

A framework for assessing the vulnerability of species to climate change: a case study of the Australian elapid snakes

Abigail L. Cabrelli · Adam J. Stow · Lesley Hughes

Received: 18 October 2013 / Revised: 12 May 2014 / Accepted: 4 July 2014 /
Published online: 1 August 2014
© Springer Science+Business Media Dordrecht 2014

Abstract Frameworks that provide a system for assessing species according to their vulnerability to climate change can offer considerable guidance to conservation managers who need to allocate limited resources among a large number of taxa. To date, climate change vulnerability assessments have largely been based on projected changes in range size derived from the output of species distribution models (SDMs). A criticism of risk assessments based solely on these models is that information on species ecological and life history traits is lacking. Accordingly, we developed a points-based framework for assessing species vulnerability to climate change that considered species traits together with the projections of SDMs. Applying this method to the Australian elapid snakes (family Elapidae), we determined which species may be particularly susceptible in the future and assessed broad-scale biogeographic patterns in species vulnerability. By offering a more comprehensive and rigorous method for assessing vulnerability than those based solely on SDMs, this framework provides greater justification for resource allocation, and can help guide decisions regarding the most appropriate adaptation strategies.

Keywords Climate change · Conservation priorities · Elapidae · Species distribution modelling · Species traits · Vulnerability assessment

Introduction

Australia has warmed by almost 1 °C over the last 100 years, consistent with global trends (Braganza and Church 2011). This warming has been accompanied by changing rainfall

Communicated by David Westcott.

Electronic supplementary material The online version of this article (doi:10.1007/s10531-014-0760-0) contains supplementary material, which is available to authorized users.

A. L. Cabrelli (✉) · A. J. Stow · L. Hughes
Department of Biological Sciences, Macquarie University, North Ryde, NSW 2109, Australia
e-mail: abby.cabrelli@gmail.com

patterns, rising sea levels and an increased frequency of extreme weather events (CSIRO and BOM 2012). There is accumulating evidence that species are already responding to these climatic changes via shifts in their distribution, demography, behaviour, phenology and genetic composition (Bull and Burzacott 2002; Umina et al. 2005; Steffen et al. 2009; Telemeco et al. 2009; Chambers et al. 2013). Climate models predict that Australia could warm by as much as 2.8 °C by 2050 and 5 °C by 2070 (Whetton 2011), leading to widespread expectations that over the coming decades, many species will face dramatic reductions in the amount and connectivity of suitable habitat, temporal and spatial mismatches with other species on which they depend, and catastrophic declines in population size (Beaumont and Hughes 2002; Williams et al. 2003; Fitzpatrick et al. 2008; Reside et al. 2012). A current challenge facing ecologists and managers is to identify which species are likely to be most vulnerable to these impacts so that conservation efforts can be prioritised.

To date, assessments of species vulnerability to climate change have largely been based on the output of correlative species distribution models (SDMs). SDMs relate species occurrences and environmental variables to describe the environmental conditions under which a species is likely to occur. The spatial distribution of environments suitable for the species can then be projected into the future under various climate change scenarios (Guisan and Zimmermann 2000; Franklin 2009). Many researchers consider correlative SDMs a valuable step in assessing the potential responses of species to climate change, primarily because their ease of use and low data requirements make them suitable for the rapid evaluation of large numbers of species. Consequently, they have proved popular tools for conducting broad-scale vulnerability assessments across multiple taxa, allowing species to be ranked according to their risk of future range contractions (e.g. Beaumont and Hughes 2002; Berry et al. 2002; Attorre et al. 2011).

The limitations of correlative SDMs are well recognised, and have been reviewed extensively elsewhere (Heikkinen et al. 2006; Sinclair et al. 2010). A major criticism of these models is that they often lack a mechanistic underpinning. An alternative approach is to use models that explicitly incorporate mechanistic links between the functional traits of species and their environment (Kearney and Porter 2009). The advantage of these mechanistic models is their ability to unveil the processes underlying species distributional patterns, which may make them more robust when extrapolating into new environments. However, these models can only be used for well-studied taxa because they require an understanding of the key processes that limit a species range, as well as estimates of numerous phenotypic parameters under a range of environmental conditions. Mechanistic models also require considerably more time and effort to parameterise because they are typically developed for specific species and require parameterisation for each species considered (Buckley et al. 2010).

In the present study, we used a third approach for assessing species vulnerability to climate change that considers the ecological and life history traits of species alongside the projections of correlative SDMs (Heikkinen et al. 2010). We integrated these two sets of information in an easy-to-apply framework using a system that awarded points to species for a number of different variables. This approach provides a more comprehensive insight into the risk a species may face in the future than assessments based solely on the projections of correlative SDMs, without the need for extensive ecological and biophysical data. We applied this framework to Australia's venomous land snakes (family Elapidae), a monophyletic group comprising 27 genera and almost 100 species (Wilson and Swan 2008). Globally, elapids occur widely in the tropics and subtropics of Asia, Africa and the Americas, but their diversity reaches a peak in Australia where they comprise nearly 70 %

of the snake fauna. We chose this group for three principle reasons. First, elapids can be found throughout the Australian continent, including the cool temperate regions of Victoria and Tasmania where low temperatures exclude all other snake families (Cogger and Heatwole 1981; Nix 1989). They are therefore ideal for investigating broad-scale biogeographic patterns in species vulnerability. Second, their ecology and life histories have been relatively well studied, and data on species traits are widely available (e.g. Shine 1994). Third, studies assessing the potential impacts of climate change on Australian elapids have until now focused on single species (Aubret and Shine 2010; Penman et al. 2010). To identify the species most in need of conservation attention, a multi-species assessment of this taxonomic group is warranted.

The principle objectives of this study were to determine which species may be at greatest risk in the future, identify the main factors contributing to their vulnerability to climate change and assess broad-scale biogeographic patterns in species vulnerability.

Methods

Variables derived from the output of SDMs

We followed the nomenclature of a comprehensive field guide to Australia's reptiles which describes 97 species of elapid snakes (Wilson and Swan 2008). Geo-referenced locality records were downloaded from the Global Biodiversity Information Facility (www.gbif.org) and BioMaps (www.biomaps.net.au), and were supplemented by records obtained directly from the Australian Museum, the Western Australian Museum (via NatureMap), the Tasmanian Museum and Art Gallery, the Atlas of NSW Wildlife and the Australian National Wildlife Collection. These records were plotted and compared with distribution maps from Wilson and Swan (2008) and other reptile field guides. Duplicate points, those with a recorded spatial precision of >5 km, those with a recorded collection date prior to 1960 and those that were questionable due to their geographic location were removed.

We omitted species that had fewer than 15 records from further analyses because low sample sizes have been shown to limit model accuracy (Online Resource 1) (Wisz et al. 2008). Generally, little is known about the ecology of these species due to their rarity, making them unsuited to our vulnerability assessment which is reliant on ecological information. Nevertheless, many of these species occupy ranges that span only a narrow range of climatic conditions and may be less able to tolerate changes in climate (Thuiller et al. 2005). We therefore recommend that, relative to the group as a whole, these species are considered highly vulnerable to the impacts of climate change until further data on their distributions and life history traits are collected.

We derived a suite of five bioclimatic variables (Busby 1991) from current climate data (1960–2000) provided by the Bureau of Meteorology (www.bom.gov.au)—annual mean temperature, temperature seasonality, minimum temperature of the coldest month, maximum temperature of the hottest month, and annual precipitation. Future climate projections for 2050 were obtained from four global circulation models (GCMs) believed to produce reliable projections of future climate in Australia (BCCR, CSIRO Mk3.5, INMCM3.0 and MIROC3.2-medres) (CSIRO and BOM 2007). These projections were based on the A2 emissions scenario from the IPCC Special Report on Emissions Scenarios (SRES) (Nakicenovic and Swart 2000), which has been shown to closely match recently observed atmospheric CO₂ levels (Raupach et al. 2007). We standardised all data to a 0.05×0.05 degree grid (approximately 5×5 km).

We used six modelling algorithms to model the current and 2050 climatic ranges of each species. Generalised linear models, generalised additive models, boosted regression trees, artificial neural networks and multivariate adaptive regression splines were all generated using the R statistical package BIOMOD (Thuiller 2003), and maximum entropy models were built using Maxent v3.3.2 (Phillips et al. 2006). These algorithms have all been shown to perform well compared to other modelling approaches (Elith et al. 2006). Pseudo-absence points were obtained by collating the locality records of all species to help account for spatial autocorrelation in the species occurrence data (Phillips et al. 2009; Mateo et al. 2010). To reduce the prevalence of false absences, we excluded all points that fell within 2° (≈ 200 km) of each presence point, except in the case of Maxent which is designed to work with background data containing both presences and absences (Phillips and Dudik 2008; Phillips et al. 2009; VanDerWal et al. 2009).

The performance of each algorithm was assessed by calculating the area under the receiver operating characteristic curve (AUC) using a tenfold cross-validation procedure. By convention, an algorithm is considered excellent if the average AUC score across all model replicates is >0.9 , good if $0.8\text{--}0.9$, fair if $0.7\text{--}0.8$ and poor if <0.7 . For each species, we eliminated the two algorithms with the poorest performance (lowest average AUC scores) from further analysis. The average AUC score of the remaining algorithms across all species was 0.98, indicating their performance was excellent.

For each of the four best performing algorithms, a ‘full model’ was built using all presence points and used to project the species current and 2050 climatic ranges. This process generated maps comprising a series of grid cells, each containing a climate suitability value ranging from 0 (entirely unsuitable for the species) to 1 (entirely suitable). For each GCM, we averaged the maps produced by the four algorithms to obtain a mean projection for 2050. Each map was then converted into a presence-absence map using the average sensitivity–specificity equality threshold of the four algorithms.

We used these maps to derive the following four variables.

Change in climatic range size

We calculated the change in climatic range size between the current and 2050 maps as the percentage change in the number of suitable grid cells. This was repeated using each of the four 2050 maps (one for each GCM), resulting in four estimates for the change in climatic range size per species. A high percentage loss of suitable area indicates high vulnerability, whereas a low percentage loss of suitable area, or a gain in suitable area, indicates low vulnerability.

Overlap between the current and 2050 climatic ranges

The pressure a species will be under to disperse to new areas can be inferred from the degree of overlap between its current and future climatic ranges: a spatially disjunct future range implies the species will have to disperse from areas within its current climatic range to reach climatically suitable areas by 2050. In contrast, a large degree of overlap indicates much of the current climatic range will remain suitable by 2050, and therefore the need for dispersal will be less. We calculated the percentage overlap between the current and 2050 climatic ranges for each 2050 map. A low percentage overlap indicates high vulnerability, whereas a high percentage overlap indicates low vulnerability.

Change in climatic suitability

We used the non-thresholded current and 2050 maps to calculate the change in climatic suitability between the current and 2050 time periods. For each map, we conserved all grid cell values above the threshold, but set the values of all grid cells that fell below the threshold to 0. This generated a heterogeneous distribution comprising varying values of climatic suitability. We then calculated the percentage change in average suitability of cells between the current and 2050 climatic ranges. A value $<100\%$ indicates conditions within the future range are less favourable for the species than those in its current range (high vulnerability), and a value $>100\%$ indicates future conditions are more favourable (low vulnerability).

Overlap with the protected area network

To assess whether climate change may drive species out of reserves, we overlaid the current and 2050 maps with a GIS layer of Australia's protected area network obtained from the Collaborative Australia Protected Area Database (CAPAD: www.environment.gov.au/parks/nrs/science/capad). We then calculated the percentage change in the number of suitable grid cells that fell within protected areas for each of the four 2050 maps. A value $<100\%$ indicates a lower proportion of the 2050 range overlaps with the network compared to the current range (high vulnerability), whereas a value $>100\%$ indicates a greater proportion of the 2050 climatic range overlaps with the network compared to the current climatic range (low vulnerability).

Variables based on species traits

A number of species traits have been proposed as correlates of climate change vulnerability (Williams et al. 2008). These include geographic range size, population size, degree of specialisation and environmental niche breadth, which are all expected to increase the sensitivity of species to environmental change. The adaptive capacity of species is influenced by attributes such as dispersal ability, phenological and behavioural plasticity, genetic variability, fecundity and generation length. We eliminated the traits for which little data were available for the majority of species as well as those that were strongly correlated with other factors to minimise redundancy. For example, we chose to include 'threatened status' as a variable but exclude 'geographic range size' and 'abundance' under the rationale that these factors are criteria used in determining a species threatened status and are therefore likely to be highly correlated, and also because data on species range sizes and abundances are not widely available at a continental scale. Following these considerations, four traits were identified as being suitable for inclusion in the vulnerability assessment: habitat specialisation, dietary specialisation, clutch/litter size and threatened status.

We assessed these traits as follows.

Habitat specialisation

We used vegetation specialisation as a proxy for habitat specialisation. A GIS layer of Australia's major vegetation types was obtained from the National Vegetation Information System (NVIS: www.environment.gov.au/erin/nvis/index.html), which describes 30 distinct types of native vegetation containing different mixes of plant species, but which are

structurally similar and often dominated by a single genus. For each species we extracted the vegetation type at each occurrence point, and calculated Simpson's index (Simpson 1949) of vegetation types across all occurrence records as an index of habitat specialisation. High habitat specialisation indicates high vulnerability and low habitat specialisation indicates low vulnerability.

Dietary specialisation

Data on diet were sourced from the literature using Shine (1994) as a primary reference. We identified seven major prey types (insects, fish, frogs, reptiles, reptile eggs, birds and mammals) and classified species as *specialist* if one prey type comprises 100 % of its diet (high vulnerability), *borderline specialist* if one prey type comprises 90–100 % of its diet (moderate vulnerability) and *generalist* if no prey type comprises ≥ 90 % of its diet (low vulnerability). Dietary information was not available for 7 species (≈ 9 %). As the diets of many elapids appear to be phylogenetically conserved (Shine 1989, 1994), we inferred these data from those of congeneric species.

Because information on the dietary preferences of juveniles is scarce, we considered the diets of adult snakes only. We note, however, that some snakes do vary in their dietary preferences at different life stages; adults of some larger species, for example, have quite generalist diets whereas juveniles consume mostly lizards (Shine 1980). In these instances our assessment will have underestimated species vulnerability.

Clutch/litter size

We sourced estimates of mean clutch and litter sizes from published data, again using Shine (1994) as a primary reference. Values were not found for 10 species (≈ 12 %). In these instances, we inferred values from their closest relatives as the reproductive biology of elapids also appears to be phylogenetically conservative (Shine 1989). Species were categorized according to their clutch/litter size based on the median value for the entire family. We classed species with clutch/litter sizes \geq median as having *large* clutch/litter sizes (low vulnerability) and those with clutch/litter sizes $<$ median as having *small* clutch/litter sizes (high vulnerability). Where there is documented evidence that species do not reproduce annually, we adjusted these estimates accordingly. We acknowledge that offspring survival is also a critical determinant of reproductive output, however data on this trait are lacking for the majority of the species considered here.

Threatened status

Species were classed as *threatened* (high vulnerability) if they are currently listed as 'near threatened', 'vulnerable', 'endangered' or 'critically endangered' under the Environment Protection and Biodiversity Conservation (EPBC) Act (www.environment.gov.au/epbc), or according to the 2008 IUCN Red List of Threatened Species (www.iucn.org).

Constructing the framework

The eight variables described above are unlikely to be equally important determinants of species vulnerability to climate change. Accordingly, we chose to rank the variables in order of perceived importance and weight them by assigning the highest number of points

to the most important variable, fewer points to the second most important variable, and so on. To reduce the subjectivity of this process, we identified a group of eight experts in Australian reptile ecology whose research interests include climate impacts, and asked them to rank the eight variables in order of importance via an on-line questionnaire. The results of the questionnaire were collated and returned anonymously to each participant. The experts were then asked to rank the eight variables a second time. This process, based on the Delphi method, is a recognised technique for increasing consensus among a panel of experts (Hsu and Sandford 2007).

We used the averaged results of the second questionnaire round to construct the vulnerability assessment framework (Table 1). We allocated a maximum point score of nine to ‘threatened status’, the variable considered by the experts to be the most important. The second most important variable, ‘overlap between the current and 2050 climatic ranges’ was allocated a maximum point score of eight, and so on. We assigned a minimum point score of one to each variable. Within each variable, points were assigned to the different categories in equal increments. For example, dietary specialisation, which comprised three categories, was allocated a maximum point score of three. We therefore assigned three points to the most vulnerable category (dietary specialist), two points to the intermediate category (borderline specialist) and one point to the least vulnerable category (dietary generalist).

A vulnerability score for each species was obtained by calculating the geometric mean of the points awarded for each of the eight variables. We repeated this process four times using the maps corresponding to each of the GCMs, resulting in four vulnerability scores for each species. The mean of these overall vulnerability scores was then used to rank species according to their vulnerability to climate change. Three vulnerability groups were defined: species with a mean score \geq the 66th percentile were classed as *high vulnerability*, species with a mean score in between the 33rd and 66th percentiles were classed as *moderate vulnerability*, and species with a mean score $<$ 33rd percentile were classed as *low vulnerability*, relative to the group as a whole.

Analysis

To investigate broad-scale regional patterns in species vulnerability to climate change, we assigned species to one of six categories according to their biogeographic distribution, based on information in Wilson and Swan (2008) and Nix (1989): temperate, tropical, arid, east coast, eastern interior and multiregional (species occurring in several biogeographical regions). Differences in vulnerability among biogeographic groups were analysed using non-parametric statistical tests. A second analysis was performed by overlaying the current climatic range maps of the 27 species assigned to the high vulnerability category to identify areas of high climatic suitability for the most vulnerable species.

Results

SDM projections

SDM projections varied widely among species (Online Resource 2), consistent with other studies that have modelled distribution shifts in reptiles on other continents (Araújo et al. 2006; Carvalho et al. 2010). Eighteen species (22 %) were projected to experience climatic range contractions by 2050 according to all four ensemble projections, and 53 species

Table 1 Summary of the vulnerability assessment framework

Variable	Assigned points
1. Threatened status	
(a) Threatened	9.0
(b) Not threatened	1.0
2. Overlap between the current and 2050 climatic ranges	
(a) $x < 1\text{st quartile}$	8.0
(b) $1\text{st quartile} \leq x < \text{median}$	5.7
(c) $\text{Median} \leq x < 3\text{rd quartile}$	3.3
(d) $x \geq 3\text{rd quartile}$	1.0
3. Change in climatic range size	
(a) $x < 1\text{st quartile}$	7.0
(b) $1\text{st quartile} \leq x < \text{median}$	5.0
(c) $\text{Median} \leq x < 3\text{rd quartile}$	3.0
(d) $x \geq 3\text{rd quartile}$	1.0
4. Habitat specialisation	
(a) $x < 1\text{st quartile}$	6.0
(b) $1\text{st quartile} \leq x < \text{median}$	4.3
(c) $\text{Median} \leq x < 3\text{rd quartile}$	2.7
(d) $x \geq 3\text{rd quartile}$	1.0
5. Change in climatic suitability	
(a) $x < 1\text{st quartile}$	5.0
(b) $1\text{st quartile} \leq x < \text{median}$	3.7
(c) $\text{Median} \leq x < 3\text{rd quartile}$	2.3
(d) $x \geq 3\text{rd quartile}$	1.0
6. Overlap with the protected area network	
(a) $x < 1\text{st quartile}$	4.0
(b) $1\text{st quartile} \leq x < \text{median}$	3.0
(c) $\text{Median} \leq x < 3\text{rd quartile}$	2.0
(d) $x \geq 3\text{rd quartile}$	1.0
7. Dietary specialisation	
(a) Specialist	3.0
(b) Borderline specialist	2.0
(c) Generalist	1.0
8. Clutch/litter size	
(a) Small	2.0
(b) Large	1.0

(65 %) were projected to experience climatic range contractions according to at least two ensemble projections (Online Resource 3). Thirteen species (16 %) were projected to experience climatic range expansions according to all four ensemble projections. The most vulnerable species according to projected changes in climatic range size included the brown-headed snake (*Furina tristis*), with an average reduction in climatic range size of 78.2 % by 2050, and the robust burrowing snake (*Antairosepens warro*), with an average reduction of 62.6 %. The least vulnerable species according to the model projections were the northern shovel-nosed snake (*Brachyuophis roperi*), the Rufous whipsnake (*Demansia*

rufescens) and the Pilbara bandy-bandy (*Vermicella snelli*), which were all projected to experience an average climatic range expansion of over 240 % and have an average percentage overlap between their current and 2050 climatic ranges of at least 65 %.

Overall vulnerability

As a consequence of their highly variable SDM projections and considerable diversity in species traits, vulnerability scores varied widely, ranging from 1.361 to 3.554 out of a possible 4.954 (Table 2). Species classed as ‘high vulnerability’ included the ornamental snake (*Denisonia maculata*), the unbanded shovel-nosed snake (*Brachyuropis incinctus*) and the black striped snake (*Cryptophis nigrostriatus*). Species scored as ‘low vulnerability’ were characterised by projected range expansions with high levels of overlap, generalist habits and large clutch sizes, and included the lesser black whipsnake (*Demansia vestigiata*), the spotted black snake (*Pseudechis guttatus*) and the yellow-faced whipsnake (*Demansia psammophis*).

Number of points for SDM-related variables vs number of points for trait-related variables

Species assigned to the high vulnerability group were generally projected to lose climatically suitable area and have low degrees of overlap (<50 %) between their current and 2050 climatic ranges, but they differed in the traits that contributed to their high scores (Online Resource 3). The ornamental snake (*Denisonia maculata*), for instance, is a habitat specialist and is currently listed as vulnerable to extinction under the federal EPBC Act and on the IUCN Red List, whereas the unbanded shovel-nosed snake (*Brachyuropis incinctus*) has highly specialised habitat and dietary requirements and a small clutch size. Unsurprisingly, therefore, the number of points awarded for SDM-related variables was not correlated with the number of points allocated for trait-related variables ($r = 0.082$, $df = 322$, $p = 0.142$). This suggests that species traits offer additional information about climate change vulnerability that is not provided by model projections.

Biogeographic analysis

There were significant differences among biogeographic zones in terms of the proportion of species assigned to each vulnerability group (Fisher’s exact test: $p = 0.037$; Fig. 1). Overall, multiregional species appeared least vulnerable, with no species assigned to the high vulnerability group. In contrast, coastal and temperate regions had the greatest proportions of species represented in the high vulnerability group. Areas of high climatic suitability for the species assigned to the high vulnerability group occur predominantly along the tropical east coast, in the northern interior and along the south coast of the Australian continent (Fig. 2).

Discussion

The vulnerability of Australia’s terrestrial elapid snakes to climate change

In this study we developed a system for assessing species vulnerability to climate change. Applying this system to Australia’s terrestrial elapid snakes, we found that vulnerability

Table 2 The vulnerability scores of each species, and the vulnerability groups to which they were assigned

Species name	Common name	Mean score	Vulnerability group
<i>Denisonia maculata</i>	Ornamental snake	3.554	H
<i>Brachyuropis incinctus</i>	Unbanded shovel-nosed snake	3.391	H
<i>Cryptophis nigrostriatus</i>	Black-striped snake	3.349	H
<i>Drysdalia mastersii</i>	Masters' snake	3.320	H
<i>Cacophis churchilli</i>	Northern dwarf crowned snake	3.174	H
<i>Rhinoplocephalus bicolor</i>	Square-nosed snake	3.153	H
<i>Antairoserpens warro</i>	Robust burrowing snake	3.105	H
<i>Parasuta nigriceps</i>	Mitchell's short-tailed snake	3.102	H
<i>Pseudonaja ingrami</i>	Ingram's brown snake	3.093	H
<i>Demansia torquata</i>	Collared whipsnake	3.085	H
<i>Parasuta flagellum</i>	Little whipsnake	3.033	H
<i>Demansia rimicola</i>	Channel country whipsnake	2.965	H
<i>Cryptophis boschmai</i>	Carpentaria snake	2.916	H
<i>Furina tristis</i>	Brown-headed snake	2.903	H
<i>Cacophis harriettae</i>	White-crowned snake	2.882	H
<i>Pseudechis colletti</i>	Collett's snake	2.845	H
<i>Oxyuranus microlepidotus</i>	Inland taipan	2.780	H
<i>Hoplocephalus bungaroides</i>	Broad-headed snake	2.677	H
<i>Pseudonaja guttata</i>	Speckled brown snake	2.675	H
<i>Echiopsis curta</i>	Bardick	2.649	H
<i>Drysdalia rhodogaster</i>	Mustard-bellied snake	2.644	H
<i>Pseudechis butleri</i>	Spotted mulga snake	2.633	H
<i>Simoselaps anomalus</i>	Desert banded snake	2.616	H
<i>Hoplocephalus stephensii</i>	Stephens' banded snake	2.599	H
<i>Cryptophis nigrescens</i>	Eastern small-eyed snake	2.544	H
<i>Cacophis krefftii</i>	Southern dwarf crowned snake	2.509	H
<i>Parasuta spectabilis</i>	Mallee black-headed snake	2.482	H
<i>Drysdalia coronoides</i>	White-lipped snake	2.455	M
<i>Pseudonaja inframacula</i>	Peninsula brown snake	2.385	M
<i>Oxyuranus scutellatus</i>	Coastal taipan	2.352	M
<i>Neelaps calonotos</i>	Black-striped snake	2.337	M
<i>Denisonia devisi</i>	De vis' banded snake	2.325	M
<i>Parasuta dwyeri</i>	Dwyer's snake	2.312	M
<i>Suta fasciata</i>	Rosen's snake	2.305	M
<i>Austrelaps labialis</i>	Pygmy copperhead	2.298	M
<i>Austrelaps superbus</i>	Lowlands copperhead	2.293	M
<i>Acanthophis pyrrhus</i>	Desert death adder	2.282	M
<i>Vermicella annulata</i>	Bandy-bandy	2.269	M
<i>Notechis scutatus</i>	Tiger snake	2.229	M
<i>Hemiaspis damelii</i>	Grey snake	2.219	M
<i>Austrelaps ramsayi</i>	Highlands copperhead	2.164	M
<i>Simoselaps littoralis</i>	West coast banded snake	2.148	M
<i>Hemiaspis signata</i>	Black-bellied swamp snake	2.133	M

Table 2 continued

Species name	Common name	Mean score	Vulnerability group
<i>Elapognathus coronatus</i>	Western crowned snake	2.121	M
<i>Hoplocephalus bitorquatus</i>	Pale-headed snake	2.120	M
<i>Suta suta</i>	Myall snake	2.107	M
<i>Brachyuropis semifasciatus</i>	Southern shovel-nosed snake	2.098	M
<i>Simoselaps bertholdi</i>	Jan's banded snake	2.093	M
<i>Brachyuropis fasciolatus</i>	Narrow-banded shovel-nosed snake	2.068	M
<i>Brachyuropis approximans</i>	North-western shovel-nosed snake	2.060	M
<i>Pseudechis porphyriacus</i>	Red-bellied black snake	2.048	M
<i>Parasuta monachus</i>	Monk snake	2.026	M
<i>Brachyuropis roperi</i>	Northern shovel-nosed snake	2.024	M
<i>Acanthophis antarcticus</i>	Common death adder	2.013	M
<i>Pseudonaja affinis</i>	Dugite	2.013	L
<i>Demansia calodera</i>	Black-necked whipsnake	2.005	L
<i>Vermicella intermedia</i>	Wide-banded northern bandy-bandy	2.003	L
<i>Furina diadema</i>	Red-naped snake	1.991	L
<i>Cacophis squamulosus</i>	Golden-crowned snake	1.971	L
<i>Elapognathus minor</i>	Short-nosed snake	1.970	L
<i>Brachyuropis australis</i>	Australian coral snake	1.928	L
<i>Pseudonaja textilis</i>	Eastern brown snake	1.866	L
<i>Demansia rufescens</i>	Rufous whipsnake	1.856	L
<i>Neelaps bimaculatus</i>	Black-naped snake	1.854	L
<i>Furina ornata</i>	Orange-naped snake	1.789	L
<i>Tropidechis carinatus</i>	Rough-scaled snake	1.787	L
<i>Acanthophis wellsi</i>	Pilbara death adder	1.762	L
<i>Parasuta gouldii</i>	Gould's hooded snake	1.749	L
<i>Demansia simplex</i>	Grey whipsnake	1.733	L
<i>Demansia olivacea</i>	Olive whipsnake	1.727	L
<i>Demansia papuensis</i>	Greater black whipsnake	1.690	L
<i>Pseudonaja modesta</i>	Ringed brown snake	1.660	L
<i>Suta punctata</i>	Little spotted snake	1.619	L
<i>Cryptophis pallidiceps</i>	Northern small-eyed snake	1.607	L
<i>Vermicella snelli</i>	Pilbara bandy-bandy	1.600	L
<i>Acanthophis praelongus</i>	Northern death adder	1.508	L
<i>Pseudonaja nuchalis</i>	Western brown snake	1.477	L
<i>Pseudechis australis</i>	King brown snake	1.477	L
<i>Pseudechis guttatus</i>	Spotted black snake	1.477	L
<i>Demansia vestigiata</i>	Lesser black whipsnake	1.406	L
<i>Demansia psammophis</i>	Yellow-faced whipsnake	1.361	L

H high, *M* moderate, *L* low vulnerability

scores varied widely among species, even those with similar distributions that will be exposed to comparable levels of environmental change. Many elapids were projected to lose climatically suitable area by 2050, and some species, including the Master's snake

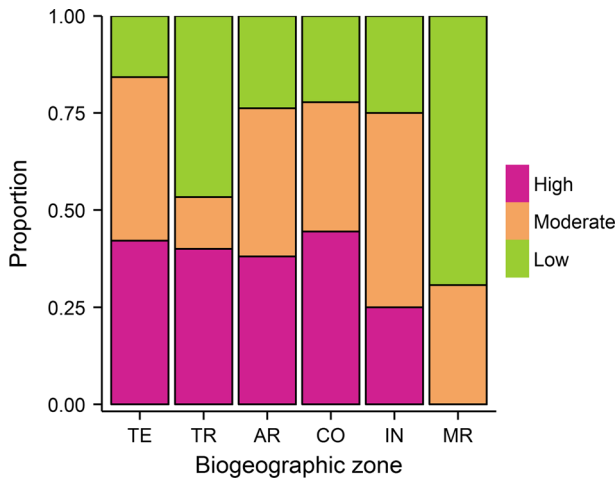


Fig. 1 The proportion of species assigned to each vulnerability group among biogeographic zones. *TR* tropical (15 species), *TE* temperate (19 species), *AR* arid (21 species), *CO* east coast (9 species), *IN* eastern interior (4 species) and *MR* multiregional (13 species)

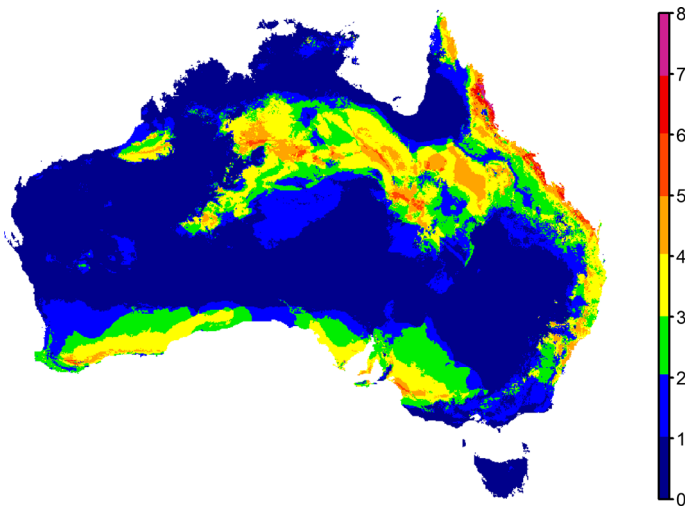


Fig. 2 Climatic suitability map highlighting areas of high climatic suitability for the species assigned to the high vulnerability group

(*Drysdalia mastersii*) and the collared whipsnake (*Demansia torquata*), also possess traits, such as high habitat and dietary specialisation, that are likely to limit their ability to reach and establish populations in new locations, or persist in areas of their current range that become climatically unsuitable. These species may be particularly susceptible to climate change and warrant targeted monitoring.

There were no multiregional species assigned to the high vulnerability group, probably a consequence of their generally wide climatic niches and generalist habits. Conversely,

east coast and temperate regions had the highest proportions of species assigned to the high vulnerability group. Levels of warming and drying are predicted to be greatest at higher latitudes in Australia (Whetton 2011), and there are limited opportunities for southerly expansions of species climatic ranges in temperate regions. Many coastal species were also projected to experience large reductions in the size of their climatic ranges, which tended to contract eastwards rather than shift polewards (Online Resource 2). Scores for the variable ‘habitat specialisation’ were particularly high among coastal and temperate species, and a relatively large proportion of temperate species are also currently listed as threatened. Interestingly, we did not find that tropical species were more vulnerable than those from other regions, contrasting with previous work which suggests that tropical ectotherms may be particularly sensitive to rising ambient temperatures because they are adapted to narrow temperature ranges, and warming has the potential to raise body temperatures beyond optimal levels, reducing species fitness and survival (Deutsch et al. 2008; Tewksbury et al. 2008). Tropical regions are expected to experience the greatest increase in the number of days with a daily maximum temperature of at least 35 °C (Whetton 2011), and on these days, the ability of species to attain their preferred body temperatures, which range between 30 and 35 °C for many elapids (Shine 1979; Lillywhite 1980), may be limited. Our inability to incorporate physiological traits in the framework due to a lack of data may explain, at least in part, why tropical species were not assessed as being more vulnerable to climate change than species from other regions.

The importance of incorporating species traits in vulnerability assessments

Assessments of climate change vulnerability frequently use the projections of SDMs as the sole means of evaluation. In this study, we have extended these methods by incorporating information on species ecological and life-history traits. Traits can provide useful, additional information about species vulnerability and can thereby influence the ways in which conservation resources are allocated. A consideration of species traits can also help identify knowledge gaps. Many traits that are considered important determinants of species vulnerability to climate change, but for which few data were available, were excluded from this assessment. For example, we excluded dispersal ability because this information is lacking for most elapids. Some species appear to have fairly high vagility: radiotracking of red-bellied black snakes (*Pseudechis porphyriacus*) has shown that individuals can move several hundred metres in only a few days (Shine 1979). While these movements easily exceed the rate at which temperatures are expected to change over this century (Loarie et al. 2009), the extent of elapid movements can be highly seasonal, extremely low in gravid females, and can drop substantially during periods of drought (Shine 1979). As droughts are predicted to increase in frequency and severity over much of Australia (Hennessy et al. 2008), the ability of at least some species to move to new locations may be reduced. Dispersal ability, like many other characteristics, represents an important gap in our understanding of the ecology of this group. Addressing these knowledge gaps will help build more refined assessments of the vulnerability of elapids to climate change.

Assessments that incorporate multiple variables can also help managers understand the reasons why some species are likely to be particularly vulnerable, and guide decisions regarding the most suitable adaptation strategies (Heller and Zavaleta 2009). For example, species with low levels of overlap between their current and 2050 climatic ranges might benefit most from strategies to increase connectivity between suitable habitats to facilitate dispersal. If a species is also a habitat specialist with limited capacity to disperse along corridors, it may ultimately become a candidate for assisted colonisation (Hoegh-Guldberg

et al. 2008; Thomas 2011). The information provided from multiple variables can thus aid decision making, increasing the likelihood that conservation efforts will be effective.

Applying the framework

The point-scoring system developed in this study provides a simple method for assessing climate change vulnerability, and similar approaches have been developed for other taxa (Heikkinen et al. 2010; Gardali et al. 2012). It is sufficiently flexible to allow it to be adapted for a wide range of taxonomic groups across multiple temporal and spatial scales. Its transparency makes it amenable to be continually updated as further trait data and occurrence records are collected, and better species distribution modelling techniques are developed. Many of the variables included in the framework are general enough to be relevant to other stressors, such as habitat fragmentation and invasive species, which compound the threat posed by climate change. These additional stressors have also been incorporated, at least to some extent, by explicitly considering species threatened status. Nevertheless, in some instances it may be necessary to specifically consider climate change vulnerability alongside vulnerability to other threats. For example, the northern death adder (*Acanthophis praelongus*) was assigned to the low vulnerability group, but is currently under significant threat from the invasive cane toad in northern Australia (Phillips et al. 2010). Integrating the assessments of multiple taxa, and across multiple stressors, will help identify regions critical to the persistence of vulnerable species.

Acknowledgments We thank the Australian Museum, the Western Australian Museum, the Tasmanian Museum and Art Gallery, the NSW Parks and Wildlife Service and the Australian National Wildlife Collection for access to their reptile locality records. Thanks to P. Wilson, L. Beaumont, D. Duursma and M. Steel for help with the species distribution modelling. We are indebted to R. Shine, J. Webb, M. Bull, E. Wapstra, M. Thomson, H. Heatwole and N. Mitchell for their participation in the Delphi process, to H. Cogger for his encouragement and advice and to M. Burgman and two anonymous referees for their comments on earlier drafts of this manuscript. This research was funded by a Macquarie University Research Excellence Scholarship to AC.

References

- Araújo MB, Thuiller W, Pearson RG (2006) Climate warming and the decline of amphibians and reptiles in Europe. *J Biogeogr* 33(10):1712–1728
- Attorre F, Alfò M, De Sanctis M, Francesconi F, Valenti R, Vitale M, Bruno F (2011) Evaluating the effects of climate change on tree species abundance and distribution in the Italian peninsula. *Appl Veg Sci* 14(2):242–255
- Aubret F, Shine R (2010) Thermal plasticity in young snakes: how will climate change affect the thermoregulatory tactics of ectotherms? *J Exp Biol* 213(2):242–248
- Beaumont LJ, Hughes L (2002) Potential changes in the distributions of latitudinally restricted Australian butterfly species in response to climate change. *Glob Change Biol* 8(10):954–971
- Berry PM, Dawson TP, Harrison PA, Pearson RG (2002) Modelling potential impacts of climate change on the bioclimatic envelope of species in Britain and Ireland. *Glob Ecol Biogeogr* 11(6):453–462
- Braganza K, Church JA (2011) Observations of global and Australian climate. In: Cleugh H, Smith MS, Battaglia M, Graham P (eds) *Climate change: science and solutions for Australia*. CSIRO Publishing, Collingwood, pp 1–14
- Buckley LB, Urban MC, Angilletta MJ, Crozier LG, Rissler LJ, Sears MW (2010) Can mechanism inform species' distribution models? *Ecol Lett* 13(8):1041–1054
- Bull CM, Burzacott D (2002) Changes in climate and in the timing of pairing of the Australian lizard, *Tiliqua rugosa*: a 15-year study. *J Zool* 256(03):383–387

- Busby JR (1991) BIOCLIM - a bioclimate analysis and prediction system. In: Margules CR, Austin MP (eds) Nature conservation: cost effective biological surveys and data analysis. CSIRO, Canberra, pp 64–68
- Carvalho SB, Brito JC, Crespo EJ, Possingham HP (2010) From climate change predictions to actions – conserving vulnerable animal groups in hotspots at a regional scale. *Glob Change Biol* 16(12):3257–3270
- Chambers L, Beaumont L, Hudson I (2013) Continental scale analysis of bird migration timing: influences of climate and life history traits—a generalized mixture model clustering and discriminant approach. *Int J Biometeorol*:1–16. doi: [10.1007/s00484-00013-00707-00482](https://doi.org/10.1007/s00484-00013-00707-00482)
- Cogger HG, Heatwole H (1981) The Australian reptiles: origins, biogeography, distribution patterns and island evolution. In: Keast A (ed) Ecological biogeography of Australia, vol 2. Dr. W. Junk bv Publishers, The Hague, pp 1331–1371
- Commonwealth Scientific and Industrial Research Organisation (CSIRO), the Australian Bureau of Meteorology (BOM) (2007) Climate change in Australia - technical report 2007. CSIRO, Aspendale. Available online at: http://www.climatechangeinaustralia.gov.au/technical_report.php. Accessed 25 June 2012
- Commonwealth Scientific and Industrial Research Organisation (CSIRO), the Australian Bureau of Meteorology (BOM) (2012) The State of the Climate 2012. CSIRO, Aspendale. Available online at: <http://www.csiro.au/Outcomes/Climate/Understanding/State-of-the-Climate-2012.aspx>. Accessed 25 June 2012
- Deutsch CA, Tewksbury JJ, Huey RB, Sheldon KS, Ghalambor CK, Haak DC, Martin PR (2008) Impacts of climate warming on terrestrial ectotherms across latitude. *Proc Natl Acad Sci USA* 105(18):6668–6672
- Elith J, Graham CH, Anderson RP, Dudík M, Ferrier S, Guisan A, Hijmans RJ, Huettmann F, Leathwick JR, Lehmann A, Li J, Lohmann LG, Loiselle BA, Manion G, Moritz C, Nakamura M, Nakazawa Y, Overton JMM, Peterson AT, Phillips SJ, Richardson K, Scachetti-Pereira R, Schapire RE, Soberón J, Williams S, Wisz MS, Zimmermann NE (2006) Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29(2):129–151
- Fitzpatrick MC, Gove AD, Sanders NJ, Dunn RR (2008) Climate change, plant migration, and range collapse in a global biodiversity hotspot: the *Banksia* (Proteaceae) of Western Australia. *Glob Change Biol* 14(6):1337–1352
- Franklin J (2009) Mapping species distributions: spatial inference and prediction. Cambridge University Press, Cambridge
- Gardali T, Seavy NE, DiGaudio RT, Comrack LA (2012) A climate change vulnerability assessment of California's at-risk birds. *PLoS ONE* 7(3):e29507
- Guisan A, Zimmermann NE (2000) Predictive habitat distribution models in ecology. *Ecol Model* 135:147–186
- Heikkinen RK, Luoto M, Araújo MB, Virkkala R, Thuiller W, Sykes MT (2006) Methods and uncertainties in bioclimatic envelope modelling under climate change. *Prog Phys Geogr* 30(6):751–777
- Heikkinen RK, Luoto M, Leikola N, Pöyry J, Settele J, Kudrna O, Marmion M, Fronzek S, Thuiller W (2010) Assessing the vulnerability of European butterflies to climate change using multiple criteria. *Biodivers Conserv* 19(3):695–723
- Heller NE, Zavaleta ES (2009) Biodiversity management in the face of climate change: a review of 22 years of recommendations. *Biol Conserv* 142(1):14–32
- Hennessy K, Fawcett R, Kirono D, Mpelasoka F, Jones D, Bathols J, Whetton P, Smith MS, Howden M, Mitchell C, Plummer N (2008) An assessment of the impact of climate change on the nature and frequency of exceptional climate events. CSIRO, Bureau of Meteorology
- Hoegh-Guldberg O, Hughes L, McIntyre S, Lindenmayer DB, Parmesan C, Possingham HP, Thomas CD (2008) Assisted colonization and rapid climate change. *Science* 321(5887):345–346
- Hsu C-C, Sandford BA (2007) The Delphi technique: making sense of consensus. *Pract Assess Res Eval* 12(10):1–8
- Kearney M, Porter W (2009) Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. *Ecol Lett* 12(4):334–350
- Lillywhite HB (1980) Behavioral thermoregulation in Australian elapid snakes. *Copeia* 1980(3):452–458
- Loarie SR, Duffy PB, Hamilton H, Asner GP, Field CB, Ackerly DD (2009) The velocity of climate change. *Nature* 462(7276):1052–1055
- Mateo RG, Croat TB, Felicísimo ÁM, Muñoz J (2010) Profile or group discriminative techniques? Generating reliable species distribution models using pseudo-absences and target-group absences from natural history collections. *Divers Distrib* 16:84–94
- Nakicenovic N, Swart RJ (2000) Emission scenarios 2000 - special report of the intergovernmental panel on climate change. Cambridge University Press, Cambridge

- Nix H (1989) A biogeographic analysis of Australian elapid snakes. In: Longmore R (ed) Atlas of elapid snakes of Australia. Australian Government Publishing Service, Bureau of Flora and Fauna, Canberra
- Penman TD, Pike DA, Webb JK, Shine R (2010) Predicting the impact of climate change on Australia's most endangered snake, *Hoplocephalus bungaroides*. *Divers Distrib* 16(1):109–118
- Phillips SJ, Dudik M (2008) Modeling of species distributions with maxent: new extensions and a comprehensive evaluation. *Ecography* 31:161–175
- Phillips SJ, Anderson RP, Schapire RE (2006) Maximum entropy modeling of species geographic distributions. *Ecol Model* 190(3–4):231–259
- Phillips SJ, Dudik M, Elith J, Graham CH, Lehmann A, Leathwick J, Ferrier S (2009) Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. *Ecol Appl* 19(1):181–197
- Phillips BL, Greenlees MJ, Brown GP, Shine R (2010) Predator behaviour and morphology mediates the impact of an invasive species: cane toads and death adders in Australia. *Anim Conserv* 13(1):53–59
- Raupach MR, Marland G, Ciais P, Le Quere C, Canadell JG, Klepper G, Field CB (2007) Global and regional drivers of accelerating CO₂ emissions. *Proc Natl Acad Sci USA* 104(24):10288–10293
- Reside AE, VanDerWal J, Kutt AS (2012) Projected changes in distributions of Australian tropical savanna birds under climate change using three dispersal scenarios. *Ecol Evol* 2(4):705–718
- Shine R (1979) Activity patterns in Australian elapid snakes (Squamata: Serpentes: Elapidae). *Herpetologica* 35(1):1–11
- Shine R (1980) Ecology of the Australian death adder *Acanthophis antarcticus* (Elapidae): evidence for convergence with the Viperidae. *Herpetologica* 36(4):281–289
- Shine R (1989) Constraints, allometry, and adaptation: food habits and reproductive biology of Australian brownsnakes (Pseudonaja: Elapidae). *Herpetologica* 45(2):195–207
- Shine R (1994) Allometric patterns in the ecology of Australian snakes. *Copeia* 1994(4):851–867
- Simpson EH (1949) Measurement of diversity. *Nature* 163:688
- Sinclair SJ, White MD, Newell GR (2010) How useful are species distribution models for managing biodiversity under future climates? *Ecol Soc* 15(1):8
- Steffen W, Burbidge AA, Hughes L, Kitching R, Lindenmayer D, Musgrave W, Stafford Smith M, Werner PA (2009) Australia's biodiversity and climate change: a strategic assessment of the vulnerability of Australia's biodiversity to climate change. A report to the Natural Resource Management Ministerial Council Commissioned by the Australian Government. CSIRO Publishing, Collingwood
- Telemeco RS, Elphick MJ, Shine R (2009) Nesting lizards (*Bassiana duperreyi*) compensate partly, but not completely, for climate change. *Ecology* 90(1):17–22
- Tewksbury JJ, Huey RB, Deutsch CA (2008) Putting the heat on tropical animals. *Science* 320:1296–1297
- Thomas CD (2011) Translocation of species, climate change, and the end of trying to recreate past ecological communities. *Trends Ecol Evol* 26(5):216–221
- Thuiller W (2003) BIOMOD - optimizing predictions of species distributions and projecting potential future shifts under global changes. *Glob Change Biol* 9:1353–1362
- Thuiller W, Lavorel S, Araújo MB (2005) Niche properties and geographical extent as predictors of species sensitivity to climate change. *Glob Ecol Biogeogr* 14(4):347–357
- Umina PA, Weeks AR, Kearney MR, McKechnie SW, Hoffmann AA (2005) A rapid shift in a classic clinal pattern in *Drosophila* reflecting climate change. *Science* 308(5722):691–693
- VanDerWal J, Shoo LP, Graham C, Williams SE (2009) Selecting pseudo-absence data for presence-only distribution modeling: How far should you stray from what you know? *Ecol Model* 220(4):589–594
- Whetton P (2011) Future Australian climate scenarios. In: Cleugh H, Smith MS, Battaglia M, Graham P (eds) Climate change: science and solutions for Australia. CSIRO Publishing, Collingwood, pp 35–44
- Williams SE, Bolitho EE, Fox S (2003) Climate change in Australian tropical rainforests: an impending environmental catastrophe. *Proc R Soc B Biol Sci* 270(1527):1887–1892
- 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(12):2621–2626
- Wilson S, Swan G (2008) A complete guide to reptiles of Australia. 2nd edn. New Holland Publishers (Australia) Pty Ltd, Sydney
- Wisz MS, Hijmans RJ, Li J, Peterson AT, Graham CH, Guisan A (2008) Effects of sample size on the performance of species distribution models. *Divers Distrib* 14(5):763–773