Original article

Potential effects of predicted climate change on the endemic South African Dwarf Chameleons, *Bradypodion*

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Abstract.— The niche concept implies that a relationship exists between a species and its environment, while macro-ecological theory suggests that an important attribute of a species' environment is climate. Thus, changes in climate could affect individual species, but also communities. Here, we analysed the potential impacts of climate change on dwarf chameleons. A niche-based modelling technique was used to predict current suitable climatic habitat for most *Bradypodion* species and for their phylogenetic clades. Additionally, the models were projected into the future (2080) using the IPCC climate change scenarios. All models for *Bradypodion* species and clades showed responses to predicted climate change, however, the degree and extent of these responses were individualistic. Most species responded with a contraction in predicated climatic suitability, but some registered an expansion or a shift. These results have important implications in understanding the vulnerability of biodiversity to climate change, and for the importance of considering the effects of predicted climatic shifts on the protection of biodiversity.

Key words.— Africa, bioclimatic models, Maxent, reptiles, species distribution models.

Some predictions indicate that temperatures for southern Africa could increase by approximately 3-7°C by 2100 and, dependent on region, rainfall could increase or decrease by up to 20% of current levels (Boko *et al*. 2007). Presumably, changes in climate will have an affect on life history traits, physiology, and geographical distributions of species, possibly resulting in whole community shifts (Hughes 2000; Parmesan *et al*. 2000; Root *et al*. 2003; Root *et al*. 2005; Parmesan 2006). Clearly, these predictions are of growing concern in a conservation context because it is unknown whether the current conservation plans will provide sufficient protection a mere 100 years into the future. It appears that some species have already responded to recent climate change trends (Hughes 2000; Parmesan *et al*. 2000; McCarty 2001; Burns *et al*. 2003; Root *et al*. 2003; Thomas *et al*. 2004; Foden *et al*. 2007) and that community changes have begun (Brown *et al*. 1997; Hughes 2000). Although species distributions have altered naturally throughout the millennia, recent rapid trends are not to be taken lightly in the face of our anthropogenically altered environment.

Although there is a wealth of literature on species-environment relationships in connection with the impacts of predicted climate change (e.g. 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 & Hu 2005; Thuiller *et al*. 2006; Tolley *et al*. 2009 and references therein), reptiles are an under-represented group in this line of research. Furthermore, some current reptile declines are arguably linked to climate change

(Gibbons *et al*. 2000; Araújo *et al*. 2006) and, together with the low dispersal rate inferred for reptiles (Kearney & Porter 2004; Araújo *et al*. 2006), they may be especially vulnerable to predicted changes (Araújo & Pearson 2005; Tolley *et al*. 2009).

One group of reptiles potentially vulnerable to climate change are the southern African dwarf chameleons (*Bradypodion*). They are medium to small chameleons and are widespread in South Africa as a genus. Most species have relatively small, allopatric distributions, and are limited to distinct habitat/vegetation types (Branch 1998; Tolley *et al*. 2006; Tolley & Burger 2007). Anecdotal information suggests their migration potential is low (K.A. Tolley, unpubl. data), which together with their distinctly allopatric distributions (often confined to a single vegetation type) suggests a high vulnerability to predicted rapid climate change. Nevertheless, recent studies show that on an evolutionary time scale, they are labile and can adapt to novel environments (Tolley *et al*. 2008). Thus, it appears that dwarf chameleons have the ability to adapt to, and thrive in novel niches, but these occurrences are not on the multi-decadal time scale which is predicted for acute climate shifts. Because climatic factors have been shown to affect species distributions (e.g. Glor *et al*. 2003; Thomas *et al*. 2004; Wiens 2004; Broennimann *et al*. 2007), we assume that climatic changes could also alter *Bradypodion* distributions and that niche-based models could provide information on the nature of these potential shifts. In this study we address two main questions. Firstly, will the future potentially suitable climatic habitat be affected by climate change for *Bradypodion*? Secondly, will responses to climate change scenarios be species specific? To investigate these questions, habitat suitability maps were constructed for various *Bradypodion* taxa using niche-based modelling. We hypothesised that climate shifts as predicted by the Intergovernmental Panel on Climate Change (IPCC) might lead to changes in climatically suitable habitat, which in turn could influence chameleon distributions, but that the intensity and direction of predicted shifts will vary according to species. While the study is focused on one genus, the results should not be considered trivial. South Africa contains three of the world's most important biodiversity hotspots (Myers *et al.* 2000). It has the 3rd most biologically rich lizard fauna on the globe, numbering approximately 300 species and more than 60% endemicity (see Branch 1998). Although broad extrapolations based on our results cannot be made, chameleons make an excellent study species as they are poor dispersers with limited distributions and have distinct habitat preferences (Tolley *et al.* 2004; Tolley & Burger 2007). These qualities suggest that they would have limited migrational movements or distribution shifts under rapid climatic changes. Thus, using chameleons as a model could provide a preliminary indication of potential risks to these centres of biodiversity.

MATERIALS AND METHODS

Data sets.—Chameleon locality data were obtained from six national databases, as well as dedicated field surveys to increase sampling for selected species. A total of 446 individuals encompassing nine taxa (*B. pumilum* (n = 122), *B. damaranum* (n = 20), *B. gutturale* (n = 75), *B. occidentale* (n = 23), *B. melanocephalum* (n = 31), *B. ventrale* (n = 89), *B. transvaalense* (n = 47), *B. taeniabronchum* (n = 19), and one undescribed species (*B*. sp. 1; n = 20) were used. Seven additional species in the genus were not analysed due to the lack of a comprehensive set of point localities for those species. In addition to the investigation carried out at the taxon level, analyses were also carried out at the level of phylogenetic clade. For this, data from all taxa from each of three major phylogenetic clades identified by Tolley *et al*. (2004, 2006; Fig. 1) were combined and analysed to examine potential climatic niche changes for these clades.

Environmental data were obtained from Schulze (1997) comprising interpolated data at 1 x 1 minute grid cells for South Africa, and included mean maximum annual temperatures (°C), annual evapotranspiration (mm), mean winter and summer precipitation (mm). 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 and served as a conservative estimate for future human impacts (e.g. Thuiller *et al*. 2006).

Future climatic scenarios.—Climate scenarios for ~2080 were obtained from the IPCC (Intergovernmental Panel on Climate Change) Special Report on Emission Scenarios (Nakicenovic & Swart 2000). The “A2” storyline describes a heterogeneous world characterised by a continuously increasing population and regionally orientated economic development. It represents an average global temperature increase of almost 4°C by ~2100. The “B2” storyline is also characterised by a continuously growing population, slower than the A2 storyline, and intermediate economic growth. It represents an average global temperature increase of just above 2.5°C by ~2100 (IPCC 2007).

Niche based distribution modelling.—We used MAXENT 2.3 (Phillips *et al*. 2006), a presence-only niche-based model, to estimate species probability distribution. Analyses were conducted for taxa having 20 or more data points. An exception was *B. taeniabronchum* which was included despite having only 19 data points. Given its listing as Critically Endangered (IUCN 2006, CR B1 + 2c), we considered it important to include in the analysis. We used the default parameterisation of Maxent, and evaluated variable performance by the highest AUC statistic, and by generating a suitability map that best matched the known distribution.

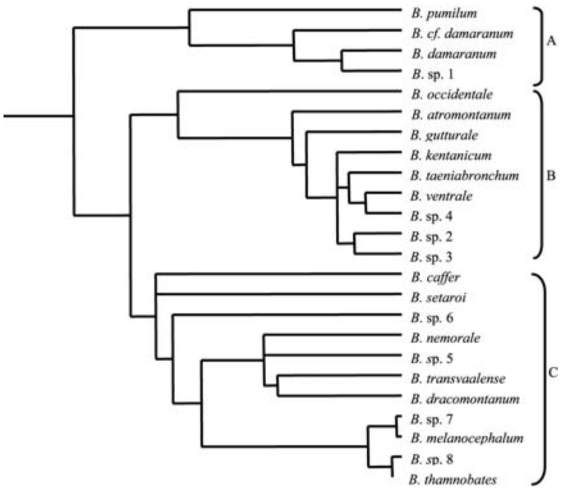


Figure 1. *Bradypodion* phylogenetic tree, showing terminal taxa and the three clades used in analysis (Adapted from Tolley *et al*. 2004, 2006).

RESULTS

Taxon level analysis.—The models for all taxa, except *B. occidentale*, showed a decrease in potentially suitable climatic habitat by 2080 regardless of IPCC scenario (Figs. 2 & 3; Appendix). When all cells within the category of 90-100% suitability ("fully suitable cells") were totalled for each species, most species (*B. pumilum, B. damaranum, B. gutturale, B. melanocephalum, B. ventrale, B. taeniabronchum, B.* sp. 1) displayed a loss of suitable climatic habitat. Fourteen to 66% of these fully suitable cells were lost under the A2 scenario while 21%-63% were lost under the B2 scenario, depending on species. In contrast, *B. occidentale* demonstrated an increase in the number of fully suitable cells (34% and 35% increases under the A2 and B2 scenario's, respectively). One species (*B. transvaalense*) displayed a loss of suitable climatic habitat coupled with a southward shift (Fig. 2). Thus,

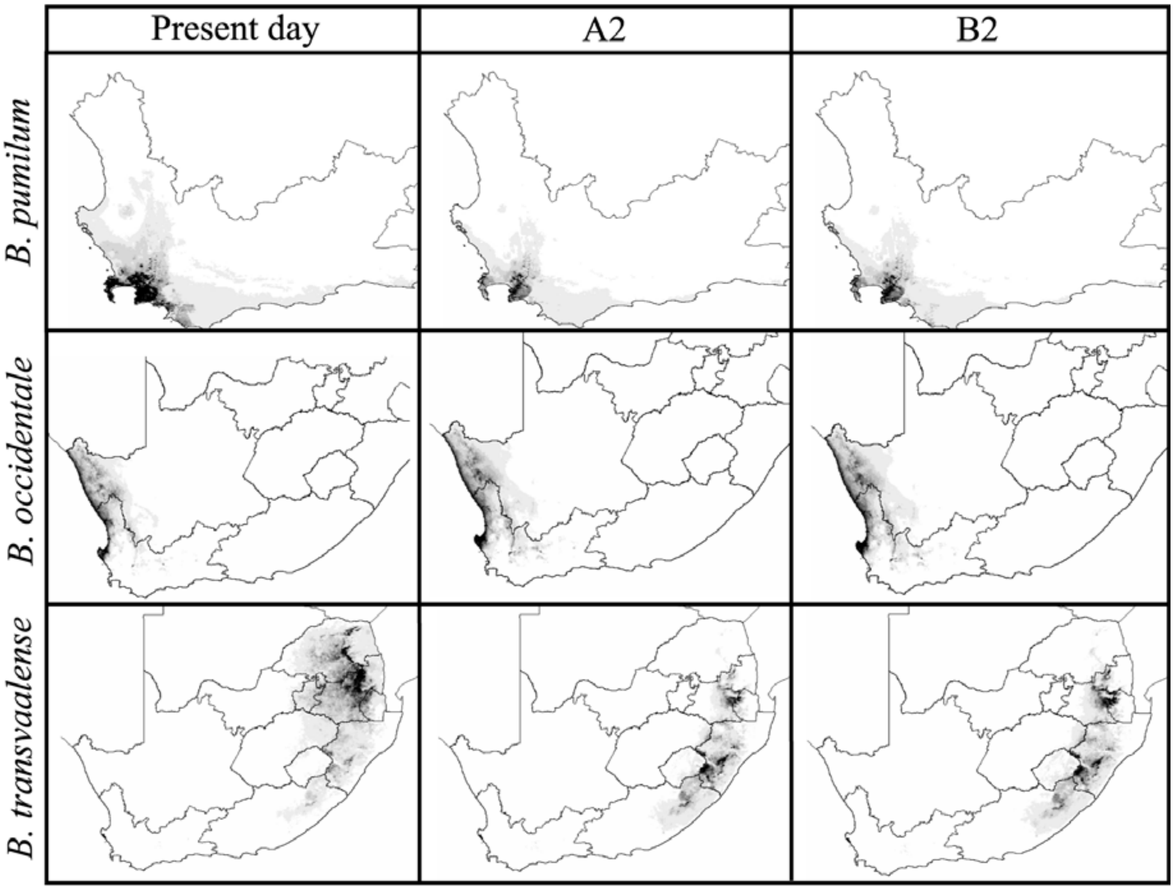


Figure 2. Habitat suitability maps for *Bradypodion pumilum* (top row, geographic area enlarged), *B. occidentale* (centre), and *B. transvaalense* (bottom) for the present day, A2 scenario, and B2 scenario. Darkest areas represent most suitable climatic habitat while lightest areas represent least suitable.

the degree and extent of response was species specific with three different types of responses of climatic habitat suitability: loss, southward shift, and increase. Overall, there was little difference in model outputs between the A2 and B2 scenarios (Fig. 3).

Phylogenetic clades.—The models for phylogenetic clades showed a loss of climatically suitable habitat by 2080, but the extent of this loss was clade specific (Fig. 3). Clade B lost approximately half its predicted fully climatically suitable cells (51% and 48% under A2 and B2, respectively), whilst clades A and B showed less substantial losses of fully suitable cells (Fig. 3).

DISCUSSION

All *Bradypodion* taxa investigated were predicted to respond to climatic change given the IPCC climate scenarios used in this study. The most common response of species (and clades) within the *Bradypodion* were contractions. However, in terms of degree and direction of responses, the models showed species responses to be individualistic. For example, *B. occidentale* was predicted to display an expansion, while all others displayed contractions. In addition, *B. transvaalense* displayed both a contraction and a strong southward shift. When taxa were grouped into clades, contractions were still observed suggesting that entire phylogenetic clades could undergo reductions in climatically suitable habitat. Although the uncertainty inherent in the models must be acknowledged (Pearson 2006; Dormann 2007), the results suggest that careful attention should be paid to these species, and to entire phylogenetic clades, to ensure they are not vulnerable to future climatic shifts.

Even in species such as *B. occidentale* and *B. transvaalense*, which showed an expansion and shift respectively, the slow migration rate suggested for some reptiles (Kearney & Porter 2004; Araújo *et al*. 2006) still makes these results notable. It is likely that chameleons could not keep pace with any range shifts that would be required to remain within a suitable climatic envelope. Compounding the problem of the implied range shifts is the effect of shifting community compositions (Burns *et al*. 2003). For example, in the event that *B. transvaalense* was forced to shift out of its present range and if that shift could keep pace with the model predictions, those areas will be occupied by other chameleon species. At the moment no two species occur sympatrically, suggesting that competition or some other factor is partially limiting distribution. This leads to the question as to whether range shifts would be impeded by biotic interactions, even in cases where a species has the ability to migrate in pace with the shift in suitable climate. This is a factor that present models cannot take into account, but one that is clearly imperative in order to accurately predict the effects of the IPCC climate scenarios.

While these predictions regarding potentially suitable climatic habitat shifts suggest that dwarf chameleons could experience range changes in the future, the limitations of this modelling exercise are multifaceted, and include compounded uncertainty in climate change scenarios (IPCC 2007), lack of the inclusion of biotic interactions, adaptation potential, or dispersal ability (Pearson & Dawson 2003; Heikkinen *et al*. 2006; Dormann 2007). Regardless, work on Malagasy chameleons demonstrated that niche-based models were useful in understanding present-day species distributions in both sampled and unsampled regions, and provided a useful tool for conservation and conservation planning (Raxworthy *et al*. 2003). Thus, despite the inherent uncertainties, the models could be used as framework to support conservation planning and to provide a first step in understanding the possible effects of rapid climate change (Guisan & Thuiller 2005). For dwarf chameleons, ecological niche modelling may be informative in the estimation of future range changes, and the losses in climatically suitable habitat predicted by the models can be taken as a first warning that these species could be sensitive to rapid climate shifts.

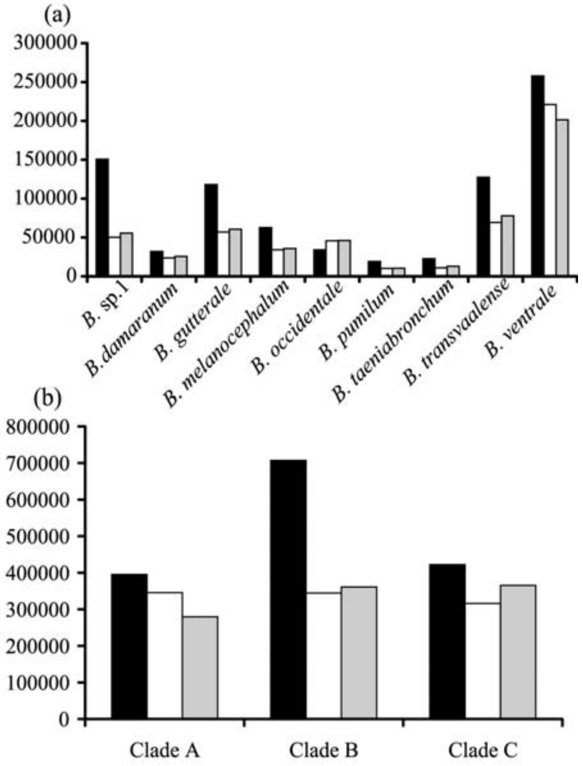


Figure 3. Total area (km^2) of climatically suitable habitat (90-100% category) for *Bradypodion* a) individual taxa and b) clades. Shaded bars indicate the total climatically suitable area (km^2 on y-axis) at present (black), under the A2 scenario (white), and the B2 scenario (grey).

ACKNOWLEDGEMENTS

We would like to thank CapeNature and the City of Cape Town (C. Dorse and D. Gibbs) for access to reserves, and A. de Villiers and A. Turner who provided useful logistical information. We are also grateful to all private landowners and reserve managers who provided access to areas under their control (Vogelgat, Mizpah, Paarl Tortoise Reserve, Farm 215, Elim and Grootbos, Elandsberg Farm). The South African National Biodiversity Institute (SANBI), University of Cape Town (Animal Demography Unit) and the Laboratoire d'Ecologie Alpine (CNRS, Université Joseph Fourier) provided funding and support. Locality data was provided by K. Hopkins, G.J. Measey, SANBI, Port Elizabeth Museum (Bayworld), the South African Museum, the Transvaal Museum, the National Museum, the Natal Museum, and the Durban Museum. Finally, we thank the members of the SANBI "Chameleon Club" for a number of useful discussions regarding this work.

LITERATURE CITED

ARAÚJO, M.B. & PEARSON, R.G. 2005. Equilibrium of species' distributions with climate. Ecography 28: 693-695.

ARAÚJO, M.B., THUILLER, W. & PEARSON, R.G. 2006. Climate warming and the decline of amphibians and reptiles in Europe. J. Biogeog. 33: 1712-1728.

BOKO, M., NIANG, I., NYONG, A., VOGEL, C., GITHEKO, A., MEDANY, M., OSMAN-ELASHA, B., TABO, R. & YANDA, P. 2007. Africa. Climate Change 2007: impacts, adaptation and vulnerability. In: Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change, (eds) M.L. Parry, O.F. Canziani, J.P. Palutikof, P.J. van der Linden & C.E. Hanson, pp. 433-467. Cambridge University Press, Cambridge.

BRANCH, B. 1998. Field Guide to Snakes and Other Reptiles of Southern Africa. Struik, Cape Town.

BROENNIMANN, O., TREIER, U.A., MÜLLER-SCHÄRER, H., THUILLER, W., PETERSON, A.T. & GUISAN, A. 2007. Evidence of climatic niche shift during biological invasion. Ecol. Lett. 10: 701-709.

BROWN, J.H., VALONE, T.J. & CURTIN, C.G. 1997. Reorganization of an arid ecosystem in response to recent climate change. Proc. Nat. Acad. Sci. 94: 9729-9733.

BURNS, C.E., JOHNSTON, K.M. & SCHMITZ, O.J. 2003. Global climate change and mammalian species diversity in U.S. national parks. Proc. Nat. Acad. Sci. 100: 11474-11477.

DORMANN, C.F. 2007. Promising the future? Global change projections of species distributions. Basic Appl. Ecol. 8: 387-397.

ENGLER, R., GUISAN, A. & RECHSTEINER, L. 2004. An improved approach for predicting the distribution of rare and endangered species from occurrence and pseudo-absence data. J. Appl. Ecol. 41: 263-274.

FODEN, W., MIDGLEY, G.F., HUGHES, G., BOND, W.J., THUILLER, W., HOFFMAN, M.T., KALEME, P., UNDERHILL, L.G., REBELO, A. & HANNAH, L. 2007. A changing climate is eroding the geographical range of the Namib Desert tree Aloe through population declines and dispersal lags. Divers. Distrib. 13: 645-653.

GAVIN D.G. & HU, F.S. 2005. Bioclimatic modelling using gaussian mixture distributions and multiscale segmentation. Global Ecol.Biogeogr. 14: 491-501.

GIBBONS, J.W., SCOTT, D.E., RYAN, T.J., BUHLMANN, K.A., TUBERVILLE, T.D., METTS, B.S., GREENE, J.L., MILLS, T., LEIDEN, Y., POPPY, S. & WINNE, C.T. 2000. The global decline of reptiles, déjà vu amphibians. BioScience 50: 653-666.

GLOR, R.E., KOLBE, J.J., POWELL, R., LARSON, A. & LOSOS, J.B. 2003. Phylogenetic analysis of ecological and morphological diversification in hispaniolan trunk-ground Anoles (*Anolis cybotes* group). Evolution 57: 2383- 2397.

GUISAN, A., & THUILLER, W. 2005. Predicting species distributions: Offering more than simple habitat models. Ecol. Lett. 8: 993-1009.

HEIKKINEN, R. K., LUOTO, M., ARAJO, M. B., VIRKKALA, R., THUILLER, W. & SYKES, M. T. 2006 Methods and uncertainties in bioclimatic envelope modeling under climate change. Prog. Phys. Geog. 30: 751-777.

HOULAHAN, J.E., FINDLAY, C.S., SCHMIDT, B.R., MEYER, A.H. & KUZMIN, S.L. 2000. Quantitative evidence for global amphibian population declines. Nature 404: 752-755.

HUGHES, L. 2000. Biological consequences of global warming: is the signal already. Trends Ecol. Evol. 15: 56-61.

INTERGOVERNMENTAL PANEL ON CLIMATE CHANGE (IPCC). 2007. Summary for policymakers. In: Climate change 2007: the physical science basis.Contribution of working group I to the fourth assessment report of the Intergovernmental Panel on Climate Change, (eds) Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., Tignor, M. & Miller, H.L. Cambridge University Press, Cambridge.

IUCN. 2006. 2006 IUCN Red List of Threatened Species (www.iucnredlist.org). Downloaded on 15 June 2007.

JANZEN, F.J. 1994. Climate change and temperature-dependent sex determination in reptiles. Proc.Nat. Acad. Sci. 91: 7487-7490.

KEARNEY, M. & PORTER, W.P. 2004. Mapping the fundamental niche: physiology, climate, and the distribution of a nocturnal lizard. Ecology 85: 3119-3131.

MCCARTY, J.P. 2001. Ecological consequences of recent climate change. Cons. Biol. 15: 320-331.

MYERS, N., MITTERMEIER, R.A., MITTERMEIER, C.G., DA FONSECA, G.A.B. & KENT, J. 2000. Biodiversity hotspots for conservation priorities. Nature 403: 853-858.

NAKICENOVIC, N. & SWART, R. (eds). 2000. Emissions Scenarios: a Special Report of Working group III of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge.

PARMESAN, C. 2006. Ecological and evolutionary responses to recent climate change. Ann. Rev. Ecol. Evol. Syst. 37: 637-669.

PARMESAN, C., ROOT, L.T. & WILLIG, M.R. 2000. Impacts of extreme weather and climate on terrestrial biota. Bull. Am. Meteorol. Soc. 81: 443-450.

PEARSON, R.G. 2006. Climate change and the migration capacity of species. Trends Ecol. Evol. 21: 111-113.

PEARSON, R.G. & DAWSON, T.P. 2003. Predicting the impacts of climate change on the distribution of species: are bioclimatic envelope models useful? Global Ecol. Biogeogr. 12: 361-371.

PHILLIPS, S.J., ANDERSON, R.P. & SCHAPIRE, R.E. 2006. Maximum entropy modelling of species geographic distributions. Ecol Model. 190: 231-259.

RAXWORTHY, C.J., MARTINEZ-MEYER, E., HORNING, N., NUSSBAUM, R.A., SCHNEIDER, G.E., MIGUEL A. ORTEGA-HUERTA, M.A. & PETERSON, A.T. 2003. Predicting distributions of known and unknown reptile species in Madagascar. Nature 426: 837-841.

ROOT, T.L., MACMYNOWSKI, D.P., MASTRANDREA, M.D. & SCHNEIDER, S.H. 2005. Human-modified temperatures induce species changes: joint attribution. Proc.Nat. Acad. Sci. 102: 7465-7469.

ROOT, T.L., PRICE, J.T., HALL, K.R., SCHNEIDER, S.H., ROSENZWEIG, C. & POUNDS, J.A. 2003. Fingerprints of global warming on wild animals and plants. Nature 421: 57-60.

SALA, O.E., CHAPIN III, S.F., ARMESTO, J.J., BERLOW, E., BLOOMFIELD, J., DIRZO, R., HUBER-SANWALD, E., HUENNEKE, L.F., JACKSON, R.B., KINZIG, A., LEEMANS, R., LODGE, D.M., MOONEY, H.A., OESTERHELD, M., POFF, L.N., SYKES, M.T., WALKER, B.H., WALKER, M. & WALL, D.H. 2000. Global biodiversity scenarios for the year 2100. Science 287: 1770-1774.

SANDERSON, E.W., JAITEH, M., LEVY, M.A., REDFORD, K.H., WANNEBO, A.V. & WOOLMER, G. 2002. The human footprint and the last of the wild. BioScience 52: 891-904.

SCHULZE, R.E. 1997. South African Atlas of Agrohydrology and-Climatology. Water Research Commission. Report TT82/96, Pretoria.

THOMAS, C.D., CAMERON, A., GREEN, R.E., BAKKENES, M., BEAUMONT, L.J., COLLINGHAM, Y.C., ERASMUS, B.F.N., DE SIQUEIRA, M.F., GRAINGER, A., HANNAH, L., HUGHES, L., HUNTLEY, B., VAN JAARSVELD, A.S., MIDGLEY, G.F., MILES, L., ORTEGA-HUERTA, M.A., TOWNSEND PETERSON, A., PHILLIPS, O.L., & WILLIAMS, S.E. 2004. Extinction risk from climate change. Nature 427: 145-148.

THUILLER, W., BROENNIMANN, O., HUGHES, G.O., ALKEMADE, J.R.M., MIDGLEY, G.F. & CORSI, F. 2006. Vulnerability of African mammals to anthropogenic climate change under conservative land transformation assumptions. Global Change Biol. 12: 424-440.

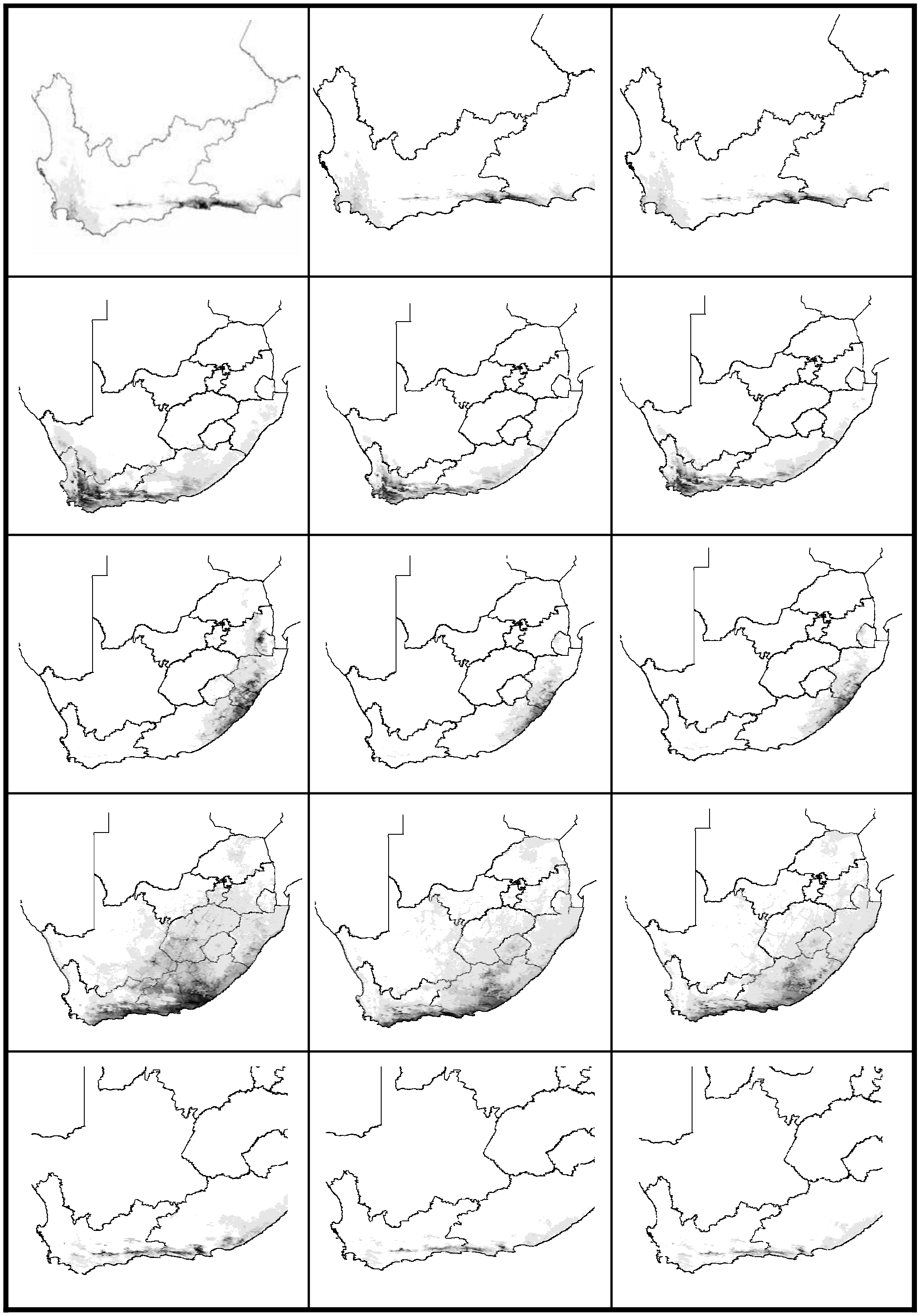
THUILLER, W., LAVOREL, S., MIDGLEY, G., LAVERGNE, S. & REBELO, T. 2004. Relating plant traits and species distributions along bioclimatic gradients for 88 *Leucadendron* taxa. Ecology 85: 1688-1699.

TOLLEY, K.A. & BURGER, M. 2007. Chameleons of Southern Africa. Struik, Cape Town.

TOLLEY, K.A., BURGER, M., TURNER, A.A. & MATTHEE, C.A. 2006. Biogeographic patterns and phylogeography of dwarf chameleons (*Bradypodion*) in an African biodiversity hotspot. Mol. Ecol. 15: 781-793.

TOLLEY, K.A., CHASE, B.M. & FOREST, F. 2008. Speciation and radiations track climate transitions

Received: 16 March 2009 *Final acceptance: 1 June 2009*



Appendix. Habitat suitability maps for the present (left), A2 scenario (centre) and B2 scenario (right). Species shown are (top to bottom) *Bradypodion damaranum* (geographic area is enlarged), *B. gutturale*, *B. melanocephalum*, *B. ventrale*, *B. taeniabronchum* (geographic area is enlarged). Darkest areas represent most suitable climatic habitat while lightest areas represent least suitable.