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Predicting the effect of climate change on a range-restricted lizard in southeastern Australia

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Abstract

Climate change is ranked as one of the most severe threats to global biodiversity. This global phenomenon is particularly true for reptiles whose biology and ecology are closely linked to climate. In this study, we used over 1,300 independent occurrence points and different climate change emission scenarios to evaluate the potential risk of changing climatic conditions on the current and future potential distribution of a rock-dwelling lizard; the velvet gecko. Furthermore, we investigated if the current extent of protected area networks in Australia captures the full range distribution of this species currently and in the future. Our results show that climate change projections for the year 2075 have the potential to alter the distribution of the velvet gecko in southeastern Australia. Specifically, climate change may favor the range expansion of this species to encompass more suitable habitats. The trend of range expansion was qualitatively similar across the different climate change scenarios used. Additionally, we observed that the current network of protected areas in southeast Australia does not fully account for the full range distribution of this species currently and in the future. Ongoing climate change may profoundly affect the potential range distribution of the velvet gecko population. Therefore, the restricted habitat of the velvet geckos should be the focus of intensive pre-emptive management efforts. This management prioritization should be extended to encompass the increases in suitable habitats observed in this study in order to maximize the microhabitats available for the survival of this species.

Key words: bioclimatic variables, climate change, environmental niche models, range expansion, reptiles.

Climate change is considered as one of the major threats to global biodiversity in the 21st century (Walther et al. 2002). Changes in future climatic conditions are predicted to alter the distribution and abundance of species, and coupled with increases in habitat fragmentation may lead to species extinction (Brown et al. 1997; Walther et al. 2002; Root et al. 2003; Wake 2007). Species with limited dispersal abilities, small geographic ranges, or confined to specialized habitats are particularly vulnerable to extinction (Pounds et al. 1999; Sodhi and Ehrlich 2010). Predictive models suggest that if climate change continues unchecked, 37% of global species might be extinct by the end of 2050 (Thomas et al. 2004).

Over the past century, global temperatures has increased by ~0.74 °C, and one of the most important bioclimatic effects seems to be an increase in the mean surface temperature (Stocker et al. 2013). Therefore, assessing species' responses to climate change is one of the greatest challenges that conservation biologists face. Notwithstanding, the effects of raising temperatures have been felt from species to community levels (Pounds et al. 1999; Walther et al. 2002; Thomas et al. 2004). Hence, identifying the most vulnerable species or group of species likely to be affected by changing climatic conditions is the first appropriate step in mitigating the impacts on biodiversity.

For reptiles in particular, decline and extirpations of large populations have occurred in many parts of the world, and climate change is one of the leading causal agents postulated to explain these declines (Araújo et al. 2006; Sinervo et al. 2010; Clusella-Trullas et al. 2011). This is mainly because, their biology and ecology are closely tied to climate; especially changes in environmental temperature (Araújo et al. 2006; Tewksbury et al. 2008; Sinervo et al. 2010). Specifically, several populations of lizards around the globe have been significantly threatened by changing climatic conditions, and recent research has predicted significant declines over the next century (Sinervo et al. 2010). This is particularly true for tropical species, which are already living close to their physiological optimum levels (Deutsch et al. 2008). Body temperatures higher than optimum creates physiological stress, reduced performance, and increased disease susceptibility; ultimately leading to population declines and extinction (Root et al. 2003; Sinervo et al. 2010; Huey et al. 2012). For example, projected temperature increases of between 1.1 °C and 6.4 °C by the year 2100 would increase the metabolic rates of ectotherms by 10–75% (Bickford et al. 2010). A rise in metabolic rates coupled with reduced foraging time could negatively affect reproduction and subsequently population growth rates (Bickford et al. 2010; Logan et al. 2014). However, the vulnerability of a species depends on its sensitivity to environmental change, its exposure to that change, its resilience or ability to recover, and its potential to adapt to these changes (Williams et al. 2008). Ideally, to predict species at risk from global warming and climate change, we need information about their habitat selection and colonization ability. For example, species with lower dispersal ability may face difficulties to colonize suitable habitats due to specialized habitat requirements (Hughes 2000, 2003; Araújo et al. 2006; Huey et al. 2012). Therefore, investigating how reptiles, especially the range-restricted ones, will respond to a new climatic regime is critical if we are to mitigate the impacts of climate change from a conservation point of view.

Lately, researchers have developed tools that enable the evaluation of the potential geographic distribution of a species' abiotic niche from changing climatic conditions. Of the many different tools available, species ecological niche models (ENMs) have been widely used (Cabrelli and Hughes 2015, Melville et al. 2016; Tingley et al. 2016). These models relate data on species' occurrence (i.e., presence/absence) to the bioclimatic conditions of a given area, therefore allowing us to determine the potential climate envelope of a species. In so doing, geographic areas that fall within or outside of the current range distribution of the species could be identified (Thuiller et al. 2005). Such approaches have found major applications in biological conservation science. For example, mapping where rare and endangered species are most likely to occur in the landscape, species discovery; prioritizing conservation sites; and identifying potential restoration sites, especially after invasion amongst others (Williams et al. 2009). In constructing climate envelopes for conservation purpose, some challenges have emerged especially for range-restricted rock-dwelling lizards such as the velvet gecko *Amalosia lesueurii* (our study species) in southeastern Australia. Among others, the species occurrence data and the spatial resolution at which bioclimatic or microclimatic data are downscaled have increasingly been cited in the scientific literatures (see also Wisz et al. 2008; Rebaudo et al. 2016; and references therein). To contribute to the growing body of knowledge on this topic, we used a range-restricted species *A. lesueurii*, to evaluate the effect of current and future climate change on the range distribution in southeastern Australia, employing an ENM approach. Additionally, we investigate if the current extent of protected area networks in Australia captures the full range distribution of this species currently and in the future.

Materials and Methods

Species' occurrence data

A total of 1,320 independent occurrences for *A. lesueurii* were collected from the Atlas of Living Australia (www.ala.org.au). These occurrence data were supplemented with our survey data collected between September 2013 and November 2015.

Climatic data

Spatially continuous current and future climate data were downloaded from the WorldClim database (www.worldclim.org; Hijmans et al. 2005). The current data represented interpolation of average monthly climatic records obtained from weather stations between 1950 and 2000, while projected future climate for the year 2075 was estimated using the Commonwealth Scientific and Industrial Research Organization (CSIRO-MK30) general circulation models (GCM) at 2.5 arcmin resolution. Although the spatial resolution of WorldClim dataset used to infer the thermal niche of small ectotherms affects the final model outputs (Hannah et al. 2014 and references therein), this topic is still highly debatable in scientific literatures (see Bennie et al. 2014; Hannah et al. 2014; Storlie et al. 2014; Rebaudo et al. 2016). In this study, we used the WorldClim datasets following the same line of thought as Rebaudo et al. (2016) and included all 19 bioclimatic variables as potential predictors (see Supplementary Table S1). For future climate projections, we considered 3 representative concentration pathways (RCPs) or emission scenarios, to account for differences across climate scenarios. For the current study, we choose 3 scenarios representing different magnitudes of greenhouse gas emissions: a high RCP 6.0 characterized by a rising radiative forcing pathway leading to ~1370 ppm CO_2 with a global mean temperature rise of 2.2 °C; a medium RCP 4.5 where greenhouse gas emissions stabilizes at ~650 ppm CO_2 with a global mean temperature rise of 1.8 °C; and lastly, the lowest RCP3PD 3.0 where greenhouse gas emissions peak at ~490 ppm CO_2 with a global mean temperature rise of 1.0 °C by 2100 (Riahi et al. 2011; Thomson et al. 2011; van Vuuren et al. 2011). For convenience, in this study we refer to these RCPs as "low mitigation" (RCP3PD), "medium mitigation" (RCP4.5), and "high mitigation" (RCP6.0).

Evaluation of suitable habitat for *A. lesueurii*

We applied an ENM approach that relies on presence of species and background data to generate correlative models for both current and future habitat suitability for *A. lesueurii* species. We used MaxEnt version 3.3.3 (Phillips et al. 2006) as it outperforms similar modeling algorithms [but see also Elith et al. (2006) for some of its numerous advantages]. We used 70% of our occurrence data for model training while withholding the remaining 30% for model evaluation. Although we lacked actual absence data for this study species, background or pseudo-absence data was generated assuming 1.5 times the number of presence points, which characterizes the environmental conditions of the study area (Phillips et al. 2009; Bezeng et al. 2017). Model performance was evaluated using the area under the curve (AUC) statistics. We then ran 15 subsampling replicates employing 5,000 iterations for each model. These replicates and iterations were considered sufficient for model convergence. Finally, to reduce model extrapolation errors caused by
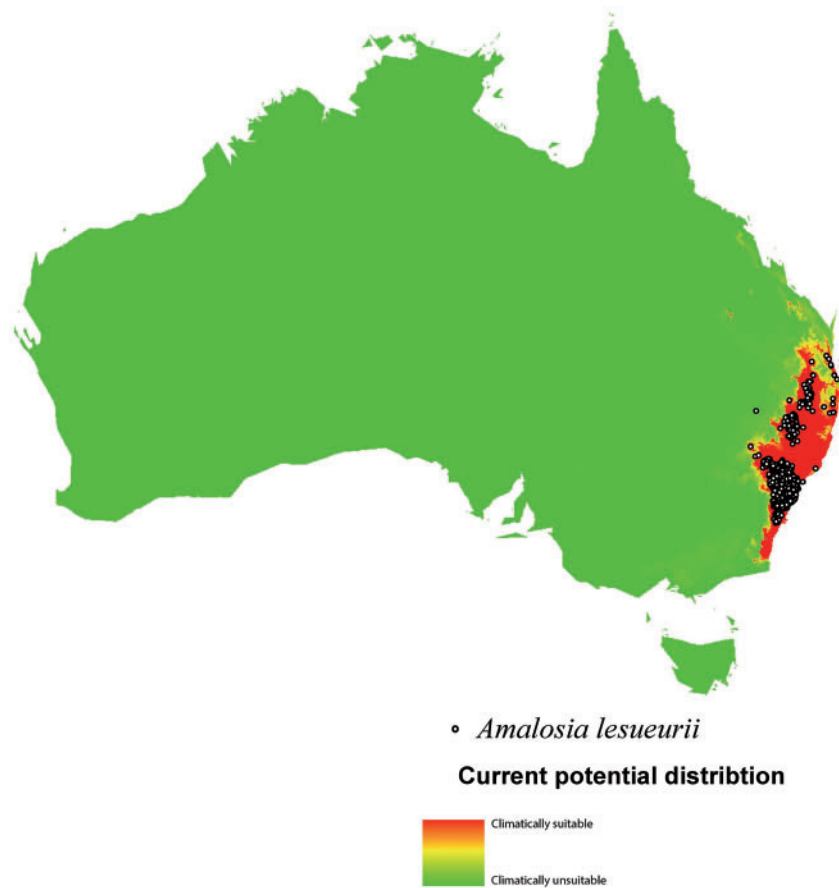
Figure 1. Current climate suitability map of *A. lesueurii* species distribution. Red color indicates areas that are climatically suitable for species occurrence while green color indicates areas that are climatically unsuitable for species occurrence. The dots indicate field observations of study species.

non-analogous climatic conditions (see Fitzpatrick and Hargrove 2009), we used a multivariate environmental similarity surface (MESS) analysis to restrict model projections to analogous environments where true presence and background records were sampled (see also Elith et al. 2010).

ENM outputs followed a logistic distribution, ranging from 0 (climatically unsuitable areas) to 1 (climatically suitable areas). For all model runs, we quantified the difference in geographical range extent of projected distributions between current and future climate scenarios, in which the extent of potential ranges could be determined by negative values (indicating a net reduction in climatically suitable areas with climate change) or positive values (indicating a net expansion of climatically suitable areas with climate change). We explored potential bioclimatic variables that might be driving range change for our study species by running a regression of change in predicted climate suitability against change in each bioclimatic variable, in turn.

Protected area data

To evaluate if the current extent of protected areas in Australia captures the full range distribution of this gecko species under climate change, we overlaid the current and future potential range distribution with a shapefile of currently protected area network in Australia downloaded from the Collaborative Australian Protected Areas Database (CAPAD 2014). This database provides spatial information about government, indigenous, private and jointly managed protected areas for the Australian continent and also meets the criteria for defining protected areas according to the IUCN standards. This analysis was performed using ArcGIS version 10.3 software.

Results

Model performances across all the species' ENMs using MaxEnt were high (AUC > 0.995 ± 0.014). Under current climatic conditions, areas that are climatically suitable for the range-restricted velvet gecko are coastal regions and ranges of New South Wales and far southeastern Queensland, which matches the areas where field observations were carried out (Figure 1).

Our results from models projected into the future, shows that climate change projections for the year 2075 have the potential to alter the distribution of the velvet gecko in southeastern Australia. Specifically, climate change may favor the range expansion of this species to encompass more suitable habitats (Figure 2, but see also Supplementary Figures S1 and S2 for alternative RCPs). Under the "low mitigation" (i.e., RCP3PD), the potential area of range expansion was $\sim726 \times 10^3$ km^2. This trend was qualitatively consistent across the different climate change scenarios, and we observed no significant difference when alternative RCPs were used (see Table 1; $P > 0.05$).
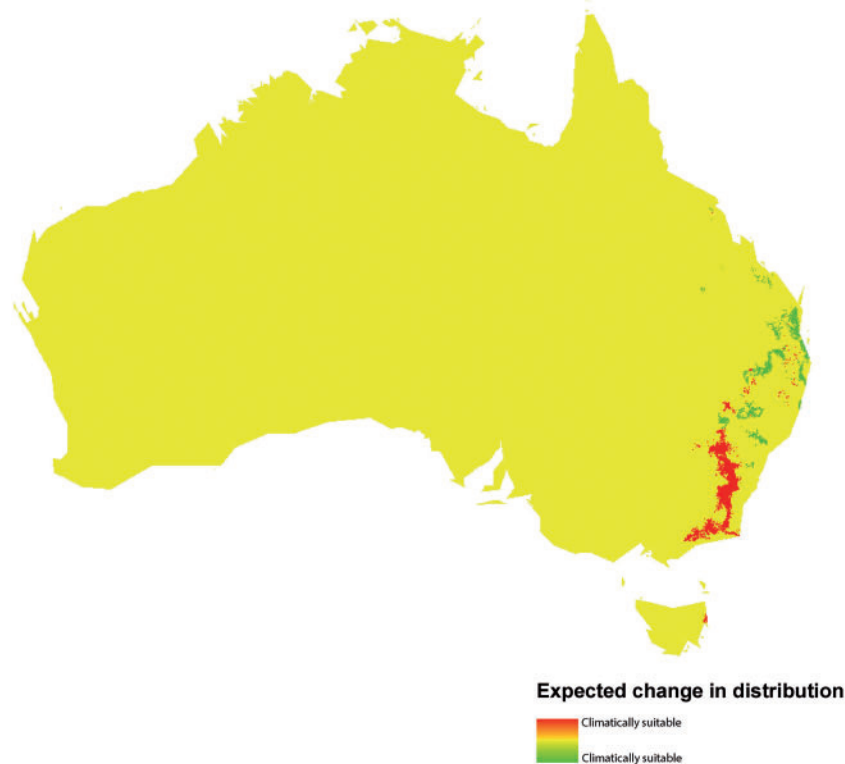
Expected change in distribution

Climatically suitable

Climatically suitable

Figure 2. Change in potential species distribution between current and projected climate for the year 2075 employing the "low mitigation" (i.e., RCP3PD) emission scenario. Red color indicates areas that are climatically suitable for species occurrence while green color indicates areas that are climatically unsuitable for species occurrence.

Table 1. Projected impacts of climate change by 2075 in terms of changes in range size for the velvet gecko in southeastern Australia across 3 climate change scenarios

Low mitigation			Medium mitigation			High mitigation		
Current	Future	PARC	Current	Future	PARC	Current	Future	PARC
7,781	8,507	726	7,781	8,510	729	7,781	8,388	607

PARC, potential area of range change ($\times 10^3$ km^2).

From the regression analysis, we found that similar temperature and precipitation bioclimatic variables were important in driving range change for *A. lesueurii* in southeast Australia. Particularly, we found that minimum temperature of coldest month, annual precipitation, precipitation of wettest month, precipitation of driest month, precipitation of wettest quarter, precipitation of driest quarter, and precipitation of warmest quarter (see Supplementary Table S2 for correlation coefficients) were important in driving range change.

Lastly, we evaluated the area of overlap between the current protected area network and the range shift of the velvet gecko in order to determine if the current extent of protected areas in southeast Australia accounts for the range expansion of this species. Surprisingly, we found that the current network of protected areas in southeast Australia does not fully account for the full range distribution of this species currently and in the future. For example, we found that, of the 2,009 protected areas that overlapped with the current distribution of this species, a significant number (i.e., 103) were outside the species' current range distribution. Likewise, of the 2,099 protected areas that overlapped with the future distribution of

this species, 118 of them were outside the species' future range distribution, representing ∼30% of the species' future range area (see Figure 3A and B).

Discussion

The recent report from the Intergovernmental Panel on Climate Change (IPCC) predicts that human activities are driving global climate change, which is likely to further increase in the future (IPCC, 2014). Thus, many species are expected to shift their current distribution to track future climate change. For example, there are growing evidences documenting the movement of species northward and upward in elevation (Parmesan 2006; Kelly and Goulden 2008; Lenoir et al. 2008; Moritz et al. 2008). In the past, many studies have attempted to model the potential current and future distribution of range-restricted species using an environmental niche modeling approach (Williams et al. 2009; Cabrelli and Hughes 2015; Melville et al. 2016). However, using ENM for range-restricted or specialized habitat species is particularly challenging. First, the
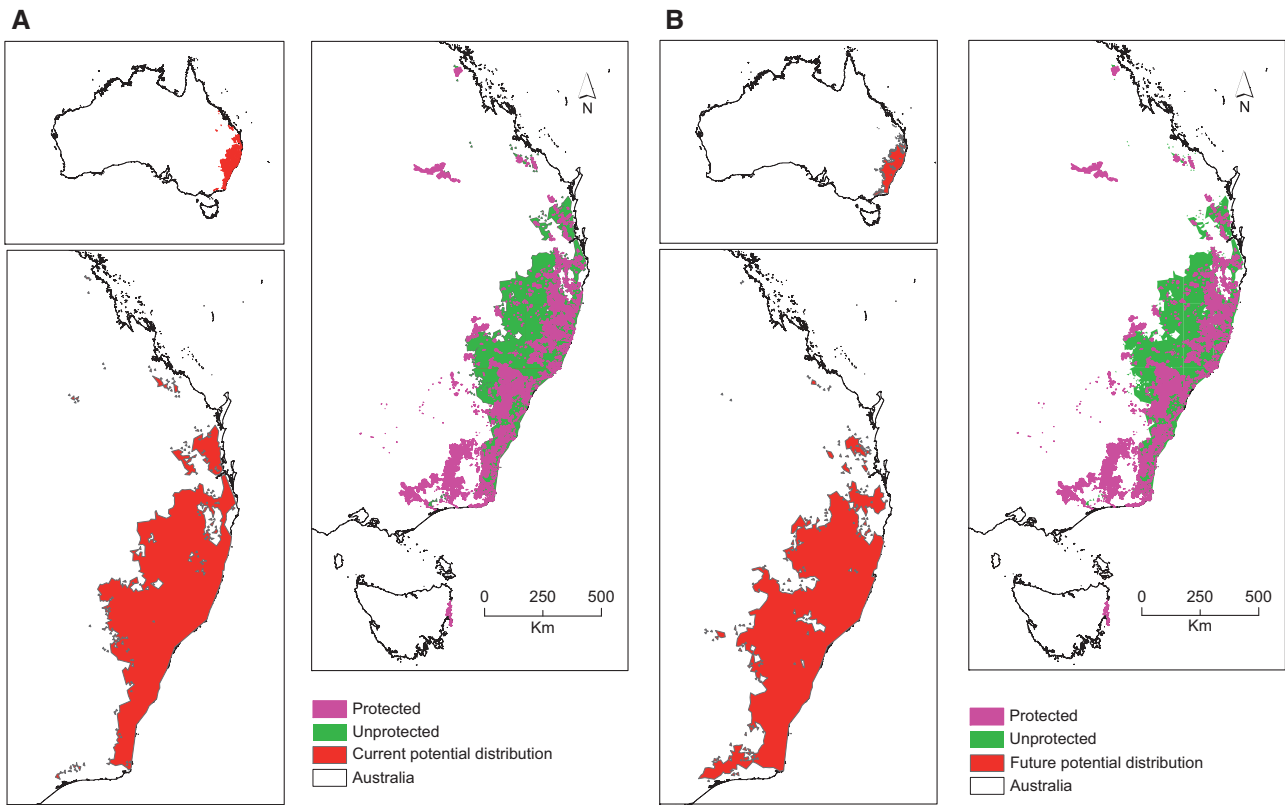
Figure 3. Overlap between current network of protected areas in southeastern Australia with **(A)** current potential distribution and **(B)** future potential distribution. Both panels represent the species' distribution in southeastern Australia in relation to the entire country and the current protected and unprotected areas.

narrow distribution and sample sizes for such species come with an additional challenge for model robustness from a statistical point of view (Stockwell and Peterson 2002; Pearson et al. 2007; Wisz et al. 2008). Second, the occurrence data for range-restricted species are often sporadic, adding more bias to modeling their potential distribution. Therefore, defining their full extent becomes less reliable from a management perspective as opposed to understanding their habitat occupancy (Williams et al. 2009). Consequently, data consideration for range-restricted species imposes a huge challenge for ENMs because they are meant to identify the full extent of a species' potential distribution but may underestimate this range if data are sporadic or intermittent (McPherson and Jetz 2007).

In this study, we used an environmental niche modeling approach as implemented in the MaxEnt algorithm since this method is especially good in handling species with few occurrences (Elith et al. 2006; Phillips et al. 2006; Wisz et al. 2008) together with future climate projections, to evaluate how changing climatic conditions will affect the potential distribution of a range-restricted lizard species in southeast Australia. Our results demonstrate that, climate change projections for the year 2075 have the potential to alter the distribution of the velvet gecko in southeastern Australia. Specifically, climate change may favor the range expansion of this species to encompass more suitable habitats. However, the magnitude of the effects of warming on the velvet gecko and on reptiles in general will depend on physiological and/or behavioural plasticity or evolutionary adaptations of different species (Williams et al. 2008; Chevin et al. 2010; Hoffmann 2010; Hoffmann et al. 2013; Monasterio et al. 2013). Therefore, as a potential source of resilience, ectotherms like the velvet gecko have *in situ* capabilities to

deal with extreme climates (see also Sunday et al. 2014). For example, this species inhabits closed systems (i.e., loose surface rocks), but in most rocky flat forms there are few loose surface rocks for animals to settle under. As a result, adult lizards may experience higher temperature during the summer. Additionally, over the last 25 years, female velvet geckos at our study sites near Nowra have continuously used the same communal nest sites for oviposition, suggesting rather limited plasticity in their choice of nest sites. Therefore, as a survival strategy, this species must leave these sites but employing this strategy is not possible. Thus, to prevent overheating, the geckos will need to move between hotter and cooler surfaces more often, potentially exposing them to avian predators and lowering their chances of survival. Notwithstanding, projecting future distributions under 3 RCPs, we identified suitable climate refugia where this species is likely to occupy. This includes southeastern New South Wales particularly toward the Australian Capital Territory. We found that similar temperature and precipitation bioclimatic variables were important in driving range change for *A. lesueurii* in southeast Australia. Additionally, we revealed some mismatches in the potential area of overlap in the range distribution of this gecko species currently and in the future with the network of protected areas in southeastern Australia.

Although our results show qualitatively a similar range expansion across the different climate change scenarios for this species, we caution that results from environmental niche models should be interpreted with some precaution. This is especially true for species with narrow geographical distributions or specialized habitat requirements like the velvet gecko and the quality of data use for characterizing their climate envelopes (see also Wisz et al. 2008;

Rebaudo et al. 2016). However, ENMs work on the assumption that a species is at equilibrium with its environment (i.e., a species is present in all suitable habitats and is absent from all unsuitable habitats (Guisan and Thuiller 2005). Notwithstanding, the climatic niche at equilibrium of a species is limited by both the small-scale abiotic and biotic interactions (e.g., competition, predation, pathogens, dispersal limitations), which are rarely incorporated in ENMs (Le Maitre et al. 2008; Guisan et al. 2014). Additionally, major weaknesses have been observed using WorldClim data to infer the thermal niche for small ectotherms (see Hannah et al. 2014 and references therein). However, this topic is still highly debatable in scientific literatures as there are protagonists (Hannah et al. 2014; Storlie et al. 2014) as well as antagonists (Bennie et al. 2014). In a recent analysis by Rebaudo et al. (2016), they used 3 different climatic datasets at different spatial scales (i.e., WorldClim, weather station, and microclimatic) to calibrate species ENMs. They showed that models calibrated with microclimatic dataset predicted the observed abundance of the study species but was however less accurate than the WorldClim datasets when performed at a coarse scale. Therefore, in the absence of microclimatic datasets, WorldClim datasets are well suited for calibrating the thermal niche of small ectotherms, given that, the availability of microclimatic data sets still represents a major challenge to overcome (Rebaudo et al. 2016). Nevertheless, we used WorldClim data to calibrate the thermal niche of the velvet gecko, but we further stress the point that ENMs provide only a probabilistic framework for a species' potential distributions, which needs to be verified using empirical data on many factors acting in a synergetic manner to determine the realized niche of a species.

Implications for the management of *A. lesueurii*

The velvet gecko is a nocturnal lizard (Cogger 2000), which relies on sandstone rocks for shelter sites, and this habitat is threatened by the illegal removal of "bush rocks" (Shine et al. 1998). For example, in Dharawal National Park and Morton National Park, the velvet gecko's habitats (i.e., rock platforms) are not connected to each other but rather separated by a minimum distance of approximately 2–3 km (Webb et al. 2008; Pike et al. 2010). Therefore, it is highly unlikely that they would shift rocky platforms due to higher temperatures, although shifting habitats (suitable microhabitats) or finding suitable retreat sites represent possible survival mechanisms to avoid lethally high temperatures in the future. In addition, the endangered broad-headed snake *Hoplocephalus bungaroides* is a major prey of this gecko species and its viability is critical for the persistence of broad-headed snakes (Pike et al. 2010).

Therefore, the relative rarity of *A. lesueurii*, together with its range-restricted nature and absence of population data, presents a daunting scenario for its conservation. Furthermore, human activities through the illegal removal of "bush rocks" and constant disturbance by reptile collectors provide a further threat to this species' survival. This phenomenon is further compounded by increases in air temperatures, which in turn increase their nest temperatures. Thus, the hatchlings survival is significantly affected which might lead to a higher probability of extinction (Dayananda et al. 2016). If the frequency and duration of summer heat waves increases in the future, coupled with anthropogenic habitat destruction, this may have profound effects on the velvet gecko population. In turn, local extinctions of geckos will have negative consequences for an endangered predator (broad-headed snake) that feeds almost entirely on velvet geckos. These findings have important implications for conservation of both predators and prey. We therefore suggest that the restricted habitat of the velvet gecko currently as predicted by climate should be a focus of intensive pre-emptive management in order to conserve this species from extinction. These results are consistent with previous studies, and in some cases management initiatives are already in place to restore the habitat of this species (see Croak et al. 2010; 2013). For example, artificial refugia have been constructed to allow crevices where this species can hide from lethal temperatures (Croak et al. 2010). These artificial rocks help to increase the colonization of both adults and juvenile geckos and we suggest that the addition of these artificial refugia should be continued in an effort to conserve this species. This is especially evident in the Dharawal National Park (67 km south of Sydney) and Morton National Park (160 km south of Sydney), which were important habitats for the velvet gecko but heavily degraded by bush-rock collection. Additionally, we show that the current network of protected areas in southeast Australia does not fully account for the full range distribution of this species currently and in the future. Therefore, present conservation actions to protect this species from anthropogenic activities should be increased to encompass the slight increases in suitable habitats of this endemic species in southeastern Australia as shown by this study. All these opportunities should be seized as they represent important conservation measures to protect this range-restricted species from anthropogenic activities.

Supplementary material

Supplementary material can be found at https://academic.oup.com/cz.

References

Araújo MB, Thuiller W, Pearson RG, 2006. Climate warming and the decline of amphibians and reptiles in Europe. *J Biogeogr* **33**:1712–1728.

Bennie J, Wilson RJ, Maclean IMD, Suggitt AJ, 2014. Seeing the woods for the trees: when is microclimate important in species distribution models? *Glob Change Biol* **20**:2699–2700.

Bezeng BS, Morales-Castilla I, van der Bank M, Yessoufou K, Daru BH et al., 2017. Climate change may reduce the spread of non–native species. *Ecosphere* **8**:e01694.

Bickford D, Howard SD, Ng DJ, Sheridan JA, 2010. Impacts of climate change on the amphibians and reptiles of Southeast Asia. *Biodivers Conserv* **19**:1043–1062.

Brown JH, Valone TJ, Curtin CG, 1997. Reorganization of an arid ecosystem in response to recent climate change. *Proc Natl Acad Sci USA* **94**:9729–9733.

Cabrelli AL, Hughes L, 2015. Assessing the vulnerability of Australian skinks to climate change. *Clim Change* **130**:223–233.

Chevin LM, Lande R, Mace GM, 2010. Adaptation, plasticity, and extinction in a changing environment: towards a predictive theory. *PLoS Biol* **8**:e1000357.

Clusella-Trullas S, Blackburn TM, Chown SL, 2011. Climatic predictors of temperature performance curve parameters in ectotherms imply complex responses to climate change. *Am Nat* **177**:738–751.

Cogger HG, 2000. *Reptiles and Amphibians of Australia*. 6th edn. Sydney: Reed Books.

Croak BM, Pike DA, Webb JK, Shine R, 2010. Using artificial rocks to restore nonrenewable shelter sites in human-degraded systems: colonization by fauna. *Rest Ecol* 18:428–438.

Croak BM, Webb JK, Shine R, 2013. The benefits of habitat restoration for rock-dwelling velvet geckos Oedura lesueurii. *J Appl Ecol* 50:432–439.

Dayananda B, Gray S, Pike D, Webb JK, 2016. Communal nesting under climate change: fitness consequences of higher nest temperatures for a nocturnal lizard. *Glob Chang Biol* 22:2405–2414.

Deutsch CA, Tewksbury JJ, Huey RB, Sheldon KS, Ghalambor CK et al., 2008. Impacts of climate warming on terrestrial ectotherms across latitude. *Proc Natl Acad Sci USA* 105:6668–6672.

Elith J, Kearney M, Phillips S, 2010. The art of modelling range-shifting species. *Methods Ecol Evol* 1:330–342.

Elith J, Graham CH, Anderson RP, Dudík M, Ferrier S et al., 2006. Novel methods improve prediction of species' distributions from ccurrence data. *Ecography* 29:129–151.

Fitzpatrick MC, Hargrove WW, 2009. The projection of species distribution models and the problem of non-analog climate. *Biodivers Conserv* 18:2255–2261.

Guisan A, Thuiller W, 2005. Predicting species distribution: offering more than simple habitat models. *Ecol Lett* 8:993–1009.

Guisan A, Petitpierre B, Broennimann O, Daehler C, Kueffer C, 2014. Unifying niche shift studies: insights from biological invasions. *Trends Ecol Evol* 29:260–269.

Hannah L, Flint L, Syphard AD, Moritz MA, Buckley LB et al., 2014. Fine-grain modeling of species' response to climate change: holdouts, stepping-stones, and microrefugia. *Trends Ecol Evol* 29:390–397.

Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A, 2005. Very high resolution interpolated climate surfaces for global land area. *Int J Climatol* 25:965–1978.

Hoffmann A, 2010. Physiological climatic limits in Drosophila: patterns and implications. *J Exp Biol* 213:870–880.

Hoffmann AA, Chown SL, Clusella-Trullas S, 2013. Upper thermal limits in terrestrial ectotherms: how constrained are they? *Funct Ecol* 27:934–949.

Huey RB, Kearney MR, Krockenberger A, Holtum JA, Jess M et al., 2012. Predicting organismal vulnerability to climate warming: roles of behaviour, physiology and adaptation. *Proc R Soc B: Bio Sci* 367:1665–1679.

Hughes L, 2000. Biological consequences of global warming: is the signal already apparent? *Trends Ecol Evol* 15:56–61.

Hughes L, 2003. Climate change and Australia: trends, projections and impacts. *Aust Ecol* 28:423–443.

Kelly AE, Goulden ML, 2008. Rapid shifts in plant distribution with recent climate change. *Proc Natl Acad Sci USA* 105:11823–11826.

Le Maitre DC, Thuiller W, Schonegevel L, 2008. Developing an approach to defining the potential distributions of invasive plant species: a case study of Hakea species in South Africa. *Glob Ecol Biogeogr* 17:569–584.

Lenoir J, Gegout JC, Marquet PA, De Ruffray P, Brisse HA, 2008. Significant upward shift in plant species optimum elevation during the 20th century. *Science* 320:1768–1771.

Logan ML, Fernandez SG, Calsbeek R, 2014. Abiotic constraints on the activity of tropical lizards. *Funct Ecol* 29:694–700.

McPherson JM, Jetz W, 2007. Effects of species' ecology on the accuracy of distribution models. *Ecography* 30:135–151.

Melville J, Haines ML, Hale J, Chapple S, Ritchie EG, 2016. Concordance in phylogeography and ecological niche modelling identify dispersal corridors for reptiles in arid Australia. *J Biogeogr* 43(9):1844–1855.

Monasterio C, Shoo LP, Salvador A, Iraeta P, Díaz J, 2013. High temperature constrains reproductive success in a temperate lizard: implications for distribution range limits and the impacts of climate change. *J Zool* 291:136–145.

Moritz C, Patton JL, Conroy CJ, Parra JL, White GC et al., 2008. Impact of a century of climate change on small-mammal communities in Yosemite National Park, USA. *Science* 322:261–264.

Parmesan C, 2006. Ecological and evolutionary responses to recent climate change. *Annu Rev Ecol Evol Syst* 37:637–669.

Pearson RG, Raxworthy CJ, Nakamura M, Peterson AT, 2007. Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. *J Biogeogr* 34:102–117.

Phillips SJ, Anderson RP, Schapire RE, 2006. Maximum entropy modelling of species geographic distributions. *Ecol Model* 190:231–259.

Phillips SJ, Dudík M, Elith J, Graham CH, Lehmann A et al., 2009. Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. *Ecol Appl* 19:181–197.

Pike DA, Webb JK, Shine R, 2010. Nesting in a thermally challenging environment: nest-site selection in a rock-dwelling gecko Oedura lesueurii (Reptilia: Gekkonidae). *Biol J Linn Soc* 99:250–259.

Pounds JA, Fogden MP, Campbell JH, 1999. Biological response to climate change on a tropical mountain. *Nature* 398:611–615.

Rebaudo F, Faye E, Dangles O, 2016. Microclimate data improve predictions of insect abundance models based on calibrated spatiotemporal temperatures. *Front Physiol* 7:139.

Riahi K, Rao S, Krey V, Cho C, Chirkov V et al., 2011. RCP 8.5: a scenario of comparatively high greenhouse gas emissions. *Clim Change* 109:33–57.

Root TL, Price JT, Hall KR, Schneider SH, Rosenzweig C et al., 2003. Fingerprints of global warming on wild animals and plants. *Nature* 421:57–60.

Shine R, Webb JK, Fitzgerald M, Sumner J, 1998. The impact of bush-rock removal on an endangered snake species Hoplocephalus bungaroides (Serpentes: Elapidae). *Wild Res* 25:285–295.

Sinervo B, Mendez-De-La-Cruz F, Miles DB, Heulin B, Bastiaans E et al., 2010. Erosion of lizard diversity by climate change and altered thermal niches. *Science* 328:894–899.

Sodhi NS, Ehrlich PR, 2010. *Conservation Biology for All*. Oxford: Oxford University Press.

Stocker T, Qin D, Plattner G, Tignor M, Allen S et al., 2013. IPCC, 2013: Climate Change 2013: The Physical Science Basis. *Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge: Cambridge University Press.

Stockwell DRB, Peterson AT, 2002. Effects of sample size on accuracy of species distribution models. *Ecol Model* 148:1–13.

Storlie C, Merino-Viteri A, Phillips B, Van Der Wal J, Welbergen J et al., 2014. Stepping inside the niche: microclimate data are critical for accurate assessment of species' vulnerability to climate change. *Biol Lett* 10:20140576.

Sunday JM, Bates AE, Kearney MR, Colwell RK, Dulvy NK et al., 2014. Thermal-safety margins and the necessity of thermoregulatory behavior across latitude and elevation. *Proc Natl Acad Sci USA* 15:5610–5615.

Tewksbury JJ, Huey RB, Deutsch CA, 2008. Putting the heat on tropical animals. *Science* 320:1296–1297.

Thomas CD, Cameron A, Green RE, Bakkenes M, Beaumont LJ et al., 2004. Extinction risk from climate change. *Nature* 427:145–148.

Thomson AM, Calvin KV, Smith SJ, Kyle GP, Volke A et al., 2011. RCP4.5: a pathway for stabilization of radiative forcing by 2100. *Clim Change* 109:77–94.

Thuiller W, Lavorel S, Araújo MB, Sykes MT, Prentice IC, 2005. Climate change threats to plant diversity in Europe. *Proc Natl Acad Sci* USA 102:8245–8250.

Tingley R, Thompson MB, Hartley S, Chapple DG, 2016. Patterns of niche filling and expansion across the invaded ranges of an Australian lizard. *Ecography* 39:270–280.

van Vuuren DP, Stehfest E, den Elzen MGJ, Kram T, van Vliet J et al., 2011. RCP2.6: exploring the possibility to keep global mean temperature increase below 2 degrees C. *Clim Change* 109:95–116.

Wake DB, 2007. Climate change implicated in amphibian and lizard declines. *Proc Natl Acad Sci USA* 104:8201–8202.

Walther GR, Post E, Convey P, Menzel A, Parmesan C et al., 2002. Ecological responses to recent climate change. *Nature* 416:389–395.

Webb JK, Pike DA, Shine R, 2008. Population ecology of the velvet gecko Oedura lesueurii in south eastern Australia: implications for the persistence of an endangered snake. *Aust Ecol* 33:839–847.

Williams JN, Seo C, Thorne J, Nelson JK, Erwin S et al., 2009. Using species distribution models to predict new occurrences for rare plants. *Divers Distrib* 15:565–576.

Williams SE, Shoo LP, Isaac JL, Hoffmann AA, Langham G, 2008. Towards an integrated framework for assessing the vulnerability of species to climate change. *PLoS Biol* 6:e325.

Wisz MS, Hijmans RJ, Li J, Peterson AT, Graham CH et al., 2008. Effects of sample size on the performance of species distribution models. *Divers Distrib* 14:763–773.