The effects of environment and niche on the distributions of dwarf chameleons, present and future.

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Abstract

The niche and niche breadth of Dwarf Chameleons, *Bradypodion*, was assessed in terms of broad scale climatic factors. A niche-based modelling method was then used to construct present and future habitat suitability maps for 2050 and 2080, for species in the genus. Additionally, the relationship between environment and morphology was analysed for a representative *Bradypodion* species, the Cape Dwarf Chameleon, *B. pumilum*.

The niche and niche breadth of species and phylogenetic clades were analysed and described via an ordination technique, the outlying mean index (OMI) analysis. Maxent (v2.3), a presence only niche modelling method, proved very useful in the construction of present and future habitat suitability maps for species within the genus. For analysis of the correspondence between environment and morphology for *B. pumilum*, regression trees were employed.

Rainfall seasonality and maximum annual temperatures were shown to strongly effect the current distributions of the genus *Bradypodion* at both the species and clade level. Additionally, as closely related species inhabited similar environmental niches, the genus was shown to display a degree of niche conservatism. All species and clades were shown to respond to climate change scenarios for 2050 and 2080, but responses were individualistic. However, most demonstrated range contractions under predicted climate scenarios. Additionally, a strong correlation ($p < 0.05$) was found between the morphology of *B. pumilum* and its environment. Environmental factors explained over 40% of the variation in snout-vent length and tail length, and over 20% of the variation in head width and head height, thus supporting the hypothesis of a correspondence between vegetation and morphology in *Bradypodion*.

These results have provided an understanding of the relationship between *Bradypodion* and their environments that could provide valuable information regarding their ecology. Additionally, the habitat suitability maps for 2050 and 2080 could prove useful in the construction of any future conservation plans for these species. Furthermore, the results support the hypothesis of a correspondence between environmental factors and morphological traits within the genus *Bradypodion*.

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Chapter 1

General Introduction

Chameleons

The majority of Chameleons are distributed through Africa and Madagascar, including some of the neighbouring islands, and also occur in restricted areas of southern Europe, Arabia and India (Hofer *et al.* 2003, Tolley and Burger 2007). There are about 150 species, comprising nine genera: *Brookesia*, *Calumma*, *Furcifer*, *Bradypodion*, *Rhampholeon*, *Rieppeleon*, *Kinyongia*, *Nadzikambia* and *Chamaeleo* (Tolley and Burger 2007). Six of the genera occur in Africa, and two, *Chamaeleo* (typical chameleons) and *Bradypodion* (Dwarf Chameleons), are represented in South Africa (Tolley and Burger 2007). These two South African genera comprise two *Chamaeleo* species and currently 15 recognised *Bradypodion* species (Tolley and Burger 2007).

Bradypodion

The genus *Bradypodion* is endemic to, and widespread throughout, South Africa. They are small (generally not longer than 15 cm), allopatrically distributed and have potential contact zones between them (Branch 1998, Tolley *et al.* 2006, Tolley and Burger 2007). Although allopatrically distributed, there are areas in South Africa where their distribution overlaps with that of the two *Chamaeleo* species (Tolley and Burger 2007). *Bradypodion* are highly dependent on crypsis, thus dependent on vegetation for predator avoidance and obtaining food (Tolley *et al.* 2006).

The morphological and genetic variation within and between species of the genus *Bradypodion* makes species description complicated, thus there are still a number of undescribed species (Tolley *et al.* 2006, Tolley and Burger 2007, Tolley *et al.* in review). There can be a number of morphological forms comprising just one species, such as in *B. transvaalense* and in *B. pumilum*, while two different species can look very similar, such as one form of *B. pumilum* resembling *B. occidentale* (Tolley and Burger 2007). Thus, the factors driving the morphology of these species differ to those driving genetic variation (Tolley *et al.* 2006).

The genus *Bradypodion* occurs in a wide array of vegetation types, these can be broadly classified into open and closed habitats (Tolley *et al.* 2004, 2006, Tolley and Burger 2007). However, they are absent from the very dry areas such as in areas of the Karoo and in areas of the Kalahari (Tolley and Burger 2007). In general, closed habitats are characterised by tall trees with a high canopy, typical of forested or semi-forested areas and can include both exotic and native trees. Open habitats are generally dominated by low shrubs and small bushes and are typical of areas dominated by Mediterranean scrub, such as fynbos, but also include grasslands. Additionally, *Bradypodion* species show morphological variation within these different habitat types (Tolley *et al.* 2006, Tolley and Burger 2007, Measey *et al.* in review) that is thought to provide a survival advantage in these structurally different habitats (Tolley *et al.* 2006, Stuart-Fox and Moussalli

2007, Measey *et al.* in review). Individuals occurring in closed habitats tend to be large, with a high casque and bright colours. In contrast individuals from open habitats tend to be smaller, with a small casque and drab colouration (Tolley *et al.* 2006, Stuart-Fox and Moussalli 2007, Tolley and Burger 2007, Measey *et al.* in review).

Bradypodion pumilum is a large dwarf chameleon, reaching *c.* 14cm in length (Tolley and Burger 2007) and is considered an active forager of insects (Branch 1998, Butler 2005, Tolley and Burger 2007). It occurs within the southwestern corner of the Western Cape, South Africa (Tolley and Burger 2007), and despite occupying a relatively restricted range, it is found within a variety of habitats where two morphological forms (ecomorphs) occur within different vegetation types (Tolley *et al.* 2006, Tolley and Burger 2007). The typical ecomorph tends to be large, long-tailed and colourful, occurring predominantly in closed habitats comprising closed canopy vegetation types such as urban gardens, forests, scrub and thickets. The second ecomorph is smaller, has a short tail and dull colouration, and inhabits open habitats such as montane and lowland fynbos areas (Tolley *et al.* 2006, Tolley and Burger 2007, Measey *et al.* in review). Thus, *B. pumilum* was selected as a representative species of the genus *Bradypodion*, and particular focus is given to this species in the present study.

The ***Bradypodion*** niche

Understanding the relationship between species and their environments is essential in understanding aspects of their ecology (Ter Braak 1986), and given the variety of habitats occupied by different chameleon species (Bickel and Losos 2002), this could be especially true for this group of reptiles. However, individual species generally occur within specific environments and are subsequently affected by a limited combination of environmental factors (Wiens 2004). The occurrence of species inhabiting a restricted environmental niche within a large geographic area has been demonstrated in various lizard species (e.g. Vitt 1991, Vanhooydonck and Van Damme 1999, Losos 2001, Zaaf and Van Damme 2001, Langerhans *et al.* 2006). For example, different populations of the southwestern American lizard *Urosaurus ornatus* occupy structurally different microhabitats (e.g. rocks and trees; Herrel *et al.* 2001), while some species of anoles occupy aquatic environments (Leal *et al.* 2002). Additionally, individual *Bradypodion* species occur within specific habitats, including fynbos, renosterveld, indigenous and exotic forests, urban gardens, grasslands and even limited areas in the Karoo (Tolley and Burger 2007).

Various definitions have been formulated to define the concept of a niche (e.g. Green 1971, Leibold 1995). However, for the purposes of this study I made use of Hutchinson's (1957) definition, as it is widely used (e.g. Green 1971, Dolédec *et al.* 2000, Guisan and Zimmerman 2000, Jackson and Overpeck 2000, Pearson and Dawson 2003, Thuiller *et al.* 2004, Knouft *et al.* 2006, Pearson *et al.* 2007) and fairly general. According to Hutchinson (1957), an ecological niche is an imaginary *n*-dimensional space, in which each dimension represents a particular environmental factor necessary for the survival of a species, and in which an individual's fitness and net population growth rate is positive (Green 1971, Leibold 1995, Dolédec *et al.* 2000, Pulliam 2000, Thuiller *et al.* 2004). Thus, the niche of a particular *Bradypodion* species would consist of the range of environmental variables that the species could tolerate and include that geographical area within an ecological space where the species could survive indefinitely.

Niches and climate change

As a relationship exists between a species and its environment that could determine its range, it is expected that changes in climate (*i.e.* environment) could affect the range of a species. The earth's climate is continually changing, but for the past 65 million years paleoclimate records show fluctuations from periods of extreme warmth to periods of extreme cold (Zachos *et al.* 2001). The start of the Cainozoic (*c.* 65 million years ago) was characterised by global temperatures which were warmer than present (Williams *et al.* 1998). Following this was a gradual global cooling trend that continued through this period up until the early Pliocene when conditions warmed slightly (Williams *et al.* 1998). However, the entire period was punctuated by a series of fluctuations (Williams *et* *al.* 1998, Zachos *et al.* 2001). Conditions then cooled in the late Pliocene and subsequent warm and cold fluctuations occurred in the Quaternary period, with present day conditions representing a Quaternary warm phase (Williams *et al.* 1998). Very recent global warming trends (*i.e.* the last 150 years) are the likely result of increases in anthropogenic green house gas concentrations (IPCC 2007).

Between 1850 and 2005 global temperatures increased by *c.* 0.6°C, and it has been predicted that during the 21st century temperatures could on average increase another 3 – 6°C (Midgley *et al.* 2005). Although predictions vary, for southern Africa they generally show an increase of approximately 3 – 7°C by *c.* 2100 (Boko *et al.* 2007). Changes in rainfall are more difficult to predict (Midgley *et al.* 2005, Boko *et al.* 2007), but it is thought that rainfall will not change by more than *c.* 20% of current levels (Midgley *et al.* 2005). However, this varies from region to region and it is uncertain whether the change will represent an increase or decrease in rainfall from present figures (Midgley *et al.* 2005). These predicted rapid climatic shifts, together with other stressors such as habitat transformations (Root *et al.* 2003) pose serious challenges for future species conservation. Furthermore, predictions on how these changes will affect species in the future are becoming increasingly vital in protected area management (Midgley *et al.* 2002).

Climate change may affect species in various ways (Hughes 2000, Parmesan *et al.* 2000, Root *et al.* 2003, Root *et al.* 2005, Parmesan 2006) and it has been suggested that many species have responded to current climatic trends (Hughes 2000, Parmesan *et al.* 2000, McCarty 2001, Burns *et al.* 2003, Root *et al.* 2003, Foden *et al.* 2007). Due to the uncertainties of species responses to climate change, it is uncertain how the present day protected areas will be able to continue to conserve the species within them (Burns *et al.* 2003, Araújo *et al.* 2004, Thuiller *et al.* 2006).

Reptiles and climate change

Linkages have been postulated between current amphibian population declines and climate change (Alford and Richards 1999, Gibbons *et al.* 2000, Houlahan *et al.* 2000, Kiesecker *et al.* 2001, Collins and Storfer 2003, Corn 2005, Pounds *et al.* 2006). Reportedly due to climate change, current reptile declines are believed to be similar to those of amphibians regarding geographic distributions and severity (Gibbons *et al.* 2000, Araújo *et al.* 2006). However, few studies have addressed the effects climate change could have on reptiles (Guisan and Hofer 2003, Araújo *et al.* 2006). Climate change effects are further compounded by the suggestion that reptiles are generally poor dispersers (Araújo *et al.* 2006) and thus highly vulnerable to rapid climate change (Araújo and Pearson 2005).

The dependence of the genus *Bradypodion* on crypsis (Tolley *et al.* 2006) implies they are vulnerable to climatic fluctuations that lead to shifts in vegetation structure (Tolley *et al.* 2006). Additionally, habitat shifts in connection with climatic fluctuations were shown to impact on the phylogenetic pattern within the genus (Tolley *et al.* in review). To understand whether chameleons in this genus are vulnerable to rapid climatic shifts, an analysis that considers and predicts these impacts would be extremely useful. On a global context, such an analysis would add to the sparse information available on the effects of climate changes on reptiles in general. The analysis could be achieved via a niche-based modelling approach. Such aspects have already been considered in Madagascar, whereby a niche-based modeling approach proved useful in providing information relating to the expansion of conservation networks (Raxworthy *et al.* 2003).

Niche and morphology

The morphological traits of a species often correspond to its environmental niche (Knouft *et al.* 2006) and natural selection on these traits may lead to the establishment of different morphological forms within different environments (Wiens 2004). This species-environment relationship has been documented in many species, including lizards (e.g. Fleishman 1992, Vitt *et al.* 1997, Butler *et al.* 2000, Herrel *et al.* 2001, Kohlsdorf *et al.* 2001, Losos and Miles 2002, Ackerly 2003, Glor *et al.* 2003) and fish (e.g. Chapman *et al.* 2000, Bouton *et al.* 2002, Langerhans *et al.* 2007). Furthermore, the common occurrence of distinct phenotypes in different environments suggests the adaptive value of distinct morphological traits within different habitats (Ackerly 2003).

In general chameleons show substantial morphological variation within the wide array of habitats occupied (Bickel and Losos 2002). However, as morphologically variable as they are, their morphology has largely adapted towards an arboreal lifestyle (Losos *et al.* 1993, Hofer *et al.* 2003), but the degree of arboreality between species varies (Losos *et al.* 1993, Bickel and Losos 2002). Despite being well studied in various lizard species (Scheibe 1987, Pounds 1988, Vitt *et al.* 1997, Vanhooydonck and Van Damme 1999, Kohlsdorf *et al.* 2001, Zaaf and Van Damme 2001, Leal *et al.* 2002), chameleons have been subject to few ecomorphological analyses (Losos *et al.* 1993, Bickel and Losos 2002). This is largely due to the lack of ecological, morphological and distributional information for many chameleon species (Bickel and Losos 2002).

Bradypodion demonstrate an apparent correspondence between phenotypes and structurally different vegetation types (Tolley *et al.* 2006, Tolley and Burger 2007, Measey *et al.* in review). These ecomorphs are most likely the result of strong selection brought about by long-term vegetation shifts and colonisation of these novel habitats (Tolley *et al.* 2006). The presence of different ecomorphs in structurally different habitats could be the result of selective pressures favouring predator avoidance over signalling ability in open habitats (Stuart-Fox *et al.* 2006, Measey *et al.* in review). Individuals in open habitats are more exposed and therefore likely to be more vulnerable to predation than individuals in closed habitats, and are thus under strong phenotypic selection to maintain the duller and smaller ecomorph (Measey *et al.* in review). Additionally, within closed habitats, mating is often accompanied by both male and female courtship displays (Stuart-Fox and Whiting 2005, Stuart-Fox *et al.* 2006). Thus, communication at a distance is far less effective in the open habitat phenotype and it is expected that displays occur at much closer quarters (Measey *et al.* in review), reducing the need for secondary sexual characters such as large, brightly coloured casques.

Study aims

Species within the genus *Bradypodion* occupy a wide variety of habitats and an understanding of the niches occupied by the species could prove useful in understanding species ecology. Furthermore, due to their dependence on vegetation, and in light of the demonstrated association between paleoclimatic shifts and phylogenetic patterns, *Bradypodion* can be used as a model to study the vulnerability of species to climate change. Additionally, there is an apparent correspondence between phenotypes and their respective environments. This implies strong environmental selection on species morphology.

To understand and predict effects of shifting environments on the *Bradypodion*, this study has three main aims:

1) To distinguish and describe the ecological niche occupied by *Bradypodion*, based on broad scale environmental variables.
2) To examine the possible effects climate change could have on these species, particularly *B. pumilum*.
3) To assess the relationship between the morphology of *B. pumilum* and a suite of habitat variables.

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Chapter 2

Ecological niche of *Bradypodion*, the endemic South African Dwarf Chameleons

Abstract

A range of environmental factors affect species niches, and these presumably influence the current distribution of a species. Furthermore, closely related species can share similar environmental niches, with species often tracking their preferred habitats rather than adapting to new ones. In the present study, an ordination technique was applied to determine the principal environmental factors governing the distributions of the endemic South African Dwarf Chameleons (*Bradypodion*). In addition, the presence of niche conservatism in the genus was tested by incorporating phylogenetic information. Rainfall seasonality and maximum annual temperature were found to strongly constrain the niche breadth of *Bradypodion*, thereby influencing distributions of the species. There was no general rule regarding niche conservatism, as some species were shown to demonstrate conservatism, whereas other species did not. These results provide important ecological knowledge on some of the environmental factors governing the distributions of species within the genus *Bradypodion*.

Introduction

Species can occur across a wide array of environments, but often have local occurrences limited by quite specific combinations of environmental factors (Wiens 2004). This is demonstrated in various lizard species that inhabit limited environmental niches within larger geographic areas that are tolerable by lizards overall (e.g. Vitt 1991, Vanhooydonck and Van Damme 1999, Zaaf and Van Damme 2001). For example, lizards occurring within the cerrado vegetation of South America segregate spatially based on differing microhabitats, such as exposed terrestrial areas, trees and grasses, within a large geographic range (Vitt 1991). Anoles on individual islands of the Greater Antilles make use of microhabitats by spatial segregation based on habitat structural characteristics (Losos 2001, Langerhans *et al.* 2006). Given this pattern of habitat partitioning in reptiles, understanding the relationship between a species and its environment at fine and course resolutions is essential for answering questions relating to their ecology.

An important assumption of ecological models predicting species distributions is that related to the concept of a niche (Guisan and Zimmermann 2000, Guisan and Thuiller 2005). Hutchinson (1957) defined an ecological niche as an imaginary, *n*-dimensional space, in which each dimension represents a particular environmental factor necessary for the survival of a species, and in which an individual's fitness, and net population growth rate, would be positive (Green

1971, Leibold 1995, Dolédec *et al.* 2000, Pulliam 2000, Thuiller *et al.* 2004). This concept was further extended to include the fundamental and realised niche (Pulliam 2000, Ackerly 2003, Thuiller *et al.* 2004). The fundamental niche theoretically defines the total range of environmental variables, without the influence of biotic factors, within which a species can exist indefinitely, and therefore relies predominantly on a species' physiological tolerances (Hutchinson 1957, Liebold 1995, Guisan and Zimmermann 2000, Thuiller *et al.* 2004, Knouft *et al.* 2006). The realised niche is a subset of the fundamental niche that reflects further constraints by biotic and stochastic factors, *i.e.* as revealed by the actual geographic distribution of a species (Austin and Smith 1989, Liebold 1995, Pulliam 2000, Thuiller *et al.* 2004).

It has been suggested that competing species within a community preferentially occupy habitats closely matching those in which they have evolved (Ackerly 2003, Wiens 2004; see also Webb *et al.* 2002 who review the link between habitat use, phenotypes and phylogenies). This "sorting" of species could promote stabilising selection (Ackerly 2003), resulting in niche conservatism over time (Webb *et al.* 2002, Ackerly 2003); in contrast, Broennimann *et al.* (2007) discussed the potential of a species to invade novel habitats. Due to a species' failure to adapt to novel environments, niche conservatism could play an important role in allopatric speciation (Wiens 2004). Numerous lineages of *Anolis* lizards demonstrate long-term stability in macro-habitat affinities, with some macro-habitats containing ancient lineages, indicating niche conservatism over an extended period (Glor *et al.* 2003). However, Knouft *et al.* (2006) found no evidence for niche conservatism in the *Anolis sagrei* group in Cuba. Some closely related species were found to occupy contrasting niches, while other more distantly related species occupied very similar niches (Knouft *et al.* 2006). Thus, the relationship between reptile species and their environments seems extremely variable and complex.

Competitive interactions between species and populations of *Anolis* lizards have been suggested as a major contributing factor towards their being able to invade and adapt to novel environments (see Losos 2001, who discusses this link in anole lizards occurring within the Greater Antilles). In two sympatric species, for example, phenotypic plasticity and competitive interactions may allow one to better exploit a particular niche. Initially, due to the lack of a genetic basis this does not represent an evolutionary change, but over time genetic differences may develop (Losos 2001). When the competitive influences (biotic interactions) are removed from a system species are able to fill a broader niche, which may not previously have been available to them (Losos 2001, Broennimann *et al.* 2007).

There have been numerous hypotheses to explain niche conservatism: "a lack of variability, natural selection, pleiotropy, and gene flow" (Wiens 2004). Natural selection could maintain ecological niches over time by the reduction of fitness for a species or population in surrounding, alternate niches (Wiens 2004). Thus, traits favouring a species' ancestral niche would be maintained (Lord *et al.* 1995, Wiens 2004). Behavioural habitat selection has also been suggested as a possible factor as a species cannot adapt to new habitats if it is not exposed to them (Wiens 2004). It can thus be argued, that even when species have the ability to adapt to new environments, natural selection and habitat preferences should work towards maintaining that species within its ancestral niche (Wiens 2004).

Pre-existing locality records have been valuable in various studies for quantifying the concept of a realised niche, and to model and understand ecological distributions of both plants and animals (e.g. Guisan and Hofer 2003, Raxworthy *et al.* 2003, Brotons *et al.* 2004, Engler *et al.* 2004, Thuiller *et al.* 2004, Thuiller *et al.* 2006). To date, few of these have focused on reptiles (Guisan and Hofer 2003, Raxworthy *et al.* 2003, Araújo *et al.* 2006, Knouft *et al.* 2006, Pearson *et al.* 2007). Various ordination methods have been implemented in an attempt to quantify species niche and niche breadths (Hurlbert 1978); including correspondence analysis (Hill 1974, Ter Braak 1985), canonical correspondence analysis (Ter Braak 1986) and Outlying Mean Index (OMI) analysis (Dolédec *et al.* 2000). When describing the application of an ordination technique in ecology, Green (1971) stated that these analyses are useful in reducing niche dimensionality by focusing on the most important variables, and in assessing the contribution of each dimension to the species niche. OMIs have been proposed to provide a relatively equal weight to species rich and poor sites, and are well suited to deal with the large variety of species-environment responses (Dolédec *et al.* 2000). This method places species along environmental gradients (Dolédec *et al.* 2000, Thuiller *et al.* 2004), along which the variability of habitats occupied by species (niche breadth) can be analysed (Thuiller *et al.* 2004). These gradients represent abstract constructs of ecological space where the position of sites along the gradient represent similarities in environments, and there is no spatial relationship between these sites along this gradient (Austin 1985). It must also be noted that correlative methods such as these only infer causality. However, such methods are still extremely useful in determining ecological patterns and in attempting to describe these.

In this study, OMI analysis was used to describe and understand the niche and niche breadth of Dwarf Chameleons (*Bradypodion*). *Bradypodion* are small, arboreal chameleons, widespread and endemic to South Africa, and allopatrically distributed with potential contact zones (Branch 1998, Tolley *et al.* 2006, Tolley and Burger 2007; figure 1). There are currently 15 recognised species, with a number of species still to be described (Tolley and Burger 2007). Additionally, the concept of niche conservatism was examined with respect to closely related species occupying similar environmental niches. Genetic analysis suggested the presence of a number of clades (Tolley *et al.* 2006), making *Bradypodion* a good candidate for a study of niche conservatism.

The suggestion by Glor *et al.* (2003) that closely related species often share discrete macrohabitats forms an underlying hypothesis in this study. OMI analysis was conducted at two levels: 1) for each terminal taxon, and 2) for each phylogenetic clade, to investigate the correspondence between a species niche and evolutionary relationship. I propose the hypothesis that closely related species within a clade will share similar environmental niches, and from this aim to answer two main questions:

1) Do fundamental environmental factors separate the *Bradypodion* species and clades? These can be examined in relation to the present geographic distributions of the various species within this genus. 2) Do closely related *Bradypodion* species share similar environmental niches? By assessing this, inferences as to the extent of niche conservatism within this genus can be made.

Materials and methods

Data sets

Location and data collection

Nine hundred and seventy data points, representing individual chameleons, for the genus *Bradypodion* were obtained from the specimen collections and databases housed at Bayworld (Port Elizabeth Museum), South African Museum, Transvaal Museum, National Museum, Natal Museum, Durban Museum and South African National Biodiversity Institute (SANBI). Additionally, surveys were conducted at 26 sites distributed throughout the range of *Bradypodion pumilum*, from January through December 2006. Chameleons were located at night with torchlight by two to five observers and coordinates were recorded for each individual using a hand-held GPS unit. A total of 115 *B. pumilum* individuals were captured in this manner at 15 sites. Thus, a total of 1085 data points was used in analysis (Figure 1); of which *B. atromontanum* comprised 19 data points, *B. caffer* 6 data points, *B. damaranum* 65 data points, *B. dracomontanum* 19 data points, *B. gutturale* 98 data points, *B. kentanicum* 10 data points, *B. melanocephalum* 62 data points, *B. nemorale* 11 data points, *B. occidentale* 45 data points, *B. pumilum* 245 data points, *B. setaroi* 38 data points, *B. taeniabronchum* 27 data points, *B. thamnobates* 39 data points, *B. transvaalense* 165 data points, *B. ventral* comprised 125 data points, *B. Sp. 1* 34 data points, *B. sp. 2* 13 data points, *B. sp. 3* 21 data points, *B. sp. 4* 11 data points, *B. sp. 5* 7 data points, *B. sp. 6* 12 data points, *B. sp. 7* 10 data points and *B. sp. 8* 3 data points.

Environmental variables

One topographic and 11 climatic variables were used. Data were obtained from Schulze (1997) and included annual evapotranspiration (mm), winter and summer precipitation (mm), winter and summer relative humidity (%), winter and summer solar radiation (MJ.m^{-2}.day^{-1}), winter and summer average monthly temperatures (°C), maximum annual temperature (°C), minimum annual temperature (°C) and altitude (m). This data set comprised interpolated data at 1 x 1 minute grid cells (which on average cover an area of 2.97km^2) for the whole of South Africa.

Mucina and Rutherford (2004) and Low and Rebelo (1998) provided a detailed vegetation and biome map of South Africa, Lesotho and Swaziland respectively. Vegetation data were extracted from these databases. The biome map comprised categorical data describing the position of seven biomes in South Africa, Lesotho and Swaziland including the Forest, Thicket, Savanna, Grassland, Nama Karoo, Succulent Karoo and Fynbos Biomes (Low and Rebelo 1998). In addition, the vegetation map comprised categorical data identifying the vegetation types of South Africa, Lesotho and Swaziland (Mucina and Rutherford 2004). An index of human influence on the land surface, known as the "Human Footprint" (Sanderson *et al.* 2002), was also incorporated into the analysis. Four proxies for human influence were combined to create this scale. They included population density, land transformation, accessibility and electrical power infrastructure (Sanderson *et al.* 2002). This spatial index expresses the relative human influence, as a percent, across all terrestrial biomes at a global level (Sanderson *et al.* 2002).

Niche separation

Taxon and clade level analysis

OMI analysis, available in the ADE-4 software (Thioulouse *et al.* 1997) and library under the R environment (R Development Core Team 2005), was carried out for all terminal taxa identified in a previous phylogenetic analysis, 23 in total (Tolley *et al.* 2006, Figure 2). Additionally, the analysis was carried out by grouping terminal taxa into phylogenetic clades (five in total). Therefore, two sets of analysis were performed at two different levels. The data format needed for the OMI analysis consisted of a matrix where rows represented X and Y coordinates for each point locality for every species and columns represented both species (where presence or absence at each point locality was noted by using a binary indicator; '0' represented present and '1' represented absent) and environmental variables. The OMI outputs provided both graphical and numerical results.

In order to test the effects of variable selection on model outputs, four sets of environmental variables (A, B, C, D) were compared using the OMI analysis. Variable set A contained climatic and topographic variables; variable set B incorporated climatic and topographic variables as well as spatial Human Footprint; variable set C included all the variables in 'B' as well as biomes; variable set D included all the variables in 'B' as well as the vegetation map.

Additionally, a scatter plot and regression line of niche breadth versus species age was constructed to examine whether older species had relatively narrower niche breadths than younger species. Niche breadth was obtained from the present analysis, whereas species age was obtained from Tolley *et al.* (in review).

Niche conservatism

Niche conservatism was assessed by examining the correspondence between the environmental niche, as indicated by the OMI analysis, occupied by individual taxa and their respective clades. Thus it could be determined whether individual taxa occupied an environmental niche that differed from that of their clade.

Results

Taxon level analysis

Of the four sets of environmental variables selected, 84% of the variation within data set A is explained by the first two OMI axis alone, in data set B the first two OMI axis explain 83% of the variation, in data set C the first two OMI axis explain 66% of the variation and in data set D the first two OMI axis explain 35% of the variation (Table 1). Only the results for set A are reported here because it explained the greatest amount of variation within the data.

The first OMI axis for variable set A explained *c.* 51% of the total variation (Table 1), and was interpreted as a gradient influenced predominantly by summer and winter rainfall ("rainfall seasonality") and maximum annual temperatures (Table 2). Most species displayed narrow niche breadths (from here on referred to as "niche specialist" species) along this gradient, indicating this gradient was highly niche restrictive for species. Thus, only the niche breadth obtained from this axis was used in further analysis. However, a few species, (*e.g. B. pumilum* and *B. occidentale)* did display wide niche breadths (from here on referred to as "niche generalist" species) along this axis. *Bradypodion pumilum's* range included warm, winter rainfall environments with *B. occidentale* extending into both hot, summer and warm, winter rainfall environments (Figure 3a).

There was not always a correspondence between niche generality and extent of distribution. *Bradypodion pumilum* was considered a niche generalist (Figure 3a) but has a restricted geographic distribution (Figure 4). *Bradypodion transvaalense*, on the other hand, was considered a niche specialist, but covers a relatively large geographic extent (Figure 5).

The second OMI axis explained *c.* 33% of the total variation (Table 1) and was interpreted as being an altitude-minimum temperature gradient (Table 2). Predominantly, species were considered niche generalist along, and therefore less restricted by, this axis (Figure 3b). Therefore, due to the predominantly large niche breadth of species along this gradient, their OMI placements could not be related directly to their geographical distributions.

No significant relationship between species age and niche breadth was found (r^2 = 0.36, p = 0.09; Appendix 2). *Bradypodion pumilum* displayed an unusually large niche breadth, and was therefore removed to investigate whether its inclusion biased the analysis. After its removal, the relationship between species age and niche breadth was weaker (r^2 = 0.07, p = 0.24) suggesting that its inclusion had actually biased the relationship upwards.

Clade level analysis

Variable set A and variable set B explained *c.* 88% of the variation, C explained *c.* 85% and D explained *c.* 76% within the data (Table 3). As with the taxa level analysis, variable set A was used for all further analyses.

The first OMI axis, interpreted as a seasonal rainfall-maximum temperature gradient (Table 4 and Figure 6a), explained *c.* 66% of the variation (Table 3). Clade A, a niche generalist, occupied warm, winter rainfall environments, while clade B, also a niche generalist, occurred in both environments (Figure 6a). All other clades (C, D, E) occurred within hot, summer rainfall environments and displayed narrow niche breadths (Figure 6a). Additionally, there was little overlap of niche breadth for most clades along this axis (Figure 6a). However, there was overlap between clade A and clade B, and clade E and clade D (Figure 6a).

The second OMI axis explained *c.* 21% of the variation and was interpreted as a minimum temperature gradient (Tables 3 and 4). Clades A, B and E extended into both environmental zones along the gradient; clades C and D occurred within the cool environments (Figure 6b). Again, the OMI placements along this axis could not be related directly to their geographical distributions.

Niche conservatism

Because the first OMI axis was consistently more restrictive than the second, niche conservatism assessments were based on this axis. All species within each clade shared a similar environmental niche (Figures 3 and 6). However, clade C and clade D contained a single species each (Figure 2). Clade B contained species that occupied warm, winter rainfall environments (*e.g. B. gutturale*, *B. atromontanum*, *B. taeniabronchum*) and hot, summer rainfall environments (*e.g. B. kentanicum*, *B. ventral*; Figure 6a). Additionally, the clade contained individual species with niche breadths that extended into both environmental zones, such as *B. occidentale*, as well as two undescribed species, *B. sp. 4* and *B. sp. 2* (Figure 3a). Therefore the niche breadth of Clade B covered both environmental zones along the gradient (Figure 6a).

Discussion

Distributions of species and of phylogenetic clades of the endemic South African *Bradypodion* are strongly influenced by rainfall seasonality and maximum temperatures (Figures 3 and 6). These variables strongly constrained the niche and niche breadths of the taxa, and are therefore likely to be the major drivers effecting the current geographic distributions of these taxonomic groups. Additionally, there was evidence for niche conservatism within this genus. This was demonstrated by all closely related species occupying similar environmental niches.

Taxon level analysis

Niche conservatism within the genus *Bradypodion* was well supported, as all closely related taxa inhabited similar niches. In contrast, many distantly related taxa were found to occur in the same niche. For example, *B. caffer*, forming clade C, and *B. transvaalense*, occurring in clade E, are both found within hot, summer rainfall environments. This could indicate a retained ancestral state, demonstrating niche conservatism over an extended time period (see Martinez-Meyer *et al.* 2004, demonstrating this pattern of niche conservatism over extended periods in United States mammals). However, over evolutionary time, different taxa can adapt to different environmental niches. Therefore, there is obvious variability in the niches of distantly related taxa. For example, *B. pumilum* in clade A is located in warm, winter rainfall environments, while *B. transvaalense* in clade C is found within hot, summer rainfall environments.

Long-term niche stability, and the ability of a species to track preferred habitats, has been implicated in the formation of new evolutionary lineages (Kozak *et al.* 2005). This has been observed in the *Bradypodion* genus, as a relationship between cladogenesis and lineage losses with paleoclimatic fluctuations has been shown (Tolley *et al.* in review). Additionally, there is a relationship between *Bradypodion* phylogenetic diversity and species richness with past, rapid climate shifts (Tolley *et al.* in review). Since *Bradypodion* arose, approximately 14.8 mya (Tolley *et al.* in review), the earth's climate has been experiencing a cooling trend (Williams *et al.* 1998). However, this general cooling was disrupted by a series of warmer periods; for example in the middle Miocene and early Pliocene (Williams *et al.* 1998, Zachos *et al.* 2001). Rapid climatic change may have resulted in a contraction of available ancestral forest habitat, leading towards initial extinction events. A period of rapid radiation followed this as exploitation of novel habitats occurred (Tolley *et al.* in review). Tropical vegetation may still have been present in the Cape during the Miocene, approximately 22.5 – 5 mya (Williams *et al.* 1998, Linder 2003), but the rapid appearance of novel habitats, such as the fynbos biome approximately 8 – 10 mya (Linder 2003), and subsequent lack of competitors may have allowed species to exploit these new habitats. Several diversification phases for *Bradypodion* have been dated to approximately this time (Tolley *et al.* 2006). Furthermore, *B. ventrale* and *B. pumilum* are able to exist in a wide variety of vegetation types (Tolley and Burger 2007) and are therefore able to exploit a variety of habitats. Thus, when novel habitats form, some *Bradypodion* species (e.g. *B. ventrale* and *B. pumilum*) would be able to occupy those areas.

Niche stability has been demonstrated in other species; for example, *Plethodon* salamander clades also show long-term ecological niche maintenance (Kozak *et al.* 2005). However, as in *B. pumilum*, *Plethodon* populations can, and have, expanded rapidly into niches when these are not occupied by any other close relatives (Kozak *et al.* 2005). Occupation of new niches also extends to plants as shown by the Spotted Knapweed (*Centaurea maculosa*), which demonstrates an ability to shift climatic niches, possibly when released from biotic constraints (Broennimann *et al.* 2007).

Niche generalists are expected to display relatively larger geographic ranges than niche specialists. Contrary to this expectation, *B. pumilum* displayed a much wider niche breadth (Figure 3a), but also occupied a relatively smaller geographic range (Figure 4) than *B. transvaalense* (Figure 3a and 5). Although occurring within a small area, *B. pumilum* does however occupy a wide variety of vegetation types and habitats, while *B. transvaalense* occupies a more limited range of habitats, occurring mainly in closed canopy vegetation (Tolley and Burger 2007). The patchy distribution of *B. transvaalense* means that although the entire extent of occurrence is larger, its true area of occupancy is probably smaller. In another example, *B. ventrale* also displayed a narrow niche breadth (Figure 3a), but occupied a relatively large geographic range (Figure 7) and despite its narrow niche breadth, naturally occurs within a wide array of habitats (Tolley and Burger 2007). Therefore, although maximum temperatures and rainfall seasonality may constrain *Bradypodion* taxa, microhabitat use and thermoregulatory ability form important aspects of species ecology. A relationship between degree of generality, based on broad climatic factors, and geographic range can therefore not be assumed. However, the relationship between the size of geographic range and niche generality for *Bradypodion* should be investigated in the future.

The total explained variance, known as inertia, provided by the OMI analysis quantifies the influence the environmental variables had on the species niches (Dolédec *et al.* 2000). The addition of the human footprint in the analysis made little difference towards the cumulated explained inertia (Table 1 and 3). This lack of correspondence between the human footprint variable and the explained inertia should, however, be interpreted with caution. Most likely, the human footprint data may not be at a fine enough resolution to indicate any effect humans may have on these chameleons. Alternatively, the four proxies used to create the human footprint variable (Sanderson *et al.* 2002) may not be those influencing chameleon distributions. Humans, after all, bring with them a greater suite of influences. The establishment of gardens and parks may actually benefit some species, as these areas are usually associated with dense bush cover and a continuous supply of water. Additionally, the inclusion of vegetation variables decreased explained inertia. However, the vegetation map is categorical. Thus, the decrease in explained inertia is the result of an increase in the number of axis when using this variable.

Clade level analysis

Given the increased time period available for adaptation and specialisation, we assumed that older clades (and species) would display narrower niche breadths than younger clades. However, this was not found (Appendix 2). Additionally, this analysis is based on empirical data and, as a clade generally consists of numerous species, the niche breadth of any one clade is a function of the species constituting that clade. For example, clade B consists of species occurring on both sides of the OMI plots, while clade C and clade D consist of one species each found in hot, summer rainfall environments along the OMI plots (Figures 3a and 6a). Therefore, clade B, as a whole, appears to be a niche generalist, while clades C and D do not. Furthermore, some of the older species, such as *B. pumilum*, were niche generalist, while others, such as *B. damaranum*, were niche specialist. Likewise, some of the younger species, such as *B. gutturale*, were considered niche generalist, while others, such as *B. kentanicum*, were niche specialist (Figure 3a).

Niche conservatism

All closely related species occupied similar environmental niches indicating that *Bradypodion* can be considered a niche conservative genus. However, some of the clades were fairly broad and incorporated many species. As the phylogenetic tree of the genus becomes more refined, differences between the niches of closely related species may be found. This should be expected, as many of the species (e.g. *B. pumilum* and *B. ventrale*) do have the ability to occupy and survive in many different habitat types (Tolley and Burger 2007), and thus occur within a range of niches. However, some lineages have been lost due to habitat shifting from closed to open environments and a failure to colonise these novel habitats (Tolley *et al.* in review). This is demonstrated in clades C and D, which now have one species each (Tolley *et al.* 2004). They have long branch lengths and no sister species (Tolley *et al.* in review). Therefore, although it is a predominantly niche conservative genus, some species do have the ability to invade novel environments.

Additionally, some clades displayed narrow niche breadths. Even clade E, which comprised several species, still displayed a narrow niche. This added further support to the niche conservative nature of these species. An exception was clade A as it displayed a wide niche breadth. However, one of the four lineages (*B. sp. 1*) has successfully colonised the open-habitat fynbos vegetation (Tolley *et al.* 2006). This clade isn't as conservative as the others and again demonstrates the evolutionary potential of these species to invade and colonise novel environments.

The overlap in niche breadth between clades A and B is due to the recent radiation of *B. sp. 1* into the fynbos, whereas the other lineages do not have representatives within fynbos vegetation. *Bradypodion sp. 1* overlaps with other fynbos species in clade B. This again shows that while niches are conserved to a degree, there is the evolutionary potential within each clade to radiate into a novel environment.

Conclusion

These analyses suggest that fundamental climatic factors influence distributions of *Bradypodion* species across the landscape and can be considered as major drivers in their current geographic distributions. However, the effect of biotic interactions and microhabitat use on species distributions should not be ignored. In addition, species within the genus *Bradypodion* appeared to be niche conservative, as all closely related taxa inhabited similar niches. However, due to different taxa adapting to different environmental niches over evolutionary time, there was variability in the niches occupied by distantly related taxa. This may be linked to the several diversification phases that have occurred throughout their evolutionary history and may be a key factor in the distributions of present day species.

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Figures

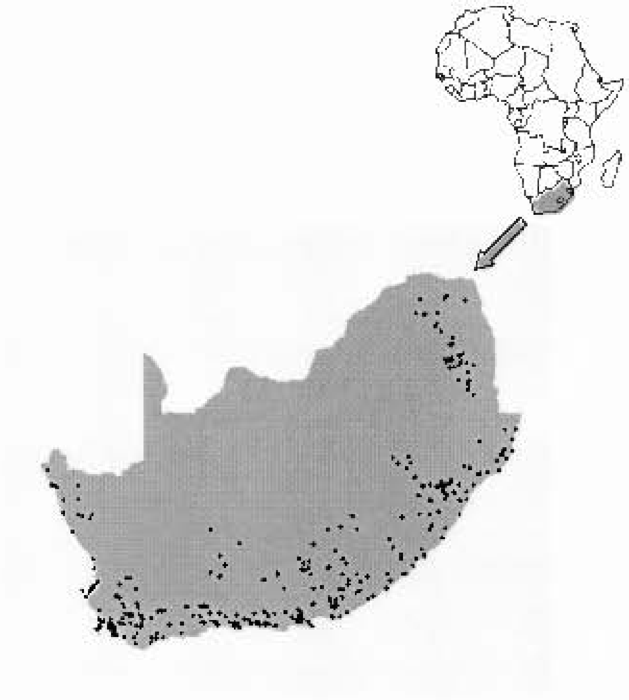


Figure 1 Locality records for the genus *Bradypodion*, occurring in South Africa. Black points indicate presence records and are based on a combined data set obtained from field surveys and additional contributions from Bayworld (Port Elizabeth Museum), South African Museum, Transvaal Museum, National Museum, Natal Museum, Durban Museum and South African National Biodiversity Institute (SANBI).

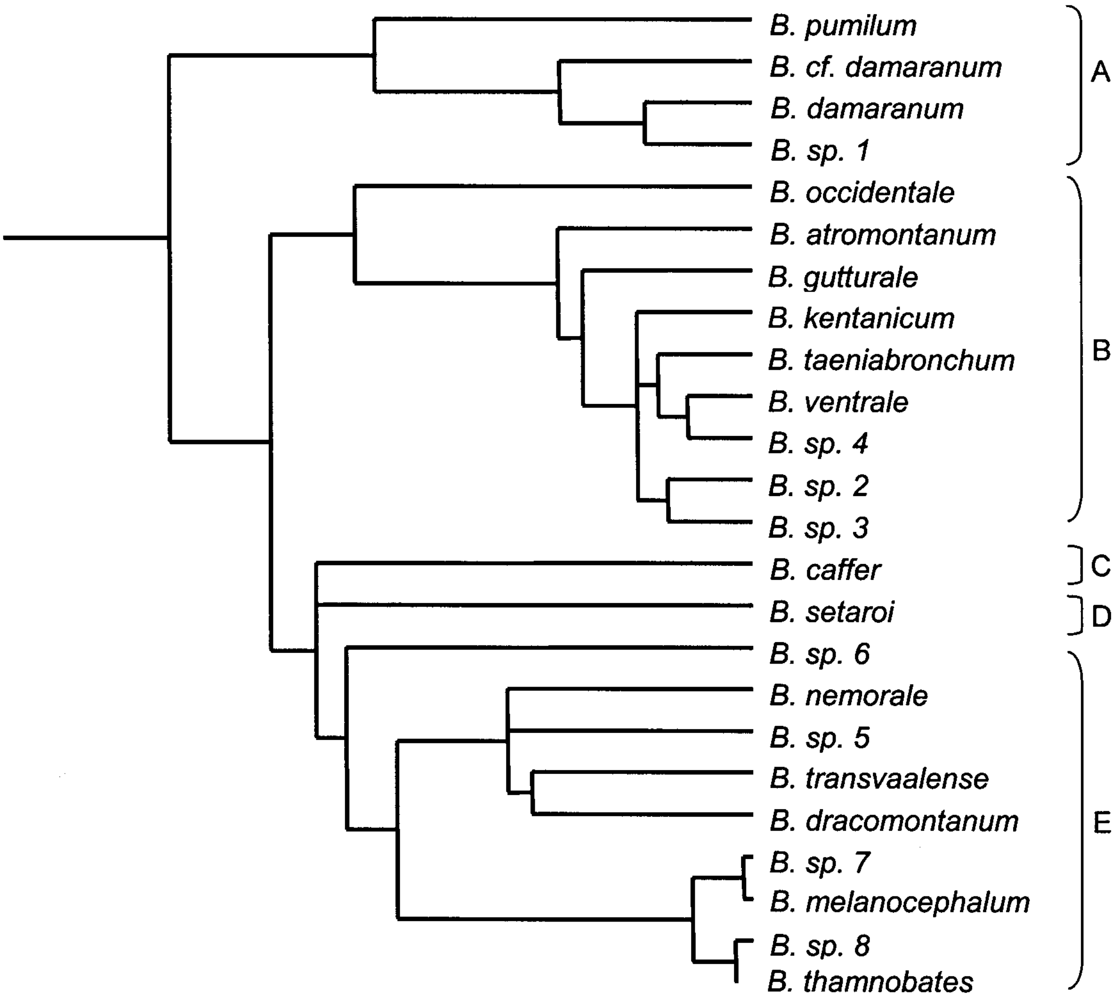
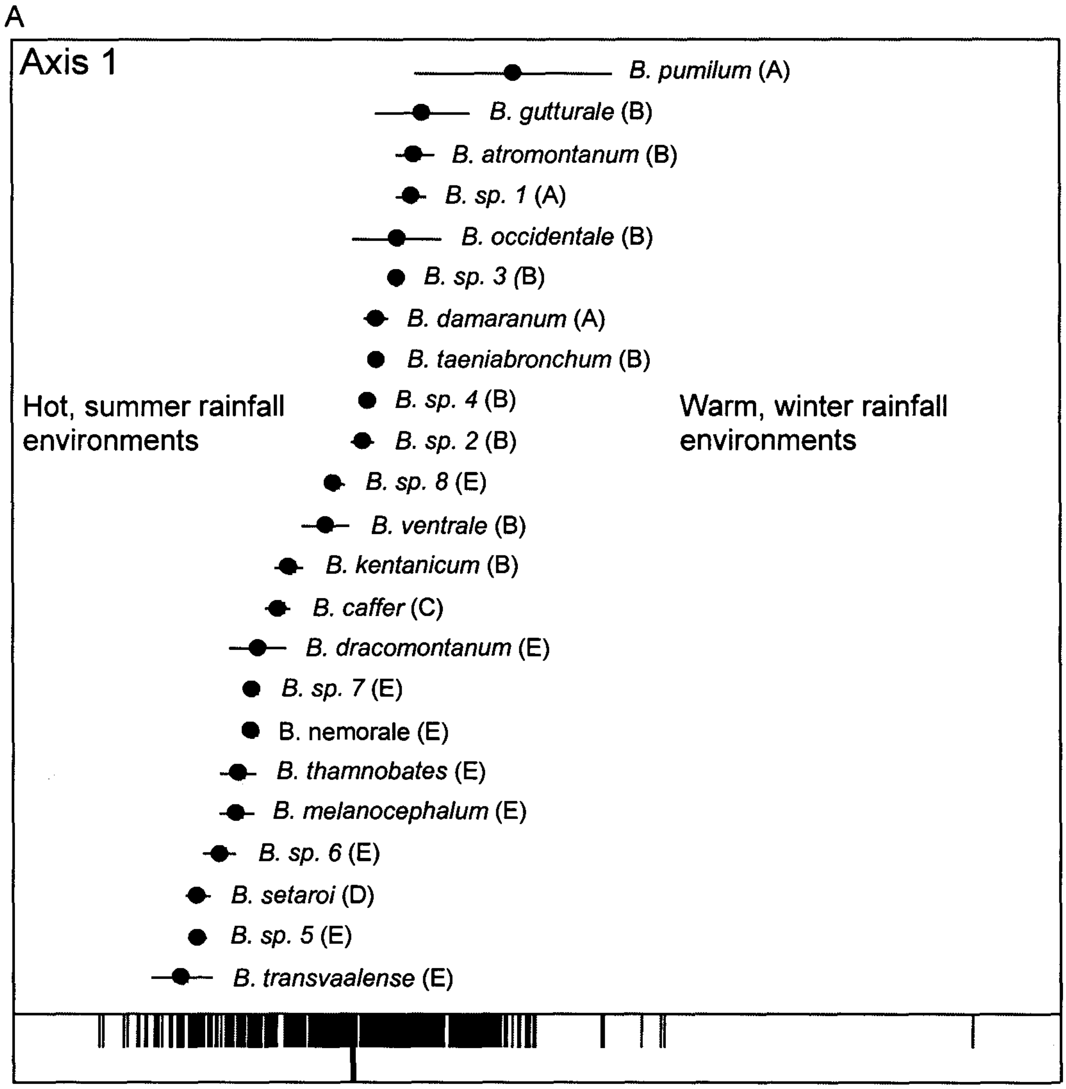


Figure 2 *Bradypodion* phylogenetic tree, representing terminal taxa and clades used in analysis (Adapted from Tolley *et al.* in review, K. A. Tolley. pers.comm.). Clades A – E on diagram are well supported. Currently undescribed species are included.


A
Axis 1
B. pumilum (A)
B. gutturale (B)
B. atromontanum (B)
B. sp. 1 (A)
B. occidentale (B)
B. sp. 3 (B)
B. damaranum (A)
B. taeniabronchum (B)
Hot, summer rainfall environments
B. sp. 4 (B)
Warm, winter rainfall environments
B. sp. 2 (B)
B. sp. 8 (E)
B. ventrale (B)
B. kentanicum (B)
B. caffer (C)
B. dracomontanum (E)
B. sp. 7 (E)
B. nemorale (E)
B. thamnobates (E)
B. melanocephalum (E)
B. sp. 6 (E)
B. setaroi (D)
B. sp. 5 (E)
B. transvaalense (E)

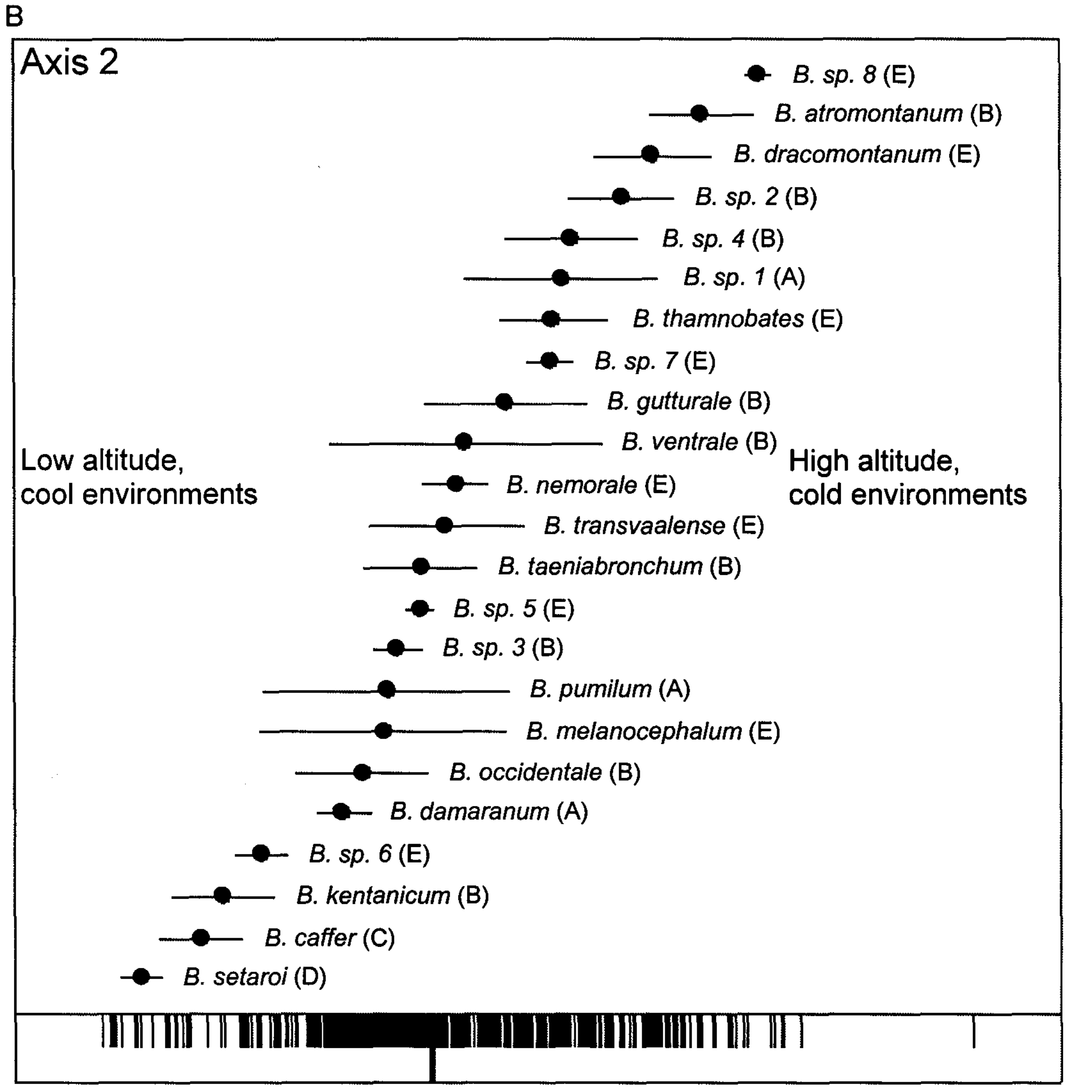


Figure 3 Species niche positions as well as species niche breadths (horizontal lines adjacent to species names) for *Bradypodion*. Constructed using variable set 'A' on the two retained OMI axis, together explaining approximately 84% of the variation: (A) represents OMI axis 1, a seasonal rainfall-maximum temperature gradient; (B) represents OMI axis 2, an altitude-minimum temperature gradient. Phylogenetic clades are indicated in parentheses. Vertical lines at the bottom of the plots indicate the position of sample localities along the gradient. The plot is

viewed as a continuous gradient. Species displaying wide niche breadths and/or species occurring along the central line (darkened vertical line at the bottom of the plot) of the plots are considered as niche generalist.

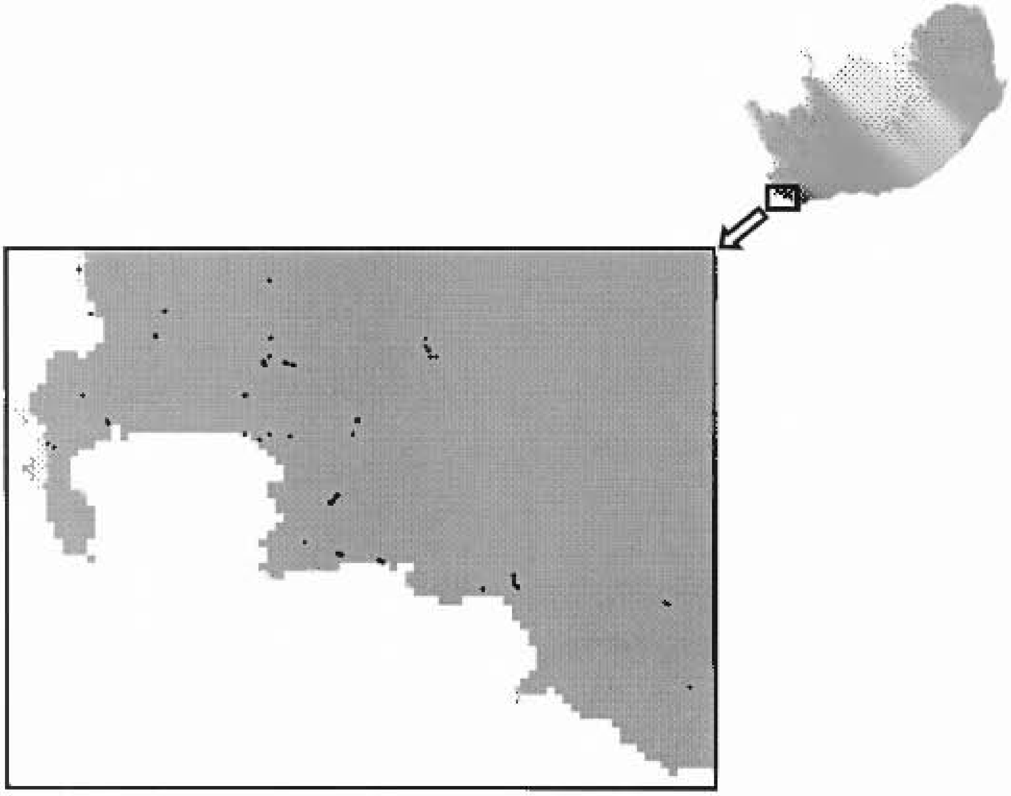


Figure 4 Map depicting distribution of *Bradypodion pumilum*, occurring in the southwestern corner of South Africa. The distribution is based on sample points, indicated by dots.

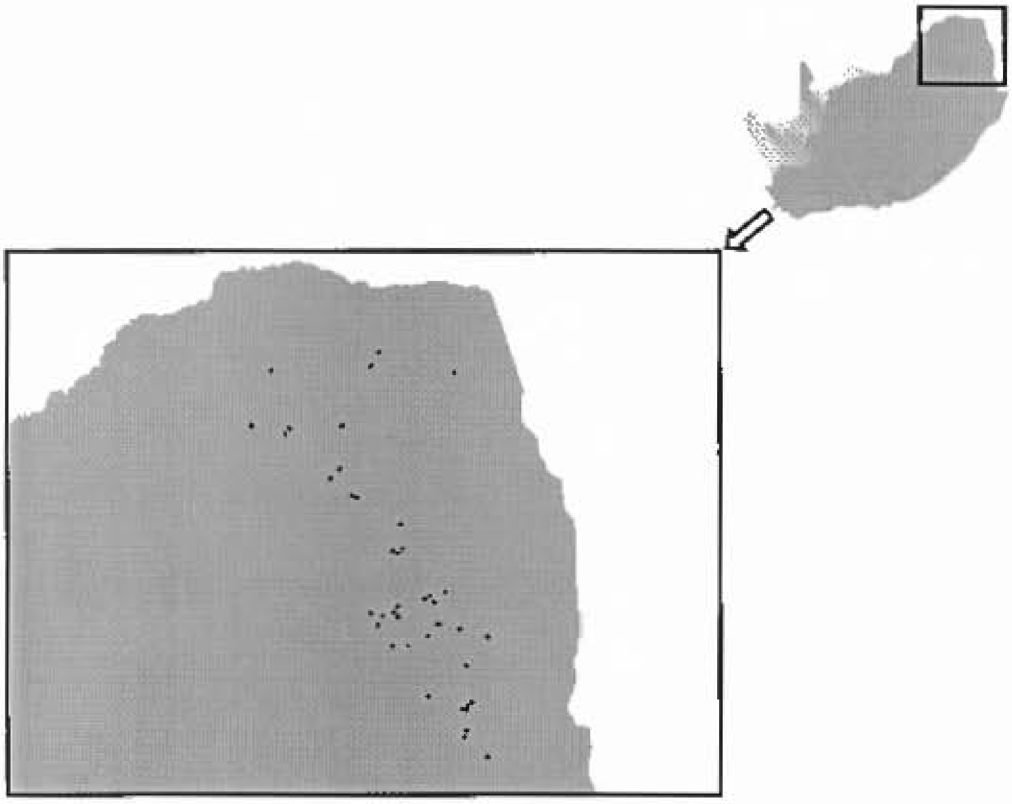
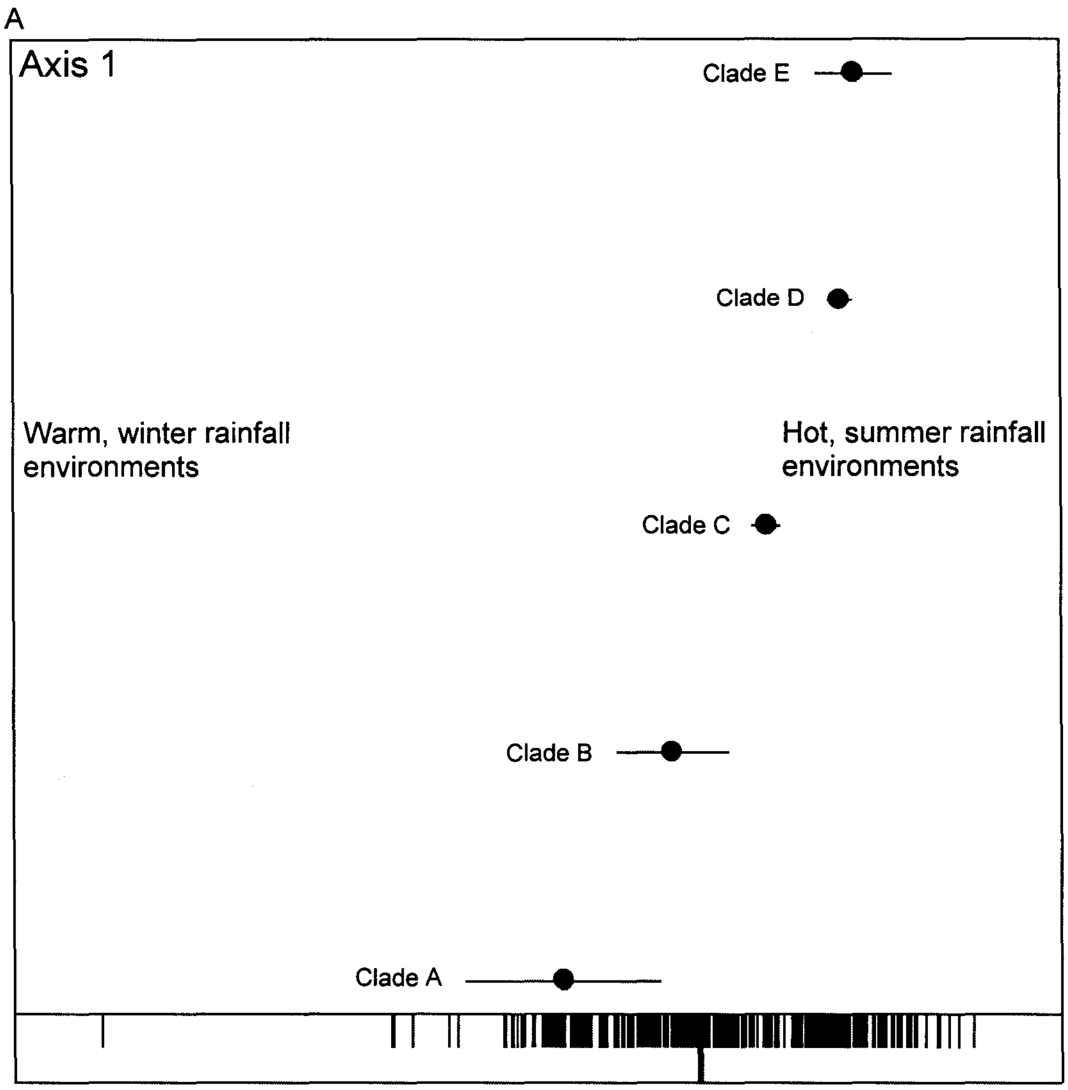


Figure 5 Map depicting distribution of *Bradypodion transvaalense*, displaying a northeast distribution within South Africa. The distribution is based on sample points, indicated by dots.


A
Axis 1
Clade E
Clade D
Warm, winter rainfall environments
Hot, summer rainfall environments
Clade C
Clade B
Clade A

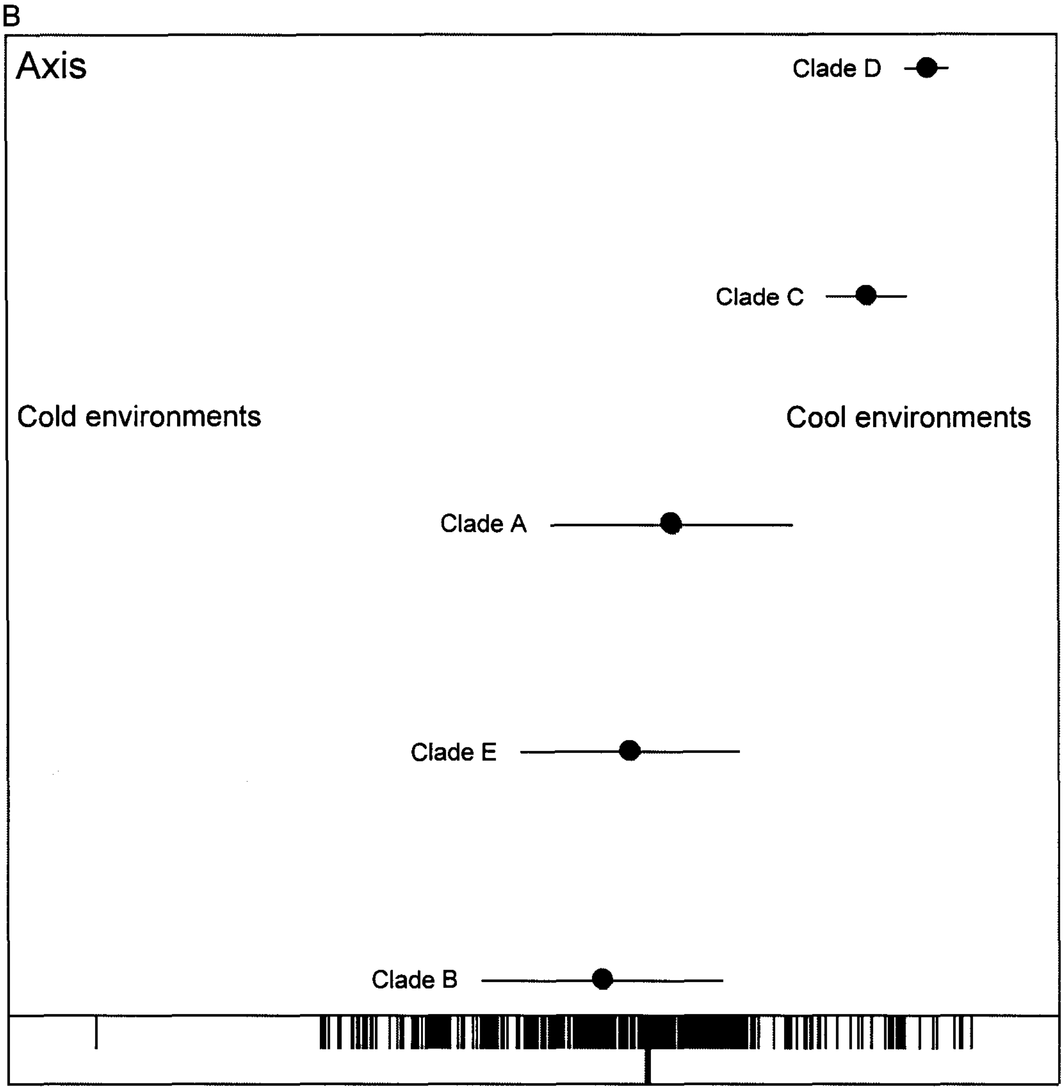


Figure 6 Niche positions and niche breadths (horizontal lines adjacent to clade names) for *Bradypodion* at the level of phylogenetic clade. Constructed using variable set ‘A’ on the two retained OMI axis together explained approximately 88% of the variation: (A) represents OMI axis 1, a seasonal rainfall-maximum temperature gradient; (B) represents OMI axis 2, a predominantly minimum temperature gradient. Vertical lines at the bottom of the plots indicate the position of clade localities along the gradient. The plot is viewed as a continuous gradient.

Clades displaying wide niche breadths and/or clades occurring along the central line (darkened vertical line at the bottom of the plot) of the plots are considered as niche generalist.

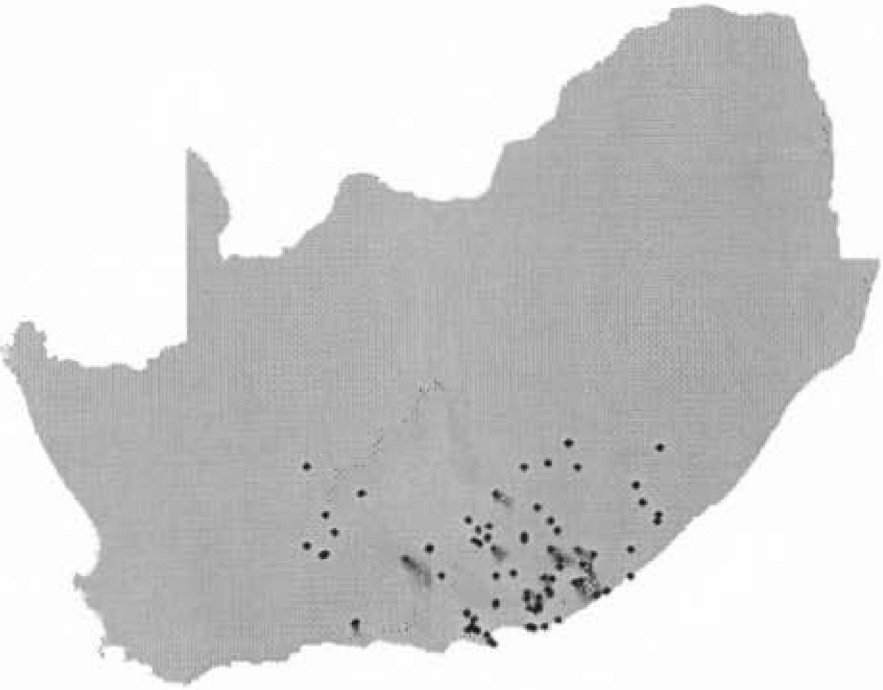


Figure 7 Distribution of *Bradypodion ventrale* within South Africa. The distribution is based on sample points, indicated by dots.

Table 1 Percentages of explained inertia (quantifies the influence the environmental variables had on the species niche; Dolédec *et al.* 2000) as well as cumulated explained inertia. OMI analysis performed at a taxa level. A = climatic and topography, B = climatic, topography and the human footprint, C = climate, topography, human footprint and biomes, D = climate, topography, human footprint and the vegetation map.

	Explained inertia (%)				**Cumulated explained inertia (%)**			
Axis	A	B	C	D	A	B	C	D
1	50.96	50.25	42.81	20.55	50.96	50.25	42.81	20.55
2	32.95	32.77	23.59	14.42	83.91	83.02	66.41	34.97

Table 2 Canonical correlations of environmental variables along the first two OMI axes of variable set A for the species level analysis by each of the environmental variables for *Bradypodion*.

Environmental variables	**Axis 1**	**Axis 2**
Annual evapotranspiration (mm)	-0.45	-0.35
Winter precipitation (mm)	0.68	0.00
Summer precipitation (mm)	-0.69	0.00
Winter relative humidity (%)	0.12	-0.58
Summer relative humidity (%)	-0.50	-0.68
Winter solar radiation (MJ.m^{-2}.day^{-1})	-0.93	-0.03
Summer solar radiation (MJ.m^{-2}.day^{-1})	-0.14	0.22
Winter average monthly temperatures (°C)	-0.51	-0.91
Summer average monthly temperatures (°C)	-0.60	-0.66
Maximum annual temperatures (°C)	-0.71	-0.54
Minimum annual temperatures (°C)	-0.40	-0.95
Altitude (m)	-0.46	0.72

Table 3 Percentages of explained inertia (quantifies the influence the environmental variables had on the species niche; Dolédec *et al.* 2000) as well as cumulated explained inertia, describes total variation explained by each axis for *Bradypodion*. OMI analysis performed at level of phylogenetic clade. A =

climatic and topography, B = climatic, topography and the human footprint, C = climate, topography, human footprint and biomes, D = climate, topography, human footprint and the vegetation map.

	Explained inertia (%)				Cumulated explained inertia (%)			
Axis	A	B	C	D	A	B	C	D
1	66.32	66.10	65.82	50.40	66.32	66.10	65.82	50.40
2	21.49	21.41	19.54	25.82	87.80	87.50	85.37	76.23

Table 4 Canonical correlations of environmental variables along the first two OMI axis of variable set A for the clade level analysis by each of the environmental variables for *Bradypodion*.

Environmental variables	Axis 1	Axis 2
Annual evapotranspiration (mm)	0.41	0.38
Winter precipitation (mm)	-0.70	0.23
Summer precipitation (mm)	0.72	0.07
Winter relative humidity (%)	-0.17	0.57
Summer relative humidity (%)	0.45	0.72
Winter solar radiation (MJ.m^{-2}.day^{-1})	0.94	0.08
Summer solar radiation (MJ.m^{-2}.day^{-1})	0.13	-0.22
Winter average monthly temperatures (°C)	0.44	0.92
Summer average monthly temperatures (°C)	0.54	0.68
Maximum annual temperatures (°C)	0.65	0.56
Minimum annual temperatures (°C)	0.33	0.96
Altitude (m)	0.53	-0.67

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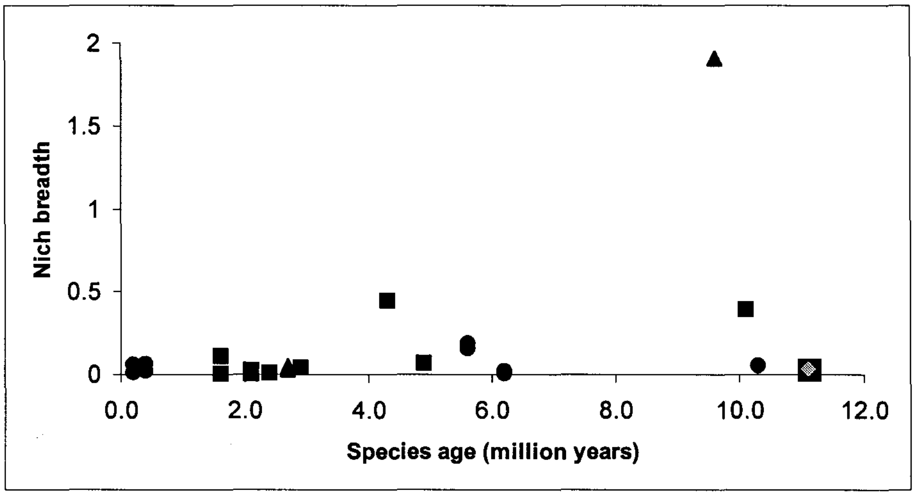
Appendix

Appendix 1 Sites visited on *Bradypodion pumilum* surveys and the total number of chameleons found.

Site 1	Site name	GPS (S)	GPS (E)	Number of chameleons
1	Koegelberg Biosphere Reserve	34° 19. 29'	18° 58. 20'	20
2	Mizpah	34° 13. 12'	18° 57. 40'	18
3	Devon Valley, Stellenbosch	33° 56. 05'	18° 49. 19'	9
4	Noordhoek	34° 05. 88'	18° 22. 71'	9
5	Landroskop	34° 02. 97'	19° 02. 57'	12
6	Robben Island	33° 47. 74'	18° 22. 39'	8
7	Blauberg Conservation Area (Hilltop)	33° 45. 33'	18° 27. 93'	0
8	Blauberg Conservation Area (Base of hill)	33° 45. 83'	18° 28. 38'	0
9	Blauberg	33° 44. 79'	18° 26. 51'	7
10	Blauberg (urban garden)	33° 43. 65'	18° 26. 58'	1
11	Elandsberg Farm	33° 28. 13'	19° 02. 37'	0
12	Somerset West	34° 04. 99'	18° 52. 22'	10
13	Rondevlei Nature Reserve	34° 03. 39'	18° 30. 19'	7
14	Fernkloof Nature Reserve	34° 23. 64'	19° 15. 96'	4
15	Vogelgat Nature Reserve	34° 24. 11'	19° 19. 22'	1
16	Tygerberg Hill Nature Reserve	33° 52. 66'	18° 35. 98'	5
17	Paarl Tortoise Reserve	33° 45. 98'	18° 49. 87'	2
18	Grootbos	34° 32. 47'	19° 24. 69'	0
19	Farm 215	34° 34. 14'	19° 33. 09'	0
20	Salmonsdam	34° 25. 36'	19° 38. 19'	2
21	Elim	34° 34. 76'	19° 45. 83'	0
22	Struisbaai	34° 48. 49'	20° 02. 81'	0
23	Arniston	34° 39. 71'	20° 30. 30'	0
24	Aghulus	34° 49. 04'	20° 00. 54'	0
25	Darling	33° 22. 37'	18° 22. 62'	0
26	Clara Anna Fontein Nature Reserve	33° 49. 58'	18° 37. 20'	0

Appendix 2 Scatter plot of species age measured against niche breadth (r^2 = 0.36, p = 0.09). Triangles represent species belonging to clade A, circles represent species belonging to clade E, squares represent species belonging to clade B. Clades C and D are represented by the grey triangle within the black square.



Chapter 3

Predicted influences of climate change on the South African Dwarf Chameleons, *Bradypodion*

Abstract

The niche concept implies a relationship exists between a species and its environment, and an important attribute of a species' environment is climate. Thus changes in climate could affect both individual species and communities, so that future predicted climate change should be considered in species conservation plans. A presence-only, niche-based modelling technique was used to predict current suitable habitat for *Bradypodion* species and phylogenetic clades. Additionally, the constructed distributions were projected into the future (2050 and 2080) using climate change scenarios obtained from the Intergovernmental Panel on Climate Change. All nine *Bradypodion* species and all three clades responded to future climate change with regards to their distribution. However, the degree and extent of these responses were individualistic. Responses included range expansions, range contractions and even a range shift. Additionally, the results suggest *Bradypodion* could be a niche conservative genus. These results have important implications in understanding the vulnerability of dwarf chameleons to climate change, and the importance of considering the effects of predicted climatic shifts on the protection of biodiversity.

Introduction

It is predicted that in this century global temperatures could rise by 3 – 6°C (Midgley *et al.* 2005). For southern Africa predictions generally show an increase of approximately 3 – 7°C by 2100 (Boko *et al.* 2007), for which models predict significant species extinctions (Fischlin *et al.* 2007). Although changes in rainfall are more difficult to predict (Midgley *et al.* 2005, Boko *et al.* 2007), rainfall could change by up to 20% of current levels (Midgley *et al.* 2005). With respect to the present rate of climate change, studies suggest species have already begun to respond to these trends (Parmesan *et al.* 2000, Hughes, 2000, McCarty 2001, Burns *et al.* 2003, Root *et al.* 2003, Foden *et al.* 2007).

Assuming individualistic species responses (Gleason 1926, Parmesan 2006), future predicted climate change could result in novel communities (Gleason 1926), modifying present day community structure (Burns *et al.* 2003). Thus, due to changing climatic conditions and species distributions, it is as yet uncertain how present day protected areas will be able to continue to conserve the species within them (Burns *et al.* 2003, Araújo *et al.* 2004, Thuiller *et al.* 2006). Despite the employment of various reserve selection procedures, a possible range loss for species within European reserves, resulting from climate change, has been demonstrated (Araújo *et al.* 2004). Furthermore, climate change can lead to plant and animal population increases and decreases, and data on the direction of these changes will be important in species conservation (McCarthy 2001).

However, the effects of climate change on a community are likely to vary from region to region, and may even vary within a country (Sala *et al.* 2000, Burns *et al.* 2003, Fischlin *et al.* 2007). Therefore, specific responses to these changes would have to be dealt with on a regional scale.

Although still debated, many studies have discussed the possible link between amphibian population declines and climate change (Alford and Richards 1999, Gibbons *et al.* 2000, Houlahan *et al* 2000, Kiesecker *et al.* 2001, Collins and Storfer 2003, Corn 2005, Araújo *et al.* 2006, Pounds *et al.* 2006). It is suggested that current reptile declines are similar to those of amphibians regarding geographic distributions and severity, arguably due to climate change (Gibbons *et al.* 2000, Araújo *et al.* 2006). Although many studies have assessed the species-environment relationship, and possible changes to this (Janzen 1994, Gibbons *et al.* 2000, Houlahan *et al.* 2000, Sala *et al.* 2000, Root *et al.* 2003, Engler *et al.* 2004, Thuiller *et al.* 2004, Gavin and Hu 2005, Thuiller *et al.* 2006 and references therein), few have focused on reptiles (Guisan and Hofer 2003, Araújo *et al.* 2006).

One such study demonstrated that reptile species in Switzerland are strongly restricted by temperature-related factors (Guisan and Hofer 2003). Additionally, due to their ectothermic nature, reptiles would assumedly be more strongly affected by cooling temperatures than by warming (Araújo *et al.* 2006). Thus, the ranges of reptiles within Europe have been projected to increase as a result of climatic warming (Araújo *et al.* 2006). However, they are generally considered poor dispersers and potentially unable to colonise this increase in climatically suitable area and could therefore still suffer a loss of available, suitable habitat (Araújo *et al.* 2006). The slow rate in distribution shifts makes reptiles potentially highly vulnerable to rapid climate change (Araújo and Pearson 2005), but it is difficult to test whether climatic changes alone are causing a decline in the availability of habitat for reptile species (Araújo *et al.* 2006). Many factors are likely responsible for such declines (Araújo *et al.* 2006).

The analysis of the species-environment relationship has been central in testing ecological theory, especially because the understanding of this relationship is vital in the predictive modelling of species' geographic ranges (Guisan and Zimmermann 2000). Changes in climate (*i.e.* environment) could affect species and communities, and changes in species life history traits could result (Hughes 2000, Parmesan *et al.* 2000, Root *et al.* 2003, Root *et al.* 2005, Parmesan 2006). Predictive niche-based modelling methods have been applied to chameleons in Madagascar for constructing species distribution maps (Raxworthy *et al.* 2003) and this method will be used in the present study in order to construct such maps for various *Bradypodion* taxonomic groups. *Bradypodion* are small chameleons, widespread and endemic to South Africa, and allopatrically distributed with potential contact zones (Branch 1998, Tolley *et al.* 2006, Tolley and Burger 2007). There are currently 15 recognised species, and genetic analysis suggests the presence of a number of clades displaying close evolutionary relationships climatic warming (Araújo *et al.* 2006). However, they are generally considered poor dispersers and potentially unable to colonise this increase in climatically suitable area and could therefore still suffer a loss of available, suitable habitat (Araújo *et al.* 2006). The slow rate in distribution shifts makes reptiles potentially highly vulnerable to rapid climate change (Araújo and Pearson 2005), but it is difficult to test whether climatic changes alone are causing a decline in the availability of habitat for reptile species (Araújo *et al.* 2006). Many factors are likely responsible for such declines (Araújo *et al.* 2006).

The analysis of the species-environment relationship has been central in testing ecological theory, especially because the understanding of this relationship is vital in the predictive modelling of species' geographic ranges (Guisan and Zimmermann 2000). Changes in climate (*i.e.* environment) could affect species and communities, and changes in species life history traits could result (Hughes 2000, Parmesan *et al.* 2000, Root *et al.* 2003, Root *et al.* 2005, Parmesan 2006). Predictive niche-based modelling methods have been applied to chameleons in Madagascar for constructing species distribution maps (Raxworthy *et al.* 2003) and this method will be used in the present study in order to construct such maps for various *Bradypodion* taxonomic groups. *Bradypodion* are small chameleons, widespread and endemic to South Africa, and allopatrically distributed with potential contact zones (Branch 1998, Tolley *et al.* 2006, Tolley and Burger 2007). There are currently 15 recognised species, and genetic analysis suggests the presence of a number of clades displaying close evolutionary relationships

(Tolley *et al.* 2006, Tolley and Burger 2007). The taxonomy is still under investigation with a number of undescribed species (Branch 1998, Tolley and Burger 2007). As a representative species particular focus will be given to the Cape Dwarf Chameleon, *Bradypodion pumilum*, a relatively large dwarf chameleon found within the southwestern corner of the Western Cape, South Africa (Tolley and Burger 2007).

Assuming that changing climates influence species ranges, climate change scenarios can be applied to niche-based models to describe possible future range shifts (Pearson and Dawson 2003). Additionally, the lack of reliable absence data for *Bradypodion* species necessitates the use of a presence-only modelling method. Thus, the habitat suitability maps for *Bradypodion* taxa were projected into the years 2050 and 2080, using climate scenarios generated by the Intergovernmental Panel on Climate Change. Due to the dependence of *Bradypodion* on vegetation (Tolley and Burger 2007), past responses of vegetation towards climate change (Linder 2003) and the past responses of *Bradypodion* species to climate change (Tolley *et al.* in review), I hypothesise that *Bradypodion* taxa will respond to future changes in climate. Additionally, owing to the variety of habitats occupied by the genus *Bradypodion* (Tolley and Burger 2007), the inherent differences in species ecology between taxa, and the effects of biotic interactions on species distributions (e.g. Losos 2001, Glor *et al.* 2003, Wiens 2004, Broennimann *et al.* 2007); species responses towards climate change should be individualistic. The study therefore seeks to address two main questions. Firstly, whether future predicted climate change will affect *Bradypodion* taxa. Secondly, what individual responses to these changes will result?

Materials and methods

Data sets

Data collection

Nighttime surveys were conducted at 26 sites throughout the range of *B. pumilum* from January through December 2006. One hundred and fifteen individuals were recorded via torchlight at 15 sites, by two to five observers. Coordinates were recorded for each individual using a hand-held GPS unit.

Additional data points for *B. pumilum* and other taxa were obtained from the specimen collections and databases housed at Bayworld (Port Elizabeth Museum), South African Museum, Transvaal Museum, National Museum, Natal Museum, Durban Museum and South African National Biodiversity Institute (SANBI). A total of 446 individuals encompassing nine taxa (*B. pumilum, B. damaranum*, *B. gutturale*, *B. occidentale*, *B. melanocephalum*, *B. ventrale*, *B. transvaalense*, *B. taeniabronchum,* and one undescribed species (*B. sp. 1*); Figure 1 and 2) were used; 122 observations comprised the *B. pumilum* dataset (Appendix 2). Two sets of analyses were performed at two different levels. The first was performed for the nine taxa separately, the second for each of three main phylogenetic clades (Figure 2; Tolley *et al.* 2004, 2006). The two clades that had only one species each (*B. caffer* and *B. setaroi*) were combined into a larger, supported clade (Clade C). Described taxa excluded from the analysis due to insufficient data (see analysis description below) included *B. atromontanum*, *B. kentanicum*, *B. caffer*, *B. setaroi*, *B. nemorale*, *B. dracomontanum* and *B. thamnobates* (Figure 2).

Environmental variables

One topographic and eight climatic variables were used to construct distribution models. Data were obtained from Schulze (1997) and included mean minimum and maximum monthly winter temperatures (°C), mean monthly summer and winter temperatures (°C), mean maximum annual temperatures (°C), annual evapotranspiration (mm), mean winter and summer precipitation (mm) and altitude (m). This comprised interpolated data at 1 x 1 minute grid cells (covering an average area of 2.97km^2) for South Africa. Winter was defined as May through August and summer from November through February. An additional measure of human influence on the land surface, the "Human Footprint" (Sanderson *et al.* 2002), was included. Four proxies for human influence were combined to create this scale. They included population density, land transformation, accessibility and electrical power infrastructure (Sanderson *et al.*

2002). This spatial index expresses the relative human influence, as a percent, across all terrestrial biomes at a global level (Sanderson *et al.* 2002).
This data set was further included in the future models and so served as a conservative estimate for human impacts in 2050 and 2080.

As particular reference was given to *B. pumilum*, multiple combinations of variables were used to select those providing an output best matching the current distribution of *B. pumilum*. These variables were also used in the models for all other taxa. The final set included mean maximum annual temperatures (°C), the human footprint, annual evapotranspiration (mm), winter and summer precipitation (mm) and altitude (m).

Future climatic scenarios

Climate scenarios for ~2050 and ~2080 were based on data obtained from the IPCC (International Panel on Climate Change) Special Report on Emission Scenarios “A1 scenario” (Nakicenovic and Swart, 2000). The A1 scenario is based on rapid economic growth and introduction of new technologies (IPCC 2007). Some of the highest increases in global warming are predicted to occur under this scenario (IPCC 2007). Thus, it represented a possible global worst-case climate change scenario.

Analysis using Maxent (2.3)

Maxent is a presence-only, niche based modelling method to estimate a target probability distribution of a species (Phillips *et al.* 2006). Known distributional data were combined with environmental variables in order to construct the models. Thus, additional areas with environmental conditions similar to those in which the species was found could be identified (Pearson *et al.* 2007). The models assume that the current distribution of a species provides a strong estimate as to its environmental requirements (Pearson and Dawson 2003). Maxent estimates a probability distribution from species point localities, each providing a set of environmental variables. The probability distribution is constrained by having the expected value of each environmental variable match its empirical average (Phillips *et al.* 2006). Taxa having 20 or more different data points were used in the construction of the habitat suitability maps (Appendix 2). An exception was *B. taeniabronchum*, having 19 localities, but was included as it is Critically Endangered (IUCN 2006, CR B1 + 2c). Maxent outputs are composed of continuous data (Phillips *et al.* 2006) and for ease of interpretation the models were converted to binary presence-absence maps using a 30% threshold.

In addition to the AUC (Area Under the Curve; provides measure of model performance, Phillips *et al.* 2006) generated by Maxent, an alternative test statistic adapted from Pearson *et al.* (2007) was performed for *B. pumilum*. The predictive success of the models was calculated via a jackknife procedure. The model was run 122 times (total number of *B. pumilum* presence records), leaving out one point locality each time. A percentage success rate was calculated defining the proportion of times the model was able to correctly predict that point.

An overall evaluation of model performance was also estimated for the model by assessing the total number of recorded point localities that fell within the predicted potential habitat.

Results

Bradypodion pumilum

The final output of potentially suitable habitat closely corresponded to the current range of the species (Figure 3). The AUC generated by Maxent was used in variable selection (AUC = 0.999, Figure 3). However, due to the small sample size and large area (South Africa) over which predictions were generated, the AUC was not considered as robust as would otherwise be required for the selection of relevant variables. The selected variables also performed well in the jackknife test, and correctly incorporated 93.4% of the sample points and further displayed an overall success rate of 93.5%. The final map (Figure 3) under-predicted (areas where the model failed to incorporate data points) the distribution of the species along the west coast and over-predicted (predicted areas of distribution where there are no data points) along the southeast coast of the range.

The model showed a decrease in current potentially suitable habitat by 2050, followed by a further decrease from 2050 – 2080 (Figures 4 and 5, AUC = 0.999). Approximately half its suitable habitat was predicted to be lost by 2050 (Figure 5), most occurring along the southeastern extents of its range (Figure 4). This prediction resulted in a range contraction towards the 'core' areas of its distribution (Figure 4).

Other Bradypodion taxa

As variable selection was based on outputs obtained for *B. pumilum*, the predicted distributions of the other taxa may have been less accurate. However, the results allow for a general trend of the possible effects of climate change on the other taxa to be obtained.

The models for seven (*B. damaranum, B. gutturale, B. melanocephalum, B. ventrale, B. transvaalense, B. taeniabronchum, B. sp. 1*) of the eight taxa showed a loss of suitable habitat by 2050, with six of those (*B. damaranum, B. gutturale, B. melanocephalum, B. ventrale, B. transvaalense, B. taeniabronchum*) showing a further loss from 2050 to 2080 (Figures 6 through 10). Although most models demonstrated a large loss of potential habitat by 2050, and a smaller loss from

2050 to 2080, the degree of loss was species specific, some responded more strongly than others at different time periods. The *B. damaranum* models displayed a large loss of suitable habitat by 2050 and a smaller loss from 2050 to 2080 (Figure 10). Conversely, the models for *B. transvaalense* demonstrated a more consistent loss of predicted suitable habitat through all time periods (Figure 10). Additionally, *B. transvaalense* displayed a southward range shift in modelled suitable habitat for 2050 and 2080 (Figure 8). Interestingly, the *B. occidentale* models displayed a range expansion by 2050, followed by no change from 2050 to 2080 (Figures 7 and 10).

Phylogenetic clades

As with the species models, responses to climate change in 2050 and 2080 were clade specific. Two of the three clade models (Clade A and B) displayed a loss of suitable habitat by 2050, and all showed loss by 2080 (Figures 11 through 13). The model for clade C displayed no loss in suitable habitat by 2050, and then a loss from 2050 – 2080 (Figure 13). None of the models displayed any overall range shifts or expansions for clades (Figures 11 and 12).

Discussion

All *Bradypodion* taxa are predicted to show responses to the climate scenarios for 2050 (Figures 4 through 10), and most are predicted to respond further by

2080. However, the model shows species responses to be individualistic. For 2050, *B. occidentale* was predicted to display a range expansion, while all others displayed range contractions (Figure 10). Coupled with this, *B. transvaalense* displayed a range shift (Figure 8). Additionally, in terms of extent, the models representing phylogenetic clade displayed differential responses to the climate scenarios (Figures 11 through 13), *i.e.* responses were clade specific. By 2080, all clades were predicted to undergo a range contraction (Figure 13). As well as individual taxa being affected, overall diversity will be affected because entire phylogenetic clades could lose part of their distribution.

The conservation implications of predicted distribution shifts for *Bradypodion* involve the establishment of conservation networks and plans for the future. If niche-based models were to be used in the construction of reserve networks, the conservation requirements of individual species and/or clades would have to first be assessed. Additionally, model uncertainties would have to be considered. Discrepancies include differences between climate change scenarios (IPCC 2007) as well as between global climate models. However, the models still provide a framework on which conservation plans can be constructed as well as providing a first step in assessing the possible effects of climate change on these species.

Bioclimatic models do have limitations, including: not accounting for biotic interactions (*e.g.* competition), the potential of species to adapt to changing climates, dispersal ability, and they assume equilibrium between a species and its environment (Pearson and Dawson 2003). However, models have still proved useful in describing known range shifts of species and providing an initial assessment of species risk to climate change (Pearson and Dawson 2003, Fischlin *et al.* 2007). Furthermore, the models allow for a quantitative assessment of the effects of climate change on biodiversity (Fischlin *et al.* 2007).

At large scales, as in the present study, bioclimatic models have proved useful in making broad predictions as to the possible effects of climate change on species distributions (Pearson and Dawson 2003). At a large scale climate was shown to be more efficient at explaining reptile distributions than topography (Guisan and Hofer 2003). Thus, it was assumed that the main determinants of *Bradypodion* distributions would be climate, followed by other factors such as topography, soil-type and vegetation. This hierarchy of variable importance was described by Pearson and Dawson (2003), stating that at continental scales climate may be considered the main factor in determining species distributions. At more local scales, topography may be more important, while at even smaller scales, biotic interactions may prove more efficient (Pearson and Dawson 2003). Assuming the distributions of the *Bradypodion* taxa are already affected by biotic interactions, and that the models are therefore based on the realised niche of the species (Pearson and Dawson 2003), biotic interactions have indirectly been included. Therefore, attempts were made to include variables pertaining to a wide variety of factors possibly effecting the distributions of *Bradypodion* taxa.

The localised distribution of many *Bradypodion* species (Tolley and Burger 2007), combined with the differential effects of climate change between regions (Sala *et al.* 2000), suggests conservation is necessary at a local scale. The most common response of species within the genus *Bradypodion* was range contractions. Even in species such as *B. occidentale* (Figures 7) and *B. transvaalense* (Figure 8), displaying a range expansion and shift respectively, the slow migration rate suggested for most reptiles (Araújo *et al.* 2006) still places them at risk. Compounding the problem of range shifts in species currently occurring within protected areas is the effects of changed community compositions due to species movements (Burns *et al.* 2003). However, work on Madagascan chameleons demonstrated that niche-based models could prove very useful for the expansion of conservation networks (Raxworthy *et al.* 2003). Additionally, niche-based models have been applied to identify and understand the distributions of Madagascan chameleon species in previously unsampled regions (Raxworthy *et al.* 2003). Maxent proved effective in constructing a map of suitable habitat for *B. pumilum*, even including unsampled areas where the species is thought to occur. Therefore, this method could prove useful in describing and understanding the distributions of the other *Bradypodion* taxa, especially lesser-known species.

Due to their small size and highly cryptic nature, true absences are unavailable for *Bradypodion*. However, most species distributions are fairly certain and highly allopatric. This lack of absences, suggests the models would, and did, over-predict the amount of potential habitat for some species. Compounding this is the small number of data points for many species. However, maximum entropy analysis has been shown to perform well with limited samples, but as sample size decreases, the relative importance of each individual data point increases (Pearson *et al.* 2007). Furthermore, the number of data points required for accurate model outputs varies from species to species. For some, very few data points are required to characterise their niche, while for others larger samples would be required (Pearson *et al.* 2007). To reduce this species-specific bias of small sample sizes, only species with 20 or more samples were used. The one exception, due to its conservation status, was *B. taeniabronchum.* A further bias in the modelling was the use of potentially inaccurate data points from historical data collected prior to the time of hand-held GPS units. However, Raxworthy *et al.* (2003) found that natural history museum data proved very useful in predictive niche modelling carried out on 11 Madagascan chameleons and provided a very good understanding of species distributions on the island.

An interesting implication of the over-predictions is the possible link to niche conservatism. In terms of niche-based models, niche conservatism is demonstrated by areas of overlapping, over-prediction in closely related, allopatrically distributed species (Raxworthy *et al.* 2003). It implies that species within a community preferentially occupy habitats closely matching those to which they have evolved (Ackerly 2003, Wiens 2004), promoting stabilising selection (Ackerly 2003), and subsequent niche conservatism (Webb *et al.* 2002, Ackerly 2003). Furthermore, it has been suggested as representing an important factor in allopatric speciation (Wiens 2004), and been demonstrated to occur in the *Bradypodion* genus (Chapter 1). *Bradypodion transvaalense* does not occur as far south as was predicted by the model (Figure 8) but there are some related species (*e.g. B. nemorale* and *B. thamnobates*; Figure 2), within the same clade, found in isolated forest patches within these areas. A similar result was obtained for *B. taeniabronchum* (Figure 9); the model over-predicted the species to occur in areas occupied by a closely related species (*B. sp. 2*) occurring within the same clade.

Alternatively, species may well be able to tolerate climatic conditions in areas of over-prediction, but as a result of competitive interactions with similar species they cannot colonise them. Therefore, species could be partitioning themselves similar to anoles on Greater Antillean Islands, where species have divided the structured habitat (Langerhans *et al.* 2006). Thus the *Bradypodion* may be partitioning themselves at a larger, two-dimensional scale based on variables such as vegetation type. However, while being predominantly niche conservative, *Bradypodion* do demonstrate the ability to enter novel habitats (Chapter 1). This phenomenon has also been demonstrated in other plant and animal taxa. Spotted Knapweed (*Centaurea maculosa*), for example, has an ability to shift climatic niches, possibly when released from biotic constraints (Broennimann *et al.* 2007). *Bradypodion ventrale* is able to exist in a wide variety of vegetation types (Tolley and Burger 2007). It is therefore able to exploit a variety of habitats, and when novel habitats lacking any competitors form, the species may be able to occupy these areas. A similar situation could exist for *B. pumilum*, which has two ecomorphs (Measey *et al.* in review), a typical forest morph, and an open canopy ecomorph (Tolley *et al.* 2006, Measey *et al.* in review). The appearance of novel habitats, such as the open canopy fynbos vegetation types, and subsequent lack of competitors may have allowed the species to exploit these areas.

Niche-based modelling proved highly useful in identifying, describing and understanding the distributions of various *Bradypodion* taxonomic groups. The results suggest that these methods are useful in describing and understanding chameleon distributions. Furthermore, support for the niche conservative nature of these species, and thereby the relevance of broad-scale environmental factors coupled with biotic interactions in the determination of species distributions, was provided. Future climate change scenarios show that most species are predicted to lose potential niche space in the face of climate change, although the severity of loss is species specific. This information, as well as the locations of the predicted area changes in species distributions, could prove useful in the establishment of conservation networks and plans for the future.

Acknowledgements

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Figures

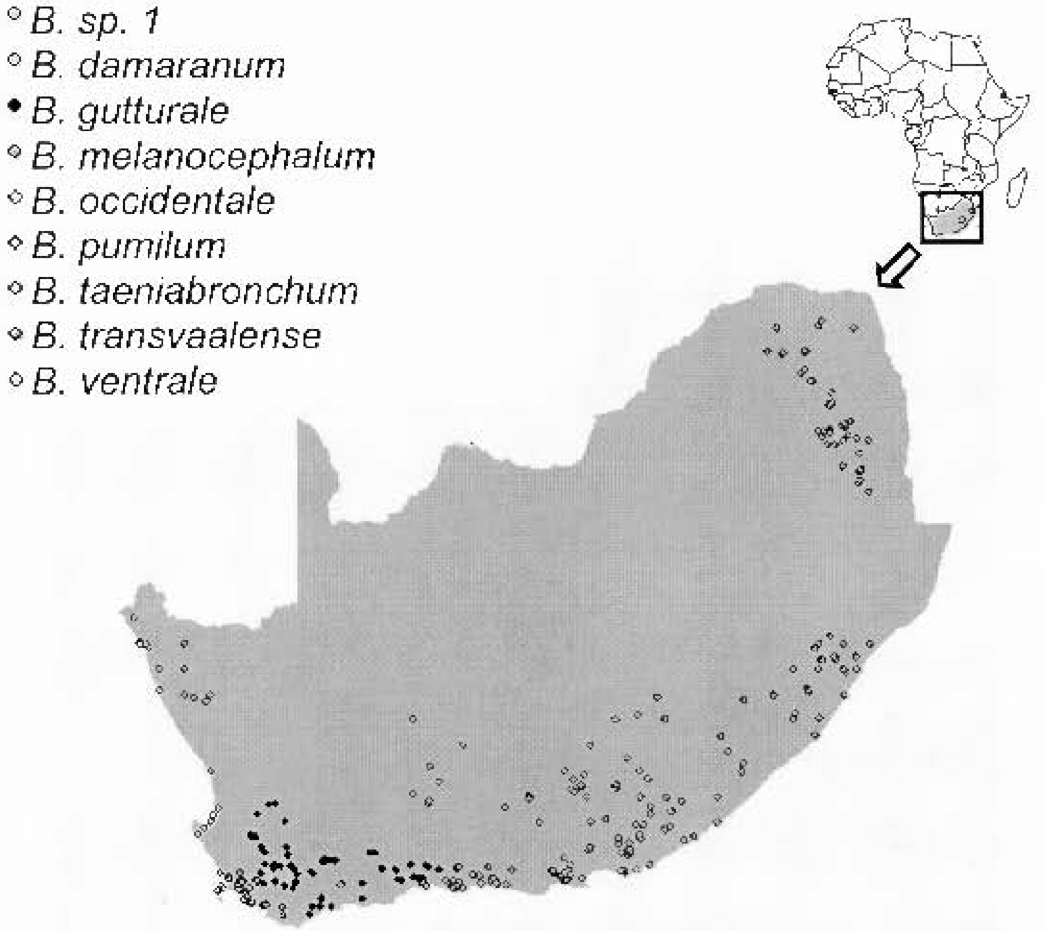


Figure 1 Map of South Africa displaying point localities for the 9 allopatrically distributed *Bradypodion* species (**n** = 446) used in this study.

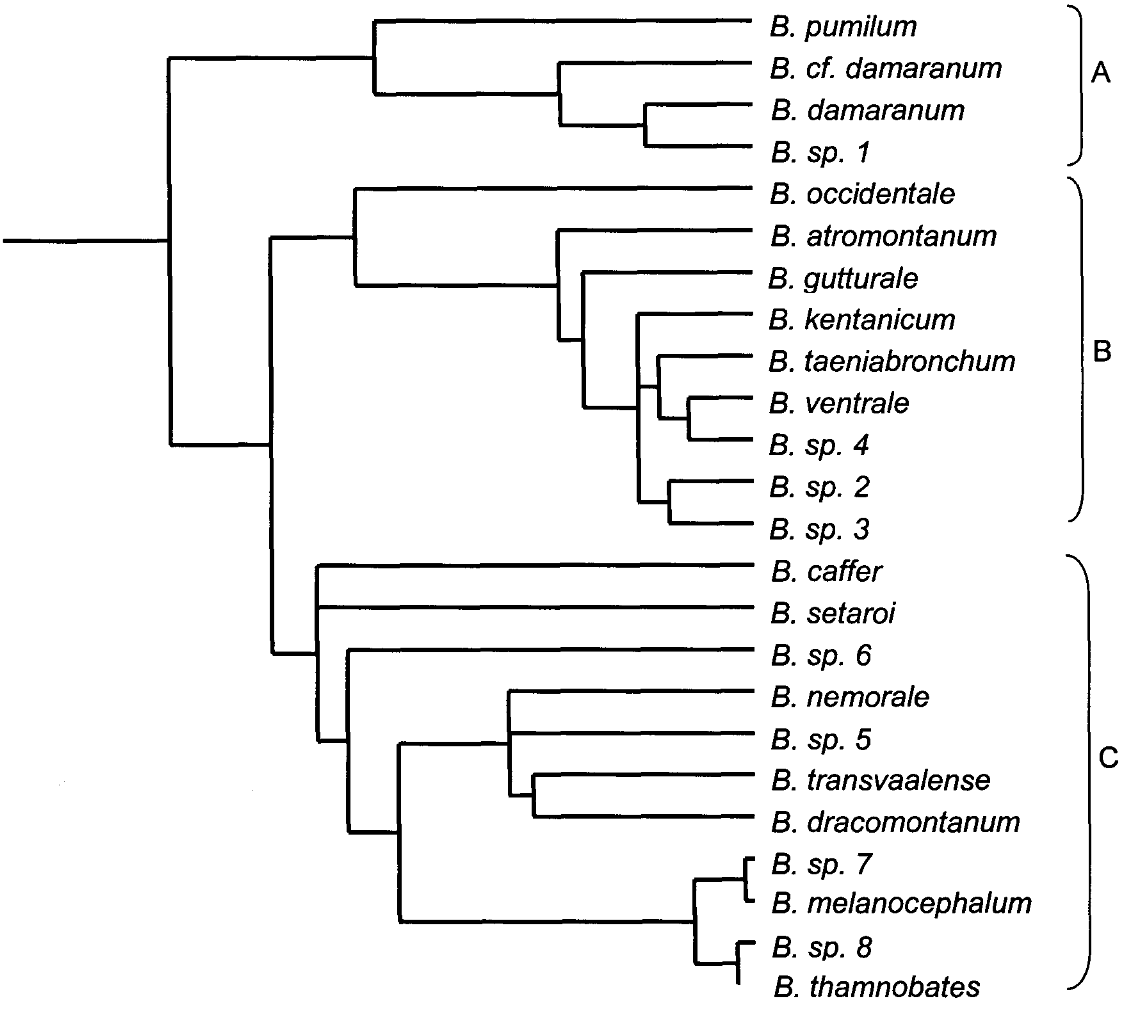


Figure 2 A *Bradypodion* phylogenetic tree, showing terminal taxa and the 3 clades used in analysis (Adapted from Tolley *et al.* in review, K. Tolley pers. com.).

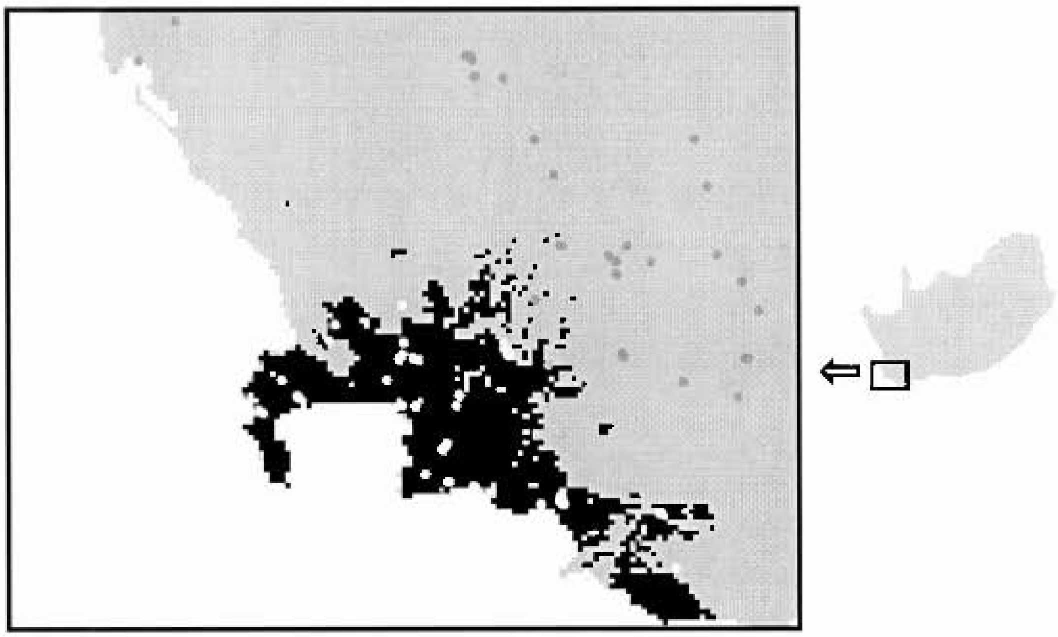
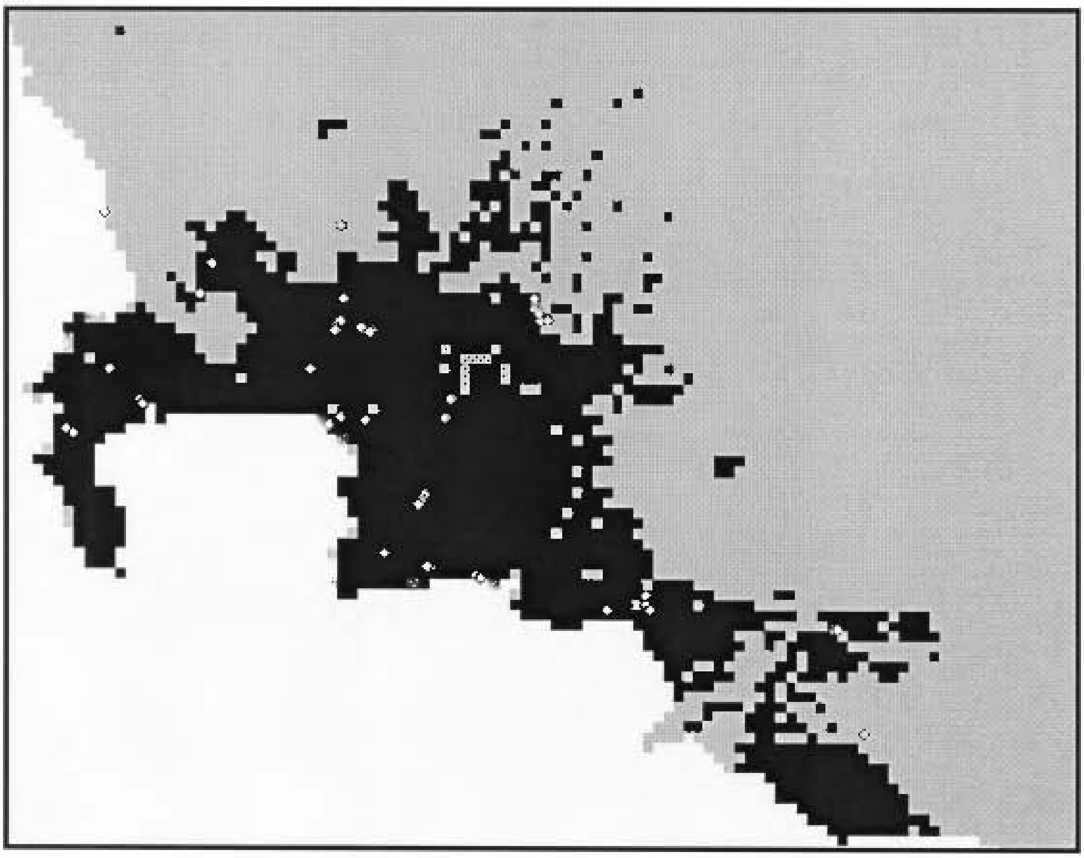
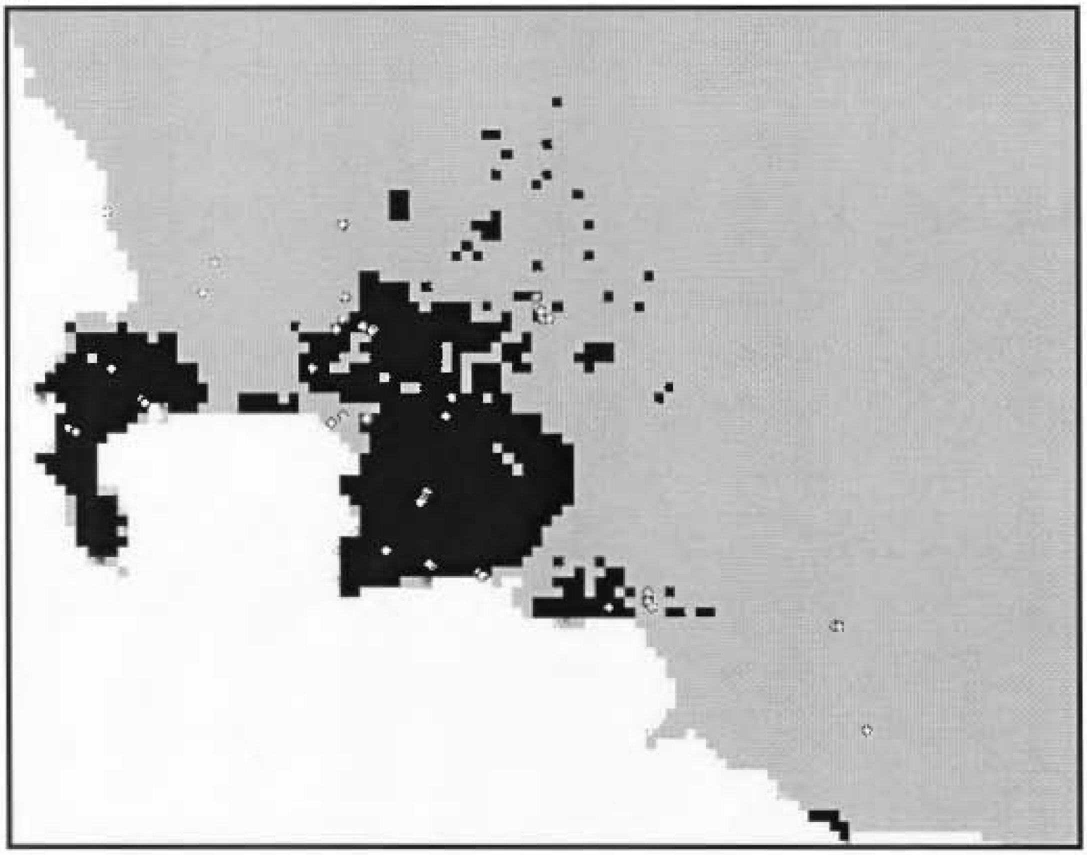


Figure 3 Shaded black region indicates the current potentially suitable habitat for *B. pumilum* (AUC = 0.999, n = 122) generated using Maxent. Yellow circles indicate locality records of *Bradypodion pumilum*, purple and red circles show neighbouring *Bradypodion* species, *B. gutturale* (n = 75) and *B. occidentale* (n = 23) respectively.

A



B



C

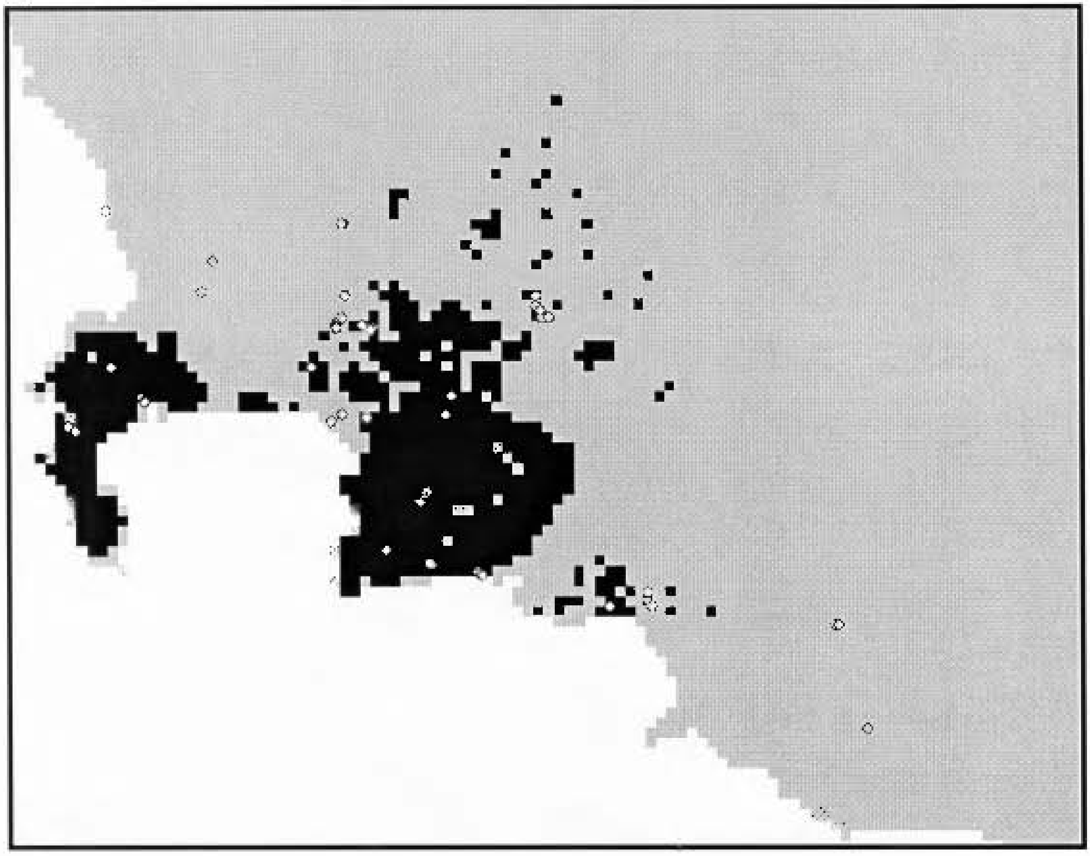


Figure 4 Potentially suitable habitat for *Bradypodion pumilum* generated using Maxent. Black shaded region indicates suitable habitat, climatic projections (2050 and 2080) were carried out using the IPCC's A1 scenario. White circles represent all point localities (n = 122). A = current potential habitat (AUC = 0.999), B = potential habitat for 2050 (AUC = 0.999), C = potential habitat for 2080 (AUC = 0.999).

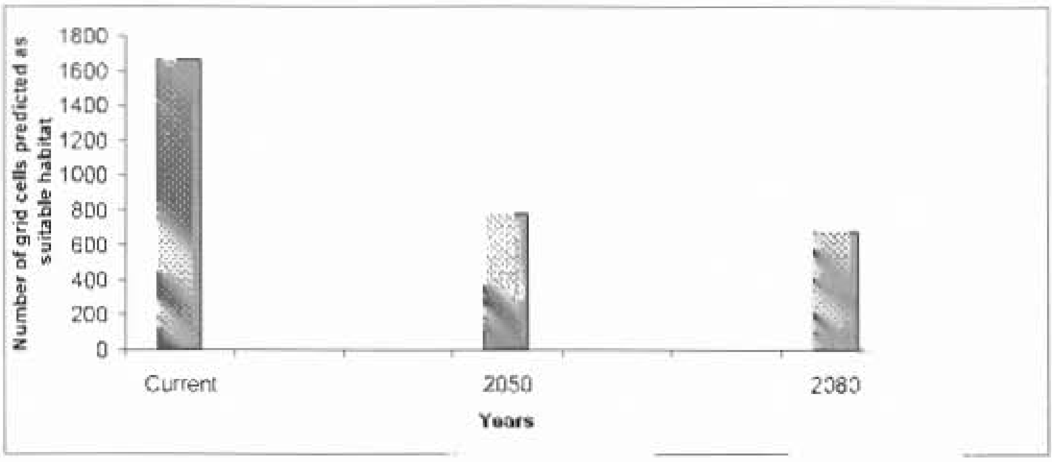
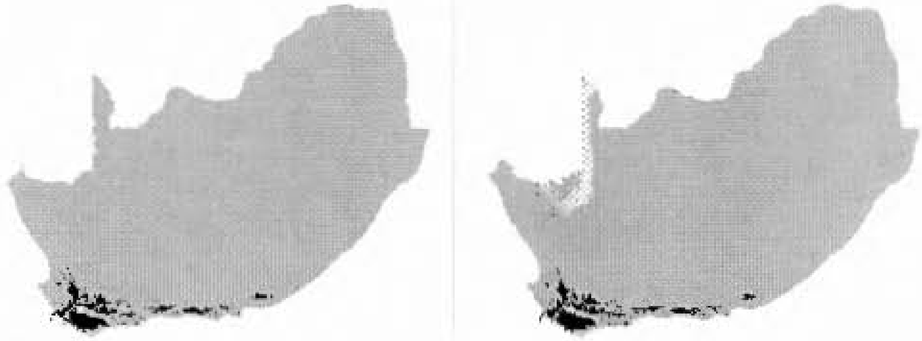
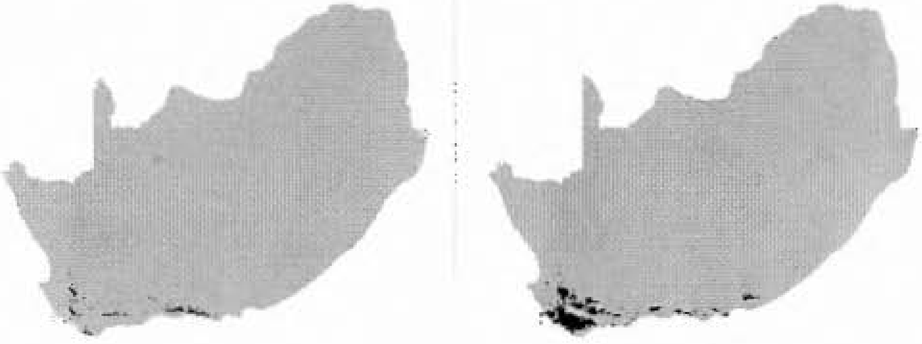


Figure 5 Frequency of 1' grid cells currently predicted as suitable habitat for *Bradypodion pumilum* and projected to be suitable in 2050 and 2080. Predictions and projections generated using Maxent.

A (AUC = 0.997) A (AUC = 0.977)

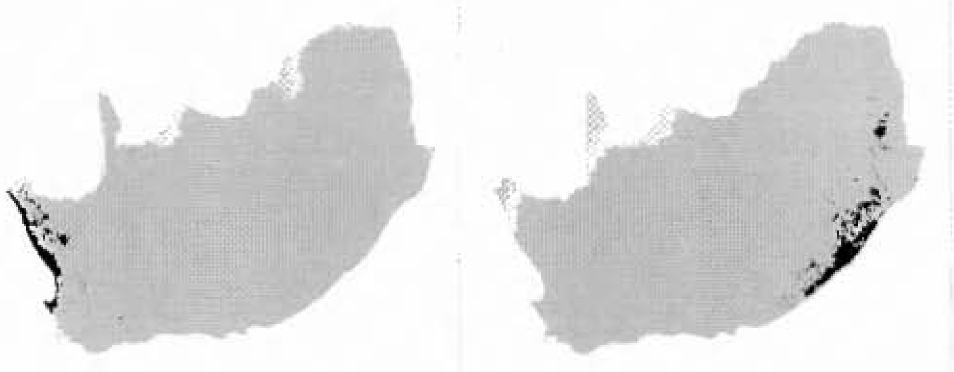


B (AUC = 0.997) B (AUC = 0.977)

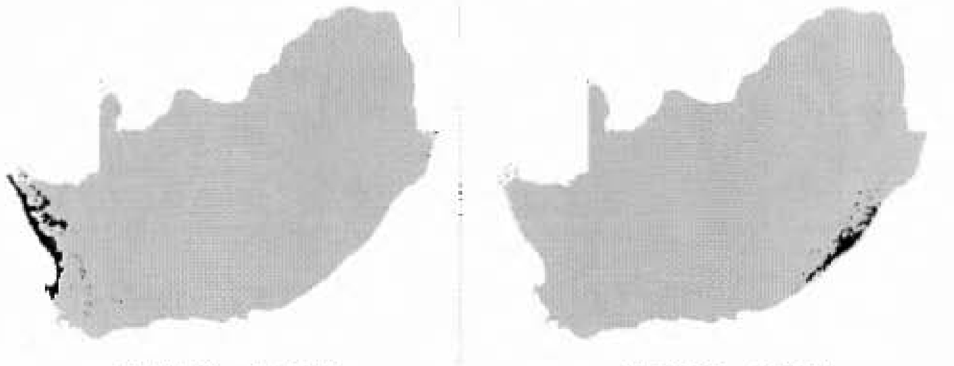


C (AUC = 0.997) C (AUC = 0.977)

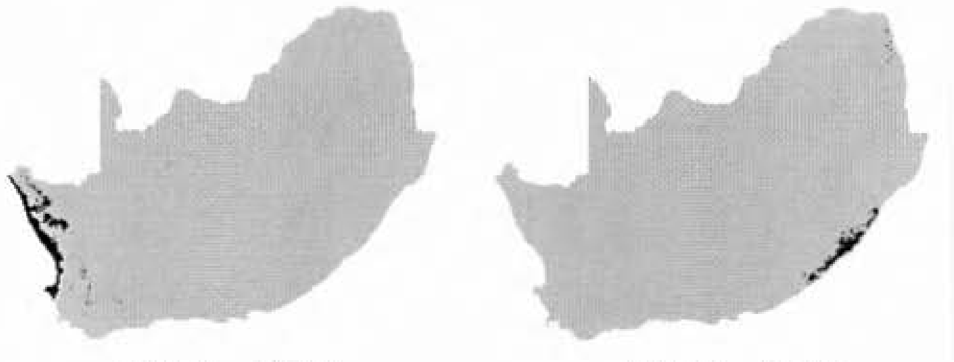
Figure 6 Shaded black regions represent current and future potentially suitable habitat for *B. sp. 1* (left column, n = 20) and *B. gutturale* (right column, n = 75). A = current potential habitat, B = potential habitat for 2050, C = potential habitat for 2080.



A (AUC = 0.990) A (AUC = 0.985)

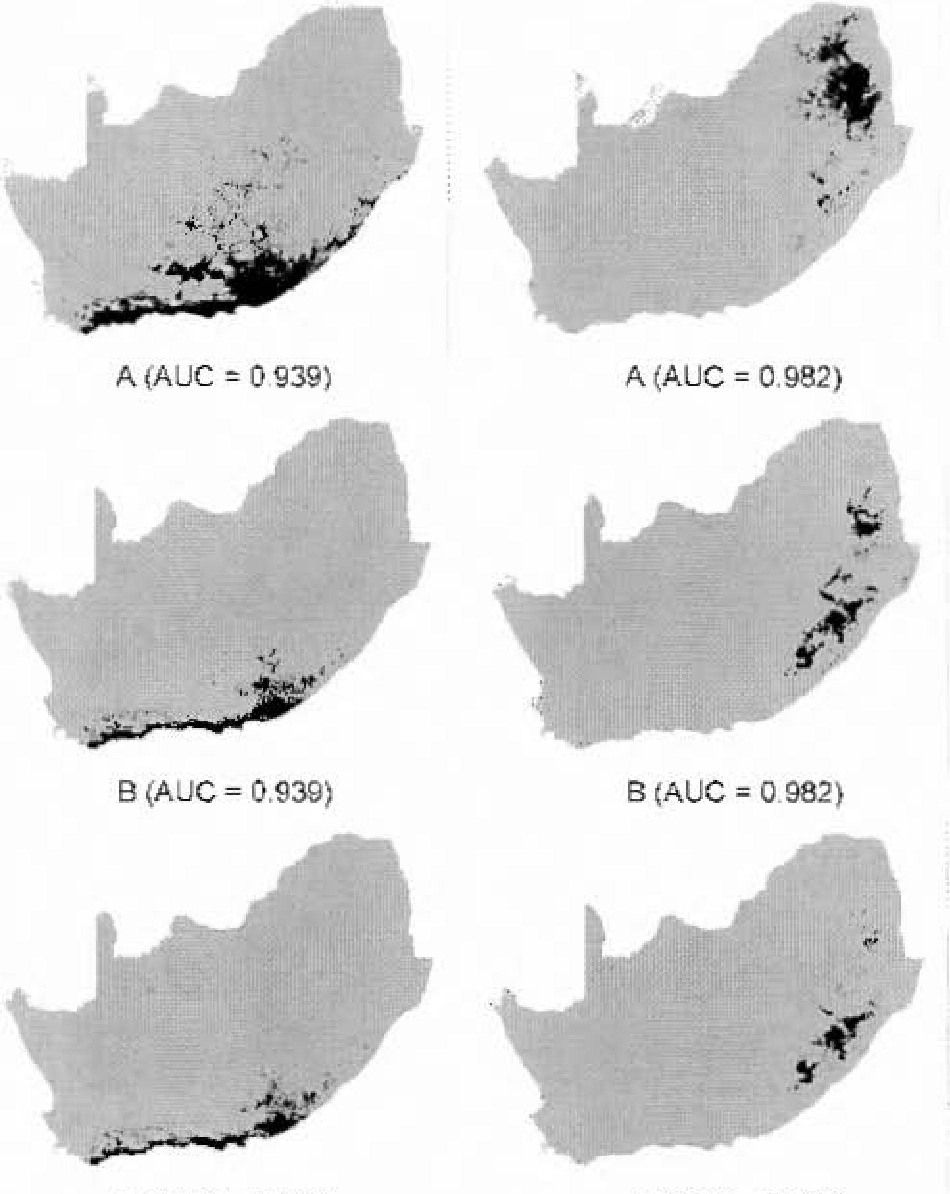


B (AUC = 0.990) B (AUC = 0.985)



C (AUC = 0.990) C (AUC = 0.985)

Figure 7 Shaded black regions represent current and future potentially suitable habitat for *B. occidentale* (left column, n = 23) and *B. melanocephalum* (right column, n = 31). A = current potential habitat, B = potential habitat for 2050, C = potential habitat for 2080.



A (AUC = 0.939)

A (AUC = 0.982)

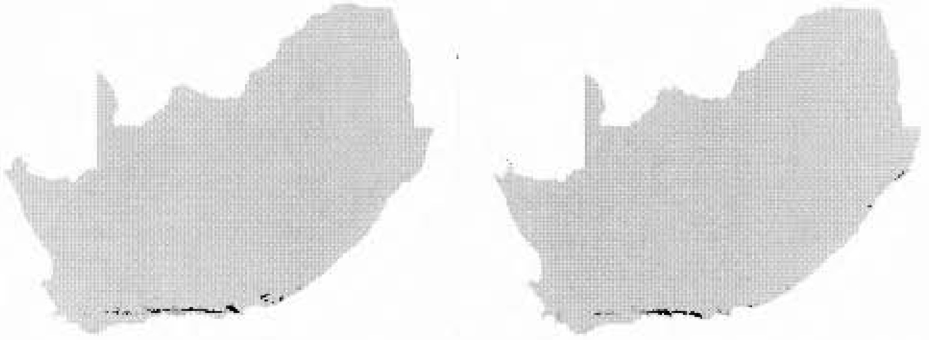
B (AUC = 0.939)

B (AUC = 0.982)

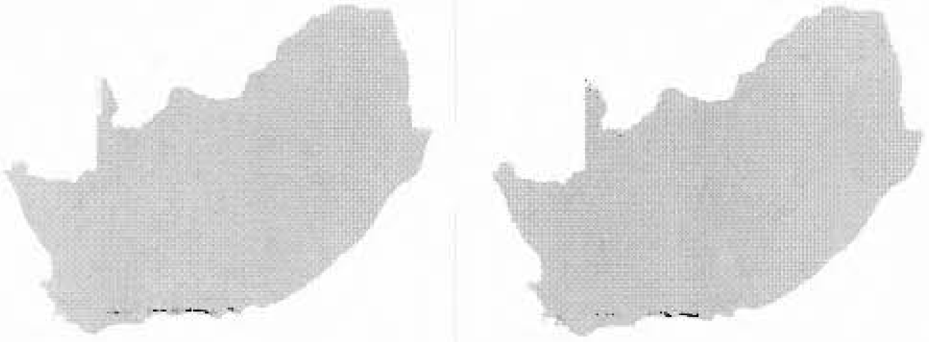
C (AUC = 0.939)

C (AUC = 0.982)

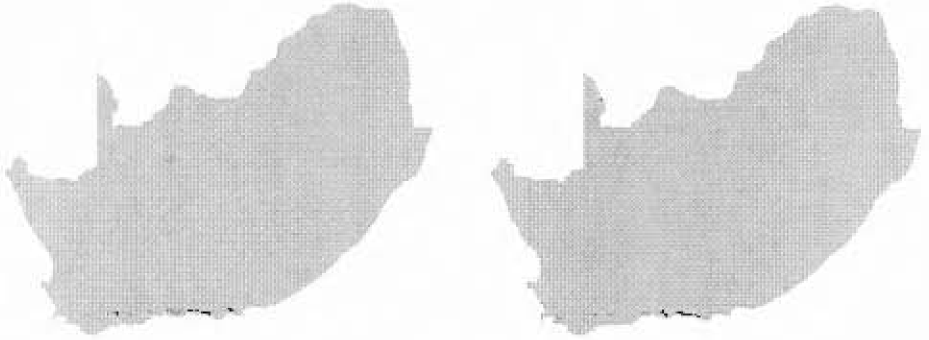
Figure 8 Shaded black regions represent current and future potentially suitable habitat for *B. ventrale* (left column, n = 89) and *B. transvaalense* (right column, n = 47). A = current potential habitat, B = potential habitat for 2050, C = potential habitat for 2080.



A (AUC = 1.000) A (AUC = 1.000)



B (AUC = 1.000) B (AUC = 1.000)



C (AUC = 1.000) C (AUC = 1.000)

Figure 9 Shaded black regions represent current and future potentially suitable habitat for *B. taeniabronchum* (left column, n = 19) and *B. damaranum* (right column, n = 20). A = current potential habitat, B = potential habitat for 2050, C = potential habitat for 2080.

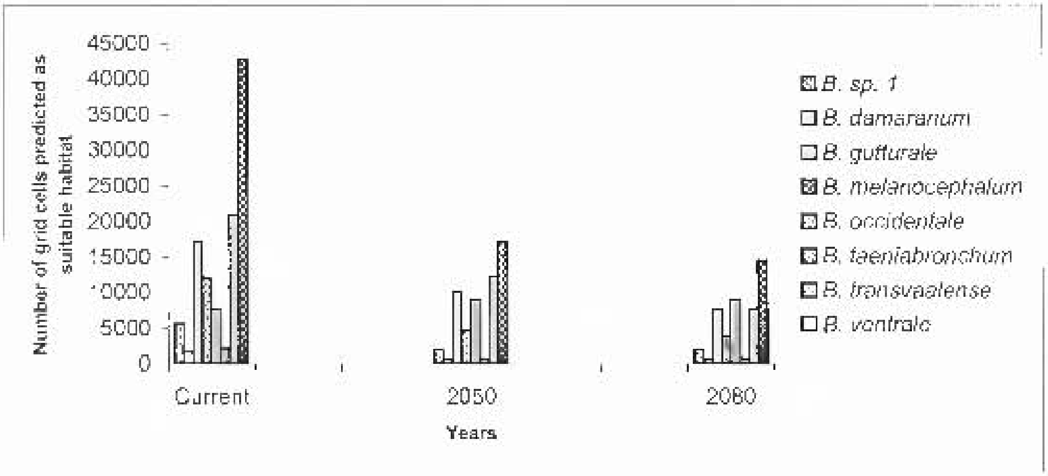
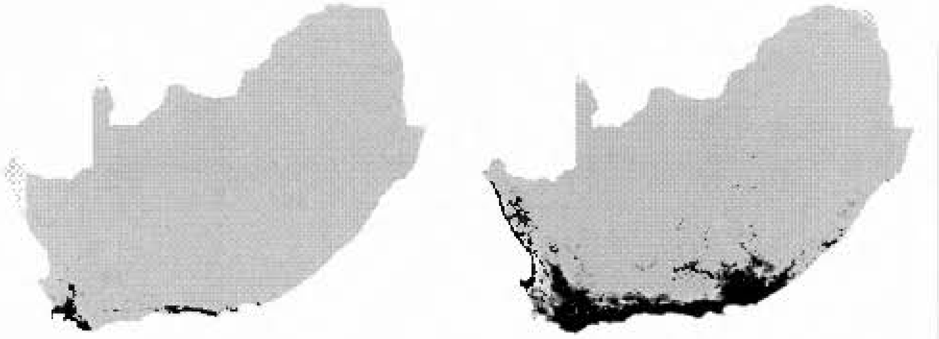
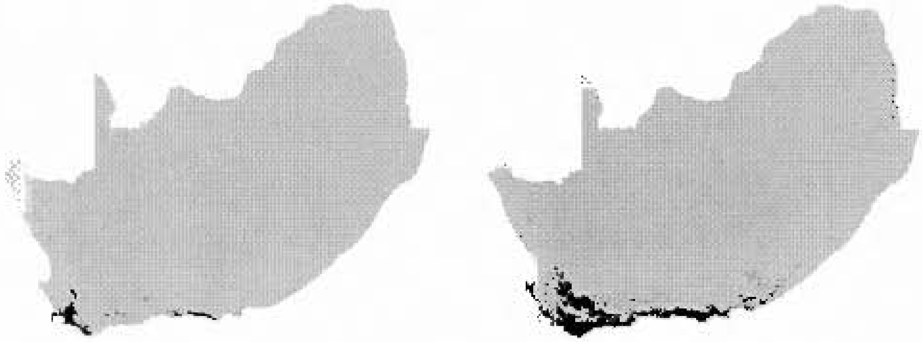


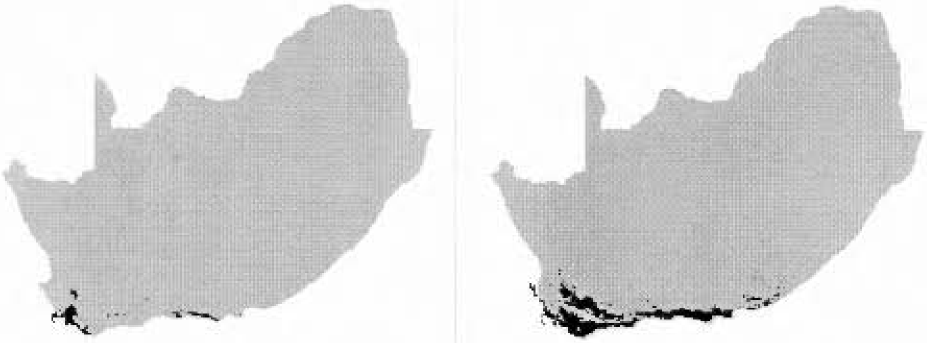
Figure 10 Frequency of 1' grid cells currently predicted as suitable habitat for additional *Bradypodion* taxa and projected to be suitable in 2050 and 2080. Predictions and projections generated using Maxent.



A (AUC = 0.997) A (AUC = 0.942)



B (AUC = 0.997) B (AUC = 0.942)



C (AUC = 0.997) C (AUC = 0.942)

Figure 11 Shaded black regions represent current and future potentially suitable habitat for Clade A (left column, n = 165) and Clade B (right column, n = 264). A = current potential habitat, B = potential habitat for 2050, C = potential habitat for 2080.

A (AUC = 0.966)

B (AUC = 0.966)

C (AUC = 0.966)

Figure 12 Shaded black regions represent current and future potentially suitable habitat for Clade C (left column, n = 152). A = current potential habitat, B = potential habitat for 2050, C = potential habitat for 2080.

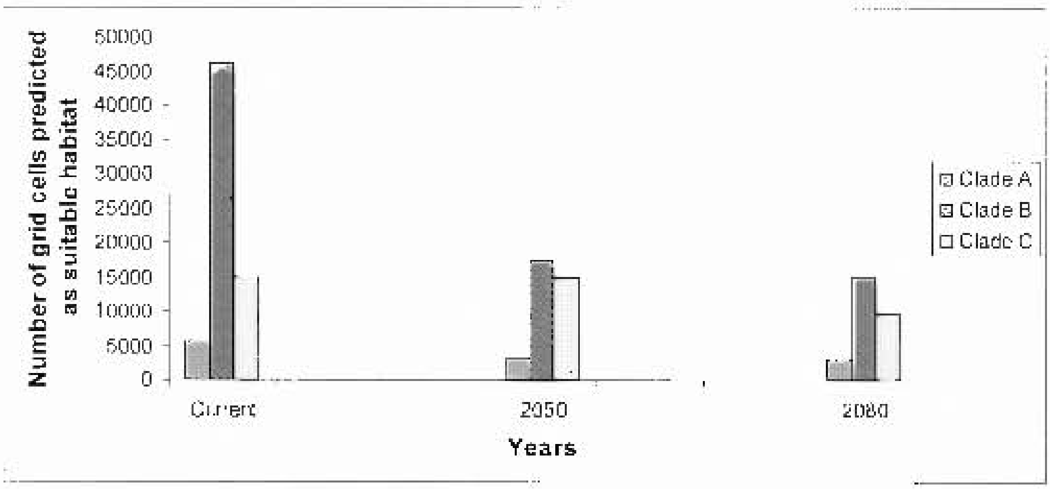


Figure 13 Frequency of 1' grid cells currently predicted as suitable habitat for all the *Bradypodion* clades and projected to be suitable in 2050 and 2080. Predictions and projections generated using Maxent.

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Appendix

Appendix 1 Sites visited for *Bradypodion pumilum* surveys and the total number of individuals found at each site.

Site 1	Site name	GPS (S)	GPS (E)	Number of individuals
1	Koegelberg Biosphere Reserve	34° 19. 29'	18° 58. 20'	20
2	Mizpah	34° 13. 12'	18° 57. 40'	18
3	Devon Valley, Stellenbosch	33° 56. 05'	18° 49. 19'	9
4	Noordhoek	34° 05. 88'	18° 22. 71'	9
5	Landroskop	34° 02. 97'	19° 02. 57'	12
6	Robben Island	33° 47. 74'	18° 22. 39'	8
7	Blauberg Conservation Area (Hilltop)	33° 45. 33'	18° 27. 93'	0
8	Blauberg Conservation Area (Base of hill)	33° 45. 83'	18° 28. 38'	0
9	Blauberg	33° 44. 79'	18° 26. 51'	7
10	Blauberg (urban garden)	33° 43. 65'	18° 26. 58'	1
11	Elandsberg Farm	33° 28. 13'	19° 02. 37'	0
12	Somerset West	34° 04. 99'	18° 52. 22'	10
13	Rondevlei Nature Reserve	34° 03. 39'	18° 30. 19'	7
14	Fernkloof Nature Reserve	34° 23. 64'	19° 15. 96'	4
15	Vogelgat Nature Reserve	34° 24. 11'	19° 19. 22'	1
16	Tygerberg Hill Nature Reserve	33° 52. 66'	18° 35. 98'	5
17	Paarl Tortoise Reserve	33° 45. 98'	18° 49. 87'	2
18	Grootbos	34° 32. 47'	19° 24. 69'	0
19	Farm 215	34° 34. 14'	19° 33. 09'	0
20	Salmonsdam	34° 25. 36'	19° 38. 19'	2
21	Elim	34° 34. 76'	19° 45. 83'	0
22	Struisbaai	34° 48. 49'	20° 02. 81'	0
23	Arniston	34° 39. 71'	20° 30. 30'	0
24	Aghulus	34° 49. 04'	20° 00. 54'	0
25	Darling	33° 22. 37'	18° 22. 62'	0
26	Clara Anna Fontein Nature Reserve	33° 49. 58'	18° 37. 20'	0

Appendix 2 The total number of individuals for each *Bradypodion* taxa used in analysis.

Species	Point localities
Bradypodion sp. 1	20
Bradypodion damaranum	20
Bradypodion gutturale	75
Bradypodion melanocephalum	31
Bradypodion occidentale	23
Bradypodion pumilum	122
Bradypodion taeniabronchum	19
Bradypodion transvaalense	47
Bradypodion ventrale	89

Chapter 4

The environmental-morphological relationship of *Bradypodion pumilum*, an endemic South African Dwarf Chameleon

Abstract

There is often a complex relationship between a species' morphology and environment, which has frequently been documented in various lizard species. Such a relationship has been hypothesised for the Cape Dwarf Chameleon (*Bradypodion pumilum*), as there are at least two distinct ecomorphs that inhabit different vegetation types. The present study employed Regression Tree Analysis to investigate the environmental-morphological relationship for the Cape Dwarf Chameleon. Using this analysis, morphological measurements were investigated for correlations with habitat variables relating to vegetation type. A strong relationship was found between the morphology of *B. pumilum* and those environmental variables pertaining specifically to vegetation structure and density ($p < 0.05$). Larger body size correlated strongest with vegetation structurally resembling closed habitats, whereas smaller body size correlated strongest with vegetation resembling open habitats. These results support previous hypotheses whereby distinct ecomorphs were presumed to occupy certain vegetation types.

Introduction

The relationship between morphology and environment can be complex (Langerhans *et al.* 2007a) and has frequently been documented in lizards (e.g. Fleishman 1992, Vitt *et al.* 1997, Butler *et al.* 2000, Kohlsdorf *et al.* 2001, Losos and Miles 2002, Ackerly 2003, Glor *et al.* 2003) and fish species (e.g. Chapman *et al.* 2000, Bouton *et al.* 2002, Langerhans *et al.* 2007a, 2007b). For example, Phrynosomatid lizards display differences in body shape and limb measurements within different habitats (Herrel *et al.* 2001), and a correspondence between macrohabitat type and various morphometric features, such as snout-vent length and limb length, has been found in the *Anolis cybotes* group (Glor *et al.* 2003). Thus, there is often a relationship between a species' morphological traits and its niche (Knouft *et al.* 2006).

Natural selection acting on a species may lead to the establishment of diverse morphological adaptations (Wiens 2004). The frequent occurrence of a relationship between phenotypes and their respective environments indicates the adaptive value of different morphological traits (Ackerly 2003). These patterns may result from phenotypic plasticity, ecological sorting or natural selection (Vitt *et al.* 1997, Chapman *et al.* 2000, Losos *et al.* 2000, Ackerly 2003) and the idea that different ecological requirements leads to differing morphologies has been well demonstrated in various lizard species (Scheibe 1987, Pounds 1988, Kohlsdorf *et al.* 2001), and in particular species of *Anolis* lizards (Vitt *et al.* 1997, Vanhooydonck and Van Damme 1999, Zaaf and Van Damme, 2001, Leal *et al.* 2002). However, very little work has been focussed towards chameleons (Losos *et al.* 1993, Bickel and Losos 2002, Stuart-Fox and Moussalli 2007). The present study aims to correlate morphology and environment for a species of chameleon known to be morphologically variable, *Bradypodion pumilum*.

Bradypodion pumilum is a relatively large dwarf chameleon found within the southwestern corner of the Western Cape, South Africa. Although the species occupies a relatively small area, it occurs within a wide variety of habitats where different morphological forms inhabit various vegetation types (Tolley and Burger 2007). The presence of these forms, occupying structurally different habitats (Tolley and Burger 2007, Measey *et al.* in review), suggests a strong relationship between morphology and environment. The typical form tends to be large, long-tailed and colourful, occurring predominantly in closed canopy vegetation types such as urban gardens, forests, scrub and thickets. Montane and lowland fynbos areas are inhabited by a form that is smaller, has a short tail and dull colouration (Tolley and Burger 2007). These forms constitute two ecomorphs, those from closed habitats, corresponding to the typical form, and those from open habitats, corresponding to the fynbos form (Measey *et al.* in review).

Overall, there appears an apparent correspondence between *Bradypodion* phenotypes and structurally different habitats (Tolley and Burger 2007), as well as a high dependence of *Bradypodion* species on vegetation (Tolley *et al.* 2006).

Therefore, I hypothesised that there is a correlation between the environment and morphology of *B. pumilum*. Consequently, the present study aims to answer two questions: (1) does a correlation between morphology and environment exist? (2) Which morphological variables are most strongly correlated to which environmental factors?

Materials and Methods

Data capture

Surveys were conducted at 26 sites throughout the range of *B. pumilum*, from January through December 2006. Individuals were located at night by two to five observers, using torchlight. A total of 116 chameleons, composed of individuals recorded from field surveys with additional individuals obtained from Measey *et al.* (in review), were used. Additionally, only individuals with a snout-vent length of 45mm or more (representing the smallest, closed-canopy morph individual able to be reliably sexed as male (Measey *et al.* in review)) were used in the analysis. Morphological measurements were collected during collaborative field surveys (Measey at al. in review, Hopkins in prep.) and included snout-vent length, tail length, head height and head width (Figure 1).

Two 10m x 10m vegetation quadrats were set up at the location of the first and the last chameleon found at each of the sites. Categorical variables assessing the general environment within these quadrats were measured and included canopy cover, canopy height, number of trees, number of shrubs, number of restionaceae clumps, dominant vegetation structure, highest visible perch, structure of highest visible perch, vegetation type, average vegetation density and slope (Appendix 2). Any woody plant with a height of 2m or more was classified as a "tree". Percentage canopy cover was assessed as "canopy density", for instance a canopy comprised of dense bushes (open habitats) would have a higher percentage canopy cover than one comprised of fewer trees (closed habitats). Additionally, the size of the quadrats often meant that within closed habitats, only a few trees were included in the quadrats. In contrast, within open habitats many bushes could be included in the quadrats. Thus, with respect to the present analysis, open habitats had a denser canopy cover than closed habitats. Chameleons were classified as belonging to one of two ecomorphs: "open", occurring in open fynbos-type vegetation (dense canopy cover), where individuals are generally small and dull coloured with a short tail and a reduced casque; and "closed", occurring in closed canopy-type vegetation (sparse canopy cover) with large, brightly coloured chameleons with long tails and large casques (Tolley *et al.* 2006, Tolley and Burger 2007, Measey *et al.* in review).

Analysis

To address which environmental variables best explained overall morphological traits within *B. pumilum*, all sizes, females, males, and both ecomorphs, were included in a single analysis. All morphological variables were tested for normality and log-transformed when necessary (using SPSS v12). Regression tree analysis (RTA) was carried out using the programme R (v2.3). RTA allows for a simplistic representation of the variation generated from categorical or numeric explanatory variables on a numeric response variable (De'Ath and Fabricius 2000, Moisen and Frescino 2002). The morphological variables functioned as response variables in all trees while the categorical environmental factors functioned as explanatory variables. RTA models place explanatory variables in a hierarchical manner based on explained deviance (variation), with the first variable at the top of the tree explaining the most variation (Franklin 1998, Thuiller *et al.* 2003). In this case the explained deviance was graphically represented by branch length, longer branches explaining more deviance. To test goodness of fit, and thus how well the model fitted the data, a linear regression was used to obtain an adjusted r^2 and corresponding p value for each of the trees.

Results

Regression trees for snout-vent length and tail length explained over 40% of the variation within the data and were most strongly correlated to canopy cover (the habitat variable at the "top" of the regression tree) followed by dominant vegetation structure (Figures 2 and 3). Regression trees for head width and head height explained 26% and 27% of the variation within the data respectively

(Figures 4 and 5). Dominant vegetation structure was the first habitat variable on both of these regression trees (Figures 4 and 5) indicating that the variation within head width and head height was best explained by dominant vegetation structure.

Areas with sparse canopy cover comprised individuals with the largest snout-vent length ($\bar{x}$ = 65.25mm; 1 – 5%, Figure 2). Smaller individuals, $\bar{x}$ = 50.43mm and $\bar{x}$ = 55.64mm, were found in areas with a denser canopy cover comprising shrubs and reeds/restioids respectively (Figure2). A similar pattern was seen with tail length. Individuals with longer tails were found in areas with low canopy cover (1 – 5%, Figure 3). Areas with a higher percentage canopy cover comprising shrubs and reeds/restioids contained individuals with shorter tails ($\bar{x}$ = 48.26mm and $\bar{x}$ = 55.13mm respectively; Figure 3).

Individuals with a smaller head width ($\bar{x}$= 6.82mm) were found in habitats dominated by shrubs, while individuals displaying the largest head widths were in reed/restioid dominated vegetation with sparse canopy cover (Figure 4). However, unlike the regression trees for snout-vent length and tail length, this result did not distinguish between open and closed habitats. Individuals with the smallest head heights ($\bar{x}$ = 7.94mm), were found in areas dominated by shrubs while individuals with the largest head heights ($\bar{x}$ = 9.62mm) were found in reed/restioid dominated areas with sparse canopy cover (Figure 5).

Snout-vent length and tail length were found to be non-normal. After log transformation tail length was found to be normally distributed, while snout-vent length was still non-normal. As snout-vent length data were not normally distributed, results should be viewed with some caution. However, the regression trees may still be valid (Vayssiéres *et al.* 2000), and, as the results agreed with the regression tree for tail length it allowed for general patterns to be examined. Furthermore, RTA procedures are non-parametric by nature (Vayssiéres *et al.* 2000), but the linear regression employed to test for goodness of fit was not. The goodness of fit test, describing model strength, indicated that all regression trees constructed for the four morphological variables (snout-vent length, tail length, head width and head height) were significant ($p < 0.05$).

Discussion

Morphological traits of the Cape Dwarf Chameleon, *Bradypodion pumilum*, are strongly correlated to habitat variables supporting the hypothesis that a strong correspondence exists between morphology and vegetation type for *Bradypodion* (Tolley *et al.* 2006). For *B. pumilum*, considerable morphological variation has been demonstrated between the two ecomorphs, and it was hypothesised that the observed variation is correlated to habitat differences (Tolley *et al.* 2006, Tolley and Burger 2007, Measey *et al.* in review). The habitat variables most strongly correlated to species morphology were those pertaining to vegetation density and structure (Figures 2 – 5), and this variation in morphology presumably provides a survival advantage to those individuals occupying their respective habitats (Vitt *et al.* 1997, Measey *et al.* in review).

Within the genus, previous studies have noted the presence of different phenotypes within different habitats (e.g. Tolley *et al.* 2004, 2006, Stuart-Fox and Moussalli 2007, Measey *et al.* in review). Generally, species with higher casques and longer tails were associated with closed canopy habitats, while individuals in areas with a high shrub and perch density (fynbos) were shown to have a smaller body size and shorter tails (Tolley *et al.* 2006, Stuart-Fox and Moussalli 2007, Measey *et al.* in review). In the present study, the presence of individuals with large snout-vent and tail lengths correlated strongly with a sparse canopy cover (Figures 1 and 2), in this case indicating closed habitats that had a lower canopy density than shrub dominated open habitats. Therefore, the largest individuals were found within closed canopy habitats. Additionally, individuals with the smallest head width and head heights were found in areas dominated by shrubs (fynbos).

Numerous ideas have been formulated to explain the morphological diversity seen in *Bradypodion* species occupying structurally different habitats. These include predator avoidance (Stuart-Fox *et al.* 2006, Stuart-Fox *et al.* in press, Measey *et al.* in review), sexual selection (Stuart-Fox *et al.* 2006), fire frequency (Stuart-Fox *et al.* 2007), locomotive and movement restrictions (Stuart-Fox *et al.* 2007), perch density (Stuart-fox *et al.* 2007) and phylogenetic constraint (Tolley *et al.* 2006, Stuart-Fox *et al.* 2007). Although the present study was not designed to directly test these hypotheses, it provides the first quantitative results showing morphological differences associated with different habitats for chameleons.

Similarly, morphology and habitat have been linked in various *Anolis* lizard species (e.g. Losos and Miles 2002, Ackerly 2003, Glor *et al.* 2003). Some lineages have shown long term morphological stability based on macrohabitat affinities, while others display evolutionary divergence in novel habitats (Glor *et al.* 2003). Additionally, long-term stability in habitat affinities for *B. pumilum* has been suggested (Chapter 1). Therefore, being able to respond morphologically to environmental selective pressures, may aid *B. pumilum* in adapting to novel environments when these become available.

The strong link between morphology and habitat suggest that environmental factors place strong selective pressures on the morphology of *B. pumilum*. The particular morphological outcome of these pressures will therefore be habitat specific, presumably offering a survival advantage to individuals within that particular habitat. The ability to respond to environmental selective pressures may also have been a major factor responsible for the morphological divergence of *B. pumilum* into open and closed habitats.

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Figures

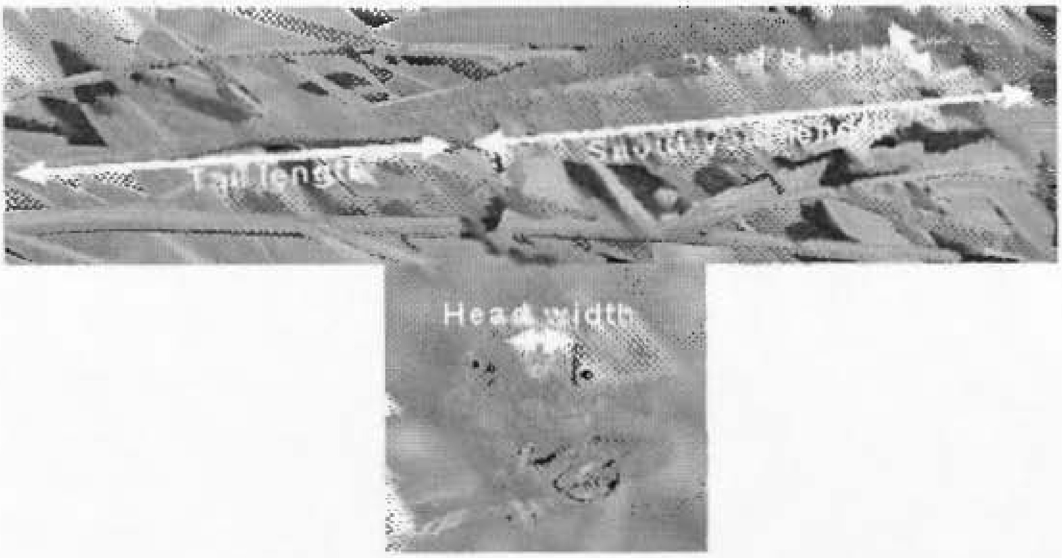

Figure 1 Morphological measurements taken for each chameleon, and subsequently employed in all analysis.

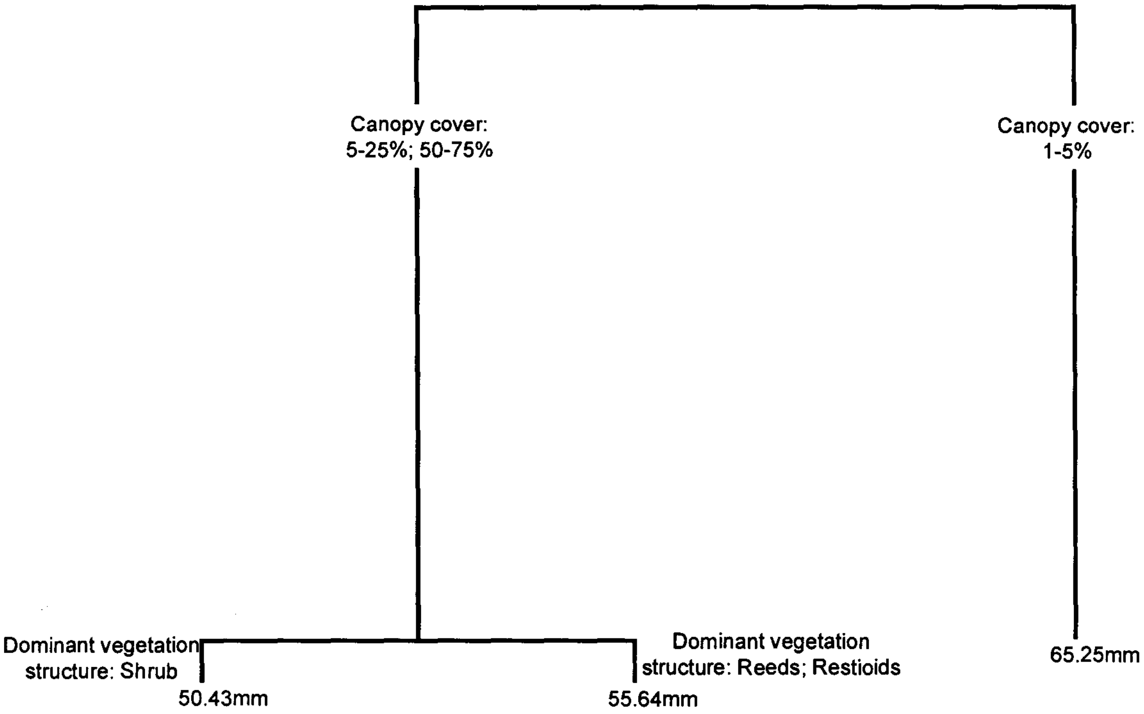

Figure 2 Regression Tree Analysis of snout-vent length with measured habitat variables for *Bradypodion pumilum*. The tree shows variables in hierarchical order of correlation, with longer branches indicating a larger proportion of explained deviance ($r^2 = 0.42$, $p < 0.05$). Categories that correlate to each variable are listed along each branch (Appendix 2). Numbers at tips of branches represent means for each morphological measurement in their respective habitats.

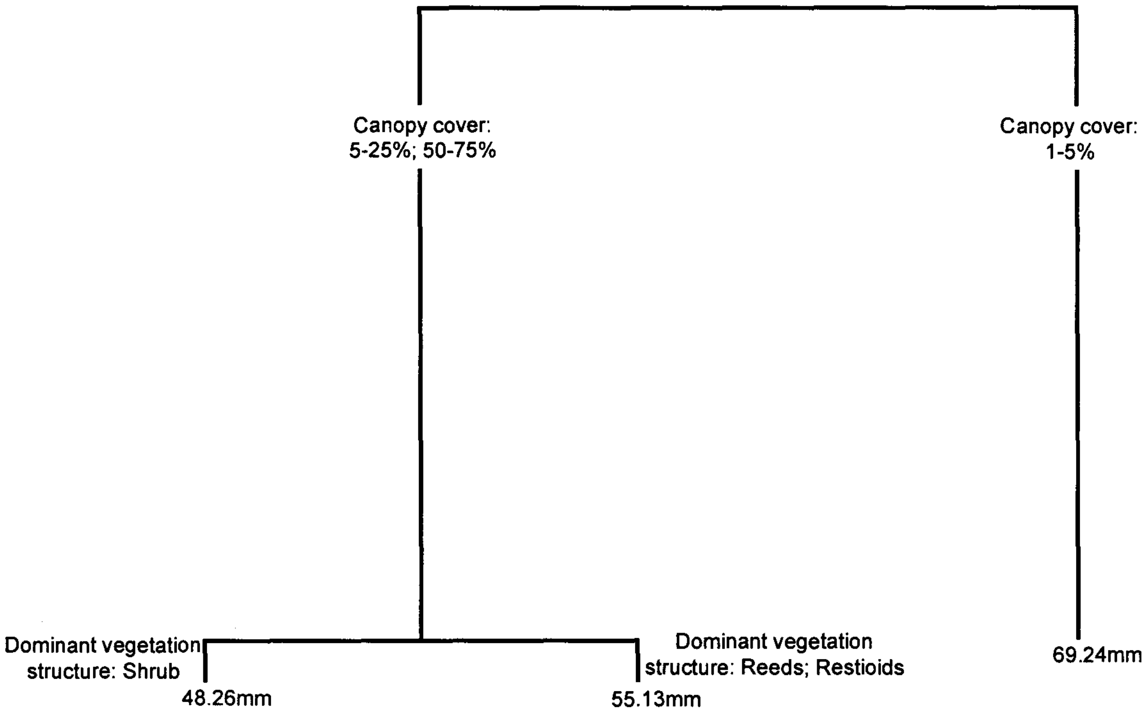

Figure 3 Regression Tree Analysis of tail length with measured habitat variables for *Bradypodion pumilum*. The tree shows variables in hierarchical order of correlation, with longer branches indicating a larger proportion of explained deviance ($r^2 = 0.48$, $p < 0.05$). Categories that correlate to each variable are listed along each branch (Appendix 2). Numbers at tips of branches represent means for each morphological measurement in their respective habitats.

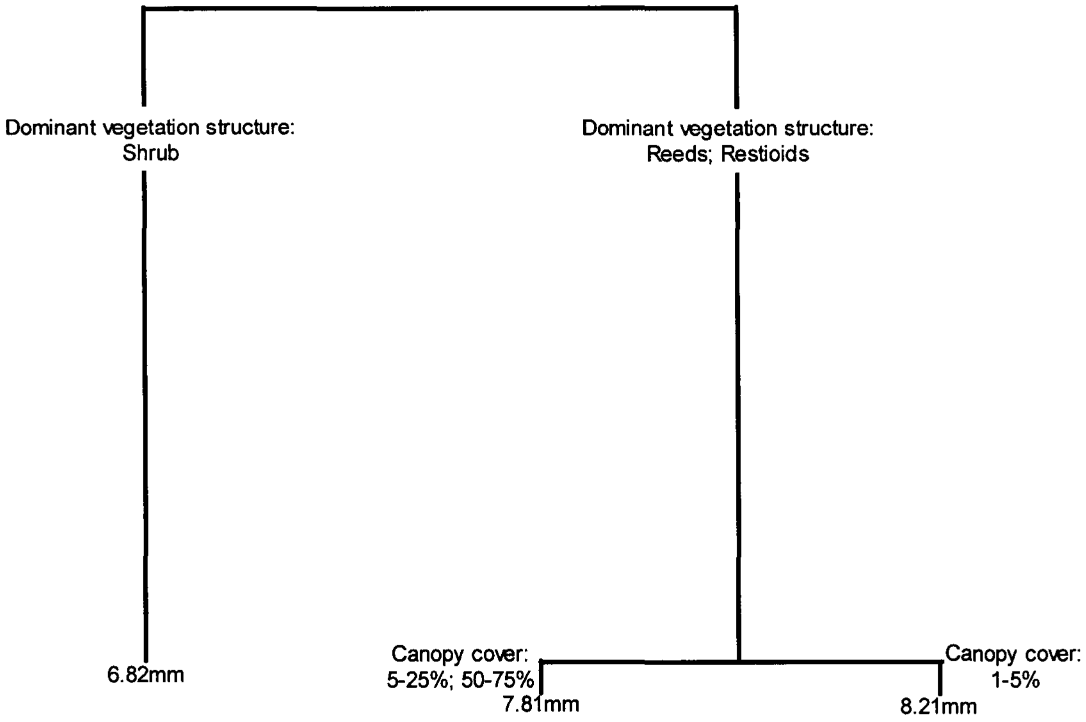

Figure 4 Regression Tree Analysis of head width with measured habitat variables for *Bradypodion pumilum*. The tree shows variables in hierarchical order of correlation, with longer branches indicating a larger proportion of explained deviance ($r^2 = 0.26$, $p < 0.05$). Categories that correlate to each variable are listed along each branch (Appendix 2). Numbers at tips of branches represent means for each morphological measurement in their respective habitats.

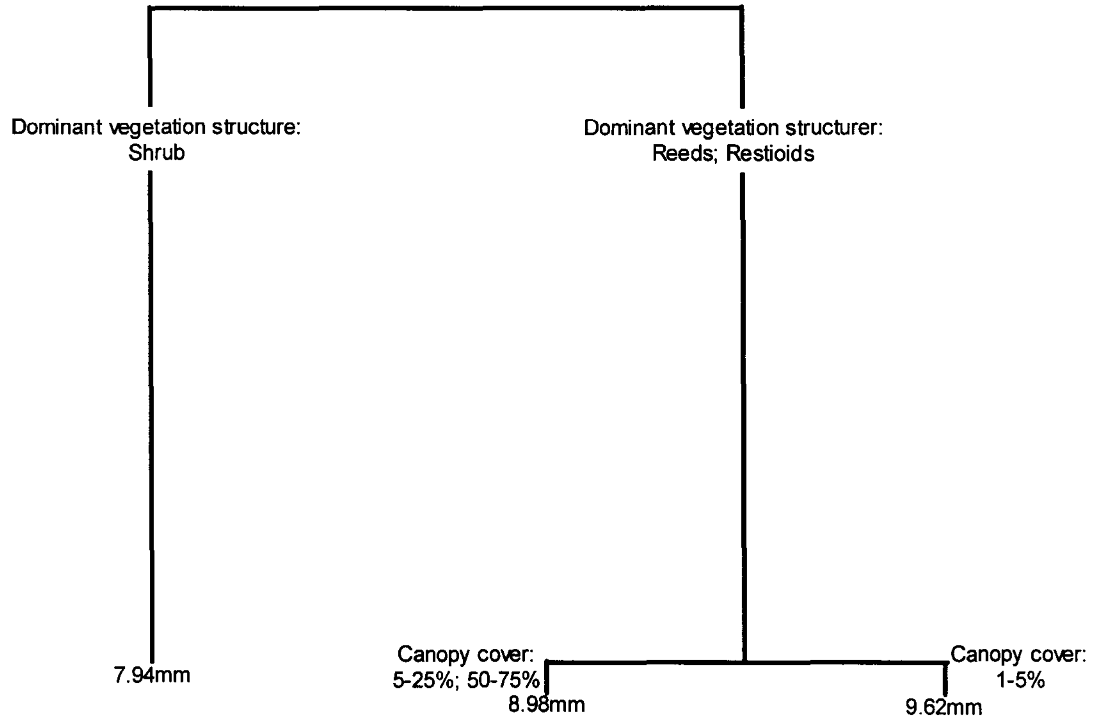

Figure 5 Regression Tree Analysis of head height with measured habitat variables for *Bradypodion pumilum*. The tree shows variables in hierarchical order of correlation, with longer branches indicating a larger proportion of explained deviance ($r^2 = 0.27$, $p < 0.05$). Categories that correlate to each variable are listed along each branch (Appendix 2). Numbers at tips of branches represent means for each morphological measurement in their respective habitats.

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Appendix

Appendix 1 Localities and sample sizes (n) of *Bradypodion pumilum* used in this study. A representative average point locality is also indicated for each area.

Habitat	**n**	**Location**	**DDS**	**DDE**
Open	22	Koegelberg Biosphere Reserve	-34.32	18.97
Open	14	Mizpah	-34.22	18.96
Open	5	Landdroskop	-34.05	19.01
Open	1	Fernkloof Reserve	-34.39	19.27
Open	1	Salmansdam Reserve	-34.42	19.64
Closed	50	Stellenbosch	-33.93	18.82
Closed	9	Noordhoek	-34.11	18.39
Closed	3	Robben Island	-33.80	18.37
Closed	1	Bloubergstrand, urban garden	-33.74	18.44
Closed	6	Somerset West	-34.08	18.87
Closed	4	Rondevlei Reserve	-34.06	18.50

Appendix 2 Categorical classification for habitat data measured per vegetation quadrat for *Bradypodion pumilum*.

	1	**2**	**3**	**4**	**5**	**6**	**7**
Canopy cover (%)	<1	1-5	5-25	25-50	50-75	>75	
Canopy height (cm)	0-50	50-100	150-200	>200			
Number of trees	Few	Many	Dense				
Number of shrubs	Few	Many	Dense				
Number of restios	Few	Many	Dense				
Dominant vegetation structure	Tree	Shrub	Reeds	Restioid	Graminoid	Urban/Mixed	Other
Highest visible perch	<1	1-5	5-25	25-50	50-75	>75	
Structure highest visible perch	Tree	Shrub	Reeds	Restioid	Graminoid	Urban/Mixed	Other
Vegetation type	Fynbos	Renosterveld	Dune thicket	Afro-montane forest	Urban closed canopy	Disturbed and invaded	Other
Average vegetation density	Sparse	Medium	Dense	Very dense			
Slope	Level	Gentle	Moderate	Steep	Very steep	Precipitous	

Chapter 5

Summary

There were three main aims to the present study. The first was to distinguish and describe the ecological niche occupied by *Bradypodion* species, based on broad scale environmental variables. The second was to analyse the possible effects climate change could have on these species. Finally, the relationship between the morphology of *B. pumilum* and corresponding habitat variables was assessed.

Analysis of the ecological niche of *Bradypodion* taxa and clades indicated that rainfall seasonality and annual maximum temperatures strongly influence the niche and niche breadths of these taxonomic groups. Although these methods only infer causality and, although there are likely multiple factors influencing the current geographic distributions of these groups, these climatic variables can be considered major drivers affecting their current ranges.

Analysis of the *Bradypodion* niche indicated the presence of closely related species occupying similar environmental niches. The presence of closely related species occurring within similar niches is termed niche conservatism. Therefore, *Bradypodion* display a degree of niche conservatism. However, species can, and presently do, occur in a wide variety of vegetation types and therefore different ecological niches. In addition many species show phenotypic variation within these different habitats (Tolley and Burger 2007), presumably providing a survival advantage (Vitt *et al.* 1997, Measey *et al.* in review). Although being niche conservative, *Bradypodion* species do have an ability to invade and occupy novel habitats when these become available.

The link between the current geographic distributions of *Bradypodion* and climate suggests that members of the genus would be vulnerable to predicted changes in current climates. All species and clade models demonstrated a response towards the climate change scenarios, however species responses were individualistic. Some species models showed range contractions (e.g. *B. pumilum*), others range expansions (e.g. *B. occidentale*), while one model (*B. transvaalense*) even showed a range shift. Therefore, any future conservation plans for *Bradypodion* would have to consider the individualistic responses of these species to predicted climate change. Additional considerations should be the localised distribution of many *Bradypodion* species (Tolley and Burger 2007), the differential effects of climate change between regions (Sala *et al.* 2000) and very importantly, the suggested slow migration rate expected for most reptiles (Araújo *et al.* 2006).

The hypothesis that a strong link exists between morphology and vegetation type for *Bradypodion* proposed that phenotypic variation exists within species in different habitats (Tolley *et al.* 2006, Tolley and Burger 2007). This hypothesis was supported in the present study, as a correlation between morphological traits and habitat was found for *Bradypodion pumilum*. Furthermore, the habitat variables shown to be important in species morphology were those related to vegetation density and structure. This phenotypic variation brought about by environmental selective pressures provides *Bradypodion* an ability to respond to changing environments and may aid in them being able to occupy novel habitats formed as a result of predicted climate change.

These results add to the current small number of studies assessing the effect predicted climate change may have on reptiles. It also adds to the low number of ecomorphological studies analysing the relationship between chameleon morphology and their respective habitats. Understanding the relationship between a species and its environment provides important information regarding its ecology. Thus, this information may prove useful in any future conservation plans for these endemic South African reptiles, as chameleons may be sensitive to climatic changes. Furthermore, while some species may not be niche conservative, the majority may not be able to keep pace with the rate of current predicted climatic trends.

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