).

Finally these themes, namely range size, niche breadth and niche preference were subject to correlation analysis to assess their utility in detecting trends in climatic vulnerability among the species. First a correlation analysis was performed on the relationship between (a) range size and niche breadth, range size and current extent of CSH niche, range size and the proportion of remaining CSH by 2050 as well as niche breadth and the proportion of remaining CSH by 2050. This was then followed by a correlation analysis on the eight environmental variables which best polarised the differences amongst the two species groups.

Results

Estimated range sizes, vary (**Table 1**), from 8957 km^2 for the widest ranging species (*B. melonocephalum*) to 10 km^2 (*B*. sp. 7). From this it is apparent that the study group can be divided, broadly, into two main groups; inland species that are predicted to experience a contraction in the extent of CSH (*B. dracomontanum*, *B. nemorale*, *B. ngomeense*, *B*. sp. 8, *B*. sp. 7, *B. thamnobates*) and more coastal species predicted to either expand (*B. caeruleogula and B. setaroi*) or roughly maintain (*B. melanocephalum*) their current area of climatically suitable habitat (CSH) as shown in **Table 1**.

Table 1. Range estimates, modelled extent of current CSH and amount predicted to remain by 2050 expressed as a proportion of their current CSH. Species are ordered from lowest (top) to highest (bottom) remaining CSH. Inland species are those considered to experience a reduction in while more coastal species are predicted to either maintain or experience an expansion in the extent of CSNH by 2050.

Group	Species	Range (km^2)	Current CSH (km^2)	Remaining CSH by 2050 (%)
1	*B. ngomeense*	26	574.11	0
1	*B*. sp. 8	1376	4982.71	9.95
1	*B. nemorale*	39	4504.43	31.29
1	*B*. sp. 7	10	788.48	31.95
1	*B. dracomontanum*	2975	6168.13	52.15
1	*B. thamnobates*	3295	8121	55.43
2	*B. melanocephalum*	8957	35769.83	97.19
2	*B. caeruleogula*	44	1139.99	421.17
2	*B. setaroi*	5303	10741.2	473.98

Two principal components were extracted, which encompassed 80% of the variation in environmental data associated with point localities (**Figure 1, Table 2**). Analyses of variance for PC1 and PC2 using species group as the fixed factor, revealed significant differences between groups for PC1 ($F_{(1,929)} = 1870.76$; $P \leq 0.001$), but not for PC2 ($F_{(1,1159)} = 0.14$; $P = 0.71$). This suggests that climatic niche space is different for these two groups for the variables associated with PC1 (**Table 2**).

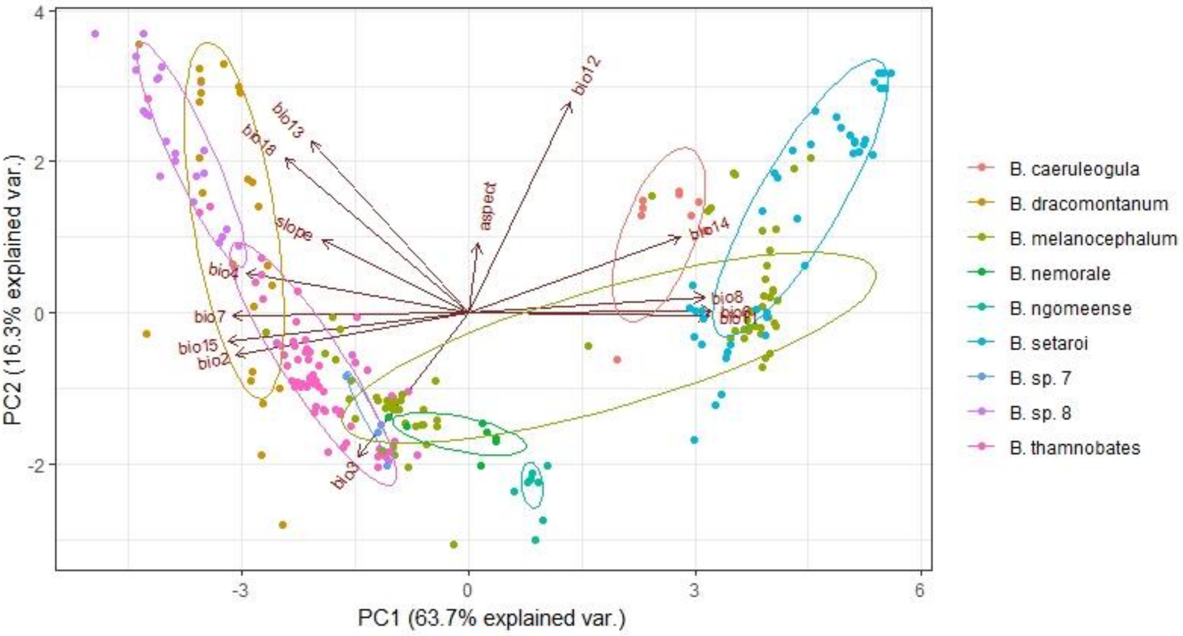

Figure 1: Principal component scatterplot for the study species in relation to environmental variables. Each species has been assigned a 95% CI ellipse.

Table 2. Rotated factor matrix for the principal components analysis. Bold text denotes variables that have the strongest association with each principal component. Percentage variation and eigenvalues for each PC are given.

Variables	Description	Factors	
		1	2
bio4	Temperature seasonality	**0.9637**	0.1744
bio7	Temperature annual range	**0.9528**	0.1323
bio6	Minimum temperature of coldest month	**-0.9455**	-0.1428
bio11	Mean temperature of the coldest quarter	**-0.9328**	-0.1455
bio2	Mean diurnal temperature range	**0.8964**	0.0675
bio8	Mean temperature of wettest quarter	**-0.8626**	-0.126
bio15	Precipitation seasonality	**0.8588**	0.1252
bio14	Precipitation of driest month	**-0.7152**	0.0567
bio13	Temperature seasonality	0.4536	**0.8479**
bio18	Temperature annual range	0.5959	**0.7636**
bio12	Minimum temperature of coldest month	-0.4761	**0.749**
Eigenvalue		8.9191	2.2842
% variation		63.7%	16.3

From the PCA plot it is also apparent that the niche breadth (as indicated by the 95% CI ellipses) varies considerably among species. Analysis of the homogeneity of dispersion (variance) from group centroids suggests that significant differences exist in the niche breadths of the study species ($F_{(8,151)} = 224.4$; $P \leq 0.001$). Post hoc (Tukey-Kramer) comparisons revealed that the majority of pairwise species combinations (64%) differed significantly in their degree of environmental dispersion from one another ($P \leq 0.05$). From these tests it is also apparent that *B. dracomonatanum* and *B. melanocephalum* occupy a considerably larger range of environmental conditions than all the other species ($P \leq 0.001$) but not from one another ($P = 0.55$, *ns*) while the opposite is true for *B.* sp. 7 (except when compared *B. caeruleogula*, $P = 0.07$, *ns*) and *B. ngomense* ($P \leq 0.05$) which occupy a significantly smaller range of conditions. The species *B. caeruleogula, B. nemorale, B setaroi, B.* sp.8 and *B. thamnobates* do not differ appreciably niche breadth from one another ($P \geq 0.05$). The pairwise comparison table is provided in **Appendix 1**.

When considering niche preference it was found that inland species occupy areas that are significantly colder during both summer ($F_{(1,820)} = 1900.66$; $P \leq 0.001$) and winter ($F_{(1,1014)} = 2209.21$; $P \leq 0.001$) months as well as being notably drier during the colder months ($F_{(1,620)} = 936.01$; $P \leq 0.001$) than those situated closer to the coast. Additionally, the conditions experienced by inland species are considerably more seasonal with regards to annual ($F_{(1,1045)} = 1433.9$; $P \leq 0.001$) and diurnal temperature range ($F_{(1, 750)} = 1211.68$; $P \leq 0.001$) as well as overall temperature ($F_{(1,1180)} = 1685.28$; $P \leq 0.001$) and precipitation seasonality ($F_{(1, 748)} = 1734.47$; $P \leq 0.001$). A proximity analysis performed in ArcMap^{tm} revealed that species defined in this study as “inland species” do indeed occur significantly further inland than those defined as being “more coastal” ($F_{(1,1233)} = 2568.85$; $P \leq 0.001$). An additional analysis on niche disparity (differences in the position of the niche within ordinal space) revealed that although some overlap occurs among species (**Figure 2**), significant differences exist in the environmental niche spaces occupied by the study species ($F_{(1,1223)} = 254.57$; $P \leq 0.001$). Post hoc comparisons using Tukey’s honestly significant difference test (Tukey's HSD) with Bonferroni corrections reveal that that all of the study species, with the exception of *B. melanocephalum* and *B. nemorale* ($P \geq 0.05$) and *B. dracomontanum* and *B.* sp. 7 occupy significantly different niche spaces ($P \leq 0.05$).

Correlation analysis revealed a strong and positive association between range size and the current extent of CSH ($r = 0.932$; $P \leq 0.001$) as well as a positive relationship ($r = 0.67$; $P \leq 0.05$) between range size and niche breadth (**Figure 2a-b**). However, no correlation between range size and remaining amounts CSH by 2050 (**Figure 2c**) was observed ($r = 0.197$; $P =$ *ns*). Additionally, no association between niche breadth and remaining amounts CSH by 2050 (**Figure 2d**) was found ($r = 0.032$; $P =$ ns). A strong positive, linear correlation ($r = 0.83$; $P \leq 0.01$) between the variance in winter rainfall (SD of bio 11) and the amount of remaining CSH by 2050 was uncovered (**Figure 3f**). Additionally, five of the eight PC1 associated variables namely mean diurnal temperature range (bio2), mean temperature of wettest quarter (bio8), mean temperature of the coldest quarter (bio11), precipitation of driest month (bio14) and precipitation seasonality (bio15) were found to be significantly correlated ($P \leq 0.05$) with the amount of remaining CSH by 2050 (**Figure 3, Appendix 2**).

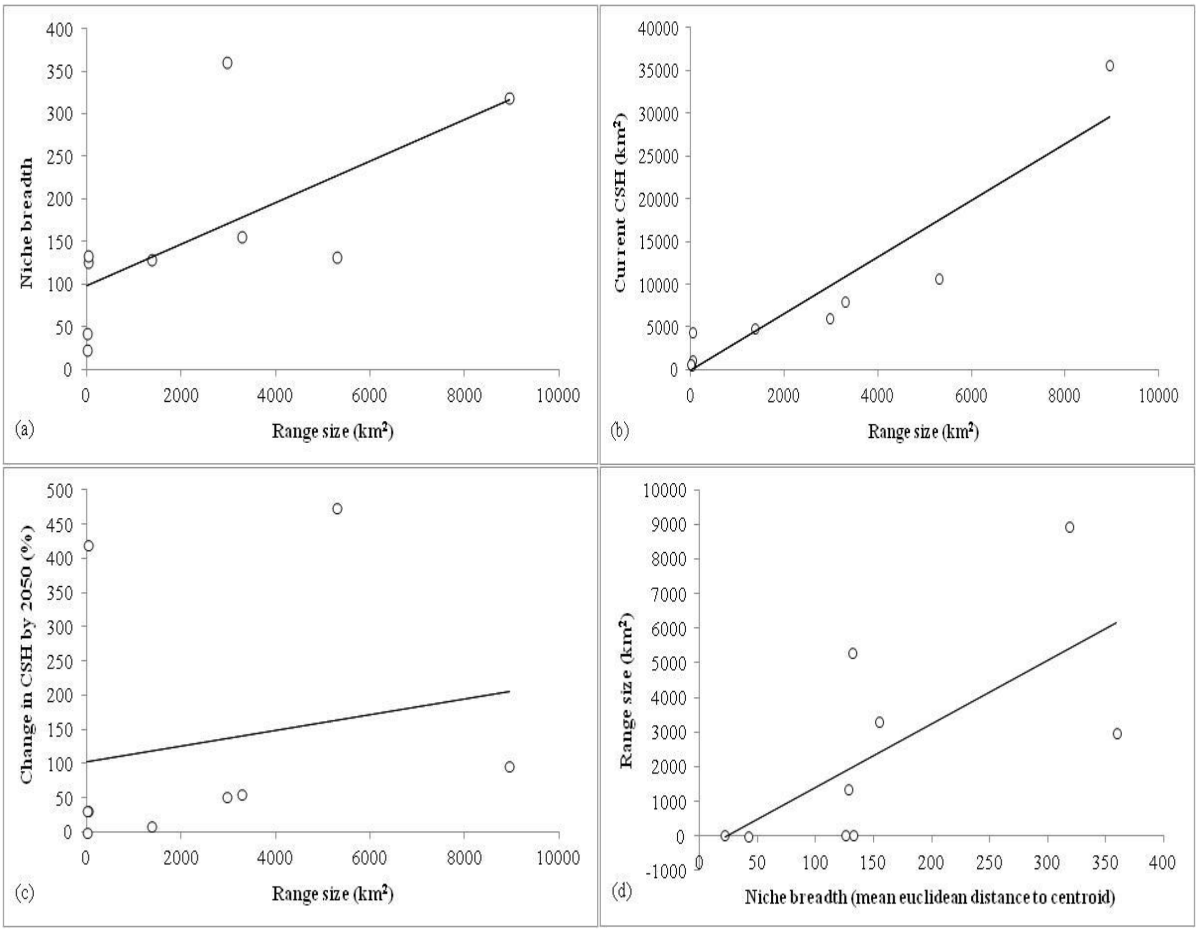

Figure 2: Results of the correlation analysis showing the relationship between (a) range size and niche breadth, (b) range size and current extent of CSH niche, (c) range size and the proportion of remaining CSH by 2050 and (d) niche breadth and the proportion of remaining CSH by 2050.

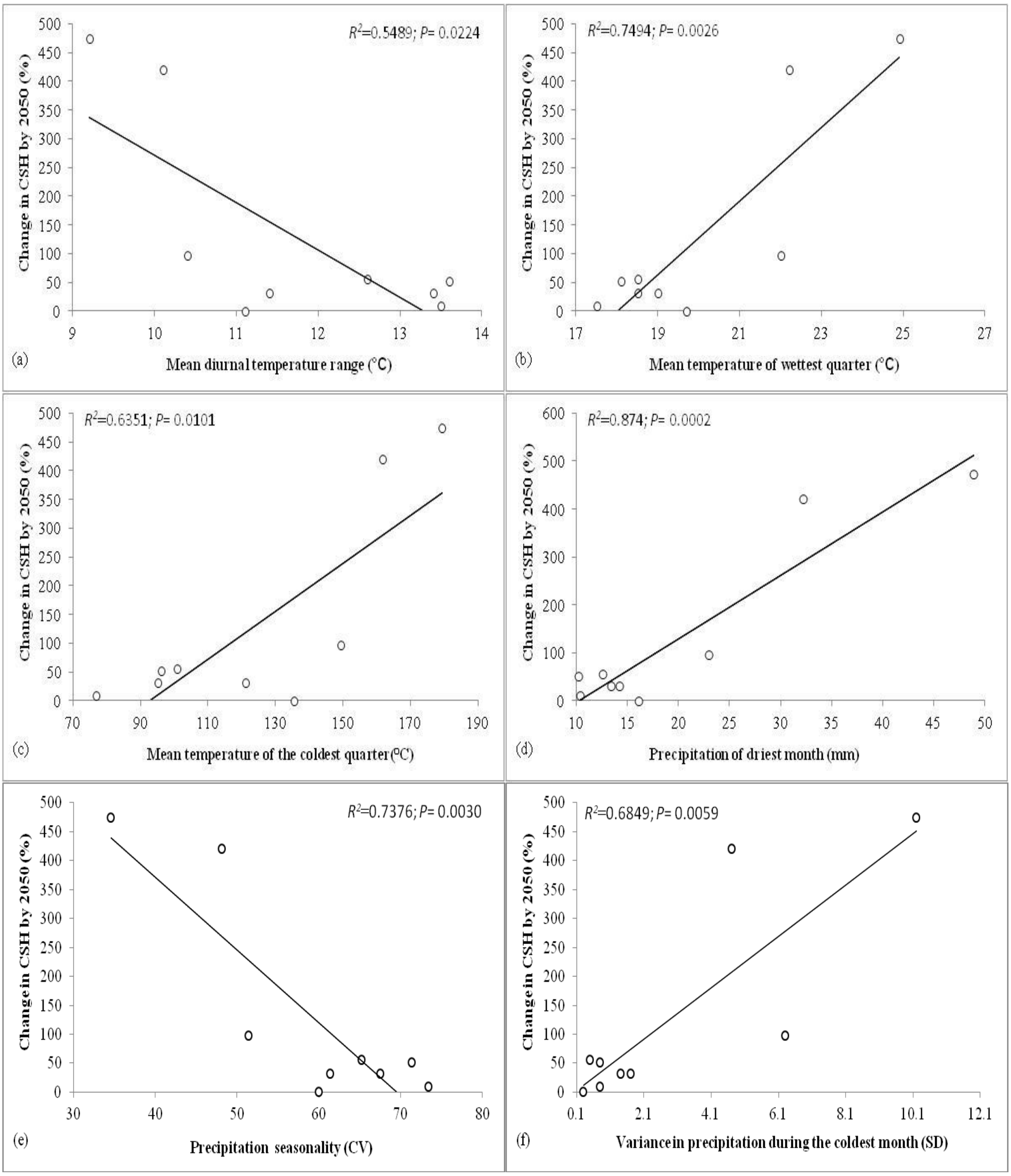

Figure 3: Results of the correlation analysis for the study species showing the significant relationships for (a) mean diurnal temperature range, (b) mean temperature of the wettest quarter, (c) mean temperature of the coldest quarter, (d) precipitation of the driest month, (e) mean temperature of the coldest quarter and (f) precipitation seasonality with the proportion of remaining CSH by 2050.

Discussion

Building on the findings from a previous study (Chapter 2) a distinction can be made in the modelled responses of KZN dwarf chameleons to future climate change. Specifically, between inland species, whose responses are marked by contractions in the availability of future climatically suitable habitat (CSH), and coastal species characterised by a maintenance or expansion in their extent of future CSH. In this investigation of some the most widely implicated macro-ecological predictors of climatic vulnerability (i.e. range size, niche breadth and niche preference), it is shown that although range size and niche breadth are correlated with one another, neither are appreciably correlated with the amount of CSH predicted to remain by 2050 as estimated by the modelling algorithm (Maxent) in Chapter 1. Instead it appears that the future availability of a specific set of climatic conditions (variables) typically associated with a species' occurrence, or its niche preference, better explained the modelled responses. More specifically, that species occupying climatically seasonal habitats where conditions are drier and cooler were more likely to contract as the climate becomes ever warmer and disproportionately drier inland. These species were also associated with a much lower variance in precipitation during winter suggesting that moisture may play a role in limiting species occurrence. Studies such as this are, however, subject to a number of limitations, at least until such time as a greater body of empirical ecophysiological information becomes available.

Perhaps the most well established macro-ecological pattern is the relationship between range size and niche breadth (Brown, 1984, Botts *et al*. 2013; Slatyer *et al*. 2013). In support of this view, this study suggests that, with some exceptions, KZN dwarf chameleons that tolerate a broader range of climatic conditions tend to occupy larger distributions. Slight outliers to this correlation included *B. dracomontanum* which was found to have a larger niche breadth than would be expected given the size of its range, and *B. melanocephalum* for which the opposite was true. Deviations such as this might be expected when considering the well-established positive correlation between topographical complexity and climatic diversity (Anderson *et al*. 2014; Stein *et al*. 2014; Badgley *et al*. 2017; Wang *et al*. 2018) and the spatial arrangement of these variables in KZN. *Bradypodion dracomontanum* occurs in the greatly incised terrain of the Drakensberg Mountains and surrounding foothills which, albeit far less extensive, is likely to be considerably more climatically diverse than the Indian Ocean Coastal Belt and adjacent lowland hills, occupied by *B. melanocephalum*. An additional pattern of increasing range restriction and climatic conservatism with increasing dependence on closed canopy habitats (habitat descriptions from Tolley and Burger; 2007 and Tolley *et al*. 2008) is inferred. An expected observation, given our current understanding of the evolutionary radiation of these chameleons (Tolley *et al*. 2008) and other ancestrally forest dwelling fauna (Lawes *et al*. 2007) and specifically, how they have responded to paleoclimatic induced vegetation shifts that has seen the progressive conversion forests to grassland and savanna over time (Mucina & Geldenhuys, 2006; Lawes, 1990). However, contrary to conventional macro-ecological theory, neither range size nor niche breadth (defined here as the range of climatic conditions associated with a species' occurrence) were found to be associated with the predicted amount of remaining CSH in future. Such results bear testament to the correlative nature of the modelling algorithm used, which does not account for ecological trends and biotic effects in its predictions but simply portrays the future availability of the suite of environmental conditions currently observed to be experienced by the species.

When considering niche preference, a number of distinctions can be made between the two main species groups. Most readily apparent is their position in ordinal space as evidenced by the PCA scatterplot (**Figure 1**). When considering the eight variables most strongly associated with PC1 (**Table2**) it was found that inland species tend to occupy habitats that are significantly cooler, drier and less seasonal (in terms of diurnal temperature range as well as temperature and precipitation seasonality) than those situated closer to the coast. This makes sense when considering oceanic effects. Nearer the coast, conditions are warmer, wetter and more buffered from large fluctuations in temperature and precipitation due to the presence of the warm Agulhas current (Reason *et al*. 2001). Additionally the correlation analysis revealed that five of these variables namely mean diurnal temperature range (bio2), mean temperature of wettest quarter (bio8), mean temperature of the coldest quarter (bio11), precipitation of driest month (bio14) and precipitation seasonality (bio15) are important in explaining the trend in climatic vulnerability observed among the species (defined as the amount of CSH predicted to remain suitable by 2050 as a proportion of their current extent of CSH). Additionally, a strong positive, correlation between the variance in winter rainfall and the amount of remaining CSH by 2050 was revealed (**Figure 3**). These results suggest that inland species tend to be more conservative in the range of precipitation they tolerate during winter months and as a consequence of their specificity are less likely to find their more specific suite of conditions in future. This suggests that inland species may be occupying habitats closer to the lower limits of their water balance thresholds and may be limited by the availability of precipitation during the driest months. The niche models (as provided in Chapter 2) also suggest that these species are less likely to find their more specific, combination of temperature and precipitation consistency as temperatures become hotter and disproportionally drier (and more irregular) westwards through the interior. Conversely, coastal species are less likely to experience as drastic a change in precipitation and are thus predicted to maintain a greater proportion of the current extent of CSH. Furthermore precipitation is less likely to be limiting for coastal species both at present and as predicted in future. Inland species are also significantly less specific with regards to variation in precipitation during the driest months, and are thus considered better able to capitalise on the expansion of warmer climate into wetter parts of KZN's interior.

Precipitation and temperature may be important in governing the current and future distribution of KZN dwarf chameleons. Indeed, when comparing their occurrences and climatic suitability with the environmentally defined floristic domains of KZN as modelled by Jewitt *et al*. (2015a) a clear lack of representation in drier areas of the province is apparent. This might be explained when considering that forest habitat is ancestral for dwarf chameleons and that some of the study species are still in the early stages of an evolutionary transition to more open habitats (Tolley *et al*. 2008) which are comparatively more desiccating. Over and above physiological adaption, for which there are inherent limitations, lizards most often manage to survive desiccating conditions through behavioural and microhabitat adjustments (Huey and Tewksbury 2009; Kearney *et al*., 2009; Ryan *et al*. 2015). Water constraints have been shown to negatively affect growth rate, activity and body temperature of lizards (Stamps and Tanaka 1981; Lorenzon *et al*. 1999) and as such movements, breeding and foraging tend to peak during wetter periods (Duda, Krzysik & Freillich, 1999; Shine and Brown, 2008). Although the overwintering behaviour of dwarf chameleons has not been formally documented, considerable anecdotal accounts suggests that at least some of the inland species seek shelter in areas of higher cover such as in cliff faces, houses and beneath logs and rocks. This is undoubtedly a response to the colder temperatures during winter but may also be response to the more desiccating conditions during this time. Certainly thermal stress and desiccation have been shown to be highly correlated in lizards (Crowley, 1987). Indeed it is becoming increasingly evident that water availability may have an equally if not greater influence on the behaviour of lizards (Davis & DeNardo, 2009; Ryan *et al*. 2015). Furthermore the results of this study are in alignment with the future distribution of forests in KZN as predicted by (Eeley *et al*. 1999) which suggest that inland forests, specifically Mistbelt and Afromontane forests, are likely to contract while expansions are predicted for coastal forests. All of the inland (predicted reduction in CSH), species are associated with Mistbelt or Afromontane forests and their surrounding grasslands, whereas all of the more coastal species (predicted expansion in CSH) are associated with coastal forests and their surrounding grassland and thicket.

It should be noted, however, that the models upon which this study is based, as with others of their type, simply provide a depiction of the spatial arrangement of the climatic associated with the observed tolerances drawn from the currently available distribution records. As such they are inherently limited by an assumption that where a species occurs is a fairly good approximation of the range of conditions it can tolerate (Phillips *et al*. 2006). It is important to note that the analyses presented here have the potential to be influenced by sampling inadequacies and / or bias as well as the resolution of the environmental data. Inadequate survey coverage and sampling bias may lead to an under prediction in the range of possible conditions tolerated by a species while the 30 arc-second resolution of the climatic has the potential to over generalise, particularly for the smaller ranging species. A possible solution to this limitation (not investigated here) might be to collect a large set of random pseudo-presences from the ecological niche model instead of using only data associated with true presences (known locality records). Additionally the models are somewhat limited in that they assume that climates, which may be wet enough eastwards, are too hot. However, it may be that the species are physiologically prepared to deal with an increase in temperature provide they can meet there water balance requirements. As such the models have the potential to be over pessimistic in their predictions of the species' responses to climate change. Nevertheless, inspection of the current and future spatial distribution of precipitation during the coldest months (bio 14) over KZN suggests that aridification is predicted to increase from east to west but that it is does so disproportionately in a large area in the provinces interior. If inland species were to meet their water requirements, in future, they would need to make a considerable shift closer to the coast where the aridification is not predicted to be as intense. However, this is unlikely to be a realistically viable for this group of small chameleons that are not renowned for their vagility. As such, although the models likely over predict range contraction to some degree they are not considered to do so drastically. This highlights the importance of physiological studies in refining such predictions. The results of this study allude to the importance of precipitation and temperature on shaping the biogeography of KZN dwarf chameleons and likely other biota. More ecophysiological studies are required that focus not only on the importance temperature but also precipitation and its relationship with temperature (the point at which moisture becomes limiting) in shaping species distributions.

Overall this study suggests that KZN dwarf chameleons differ not only in their spatial distributions but also in terms of their niche breadths and preferences, more so than would be expected by chance. These differences are reflected in their differing evolutionary paths in response to paleoclimatic change, and hint at their possible responses to climatic changes in the future. Furthermore the findings of this study suggest that the direction of a species' response, as predicted by correlative niche models, is largely contingent on its climatic niche preference and its alignment with a set of key variables likely to become limiting under the forecasted conditions. More specifically, that species occupying seasonal habitats where conditions are more desiccating during winter are more likely to contract as the climate becomes warmer and disproportionately drier inland.

Chapter 4: Conclusion

This work was founded on a growing concern for the way in which human-induced changes are accelerating species extinctions globally, and the pressing need for practical and pre-emptive information to guide conservation prioritisation. Today the deleterious human-induced erosion of biodiversity and ecosystem services continues unabated and has triggered a cascade of co-extinctions that may come to be known as the period of "biological annihilation" during what is already known as the sixth, ongoing mass extinction (Ceballos *et al.*, 2019; Strona *et al.*, 2018). A seminal paper by Myers *et al.*, (2000) highlighted that biodiversity is not distributed evenly across the world but instead is concentrated in hotspots and that these locations, particularly those supporting high species endemism that also face high levels of threat, should be prioritised for conservation. With this in mind it was of upmost importance that this thesis was focussed on providing important practical information that could contribute towards the protection of threatened hotspots of species endemism. In response I chose to investigate the effects of two of the greatest threats to global biodiversity (climate and land use change) on a genus of chameleons largely endemic to the rapidly developing province of KwaZulu-Natal, South Africa.

Through the production of this thesis important spatial information was generated on the extent of climatically suitable natural habitat (CSNH) available to each of KwaZulu-Natal's (KZN) nine dwarf chameleon species, at present and under future scenarios of climate and land use change. Using these data, it was found that the dwarf chameleons of KZN do indeed show varying degrees of susceptibility to the combined effects of these global change drivers (Chapter 2). This susceptibility was in turn shown to be associated with niche preference and how that preference is anticipated to align with the forecasted conditions.

While losses of CSNH were predicted for the inland species a maintenance or expansion in CSNH was predicted for those situated closer to the coast. As climate was found to be the dominant driver responsible for the losses predicted within the inland species, this became the focus of a subsequent investigation to uncover traits which may infer higher vulnerability (Chapter 3). This investigation revealed that the susceptibility of inland species was linked to niche preference and the degree to which a given species was associated with a key set of climatic variables forecasted to become limiting in future. More specifically, inland species tend to occupy habitats that are significantly cooler, drier and less seasonal (in terms of diurnal temperature range as well as temperature and precipitation seasonality) than species situated closer to the coast. The models suggest that inland species are less likely to find their more specific suite of climatic conditions, particularly with regards to precipitation during winter, as the climate becomes ever warmer and disproportionately drier inland.

With this in mind my attention turned towards estimating how much of each species' CSNH coincides with the provinces protected areas network both at present and as predicted by 2050. In so doing, the crucial role that the Ezemvelo KZN Wildlife (EKZNW) protected areas network has played in preserving crucial pockets of land for these chameleons became evident. A prime example being *B. caeruleogula, B. ngomeense and B. nemorale*, for which precious little of their forest habitat occurs outside of reserves. However, this investigation revealed that CSNH for three species (*B. melanocephalum, B. thamnobates and B. sp. 7*) is negligible within the EKZNW protected areas network (< 11%). More concerning still is that by 2050 notable reductions in the extent of CSNH within protected areas are predicted for all but two (*B. caeruleogula* and *B. dracomontanum*) of the province's dwarf chameleon species. Consequently, it would appear that several species may warrant higher levels of conservation attention than would otherwise be assumed given their current threat status.

Considering the relative contributions of each change driver to overall loss it is recommended that an adaptive approach to habitat preservation be adopted for the species within each group. For inland species the continued availability of climatically suitable habitat is likely to be a considerably more limiting factor than the availability of untransformed habitat. For these species it is suggested that protected areas expansion be focused on protecting areas predicted to remain climatically suitable in future especially those which overlap known populations. Incised terrain might prove particularly important as refugia for these species due to the strong correlation between climatic diversity and topographic complexity and the scope it provides in terms of behavioural responses that may allow for persistence in microhabitat refugia (e.g. sheltering in gorges or movements up or down slopes). In contrast, species occupying areas closer to the coast are anticipated to be more climatically resilient, and for these species conservation of as much of their limited amount of remaining natural habitat is particularly important. Ultimately however, the effective designation of conservation areas for these species needs to be informed by a multitude of other information not provided here. For example more information is required on the habitat associations of these species and their tolerance towards habitat degradation.

Such information would help to inform potential relocation or habitat rehabilitation efforts in future.

Although this study takes important preliminary steps towards anticipating how KZN's dwarf chameleons may respond to climate and land use change, refinements in spatial datasets and a considerable amount of further research are required to better complete the picture. Firstly, the overall accuracy of the models was limited by the resolution of the climatic variables and the lack of detailed future land use change data produced under different management scenarios. Additionally, the models are limited by the assumption that the current set of locality records upon which they are based represent the full spectrum of conditions tolerated by the species, which may not be the case. This highlights the need for more empirical ecophysiological studies on these species to refine model predictions. Lastly, it is important to remember that the actual response taken by these species is also likely to be contingent on how well they will be able to track suitable climate as well as cope with the changing conditions through adaption and persistence in climatic refugia. Although dispersal to novel areas in response to climate is considered unlikely, research on the patch connectivity, demographics and movement ecology of these species is required to make informed predictions in this regard. Likewise, more studies are required on the genetic and phenotypic adaptability of these species in the face of impending climate change, while studies on population changes in anthropogenically transformed habitats may help to establish their resilience to land use change. Perhaps more challenging to quantify, yet equally important will be the role that behavioural responses may play in allowing species to persist in microhabitat refugia, not captured by the landscape-scale spatial data used in this study.

In spite of the limitations, this study provides useful and urgently needed information which can be used to better guide conservation efforts for the provinces largely endemic dwarf chameleon assemblage. It would appear that some species may be more susceptible than others to the effects of climate and land use change. These findings may have similar implications for other fauna that have taken similar evolutionary paths in response to paleoclimatic induced shifts in forest habitats within this biodiverse region. The importance upholding and pre-emptively expanding the provinces protected areas network to keep pace with the impending changes cannot be stressed enough.

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Appendices

Appendix 1: Results of the post-hoc Tukey’s honestly significant difference test (Tukey's HSD) conducted with Bonferroni corrections for the permutational MANOVA on niche disparity among species.

Pairs	df.	Sums of Sqs.	F. Model	r^2	*P.* value
B. thamnobates vs B. melanocephalum	137018791.7	1634.51	0.68	0.001	P<0.05
B. thamnobates vs B. sp. 8	14185296.4	470.11	0.48	0.001	P<0.05
B. thamnobates vs B. dracomontanum	1562853.6	32.06	0.08	0.001	P<0.05
B. thamnobates vs B. sp. 7	2386632	74.99	0.17	0.001	P<0.05
B. thamnobates vs B. setaroi	77415630.3	2493.08	0.84	0.001	P<0.05
B. thamnobates vs B. ngomeense	46977119.8	1518.51	0.8	0.001	P<0.05
B. thamnobates vs B. nemorale	12740648	374.5	0.51	0.001	P<0.05
B. thamnobates vs B. caeruleogula	35800051.4	1067.93	0.74	0.001	P<0.05
B. melanocephalum vs B. sp. 8	164222421.2	1729.31	0.74	0.001	P<0.05
B. melanocephalum vs B. dracomontanum	16733930.9	132.27	0.22	0.001	P<0.05
B. melanocephalum vs B. sp. 7	9390664.4	82.15	0.15	0.001	P<0.05
B. melanocephalum vs B. setaroi	2225689.1	22.22	0.04	0.001	P<0.05
B. melanocephalum vs B. ngomeense	3326464.9	29.73	0.06	0.001	P<0.05
B. melanocephalum vs B. nemorale	135265.5	1.14	0	0.284	P>0.05
B. melanocephalum vs B. caeruleogula	4436292.7	37.9	0.08	0.001	P<0.05
B. sp. 8 vs B. dracomontanum	7675423	150.8	0.43	0.001	P<0.05
B. sp. 8 vs B. sp. 7	10656038.9	580.29	0.75	0.001	P<0.05
B. sp. 8 vs B. setaroi	107875527.6	5025.68	0.95	0.001	P<0.05
B. sp. 8 vs B. ngomeense	70776497.5	4080.28	0.95	0.001	P<0.05
B. sp. 8 vs B. nemorale	23345629.7	1075.74	0.86	0.001	P<0.05
B. sp. 8 vs B. caeruleogula	51876013.2	2456.19	0.93	0.001	P<0.05
B. dracomontanum vs B. sp. 7	592116.4	5.95	0.08	0.009	P>0.05
B. dracomontanum vs B. setaroi	16881826	289	0.64	0.001	P<0.05
B. dracomontanum vs B. ngomeense	18798225.1	217.07	0.73	0.001	P<0.05
B. dracomontanum vs B. nemorale	6245126.4	47.64	0.46	0.001	P<0.05
B. dracomontanum vs B. caeruleogula	17592216.7	148.4	0.71	0.001	P<0.05
B. sp. 7 vs B. setaroi	10841486.7	601.09	0.79	0.001	P<0.05
B. sp. 7 vs B. ngomeense	12694620	5259.4	0.99	0.001	P<0.05
B. sp. 7 vs B. nemorale	3878396.6	343.77	0.88	0.001	P<0.05
B. sp. 7 vs B. caeruleogula	13448167.9	1288.47	0.96	0.001	P<0.05
B. setaroi vs B. ngomeense	3138303.5	186.82	0.53	0.001	P<0.05
B. setaroi vs B. nemorale	750299.4	33.7	0.19	0.001	P<0.05
B. setaroi vs B. caeruleogula	2620750.2	121.85	0.45	0.001	P<0.05
B. ngomeense vs B. nemorale	854969.2	95.8	0.62	0.001	P<0.05
B. ngomeense vs B. caeruleogula	1138670	135.02	0.68	0.001	P<0.05
B. nemorale vs B. caeruleogula	2065867.6	91.06	0.69	0.001	P<0.05

Appendix 2a: Means of the Euclidean distances to centroid for each species, their standard deviation and code for the pairwise comparisons in (b).

Code	Species	N	Mean Euclidean distance to centroid	Std. Dev.
1	*B. caeruleogula*	24	127.81	56.23
2	*B. dracomontanum*	39	361.83	209.05
3	*B. melanocephalum*	444	327.63	120.44
4	*B. nemorale*	18	147.56	54.64
5	*B. ngomeense*	42	24.68	34.69
6	*B. setaroi*	127	134.14	59.67
7	*B.* sp. 7	32	44.33	34.06
8	*B.* sp. 8	164	128.93	67.26
9	*B. thamnobates*	344	156.11	99.86

Appendix 2b: Post hoc (Tukey-Kramer) pairwise comparisons between species with regard to their niche breadth. The P values were adjusted using least squares means adjustments for multiple comparisons. See (a) for species codes.

Pr > |t| for H0: LS Mean (i) = LS Mean(j)

i/j	1	2	3	4	5	6	7	8	9
1		***	***	ns	**	ns	ns	ns	ns
2	***		ns	***	***	***	***	***	***
3	***	ns		***	***	***	***	***	***
4	ns	***	***		***	ns	*	ns	ns
5	**	***	***	***		***	ns	***	***
6	ns	***	***	ns	***		***	ns	ns
7	ns	***	***	*	ns	***		***	***
8	ns	***	***	ns	***	ns	***		ns
9	ns	***	***	ns	***	ns	***	ns	

* p<0.05; ** p < 0.01; *** p<0.001; ns=not significant