

The impacts of climate change on Australian reptiles

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For Simon

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SUMMARY

Climate change is anticipated to develop into one of the most significant threats to biodiversity this century. Reptiles are expected to be particularly vulnerable, yet they have received less attention in the climate change literature than some other taxonomic groups. In this thesis, I addressed this knowledge gap by investigating the impacts of climate change on the reptiles of Australia. In the first part of this thesis, I reviewed the published literature to assess why reptiles may be particularly vulnerable to climate change, and whether they have already started to respond in Australia. In the second part, I developed novel frameworks for evaluating the climate change vulnerability of three groups of reptiles – the elapid snakes, the skinks and the freshwater turtles – which integrated the output of environmental niche models and species ecological traits. In the final part, I performed a conservation planning exercise to identify areas within Australia that are important for reptile conservation, and remain important under future climate change. The results of this work were used to determine the species likely to be most vulnerable to climate change, and identify areas that may be particularly valuable additions to the existing National Reserve System.

STATEMENT OF CANDIDATE

I certify that the work in this thesis entitled ‘The Impacts of Climate Change on Australian Reptiles’ has not previously been submitted for a degree, nor has it been submitted as part of the requirements for a degree, to any other university or institution other than Macquarie University. This thesis is an original piece of work, and any help and assistance that I have received in my research, and in the preparation of the thesis itself, have been appropriately acknowledged. I estimate my specific contributions to each thesis chapter has been:

- Chapter 1** Writing (95%)
- Chapter 2** Sourcing literature (100%), writing (90%)
- Chapter 3** Sourcing literature (100%), writing (90%)
- Chapter 4** Study design (50%), data collection (100%), modelling (100%), data analysis (100%), writing (90%)
- Chapter 5** Study design (50%), data collection (100%), modelling (100%), data analysis (100%), writing (90%)
- Chapter 6** Study design (80%), data collection (100%), modelling (100%), data analysis (100%), writing (90%)
- Chapter 7** Study design (95%), data collection (100%), modelling (100%), data analysis (100%), writing (90%)
- Chapter 8** Writing (95%)

The research presented in this thesis was approved by the Macquarie University Ethics Review Committee (reference number: 5201001302) on the 2nd November 2010.

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CHAPTER 1

Introduction

BACKGROUND

Australia is a remarkable place in terms of its biodiversity. Between 7 and 10% of all described species occur here, making Australia one of the 17 mega-diverse countries that collectively hold about 70% of the world's flora and fauna (Mittermeier *et al.* 2005). Its marine ecosystems support one of the most diverse fish faunas in the world, with almost 5000 described species (Chapman 2009). More than two-thirds of the world's marsupial species are found in Australia, filling an extraordinary range of ecological niches that in other countries are occupied by placental mammals (Archer 1981). There are more than twice as many species of reptiles in Australia as there are in the United States, and its deserts in particular support more lizard species than any other comparable environment (Cogger and Heatwole 1981; James and Shine 2000; Steffen *et al.* 2009). Even more extraordinary is the unusually large proportion of species that occur nowhere else – approximately 92% of its vascular plants, 87% of its mammals, 93% of its reptiles and 94% of its frogs are endemic to the continent – reflecting Australia's long history of geographic isolation from the rest of the world (Keast 1981; Chapman 2009).

Australia's extinction record is also unprecedented. In the 200 years since European settlement, Australia has witnessed the largest documented decline in biodiversity of any continent. Forty-two species of plants and 55 species of animals, including 27 mammals, 23 birds, four frogs and one invertebrate, have been listed as extinct under the Environment Protection and Biodiversity Conservation (EPBC) Act. Almost half of all global mammal extinctions in the last 200 years have occurred in Australia (Johnson 2006). Today, approximately 13% of all Australia's vertebrate species are listed as vulnerable under the EPBC Act, and a further 32% are in some form of serious decline in one or more parts of

their range (Mackey *et al.* 2008). Habitat degradation and fragmentation, inappropriate fire regimes, soil enrichment, feral predators, hunting and invasive plants have been collectively responsible for most of these declines (Evans *et al.* 2011). Over recent years, anthropogenic climate change has emerged as an additional threat, and is now expected to become one of the primary drivers of biodiversity loss in the 21st century and beyond (Steffen *et al.* 2009).

Despite the relatively modest climatic changes that have occurred to date, documented evidence of its impacts on species is already mounting, both in Australia and elsewhere (Hughes 2003; Rosenzweig *et al.* 2008; Steffen *et al.* 2009; Chen *et al.* 2011). Species have shifted their distributions, changed the timing of their life cycle events, altered their behaviours and undergone genetic changes (Parmesan 2006), although the magnitude and direction of these responses often vary markedly among species (Chen *et al.* 2011). These impacts are expected to increase over the coming decades as the pace of climate change accelerates (Thomas *et al.* 2004; Thuiller *et al.* 2005; Carpenter *et al.* 2008; Maclean and Wilson 2011).

In this thesis, I investigate the potential impacts of climate change on one particularly diverse group of Australian animals, the reptiles (Class Reptilia). Specifically, I address the following three questions:

1. What evidence is there that reptiles will be particularly vulnerable to climate change, and are species already starting to respond in Australia?
2. Which species are likely to be most vulnerable in the future?

3. What can be done, from a conservation planning perspective, to protect Australia's reptiles under future climate change?

These three questions give rise to the three main parts of this thesis.

STRUCTURE OF THESIS

What evidence is there that reptiles will be particularly vulnerable to climate change, and are species already starting to respond in Australia?

Reptiles are expected to be particularly susceptible to the impacts of climate change primarily because, as ectotherms, many aspects of their biology are sensitive to environmental temperature. In Chapter 2, I conduct a literature review to investigate this expectation, making particular reference to the impacts of changes in air temperature, rainfall, water temperature and sea level. In Chapter 3, I focus on Australian reptiles and explore the scientific literature for evidence that species are already responding to climate change, and for predictions of how they may continue to respond in the future. These reviews highlight several knowledge gaps and promising areas for future research.

Which species are likely to be most vulnerable in the future?

Correlative environmental niche models (ENMs) have become popular tools for forecasting the potential impacts of future climate change on species distributions. These

models generate projections of future range shifts by correlating records of a species' occurrences with a set of environmental variables under a range of climate change scenarios (Guisan and Zimmermann 2000; Franklin 2009). The advantages of ENMs stem from their relatively low data requirements and ease of use, which permit the rapid assessment of large numbers of species. As a consequence, ENMs have been used to assess species vulnerability to climate change across numerous taxonomic groups, and in many regions of the world (e.g. Araújo *et al.* 2006; McKenney *et al.* 2007; Bond *et al.* 2011; Maiorano *et al.* 2011).

ENMs model changes in habitat (or climate) suitability, rather than the realised distributions of species *per se*. Because a decline in the suitability of a species' habitat does not necessarily imply a decline in the population size of the species, assessments of climate change vulnerability based solely on model projections have the potential to be misleading. Whether the population size of a species does decline under climate change will be contingent not only on how the suitability of its habitat changes, but also to what extent it is able to buffer these changes, which in turn will be influenced by its ecological and life history traits.

To assess the vulnerability of Australia's reptiles to future climate change, I use ENMs to model changes in habitat suitability for over 400 species, representing the first large-scale assessment of this taxonomic group in Australia. I design three novel assessment frameworks for quantifying species vulnerability to climate change that integrate the model projections with information on species traits. I apply these frameworks to three groups of Australian reptiles, the terrestrial elapid snakes (Chapter 4), the skinks (Chapter 5) and the freshwater turtles (Chapter 6), to identify which species may be particularly vulnerable to

climate change in the future, and explore geographical and phylogenetic patterns in vulnerability across each group. This work represents one of the few attempts to combine these two sets of information to assess the vulnerability of Australia's biodiversity to climate change.

What can be done, from a conservation planning perspective, to protect Australia's reptiles under future climate change?

In Chapter 7 I couple model projections of all three groups with a conservation planning tool to identify important areas for reptile conservation that remain important under climate change. In my final discussion chapter (Chapter 8), I review the principal findings of the preceding chapters, identify future research directions and discuss other conservation actions that may be valuable additions to a strategy aimed at protecting Australia's reptiles under climate change.

FORMAT OF THESIS

Chapters 2-7 of this thesis are written as standalone papers in order to comply with a 'thesis by publication' format. As a consequence, there is some inevitable repetition between them, particularly among the introductions and methods sections. All chapters use plural pronouns in preparation for their publication as multi-authored papers. My contribution to each chapter is explicitly outlined in the Statement of Candidate on page iii.

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CHAPTER 2

The vulnerability of reptiles to climate change

ABSTRACT

Many aspects of reptilian biology are closely tied to climate, suggesting that this group might be particularly susceptible to the impacts of climate change. Until recently, however, reptiles have been poorly represented in the climate change literature. In this paper, we review the vulnerability of the world's reptiles to the impacts of climate change, with particular reference to changes in air temperature, rainfall, water temperature and sea level. We find that increasing empirical and theoretical evidence confirms reptiles are already responding to recent changes in climate, and that range contractions and population extinctions are likely in the near future. We identify three areas for further research, including better understanding the traits quantifying species thermal tolerance limits, investigating how different environmental factors are likely to interact, and assessing the capacity of species to buffer the impacts of climate change *in situ*. A greater understanding of these factors will help inform management practices aimed at protecting reptiles under future climate change.

Keywords: extinction risk, range shifts, reproductive output, rising temperatures, sea level rise, TSD, vulnerability

INTRODUCTION

The class Reptilia comprises over 9000 species, including 322 species of turtles and tortoises (order Testudines), 23 species of crocodiles and alligators (order Crocodylia), over 8000 species of snakes and lizards (order Squamata) and one species of tuatara (order Rhynchocephalia). They are found in every continent with the exception of Antarctica, although diversity tends to be greatest in tropical and subtropical regions (Fig. 1). A number of threats, including habitat destruction, invasive species, pollution, disease and overexploitation have already resulted in the listing of approximately 22% of reptile species as threatened with extinction, many of which occur in those regions where reptile diversity is greatest (Fig. 2) (Gibbons *et al.* 2000; IUCN 2009).

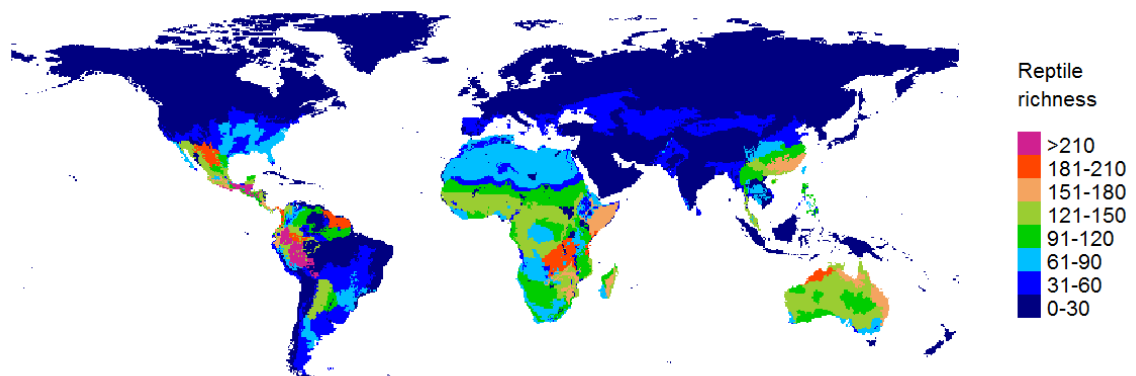


Figure 1. Reptile species richness among the world's ecoregions. Data sourced from World Wildlife Fund. WildFinder: Online database of species distributions, ver. 01.06 gis.wwfus.org/wildfinder.

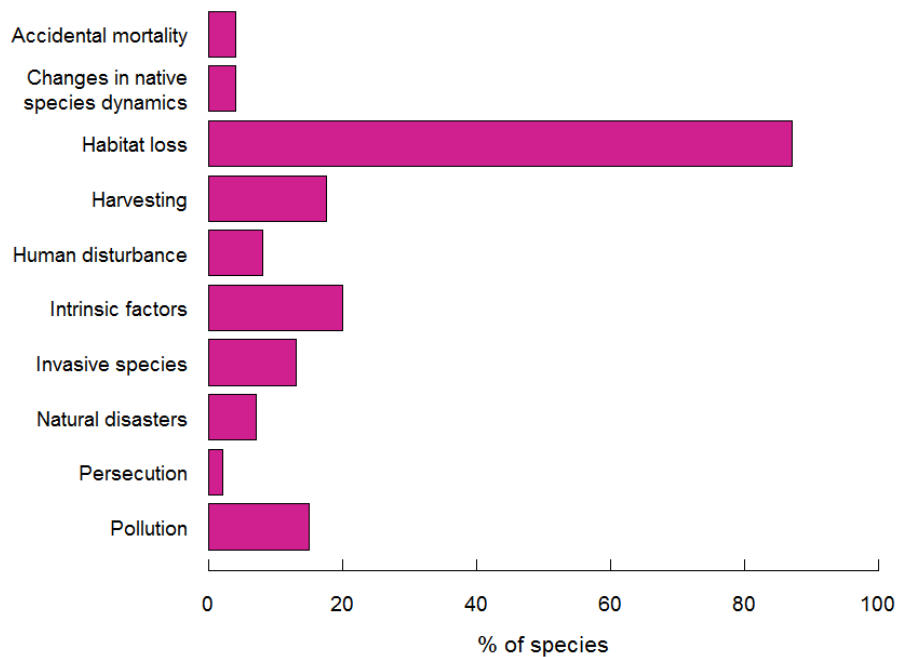


Figure 2. The major threats to the world's reptiles. Adapted with permission from IUCN (2009) *Wildlife in a changing world: an analysis of the 2008 IUCN red list of threatened species*. IUCN, Gland, Switzerland.

Anthropogenic climate change now presents the world's reptiles with an additional challenge. Over the past five decades, air temperatures have risen by an average of 0.46°C across the globe, accompanied by changes in rainfall patterns, water temperatures, sea level and the frequency and intensity of extreme weather events (WMO 2012). Although to date the magnitude of these trends has been relatively modest, there is now mounting evidence that they have already had, and are continuing to have, discernible impacts on the world's biodiversity (Parmesan and Yohe 2003; Root *et al.* 2003; Parmesan 2006; Rosenzweig *et al.* 2008; Chen *et al.* 2011; Maclean and Wilson 2011). Until recently, however, the impacts of climate change on reptiles have received relatively little attention (but see Janzen 1994a). Few long-term datasets suitable for identifying climate change-

related trends exist for reptiles, and as a consequence, only three species were included in a global analysis of phenological and distributional changes of more than 1700 species to climate change (Parmesan and Yohe 2003). Another meta-analysis of 78 studies across multiple physical and biological systems did not include any studies on reptiles (Rosenzweig *et al.* 2008).

This poor representation of reptiles in the climate change literature is concerning. Although reptiles have survived extreme climatic trends in the past, average global temperatures could reach 4°C above pre-industrial levels by the 2060s (Betts *et al.* 2011), a rate that would far exceed prehistoric climatic changes of similar magnitude. In addition, landscape transformation by humans has created dispersal barriers of agricultural and urban land, which will prevent most species from shifting their distributions as they have in the past (Peters and Darling 1985). The increasing fragmentation of populations has also led to the loss of genetic variation (Delaney *et al.* 2010), and coupled with the long generation lengths of many reptiles, is expected to limit the potential of many species to adapt genetically to rising temperatures. Climate change therefore presents a novel and potentially substantial threat to this taxonomic group, and further research on its impacts is needed if species extinctions are to be prevented (Janzen 1994a; McCallum *et al.* 2009).

Here, we review the published literature on the vulnerability of the world's reptiles to climate change, with specific reference to changes in air temperatures, rainfall patterns, water temperatures and sea levels. Finally, we highlight research directions that warrant further attention if we are to obtain a more thorough understanding of the potential impacts of climate change on this taxonomic group.

RISING AIR TEMPERATURES

Temperature is arguably the most important physical factor in the ecology of reptiles because unlike mammals or birds that maintain body temperatures via their own metabolic processes, reptiles rely on their external environment as a thermal source (Heatwole and Taylor 1987). Despite fluctuating environmental conditions, most reptiles are able to control their body temperatures precisely by employing a number of behavioural strategies, and may therefore have the capacity to buffer moderate levels of warming very effectively, provided the thermal environment is relatively heterogeneous (Kearney *et al.* 2009; Huey *et al.* 2012). However, future climate change is expected to push environmental conditions beyond the range to which many species have become adapted (Davis and Shaw 2001; Calosi *et al.* 2008). This is most likely to occur in tropical environments where species already live close to their physiological optimum (Deutsch *et al.* 2008; Tewksbury *et al.* 2008). Indeed, biophysical models have shown that ectotherms at tropical sites could exceed stressfully high temperatures 63% of the time following a 3°C rise in temperature (Kearney *et al.* 2009). In Puerto Rico, for example, a 3°C rise in air temperature would result in daytime summer temperatures just $3.5 \pm 0.9^{\circ}\text{C}$ below the thermal maximum of several *Sphaerodactylus* geckos (Huey *et al.* 2009). With body temperatures higher than optimum, physiological stress, reduced performance and increased disease susceptibility may ensue, ultimately leading to population declines and extirpation.

Although thermal refugia may provide tropical reptiles with some capacity to buffer small increases in ambient temperature, retreating to thermal refuges will limit the time available for foraging. This is particularly problematic given the direct influence of warming on metabolic functions. Bickford *et al.* (2010) predicted that the metabolic rates of ectotherms

could increase by 10-75% following a 1.1-6.4°C rise in temperatures. A rise in metabolic rates, compounded by reduced foraging time, is likely to compromise energy budgets, thereby undermining population growth rates and raising extinction risk. Indeed, ecophysiological models have predicted that activity restrictions could drive almost 40% of all global lizard populations, and 20% of all lizard species, extinct by 2080 (Sinervo *et al.* 2010). These processes already appear to have resulted in the local extinctions of *Sceloporus* lizards in Mexico (Sinervo *et al.* 2010).

In contrast to species from tropical regions, temperate reptiles generally inhabit environments that are on average cooler than optimal (Deutsch *et al.* 2008). These species may therefore benefit from rising temperatures which have the potential to open up new areas suitable for colonisation, leading to range expansions and an increase in population carrying capacity (Araújo *et al.* 2006). Increased thermoregulatory opportunities may also shorten the time spent basking, reducing the length of time the animal is most exposed to predators and allowing more time for foraging. In turn, these effects may improve survival rates and provide a greater opportunity to grow and reproduce, with concomitant impacts on population persistence.

Evidence from temperate regions suggests that some species are already starting to benefit from recent increases in ambient temperatures. In France, positive correlations have been found between rising summer temperatures and the body sizes, clutch sizes and total reproductive effort of common lizards (*Lacerta vivipara*), which are thought to be a result of increased food resources and/or a rise in metabolic rates (Chamaille-Jammes *et al.* 2006). A positive relationship between the length of the seasonal activity period of the Mediterranean snake *Malpolon monspessulanus* and annual mean temperature has also

been documented (Moreno-Rueda *et al.* 2009). In North America, higher night-time temperatures have been shown to increase reproductive success, hatchling size and hatchling survival in side-blotched lizards (*Uta stansburiana*) (Clarke and Zani 2012).

However, levels of warming are projected to be greatest at high latitudes, and even temperate reptiles may soon become susceptible to temperature stress. Some temperate species may be able to buffer small temperature changes *in situ* because environmental temperatures are generally more heterogeneous in space and time than in the tropics, providing reptiles with more thermoregulatory options (Huey *et al.* 2009). Large temperature increases, however, may force many species to shift their distributions to cooler climates. In Spain, the northern boundaries of 22 reptile species have already shifted polewards by an average of 15.2 km from 1940-1975 to 1991-2005, equivalent to approximately 0.5 km/year (Moreno-Rueda *et al.* 2012). Although this rate of dispersal is similar to the average shift in terrestrial climate zones predicted for the 21st century (0.42 km/year) (Loarie *et al.* 2009), many reptiles are unlikely to keep pace with the changing climate because habitat fragmentation, mountain ranges and oceans will present insurmountable barriers to species movement. Further, the intrinsic dispersal ability of some reptiles may be directly inhibited by changes in temperature. For example, juvenile dispersal of the common lizard (*Lacerta vivipara*) decreases with higher prenatal temperatures and has declined dramatically over recent years in an area of southern France, paralleling the rise in spring temperatures (Massot *et al.* 2008). Consequently, many species are expected to be at risk of range contractions under future climate change. Environmental niche models (ENMs), which forecast species range shifts under climate change, support these expectations. Assuming no dispersal capacity, ENMs have estimated that 98% of reptiles in Europe may experience range contractions by 2050 (Araújo *et al.*

2006). In the Iberian peninsula, 92% of reptiles and amphibians are projected to lose climatically suitable area by 2080, with 27% of species projected to lose their entire climatic envelope (Carvalho *et al.* 2010). Modelling of range shifts among freshwater turtles have revealed similar findings, with 86% of species projected to experience range contractions by 2080, and nearly 12% losing all climatically suitable area (Ihlow *et al.* 2012).

Distributional shifts along altitudinal gradients may be more feasible for reptiles, because small shifts upslope correspond climatically to much larger shifts across latitudes. Upslope range shifts of several reptile, amphibian and bird communities, associated with a decline in dry-season mist frequency, have already been documented within a mountainous region in Costa Rica (Pounds *et al.* 1999), and similar elevational shifts among reptiles have been recorded in Madagascar (Raxworthy *et al.* 2008). However, upslope migrations place species at risk of range losses and population declines because the area of suitable habitat decreases as they move upwards in elevation (Krajick 2004). Ultimately, reptiles that inhabit montane environments will become locally extinct if rising temperatures cause their habitat to disappear entirely.

Effects of warming during embryonic development

Some of the most significant impacts of climate change on reptiles are expected to derive from the effects of warming during embryonic development. Warmer temperatures and increased basking opportunities influence the timing and duration of incubation/gestation (Wapstra *et al.* 2004; Telemeco *et al.* 2009), as well as several fitness-related traits of

hatchlings including their body size and morphology (Van Damme *et al.* 1992; Elphick and Shine 1998; Booth *et al.* 2004; Deeming 2004; Andrews 2008), locomotor speeds (Elphick and Shine 1998; Shine and Elphick 2001), cognitive ability (Amiel and Shine 2012), and growth (Andrews 2008; Dubey and Shine 2011). The direction of these effects appears to vary between species. For example, improved locomotor performances of the sub-alpine skink *Acritoscincus duperreyi* occur following only a very brief exposure to high temperatures during development (Shine and Elphick 2001), and pine snakes (*Pituophis melanoleucus*) incubated in warmer conditions build more tunnels and are more responsive, potentially making them less vulnerable to predation (Burger 1998). In contrast, the common wall lizard (*Podarcis muralis*), the Mary River turtle (*Elusor macrurus*) and the Green turtle (*Chelonia mydas*) all exhibit slower locomotor speeds following incubation at higher temperatures (Van Damme *et al.* 1992; Booth and Evans 2011; Micheli-Campbell *et al.* 2011).

Offspring gender is also determined by incubation temperature in some reptiles, providing a mechanism through which climate warming could adversely skew offspring sex ratios (Janzen 1994a). Temperature-dependent sex determination (TSD) is present in all four reptile orders, having been observed in all crocodilians, the tuatara, most turtles and some lizards. It occurs in both oviparous and viviparous reptiles, and frequently occurs alongside genotypic sex determination (GSD) within a family (Ciofi and Swingland 1997), and even within a single species (Shine *et al.* 2002; Telemeco *et al.* 2009). Pivotal temperatures are those that produce a 1:1 sex ratio among eggs reared at constant temperature and variations in incubation temperature around this threshold result in skewed sex ratios (Valenzuela 2004). The sex ratios produced at different incubation temperatures define the three main patterns of TSD (Fig. 3).

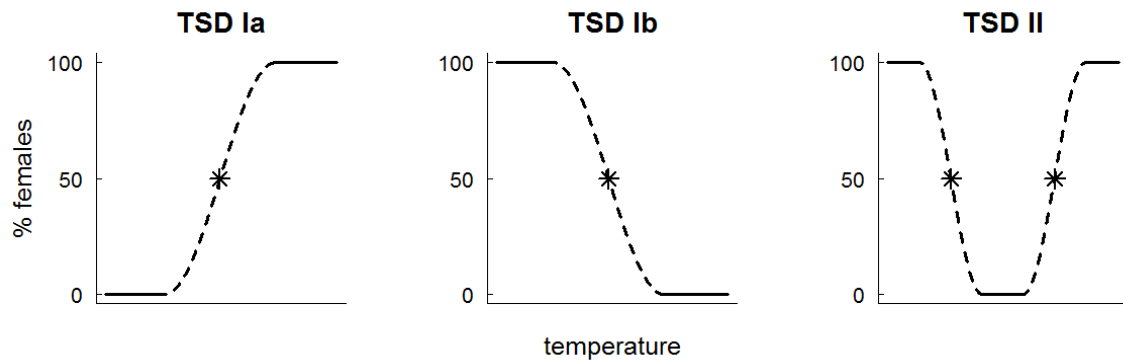


Figure 3. The three patterns of TSD. Species with TSD Ia (male-female, MF) produce males at low temperatures and females at high temperatures, while those with TSD Ib (female-male, FM) produce females at low temperatures and males at high temperatures. Species with TSD II (female-male-female, FMF) produce females at low and high temperatures and males at intermediate temperatures. TSD Ia has been reported for turtles, TSD Ib for tuatara, lizards and crocodilians (but see Mitchell *et al.* 2006) and TSD II for turtles, lizards and crocodilians. Stars represent pivotal temperatures and dotted lines represent the transitional range of temperatures (TRT) (Valenzuela 2004).

The narrower the transitional range of temperatures (TRT) over which sex ratios shift from being 100% male to being 100% female, the greater the probability of unequal sex ratios under future climate warming because a small change in temperature around the pivotal temperature has the potential to lead to dramatic changes in offspring sex ratios. The degree of warming required to produce unisex clutches in many species is well within the climate change projections for the coming decades (Betts *et al.* 2011). For example, populations of Loggerhead turtles (*Caretta caretta*) could become extremely female biased following a warming of only 1°C and experience high rates of mortality if warming were to exceed 3°C (Hawkes *et al.* 2007). Under an extreme climate change scenario, a near complete feminisation of hatchling Green turtles (*Chelonia mydas*) in the northern Great

Barrier Reef could occur by 2070 (Fuentes *et al.* 2010). Similarly, an increase of only 4°C in mean July air temperatures could eliminate the production of male offspring in populations of painted turtles (*Chrysemys picta*) (Janzen 1994a). It should be noted, however, that these estimates are based solely on extrapolation, and do not allow for a phenological shift in nesting dates.

If offspring sex ratios translate into adult sex ratios, the impacts of climate change on offspring gender have the potential to alter population dynamics and adversely affect species persistence due to the reduction in effective population size (Frankham *et al.* 2002). Population viability analyses have shown that the current population of tuatara (*Sphenodon punctatus*) would be expected to persist for at least 2000 years at hatchling sex ratios of up to 75% male, but if this bias increased to 85% male, the population could become extinct within approximately 300 years (Mitchell *et al.* 2010). A lower effective population size, as a consequence of shifting sex ratios, will also lead to higher levels of inbreeding depression and a greater loss of genetic variation (Briton *et al.* 1994), thereby affecting the potential to adapt genetically to climate change.

Not all species will be vulnerable to the negative demographic consequences of sex ratio skewing. If females are produced at higher temperatures, polygamous mating systems and/or an increased frequency of breeding among males compared to females may mean that skewed sex ratios will pose little immediate threat (Wapstra *et al.* 2009; Hays *et al.* 2010; Wright *et al.* 2012). Warming may help equalise sex ratios in populations that nest in high latitude regions where a bias currently exists due to the cooler conditions, potentially leading to an increase in population density (Kallimanis 2010). For others, a number of environmental, behavioural, demographic and genetic factors are expected to provide some

protection against the impacts of climate warming on sex ratios. For example, sand albedo, nest substrate, soil moisture, nest depth, clutch size, vegetation cover and cloud cover have all been shown to influence incubation temperature and may help ensure offspring of both sexes are produced (Janzen 1994b; Hays *et al.* 2003; Morjan 2003b; Doody *et al.* 2006; Patino-Martinez *et al.* 2012). Highly fluctuating temperatures may also help protect species against a skewing of sex ratios (Booth 2006), and changes in nesting phenology may ensure the critical thermosensitive period when sex is determined occurs during cooler parts of the year. Mechanistic modelling of tuatara (*Sphenodon punctatus*), for instance, has shown that all-male clutches could be produced by the mid-2080s under extreme climate change, but that tuatara could behaviourally compensate for these effects by nesting later in the season or by selecting shadier nest sites (Mitchell *et al.* 2008). Viviparous species with TSD, such as the spotted skink (*Niveoscincus ocellatus*), may also have the capacity to buffer some degree of warming by adjusting basking behaviours (Wapstra *et al.* 2004).

Species whose distributions span a broad latitudinal or altitudinal range are expected to be more resilient to shifts in sex ratios than those that nest over much smaller areas. This is because large geographic ranges are more likely to encompass a range of nest sites with varying thermal characteristics, increasing the probability that cooler nests will be available in at least some areas. Some sea turtles, however, demonstrate a strong fidelity to beaches within a small region and are therefore expected to be particularly vulnerable to a skewing of sex ratios if these beaches are climatically very similar (Davenport 1989). These species may become increasingly reliant on the migration of the rarer sex from cooler regions to help supplement heavily biased populations in warmer areas.

Clinal variation in certain behavioural traits, such as female nest site choice, is also likely to increase adaptability as it implies adjustments to such behaviours are possible (Doody 2009). Variation in behaviours is evident among Australian water dragons (*Physignathus lesueurii*), for example, that are able to select remarkably similar thermal characteristics across broad latitudinal and elevational gradients by preferring more shaded nest sites, or by building deeper nests, in warmer areas (Doody *et al.* 2006; Doody 2009). However, examples of temporal modifications in behaviours that have already occurred in response to warming suggest these adjustments may not be sufficient to counter climate change in a number of species (Schwanz and Janzen 2008; Telemeco *et al.* 2009). For example, nest temperatures of the Australian skink *Acrیتoscincus duperreyi* have continued to rise in line with rising air temperatures, despite adjustments in both nest depth and in the timing of oviposition (Telemeco *et al.* 2009). For some species with small geographic ranges, human assistance by artificially harvesting and incubating eggs, providing nest shading and translocating eggs to cooler environments may be necessary to avoid the demographic consequences of skewed sex ratios (Mitchell *et al.* 2010).

Shifts in the pivotal temperature and/or the TRT provide another potential adaptation strategy for species with TSD. The width of the TRT is positively correlated with the proportion of nests producing both sexes, suggesting that populations with wider TRTs will be more likely to evolve in response to new thermal conditions because a higher proportion of mixed nests favours the expression of genetic variation (Hulin *et al.* 2008; Hulin *et al.* 2009). However, such shifts are generally considered unlikely. For many species, pivotal temperatures do not appear to be under strong selection pressure because they tend to be similar among populations (Doody *et al.* 2006; Hawkes *et al.* 2009; but see Ewert *et al.* 1994). Evolutionary responses also require sufficient time for genetic changes

to occur, and as a consequence, the rapid rate of climate change is expected to limit the capacity of many long-lived species, particularly reptiles that have some of the longest generation lengths of any animal, to adapt genetically (Morjan 2003a).

CHANGING RAINFALL PATTERNS

Over the coming century, rainfall patterns across the globe are expected to change, with an increase in very heavy precipitation in wet areas, and increases in drought in dry areas (Allison *et al.* 2009). Terrestrial reptiles may be less sensitive to these climatic changes than some other taxa, such as amphibians, because they possess a number of adaptations that allow them to cope with water scarcity, such as scaled skin, which have allowed them to colonise and even flourish in areas with very little rainfall. Desert species that are already very well adapted to arid conditions may be particularly resilient to increasing rainfall variability, provided that years with good resource availability occur sufficiently frequently to allow them to build up energy reserves and improve body condition.

Other reptile groups may be less resilient to changes in rainfall. The eggs of a number of species, including many lizards, are permeable to water with a thin, flexible shell that lacks a well-defined calcareous layer, and under particularly dry conditions these eggs may desiccate, resulting in reduced hatching success (Belinsky *et al.* 2004). Increasingly dry conditions may also negatively affect activity levels, body condition and growth rates by causing dehydration (Lorenzon *et al.* 1999; Fernández-Chacón *et al.* 2011), and may aggravate the impacts of warming on offspring sex ratios by reducing soil moisture, which in turn may increase nest temperatures further (Houghton *et al.* 2007). An increased

frequency of heavy rainfall events, such as storms and cyclones, may lead to nest flooding, resulting in a rise in embryo mortality rates. In some reptiles, life cycle events such as nesting and hatching are synchronised with rainfall – Loggerhead sea turtles (*Caretta caretta*), the Murray river turtle (*Emydura macquarii*) and the broad-shelled river turtle (*Chelodina expansa*), for example, have all been shown to prefer to nest during or after rainfall (Bowen *et al.* 2005; Pike 2008), while Olive Ridley turtles (*Lepidochelys olivacea*) have been found to postpone nesting during periods of heavy rain (Plotkin *et al.* 1997). The timing of these life cycle events may therefore alter in response to changes in precipitation. Such phenological changes have the potential to alter interactions between hatchlings and their prey and predators, with important consequences for hatchling survival (Stenseth and Mysterud 2002).

The most significant impacts of changing rainfall patterns on many reptiles are expected to be mediated via changes in habitat and prey availability. Rainfall-induced resource shortages have been correlated with alterations in growth rates, condition, activity, reproductive effort and survival, and have been shown to influence population dynamics in a number of reptile species (Dickman *et al.* 1999; Kerr and Bull 2006; Madsen *et al.* 2006; Brown and Shine 2007; Sperry and Weatherhead 2008; Fernández-Chacón *et al.* 2011). Flooding events that occurred in the early 1990s, for example, caused substantial seagrass loss along the east coast of Australia and may have contributed to the poor growth rates of Green turtles (*Chelonia mydas*) in subsequent years (Chaloupka *et al.* 2004). The declines of two species of freshwater turtle in Australia have been primarily attributed to drought-induced losses of critical floodplain habitat (Chessman 2011). In Costa Rica, increasingly wet and warm conditions over the past two decades is thought to have led to a reduction in the quantity of standing leaf litter, an important microhabitat for many reptile species,

which may in turn have contributed to marked reptile declines in the area (Whitfield *et al.* 2007). Microhabitat losses will reduce adaptation potential by lowering the capacity to buffer the impacts of climate change *in situ*, and by reducing the availability of dispersal corridors.

RISING WATER TEMPERATURES

Water temperature has been directly linked to fitness and reproductive traits in aquatic and semi-aquatic reptiles (Elsworth *et al.* 2009; Booth and Evans 2011), and has been correlated with nesting dates in turtles (Weishampel *et al.* 2004; Pike *et al.* 2006; Mazaris *et al.* 2008). Water temperature is also one of the most important determinants of sea turtle and sea snake distributions. For example, satellite tracking of Leatherback turtles (*Dermochelys coriacea*) in the North Atlantic has shown that the northern boundary of their distribution is correlated with the position of the 15°C isotherm which has moved 330 km north over the last 17 years (McMahon and Hays 2006). Jellyfish, the main prey of Leatherback turtles, have also increased substantially in biomass in many regions (e.g. Brodeur *et al.* 2002; Atrill *et al.* 2007), suggesting that this species may benefit from rising water temperatures in some areas. An increase in the number of sightings of Leatherback turtles in UK waters supports the suggestion that warming has opened up new foraging areas for this species (Witt *et al.* 2007).

The indirect effects of rising water temperatures on the availability of prey and habitat are likely to pose substantial threats to many other aquatic and semi-aquatic reptiles. For example, ocean warming, coupled with changes in UV light penetration, salinity and

eutrophication, are expected to lead to a redistribution of seagrass habitats (Short and Neckles 1999) which form vital foraging areas for Green turtles (*Chelonia mydas*). As variations in resources are related to the interval between breeding seasons for this species (Broderick *et al.* 2003), these changes will have important implications for growth, condition and reproductive output. Indirect impacts of warming water temperatures on aquatic reptiles are already evident. A decrease in ocean productivity and prey abundance in the core foraging areas of Pacific Loggerhead turtles (*Caretta caretta*), as a consequence of warming sea temperatures, are thought to have already contributed to a reduction in nesting for this species (Chaloupka *et al.* 2008). Specialists will be particularly vulnerable to these effects. Species confined to coral reefs for instance, such as the olive sea snake (*Aypisurus laevis*), may be particularly vulnerable to range contractions due to the impacts of warming sea temperatures on coral health (Hoegh-Guldberg 1999).

RISING SEA LEVELS

Global sea levels are predicted to rise by 0.5-2.0 m over the next century (Nicholls *et al.* 2011) and will contribute to a loss of habitat and potential nesting sites for many reptiles, particularly those that inhabit coastal areas and small, low-lying islands. Topographic models have shown that up to 32% of the total current beach area around the Caribbean island of Bonaire, an important nesting ground for both Hawksbill (*Eretmochelys imbricata*) and Loggerhead (*Caretta caretta*) turtles, could be lost if sea levels rise by 0.5 m (Fish *et al.* 2005), and up to 40% of Green turtle (*Chelonia mydas*) nesting beaches could be lost following a 0.9 m sea level rise in the northwestern Hawaiian islands (Baker *et al.* 2006). Coastal development in these areas will prevent the landward migration of

beaches and limit the number of alternative nesting sites along neighbouring coastlines. A lack of space may increase the risk of nest destruction by other nesting females due to the greater density of nests (Mazaris *et al.* 2009), or may force turtles to nest nearer the water's edge, making their nests more prone to high-tide inundations.

Rising sea levels are also predicted to lead to the saltwater intrusion of freshwater habitats in many regions, with important consequences for freshwater reptiles, including crocodiles, alligators and turtles. Even relatively modest changes in sea level have already led to the saltwater intrusion of a tidal creek system in Northern Australia, extending some creeks a further 30km inland and causing them to invade freshwater wetlands (Mulrennan and Woodroffe 1998). Salinization of freshwater habitats has been shown to influence the distribution of the American alligator (*Alligator mississippiensis*) (Mazzotti and Brandt 1994), and has been correlated with reduced growth rates and survival in the American crocodile (*Crocodylus acutus*), with subsequent restoration of freshwater flows linked to an improvement in nesting effort and success (Mazzotti *et al.* 2007).

CONCLUSIONS

Although reptiles have attracted less attention from climate change scientists than some other taxonomic groups, evidence that climate change is already affecting several reptile species is accumulating. These impacts will become more pervasive as the Earth's climate continues to change at an ever increasing rate over the 21st century. While much progress has been made towards understanding the impacts of climate change on reptiles, important

knowledge gaps remain that currently limit our ability to identify which species are likely to be most vulnerable in the future. These include:

1. An understanding of the traits which are likely to be important in determining the vulnerability of reptiles to warming, and of the heritability of these traits. Thermal tolerance limits, for instance, influence the capacity of species to cope with environmental change, yet have only been established for a relatively small number of taxa.
2. An understanding of how different environmental factors are likely to interact. For instance, how might factors such as rainfall, soil moisture, substrate and sand albedo, interact to either buffer or exacerbate the impacts of warming on nest temperatures?
3. An understanding of the capacity of reptiles to buffer the impacts of climate change *in situ*, for example by exploiting thermal refuges within their home ranges, or by shifting the timing of their activity periods and life cycles. It is also important to understand what effect these buffering mechanisms might have on energy budgets and interactions with other species. As yet, the capacity of species to adapt to climate change *in situ* has been largely unexplored.

Further progress in these three research areas would help provide more accurate predictions of demographic and distribution shifts under climate change, and refine predictions about relative vulnerabilities.

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CHAPTER 3

The responses of Australian reptiles to climate change

ABSTRACT

Renowned for its remarkably diverse reptile fauna, Australia is currently undergoing significant climatic changes. How Australia's reptiles may respond to these changes has received less attention than many other taxonomic groups. Here, we outline recent and projected climate trends within Australia, and review the impacts these have had, and may continue to have, on Australia's reptile fauna. We find that relatively few examples of responses among Australia's reptiles have yet been documented, and that most of these have described changes in phenology or behaviour. There is, however, substantial evidence that many aspects of their biology are highly sensitive to temperature and precipitation, indicating that future impacts on this taxonomic group could be severe. We suggest that further research on the reptilian traits that are likely to promote vulnerability to climate change, coupled with comprehensive assessments that model range shifts among the taxonomic group, will help identify those species likely to be most in need of conservation attention.

Keywords: Australia, behavioural adaptation, distribution shift, extinction, genetic adaptation, phenology, population dynamics, species interactions

INTRODUCTION

Over the past century, Australia has experienced significant climatic changes, consistent with those around the globe. These changes have included a warming of almost 0.9°C since 1910, coupled with shifts in rainfall patterns, increased sea surface temperature (SST) and changes in the incidence and intensity of droughts, fires and floods (CSIRO and BOM 2012). These trends have already had a discernible impact on Australia's biota, with documented changes in the distribution, phenology, genetics and community dynamics of many taxa including birds, insects, plants and coral reefs (Hoegh-Guldberg 1999; Hughes 2003; Umina *et al.* 2005; Beaumont *et al.* 2006; Chambers 2008; Steffen *et al.* 2009; Kearney *et al.* 2010). In this paper, we examine the climate change vulnerability of a relatively understudied taxonomic group, the reptiles. Specifically, we outline recent and predicted climate trends for Australia, review what is known about how Australia's reptile species have already responded to these changes, and suggest how they may continue to do so over coming decades. A greater understanding of the adaptive capacity of reptiles to climate change is particularly important, given the likelihood that future impacts on this taxonomic group could be severe (Araújo *et al.* 2006; Sinervo *et al.* 2010; Ihlow *et al.* 2012).

THE REPTILES OF AUSTRALIA

Australia is home to an enormously diverse reptile fauna. Over 900 species, including representatives of the orders Squamata (snakes and lizards), Crocodilia (crocodiles) and Testudines (turtles), have been described, together amounting to approximately 10% of the

known global reptile fauna (Chapman 2009). Australia's lizards are particularly diverse, especially in the arid zone where there is greater species richness than in any other continental desert, and as many as 40 species have been found living sympatrically (Pianka 1973). The diversity of Australia's venomous land snakes (family Elapidae) is also extremely high, making Australia unique in being the only continent with a greater diversity of venomous than non-venomous snakes (Cogger 2000; Wilson and Swan 2008). Reptiles are found throughout the continent but, like other areas of the globe, diversity tends to be greater in the warm tropical and subtropical regions of the north and east, and decreases towards the cooler temperate regions of the south (Fig. 1) (Wilson and Knowles 1988). Range sizes vary markedly; there are species that are distributed nearly throughout the continent, such as the Bynoe's gecko (*Heteronotia binoei*), and those with very localised, restricted distributions, such as the red-throated skink (*Niveoscincus palfreymani*) which is confined to a small, rocky islet off the southern coast of Tasmania (Cogger 2000).

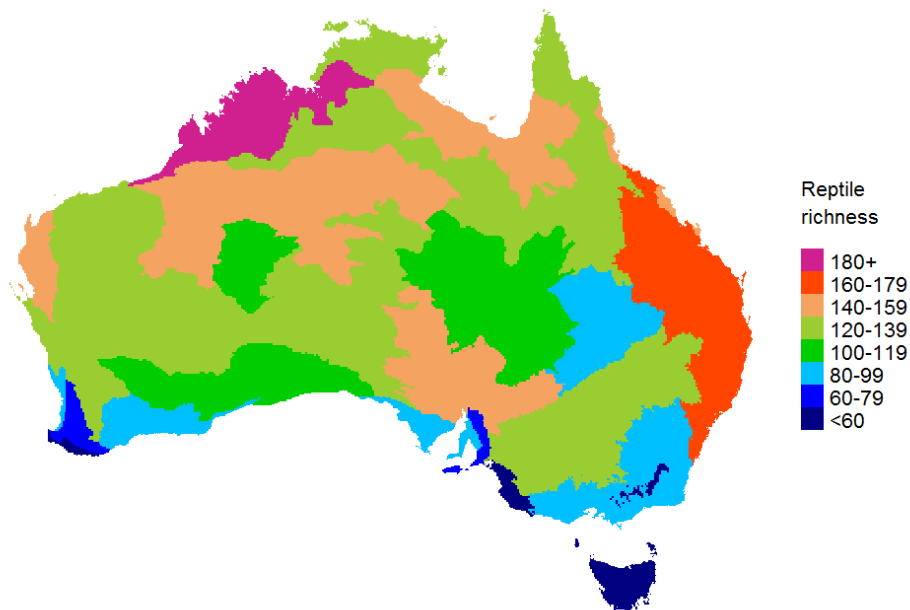


Figure 1. Reptile species richness among Australia's ecoregions. Data sourced from World Wildlife Fund. WildFinder: Online database of species distributions, ver. 01.06 gis.wwfus.org/wildfinder.

Most of Australia's reptiles are considered to be descendants of Asian immigrants that arrived in Australia after it had split from the southern supercontinent Gondwanaland and migrated northwards (Cogger and Heatwole 1981; Oliver and Sanders 2009). The remainder, which include the freshwater side-necked turtles and the diplodactyloid geckos, are thought to have Gondwanan origins. Throughout its movement northwards, Australia was subject to major shifts in climate, vegetation and geography, and subsequent alterations in habitat boundaries and dispersal corridors are thought to have led to the isolation of conspecific populations that subsequently diverged. These processes have resulted in a remarkable level of endemism among Australia's reptile fauna; approximately 93% of species are found nowhere else, the highest level of reptile endemism in the world (Chapman 2009).

According to the IUCN Red List, Australia has one of the largest numbers of threatened reptiles, surpassed only by New Caledonia, Mexico and Madagascar (IUCN 2012). Fifty-four (approximately 5.9%) of Australia's reptiles are listed as threatened under the federal *Environment Protection and Biodiversity Conservation (EPBC) Act 1999* and a further 63 species (approximately 6.9%) are listed under state acts. Two of these species have been listed as critically endangered under the EPBC Act; the Western Swamp turtle (*Pseudemydura umbrina*) found in Western Australia and the Nangur spiny skink (*Nangura spinosa*) found in Southern Queensland. To date, the most significant threat to Australia's reptiles has been habitat loss and degradation from land clearing for agriculture and urbanisation, although invasive species, notably cane toads, foxes and pigs, are also a major source of mortality (Cogger *et al.* 1993; Heard *et al.* 2006; Johnson *et al.* 2007; Letnic *et al.* 2008; Doody *et al.* 2009).

Anthropogenic climate change now presents an additional challenge to Australia's reptiles. In the short term, many reptile species are likely to be relatively resilient to changes in their environment. This is because the Australian climate is characterised by great climatic extremes and a high degree of variability, which has led to the evolution of organisms that are adapted to warm, dry and unpredictable conditions (Steffen *et al.* 2009). In addition, reptiles have relatively low energy and water requirements, many have highly opportunistic diets, and some have the ability to aestivate during periods unfavourable for activity (Dickman *et al.* 1999). Some reptiles have reproductive strategies that are also highly opportunistic; hatching of pig-nosed turtles (*Carettochelys insculpta*), for example, is prompted by the onset of the monsoonal rains (Doody *et al.* 2001). However, future climate change is expected to push Australia's environment well beyond the limits of

natural variability to which species are adapted, and therefore has the potential to develop into one of the most significant threats to the reptile fauna.

CLIMATE CHANGE IN AUSTRALIA

Consistent with global averages, Australia has warmed by approximately 0.9°C since 1910 (CSIRO and BoM 2012). The rate of warming has increased since the mid-20th century, with 2009 ending Australia's warmest decade on record (CSIRO and BoM 2010). The strongest and weakest warming trends have occurred inland and in the northwest respectively (Nicholls 2006; Braganza and Church 2011). Climate models predict mean temperatures in some areas may rise by up to 5°C by 2070, with expected levels of warming lowest for coastal areas and Tasmania and highest inland (Whetton 2011). Projected changes in maximum and minimum temperatures indicate an increase in the diurnal temperature range in the south of Australia, and a decrease in the north. An increase in heatwave duration and a decrease in frost and cold days has also been projected (Alexander and Arblaster 2009).

Significant rainfall trends have been difficult to distinguish against the background of high, natural, year-to-year rainfall variability, and future projections are considerably less certain than those for temperature (Braganza and Church 2011). Generally, both rainfall variability and unpredictability are expected to increase, with a decrease in the frequency of rainfall and an increase in the intensity of extreme rainfall events. Decreases in rainfall have been projected for southern areas, increases in rainfall have been projected for the north, and little change has been projected for central regions (Pitman and Perkins 2008; Whetton

2011). In some areas, increases in precipitation will be offset by the rise in evaporation associated with higher temperatures, leading to a decrease in soil moisture, a reduction in water flows through many freshwater systems and an increase in drought frequency and severity (Hennessy *et al.* 2008; Hobday and Lough 2011).

Recent changes in air temperature and rainfall have been accompanied by changes in sea level, sea temperature and extreme climatic events. Sea levels in the north and northwest of the Australian continent have risen by 7-11mm/year since 1993, almost three times the global average (CSIRO and BoM 2012). Sea surface temperatures have increased over every decade since 1900, and those recorded in 2010 were the warmest on record (CSIRO and BoM 2012). The El Niño Southern Oscillation (ENSO), which is associated with reduced rainfall and drought over much of northern and eastern Australia, has also been increasing in frequency and severity since the early 1900s, and a trend towards more El Niño-type conditions in the future is expected (Collins 2005; Hennessy *et al.* 2008). Trends in the patterns of extreme weather events, including an increased frequency of floods, more intense cyclones and an increase in the number of days with a very high and extreme fire danger, are also expected to continue (Hennessy *et al.* 2008).

ECOLOGICAL RESPONSES OF AUSTRALIA'S REPTILES TO CLIMATE CHANGE

Changes in behaviour

Many reptilian traits exhibit considerable plasticity in response to environmental factors, and a modification of these traits may therefore allow a degree of adaptation to take place *in situ* (Gvoždík 2012). Alterations in behavioural traits in particular may buffer rapid changes in climate because they can be adjusted by individuals almost immediately (Telemeco *et al.* 2009). Modifications to behaviour, particularly through changes in thermoregulation and nest site choice, are therefore considered one of the principal ways in which reptiles might respond to warming.

Behavioural thermoregulation

Behavioural thermoregulation refers to the ability of reptiles to adjust body temperatures by behavioural means, which they can do so very precisely and over a considerable thermal range (Shine 2005). The behavioural responses required to buffer (or exploit) the impacts of climate change will vary by site. Under warmer climates, reptiles that inhabit cooler regions may be able to use behavioural adjustments to take advantage of the warming air temperatures (Kearney *et al.* 2009). In tropical and desert areas where the primary thermal challenge is staying cool, reptiles may alter their behaviour to spend less time exposed to direct sun during basking and other activities (Huey and Tewksbury 2009; Kearney *et al.* 2009). Fossorial reptiles may simply burrow deeper into the soil, while

others may be able to utilise different microhabitats to achieve their preferred thermal surroundings. In the Northern Territory, for example, freshwater crocodiles (*Crocodylus johnstoni*) have been found aestivating in caves during particularly warm, dry conditions (Walsh 1989).

For viviparous species with temperature-dependent sex determination (TSD), modifications to thermoregulatory behaviours may also buffer the impacts of warming on sex ratios. Female spotted skinks (*Niveoscincus ocellatus*), for example, produce female-biased sex ratios among their offspring when given access to greater basking opportunities during gestation (Wapstra *et al.* 2004). In many species, basking time also influences traits such as body mass, morphology and growth rate, suggesting that behavioural thermoregulation may also assist reptiles to maximise the fitness of their offspring under changing environmental conditions (Autumn and Nardo 1995; Wapstra *et al.* 2004).

However, behavioural changes are not without trade-offs and complications because a species ability to buffer the impacts of climate change is constrained by its energy requirements (Kearney *et al.* 2009). For example, in areas where temperatures are already optimal or above optimal for species performance, warming may induce species to spend greater lengths of time in thermal refugia, reducing the time available for foraging (Sinervo *et al.* 2010). In turn, these constrictions may have deleterious effects on an animal's energy stores due to the impact of warming on metabolic rates.

For some species, the ability to behaviourally escape from the impacts of warming temperatures may also be constrained by the environmental conditions to which they have become acclimated. Captive-born tiger snakes (*Notechis scutatus*), for instance, are unable

to maintain optimal body temperatures when they are suddenly shifted to a new thermal environment, because they continue to thermoregulate in the same way they have done previously (Aubret and Shine 2010). How long these suboptimal thermoregulatory tactics may persist is unknown because the snakes were only monitored for two months following the thermal shift. Nevertheless, even short periods of body temperatures outside an animal's preferred range are expected to have adverse effects on fitness. These findings suggest that the ability of at least some species to successfully buffer increased year-to-year climatic variability by altering their thermoregulatory behaviours may be limited.

Nest site choice

For oviparous reptiles that exhibit TSD, a potential means of buffering the impacts of warming on offspring sex ratios is via active nest site choice (Warner and Shine 2007). This may also be an important strategy for reptiles with genotypic sex determination (GSD) because incubation temperature has been shown to influence other fitness characteristics, including development rate, hatching success, locomotor ability and offspring survival (Brown and Shine 2004; Micheli-Campbell *et al.* 2011).

Rainfall, nest depth, shadiness and albedo of the substrate all affect the thermal nesting environment (Hays *et al.* 2003; Morjan 2003b; Doody *et al.* 2006; Houghton *et al.* 2007). Clutch mass can also influence nest temperatures via the effect of metabolic heating (Glen and Mrosovsky 2004). By adjusting these factors, some reptiles are able to consistently select nest microenvironments with similar thermal conditions throughout their range. Australian water dragons (*Physignathus lesueurii*), for example, are able to obtain

remarkably similar nest temperatures across broad latitudinal and elevational gradients by preferring more shaded nest sites, or by building deeper nests, in warmer areas (Doody *et al.* 2006; Doody 2009). This plasticity in nest site choice should limit the degree to which changes in ambient temperature under climate change will affect embryo development.

In other species, the efficacy of altered nesting behaviours to compensate entirely for future levels of climate change, either alone or in combination with other responses, is more doubtful (Morjan 2003a; Telemeco *et al.* 2009). Only a few hot days may be sufficient to heavily influence offspring phenotype, and extreme climate conditions may therefore override any buffering effects during particularly warm summers (Shine and Elphick 2001). In one study in which the nests of three-lined skinks (*Acritoscincus duperreyi*) in southeast Australia were monitored over a ten year period, nest temperatures continued to rise despite a progressive increase in nest depth and an advancement in the seasonal timing of oviposition (Telemeco *et al.* 2009). Further, facultative adjustment of nest conditions will only be possible if cooler nest sites are available. Rising sea levels and increased coastal erosion due to storms, for example, may reduce the number of nest sites with different attributes for some species of sea turtle that return to the same area every year to nest (Davenport 1989; Fish *et al.* 2005).

Changes in phenology

Changes in temperature and precipitation are important cues for life cycle events in most species. In reptiles, the timing of breeding, hibernation and aestivation are often tightly linked to environmental conditions and may therefore be affected by climate change. Some

species are expected to benefit from these changes: for example, a lengthening of the activity season of high-latitude reptiles, which is frequently constrained by temperature, may result in greater opportunities to feed, grow and reproduce (Moreno-Rueda *et al.* 2009; Weatherhead *et al.* 2012). Reptiles may also benefit from advances in the timing of food availability due to earlier leafing, flowering, fruiting and appearance of insects.

Compared to other taxonomic groups, relatively few examples of phenological shifts among Australian reptiles have been documented. Those that have typically involve changes in the timing of reproductive behaviours. In South Australia, shingleback lizards (*Tiliqua rugosa*), which closely associate as pairs during the weeks that precede mating, were found pairing progressively earlier over a 15 year period, associated with higher August temperatures, lower winter rainfall and higher spring rainfall (Bull and Burzacott 2002). Over a ten year period, three-lined skinks (*Acritoscincus duperreyi*) from an alpine area in southeast Australia were found nesting progressively earlier in response to rising air temperatures (Telemeco *et al.* 2009).

However, alterations in the timing of nesting appear insufficient to compensate completely for the impacts of climate change in some reptile species. Despite nesting earlier and building deeper nests, nest temperatures of three-lined skinks (*Acritoscincus duperreyi*) in southeast Australia continued to rise by approximately 1.5°C over a ten year period, mirroring mean ambient temperature rise (Telemeco *et al.* 2009). These behavioural and phenological adjustments were sufficient to achieve preferred nest temperatures at the time of laying, but the rapid rate of warming meant they were insufficient to maintain nest temperatures later in the nesting season. These findings are supported by overseas studies,

which have also demonstrated an inability of reptiles to buffer the impacts of climate change by phenological means (Schwanz and Janzen 2008).

Changes in genetic composition

Genetic adaptation provides another potential mechanism by which species could adapt to climate change *in situ*. No examples of heritable, genetic changes in response to recent climate change have yet been documented for Australia's reptiles, although they have been for insects (Umina *et al.* 2005). Many reptiles have long generation times, leading some researchers to question whether evolutionary responses among some species could occur sufficiently quickly to track the particularly rapid rates of environmental change projected in the future (Mitchell *et al.* 2008; Hawkes *et al.* 2009). Other anthropogenic effects, including overexploitation and habitat fragmentation, are expected to further limit evolutionary potential due to their effects on genetic diversity and gene flow respectively (Templeton *et al.* 2001).

Recent research, however, suggests that rapid evolutionary changes in response to environmental pressures other than climate change can occur in at least some reptile species. In Australia, reptiles have demonstrated adaptive responses since the introduction of cane toads in the 1930s. Red-bellied black snakes (*Pseudechis porphyriacus*) and green tree snakes (*Dendrelaphis punctulatus*) from cane toad-exposed localities, for instance, have demonstrated a steady increase in body length and a reduction in gape size over this time frame (Phillips and Shine 2004). *P. porphyriacus* is also showing an increased resistance to toad toxin and a decreased preference for toads as prey (Phillips and Shine

2006). These changes appear to be a consequence of natural selection, rather than phenotypic plasticity to local environmental conditions.

Distribution shifts

In conjunction with the *in situ* responses described above, many species are expected to adapt to climate change by shifting their spatial distributions polewards and upwards in elevation, tracking their specific climate preferences. This is especially likely for reptiles because thermal tolerances are a particularly important determinant of species range boundaries in this taxonomic group (Kearney and Porter 2004; Fuentes *et al.* 2009; Doody and Moore 2010). Assuming that species are capable of dispersing into their new ranges, corridors permitting dispersal exist, and suitable habitats with adequate resources are available, migration is likely to be an adaptation option for a number of species. Indeed, there is evidence that many species of animals and plants have already responded in this manner (Hughes 2003; Parmesan and Yohe 2003; Rosenzweig *et al.* 2008; Maclean and Wilson 2011), although the direction and magnitude of these distribution shifts are not always consistent with a climate change signal (Chen *et al.* 2011).

Unfortunately, these assumptions are often unrealistic with regard to reptiles, especially terrestrial species. The capacity of many reptile species to make large scale migrations within the time frames imposed by contemporary climate change, particularly those with small body sizes, is doubtful (Araújo and Pearson 2005). Species with southerly distributions, and those restricted to islands, will have limited opportunities for poleward migration because the sea presents a geographical barrier to movement. Furthermore, the

Australian landscape has become increasingly modified by human activities such as agriculture and deforestation, resulting in a significant decline in the quantity and quality of natural habitats. For reptiles, even narrow belts of unsuitable habitat such as roads can act as barriers to dispersal (Pianka 1969; Koenig *et al.* 2001; Patrick and Gibbs 2010). Upslope migrations are also unlikely to be feasible for many species, as Australia is the flattest of all continents, with less than 5% of its land surface more than 600m above sea level.

Despite the inherent dispersal limitations of reptiles, evidence of climate change-induced range shifts among a few species are now evident globally (e.g. McMahon and Hays 2006; Moreno-Rueda *et al.* 2012) but such shifts have yet to be documented in Australia, probably reflecting a lack of baseline datasets and monitoring efforts, at least in part (Fuentes *et al.* 2009). Greater attention has been given to projecting range shifts under climate change over the 21st century. In North Queensland, three reptile species were projected to retain a distribution of more than 75% by 2100 under a conservative climate change scenario, but lose a minimum of 80% of their climatic range under an extreme scenario, with the chameleon gecko (*Carphodactylus laevis*) retaining just 4% of its core range (Meynecke 2004). In New South Wales, the broad-headed snake (*Hoplocephalus bungaroides*) was projected to lose 86% of its climate space by 2070 under a high climate change scenario (Penman *et al.* 2010). Although these attempts to model future range shifts among Australia's reptiles have focused on only a few species, they suggest that reductions in range sizes could be pronounced among this taxonomic group. More comprehensive assessments that model range shifts among much larger numbers of reptile species, as have been conducted overseas (e.g. Araújo *et al.* 2006; Carvalho *et al.* 2010), are clearly warranted in Australia.

Changes in population dynamics

Direct impacts of climate change on fitness-related traits

If species are unable to adapt *in situ* or disperse to new locations in response to climate change, impacts on population dynamics are likely to occur. The severity of these impacts is expected to vary geographically. For example, tropical reptiles are expected to have less capacity to endure rising temperatures because they have evolved in these regions with relatively aseasonal, predictable environments, and tend to possess narrow thermal tolerances. Thus even fairly modest levels of warming may compromise the ability of many reptiles to maintain body temperatures within their preferred thermal ranges, leading to physiological stress, poorer body condition and reduced rates of reproduction and survival (Deutsch *et al.* 2008; Huey *et al.* 2009). In contrast, warming is predicted to have a beneficial effect on the population dynamics of reptiles in temperate regions, where conditions are currently below their thermal optima. In these areas, warming may offer new opportunities for raised activity levels and increased time available for foraging and growth, with concomitant impacts on performance, survival and reproductive effort (Chamaille-Jammes *et al.* 2006; Moreno-Rueda *et al.* 2009). Further, many fitness-related traits of reptiles that inhabit cooler regions are impaired by lower than optimal temperatures during development, and increases in incubation temperatures have been shown to confer benefits on hatching success, post-hatching growth rates, locomotor speeds, anti-predatory behaviours, and ultimately, reproductive success and survival among a number of species (Shine and Elphick 2001; Dubey and Shine 2011; Clarke and Zani 2012). For example, longer basking opportunities during pregnancy have been shown to increase offspring growth rates in the Blue Mountains water skink (*Eulamprus*

leuraensis) (Dubey and Shine 2011). Provided suitable resources are available, the populations of many of Australia's temperate reptiles may therefore increase under future warming, at least in the short term.

Climatic processes other than rising temperatures also have the potential to exert direct impacts on the dynamics of reptile populations in Australia. In the north, sea levels are projected to rise by a further 0.5-2.0 m by 2100 (Nicholls *et al.* 2011), which is expected to cause significant reductions in turtle nesting habitat, and increase embryonic mortality through nest inundations, reducing reproductive success. Three dimensional elevation models have shown, for example, that up to 38% of available nesting area across Green turtle (*Chelonia mydas*) rookeries in the northern Great Barrier Reef could be lost by 2100 as a result of sea level rise (Fuentes *et al.* 2010b). This reduction in nesting area will increase the density of nests, increasing the risk of nest destruction by other females, and increasing embryo mortality further (Mazaris *et al.* 2009). This phenomenon is already evident at some nest sites along the Great Barrier Reef during high density nesting years (Fuentes *et al.* 2010b). Population viability analyses have shown that egg survival is an important determinant of population persistence (Mazaris *et al.* 2005), hence increases in embryo mortality as a consequence of climate change may have a dramatic effect on population growth rates. On the other hand, warmer water temperatures have been shown to have beneficial impacts on the growth rates of the Western Swamp turtle (*Pseudemydura umbrina*), provided food supplies are not limited, which may therefore have a greater chance of reaching the critical mass necessary to survive long summer aestivation periods (Mitchell *et al.* 2012).

Direct effects of climate change on offspring sex ratios

Reptiles that exhibit TSD, including the crocodiles, the marine turtles, the water dragon (*Physignathus lesueurii*), and some of Australia's terrestrial lizards, may be particularly susceptible to altered population dynamics if behavioural and phenological adjustments are insufficient to buffer the impacts of warming on offspring sex ratios (Mitchell and Janzen 2010). For example, thermal models predict a near complete feminisation of hatchling Green turtles (*Chelonia mydas*) from the northern Great Barrier Reef will occur by 2070 under an extreme climate change scenario (Fuentes *et al.* 2010a). Green turtles, as for all Australia's marine turtles, are already listed as threatened under the EPBC Act, and may therefore be particularly vulnerable, at a species level, to the negative impacts of climate change on population dynamics.

Indirect impacts of climate change

In many cases, the most significant impacts of climate change on the population dynamics of Australian reptiles are likely to be mediated via indirect effects on habitat and prey availability. Climate-induced changes in vegetation patterns, primarily via changes in rainfall, atmospheric carbon dioxide concentrations (CO₂) and growing season duration, have already contributed to the establishment of woody shrubs at the expense of grasses in many areas in Australia (Bowman *et al.* 2001; Bowman *et al.* 2010), and some weeds are also expected to benefit (Kriticos *et al.* 2003). Changes in the composition of native plant communities will have concomitant impacts on the reptile communities for which these plants provide essential habitat. In central Australia, for instance, a successional change in

the dominant plant species spinifex (*Triodia spp.*), in response to changing rainfall patterns, resulted in a shift in the relative abundances of two species of agamid lizard over a period of seven years (Dickman *et al.* 1999).

The predicted increase in both the intensity and frequency of fires in Australia under climate change will also undoubtedly affect vegetation patterns across the continent, both directly and indirectly by affecting soil nutrients. The vegetation mosaics that result from small, localised fires promote reptile diversity in the arid zone, because the regenerating areas act as fire breaks and ensure mature spinifex is always present. Fires also increase the availability of dead wood that can provide habitat for reptiles. However, more severe fires can contribute to the direct mortality of many reptiles, particularly non-burrowing species (Griffiths and Christian 1996; Smith *et al.* 2012), and adversely affect the condition and survival of others. The pygmy bluetongue lizard (*Tiliqua adelaidensis*), for instance, suffered a marked decline in body condition as a result of reduced foraging activity following a major fire in South Australia in December 2005 (Fenner and Bull 2007).

Australia's aquatic and semi-aquatic reptiles are also likely to be sensitive to climate change-induced alterations in prey and habitat availability. The amount and timing of wet season rainfall, for instance, has been shown to drive rat abundances in northern Australia, which in turn influences reproduction and population dynamics in water pythons (*Liasis fuscus*) (Shine and Madsen 1997; Madsen *et al.* 2006). An inverse relationship between nesting abundance and mean annual SST in core foraging areas has been found among populations of Loggerhead turtle (*Caretta caretta*) in east Australia, indicating that climate warming is already reducing nesting and recruitment in this species via its impact on ocean productivity and prey abundance (Chaloupka *et al.* 2008). Freshwater turtles are expected

to be particularly vulnerable to habitat loss as a consequence of climate change. Shorter hydroperiods of temporary wetlands are expected to impose longer aestivation periods, or greater travelling distances between water sources, increasing the risk of predation and desiccation (Roe and Georges 2009). Loss of critical floodplain habitat and increased predation following a severe drought from 2001 to 2010 has already contributed to the population declines of two species of freshwater turtles in the Murray Darling Basin (Chessman 2011).

Impacts of climate change on species interactions

Climate change is also expected to be a significant driver of altered interactions with predators and invasive species, and such changes are already evident among Australia's reptiles. Alpine skinks (*Liopholis guthega*) have recently become exposed to a new predator, the kookaburra (*Dacelo novaeguineae*), which is now hunting at higher elevations as a consequence of rising air temperatures (Low 2007). The highly toxic cane toad (*Bufo marinus*) has already contributed to the declines of three species of monitor lizards, *Varanus panoptes*, *V. mitchelli* and *V. mertensi* (Doody *et al.* 2009), and the massive mortality of freshwater crocodiles (*Crocodylus johnstoni*) at the toad invasion front (Letnic *et al.* 2008) in northern Australia. Long-term monitoring of populations of Northern death adders (*Acanthophis praelongus*) has also revealed massive declines of >89% in recent years, coincident with the arrival of toads (Phillips *et al.* 2010). The cane toad is expected to expand its range under climate change (Urban *et al.* 2007; Kearney *et al.* 2008), suggesting that an increase in encounter rate with their reptilian predators, and further population declines, are likely to occur.

Many reptilian pathogens are sensitive to environmental factors, and are therefore also likely to experience climate-driven changes in their distributions and population dynamics. Warmer sea temperatures are thought to be related to increases in the incidence of fibropapillomatosis among Green turtles (*Chelonia mydas*) since the 1980s (Aguirre and Lutz 2004; Ward and Lafferty 2004). A sequence of high rainfall years resulted in a shift of 1-2 km in the parapatric boundary between two reptile ticks in South Australia, and as a consequence, the density of ticks on lizards flanking the boundary zone increased for one species of tick and decreased for the other (Bull and Burzacott 2001). Under warmer climates, overall tick infestation levels are also expected to increase as lizards are forced to retreat into cool, moist refuges where parasite densities are particularly high (Kerr and Bull 2006).

CONCLUSION

To date, responses that have been confidently attributed to long-term climatic trends have only been documented for a small number of Australia's reptile species. Most of these responses have involved changes in phenology and behaviour. This is unsurprising as research suggests these *in situ* changes typically pre-empt changes in distribution and abundance, and as such have been some of the most frequently observed responses of species to climate change (Peñuelas and Filella 2001). The fact that some Australian reptiles are already responding to the relatively modest climate change that has occurred so far raises concerns that future impacts on this taxonomic group could be severe, particularly because there is now ample evidence that many aspects of reptilian biology are extremely sensitive to temperature and precipitation. Studies from overseas justify these

concerns, with confirmation of climate change-induced range shifts and species' extirpations in this taxonomic group (Sinervo *et al.* 2010; Moreno-Rueda *et al.* 2012). Identifying the species likely to be most susceptible to future climate change is therefore becoming increasingly urgent. We suggest that amalgamating the reptilian traits that are expected to promote vulnerability into a formal assessment framework, and coupling this information with more comprehensive modelling assessments of species' distributions, would be an extremely worthwhile step towards obtaining more robust predictions of species' responses to future climate change. This knowledge will be invaluable for informing management efforts aimed at protecting Australia's reptile fauna against the impacts imposed by a rapidly changing climate.

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CHAPTER 4

A vulnerability assessment of Australian elapid snakes

ABSTRACT

In view of the accelerating rate of climate change, there is an imperative to assess species vulnerability so that conservation priorities can be set. To date, vulnerability assessments have largely been based on projected changes in range size derived from the output of environmental niche models (ENMs). A criticism of these models as risk assessment tools is that they do not incorporate information on species ecological and life history traits. Accordingly, we developed a novel framework for assessing species vulnerability to climate change that considered species traits together with the projections of ENMs. Applying this method to the Australian elapid snakes (family Elapidae), we determined which species may be particularly susceptible in the future, assessed broad-scale biogeographic patterns in species vulnerability, and identified two ecoregions that are especially rich in the most vulnerable species. By offering a more comprehensive and rigorous method for assessing vulnerability than those based solely on ENMs, 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, environmental niche 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 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; Hughes 2003; Umina *et al.* 2005; Beaumont *et al.* 2006; Steffen *et al.* 2009; Telemeco *et al.* 2009). 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). 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 environmental niche models (ENMs). ENMs 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 ENMs 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 ENMs 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. Their disadvantage, however, is that they 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. Further, mechanistic models require considerably more time and effort to build because they are typically developed for particular species and require substantial revision before they can be applied more widely (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 ENMs (Heikkinen *et al.* 2010). We integrated these two sets of information in a novel, 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 ENMs, without the need for complex ecological and biophysical data.

We applied this system 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 diversity reaches its peak in Australia where they comprise nearly 70% of the snake fauna. We chose this group for three principal reasons. First, elapids can be found throughout the Australian continent, including the cool temperate regions of Victoria and Tasmania where the 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 principal objectives of this study were to determine which species may be at greatest risk in the future and identify the main factors contributing to their vulnerability.

Specifically, we addressed the following questions:

- 1) Are species that appear most vulnerable to contractions in climatic range, as predicted using ENMs, also those that appear highly vulnerable due to specific life history and ecological traits?

- 2) Do highly vulnerable species cluster in certain regions of the elapid phylogeny?
- 3) Does vulnerability to climate change vary among species from different biogeographic zones?
- 4) Are there particular regions in Australia that appear especially rich in highly vulnerable species where conservation efforts should be focused?

METHODS

Variables derived from the output of ENMs

We followed the nomenclature of the most recently published 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. We omitted species that had fewer than 15 records from further analysis as low sample sizes have been shown to limit model accuracy (Supplementary Table 1) (Wisz *et al.* 2008). We set this threshold fairly low compared to other studies because we wanted to include as many rare species in our vulnerability assessment as possible. The locality records for the remaining 81 species were plotted and compared with distribution maps from Wilson and Swan (2008) and other reptile field

guides. Duplicate points and those that were questionable due to their geographic location were removed.

We derived a suite of 19 bioclimatic variables (Busby 1991) from current climate data (1960-2000) provided by the Bureau of Meteorology (www.bom.gov.au). Of these, five were chosen for inclusion in the modelling process – annual mean temperature, temperature seasonality, minimum temperature of the coldest month, maximum temperature of the hottest month, and annual precipitation – under the rationale that they incorporate information about climatic averages, seasonal variability and extremes, and are generally considered biologically important determinants of reptile distribution limits (Qian *et al.* 2007). These variables were checked for redundancy using a correlation analysis. We obtained future climate projections for 2050 from four global circulation models (GCMs) believed to produce reasonably 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 x 0.05 degree grid (approximately 5 x 5km).

We used an ensemble of 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° (≈200km) 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).

The performance of each algorithm was assessed by calculating the area under the receiver operating characteristic curve (AUC) using a 10-fold cross-validation procedure. By convention, an algorithm is considered excellent if the average AUC score across all model replicates is > 0.9, good if 0.8-0.9, fair if 0.7-0.8 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). We averaged the four maps corresponding to each of the four GCMs to produce a mean projection for 2050. To obtain a single projection across all algorithms for each time period we used a weighted average (WA) consensus method which weights the contribution of each algorithm according to its AUC score:

$$WA_i = \frac{\sum_m (AUC_m \times s_{mi})}{\sum_m AUC_m}$$

where i is the grid cell index, m is the model algorithm and s is the climatic suitability of grid cell i according to algorithm m . This method has been shown to provide significantly more robust predictions than other consensus methods (Marmion *et al.* 2009).

Following the method of Carvalho *et al.* (2010) we converted these consensus maps into presence-absence maps using a consensus threshold (CT). This threshold value was determined by calculating the weighted average of the sensitivity-specificity equality thresholds for each algorithm, using the AUC score of the algorithm as its weight:

$$CT = \frac{\sum_m (AUC_m \times t_m)}{\sum_m AUC_m}$$

where m is the model algorithm and t_m is the sensitivity-specificity equality threshold of algorithm m .

We used these maps to derive the following four variables:

1. Change in climatic range size

Using the current and 2050 presence-absence maps, we calculated the change in climatic range size as the percentage change in the number of suitable grid cells. 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.

We categorised species according to their projected change in climatic range size by dividing these data into quartiles (change in range size < 1st quartile; 1st quartile ≤ change

in range size < median; median \leq change in range size < 3rd quartile; change in range size \geq 3rd quartile) thereby generating four equal-sized classes to which species could be assigned. By ensuring that 25% of species fell into each class, we allowed for greater discrimination between them than if these thresholds had been chosen arbitrarily. We followed this procedure for all of the continuous variables used in the assessment.

2. 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 all 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 used the presence-absence maps to calculate the percentage overlap between the current and 2050 climatic ranges. A low percentage overlap indicates high vulnerability, whereas a high percentage overlap indicates low vulnerability.

3. Change in climatic suitability

We used the non-thresholded current and 2050 maps to calculate the change in climatic suitability, or favourability, between the current and 2050 time periods. For each map, we conserved all grid cell values above the consensus 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).

4. Overlap with the protected area network

To assess whether climate change may drive species out of reserves, we overlaid the presence-absence 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) and calculated the percentage change in the number of suitable grid cells that fell within protected areas. 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 (including clutch size) and generation length. Also important is the degree of exposure to climate change. Diurnal species, for example, will be more exposed to extreme temperatures than nocturnal species. Species that are active on the surface will also be more exposed than fossorial species, which may have greater opportunities to select cooler, more stable conditions by adjusting their burrowing behaviours.

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. Following these considerations, six traits were identified as being suitable for inclusion in the vulnerability assessment: habitat specialisation, dietary specialisation, clutch/litter size, habitat (terrestrial, fossorial or arboreal), activity (diurnal or nocturnal) and threatened status.

We assessed these traits as follows:

1. 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 (D) of vegetation types across all occurrence records as an index of habitat specialisation (Simpson 1949). High habitat specialisation indicates high vulnerability and low habitat specialisation indicates low vulnerability. We acknowledge that selecting different vegetation datasets at varying resolutions may have yielded different estimates of habitat specialisation.

2. 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 $\geq 90\%$ of its diet (low vulnerability). Dietary information was not available for approximately 9% of species. 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 vulnerability.

3. 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 approximately 15% of species. 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).

4. Habitat

Species were classified as *terrestrial* (high vulnerability), *arboreal* (high vulnerability) or *fossorial* (low vulnerability) depending on the habitat in which they are most commonly found, based predominantly on information in Wilson & Swan (2008).

5. Activity

We classified the daily activity of species into one of the following two groups: *diurnal* species that are only ever active during the daytime (high vulnerability), and *crepuscular / nocturnal* species that are predominantly active during the evenings and at night (low vulnerability). We included species that are active both day and night, and those whose activity periods shift seasonally (e.g. the red-bellied black snake, *Pseudechis porphyriacus*) or geographically (e.g. the king brown snake, *P. australis*), in the lower risk category, as

this plasticity in activity patterns may enhance the ability of these species to adapt to climate change.

6. 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). Species classified as ‘data deficient’ according to the IUCN Red List were not classed as threatened.

Constructing the framework

The ten 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 ten 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 ten variables a second time (Fig. 1). This process,

based on the Delphi method, is a recognised technique for increasing consensus among a panel of experts (Hsu and Sandford 2007).

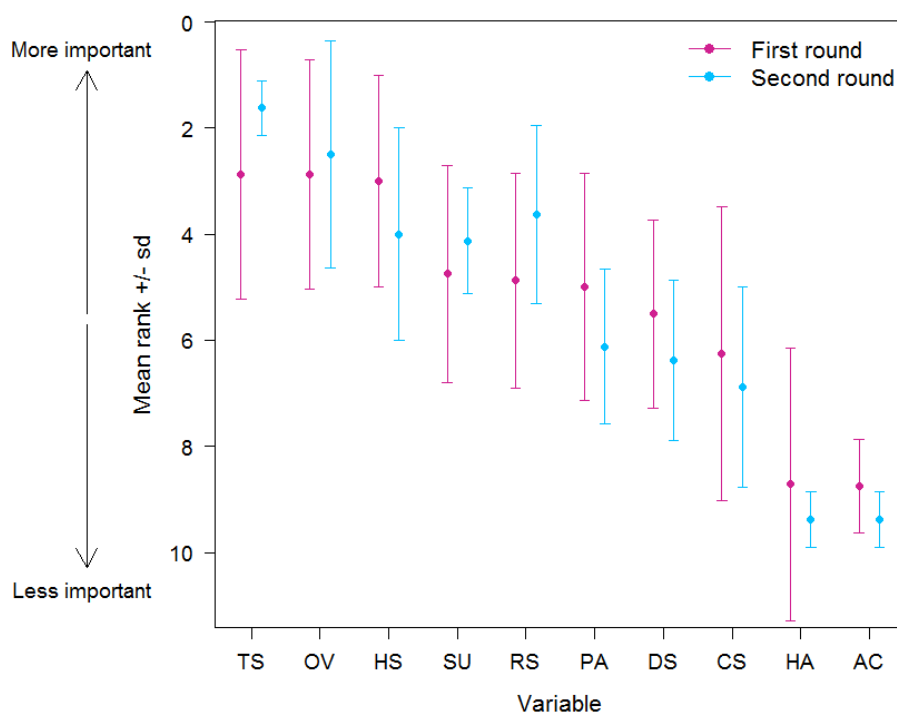


Figure 1. The mean rank (± 1 sd) of the ten variables used in the assessment following the first and second rounds of the Delphi process. TS = threatened status, OV = overlap between the current and 2050 climatic ranges, HS = habitat specialisation, SU = change in climatic suitability, RS = change in climatic range size, PA = overlap with the protected area network, DS = dietary specialisation, CS = clutch / litter size, HA = habitat, AC = activity.

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 ten 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 nine, and so on. Two variables, ‘habitat’ and

‘activity’, were considered equally important and were therefore allocated equal points. So that we could investigate both *additive* and *multiplicative* approaches to combining individual variable scores into an overall vulnerability score, we assigned a minimum point score to each variable of one. (If the minimum point score had been zero, only species that received points across all variables would receive an overall vulnerability score greater than zero using a multiplicative approach).

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 four. We therefore assigned four points to the most vulnerable category (dietary specialist), 2.5 points to the intermediate category (borderline specialist) and one point to the least vulnerable category (dietary generalist).

Table 1. Summary of the vulnerability assessment framework

Variable	Assigned Points	Variable	Assigned Points
1. Threatened status		6. Overlap with the protected area network	
(a) threatened	10.0	(a) $x < 1^{\text{st}}$ quartile	5.0
(b) not threatened	1.0	(b) 1^{st} quartile $\leq x < \text{median}$	3.7
		(c) $\text{median} \leq x < 3^{\text{rd}}$ quartile	2.3
2. Overlap between the current and 2050 climatic ranges		(d) $x \geq 3^{\text{rd}}$ quartile	1.0
(a) $x < 1^{\text{st}}$ quartile	9.0	7. Dietary specialisation	
(b) 1^{st} quartile $\leq x < \text{median}$	6.3	(a) specialist	4.0
(c) $\text{median} \leq x < 3^{\text{rd}}$ quartile	3.7	(b) borderline specialist	2.5
(d) $x \geq 3^{\text{rd}}$ quartile	1.0	(c) generalist	1.0
3. Change in climatic range size		8. Clutch / litter size	
(a) $x < 1^{\text{st}}$ quartile	8.0	(a) small	3.0
(b) 1^{st} quartile $\leq x < \text{median}$	5.7	(b) large	1.0
(c) $\text{median} \leq x < 3^{\text{rd}}$ quartile	3.3		
(d) $x \geq 3^{\text{rd}}$ quartile	1.0	9. Habitat	
4. Habitat specialisation		(a) terrestrial or arboreal	2.0
(a) $x < 1^{\text{st}}$ quartile	7.0	(b) fossorial	1.0
(b) 1^{st} quartile $\leq x < \text{median}$	5.0		
(c) $\text{median} \leq x < 3^{\text{rd}}$ quartile	3.0	10. Activity	
(d) $x \geq 3^{\text{rd}}$ quartile	1.0	(a) diurnal	2.0
5. Change in climatic suitability		(b) crepuscular or nocturnal	1.0
(a) $x < 1^{\text{st}}$ quartile	6.0		
(b) 1^{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		

We defined two methods for generating a vulnerability score: scores for each variable were summed (*additive model*) and the logarithms of each score were summed (*multiplicative model*). Thus for the *additive model*, vulnerability scores could range from 10 to 56, and

for the *multiplicative model*, scores could range from 0 to 15.8. We divided these ranges into three classes of equal size. Species awarded scores in the highest class were defined as ‘high vulnerability’ relative to the group as a whole, those awarded scores in the middle class were defined as ‘moderate vulnerability’ and those awarded scores in the lowest class were defined as ‘low vulnerability’. Finally, we grouped species according to their overall vulnerability based on the following criteria. Species that were defined as ‘high vulnerability’ according to both the *additive* and *multiplicative models* were assigned to vulnerability group 1 (highest vulnerability). Those defined as ‘high vulnerability’ according to one model, and ‘moderate vulnerability’ according to the other model were assigned to group 2. Those defined as ‘moderate vulnerability’ according to both models were assigned to group 3. Those defined as ‘moderate vulnerability’ according to one model, and ‘low vulnerability’ according to the other model, were assigned to group 4. Those species defined as ‘low vulnerability’ according to both the *additive* and *multiplicative models* were assigned to group 5 (lowest vulnerability).

Estimating uncertainty

This assessment framework, like all vulnerability assessments, involves some degree of uncertainty (Burgman 2005). Minimising, quantifying and communicating the sources of this uncertainty, where possible, should be an integral component of any vulnerability assessment so that conservation managers are able to make informed decisions with regard to the reliability of the assessment method. In this assessment, there are uncertainties associated with the data on species traits (which will have been influenced by sampling, measurement and stochastic errors), the ENM projections (which are highly sensitive to the

quality of the locality data, as well as the choice of GCM, modelling algorithm and climate variables) (Thuiller 2004; Synes and Osborne 2011), and the choice of framework design.

We have attempted to minimise uncertainty using three principal methods: 1) we have projected an ensemble of models onto the climate surfaces produced by multiple GCMs, 2) we have reduced the subjectivity associated with the weighting of variables by eliciting the opinions of experts using the Delphi process and 3) we have integrated the results of two different methods for combining variable scores into an assessment of overall vulnerability.

To extend our assessment of uncertainty, we explicitly quantified the variability among the model projections using principal component analysis (PCA) following the recommendation of Thuiller (2004). This multivariate technique determines the line that goes through the centroid of all model projections and minimises the square of the distance of each projection to that line (Araújo *et al.* 2005). An index of uncertainty is therefore provided by the first axis of the PCA which represents the greatest proportion of variance among the forecasts. Highly corroborative forecasts should instil greater confidence in their reliability, and provide managers with stronger justification for conservation action (Jones-Farrand *et al.* 2011).

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.

To perform a finer scale analysis, we obtained a GIS layer of Australia's terrestrial ecoregions from the World Wildlife Fund (Olson *et al.* 2001). These ecoregions represent large areas containing a geographically distinct assemblage of natural communities that share a large majority of their species and have similar environmental conditions. Across the globe, over 800 terrestrial ecoregions have been identified, of which 37 make up the Australian continent. We overlaid this layer with species occurrence records and identified the ecoregions that are especially rich in highly vulnerable species.

RESULTS

ENM projections

ENM projections varied widely among species (Supplementary Table 2), consistent with other studies that have modelled distribution shifts in reptiles on other continents (Araújo *et al.* 2006; Carvalho *et al.* 2010). Fifty-seven species (70%) were projected to experience range contractions by 2050, and one species, the inland taipan (*Oxyuranus microlepidotus*), was projected to lose all climatically suitable area. The least vulnerable species according to their ENM projections included the grey whipsnake (*Demansia simplex*), the northern shovel-nosed snake (*Brachyuophis roperi*) and the Pilbara bandy-bandy (*Vermicella snelli*) which were all projected to experience range expansions of over 200% and have a

percentage overlap between their current and 2050 climatic ranges of at least 95%.

Interestingly, the majority of species (57%) were projected to experience an increase in the degree of overlap with the protected area network by 2050 (mean change in overlap with the protected area network = 133%). The variability in model projections, as determined by PCA, also differed among species, ranging from 0.38 to 0.89 (Supplementary Table 2).

Species traits

The Australian elapids exhibit an enormous diversity of life history and ecological traits (Supplementary Table 2). Some species occur widely across Australia and tend to be very general in their habitat requirements, whereas others are known to prefer particular microhabitat types that appear to constrain their geographic distributions (Shea *et al.* 1993). Most individuals of the square-nosed snake (*Rhinoplocephalus bicolour*), for example, have been found in the abandoned nests of stick-ants (Shine 1986). Reptiles and frogs constitute the main dietary items for most elapids, but the degree of dietary specialisation can also vary widely. Some species feed almost exclusively on frogs (e.g. the ornamental snake, *Denisonia maculata*), typhlopids snakes (e.g. the bandy-bandies, *Vermicella sp.*) and reptile eggs (e.g. the unbanded shovel-nosed snake, *Brachyurops incinctus*) (Shea *et al.* 1993; Shine 1994). Generally, larger elapids have more generalised diets, although there are exceptions. The inland taipan (*Oxyuranus microlepidotus*), for instance, is a large elapid approximately 2m in length that feeds predominantly on rodents. Elapids include fully diurnal and nocturnal species, but there is often considerable flexibility in activity patterns within species, both geographically and seasonally. For example, the king brown snake (*Pseudechis australis*) is primarily diurnal in southern parts

of its range, but shows much more nocturnal activity in tropical regions (Cogger 2000). Many of the larger species are primarily diurnal whereas smaller species tend to be nocturnal, although again there are exceptions to this general rule. Average clutch / litter sizes range from approximately 2.5 to 19.1 (Shine 1994) and tend to increase with maternal body size, both within and amongst species (Shine 1985; Shea *et al.* 1993).

Overall vulnerability

As a consequence of their highly variable ENM projections and considerable diversity in species traits, vulnerability scores varied widely, ranging from 14.8 to 45 for the *additive model*, and 2.9 to 12.6 for the *multiplicative model* (Table 2). Eight species were categorised as ‘high vulnerability’ according to both models, and may be particularly susceptible to population declines under future climate change (Fig. 2). These included the unbanded shovel-nosed snake (*Brachyuophis incinctus*), the ornamental snake (*Denisonia maculata*), the collared whipsnake (*Demansia torquata*) and the Master’s snake (*Drysdalia mastersii*). Species categorised as ‘low vulnerability’ according to both models were characterised by projected range expansions with high levels of overlap, generalist habits and large clutch sizes, and included the northern small-eyed snake (*Cryptophis pallidiceps*) the yellow-faced whipsnake (*Demansia psammophis*) and the ringed brown snake (*Pseudonaja modesta*).

Table 2. The scores and classes awarded by the additive and multiplicative models to each species, and the overall vulnerability group to which they were assigned. Species are ordered alphabetically within vulnerability groups. H = high, M = moderate and L = low vulnerability.

Species name	Common name	ADDITIVE		MULTIPLICATIVE		Overall group
		Score	Class	Score	Class	
<i>Brachyurops incinctus</i>	Unbanded shovel-nosed snake	45.0	H	12.1	H	1
<i>Cacophis churchilli</i>	Northern dwarf crowned snake	42.0	H	11.2	H	1
<i>Demansia rimicola</i>	Channel country whipsnake	44.0	H	12.1	H	1
<i>Demansia torquata</i>	Collared whipsnake	43.0	H	12.6	H	1
<i>Denisonia maculata</i>	Ornamental snake	45.2	H	11.6	H	1
<i>Drysdalia mastersii</i>	Masters' snake	41.0	H	12.5	H	1
<i>Oxyuranus microlepidotus</i>	Inland taipan	43.0	H	12.1	H	1
<i>Pseudonaja ingrami</i>	Ingram's brown snake	44.0	H	11.7	H	1
<i>Cryptophis boschmai</i>	Carpentaria snake	39.3	M	10.6	H	2
<i>Cryptophis nigrostriatus</i>	Black-striped snake	40.1	M	11.2	H	2
<i>Drysdalia rhodogaster</i>	Mustard-bellied snake	39.6	M	12.0	H	2
<i>Parasuta flagellum</i>	Little whip snake	36.6	M	11.0	H	2
<i>Parasuta nigriceps</i>	Mitchell's short-tailed snake	34.0	M	10.6	H	2
<i>Pseudechis colletti</i>	Collett's snake	41.0	H	10.3	M	2
<i>Pseudonaja guttata</i>	Speckled brown snake	41.0	H	10.3	M	2
<i>Rhinoplocephalus bicolor</i>	Square-nosed snake	40.0	M	11.8	H	2
<i>Acanthophis pyrrhus</i>	Desert death adder	34.3	M	8.7	M	3
<i>Acanthophis wellsi</i>	Pilbara death adder	34.3	M	9.3	M	3
<i>Antairoserpens warro</i>	Robust burrowing snake	39.0	M	10.2	M	3
<i>Austrelaps labialis</i>	Pygmy copperhead	36.3	M	9.7	M	3
<i>Austrelaps ramsayi</i>	Highlands copperhead	28.6	M	8.4	M	3
<i>Austrelaps superbus</i>	Lowlands copperhead	29.3	M	8.0	M	3
<i>Brachyurops australis</i>	Australian coral snake	32.7	M	7.4	M	3
<i>Cacophis harriettae</i>	White-crowned snake	38.5	M	10.4	M	3
<i>Cacophis krefftii</i>	Southern dwarf crowned snake	28.0	M	9.1	M	3
<i>Cacophis squamulosus</i>	Golden-crowned snake	25.4	M	7.2	M	3
<i>Cryptophis nigrescens</i>	Eastern small-eyed snake	29.1	M	8.8	M	3
<i>Demansia calodera</i>	Black-necked whipsnake	27.3	M	8.1	M	3
<i>Denisonia devisi</i>	De vis' banded snake	32.3	M	9.5	M	3
<i>Drysdalia coronoides</i>	White-lipped snake	29.3	M	8.6	M	3
<i>Echiopsis curta</i>	Bardick	30.0	M	8.4	M	3
<i>Elapognathus minor</i>	Short-nosed snake	25.4	M	7.8	M	3
<i>Furina diadema</i>	Red-naped snake	30.6	M	9.1	M	3
<i>Furina tristis</i>	Brown-headed snake	40.0	M	10.1	M	3
<i>Hemiaspis damelii</i>	Grey snake	34.5	M	8.8	M	3
<i>Hoplocephalus bungaroides</i>	Broad-headed snake	37.7	M	10.2	M	3
<i>Hoplocephalus stephensii</i>	Stephens' banded snake	34.0	M	10.0	M	3
<i>Notechis scutatus</i>	Tiger snake	26.0	M	7.8	M	3
<i>Oxyuranus scutellatus</i>	Coastal taipan	28.9	M	9.2	M	3
<i>Parasuta dwyeri</i>	Dwyer's snake	29.3	M	8.2	M	3
<i>Parasuta monachus</i>	Monk snake	25.4	M	8.0	M	3
<i>Parasuta spectabilis</i>	Mallee black-headed snake	36.0	M	9.2	M	3
<i>Pseudechis butleri</i>	Spotted mulga snake	38.5	M	9.6	M	3

<i>Pseudonaja inframacula</i>	Peninsula brown snake	32.3	M	9.0	M	3
<i>Pseudonaja textilis</i>	Eastern brown snake	26.4	M	7.6	M	3
<i>Simoselaps anomalus</i>	Desert banded snake	39.0	M	10.2	M	3
<i>Suta fasciata</i>	Rosen's snake	31.3	M	9.9	M	3
<i>Suta suta</i>	Myall snake	30.3	M	8.4	M	3
<i>Vermicella annulata</i>	Bandy-bandy	29.0	M	7.7	M	3
<i>Acanthophis antarcticus</i>	Common death adder	23.4	L	6.7	M	4
<i>Brachyuropsis approximans</i>	North-western shovel-nosed snake	25.0	L	6.0	M	4
<i>Brachyuropsis fasciolatus</i>	Narrow-banded shovel-nosed snake	24.0	L	6.4	M	4
<i>Brachyuropsis semifasciatus</i>	Southern shovel-nosed snake	24.4	L	7.3	M	4
<i>Demansia rufescens</i>	Rufous whipsnake	22.7	L	5.7	M	4
<i>Demansia simplex</i>	Grey whipsnake	24.0	L	6.0	M	4
<i>Elapognathus coronatus</i>	Western crowned snake	23.4	L	6.7	M	4
<i>Hemiaspis signata</i>	Black-bellied swamp snake	24.6	L	7.1	M	4
<i>Hoplocephalus bitorquatus</i>	Pale-headed snake	23.0	L	7.2	M	4
<i>Neelaps bimaculatus</i>	Black-naped snake	21.7	L	5.4	M	4
<i>Neelaps calonotos</i>	Black-striped snake	25.0	L	6.0	M	4
<i>Pseudechis porphyriacus</i>	Red-bellied black snake	23.3	L	6.3	M	4
<i>Pseudonaja affinis</i>	Dugite	25.0	L	7.0	M	4
<i>Simoselaps littoralis</i>	West coast banded snake	24.0	L	6.4	M	4
<i>Tropidechis carinatus</i>	Rough-scaled snake	23.0	L	6.6	M	4
<i>Acanthophis praelongus</i>	Northern death adder	17.7	L	4.2	L	5
<i>Brachyuropsis roperi</i>	Northern shovel-nosed snake	21.0	L	5.2	L	5
<i>Cryptophis pallidiceps</i>	Northern small-eyed snake	16.5	L	3.2	L	5
<i>Demansia olivacea</i>	Olive whipsnake	20.0	L	5.2	L	5
<i>Demansia papuensis</i>	Greater black whipsnake	18.0	L	4.1	L	5
<i>Demansia psammophis</i>	Yellow-faced whipsnake	14.8	L	3.1	L	5
<i>Demansia vestigiata</i>	Lesser black whipsnake	18.7	L	4.9	L	5
<i>Furina ornate</i>	Orange-naped snake	18.7	L	4.5	L	5
<i>Parasuta gouldii</i>	Gould's hooded snake	22.0	L	5.1	L	5
<i>Pseudechis australis</i>	King brown snake	16.0	L	3.2	L	5
<i>Pseudechis guttatus</i>	Spotted black snake	19.3	L	4.7	L	5
<i>Pseudonaja modesta</i>	Ringed brown snake	15.2	L	2.9	L	5
<i>Pseudonaja nuchalis</i>	Western brown snake	16.0	L	3.2	L	5
<i>Simoselaps bertholdi</i>	Jan's banded snake	18.3	L	4.4	L	5
<i>Suta punctate</i>	Little spotted snake	17.3	L	4.0	L	5
<i>Vermicella intermedia</i>	Wide-banded northern bandy-bandy	19.7	L	4.9	L	5
<i>Vermicella snelli</i>	Pilbara bandy-bandy	21.0	L	4.4	L	5

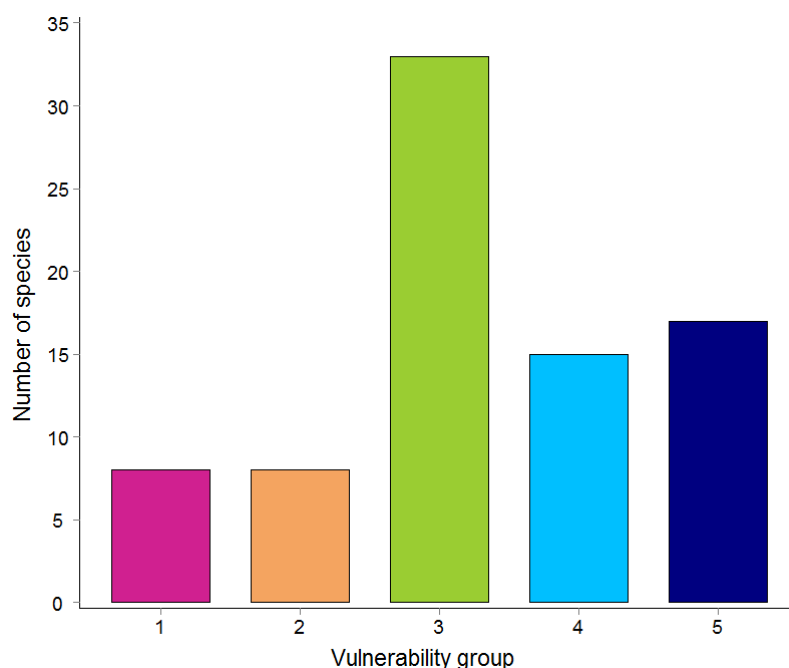


Figure 2. The number of species assigned to each vulnerability group. Group 1 represents the most vulnerable species, and group 5 represents the least vulnerable species.

Are species that appear most vulnerable to contractions in climatic range, as predicted using ENMs, also those that appear highly vulnerable due to specific life history traits?

Species assigned to vulnerability group 1 were all projected to lose large amounts of climatically suitable area and to have low degrees of overlap between their current and 2050 climatic ranges, but differed in the traits that contributed to their high scores (Supplementary Table 2). 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. The unbanded shovel-nosed snake (*Brachyuophis incinctus*) has highly specialised habitat and dietary requirements and a small clutch size, whereas the Master's snake (*Drysdalia mastersii*) is a dietary specialist and active only during the day. Unsurprisingly, therefore, the number of points awarded for ENM-related

variables was not correlated with the number of points awarded for trait-related variables for either the *additive model* ($r = 0.099$, $df = 79$, $p = 0.38$; Fig. 3a) or the *multiplicative model* ($r = 0.030$, $df = 79$, $p = 0.79$; Fig. 3b). This suggests that species traits offer additional information about climate change vulnerability that is not provided by model projections.

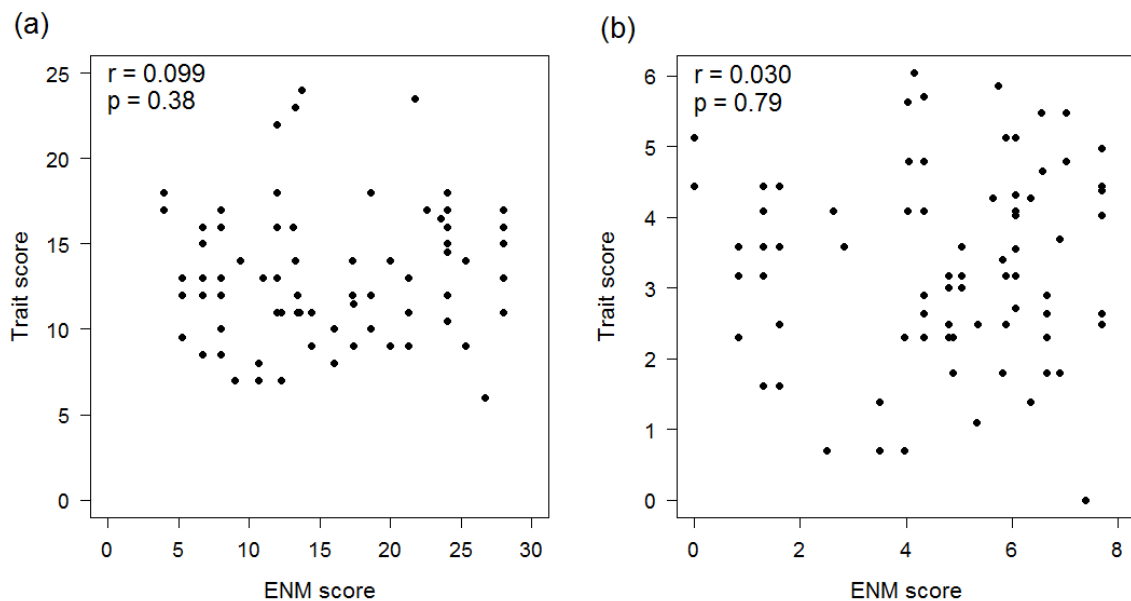


Figure 3. The relationship between the number of points awarded for ENM-related variables and the number of points awarded for trait-related variables for (a) the additive model and (b) the multiplicative model.

Do highly vulnerable species cluster in certain areas of the elapid phylogeny?

The vulnerability of species within the elapid family appears phylogenetically independent, as visual inspection revealed highly vulnerable species occur across the phylogeny (Fig. 4).

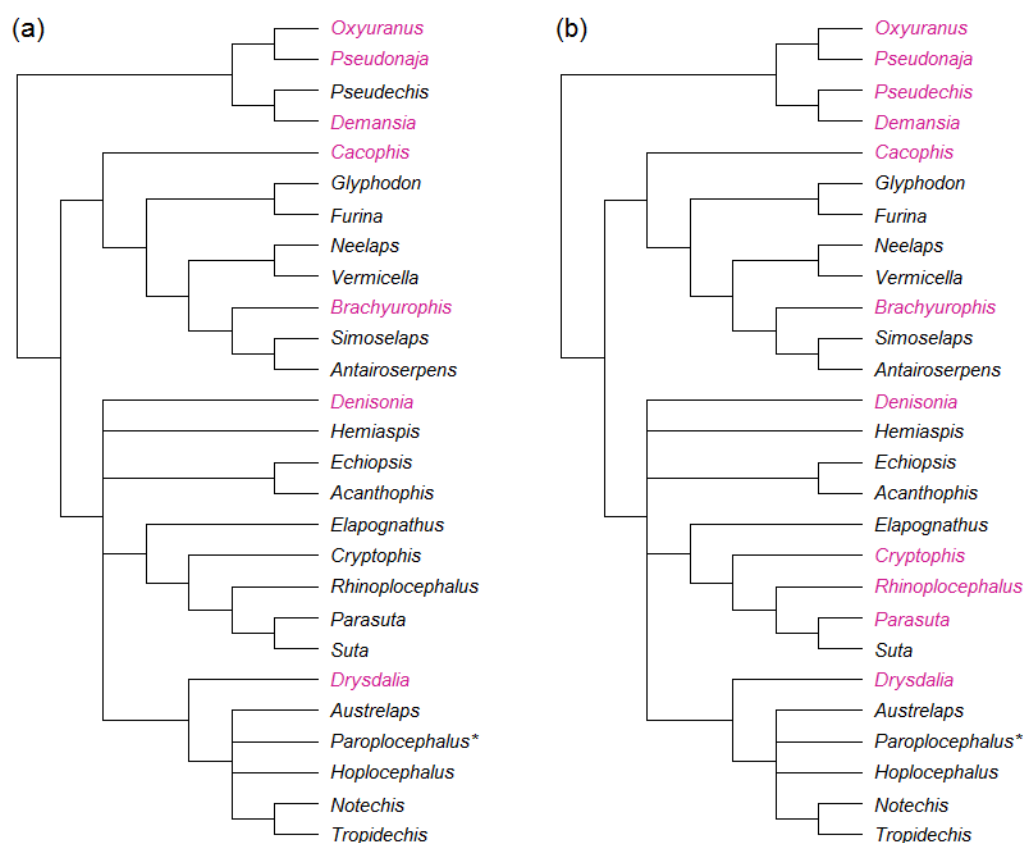


Figure 4. The phylogenetic relationships of the highly vulnerable species. The tree (adapted from Scanlon and Lee (2004)) is drawn to genera level only as the phylogenetic relationships among species are only partially resolved. Genera containing (a) the species in vulnerability group 1 and (b) the species in vulnerability groups 1 and 2 are shown in red. *The monospecific genus *Paroplocephalus* was not included in the assessment.

Does vulnerability to climate change vary among species from different biogeographic zones?

The proportion of species assigned to each vulnerability group differed among biogeographic zones (Fisher's exact test: $p = 0.026$; Fig. 5). Overall, multiregional species appeared least vulnerable, with a large proportion of species assigned to the lowest

vulnerability group (group 5) and none assigned to the highest vulnerability groups (groups 1 and 2). In contrast, tropical, temperate, arid and eastern interior regions had the greatest proportions of species represented in groups 1 and 2.

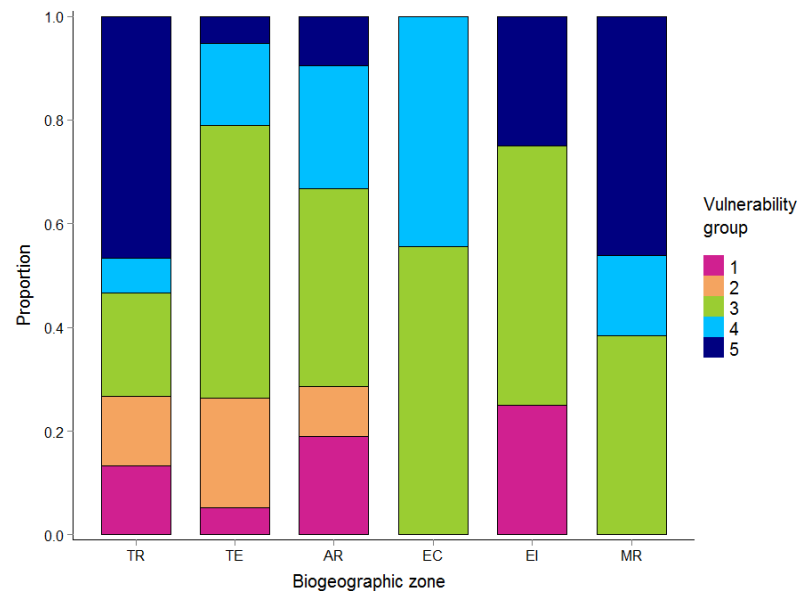


Figure 5. The proportion of species assigned to each vulnerability group among biogeographic zones. TR = tropical (15 species), TE = temperate (19 species), AR = arid (21 species), EC = east coast (9 species), EI = eastern interior (4 species) and MR = multiregional (13 species). Group 1 represents the most vulnerable species, and group 5 represents the least vulnerable species.

Are there particular regions that appear especially rich in highly vulnerable species where conservation efforts should be focused?

Analysis of the eight species assigned to group 1 highlighted the Mitchell grass downs, which spans across central west Queensland and into the Northern Territory, as the ecoregion richest in the most vulnerable species (Fig. 6a). Analysis of the 16 species

assigned to groups 1 and 2 revealed the Mitchell grass downs and the Brigalow tropical savannah, which stretches from north Queensland to the New South Wales border, as especially rich in highly vulnerable species (Fig. 6b).

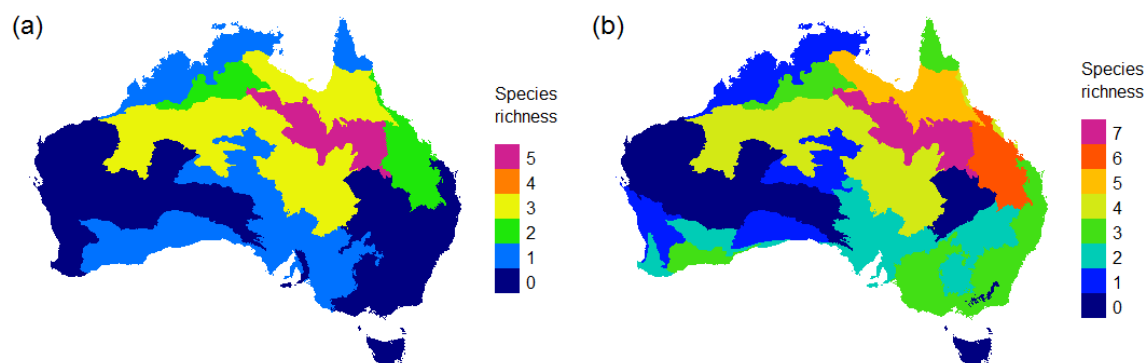


Figure 6. The richness of species assigned to (a) vulnerability group 1 and (b) vulnerability groups 1 and 2 among Australia's ecoregions.

DISCUSSION

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

In this paper, we developed a novel system for assessing species vulnerability to climate change. Applying this system to Australia's terrestrial elapid snakes, we found that 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 large amounts of climatically suitable area by 2050, and have low levels of overlap between their current and 2050 climatic ranges. Some species, including the

ornamental snake (*Denisonia maculata*) and the unbanded shovel-nosed snake (*Brachyuophis incinctus*), 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.

Previous work investigating broad-scale biogeographic patterns in species responses to climate change has suggested 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 also expected to experience the greatest increase in the number of days with a daily maximum temperature of at least 35°C (Whetton 2011). 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. Despite these expectations, we did not find that species from tropical regions were significantly more vulnerable to climate change than species from temperate or arid regions. This may be because we were unable to incorporate physiological traits in the framework due to a lack of data, or alternatively because additional factors render species from these other regions equally vulnerable, such as the limited opportunities for southerly expansions of species ranges in temperate regions and the large increases in mean annual temperatures predicted in the arid zone. Similar analyses of other taxonomic groups will be required to test the consistency of this finding.

Identifying potentially important areas for biodiversity conservation is a principal goal of climate change research. Accordingly, we identified two ecoregions that are especially rich in vulnerable elapids: the Mitchell grass downs and the Brigalow tropical savannah. In the short term, the availability of thermally sheltered microhabitats in these areas, such as the cracking, clay soils that characterise the Mitchell grass downs, may be sufficient to buffer species against the impacts of climate change. In the longer term, the low representation of these regions in the protected area network, and the large areas that are currently under threat from stressors such as land clearing, introduced predators and grazing, will need to be addressed. Conservation efforts to protect native habitat and maximise connectivity between protected areas may be necessary to enhance the resilience of vulnerable species against the impacts of climate change. These actions also have the potential to benefit other elapids found in these ecoregions, such as the threatened Dunmall's snake (*Furina dunmalli*) which was too rare to be included in this assessment due to a lack of occurrence records.

The importance of incorporating species traits in vulnerability assessments

Assessments of climate change vulnerability frequently use the projections of ENMs as the sole means of evaluation. In this study, we have extended these methods by incorporating information on species ecological and life-history traits. We believe accounting for the ecological differences between species is important for three principal reasons:

1. Ecological and life-history traits can provide useful, additional information to complement assessments based on the projections of ENMs.

Two variables, the ‘change in climatic range size’ and the ‘change in climatic suitability’, highlight areas that currently meet species environmental requirements, but are unlikely to do so in the future. However, species that possess traits that enhance their adaptive capacity to climate change, such as high phenological and behavioural plasticity and the ability to burrow, may be able to persist in areas that become climatically unfavourable. *Brachyurophis australis*, for instance, was projected to lose over 50% of its current climatic range by 2050, but its fossorial lifestyle may help it persist in areas that become unsuitable, at least in the short term. Conversely, species may have been projected to experience an increase in climatic range size, but possess traits that prevent them from expanding their realised distributions into novel areas. For example, the broad-headed snake (*Hoplocephalus bungaroides*) was projected to experience a range expansion of 113%, but may not be able to take advantage of this increase in climatic space if its restriction to weathered sandstone outcrops limits dispersal to new locations. In these cases, a consideration of ENM-related variables by themselves would be misleading. Including information on species traits is therefore important because, by modifying the inferences drawn from the projections of ENMs, it can influence the ways in which conservation resources are allocated.

2. A consideration of species traits can help identify knowledge gaps.

Many traits that are considered important determinants of species vulnerability to climate change, but for which little data were available, were excluded from this assessment. For example, we excluded dispersal ability as 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), whether they are constrained within an individual's home range has yet to be determined. Further, 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.

3. Multi-variable assessments can aid decision making.

Assessments that incorporate multiple variables can 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, high scores for the variable 'overlap between the current and 2050 climatic ranges' highlight species that might benefit most from strategies to increase connectivity between suitable habitats to facilitate dispersal. If that 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). Alternatively, if a species is predicted to experience dramatic reductions in the climatic suitability of certain areas within its range and does not possess traits which may enable it to buffer the impacts of climate change, efforts to encourage persistence in these areas, such as by promoting microhabitat heterogeneity through habitat restoration, may not be worthwhile. 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. 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 environmental niche 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 least vulnerable 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 provide greater justification for allocating resources to regions critical to the persistence of vulnerable species.

CONCLUSION

Frameworks that provide a system for assessing species according to their vulnerability to climate change can offer considerable guidance to conservation programs that need to allocate limited resources among a large number of taxa (Millsap *et al.* 1990).

Vulnerability assessments frequently use the projections of ENMs to identify which species are likely to be most at risk in the future, but ignore the ecological traits that may influence whether or not these projections are indeed realised. In light of the accelerating rate of climate change, and in response to increased calls for information from decision makers, there is now a need to develop more comprehensive methods for identifying vulnerable species that remain simple to apply. We believe that a consideration of species traits together with the projections of ENMs provides a means by which this can be achieved.

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CHAPTER 5

A vulnerability assessment of Australian skinks

ABSTRACT

A novel framework for assessing species vulnerability to climate change was developed and applied to the largest family of reptiles in Australia, the scincid lizards (skinks). This framework assessed vulnerability by explicitly considering species susceptibility and adaptive capacity, and integrated variables based on the projections of environmental niche models (ENMs) and species ecological and life history traits. We found vulnerability to be highly variable among species, suggesting that responses to climate change will be idiosyncratic. Importantly, we identified a number of species that, by virtue of their ecological traits and model projections, may be at risk of climate change impacts in the near future. Biogeographic patterns in vulnerability were evident, with species inhabiting Australia's arid and semi-arid zone appearing most vulnerable overall. Certain regions within the arid and semi-arid zone were also identified as being particularly rich in the most vulnerable species. The framework presented here can assist with decisions regarding resource allocation by identifying which approaches may afford the best protection to species in the face of climate change.

Keywords: adaptive capacity, climate change, environmental niche modelling, risk assessment, Scincidae, species traits, susceptibility, vulnerability

INTRODUCTION

Impacts of climate change on Australia's biota are already apparent, with evidence these changes are driving range shifts, phenological mismatches and population declines among numerous taxa (Hughes 2003; Steffen *et al.* 2009). Australia is committed to further warming (Whetton 2011), raising concerns that these impacts will increase in scope and scale over the coming decades. To successfully prepare for, and adapt to, the effects of climate change, it is imperative that susceptible species and systems are identified and appropriate management efforts initiated without delay.

Vulnerability assessments offer a key tool for helping managers prioritise conservation resources by highlighting the species and regions that are likely to face the most significant consequences of future climate change (Williams *et al.* 2008). These assessments can also identify knowledge gaps, as well as provide a basis for developing appropriate management strategies by ascertaining the specific factors contributing to vulnerability. Assessing vulnerability to climate change has received considerable attention over recent years, and systems have been developed for a variety of taxa and regions in Australia, including sharks and rays (Chin *et al.* 2010), marine ecosystems (Hobday *et al.* 2006), and the Great Barrier Reef (Johnson and Marshall 2007). In this paper, we present the first vulnerability assessment of a relatively understudied taxonomic group, the Australian scincid lizards (family Scincidae).

Scincid lizards (skinks) are a widespread family of reptiles found throughout Australia, western Asia, North Africa, Mediterranean Europe, temperate North America and northern South America (Hutchinson 1993). Diversity and endemism are especially high in

Australia where they comprise the largest family of reptiles, numbering almost 400 species across three monophyletic lineages: Sphenomorphus, Egernia and Eugongylus (Wilson and Swan 2008). Skinks exhibit an enormous variation in ecological and life history traits (Hutchinson 1993), some of which are expected to increase species vulnerability to climate change. Several species, for instance, are habitat specialists showing considerable fidelity to particular vegetation and soil types (Pianka 1969a), a few possess temperature-dependent sex determination (TSD) (e.g. Telemeco *et al.* 2009) and many have very limited dispersal capabilities (e.g. Dubey and Shine 2010). A few are restricted to montane areas, where warming may cause habitats to disappear entirely (Williams *et al.* 2003; Dubey and Shine 2011). Some species are also already under considerable threat from habitat degradation and invasive predators (Cogger *et al.* 1993), and may be less able to tolerate changes in climate.

The assessment framework presented here is built upon a previous system developed for Australia's elapid snakes (see Chapter 4). This system integrated the output of environmental niche models (ENMs), statistical tools that correlate species occurrences with environmental data to generate predictions of species future distributions, and information on species ecological and life history traits. In so doing, this approach provides a more comprehensive and rigorous method for assessing vulnerability than systems based solely on model projections. In the present study, we modified the framework presented in Chapter 4 to explicitly distinguish between the two components of vulnerability – *susceptibility* and *adaptive capacity* (Fig. 1) – to provide a stronger basis for decision-making. For example, species with a high susceptibility but a high adaptive capacity may be similar to species with a low susceptibility and a low adaptive capacity in terms of overall vulnerability, but may require different management interventions. Thus,

considering these two components separately should help define appropriate conservation strategies, and increase the likelihood such strategies will be effective.

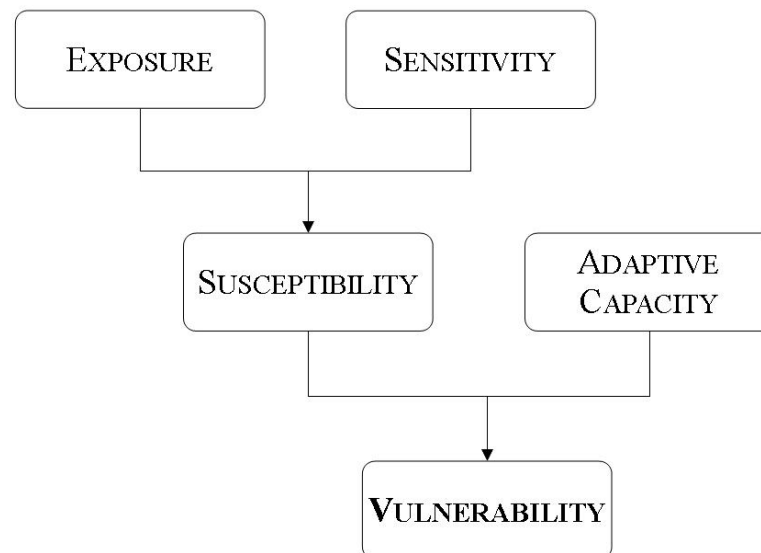


Figure 1. The vulnerability of a species to climate change is a function of its susceptibility to climate change and its adaptive capacity. Susceptibility relates to the potential for adverse consequences to occur and is determined by the magnitude of climatic changes across the species range (exposure) and the degree to which the species will be affected by these changes in the absence of an adaptive response (sensitivity). Susceptibility can be assessed using ENMs, but is also influenced by species attributes such as habitat and dietary specialisation, geographic range size and environmental niche breadth. Adaptive capacity refers to a species ability to adjust to climate change, take advantage of opportunities, and recover following environmental perturbations. Traits that are expected to influence the adaptive capacity of species include dispersal ability, behavioural and phenological plasticity, reproductive output and evolutionary potential.

METHODS

The framework adopted a points-based system in which species were allocated points for a number of variables, including those based on the output of ENMs and those based on ecological and life history traits. These variables were derived as follows:

Variables based on the output of ENMs

We assembled a species list using the most recently published field guide to Australia's reptiles which describes 387 species of skinks (Wilson and Swan 2008), updated with recent changes in nomenclature (Gardner *et al.* 2008; Mecke *et al.* 2009). Occurrence data were compiled from the Global Biodiversity Information Facility (www.gbif.org) and Biomaps (www.biomaps.net.au), and were supplemented with records obtained directly from the Western Australian Museum (via NatureMap), the Tasmanian Museum and Art Gallery and the Atlas of NSW Wildlife. We excluded species with fewer than 15 geographically distinct records to reduce errors associated with small sample sizes (Supplementary Table 1) (Wisz *et al.* 2008), leaving 315 species to be included in the assessment. Records that were clearly erroneous due to incorrect geocoding were subsequently removed.

Current climate data (1960-2000) were obtained from the Australian Bureau of Meteorology (www.bom.gov.au) and were used to derive five climatic variables (Busby 1991): annual mean temperature, temperature seasonality, minimum temperature of the coldest month, maximum temperature of the hottest month and annual precipitation. These

variables were chosen because of their presumed influence on the physiological limits of reptiles, and have been used successfully in previous work to model range shifts in this taxonomic group (see Chapter 4). Climate projections for 2050 were obtained from four global circulation models (GCMs) believed to produce reasonably reliable projections of future climate in Australia (CSIRO and BoM 2007). These were based on the A2 emission scenario, which has been found to closely match observed atmospheric CO₂ levels (Raupach *et al.* 2007).

We used an ensemble of six, widely adopted algorithms to model the current and 2050 climatic ranges of each species: generalised linear models, generalised additive models, boosted regression trees, artificial neural networks, multivariate adaptive regression splines and maximum entropy models (Thuiller 2003; Phillips *et al.* 2006). We assessed the performance of the algorithms by calculating the area under the receiver operating characteristic curve (AUC) using a 10-fold cross-validation procedure. By convention, an AUC score > 0.9 indicates excellent performance, 0.8-0.9 indicates good performance, 0.7-0.8 indicates fair performance and < 0.7 indicates poor performance. For each species, the two worst-performing algorithms (lowest AUC scores) were eliminated from further analysis. The average AUC score of the remaining algorithms across all species was very high (0.964) indicating the algorithms generally performed extremely well.

We used the remaining four algorithms to model the current and 2050 climatic ranges for each species. The resulting maps comprised a series of grid cells, each containing a climate suitability value ranging from 0 (entirely unsuitable for the species) to 1 (entirely suitable). To obtain a single projection for each time period we calculated a weighted mean by weighting each projection according to that algorithm's AUC score (Marmion *et al.* 2009).

These final range maps were then converted into presence-absence maps using a threshold equal to the weighted average of the sensitivity-specificity equality thresholds for each algorithm.

To provide an index of uncertainty in the model projections, we used principal component analysis (PCA; see Thuiller (2004) for more details of this method). The first axis of the PCA represents the greatest proportion of variation among the model forecasts, and can provide a guide for decision makers as to how reliable these forecasts are.

The consensus maps were used to calculate the following four variables:

1. Change in climatic range size

We used the presence-absence maps to calculate an estimate of the change in climatic range size by 2050 based on the percentage change in the number of suitable grid cells. A value $> 100\%$ indicates the 2050 climatic range is larger than the current climatic range (low vulnerability) and a value $< 100\%$ indicates the 2050 climatic range is smaller (high vulnerability). We categorised species according to their projected change in climatic range size by dividing the range of values into quartiles (change in range size $< 1^{\text{st}}$ quartile; 1^{st} quartile \leq change in range size $<$ median; median \leq change in range size $< 3^{\text{rd}}$ quartile; change in range size $\geq 3^{\text{rd}}$ quartile), thus creating four equal-sized classes to which species could be assigned. We followed this procedure for all of the continuous variables used in the assessment.

2. Overlap between the current and 2050 climatic ranges

Using the presence-absence maps, we calculated the percentage overlap between the current and 2050 climatic ranges to infer the pressure species will be under to disperse: ranges that are entirely disjunct indicate the species will have to disperse from all areas of its current climatic range to reach areas that become suitable in the future (high vulnerability), whereas a high percentage overlap indicates much of the current climatic range will remain suitable by 2050, and the need for dispersal will be less (low vulnerability).

3. Change in climatic suitability

Using the non-thresholded maps, we set all cell values below the consensus threshold to 0, but retained all values above the threshold, generating a heterogeneous range comprising various values of climate suitability. The change in climatic suitability between the current and 2050 ranges was calculated as the percentage change in the average grid cell value across each range. A value $>100\%$ indicates conditions in the 2050 climatic range are more suitable for the species than the current climatic range (low vulnerability) and a value $<100\%$ indicates conditions are less suitable (high vulnerability).

4. Overlap with the protected area network

We overlaid each species current and 2050 climatic ranges with a GIS layer of Australia's protected area network, downloaded from the Collaborative Australia Protected Area Database (CAPAD: www.environment.gov.au/parks/nrs/science/capad), and calculated the

percentage change in the number of suitable grid cells that fell within the network. A value $>100\%$ indicates a higher proportion of the 2050 climatic range overlaps the network compared to the current climatic range (low vulnerability), whereas a value $<100\%$ indicates a lower proportion of the 2050 climatic range overlaps the network (high vulnerability).

Variables based on species traits

The vulnerability of a species to climate change depends on a variety of biological traits, including its life history, ecology, behaviour, physiology and genetic make-up (Williams *et al.* 2008). Specifically, species susceptibility will be influenced by traits that increase its sensitivity, such as small geographic range size and a high degree of specialisation, and by traits that are related to its exposure, including whether the species is active during the daytime (and therefore more exposed to high temperatures) and whether it is able to burrow (and therefore less exposed). Traits that influence a species adaptive capacity include its degree of phenological and behavioural plasticity, reproductive output, dispersal ability and evolutionary potential.

We eliminated traits with insufficient data for our study group (e.g. abundance), as well as those that were likely to be highly correlated. For example, we chose not to include body size as a proxy for dispersal ability due to its correlation with several other traits, such as clutch / litter size. This left seven traits for inclusion in the assessment – habitat specialisation, dietary specialisation, clutch / litter size, the presence of temperature-

dependent sex determination (TSD), activity (diurnal or nocturnal), habitat (surface-dwelling or subterranean) and threatened status – which were assessed as follows:

1. Habitat specialisation

Skinks vary significantly in their habitat requirements. Some are restricted to areas containing certain vegetation types (e.g. *Ctenotus leonhardii* is most abundant in habitats dominated by *Acacia* shrubs) while others are more dependent on land form and soil (e.g. *Ctenotus brooksi* is restricted to desert sand ridges) (Pianka 1969a). Accordingly, we obtained a GIS layer of Australia's vegetation from the National Vegetation Information System (NVIS: www.environment.gov.au/erin/nvis/index) and a layer of soil types from the Australian Soil Resource Information System (ASRIS: www.asris.csiro.au/themes/Atlas). For each species, we extracted the vegetation and soil type at each occurrence point, and used Simpson's index (D) to calculate values of both vegetation and soil specialisation (Simpson 1949). These were summed to obtain an overall estimate of habitat specialisation. High habitat specialisation indicates high vulnerability and low habitat specialisation indicates low vulnerability.

2. Dietary specialisation

We classed species as *dietary generalists* (low vulnerability) if they feed on a variety of insect prey, or are omnivorous, and as *dietary specialists* (high vulnerability) if they are known to specialise on a particular prey type. Some species have been found to specialise on termites, but it is not known whether this reflects true dietary specialisation or opportunism in taking advantage of an abundant resource (Pianka 1969b; Hutchinson

1993). We took a precautionary approach and classified these species as specialists, but note that in some instances this may have caused us to overestimate vulnerability.

3. Clutch / litter size

Estimates of clutch and litter sizes were sourced from published data. Values were not found for approximately 37% of species. Because clutch / litter size is strongly related to body size in reptiles (Shine 1985), we used regression to estimate clutch / litter sizes where these data were missing. Where there was documented evidence that species did not reproduce annually, we adjusted these estimates accordingly. We classified species with clutch / litter sizes \geq the median for the entire family as having *large* clutch / litter sizes (low vulnerability) and those with clutch / litter sizes $<$ median as having *small* clutch / litter sizes (high vulnerability).

4. Presence of temperature-dependent sex determination (TSD)

Species were classed as *TSD* (high vulnerability) or *GSD* (low vulnerability). We took a precautionary approach and assigned species that possess both TSD and GSD (e.g. *Acritoscincus duperreyi*; Shine *et al.* 2002) to the high vulnerability category. If no data were available for a species, we assumed it possesses GSD as this is by far the most common sex determining mode in this taxonomic group.

5. Activity

We classified species as *diurnal* if it is only ever active during the daytime (high vulnerability), and *crepuscular* / *nocturnal* if it is predominantly active during the evenings and at night (low vulnerability). We included species that are active during both day and night in the low vulnerability category as this plasticity in activity period is expected to increase the potential for species to adapt.

6. Habitat

We classified the habitat of species into one of the following two groups: *surface dwelling* species that are active on the ground surface, are saxicolous (rock dwelling), or are arboreal (high vulnerability), and *subterranean* species which are predominantly active underground (low vulnerability).

7. Threatened status

We included threatened status as a variable to indirectly incorporate information on a species distribution size and abundance, criteria commonly used in determining extinction risk, while circumventing the need for accurate estimates of these attributes. Species were classified 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). Species that are listed

only under a state act and are geographically restricted to that state were also classified as threatened.

Constructing the framework

Because the 11 variables included in the framework are unlikely to be equally important determinants of species vulnerability to climate change, we chose to weight these variables by their perceived importance. To achieve this, we elicited the opinions of eight experts in Australian herpetology, whose research interests include climate impacts, using the Delphi process, a recognised technique for improving consensus among a panel of participants (Hsu and Sandford 2007). The experts completed an on-line questionnaire in which they were asked to rank the 11 variables in order of importance (Fig. 2). The results were collated and returned to the participants who were then asked to rank the variables a second time. The results of the second round were used to weight the variables. We assigned 11 points to the variable considered by the experts to be the most important, ‘threatened status’, ten points to the second most important variable ‘overlap between the current and 2050 climatic ranges’ and so on (Table 1). Two variables, ‘dietary specialisation’ and ‘clutch / litter size’ were considered equally important and were therefore assigned equal points. The minimum number of points that could be awarded to species for each variable was one. Within each variable, points were assigned to the different categories in approximately equal increments. We next classified each variable according to whether we considered it related to species susceptibility or adaptive capacity. We considered susceptibility to be influenced by traits related to species sensitivity (threatened status, habitat and dietary specialisation, presence of TSD) and those related to

species exposure (habitat, activity). Susceptibility can also be assessed by ENM projections, namely the projected change in range size, the percentage overlap between the current and 2050 ranges, and the change in climatic suitability, which effectively quantify the potential impact of climate change on species distributions. Clutch / litter size, as an indication of reproductive potential, was considered to influence the adaptive capacity of a species to climate change because reproductive potential is correlated with enhanced population recovery rates. Adaptive capacity was also considered to be affected by the overlap with the protected area network, as species that are well represented in protected areas are expected to be better able to recover from climate change impacts because they are less exposed to some other stressors, such as habitat degradation. This is supported by evidence that the degree of spatial overlap with protected areas is associated with stable or increasing population trends among threatened species (Taylor *et al.* 2011).

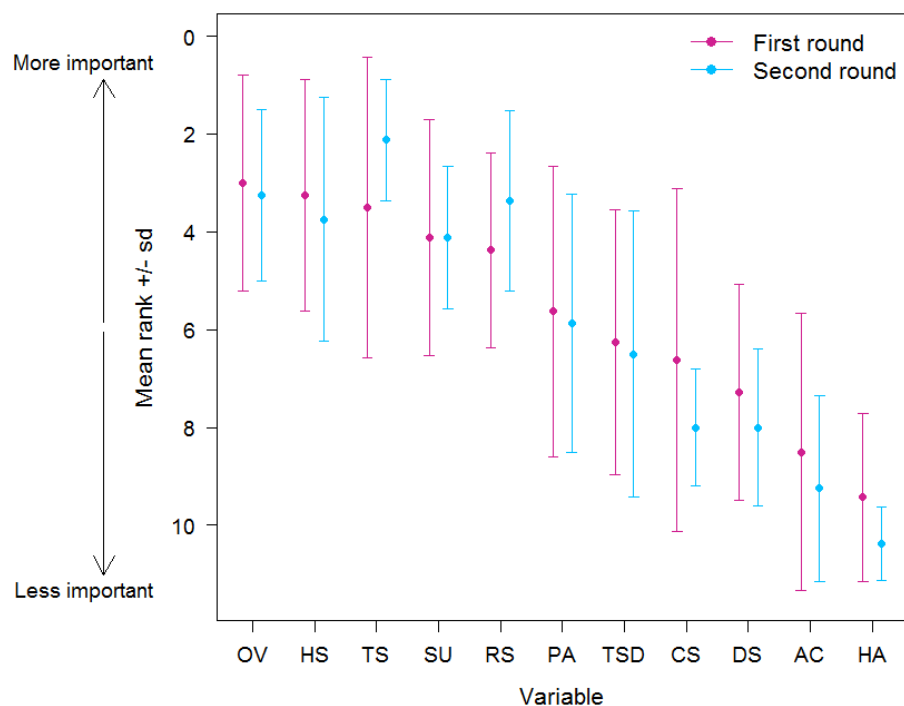


Figure 2. The mean rank (± 1 sd) of the 11 variables used in the assessment following the first and second rounds of the Delphi process. OV = overlap between the current and 2050 climatic ranges, HS = habitat specialisation, TS = threatened status, SU = change in climatic suitability, RS = change in climatic range size, PA = overlap with the protected area network, TSD = presence of temperature-dependent sex determination, CS = clutch/litter size, DS = dietary specialisation, AC = activity, HA = habitat.

Table 1. Summary of the vulnerability assessment framework

Variable	Assigned Points	Variable	Assigned Points
SUSCEPTIBILITY		6. Presence of TSD	
1. Threatened status		(a) yes	5.0
(a) threatened	11.0	(b) no	1.0
(b) not threatened	1.0		
		7. Dietary specialisation	
2. Overlap between the current and 2050 climatic ranges		(a) specialist	4.0
(a) $x < 1^{\text{st}}$ quartile	10.0	(b) generalist	1.0
(b) 1^{st} quartile $\leq x < \text{median}$	7.0		
(c) $\text{median} \leq x < 3^{\text{rd}}$ quartile	4.0	8. Activity	
(d) $x \geq 3^{\text{rd}}$ quartile	1.0	(a) diurnal	3.0
		(b) crepuscular / nocturnal	1.0
3. Change in climatic range size			
(a) $x < 1^{\text{st}}$ quartile	9.0	9. Habitat	
(b) 1^{st} quartile $\leq x < \text{median}$	6.3	(a) surface-dwelling	2.0
(c) $\text{median} \leq x < 3^{\text{rd}}$ quartile	3.7	(b) subterranean	1.0
(d) $x \geq 3^{\text{rd}}$ quartile	1.0		
		ADAPTIVE CAPACITY	
4. Habitat specialisation		1. Overlap with the protected area network	
(a) $x < 1^{\text{st}}$ quartile	8.0	(a) $x < 1^{\text{st}}$ quartile	6.0
(b) 1^{st} quartile $\leq x < \text{median}$	5.7	(b) 1^{st} quartile $\leq x < \text{median}$	4.3
(c) $\text{median} \leq x < 3^{\text{rd}}$ quartile	3.3	(c) $\text{median} \leq x < 3^{\text{rd}}$ quartile	2.7
(d) $x \geq 3^{\text{rd}}$ quartile	1.0	(d) $x \geq 3^{\text{rd}}$ quartile	1.0
5. Change in climatic suitability		2. Clutch / litter size	
(a) $x < 1^{\text{st}}$ quartile	7.0	(a) small	4.0
(b) 1^{st} quartile $\leq x < \text{median}$	5.0	(b) large	1.0
(c) $\text{median} \leq x < 3^{\text{rd}}$ quartile	3.0		
(d) $x \geq 3^{\text{rd}}$ quartile	1.0		

To quantify overall vulnerability to climate change, we adopted a similar approach to Chapter 4 and identified two models for combining species variables scores – an *additive model* and a *multiplicative model*. For the additive model, we summed the points for the relevant variables to obtain a susceptibility score (out of a possible 59) and an adaptive capacity score (out of a possible 10). For the multiplicative model we repeated this process but logged species variable scores before summing them. For each model, we calculated the range of possible values for the susceptibility and adaptive scores, and assigned species to one of three classes – ‘high-’ ‘moderate-’ or ‘low vulnerability’ – using the risk matrix illustrated in Figure 3.

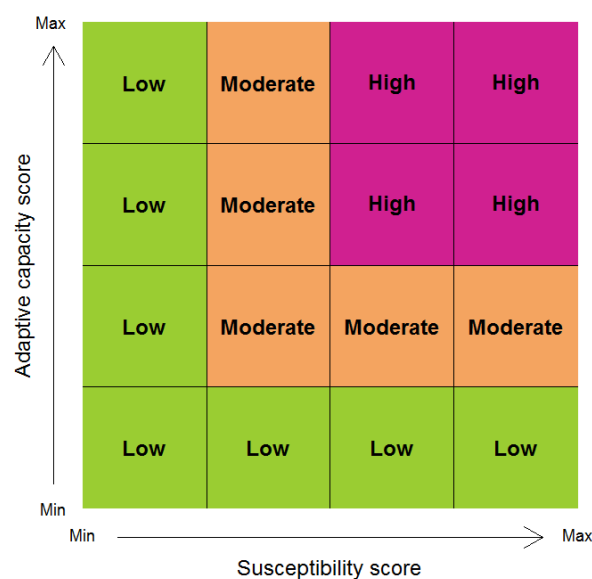


Figure 3. Risk matrix for defining species vulnerability as ‘high’, ‘moderate’ or ‘low’ depending on their susceptibility and adaptive capacity scores. Each axis covers the entire range of possible scores (e.g. the range of possible susceptibility scores for the additive model was 9 to 59) and not just the range of scores awarded to species.

To integrate the results of the additive and multiplicative models, we assigned species to overall vulnerability groups based on the following criteria. Species that were defined as ‘high vulnerability’ according to both the additive and multiplicative models were assigned to vulnerability group 1 (highest vulnerability). Those defined as ‘high vulnerability’ according to one model, and ‘moderate vulnerability’ according to the other model were assigned to group 2. Those defined as ‘moderate vulnerability’ according to both models were assigned to group 3. Those defined as ‘moderate vulnerability’ according to one model, and ‘low vulnerability’ according to the other model, were assigned to group 4. Those species defined as ‘low vulnerability’ according to both the additive and multiplicative models were assigned to group 5 (lowest vulnerability).

Analysis

We investigated broad-scale biogeographical patterns in vulnerability scores by assigning each species to one of six biogeographic zones based on their realised distributions (Wilson and Swan 2008): tropical / subtropical, temperate, arid / semi-arid, eastern, Mediterranean (southwestern Western Australia) and multiregional (species occurring in more than one zone). Differences between biogeographic groups were assessed using non-parametric statistical tests.

To perform a finer scale analysis, we obtained a GIS layer of Australia’s 37 terrestrial ecoregions, defined as large areas containing a geographically distinct assemblage of natural communities that share a large majority of species and have similar environmental conditions (Olson *et al.* 2001). Overlaying this layer with each species occurrence records,

we determined which species inhabit each ecoregion, and identified the ecoregions that appear especially rich in vulnerable species.

RESULTS

ENM projections

The projections of ENMs were highly variable among species (Supplementary Table 2). The majority of species (71%) were projected to experience contractions in their climatic range by 2050, with 21 (6.7%) species projected to lose all climatically suitable area. By default, all species that were projected to lose all climatically suitable area were also highly vulnerable according to the other three ENM-related variables. Most of these species have very restricted distributions (e.g. *Ctenotus kurnbudi*) but some are more widespread (e.g. *C. joanae*). Having a restricted distribution did not automatically confer high vulnerability, however, as there were some small-ranged species that were not projected to lose all climatically suitable area (e.g. *Lampropholis robertsi*) and some whose climatic range was even projected to expand (e.g. *Lerista allochira*). Twenty of the 21 species that were projected to lose all climatically suitable area by 2050 inhabit either arid / semiarid or tropical / subtropical regions. The least vulnerable species according to their ENM projections were *C. rutilans* and *Lerista neander* which were both projected to experience a range expansion of over 500%. These species have similar distributions, both being found in the arid western interior of Western Australia. Model variability, and therefore the reliability of the projections, also varied widely among species (Supplementary Table 2).

Species traits

Most skinks are diurnal heliotherms, and active on the ground surface (Supplementary Tables 2 and 3). The largest proportion of burrowing skinks occurs in Australia's arid zone, possibly due to the greater availability of suitable substrate in this region, such as sandy soils, and because subterranean habitats that provide more thermally stable and humid environments are more important in the arid zone where temperatures are highly variable and rainfall is infrequent. Nocturnal activity periods are also more common among arid zone skinks. Some species exhibit very high habitat specialisation, with ranges restricted to certain vegetation types or landforms. *Ctenotus brooksi*, for instance, is restricted to sand ridges, whereas *C. pantherinus* is invariably found in areas dominated by spinifex grass (*Triodia* sp.) (Pianka 1969a). The largest proportion of habitat specialists also occurs in the arid zone, possibly reflecting the relative homogeneity of vegetation and substrate in this region. Dietary specialisation is rare, with most species feeding on a variety of insect prey. Exceptions to this general rule include *Cyclodomorphus gerrardii*, which specialises on molluscs, and *Coeranoscincus reticulatus* which feeds predominantly on earthworms. Clutch / litter sizes are strongly related to body size ($F = 95.48$, $df = 196$, $r^2 = 0.324$, $p < 0.001$, this study) and range from one to approximately 15. Thirteen species are currently listed as threatened and three have been found to possess TSD.

Overall vulnerability

Fifty-four species (17%) were classified as 'high vulnerability' according to the additive and multiplicative models and assigned to vulnerability group 1 (Table 2, Fig. 4). These

species were generally characterised by large range contractions, low levels of overlap between their current and 2050 climatic ranges and specialist habitat requirements. The majority of species (81%), however, were identified as ‘moderate-’ or ‘low vulnerability’ according to both the additive and multiplicative models, and were assigned to vulnerability groups 3, 4 and 5.

Table 2. The scores and classes awarded by the additive and multiplicative models to each species, and the overall vulnerability group to which they were assigned. Species are ordered alphabetically within vulnerability groups. H = ‘high’, M = ‘moderate’ and L = ‘low’ vulnerability. SC = ‘susceptibility’ and AC = ‘adaptive capacity’.

Species name	ADDITIVE			MULTIPLICATIVE			Vulnerability group
	SC score	AC score	Class	SC score	AC score	Class	
<i>Carlia aerata</i>	39.7	6.7	H	10.0	2.4	H	1
<i>Carlia jarnoldae</i>	34.7	8.3	H	9.3	2.8	H	1
<i>Carlia johnstonei</i>	34.3	8.3	H	9.3	2.8	H	1
<i>Carlia tanneri</i>	42.0	10.0	H	10.3	3.2	H	1
<i>Ctenotus alacer</i>	42.0	10.0	H	10.3	3.2	H	1
<i>Ctenotus alleni</i>	42.0	7.0	H	10.3	1.8	H	1
<i>Ctenotus astarte</i>	35.0	7.0	H	9.3	1.8	H	1
<i>Ctenotus atlas</i>	35.0	8.3	H	10.3	2.8	H	1
<i>Ctenotus brachyonyx</i>	39.7	7.0	H	10.0	1.8	H	1
<i>Ctenotus burbridgei</i>	42.0	10.0	H	10.3	3.2	H	1
<i>Ctenotus calurus</i>	45.0	10.0	H	11.7	3.2	H	1
<i>Ctenotus dux</i>	39.7	10.0	H	10.0	3.2	H	1
<i>Ctenotus euclae</i>	39.0	10.0	H	10.0	3.2	H	1
<i>Ctenotus hebetior</i>	35.0	10.0	H	8.2	3.2	H	1
<i>Ctenotus joanae</i>	42.0	7.0	H	10.3	1.8	H	1
<i>Ctenotus kurnbudj</i>	39.7	7.0	H	10.0	1.8	H	1
<i>Ctenotus lateralis</i>	35.0	7.0	H	8.2	1.8	H	1
<i>Ctenotus mastigura</i>	42.0	7.0	H	10.3	1.8	H	1
<i>Ctenotus nasutus</i>	42.0	10.0	H	10.3	3.2	H	1
<i>Ctenotus nigrilineatus</i>	42.0	10.0	H	10.3	3.2	H	1
<i>Ctenotus olympicus</i>	39.7	7.0	H	10.0	1.8	H	1
<i>Ctenotus orientalis</i>	37.3	7.0	H	9.4	1.8	H	1
<i>Ctenotus pulchellus</i>	35.0	7.0	H	8.2	1.8	H	1
<i>Ctenotus schevilli</i>	42.0	7.0	H	10.3	1.8	H	1
<i>Ctenotus septenarius</i>	42.0	7.0	H	10.3	1.8	H	1
<i>Ctenotus striaticeps</i>	39.7	10.0	H	10.0	3.2	H	1
<i>Ctenotus tanamiensis</i>	42.0	7.0	H	10.3	1.8	H	1
<i>Ctenotus youngsoni</i>	42.0	7.0	H	10.3	1.8	H	1
<i>Ctenotus zastictus</i>	52.0	10.0	H	12.7	3.2	H	1
<i>Egernia hosmeri</i>	37.3	10.0	H	9.4	3.2	H	1

<i>Eremiascincus brongersmai</i>	40.0	7.0	H	9.2	1.8	H	1
<i>Eulamprus leuraensis</i>	39.7	7.0	H	10.6	1.8	H	1
<i>Hemiergis millewae</i>	36.7	6.7	H	8.2	2.4	H	1
<i>Lampropholis elongata</i>	42.0	7.0	H	10.3	1.8	H	1
<i>Lampropholis robertsi</i>	34.3	6.7	H	9.3	2.4	H	1
<i>Lerista apoda</i>	39.0	7.0	H	8.5	1.8	H	1
<i>Lerista carpentariae</i>	39.0	7.0	H	8.5	1.8	H	1
<i>Lerista elongata</i>	39.0	6.7	H	8.5	2.4	H	1
<i>Lerista eupoda</i>	39.0	7.0	H	8.5	1.8	H	1
<i>Lerista frosti</i>	39.0	10.0	H	8.5	3.2	H	1
<i>Lerista gascoynensis</i>	39.0	7.0	H	8.5	1.8	H	1
<i>Lerista humphriesi</i>	39.0	10.0	H	8.5	3.2	H	1
<i>Lerista kennedyensis</i>	39.0	10.0	H	8.5	3.2	H	1
<i>Lerista simillima</i>	39.0	10.0	H	8.5	3.2	H	1
<i>Lerista tridactyla</i>	39.0	10.0	H	8.5	3.2	H	1
<i>Lerista walker</i>	39.0	10.0	H	8.5	3.2	H	1
<i>Lerista yuna</i>	39.0	7.0	H	8.5	1.8	H	1
<i>Liopholis slateri</i>	42.0	7.0	H	8.8	1.8	H	1
<i>Liopholis striata</i>	36.7	8.3	H	8.2	2.8	H	1
<i>Lisssolepsis coventryi</i>	41.0	6.7	H	10.6	2.4	H	1
<i>Niveoscincus microlepidotus</i>	34.3	6.7	H	9.1	2.4	H	1
<i>Proablepharus kinghorni</i>	34.3	10.0	H	9.3	3.2	H	1
<i>Saproscincus czechurai</i>	39.0	6.7	H	10.0	2.4	H	1
<i>Tiliqua adelaidensis</i>	52.0	7.0	H	12.7	1.8	H	1
<i>Carlia schmeltzii</i>	27.6	8.3	M	7.9	2.8	H	2
<i>Ctenotus allopotropis</i>	29.6	6.7	M	8.4	2.4	H	2
<i>Ctenotus grandis</i>	29.7	7.0	M	9.1	1.8	H	2
<i>Ctenotus vertebralis</i>	32.0	6.7	M	8.9	2.4	H	2
<i>Cyclodomorphus branchialis</i>	33.0	10.0	M	8.6	3.2	H	2
<i>Egernia saxatilis</i>	32.0	6.7	M	8.9	2.4	H	2
<i>Morethia storri</i>	32.6	6.7	M	8.7	2.4	H	2
<i>Anomalopus brevicollis</i>	29.3	5.0	M	6.9	1.4	M	3
<i>Anomalopus mackayi</i>	51.0	5.0	M	12.0	1.4	M	3
<i>Anomalopus swansoni</i>	28.7	5.0	M	7.5	1.4	M	3
<i>Calyptotis temporalis</i>	24.4	5.0	M	6.1	1.4	M	3
<i>Carlia foliorum</i>	22.0	6.7	M	6.8	2.4	M	3
<i>Carlia laevis</i>	34.3	5.0	M	9.3	1.4	M	3
<i>Carlia longipes</i>	32.0	5.0	M	7.9	1.4	M	3
<i>Carlia macfarlani</i>	37.3	5.0	M	9.4	1.4	M	3
<i>Carlia mundivensis</i>	29.6	5.0	M	8.4	1.4	M	3
<i>Carlia pectoralis</i>	22.0	8.3	M	6.8	2.8	M	3
<i>Carlia rimula</i>	37.3	5.0	M	9.4	1.4	M	3
<i>Carlia rostralis</i>	29.6	5.0	M	8.4	1.4	M	3
<i>Carlia rubrigularis</i>	32.0	5.0	M	8.9	1.4	M	3
<i>Carlia sesbrauna</i>	39.7	5.0	M	10.0	1.4	M	3
<i>Carlia storri</i>	27.3	6.7	M	7.2	2.4	M	3
<i>Carlia tetradactyla</i>	26.6	5.0	M	7.8	1.4	M	3
<i>Cryptoblepharus litoralis</i>	35.0	5.0	M	8.2	1.4	M	3
<i>Ctenotus ariadnae</i>	22.0	5.3	M	5.3	1.5	M	3
<i>Ctenotus australis</i>	24.4	7.0	M	7.3	1.8	M	3
<i>Ctenotus brooksi</i>	29.3	10.0	M	7.5	3.2	M	3
<i>Ctenotus catenifer</i>	25.0	8.3	M	7.3	2.8	M	3
<i>Ctenotus coggeri</i>	24.4	5.3	M	7.3	1.5	M	3
<i>Ctenotus colletti</i>	23.7	6.7	M	6.3	2.4	M	3
<i>Ctenotus delli</i>	23.7	8.3	M	6.3	2.8	M	3
<i>Ctenotus gemmula</i>	22.4	8.3	M	6.2	2.8	M	3
<i>Ctenotus greeri</i>	39.7	5.0	M	10.0	1.4	M	3

<i>Ctenotus helenae</i>	24.4	5.3	M	7.3	1.5	M	3
<i>Ctenotus impar</i>	24.4	6.7	M	7.3	2.4	M	3
<i>Ctenotus maryani</i>	27.4	5.0	M	7.9	1.4	M	3
<i>Ctenotus piankai</i>	24.4	8.3	M	7.3	2.8	M	3
<i>Ctenotus quattuordecimlineatus</i>	36.7	5.3	M	9.6	1.5	M	3
<i>Ctenotus regius</i>	27.3	8.3	M	7.2	2.8	M	3
<i>Ctenotus spaldingi</i>	29.6	5.3	M	8.4	1.5	M	3
<i>Ctenotus strauchii</i>	22.0	6.7	M	6.8	2.4	M	3
<i>Ctenotus xenopleura</i>	42.0	5.0	M	10.3	1.4	M	3
<i>Egernia richardi</i>	32.0	5.3	M	8.9	1.5	M	3
<i>Egernia striolata</i>	24.3	5.3	M	6.6	1.5	M	3
<i>Eulamprus amplus</i>	22.0	5.3	M	5.3	1.5	M	3
<i>Eulamprus murrayi</i>	22.0	5.3	M	6.8	1.5	M	3
<i>Eulamprus tigrinus</i>	23.7	5.3	M	6.3	1.5	M	3
<i>Glaphyromorphus cracens</i>	40.0	5.0	M	9.2	1.4	M	3
<i>Hemiergis initialis</i>	22.0	8.3	M	5.5	2.8	M	3
<i>Lampropholis adonis</i>	32.0	5.0	M	8.9	1.4	M	3
<i>Lampropholis caligula</i>	23.3	8.3	M	5.3	2.8	M	3
<i>Lampropholis coggeri</i>	37.0	5.0	M	9.6	1.4	M	3
<i>Lampropholis couperi</i>	34.3	5.0	M	9.3	1.4	M	3
<i>Lerista allochira</i>	25.0	10.0	M	4.4	3.2	M	3
<i>Lerista arenicola</i>	28.3	7.0	M	6.9	1.8	M	3
<i>Lerista baynesi</i>	28.3	7.0	M	6.9	1.8	M	3
<i>Lerista bougainvillii</i>	26.6	6.7	M	6.6	2.4	M	3
<i>Lerista christinae</i>	26.6	10.0	M	6.6	3.2	M	3
<i>Lerista fragilis</i>	22.0	6.7	M	5.5	2.4	M	3
<i>Lerista ips</i>	29.0	10.0	M	7.1	3.2	M	3
<i>Lerista kalumburu</i>	26.7	10.0	M	6.4	3.2	M	3
<i>Lerista microtis</i>	22.0	7.0	M	5.5	1.8	M	3
<i>Lerista orientalis</i>	24.3	6.7	M	5.4	2.4	M	3
<i>Lerista picturata</i>	36.7	5.3	M	8.2	1.5	M	3
<i>Lerista punctatovittata</i>	26.6	7.0	M	6.6	1.8	M	3
<i>Lerista separanda</i>	29.0	6.7	M	7.1	2.4	M	3
<i>Lerista stylis</i>	36.7	5.0	M	8.2	1.4	M	3
<i>Lerista terdigitata</i>	24.4	5.3	M	6.1	1.5	M	3
<i>Lerista vermicularis</i>	22.0	10.0	M	4.0	3.2	M	3
<i>Lerista zietzi</i>	22.0	10.0	M	4.0	3.2	M	3
<i>Lerista zonulata</i>	31.3	5.0	M	7.5	1.4	M	3
<i>Liopholis guthega</i>	51.0	5.3	M	12.0	1.5	M	3
<i>Liopholis kintorei</i>	46.7	5.3	M	10.6	1.5	M	3
<i>Liopholis whitii</i>	25.6	6.7	M	7.1	2.4	M	3
<i>Menetia timlowi</i>	37.3	5.0	M	9.4	1.4	M	3
<i>Morethia boulengeri</i>	27.3	7.0	M	7.2	1.8	M	3
<i>Morethia taeniopleura</i>	24.4	10.0	M	7.3	3.2	M	3
<i>Niveoscincus coventryi</i>	29.6	5.0	M	8.4	1.4	M	3
<i>Niveoscincus greeni</i>	36.7	5.0	M	9.6	1.4	M	3
<i>Niveoscincus ocellatus</i>	39.0	5.0	M	9.8	1.4	M	3
<i>Niveoscincus pretiosus</i>	24.3	5.0	M	6.6	1.4	M	3
<i>Notoscincus butleri</i>	25.0	6.7	M	5.8	2.4	M	3
<i>Ophioscincus truncatus</i>	28.6	5.0	M	7.7	1.4	M	3
<i>Proablepharus reginae</i>	22.4	10.0	M	6.2	3.2	M	3
<i>Pseudemoia spenceri</i>	29.6	5.0	M	8.4	1.4	M	3
<i>Saproscincus basiliscus</i>	29.0	5.0	M	8.4	1.4	M	3
<i>Saproscincus challengerii</i>	24.0	6.7	M	7.3	2.4	M	3
<i>Saproscincus lewisi</i>	26.7	5.0	M	7.7	1.4	M	3
<i>Saproscincus oriarus</i>	39.7	5.0	M	10.0	1.4	M	3
<i>Saproscincus rosei</i>	24.4	6.7	M	7.3	2.4	M	3

<i>Saprosincus spectabilis</i>	24.3	5.0	M	6.6	1.4	M	3
<i>Saprosincus tetradactylus</i>	23.7	8.3	M	6.3	2.8	M	3
<i>Tiliqua rugosa</i>	22.3	6.7	M	6.1	2.4	M	3
<i>Acritoscincus platynotum</i>	24.4	3.7	L	7.3	1.0	M	4
<i>Bellatorias frerei</i>	24.3	3.7	L	6.0	1.0	M	4
<i>Calypotis ruficauda</i>	18.4	3.7	L	4.1	1.0	M	4
<i>Calypotis scutirostrum</i>	19.0	5.3	L	5.0	1.5	M	4
<i>Carlia vivax</i>	19.7	8.3	L	5.6	2.8	M	4
<i>Coeranoscincus frontalis</i>	36.3	3.7	L	10.0	1.0	M	4
<i>Cryptoblepharus carnabyi</i>	19.7	8.3	L	5.6	2.8	M	4
<i>Cryptoblepharus virgatus</i>	19.7	6.7	L	5.6	2.4	M	4
<i>Ctenotus essingtonii</i>	27.3	3.7	L	7.2	1.0	M	4
<i>Ctenotus eurydice</i>	29.0	3.7	L	8.4	1.0	M	4
<i>Ctenotus fallens</i>	17.3	5.3	L	4.4	1.5	M	4
<i>Ctenotus labillardieri</i>	17.3	7.0	L	4.4	1.8	M	4
<i>Ctenotus leae</i>	19.0	5.3	L	5.4	1.5	M	4
<i>Ctenotus leonhardii</i>	19.7	5.3	L	5.6	1.5	M	4
<i>Ctenotus pallescens</i>	17.3	10.0	L	4.4	3.2	M	4
<i>Ctenotus pantherinus</i>	17.3	5.3	L	4.4	1.5	M	4
<i>Ctenotus robustus</i>	16.7	5.3	L	4.2	1.5	M	4
<i>Ctenotus schomburgkii</i>	19.7	6.7	L	5.6	2.4	M	4
<i>Ctenotus taeniatus</i>	19.3	6.7	L	5.5	2.4	M	4
<i>Ctenotus taeniolatus</i>	24.4	3.7	L	7.3	1.0	M	4
<i>Cyclodomorphus celatus</i>	20.0	3.7	L	5.7	1.0	M	4
<i>Cyclodomorphus gerrardii</i>	17.7	3.7	L	4.5	1.0	M	4
<i>Cyclodomorphus michaeli</i>	20.0	5.3	L	5.7	1.5	M	4
<i>Cyclodomorphus praealtus</i>	42.3	3.7	L	10.6	1.0	M	4
<i>Cyclodomorphus venustus</i>	17.7	5.3	L	4.5	1.5	M	4
<i>Egernia cunninghami</i>	24.3	3.7	L	6.6	1.0	M	4
<i>Egernia Formosa</i>	19.0	10.0	L	5.4	3.2	M	4
<i>Egernia mcphreei</i>	24.4	3.7	L	7.3	1.0	M	4
<i>Egernia napoleonis</i>	17.3	5.3	L	4.4	1.5	M	4
<i>Eulamprus heatwolei</i>	24.0	3.7	L	7.3	1.0	M	4
<i>Eulamprus kosciuskoi</i>	26.6	3.7	L	7.8	1.0	M	4
<i>Eulamprus martini</i>	24.4	3.7	L	7.3	1.0	M	4
<i>Eulamprus quoyii</i>	22.0	3.7	L	6.8	1.0	M	4
<i>Eulamprus tenuis</i>	19.7	3.7	L	5.6	1.0	M	4
<i>Glaphyromorphus fuscicaudis</i>	24.7	3.7	L	6.6	1.0	M	4
<i>Glaphyromorphus mjobergi</i>	18.4	5.3	L	4.1	1.5	M	4
<i>Glaphyromorphus nigricaudis</i>	28.6	3.7	L	6.9	1.0	M	4
<i>Glaphyromorphus pumilus</i>	36.7	3.7	L	8.2	1.0	M	4
<i>Hemiergis decresiensis</i>	23.6	3.7	L	6.0	1.0	M	4
<i>Lampropholis amacula</i>	19.7	6.7	L	5.6	2.4	M	4
<i>Lampropholis delicata</i>	26.6	3.7	L	7.8	1.0	M	4
<i>Lampropholis guichenoti</i>	26.6	3.7	L	7.8	1.0	M	4
<i>Lerista aericeps</i>	21.3	6.7	L	4.8	2.4	M	4
<i>Lerista desertorum</i>	24.3	3.7	L	5.4	1.0	M	4
<i>Lerista dorsalis</i>	29.0	3.7	L	7.1	1.0	M	4
<i>Lerista edwardsae</i>	29.0	3.7	L	7.1	1.0	M	4
<i>Lerista labialis</i>	18.7	6.7	L	4.3	2.4	M	4
<i>Lerista taeniata</i>	19.0	10.0	L	5.0	3.2	M	4
<i>Lerista xanthura</i>	21.3	6.7	L	4.8	2.4	M	4
<i>Liopholis inornata</i>	21.3	8.3	L	4.8	2.8	M	4
<i>Liopholis modesta</i>	18.7	6.7	L	4.9	2.4	M	4
<i>Liopholis multiscutata</i>	18.7	8.3	L	4.9	2.8	M	4
<i>Liopholis pulchra</i>	19.3	7.0	L	4.2	1.8	M	4
<i>Menetia alanae</i>	21.4	8.3	L	5.9	2.8	M	4

<i>Menetia concinna</i>	17.3	10.0	L	4.4	3.2	M	4
<i>Menetia greyii</i>	16.7	8.3	L	4.2	2.8	M	4
<i>Menetia maini</i>	16.7	8.3	L	4.2	2.8	M	4
<i>Morethia adelaidensis</i>	29.6	3.7	L	8.4	1.0	M	4
<i>Morethia butleri</i>	19.7	5.3	L	5.6	1.5	M	4
<i>Morethia obscura</i>	16.7	5.3	L	4.2	1.5	M	4
<i>Niveoscincus orocryptus</i>	34.3	3.7	L	9.3	1.0	M	4
<i>Pseudemoia baudini</i>	39.7	3.7	L	10.0	1.0	M	4
<i>Pseudemoia entrecasteauxii</i>	24.3	3.7	L	6.6	1.0	M	4
<i>Pseudemoia pagenstecheri</i>	27.3	3.7	L	7.2	1.0	M	4
<i>Saiphos equalis</i>	19.0	3.7	L	5.0	1.0	M	4
<i>Saproscincus mustelinus</i>	29.0	3.7	L	8.4	1.0	M	4
<i>Tiliqua occipitalis</i>	19.7	3.7	L	5.6	1.0	M	4
<i>Tiliqua scincoides</i>	16.7	5.3	L	4.2	1.5	M	4
<i>Acritoscincus duperreyi</i>	31.3	2.0	L	8.8	0.0	L	5
<i>Acritoscincus trilineatus</i>	14.3	5.3	L	3.0	1.5	L	5
<i>Anepischetosia maccoyi</i>	26.6	2.0	L	6.6	0.0	L	5
<i>Anomalopus leuckartii</i>	15.7	3.7	L	3.5	1.0	L	5
<i>Anomalopus verreauxii</i>	23.3	2.0	L	5.9	0.0	L	5
<i>Bellatorias major</i>	15.7	3.7	L	3.5	1.0	L	5
<i>Calypotis lepidorostrum</i>	27.3	2.0	L	5.8	0.0	L	5
<i>Carlia amax</i>	12.0	8.3	L	1.8	2.8	L	5
<i>Carlia gracilis</i>	12.0	8.3	L	1.8	2.8	L	5
<i>Carlia munda</i>	12.0	8.3	L	1.8	2.8	L	5
<i>Carlia rhomboidalis</i>	16.7	8.3	L	3.5	2.8	L	5
<i>Carlia rufilatus</i>	12.0	10.0	L	1.8	3.2	L	5
<i>Carlia triacantha</i>	12.0	6.7	L	1.8	2.4	L	5
<i>Coeranoscincus reticulatus</i>	44.0	2.0	L	12.0	0.0	L	5
<i>Cryptoblepharus megastictus</i>	16.7	10.0	L	3.5	3.2	L	5
<i>Cryptoblepharus plagiocephalus</i>	12.0	6.7	L	1.8	2.4	L	5
<i>Ctenotus arcanus</i>	32.0	2.0	L	8.9	0.0	L	5
<i>Ctenotus arnhemensis</i>	16.7	10.0	L	3.5	3.2	L	5
<i>Ctenotus borealis</i>	16.7	7.0	L	3.5	1.8	L	5
<i>Ctenotus decaneurus</i>	14.3	8.3	L	3.0	2.8	L	5
<i>Ctenotus duricola</i>	19.0	10.0	L	3.9	3.2	L	5
<i>Ctenotus gagudju</i>	19.0	10.0	L	3.9	3.2	L	5
<i>Ctenotus hanloni</i>	14.3	2.0	L	3.0	0.0	L	5
<i>Ctenotus hilli</i>	12.0	10.0	L	1.8	3.2	L	5
<i>Ctenotus iapetus</i>	22.7	2.0	L	6.1	0.0	L	5
<i>Ctenotus ingrami</i>	26.7	2.0	L	7.7	0.0	L	5
<i>Ctenotus inornatus</i>	12.0	3.7	L	1.8	1.0	L	5
<i>Ctenotus militaris</i>	14.3	8.3	L	3.0	2.8	L	5
<i>Ctenotus mimetes</i>	14.3	2.0	L	3.0	0.0	L	5
<i>Ctenotus rimacola</i>	16.7	5.3	L	3.5	1.5	L	5
<i>Ctenotus rubicundus</i>	19.0	7.0	L	3.9	1.8	L	5
<i>Ctenotus rufescens</i>	14.3	6.7	L	3.0	2.4	L	5
<i>Ctenotus rutilans</i>	19.0	5.0	L	3.9	1.4	L	5
<i>Ctenotus saxatilis</i>	16.7	5.3	L	3.5	1.5	L	5
<i>Ctenotus serventyi</i>	16.7	5.0	L	3.5	1.4	L	5
<i>Ctenotus severus</i>	19.0	2.0	L	3.9	0.0	L	5
<i>Ctenotus storri</i>	14.3	10.0	L	3.0	3.2	L	5
<i>Ctenotus tantillus</i>	16.7	8.3	L	3.5	2.8	L	5
<i>Ctenotus uber</i>	14.3	6.7	L	3.0	2.4	L	5
<i>Cyclodomorphus casuarinae</i>	22.3	2.0	L	5.5	0.0	L	5
<i>Cyclodomorphus maximus</i>	40.0	2.0	L	9.2	0.0	L	5
<i>Cyclodomorphus melanops</i>	12.3	8.3	L	1.9	2.8	L	5
<i>Egernia depressa</i>	14.3	8.3	L	3.0	2.8	L	5

<i>Egernia kingi</i>	15.7	5.3	L	2.8	1.5	L	5
<i>Egernia pilbarensis</i>	16.7	7.0	L	3.5	1.8	L	5
<i>Egernia rugosa</i>	48.7	2.0	L	11.7	0.0	L	5
<i>Egernia stokesii</i>	12.0	5.3	L	1.8	1.5	L	5
<i>Eremiascincus douglasi</i>	10.0	5.3	L	0.7	1.5	L	5
<i>Eremiascincus fasciolatus</i>	9.0	5.3	L	0.0	1.5	L	5
<i>Eremiascincus pardalis</i>	34.3	2.0	L	7.6	0.0	L	5
<i>Eremiascincus richardsonii</i>	9.0	5.3	L	0.0	1.5	L	5
<i>Eulamprus brachysoma</i>	29.6	2.0	L	8.4	0.0	L	5
<i>Eulamprus sokosoma</i>	35.0	2.0	L	8.2	0.0	L	5
<i>Eulamprus tympanum</i>	33.6	2.0	L	10.0	0.0	L	5
<i>Glaphyromorphus crassicaudus</i>	32.0	2.0	L	6.4	0.0	L	5
<i>Glaphyromorphus darwiniensis</i>	10.0	8.3	L	0.7	2.8	L	5
<i>Glaphyromorphus gracilipes</i>	26.6	2.0	L	6.6	0.0	L	5
<i>Glaphyromorphus isolepis</i>	10.0	5.3	L	0.7	1.5	L	5
<i>Glaphyromorphus punctulatus</i>	19.7	2.0	L	4.4	0.0	L	5
<i>Gnypetoscincus queenslandiae</i>	37.7	2.0	L	8.9	0.0	L	5
<i>Harrisoniascincus zia</i>	42.0	2.0	L	10.3	0.0	L	5
<i>Hemiergis peronei</i>	16.7	5.3	L	3.8	1.5	L	5
<i>Hemiergis quadrilineata</i>	21.4	2.0	L	5.5	0.0	L	5
<i>Lerista bipes</i>	13.3	8.3	L	2.3	2.8	L	5
<i>Lerista borealis</i>	11.3	7.0	L	1.2	1.8	L	5
<i>Lerista connivens</i>	17.3	5.3	L	3.1	1.5	L	5
<i>Lerista distinguenda</i>	13.7	6.7	L	1.7	2.4	L	5
<i>Lerista elegans</i>	12.0	6.7	L	1.4	2.4	L	5
<i>Lerista flammicauda</i>	16.0	10.0	L	2.1	3.2	L	5
<i>Lerista gerrardii</i>	14.3	5.0	L	2.6	1.4	L	5
<i>Lerista greeri</i>	16.0	8.3	L	2.1	2.8	L	5
<i>Lerista griffin</i>	13.7	8.3	L	1.7	2.8	L	5
<i>Lerista karlschmidti</i>	11.3	8.3	L	1.2	2.8	L	5
<i>Lerista kendricki</i>	32.0	2.0	L	7.5	0.0	L	5
<i>Lerista lineata</i>	19.0	2.0	L	3.5	0.0	L	5
<i>Lerista lineopunctulata</i>	9.0	5.3	L	0.0	1.5	L	5
<i>Lerista macropisthopus</i>	11.3	2.0	L	1.2	0.0	L	5
<i>Lerista muelleri</i>	9.0	8.3	L	0.0	2.8	L	5
<i>Lerista neander</i>	16.0	2.0	L	2.1	0.0	L	5
<i>Lerista nichollsi</i>	19.0	2.0	L	3.5	0.0	L	5
<i>Lerista onsloviana</i>	27.4	2.0	L	6.4	0.0	L	5
<i>Lerista petersoni</i>	27.4	2.0	L	6.4	0.0	L	5
<i>Lerista planiventralis</i>	16.7	2.0	L	3.8	0.0	L	5
<i>Lerista praepedita</i>	16.7	6.7	L	3.8	2.4	L	5
<i>Lerista uniduo</i>	16.7	5.0	L	3.1	1.4	L	5
<i>Lerista varia</i>	39.0	2.0	L	8.5	0.0	L	5
<i>Liopholis margaretae</i>	38.7	2.0	L	9.3	0.0	L	5
<i>Liopholis Montana</i>	38.7	2.0	L	9.3	0.0	L	5
<i>Lissolepsid luctuosa</i>	17.7	5.3	L	3.8	1.5	L	5
<i>Menetia surda</i>	16.7	10.0	L	3.5	3.2	L	5
<i>Morethia lineocellata</i>	12.0	8.3	L	1.8	2.8	L	5
<i>Morethia ruficauda</i>	14.3	6.7	L	3.0	2.4	L	5
<i>Niveoscincus metallicus</i>	27.3	2.0	L	7.2	0.0	L	5
<i>Notoscincus ornatus</i>	14.3	5.0	L	3.0	1.4	L	5
<i>Proablepharus tenuis</i>	12.0	8.3	L	1.8	2.8	L	5
<i>Pseudemoia cryodroma</i>	44.3	2.0	L	11.7	0.0	L	5
<i>Pseudemoia rawlinsoni</i>	36.7	2.0	L	9.6	0.0	L	5
<i>Saproscincus hannahae</i>	19.0	5.0	L	3.9	1.4	L	5
<i>Tiliqua multifasciata</i>	14.3	5.3	L	3.0	1.5	L	5
<i>Tiliqua nigrolutea</i>	27.3	2.0	L	7.2	0.0	L	5

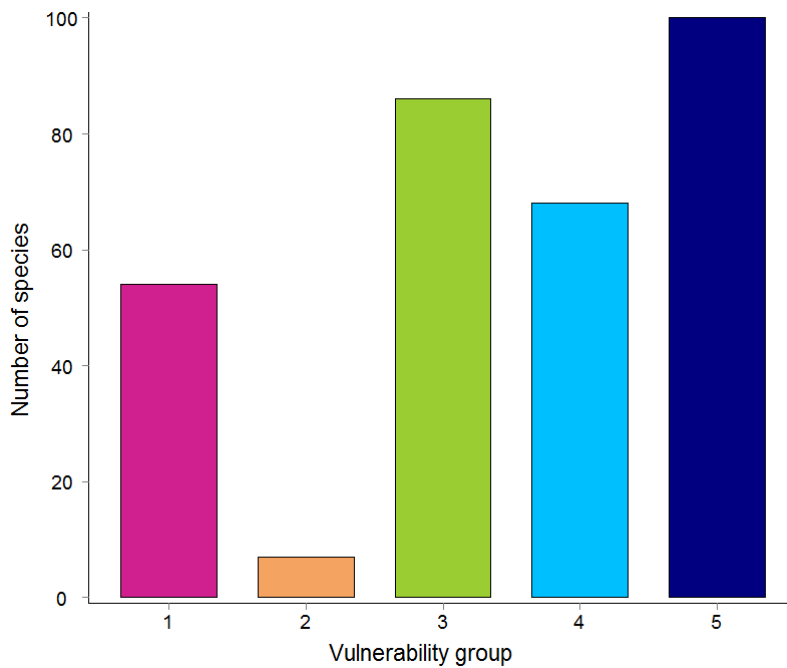


Figure 4. The number of species assigned to each vulnerability group. Group 1 represents the most vulnerable species, and group 5 represents the least vulnerable species.

The proportion of species assigned to each vulnerability group varied significantly among biogeographic zones (Fisher's exact test: $p < 0.001$; Fig. 5). Broadly, a larger proportion of arid zone species were assigned to the highest vulnerability groups (1 and 2) compared to all other zones, whereas all eastern and Mediterranean species were assigned to the lower vulnerability groups (3-5). Phylogenetic patterns in vulnerability were also evident, at least at a broad scale, with a higher proportion of species of the *Saproscincus* lineage assigned to the high vulnerability groups compared to the *Egernia* and *Eugongylus* lineages (Fig. 6). These differences among lineages were statistically significant (Fisher's exact test: $p = 0.003$).

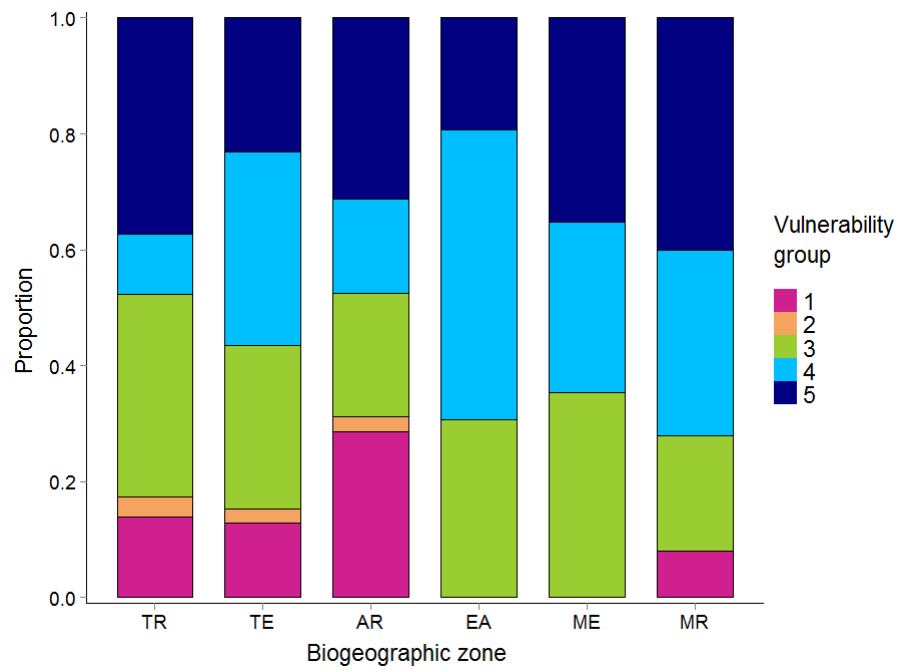


Figure 5. The proportion of species assigned to each vulnerability group among biogeographic zones. TR = tropical (86 species), TE = temperate (39 species), AR = arid (122 species), EA = eastern (26 species), ME = Mediterranean (17 species) and MR = multiregional (25 species).

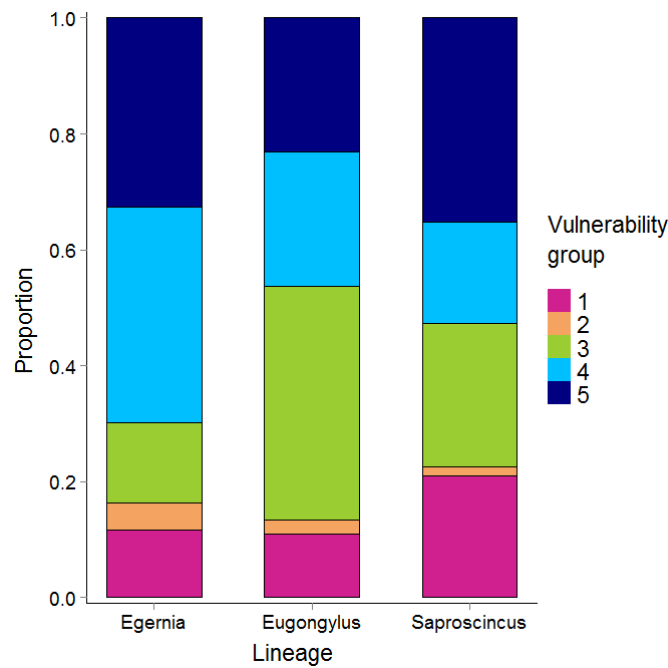


Figure 6. The proportion of species assigned to each vulnerability group among the three skink lineages: *Egernia* (43 species), *Eugongylus* (82 species) and *Saproscincus* (190 species).

Species assigned to the highest vulnerability groups inhabit almost all areas of the Australian continent (Fig. 7); however richness of vulnerable species appears especially high in arid regions of the continent. Analysis of the group 1 species revealed the Simpson Desert in central Australia as the ecoregion richest in vulnerable species (Fig. 7a). Analysis of groups 1 and 2 combined also highlighted the Kimberley tropical savannah in north Western Australia, and the Great Sandy-Tanami Desert which stretches across much of Western Australia and the Northern Territory, as ecoregions that are especially rich in vulnerable species (Fig. 7b).

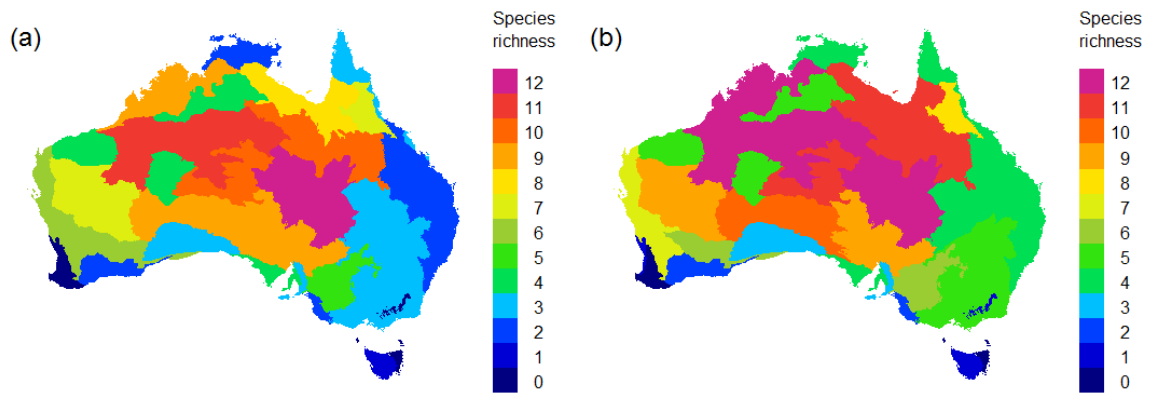


Figure 7. The richness of species assigned to (a) vulnerability group 1 and (b) vulnerability groups 1 and 2 among Australia's ecoregions.

DISCUSSION

The vulnerability of Australian skinks to climate change

Some Australian skinks may be particularly vulnerable to the impacts of climate change by virtue of their ecological attributes and the projected changes in distribution of climatically suitable habitat. Species with the highest susceptibility and adaptive capacity scores that were assigned to vulnerability group 1 included *Ctenotus zasticus* and *Tiliqua adalaidensis* which were both projected to lose more than 99% of their current climatic ranges by 2050 with no overlap between current and future suitable areas, have highly specialised habitat requirements, and are both currently listed as threatened. The least vulnerable species that were assigned to vulnerability group 5 were generally characterised by projected range expansions with high levels of overlap and possess characteristics, such as generalist habits and large clutch sizes, which may enable them to exploit any increases in climatic space. These species may therefore be advantaged under future climate change.

Vulnerability differed significantly among species from different biogeographic regions. Broadly, arid zone species appeared most vulnerable overall, with a greater proportion of species being assigned to vulnerability group 1 compared to the other biogeographic groups. This may reflect the larger climatic changes projected in this region than elsewhere on the Australian continent, coupled with the relatively high proportion of arid zone species that are habitat specialists. Interestingly, Mediterranean species did not appear to be particularly vulnerable overall, with no species being assigned to either vulnerability groups 1 or 2. This contrasts with other research investigating projected changes in range size among *Banksia* spp. in this region (Fitzpatrick *et al.* 2008). This inconsistency may be an artefact of the different modelling techniques used, or it may reflect the comparably lower sensitivity of reptiles to changing rainfall patterns.

Highly vulnerable species can be found throughout most of continental Australia, making the identification of specific areas that may warrant more focused conservation efforts challenging. Nevertheless, some regions appear especially rich in vulnerable species, including the Great Sandy-Tanami and Simpson deserts. The high frequency of burrowing and nocturnal habits among species inhabiting these arid areas may help buffer against the impacts of warming, at least in the short term. The Kimberley tropical savannah was also identified as being particularly rich in vulnerable species. Here, extensive pastoralism, inappropriate fire regimes and feral predators pose the most significant threats to biodiversity (Carwardine *et al.* 2011). Reducing the impacts of these threats, such as through pest animal control and fire management initiatives, may help increase the resilience of these species to climate change.

Applying the framework

The framework presented here is an extension of a previous assessment developed for Australia's elapid snakes (see Chapter 4). It addresses the limitations of using model projections as the sole means of assessing species vulnerability to climate change by integrating the information provided by these models with species ecological and life history traits. It therefore offers a more comprehensive picture of how species may respond in the future, and can assist with decisions regarding resource allocation.

Nevertheless, the framework remains a very coarse assessment of species vulnerability to climate change. Although we indirectly incorporated the compounding effects of other stressors by considering species threatened status, we did not consider how the strength of these stressors may change in response to climate change. We also omitted several variables considered important determinants of vulnerability where data were lacking for the majority of species. This is particularly true for our assessment of species adaptive capacity, which was based on only two variables. *Liopholis guthega* (vulnerability group 3), for example, occurs at high altitudes where much of its habitat has been degraded over recent years as a result of ski resort development (Donnellan *et al.* 2002). Adults appear to have considerable site fidelity, being restricted to areas surrounding a network of burrows, and vagility may therefore be extremely low. It is also vulnerable to altered prey dynamics as kookaburras, known skink predators, are now hunting at higher elevations in response to warming (Low 2007). By not explicitly considering these factors in the framework we will have underestimated the vulnerability of this species to climate change. The transparency of the framework, however, allows species to be easily re-ranked if additional variables are integrated into the framework as more data becomes available. Rare species could also be

included in the assessment once further occurrence data and information on their ecological attributes are collected.

To aid decision making, the framework presented here explicitly considers susceptibility and adaptive capacity as two distinct components of species vulnerability (Fig. 8). Species with a high susceptibility and a low adaptive capacity will be particularly vulnerable to climate change and are likely to require intensive intervention measures (Dawson 2011). *Ctenotus zasticus*, for instance, was one of the most vulnerable of all species. This species currently occupies a very limited distribution, restricted to an isolated patch of mallee (*Eucalyptus* sp.) on two adjacent properties in Western Australia (Cogger *et al.* 1993). Its range is surrounded by unsuitable habitat (*Acacia* shrubland), suggesting that the capacity for dispersal will be limited. Increased connectivity between patches of suitable habitat, and a reduction in other threats, particularly those posed by grazing, may be appropriate management strategies for this species. Given that the models projected a complete disappearance of climatically suitable habitat by 2050, and that dispersal is likely to be limited, *C. zasticus* may ultimately become a candidate for assisted colonisation (Thomas 2011).

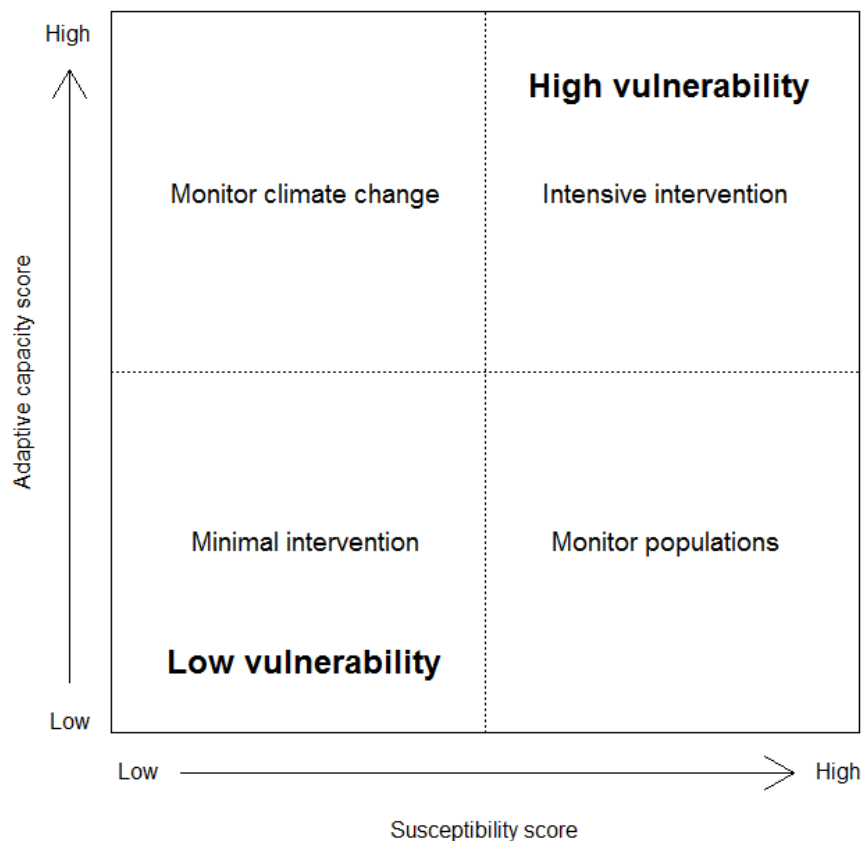


Figure 8. The relative contributions of *susceptibility* and *adaptive capacity* to a species overall vulnerability can help define management strategies.

Species with a high susceptibility, but a high adaptive capacity, are those that will be very sensitive to climatic changes across their range, but may have the capacity to disperse to new areas, adapt *in situ* and/or recover quickly following declines in population size. These species will warrant careful monitoring to ensure that population declines as a result of climate change and any difficulties repopulating are identified early, should their capacity to adapt prove insufficient. Those with a low susceptibility, but a low adaptive capacity, are those that are likely to be less exposed to climate change, or fairly resistant to its impacts in the short term, but will have limited abilities to cope should the climate change beyond their tolerance levels. Careful monitoring of climatic changes across these species

ranges is warranted as they will require reassessment should these changes ultimately occur at a rate faster than that currently projected by GCMs. Species with a low susceptibility and a high adaptive capacity will be least vulnerable to climate change, and may persist with only minimal intervention. Identifying the most appropriate adaptation strategies will increase the likelihood they will be effective, and afford the best protection to species in the face of climate change (Heller and Zavaleta 2009).

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CHAPTER 6

A vulnerability assessment of Australasian freshwater turtles

ABSTRACT

Reptiles have been proposed as one of the most vulnerable taxonomic groups to the impacts of climate change. Freshwater turtles may be particularly vulnerable as they are considered one of the most threatened groups of vertebrates worldwide, and climate change is likely to exacerbate the already precarious status of many species. We present a novel framework for assessing the vulnerability of freshwater turtles to climate change and apply this method to the fauna of Australia and New Guinea. The framework incorporates multiple variables that explicitly quantify the three components of vulnerability: exposure, sensitivity and adaptive capacity. We found that by virtue of their high exposure, high sensitivity and low adaptive capacity, climate change may pose a serious threat to some species. This framework provides a transparent and objective tool for assessing climate change vulnerability and can provide a basis upon which to develop response strategies.

Keywords: adaptive capacity, climate change, environmental niche modelling, exposure, risk assessment, sensitivity, species traits

INTRODUCTION

Freshwater ecosystems have been identified as one of the most vulnerable components of the Earth's environment to climate change (Woodward *et al.* 2010). Elevated temperatures, changing rainfall patterns, increased glacial melt and rising sea levels have already altered natural flow regimes in many areas (Jenkins *et al.* 2011). These impacts are anticipated to worsen as climate change accelerates over the coming decades, and are likely to pose a significant threat to freshwater biodiversity worldwide.

Freshwater turtles may be particularly susceptible to the adverse effects of climate change (Ihlow *et al.* 2012). As ectotherms, their physiological processes, activity patterns and development are dependent on the presence of optimal environmental conditions: higher temperatures during incubation, for instance, have been associated with lower hatching success, smaller body sizes, slower growth rates and reduced swimming performance in some species (Booth *et al.* 2004; Micheli-Campbell *et al.* 2011). Many turtles possess temperature-dependent sex determination (TSD), and warming has the potential to skew offspring sex ratios (Mitchell and Janzen 2010). Droughts may lead to higher population densities, increased competition and disease prevalence, reduced recruitment, and mass mortality if water levels recede completely (Roe and Georges 2009; Chessman 2011). Other stressors, particularly habitat loss and overexploitation, have already resulted in turtles being classified as one of the most endangered groups of vertebrates globally (van Dijk *et al.* 2011), and there is a growing concern that the exposure of these species to significant environmental change may be sufficient to drive them towards extinction without concerted conservation efforts.

Here, we assess the climate change vulnerability of the freshwater turtle fauna of Australia and New Guinea (herein Australasia). This group, numbering some 32 species, is dominated by the family Chelidae, also known as the side-necked turtles because their head and neck are withdrawn sideways into the shell. The Chelidae is a relatively large family of turtles that is restricted to Australia, New Guinea and South America and is of undisputed Gondwanan origin. The Trionychidae and Carettochelys families, which differ from the side-necked turtles by folding their necks vertically, also have representatives in the Australasian region. The diversity of turtles is highest in the tropical southern lowlands of New Guinea, and declines with increasing latitude. Approximately one third of species are already listed as threatened with extinction, largely as a consequence of habitat degradation, introduced predators and overexploitation (Georges 1994; Spencer and Thompson 2005). For some turtles, these threats have had devastating consequences. The Western swamp turtle (*Pseudemydura umbrina*) has been subject to habitat clearance, predation by foxes and other animals, inappropriate fire regimes and drainage of swamp habitat, and is currently regarded as Australia's most threatened reptile (Cogger *et al.* 1993). If we are to protect these species in the face of climate change, an assessment of how this group may fare in the future is urgently needed so that conservation management strategies can be designed and implemented without delay.

To assess species vulnerability to climate change we designed a novel framework that offers an alternative method to those presented in Chapters 4 and 5, by recognising vulnerability as comprising three distinct components: exposure, sensitivity and adaptive capacity (IPCC 2007a). The exposure of a species is related to the magnitude of climatic changes, as well as the frequency of extreme climatic events, across its range. Sensitivity is the degree to which a species will be affected by, or responsive to, these environmental

changes, and adaptive capacity refers to a species ability to adjust to climate change in order to buffer its adverse effects, take advantage of opportunities and recover following environmental perturbations. Clearly, species that inhabit the most exposed locales, are highly sensitive to environmental changes and have a low adaptive capacity will be the most vulnerable to climate change.

To quantify these three vulnerability components, the framework incorporated variables based on the projections of environmental niche models (ENMs), statistical techniques that associate a species occurrence records with environmental data to generate projections of its future potential distribution, and species traits. Species were assessed according to each variable, and then assigned to various vulnerability categories. The objectives of this study were to ascertain which species may be most vulnerable to climate change and to identify any phylogenetic or biogeographic patterns in vulnerability within this taxonomic group.

METHODS

Quantifying exposure, sensitivity and adaptive capacity

We designed three models to quantify the exposure, sensitivity and adaptive capacity of species to climate change. The structure of these models was based on the rarity model of Rabinowitz (1981) which ranks species according to their combinations of three variables: geographic range size, abundance and habitat specialisation. This rarity model was extended by Kattan (1992) to assess extinction risk among Columbian birds and has been extensively applied to other taxonomic groups (e.g. Goerck 1997; Harcourt *et al.* 2002;

Isaac *et al.* 2009). Broadly, the rarity model requires species to be assigned to one of two classes according to each variable, resulting in eight levels of extinction risk in three dimensions (Table 1). Species that are classified as rare with respect to all three variables are awarded a score of one (high extinction risk) and species that are common according to all three variables are awarded a score of eight (low extinction risk). Of the remaining cells in the model, three are rare according to two variables and are awarded 2-4 points, and three are rare in only one variable and are awarded 5-7 points.

Table 1. The rarity model of Rabinowitz (1981) and extended by Kattan (1992). The model comprises a three-dimensional matrix of eight cells, each defining a different level of extinction risk.

		<i>Geographic distribution</i>			
		Wide		Narrow	
		Broad	Restricted	Broad	Restricted
<i>Habitat specialisation</i>					
<i>Abundance</i>	Abundant	8	6	5	2
	Sparse	7	4	3	1

To assess species exposure, sensitivity and adaptive capacity, we developed three analogous models using different combinations of variables.

Exposure model

Most assessments of species exposure to climate change are based on projections of Global Circulation Models (GCMs) which are then applied in ENMs to project the location and

extent of climatically suitable habitat in the future (Dawson *et al.* 2011; Gardali *et al.* 2012). The projections of ENMs can be used to derive a number of different risk assessment variables (Ohlemüller *et al.* 2006), of which we identified three for inclusion in the exposure model: the projected change in climatic range size, the percentage overlap between the projected current and future (2050) ranges (which gives an indication of the pressure a species will be under to disperse), and the change in climatic suitability of the projected range between the current and 2050 time periods (Table 2).

Table 2. The exposure model.

		<i>% Overlap between the current and 2050 ranges</i>			
		> Median		< Median	
<i>Change in climatic range size</i>		> Median	< Median	> Median	< Median
<i>Change in climatic suitability</i>	> Median	1	3	4	7
	< Median	2	5	6	8

To align with other studies in which high scores reflect high vulnerability, we awarded a species a score of eight if it had a high degree of exposure according to all three variables and a score of one if it had a low degree of exposure according to all three variables. To assign scores to species that were highly exposed according to only one or two variables, we ranked the three variables in the following order of importance: 1) the percentage overlap between the current and 2050 climatic ranges, 2) the change in climatic range size and 3) the change in climatic suitability, based on the reasoning that a species will not be able to benefit from an expansion of its climatic range if newly suitable areas are out of reach. In other words, species whose future ranges lie beyond their dispersal capabilities are vulnerable regardless of whether or not their future climatic range is projected to

expand. In addition, a decline in climatic suitability may not negatively affect species if they are able to utilise microhabitat buffering to persist in areas that become less favourable.

Sensitivity model

Species that are expected to be highly sensitive to climate change include those with small geographic ranges, low local abundances and specialised requirements, traits effectively encapsulated by the rarity model of Rabinowitz (1981). We chose to assess sensitivity using the following variables: threatened status (because abundance data for most turtle species are lacking, and threatened status indirectly incorporates information on rarity as well as distribution size), habitat specialisation, and whether the species possesses temperature-dependent sex determination (TSD) or genotypic sex determination (GSD) (Table 3). On the basis that threatened species are characteristically rare and restricted and are therefore at greater risk of demographic stochastic processes as a consequence of climate change, and that habitat specialists are expected to be sensitive to climate change irrespective of their sex determining mode, we ranked these variables in the order of 1) threatened status, 2) habitat specialisation and 3) TSD.

Table 3. The sensitivity model.

<i>Habitat specialisation</i>		<i>Threatened status</i>			
		Not threatened		Threatened	
		Generalist	Specialist	Generalist	Specialist
<i>TSD</i>	No	1	3	4	7
	Yes	2	5	6	8

Adaptive capacity model

We assessed adaptive capacity for each species using the following variables: habitat connectivity (which will influence a species ability to disperse), body size / carapace length (which is positively correlated with dispersal ability and fecundity) (Jenkins *et al.* 2007; Gosnell *et al.* 2009), and the change in overlap of the species projected range with the protected area network between the current and 2050 time periods (because climate change may drive species out of reserves, increasing their exposure to other stressors and reducing their ability to recover from environmental perturbations) (Table 4). We acknowledge that body size provides a relatively coarse approximation of dispersal ability because there are some small species, such as the eastern long-necked turtle (*Chelodina longicollis*), that can migrate overland for considerable distances (Stott 1987). We ranked these variables in the order of 1) habitat connectivity, 2) carapace length and 3) overlap with the protected area network under the following rationale. The presence of barriers to movement will be more important than the intrinsic dispersal capabilities of species because a species may not be able to reach new areas if there are barriers impeding its movements, even if it has good dispersal capability. In addition, a species will only benefit from an increased

representation in the protected area network if it is able to reach and establish viable populations in new areas.

Table 4. The adaptive capacity model. PAN = protected area network.

<i>Carapace length</i>		<i>Habitat connectivity</i>			
		> Median		< Median	
		Large	Small	Large	Small
<i>Overlap with PAN</i>	> Median	1	3	4	7
	< Median	2	5	6	8

Environmental niche modelling

A species list was derived from a recent overview of the taxonomy of the Australasian freshwater turtles (Georges and Thomson 2010). We obtained locality records for each species from the Global Biodiversity Information Facility (www.gbif.org), Biomaps (www.biomaps.net.au) and Turtlebase (piku.org.au/cgi-bin/locations_add.cgi), removing all duplicate and anomalous points that may have arisen due to geocoding or identification errors. Four species had fewer than ten locality records and were excluded from further analysis (Supplementary Table 1). This threshold has been used successfully in other studies modelling the climate change impacts on turtle distributions (Ihlow *et al.* 2012), and while lower than some other modelling studies, our aim was to assess broad-scale patterns of vulnerability across the group as a whole, rather than to generate highly accurate projections for each species. The final dataset comprised an average of 113 records per species.

Climate data in the form of 19 bioclimatic variables for Australia and Papua New Guinea were obtained from the Worldclim database (www.worldclim.org) (Hijmans *et al.* 2005). Of these, we chose six for inclusion in the modelling process that incorporate information on climatic averages, seasonality and extremes: annual mean temperature, temperature seasonality, maximum temperature of the hottest month, minimum temperature of the coldest month, precipitation of the wettest quarter and precipitation of the driest quarter. Climate data for 2050 were obtained for four GCMs under the A2 climate scenario, which has been shown to closely match current emission rates (Raupach *et al.* 2007).

We used an ensemble of seven ENM algorithms to model the projected changes in species climatic ranges: maximum entropy, generalised linear models, generalised additive models, boosted regression trees, artificial neural networks, multivariate adaptive regression splines and random forests. These algorithms have all proven popular for modelling climate-induced range shifts, and have been shown to perform well compared to other approaches (Elith *et al.* 2006). We used a 10-fold cross-validation procedure to calculate the area under the receiver operating characteristic curve (AUC) which we then used to assess the performance of each algorithm. For each species, the algorithm that performed least well was excluded, and an ensemble projection was derived from the remaining six algorithms using the AUC as weights. We transformed these maps into presence-absence maps using a threshold equal to the weighted average of the sensitivity-specificity equality thresholds for each algorithm (Carvalho *et al.* 2010). To limit the over-prediction of species ranges, these final maps were clipped to the drainage divisions in which the species is known to occur.

To provide a measure of uncertainty in the ENM forecasts, we quantified the variability among projections using principal components analysis (see Thuiller 2004 for a more

detailed discussion of this method). Variability can range from zero (model projections are completely unrelated) to one (model projections are exactly the same).

Variables

The methods for calculating the nine variables included in the exposure, sensitivity and adaptive capacity models are outlined below. Unless otherwise stated, we dichotomised the continuous variables based on the median value across all species to provide the greatest level of discrimination.

1. Percentage overlap between the projected current and 2050 climatic ranges

We used the presence-absence maps to calculate the percentage overlap between the projected current and 2050 ranges. A value of 100% indicates the current range is entirely contained within the 2050 range, whereas a value of 0% indicates the current and 2050 ranges are entirely disjunct.

2. Change in climatic range size

We used the presence-absence maps to calculate the percentage change in climatic range size between the current and 2050 time periods, using the number of pixels as a proxy for range size.

3. Change in suitability of climatic range

To calculate the change in climatic suitability between the current and 2050 time periods, we set all cell values of the non-thresholded maps below the threshold to 0, but retained all cell values above the threshold, thereby generating a heterogeneous distribution of varying values of climatic suitability. We then calculated the percentage change in the average grid cell value across each range. A value $>100\%$ indicates that conditions within the 2050 climatic range are more suitable for the species, and a value $<100\%$ indicates conditions are less suitable.

4. Threatened status

We classified a species as threatened if they are currently listed as critically endangered, endangered or vulnerable under Australia's Environment Protection and Biodiversity Conservation (EPBC) Act and/or on the IUCN red list. Both these frameworks incorporate criteria for listing based on a species population size, geographic distribution and rate of decline.

5. Habitat specialisation

Land cover data for the Australia Pacific region were obtained from the USGS Global Land Cover Characterisation Database (edc2.usgs.gov/glcc/glcc.php). We used the International Geosphere Biosphere Programme (IGBP) classification which describes 17 land cover types. For each species, we extracted the land cover type at each occurrence

point and calculated Simpson's index (D) of land cover types across all locations as an index of habitat specialisation (Simpson 1949).

6. TSD

We determined whether a species possesses TSD or GSD based on the published literature. If no data were available, we assumed species to possess GSD as this has been the exclusive sex determining mode so far found among the Chelidae and Trionychidae families which include all but one of the Australasian freshwater turtle species.

7. Habitat connectivity

Most turtles utilise two contrasting modes of dispersal to move to new waterbodies: overland dispersal across terrestrial habitats, and dispersal through connecting waterways (streams, rivers, canals etc.). The success of overland dispersal depends primarily on the availability of waterbodies in the close vicinity, as movements over large distances (i.e. several kilometres) are likely to exceed the dispersal capabilities of most species (Roe and Georges 2009). For many species, roads will also act as dispersal barriers overland, and dams are likely to pose significant barriers to movements up and down streams, potentially causing populations to become isolated (Gibbs and Shriver 2002; Limpus *et al.* 2006). Accordingly, we obtained data on roads and streams for Australia and Papua New Guinea from DIVA-GIS (www.diva-gis.org) and data on dams from the Global Reservoir and Dam (GRanD) database version 1.1 (www.gwsp.org/85.html). Because dispersal will be positively influenced by the density of streams across each species current range, and

negatively influenced by the density of dispersal barriers, we developed an index of habitat connectivity based upon the following equation:

$$\frac{\text{habitat connectivity of species}}{\text{projected current range}} = \text{stream density} - \text{road density} - \text{dam density}$$

We used this index for all species to maximise consistency, but acknowledge that overland dispersal is uncommon for a few species, for which the influence of road and stream density will be less important.

8. Carapace length

We sourced data on adult carapace lengths from the published literature. Because many species exhibit sexual size dimorphism, and therefore carapace lengths often take a range of values, we chose an arbitrary threshold (300mm) that would allow us to dichotomise species as accurately as possible, rather than using the median value for the group.

9. Overlap with the protected area network

We downloaded GIS data on the protected areas of Australia and Papua New Guinea from the World Database on Protected Areas (www.wdpa.org). We overlaid this layer on the current and 2050 presence-absence maps for each species and calculated the percentage change in representation of the climatic range in the network between the two time periods. A value >100% indicates a greater proportion of the projected 2050 range is incorporated in the network compared to the projected current range, and vice versa, assuming no changes in the extent of the network.

Analysis

We determined the overall vulnerability of each species relative to the group as a whole by assigning each to a ‘high vulnerability’ group if they scored highly (6-8 points) in all three vulnerability components, a ‘moderate vulnerability’ group if they scored highly in two components, a ‘low vulnerability’ group if they scored highly in one component and a ‘very low vulnerability’ group if they did not score highly in any component.

To investigate biogeographic patterns in vulnerability, species were assigned to one of five biogeographic zones – northern tropical, eastern tropical and subtropical, temperate, arid and multiregional (species that occur in more than one zone) – based on broad-scale geographic patterns in their distributions (Wilson and Swan 2008; Georges and Thomson 2010). We used cluster analysis (unweighted pair-group average method with Euclidean distances) to compare the similarity of exposure, sensitivity and adaptive capacity scores among species, and identified any clumping of species from the same biogeographic zone. Fisher’s exact test was used to investigate differences in overall vulnerability among biogeographic groups due to the relatively low sample size.

RESULTS

The majority (81%) of species were projected to experience climatic range contractions by 2050, with 25% of species projected to lose more than 90% of their current climatic ranges (Supplementary Table 2). The species that were projected to experience climatic range expansions include the pig-nosed turtle (*Carettochelys insculpta*), the New Guinea long-

necked turtle (*Chelodina novaeguinea*), the Northern snake-necked turtle (*Chelodina rugosa*), the northern snapping turtle (*Elseya dentata*), the New Guinea painted turtle (*Emydura subglobosa subglobosa*) and the New Guinea giant softshell turtle (*Pelochelys bibroni*). All these species inhabit tropical areas of the Australasian region. Model variability ranged from 0.11 to 0.95 (Supplementary Table 2), indicating the reliability of the projections differed considerably among species.

Points awarded to species by the exposure, sensitivity and adaptive capacity models varied widely, suggesting that species responses to climate change will also vary (Table 5). Only one species, the western swamp turtle (*Pseudemydura umbrina*), scored highly in all three vulnerability components, and was placed in the ‘high vulnerability’ category. The majority of species (72%) scored highly in only one component, or not at all. There was no significant correlation between the points awarded by each of the three models (Table 6); thus species may be highly exposed to climate change but relatively insensitive to its impacts and so on. This finding emphasises the value of considering all vulnerability components when attempting to assess the likely impacts of climate change on species.

Table 5. Species scores according to the exposure (EX), sensitivity (SN) and adaptive capacity (AC) models, with final vulnerability categories. Species are ordered alphabetically within the categories. H = high, M = moderate, L = low and VL = very low.

Species name	Common name	EX	SN	AC	Vulnerability category
<i>Pseudemydura umbrina</i>	Western swamp turtle	8	7	7	H
<i>Chelodina steindachneri</i>	Steindachner's long-necked turtle	8	1	7	M
<i>Elusor macrurus</i>	Mary River turtle	8	4	6	M
<i>Emydura macquarii nigra</i>	Fraser Island short-necked turtle	8	3	8	M
<i>Emydura victoriae</i>	Northern red-faced turtle	8	3	8	M
<i>Myuchelys bellii</i>	Western sawshelled turtle	8	4	8	M
<i>Myuchelys georgesi</i>	Georges' helmeted turtle	2	7	7	M
<i>Myuchelys purvisi</i>	Manning River helmeted turtle	8	3	7	M
<i>Rheodytes leukops</i>	Fitzroy River turtle	8	7	5	M
<i>Carettochelys insculpta</i>	Pig-nosed turtle	1	8	1	L
<i>Chelodina burrungandjii</i>	Sandstone snake-necked turtle	1	3	8	L
<i>Chelodina canni</i>	Cann's long-necked turtle	7	1	3	L
<i>Chelodina colliei</i>	Oblong turtle	1	1	7	L
<i>Chelodina longicollis</i>	Eastern long-necked turtle	1	1	7	L
<i>Chelodina parkeri</i>	Parker's snake-necked turtle	8	4	5	L
<i>Elseya branderhorsti</i>	New Guinea snapping turtle	8	4	2	L
<i>Elseya irwini</i>	Irwin's snapping turtle	8	1	4	L
<i>Elseya lavarackorum</i>	Gulf snapping turtle	8	4	2	L
<i>Emydura macquarii emmotti</i>	Cooper Creek turtle	8	3	2	L
<i>Emydura macquarii kreftii</i>	Kreft's River turtle	1	1	7	L
<i>Emydura macquarii macquarii</i>	Macquarie River turtle	1	1	7	L
<i>Emydura subglobosa worrelli</i>	Worrell's turtle	8	3	5	L
<i>Pelochelys bibroni</i>	New Guinea giant softshell turtle	1	7	2	L
<i>Chelodina expansa</i>	Broad-shelled turtle	1	1	4	VL
<i>Chelodina novaeguineae</i>	New Guinea long-necked turtle	1	3	3	VL
<i>Chelodina rugosa</i>	Northern snake-necked turtle	1	3	5	VL
<i>Elseya albagula</i>	White-throated snapping turtle	4	1	4	VL
<i>Elseya dentata</i>	Northern snapping turtle	1	3	5	VL
<i>Emydura subglobosa subglobosa</i>	New Guinea painted turtle	1	1	5	VL
<i>Emydura tanybaraga</i>	Northern yellow-faced turtle	5	3	5	VL
<i>Myuchelys latisternum</i>	Common sawshelled turtle	1	1	3	VL
<i>Myuchelys novaeguineae</i>	New Guinea spotted turtle	1	3	3	VL

Table 6. Kendall tau rank correlation coefficients between the points awarded for each of the three models (EX = exposure, SN = sensitivity and AC = adaptive capacity). All coefficients are non-significant at the 0.05 level.

	EX	SN	AC
EX	1.000	-	-
SN	0.290	1.000	-
AC	0.115	-0.101	1.000

Under the exposure model, the majority of species (88%) were awarded either one point (least exposed) or eight points (most exposed) (Fig. 1a). This large bias towards the most extreme scores may be because the variables incorporated in the exposure model are not independent. Thus, if models project the climatic range of a species will contract in the future, they are also likely to project a decrease in climatic suitability of the future range, and a relatively low level of overlap. This finding suggests that only one of these variables is required to explain most of the variability in exposure among species, and the other two variables provide little (albeit some) additional information, at least for this taxonomic group.

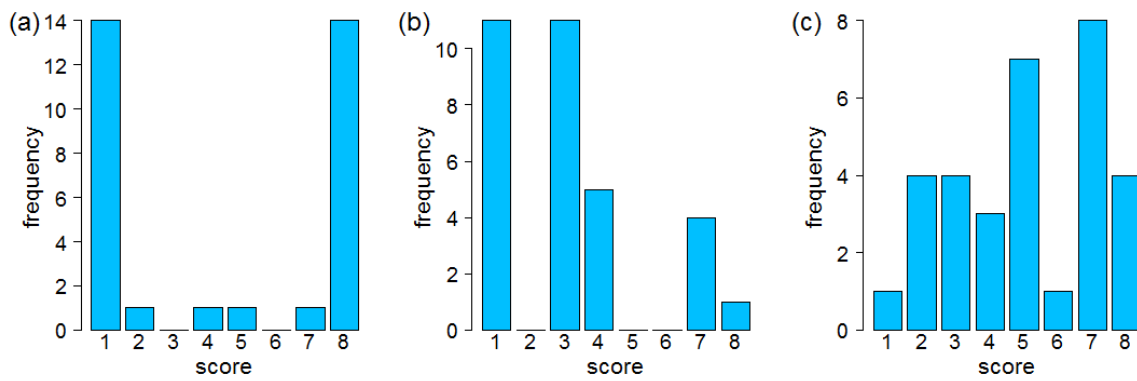


Figure 1. Frequency histograms of the points awarded for (a) the exposure model, (b) the sensitivity model and (c) the adaptive capacity model.

Most species were awarded relatively low scores for sensitivity, with only five species (16%) receiving scores greater than four (Fig. 1b). The majority of species (69%) are not listed as threatened and do not possess TSD, and were therefore awarded either one or three points, depending on their habitat specialisation. The most sensitive species was the pig-nosed turtle (*Carettochelys insculpta*) which is a habitat specialist, currently listed as vulnerable under the IUCN red list and possesses TSD. Adaptive capacity scores were more evenly distributed among species compared to the other two models (Fig. 1c).

Phylogenetic and biogeographic analyses

The cluster analysis revealed no strong phylogenetic or biogeographical effects on the similarity of species in terms of their exposure, sensitivity and adaptive capacity scores, with no obvious clumping of congeneric species or those from the same biogeographic zone (Fig. 2). With regard to overall vulnerability, there also does not appear to be any phylogenetic patterns, as species assigned to the ‘high’ and ‘moderate’ vulnerability categories occur throughout the turtle phylogeny (Fig. 3). There does, however, appear to

be a weak biogeographic signal in overall vulnerability, as the proportions of species that were assigned to each vulnerability category were not consistent among biogeographic groups (Fig.4). A greater proportion of northern tropical and multiregional species were classified as ‘low-’ or ‘very low vulnerability’ compared to the other three groups. These differences were marginally significant (Fisher’s exact test: $p = 0.076$).

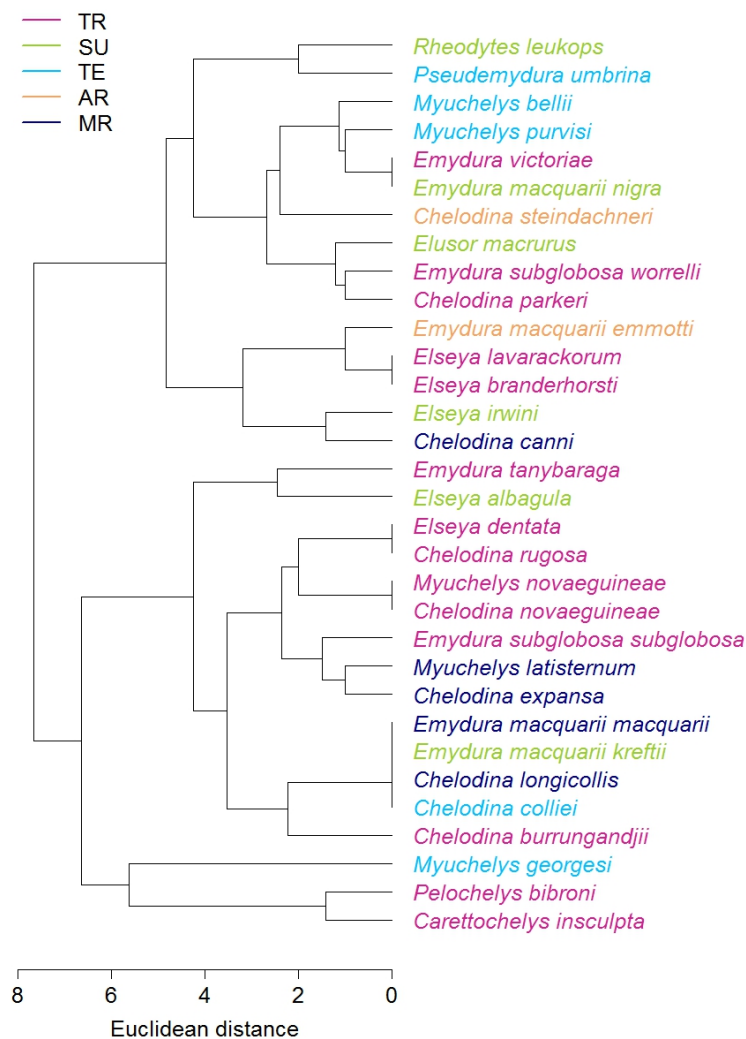


Figure 2. Cluster analysis of species in terms of their similarity in exposure, sensitivity and adaptive capacity scores. TR = northern tropical (14 species), SU = eastern tropical and subtropical (6 species), TE = temperate (5 species), AR = arid (2 species) and MR = multiregional (5 species).

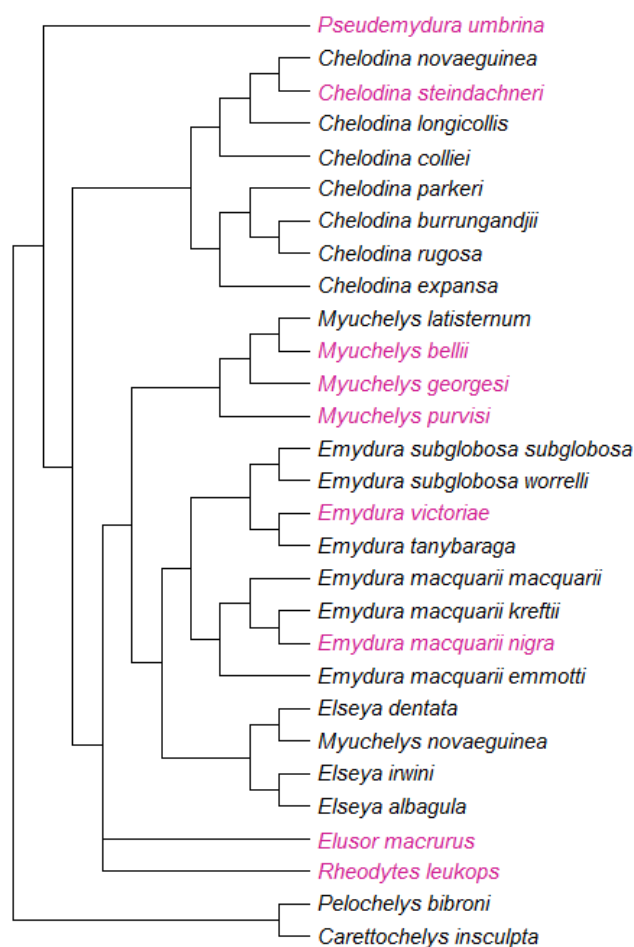


Figure 3. Cladogram of the species assessed (where evidence of their phylogenetic relationships is available) based on Georges and Adams (1992) and Georges et al. (2002). These studies both used allozyme electrophoresis to derive the phylogeny. Species categorised as ‘high’ or ‘moderate’ vulnerability are in red.

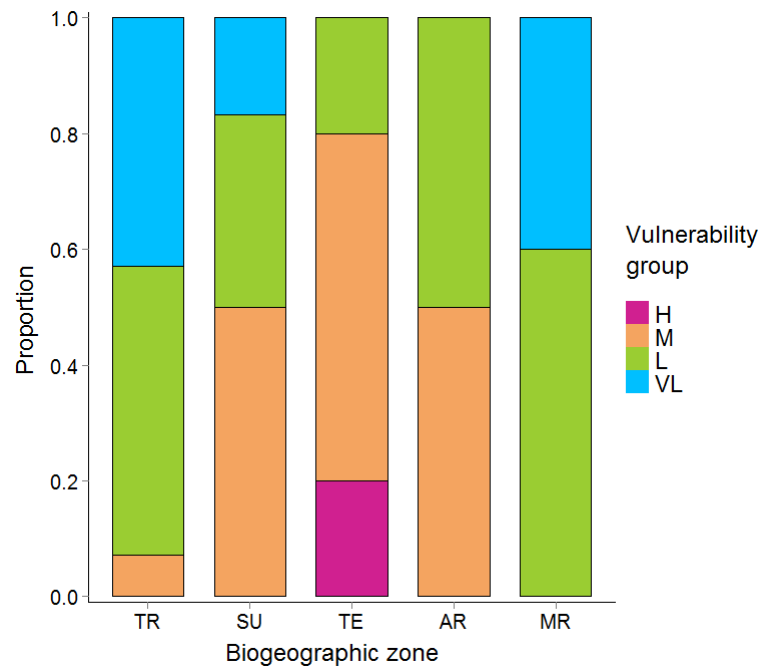


Figure 4. The proportion of species assigned to each vulnerability category (H = high, M = moderate, L = low and VL = very low) across different biogeographic groups. TR = northern tropical (14 species), SU = eastern tropical and subtropical (6 species), TE = temperate (5 species), AR = arid (2 species) and MR = multiregional (5 species).

DISCUSSION

The vulnerability of Australasian freshwater turtles to climate change

This study indicates that some Australasian freshwater turtles have high exposure, high sensitivity and low adaptive capacity, and may be extremely vulnerable to the negative impacts of climate change. Importantly, we identified four species as moderately vulnerable to climate change that are not currently listed as threatened: Steindachner's long-necked turtle (*Chelodina steindachneri*), the Fraser Island short-necked turtle (*Emydura macquarii nigra*), the northern red-faced turtle (*Emydura victoriae*) and the

Manning River helmeted turtle (*Myuchelys purvisi*). Careful monitoring over the coming decades may be required to identify any adverse effects of climate change on these species.

The western swamp turtle (*Pseudemydura umbrina*) possesses several characteristics that render it particularly susceptible to climate change, and was identified by the framework as the most vulnerable of this taxonomic group. This species is currently listed as critically endangered on the IUCN red list and under the EPBC Act. It is dependent on ephemeral swamps and has an extremely restricted and fragmented distribution, comprising only three wild populations (two of which are maintained by supplementation with translocated individuals from a captive-bred population) (Burbidge 1981). Declines in winter rainfall since the 1970s have already shortened the hydroperiod of these swamps (Mitchell *et al.* 2012), and none were projected to remain climatically suitable for the species by 2050 (Supplementary Table 2). However, these results should be treated with caution given that the occurrence records for this species were derived from only three small areas.

The western swamp turtle (*Pseudemydura umbrina*) is also the smallest of all Australasian turtles and has very low fecundity, typically producing only one clutch of 3-5 eggs per year (Burbidge 1981). This is considerably lower than most other Australasian turtles, such as the Macquarie River turtle (*Emydura macquarii macquarii*) which produces 2-3 clutches of up to 30 eggs per year (Judge 2001). Conservation efforts to ameliorate the deleterious effects of climate change, such as by identifying potential translocation sites that are projected to be climatically suitable in the future, will become increasingly important for this species (Burbidge *et al.* 2011).

Another species of conservation concern is the Fitzroy River turtle (*Rheodytes leukops*). It is restricted to a single drainage in central Queensland and was also projected to lose all climatically suitable area by 2050 (Supplementary Table 2), placing it at considerable risk of extinction if unable to adapt and persist in areas that become climatically unfavourable. In addition to the factors considered in this assessment, climate change may have important indirect effects on the Fitzroy River turtle via changes in its habitat. This species is specialised for life in fast-flowing riffles due to its unusual ability to extract oxygen from water using well-vascularised gills in its cloaca (Legler and Georges 1993), and if increased human demands in times of drought result in the construction of dams and reservoirs, this essential microhabitat could become threatened (Roe and Georges 2009). Our assessment may have therefore underestimated the vulnerability of this species to climate change.

Although we found no clear phylogenetic signal in vulnerability, climate change could still lead to a significant loss of evolutionary history within this taxonomic group. Four (50%) of the extant genera are monotypic – *Carettochelys*, *Elusor*, *Pseudemydura* and *Rheodytes* – three of which were assigned to the ‘high’ or ‘moderate’ categories. Therefore, losses of genetic diversity have the potential to exceed those at the species level if climate change drives the species within these genera towards extinction (Balint *et al.* 2011).

In relation to biogeographic patterns, there was a weak trend for northern tropical and multiregional species to be less vulnerable to climate change than those from other biogeographic zones. Not surprisingly, multiregional species generally failed to score highly because they tend to be characterised by large geographic distributions, wide environmental tolerances and generalist habits. In contrast, tropical species may not have

scored highly because the degree of warming at low latitudes is expected to be less (IPCC 2007b), reflected in the large climatic range expansions projected for many tropical species (Supplementary Table 2). In Australasia, regions in the northern tropics also have relatively low human populations densities compared to Australia's eastern and southern areas, so there are likely to be fewer anthropogenic barriers to dispersal. This, coupled with the relatively high density of streams in tropical areas, contributed to species from these regions having the highest levels of habitat connectivity compared to the other biogeographic groups (Supplementary Table 3).

Applying the framework

This framework provides a transparent and objective tool for assessing species vulnerability to climate change, and can be applied to rare species. By incorporating information on species traits alongside ENM projections, it provides a considerably more comprehensive assessment of vulnerability than assessments based on models alone. ENMs have several limitations, such as their reliance on the assumption that species conserve identical niche preferences (for a review of the limitations of ENMs, see Heikkinen *et al.* 2006; Sinclair *et al.* 2010). However, there are other assumptions and simplifications of the framework presented here that should be recognised.

First, we assumed that a large body size, via its positive correlation with dispersal ability and fecundity, would increase the adaptive capacity of species to climate change. However, a large body size has also been shown to increase the vulnerability of turtles to other threats, and has been used as a positive correlate of extinction risk in other

frameworks (e.g. Luiselli 2009). In our assessment, for example, the large pig-nosed turtle (*Carettochelys insculpta*) scored the lowest of all species for adaptive capacity, suggesting its ability to adapt and cope with climate change should be highest among this taxonomic group. However, its large size (coupled with its palatability, ease of capture and stereotyped nesting behaviour) renders it susceptible to overexploitation for food, which in turn is a suspected contributor to population declines in areas of Papua New Guinea (Eisemberg *et al.* 2011). Larger animals are also more vulnerable to illegal netting. These factors have been incorporated, at least in part, by including the threatened status of a species as a variable. For some species, however, it will be imperative that the results of this study be considered alongside information on the effects of other stressors, which will act in concert with climate change, so that a more comprehensive assessment of its risk of decline is obtained.

The framework presented here does not include the potential for behavioural adaptation, which is considered an important determinant of species vulnerability to climate change (Williams *et al.* 2008). For freshwater turtles, the highly variable rainfall patterns that characterise the Australian environment, together with increasing aridity since the Quaternary period, have favoured behavioural traits that enhance species abilities to survive when their habitats dry, and may confer a degree of resilience during the more severe and prolonged drought conditions in the future (Roe and Georges 2009; Steffen *et al.* 2009). A few species, for example, are capable of aestivating during dry conditions, including the western swamp turtle (*Pseudemydura umbrina*), the northern snake-necked turtle (*Chelodina rugosa*), the oblong turtle (*Chelodina colliei*) and Steindachner's long-necked turtle (*Chelodina steindachneri*). However, predation rates can be high during this time, and if wetlands do not re-flood before energy stores are depleted, turtles will

eventually die of starvation or dehydration (Roe and Georges 2009). For many of these species, we know little about how long they are able to remain in an aestivated state. This, coupled with the considerable uncertainty in future rainfall predictions, makes understanding the potential effectiveness of this strategy inherently difficult.

Ameliorating the adverse effects of climate change on Australasian freshwater turtles will be contingent on developing appropriate adaptation strategies for vulnerable species. By explicitly considering all three components of vulnerability, this framework can aid the decision-making process. For instance, species that are projected to be highly exposed to climate change may require additional monitoring so that population declines, as a result of environmental changes beyond their tolerance ranges, can be detected early. Species that are highly sensitive may benefit most from strategies aimed at reducing the effects of other stressors, such as constructing predator exclusion fences around important breeding areas and, if highly dependent on particular habitat types, strategies targeting native habitat regeneration. Species that have low adaptive capacity may benefit most from measures such as captive breeding programs, assisted colonisation, establishment of habitat corridors to facilitate dispersal, and an increased representation in the protected area network. Ensuring that conservation actions target the reasons contributing to a species vulnerability to climate change will increase the likelihood of their success.

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CHAPTER 7

Protecting Australia's reptiles under future climate change

ABSTRACT

The potential redistribution of species under climate change has important implications for protected areas which are fixed in space and therefore poorly suited to accommodating species range shifts. The primary aim of this study was to combine environmental niche modelling and a site prioritisation tool to identify areas of conservation value that will maintain their importance under future climate change. We modelled the current, 2030, 2050 and 2070 climatic ranges of 345 species of reptiles in Australia, and assessed the efficacy of the existing reserve network in protecting reptiles both currently and in the future. We then generated new reserve designs for each time period that maximised species representation at minimum cost, and identified areas that were consistently selected across all time frames as these are likely to represent the best candidates for investment. We found that adding these areas to the existing NRS would improve species representation, although a number of species would remain inadequately protected. This indicates that other adaptation strategies, such as assisted colonisation, may be necessary to ensure the persistence of some reptile species under climate change.

Keywords: conservation prioritisation, environmental niche modelling, MARXAN, protected areas, range shifts

INTRODUCTION

Reptiles are among the world's most threatened vertebrate groups, with declines of many populations now evident worldwide (Whitfield *et al.* 2007; Reading *et al.* 2010). These declines have been attributed to a variety of threats, including habitat loss, invasive species, pollution, disease and overexploitation (Gibbons *et al.* 2000). Over recent decades, climate change has emerged as an additional threat to biodiversity, and reptiles have been proposed as being particularly vulnerable to its impacts (Sinervo *et al.* 2010; Ihlow *et al.* 2012). As ectotherms, reptiles are highly sensitive to the temperature of their surroundings, and many species possess traits such as low vagility, low reproductive output, long life spans and temperature-dependent sex determination (TSD) that are expected to increase their sensitivity to the negative impacts of climate change (Bickford *et al.* 2010; Mitchell and Janzen 2010). Ensuring that reptiles are adequately conserved both now and in the future is essential if local and global extinctions are to be prevented.

Protected area systems, while not able to protect species from all threats, nevertheless form a major component of global efforts to conserve biodiversity (Margules and Pressey 2000), and several studies have undertaken conservation planning exercises with the aim of ensuring reptiles are adequately represented in reserve networks (Pawar *et al.* 2007; Urbina-Cardona and Flores-Villela 2010; Carvalho *et al.* 2011b). None of these, however, have considered the potential responses of species to climate change. This is problematic because the spatial relationships between species and reserves are expected to change as some species migrate to regions that are cooler or have different rainfall regimes (Araújo *et al.* 2004; Pyke *et al.* 2005; Hannah *et al.* 2007; Pressey *et al.* 2007; Hannah 2008; Carvalho *et al.* 2011a). Thus areas that adequately protect species now may not do so by the end of

the century. Adding new reserves to an existing network is one way to compensate for a loss of representation, but where should these new reserves be sited that will afford the best protection to species under a changing climate?

The aim of the present study is to identify important areas for reptile conservation that considers the potential impacts of climate change on species distributions. We focussed our assessment on Australia which supports an exceptionally diverse reptile fauna comprising 917 described species, of which 93% are endemic (Chapman 2009). Recent years have seen an expansion of Australia's National Reserve System (NRS), which currently covers 98 million hectares (12.8%) of the continent and comprises a network of over 9000 protected areas, including national parks, indigenous protected areas, regional reserves and other reserve types (Department of Sustainability, Environment, Water, Population and Communities 2008). Initiatives to extend the NRS are continuing, and have acknowledged the importance of accounting for climate change in this process (Commonwealth of Australia 2009).

The first objective of this study was to identify areas of high reptile diversity and assess how these areas may shift under future climate change. To achieve this, we used a variety of environmental niche modelling (ENM) algorithms to model the current and future climatic ranges of 345 species of reptiles. ENMs correlate the geographic occurrences of a species with a set of environmental layers that are considered important determinants of its realised niche (Guisan and Zimmermann 2000). They have great utility in conservation planning, particularly in the context of climate change, because they can be used to estimate species ranges based on relatively limited data, can derive forecasts of species

ranges under a variety of future climate scenarios, and can be applied rapidly to large numbers of species (Elith and Leathwick 2009).

The second objective of this study was to evaluate the effectiveness of the existing NRS in protecting Australia's reptiles both currently and in the future. Specifically, we aimed to identify which species are poorly represented in existing reserves, and which are expected to lose representation under future climate change. Our final objective was to use a site prioritisation tool to identify areas for reptile conservation outside the existing NRS that will remain important under climate change.

METHODS

Species data

We focused on three groups of reptiles: the terrestrial elapid snakes (Family Elapidae), the skinks (Family Scincidae) and the freshwater turtles (Families Chelidae and Carettochelydidae). Together, these families represent two of the three reptile orders found in Australia (excluding the crocodiles), number over 500 described species, and comprise almost 60% of the Australian reptile fauna. We assembled a species list based on the most recently published field guide of Australian reptiles (Wilson and Swan 2008), updated with recent taxonomic changes (Gardner *et al.* 2008; Mecke *et al.* 2009; Georges and Thomson 2010). Data on species occurrences were compiled from GBIF (www.gbif.org), Biomaps (www.biomaps.net.au) and Turtlebase (piku.org.au/cgi-bin/locations_add.cgi), and were supplemented by data 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 data were checked for geographical errors which were subsequently removed. Species with fewer than 20 geographically distinct records were excluded from further analysis as models built with low numbers of records are unlikely to have sufficient predictive power to be useful for conservation prioritisation (Elith and Leathwick 2009). Our final dataset comprised over 110,000 locality records across 345 species (mean = 328 records per species).

Environmental data

Current climate data (1960-2000) for Australia were obtained from the Bureau of Meteorology (www.bom.gov.au), and were used to derive six bioclimatic variables: annual mean temperature (AMT), maximum temperature of the hottest month (THM), minimum temperature of the coldest month (TCM), temperature seasonality (TS), precipitation of the wettest quarter (PWQ) and precipitation of the driest quarter (PDQ). These variables were chosen because they include information about climate averages, extremes and seasonality, are known to be important determinants of reptile diversity (Qian *et al.* 2007), and have been used successfully in previous studies to model distribution shifts in this taxonomic group (see Chapters 4-6). These data were supplemented with two topographical variables, slope and aspect, which were derived from digital elevation data downloaded from the CGIAR Consortium for Spatial Information via DIVA-GIS (www.diva-gis.org). We also included a land-cover variable obtained from the Global Land Cover 2000 project (bioval.jrc.ec.europa.eu/products/glc2000/glc2000.php) which describes 12 broad categories of land cover across Australia, including forests, woodlands, grasslands etc. We

chose not to include elevation, despite its known influence on reptile distribution limits, for two principal reasons. First, elevation is strongly correlated with a number of climatic factors, especially temperature, and its inclusion in the modelling process could reduce predictive power. Second, elevation has the potential to affect the accuracy of future projections because its relationship with the distributions of species is likely to change in the future as species move upslope in response to warming. Thus, including elevation in the models may underestimate future range shifts.

Climate projections were derived for 2030, 2050 and 2070 using four global circulation models (GCMs) that have been found to produce reliable projections of future climates in Australia (CSIRO & BOM 2007). These were based on the A2 emission scenario which has been shown to closely match recent trends in atmospheric CO₂ levels (Raupach *et al.* 2007). Because reliable projections of future land cover are not currently available for the Australian region, we assumed that land cover will not change over time. Including land cover as a static variable has been shown to produce better performing models than if it is excluded, even though this means making the unrealistic assumption that land cover will not change in the future (Stanton *et al.* 2012). All environmental data were rescaled to a spatial resolution of 0.05° (approx 5km).

Environmental niche modelling

We used an ensemble of five modelling algorithms to model the current, 2030, 2050 and 2070 climatic distributions of each species: maximum entropy, generalised linear models, generalised additive models, boosted regression trees and random forests. These algorithms

have been shown to perform well in comparison to other methods, and have consequently proven popular tools for predicting range shifts under climate change (Elith *et al.* 2006). For each algorithm, we performed a 10-fold cross validation procedure to calculate the area under the receiver operative curve (AUC) which we used to assess the algorithms' performance. The AUC can range from 0 to 1, with scores >0.7 generally considered to represent satisfactory performance. For each species, we excluded the algorithm that performed worst (i.e. had the lowest average AUC score across all 10 models) from further analysis. The average AUC score across all remaining algorithms, and across all species, was 0.993, indicating that the algorithms generally performed exceptionally well. With the four best-performing algorithms, we built a full model using all occurrence records for model calibration, and projected this full model onto the current, 2030, 2050 and 2070 climate surfaces to generate four projections (four algorithms) of each species current climatic range and 16 projections (four algorithms x four GCMs) of each species climatic range in 2030, 2050 and 2070. For each future time period, we calculated a mean projection across all four GCMs. We then calculated a mean projection across all four algorithms for each time period using a weighted average consensus method which weights the contribution of each algorithm according to its AUC score (Marmion *et al.* 2009).

These final maps comprised a continuous probability field, with grid cell values ranging from 0 (environment is entirely unsuitable for the species) to 1 (environment is entirely suitable). To limit the over-prediction of a species climatic range, we followed the minimum expected threshold coverage approach of Wilson *et al.* (2005). First, for each algorithm we identified a threshold determined by the point along the receiver operating curve at which the sensitivity and specificity of the model projections were equal. We then calculated the weighted average of these sensitivity-specificity equality thresholds across

all algorithms, using the AUC score of each algorithm as its weight. Second, we set the expected area of occurrence in each grid cell that contained a value below this threshold to zero. This approach prevents the loss of information associated with dichotomising the model output (i.e. converting into presence/absence) while helping to ensure that only highly suitable areas are counted towards the climatic range size of each species, and are therefore considered in the conservation planning process. The values in each grid cell were multiplied by the area of the grid cell (which varied according to latitude) and then summed to obtain an estimate of the species climatic range size.

Richness mapping

We summed the current projected maps across all species to identify areas of high reptile diversity. Because the maps reflect probabilistic distributions rather than strict presences and absences, these areas represent regions of high climatic suitability for our study group, rather than true species richness. We repeated this procedure for each future time period to determine how areas of high climatic suitability might shift under future climate change.

Evaluation of the existing National Reserve System (NRS)

To evaluate the effectiveness of the existing NRS at conserving species climatic ranges, we first defined a set of targets, which are the minimum amount of each species range that needs to be included in the NRS for that species to be considered adequately protected. A popular method is to develop targets that change as a function of range size (e.g. Rondinini

et al. 2005). Accordingly, we followed the approach of Watson *et al.* (2011) and set a target of 100% of the climatic range if it is $<1000\text{km}^2$, 1000km^2 if the climatic range is between 1000 and $10,000\text{km}^2$, or 10% of the climatic range if it is $>10,000\text{km}^2$. This set of targets is essentially arbitrary, but is based on the premise that protecting a minimum of 10% of the range of even widespread species is a reasonable expectation considering the current extent of the NRS. We defined this set of targets as the ‘low target level’.

We defined another set of targets equal to double the previous set (herein referred to as the ‘high target level’). Thus we set a target of 100% of the climatic range if it is $<2000\text{km}^2$, 2000km^2 if the climatic range is between 2000 and $10,000\text{km}^2$, or 20% of the climatic range if it is $>10,000\text{km}^2$. We included this alternate set of targets because a species climatic range represents its potential distribution rather than its actual distribution, and thus using the climatic range in a conservation planning exercise may lead to the protection of areas in which the species is not actually found. Setting a large target therefore helps reduce the likelihood that species will be inadequately protected in a new reserve network.

The current climatic range maps were intersected with a GIS layer of Australia’s NRS obtained from the Collaborative Australia Protected Area Database (CAPAD) 2008 which constitutes the most recent spatial data available. We calculated the number of gap species (species occurring entirely outside protected areas), the number of species protected at both the low and high target levels, and the average coverage of species climatic ranges by the NRS. We repeated this process for each future time period using the relevant maps.

This analysis was performed for all species, and then repeated for a subset of high priority species. We defined a species as high priority if it satisfied any one of three criteria: 1) the

species is currently listed as threatened under Australia's Environment Protection and Biodiversity Conservation (EPBC) Act or on the IUCN Red List, 2) the species was assigned to the highest vulnerability group according to the frameworks developed in Chapters 4-6 and 3) the species belongs to a monotypic genus. This third criteria provides a very coarse assessment of a species phylogenetic distinctiveness but is nevertheless included to acknowledge that the more evolutionarily unique a species is, the greater its systematic significance.

Systematic reserve selection

We used the MARXAN software package which applies a simulated annealing algorithm to identify sets of areas (solutions) that meet *a priori* targets while minimising costs, based on the principle of complementarity (Ball *et al.* 2009). It has proven an extremely popular tool for assisting in the prioritisation of lands for conservation purposes both in Australia and overseas. MARXAN requires a set of planning units which are areas of land that can be selected by the algorithm depending on the species they contain. We divided continental Australia into 69,914 grid cells using a $0.1^\circ \times 0.1^\circ$ grid and defined each grid cell as a potential planning unit. The average size of these planning units was 111.0km^2 , which is very similar to the average reserve size (105.4km^2) of the existing NRS. Because the degazettement of protected areas is unlikely, we forced MARXAN to include all existing protected areas in the final reserve system.

We performed a preliminary sensitivity analysis to determine values for two parameters required by MARXAN: the species penalty factor and the boundary length modifier,

following the procedure outlined in Ardron *et al.* (2010). The species penalty factor controls the penalty if a target is not met; the higher the penalty, the greater the likelihood that targets are met in the reserve network solution. Too high values, however, can constrain the MARXAN output. The boundary length modifier influences both the degree of fragmentation of the solution and its overall cost. Once these parameters were set, we performed 100 runs with 1,000,000 iterations to produce 100 solutions with varying spatial configurations, and selected the solution that achieved all conservation targets at the lowest cost. This procedure was repeated for each time period using the relevant maps and for each target level, resulting in eight final solutions (four time periods x two target levels). For each target level, we identified the planning units that were consistently selected across all four time periods as these reflect areas that are most likely to remain important for reptile conservation under climate change, at least until 2070. We termed these ‘priority areas’. We investigated how effective adding these priority areas to the NRS would be by calculating the number of gap species, the number of species adequately protected, and the average coverage of species ranges in a network consisting of existing protected areas plus the priority areas. We also evaluated whether any of these priority areas may be unsuitable for use in conservation because of their current land use status. An area was deemed unsuitable if its land use category was ‘intensive use’ or ‘water’ following the classification of the National Land Use version 4 dataset, obtained from the Australian Bureau of Agricultural and Resource Economics and Sciences.

RESULTS

Richness mapping

Model projections revealed reductions in climatic suitability for 80% of species by 2030, 87% by 2050 and 79% by 2070, suggesting that many reptiles may suffer range losses under climate change. The fact that fewer species were projected to experience climatic range contractions by 2070 compared with 2050 indicates that changes in climatic suitability are not always unidirectional on the time scales considered here. For example, climatic suitability for 45 species (13%) was projected to decrease between the current and 2050 time periods, but then increase by 2070. This finding highlights both the complexity of species potential responses to climate change, and the importance of considering multiple time periods when modelling species range shifts.

There are currently several regions of high climatic suitability for the target taxa in Australia (Fig. 1). The largest of these regions occur in the south-east, the mid-west, the north and the centre of the continent. Under future climate change, these regions diminish in size and retract towards the coasts, with the central region disappearing entirely by 2050. Between 2050 and 2070, new areas of high climatic suitability appear in the north and west (Fig. 1d), as a consequence of the climatic range expansions projected for some species in this time period.

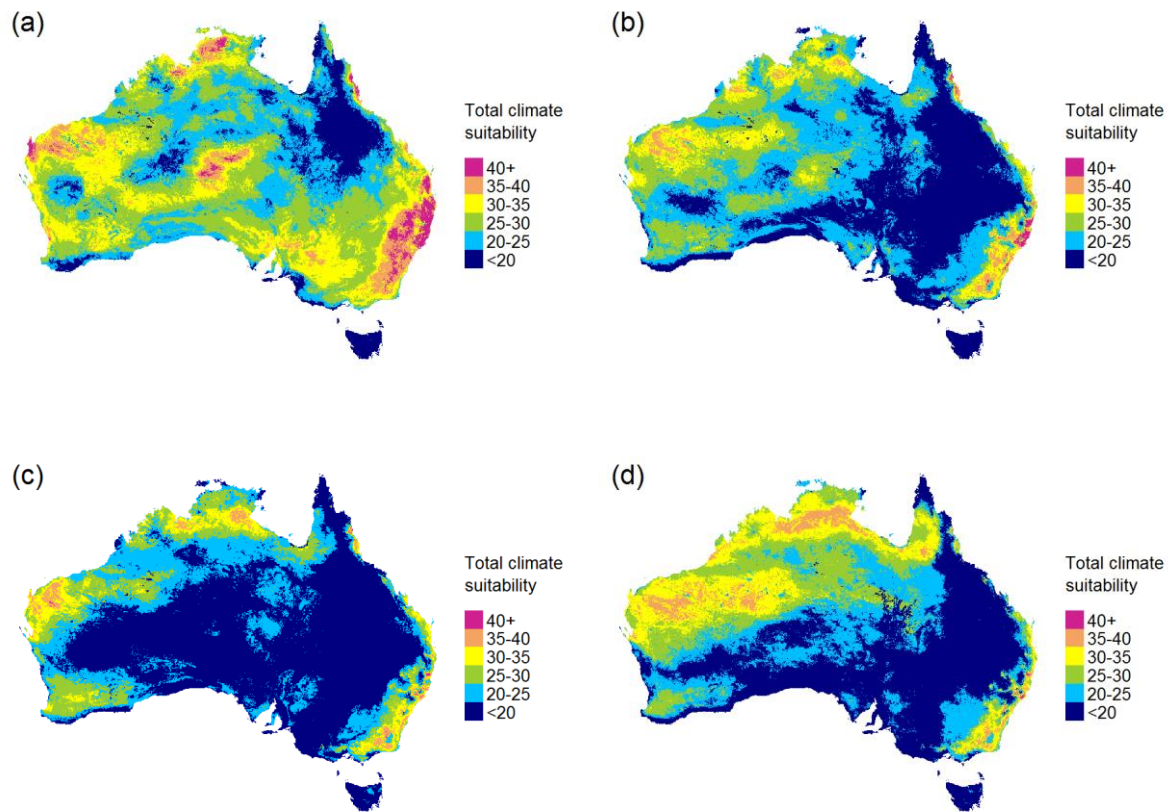


Figure 1. Total climatic suitability for the (a) current, (b) 2030, (c) 2050 and (d) 2070 time periods, derived by summing the projected maps across all 345 species.

Evaluation of the existing National Reserve System

The current climatic ranges of all species considered in this assessment are represented to some degree in the existing NRS, although not all are protected at target levels (Table 1; see Supplementary Table 1 for information on individual species). Under future climate change, the climatic ranges of an increasing number of species were projected to disappear from the reserve network, and in many instances to disappear altogether. The number of

species for which adequacy targets were met also progressively decreased under climate change.

Table 1. The average climatic range size, the number of species with climatic ranges entirely outside the existing NRS (gap species), the number of species for which the low and high targets are met, and the mean and median percentage of species climatic ranges included in the NRS. The results have been calculated for all species combined (n=345), and a subset of high priority species (n=51).

	Current	2030	2050	2070
<i>All species (n=345)</i>				
Average climatic range size (x10 ³ km ²)	594.9	497.2	445.8	510.7
Number of gap species	0 (0.0%)	21 (6.1%)	26 (7.5%)	32 (9.3%)
Number of species that meet low target	291 (84.3%)	222 (64.3%)	203 (58.8%)	192 (55.7%)
Number of species that meet high target	156 (45.2%)	116 (33.6%)	91 (26.4%)	80 (23.2%)
Mean range included in NRS	25.0%	26.8%	27.5%	27.5%
Median range included in NRS	19.2%	19.7%	19.9%	19.2%
<i>High priority species (n=51)</i>				
Average climatic range size (x10 ³ km ²)	229.4	69.4	48.6	39.1
Number of gap species	0 (0.0%)	11 (21.6%)	13 (25.5%)	13 (25.5%)
Number of species that meet low target	39 (76.5%)	16 (31.4%)	15 (29.4%)	10 (19.6%)
Number of species that meet high target	23 (45.1%)	11 (21.6%)	8 (15.7%)	5 (9.8%)
Mean range included in NRS	29.0%	24.3%	24.8%	25.0%
Median range included in NRS	21.7%	16.5%	13.0%	11.2%

The mean and median percentages of species current climatic ranges included in the NRS are 25.0% and 19.2% respectively (Table 1). This disparity between the mean and median values reflects the relatively large proportion of species that have only very small areas of their climatic ranges overlapping protected areas. When considering all species together,

these values remain relatively constant under future climate change suggesting that the loss of representation of some species climatic ranges in the NRS is balanced by a gain in representation of others.

The subset of high priority species had a higher proportion of gap species in all future time periods, and a lower proportion of species that met both the low and high target levels, compared to the group as a whole (Table 1). In the current time period, the mean and median percentages of species ranges included in the NRS are slightly larger than all species combined. Together, these results suggest that the majority of high priority species are poorly represented in the NRS, but that there are a few species with extremely high levels of overlap. This is logical if some areas have been incorporated into the NRS with the specific aim of protecting these well-represented species, or that these species have been extirpated from surrounding lands and now only persist in conservation areas. The average overlap of species climatic ranges with the NRS is considerably lower in all future time periods compared with the current, suggesting that the climatic ranges of many high priority species lose representation in protected areas as a consequence of climate change.

Systematic reserve selection

Additional areas selected by MARXAN were generally located throughout the continent, particularly along the east coast, in the south east and across the centre, although the exact spatial configuration of these areas varied among time periods and target levels (Fig. 2). This concentration of new areas along the coasts and across the centre is consistent with the projected changes in total climatic suitability under future climate change (Fig. 1). Few

planning units were consistently selected across all four time periods (red areas, Fig. 2). Under the low target scenario, only 12.4% of all selected planning units were selected in all four time periods, and only 7.6% of all selected planning units were consistently selected under the high target scenario. These priority areas were generally located near the coast, particularly in the south, east and south-west, with few areas in central regions. Very few coincide with areas of intensive human use, such as for residential, mining or intensive farming purposes (Fig. 3). Adding just these priority areas to the existing NRS would increase its size by approximately 79,000km² (6.7%) and 131,000km² (11.1%) under the low and high target scenarios respectively.

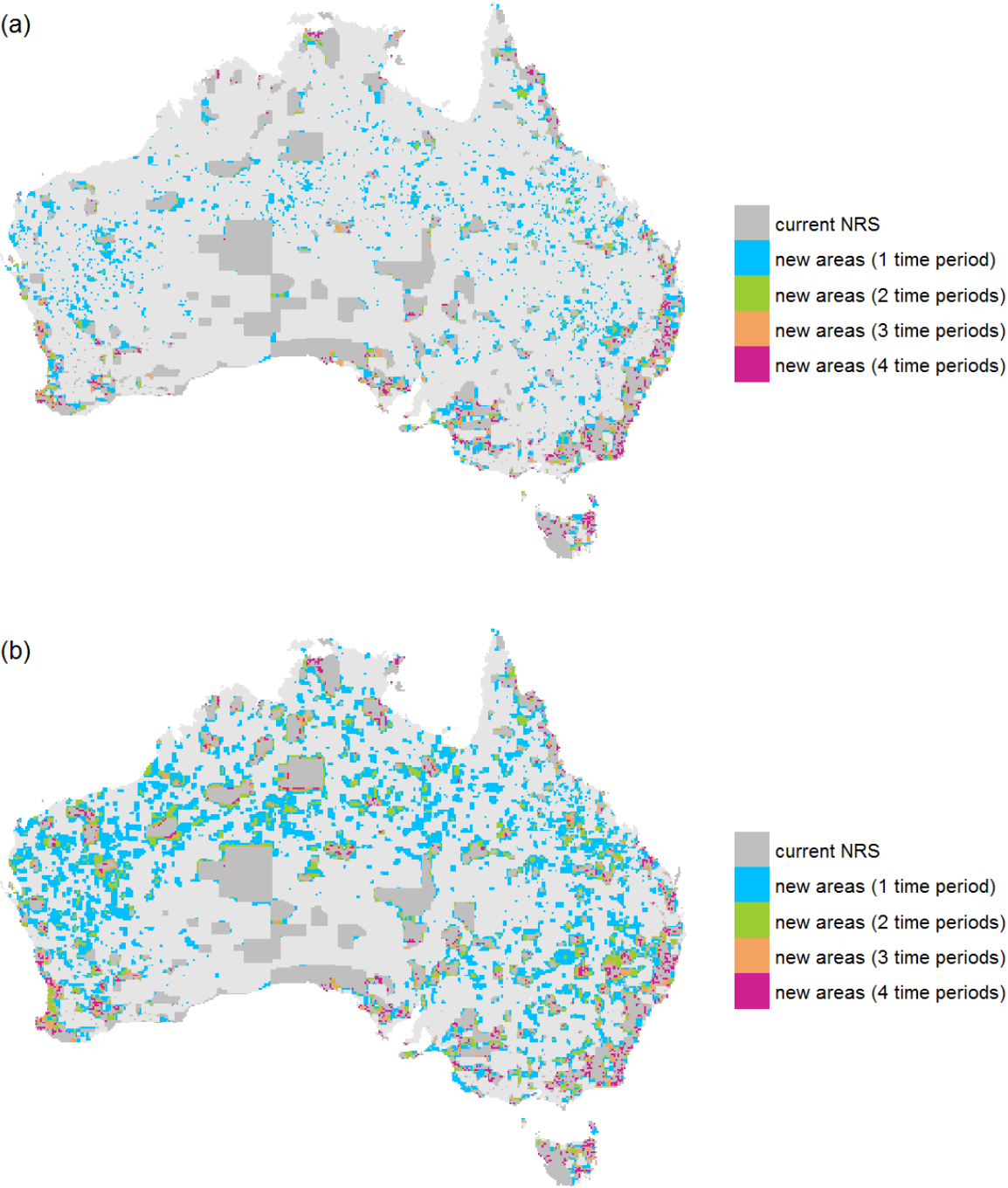


Figure 2. The additional areas selected under (a) the low target scenario and (b) the high target scenario. Areas selected in one time period are shown in blue, areas selected in two time periods are shown in green, areas selected in three time periods are shown in orange and areas selected in all four time periods (priority areas) are shown in red.

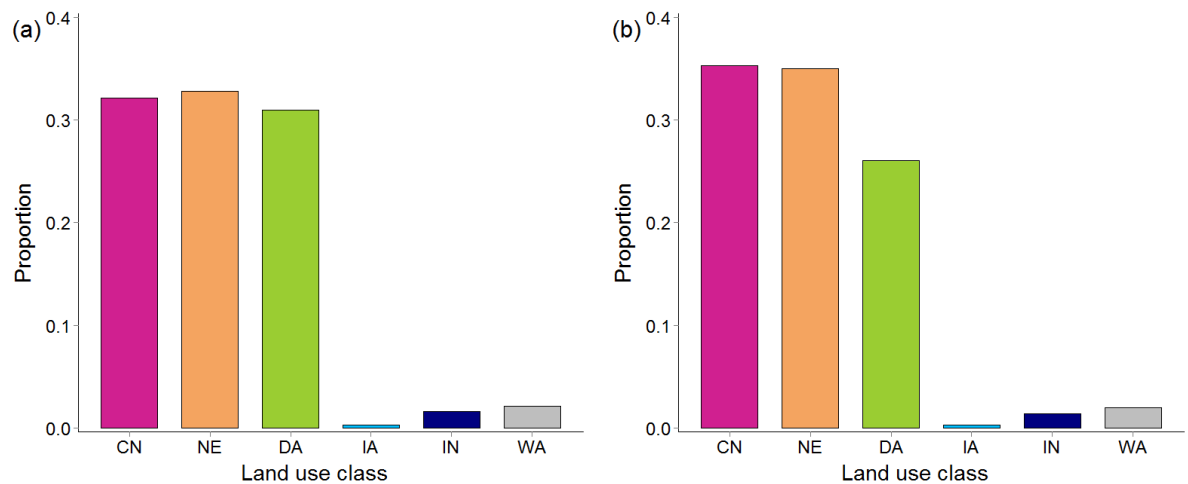


Figure 3. The proportion of priority areas coinciding with each major land use class under (a) the low target scenario and (b) the high target scenario. CN = conservation and natural environments, NE = production from relatively natural environments, DA = production from dryland agriculture and plantations, IA = productions from irrigated agriculture and plantation, IN = intensive uses (residential, mining etc.) and WA = water.

The addition of these priority areas to the existing NRS would increase the representation of species climatic ranges, with more species expected to meet the low and high targets and a higher average overlap of species ranges with the reserve network (Table 2). However, the number of gap species does not decrease under the low target scenario, and only decreases marginally under the high target scenario. This is because most of these gap species were projected to lose their entire climatic range under climate change, and would therefore classify as a gap species regardless of how much of the continent was protected.

Table 2. The efficiency of a reserve network that incorporates both existing areas and priority areas, in terms of the number of gap species, the number of species for which the low and high targets are met, and the average overlap between species ranges and the network. Results are shown for a network designed under the low target scenario and for one designed under the high target scenario.

	Current	2030	2050	2070
Network based on low target				
<i>All species (n=345)</i>				
Number of gap species	0 (0.0%)	21 (6.1%)	26 (7.5%)	32 (9.3%)
Number of species that meet low target	294 (85.2%)	231 (67.0%)	213 (61.7%)	201 (58.3%)
Number of species that meet high target	170 (49.3%)	130 (37.7%)	107 (31.0%)	104 (30.1%)
Mean range included in NRS (%)	28.2%	30.6%	31.3%	31.6%
Median range included in NRS (%)	20.5%	21.5%	21.9%	21.9%
<i>High priority species (n=51)</i>				
Number of gap species	0 (0.0%)	11 (21.6%)	13 (25.5%)	13 (25.5%)
Number of species that meet low target	39 (76.5%)	17 (33.3%)	16 (31.4%)	11 (21.6%)
Number of species that meet high target	25 (49.0%)	12 (23.5%)	10 (19.6%)	8 (15.7%)
Mean range included in NRS (%)	32.9%	28.9%	28.8%	28.9%
Median range included in NRS (%)	22.7%	18.2%	13.5%	12.7%
Network based on high target				
<i>All species (n=345)</i>				
Number of gap species	0 (0.0%)	21 (6.1%)	25 (7.2%)	31 (9.0%)
Number of species that meet low target	300 (87.0%)	236 (68.4%)	222 (64.3%)	203 (58.8%)
Number of species that meet high target	179 (51.9%)	140 (40.6%)	119 (34.5%)	107 (31.0%)
Mean range included in NRS (%)	29.4%	32.1%	32.7%	32.7%
Median range included in NRS (%)	21.7%	23.2%	23.2%	22.9%
<i>High priority species (n=51)</i>				
Number of gap species	0 (0.0%)	11 (21.6%)	13 (25.5%)	13 (25.5%)
Number of species that meet low target	40 (78.4%)	18 (35.3%)	16 (31.4%)	11 (21.6%)
Number of species that meet high target	26 (51.0%)	12 (23.5%)	10 (19.6%)	8 (15.7%)
Mean range included in NRS (%)	33.6%	30.0%	29.5%	29.6%
Median range included in NRS (%)	23.2%	19.4%	14.3%	13.4%

DISCUSSION

We used ecological niche modelling and a site prioritisation method to assess the adequacy of Australia's NRS for protecting a substantial portion of reptile species under climate change, and to identify additional areas of conservation value. We found that the existing network does not represent all species at even the low target level under current conditions, and an overall decrease in representation would be expected under climate change as species ranges contract. This decrease in representation was particularly marked for our subset of high-priority species, which is unsurprising given that this group included species that were projected to experience large range contractions under future climate change, and subsequently scored highly in the assessments described in Chapters 4-6. We also located 'priority areas' outside the existing NRS that were consistently selected across all four time periods. These areas could be particularly valuable additions to the NRS (subject to economic and socio-political considerations) because it is here where conservation efforts may yield the most consistent return.

Relatively few areas maintained their conservation value across all four time periods, highlighting the immense challenge of accounting for climate change in conservation planning exercises. The shifting of species range boundaries under climate change is a dynamic process, whereas protected areas are fixed in space. Designing reserve networks that are robust to climate change has consequently been likened to shooting a moving target (Wiens *et al.* 2011). Nevertheless, it is important that these challenges do not delay incorporating climate change into management planning, as this will result in network solutions that are more costly and less efficient than ones designed to conserve species current and future climatic ranges simultaneously (Hannah *et al.* 2007).

While the addition of these priority areas to the NRS may help slow the loss of species representation under climate change, we found that up to 70% of species would remain inadequately protected under both the low and high target levels. Almost 10% of species were projected to lose their entire bioclimatic ranges by 2070 and so would fail to meet conservation targets regardless of how much land was protected. For these species, land protection alone is unlikely to be sufficient to maximise their probability of persistence under climate change. Alternative strategies involving efforts both inside and outside protected areas, that target the species expected to be particularly vulnerable, may be necessary (Heller and Zavaleta 2009).

Because model accuracy is heavily dependent on sample size (Wisz *et al.* 2008), we were unable to include very rare species in this assessment. This is problematic because rare species tend to be restricted in their distributions, occur at low population densities, and are therefore in most need of conservation attention. A recent assessment of the capacity of Australia's NRS to protect threatened species across a variety of taxonomic groups found that a large proportion of species (80.4%) were not represented at target levels (equivalent to the low target level used in this study) (Watson *et al.* 2011). Of the 23 reptiles included in the assessment, four (17.4%) are found entirely outside the network. These extremely low levels of representation among threatened reptiles suggest that many species may have little capacity to be resilient to climate change unless new sites are added to the existing NRS. Other modelling techniques that do not require occurrence records, such as mechanistic models that associate the functional traits of species with their environment, may be useful in predicting the impacts of climate change on at least some of these rare species where sufficient data are available (Kearney and Porter 2009). Coupling these

model projections with a site prioritisation algorithm could then highlight other priority areas to augment those reported here.

Projecting species climatic ranges onto the climate surfaces of multiple future time periods proved particularly important, as the model projections did not reveal consistent climatic range contractions (or expansions) over time for all species, with some predicted to experience initial range contractions followed by expansions, and vice versa. This was a surprising finding, given the higher temperatures projected for 2070 (mean change in AMT since the current time period = 2.77°C , range = 1.70°C - 3.42°C) compared to the other time periods (2030: mean change in AMT since the current time period = 1.21°C , range = 0.64°C - 1.58°C ; 2050: mean change in AMT since the current time period = 1.73°C , range = 1.01°C - 2.21°C). Similar results have been described in other studies investigating the impacts of climate change on biodiversity (e.g. Carvalho *et al.* 2010; O'Donnell *et al.* 2012). A reserve design based on the projections from a single future time period may therefore be misleading because it fails to account for the potentially complex range dynamics of some species.

Using ENMs in conservation planning

There is a need for caution when interpreting ENM projections for conservation prioritisation purposes. ENMs are accompanied by a range of uncertainties relating to the emissions scenarios, the GCMs, the species location data and the modelling algorithm (Heikkinen *et al.* 2006; Sinclair *et al.* 2010). Different algorithms, for instance, have been shown to result in very different network designs (Loiselle *et al.* 2003). Because ENMs

project the potential distribution of a species rather than its actual distribution, there is a risk of protecting areas where the species is not actually found. Protecting areas within a species future climatic range, but not the species itself, will be more likely for those with low dispersal capabilities, such as many reptiles, which may be unable to track their shifting climatic niches. In this way, ENMs have the potential to underestimate the number of species that are inadequately protected, and the total amount of area that needs to be conserved. Setting targets higher than those usually deemed adequate for species conservation is one way to address this potential issue.

A further limitation of ENMs is their potential to overestimate species range shifts, as many species are expected to utilise microhabitat buffering, or undergo genetic, behavioural or physiological changes, that will enable them to persist in areas that become climatically unsuitable (Kearney *et al.* 2009; Huey *et al.* 2012). In these instances, establishing protected areas within the future climatic ranges of species may provide little benefit. Our current understanding of the capacity of reptiles to adapt to climate change *in situ* is relatively poor (Chapter 2). Until this knowledge gap is filled, a precautionary approach in which the potential for *in situ* adaptation is considered negligible, and both current and future climatic ranges are conserved, will be the safest course of action.

Despite these limitations, ENMs continue to prove valuable tools in conservation planning, particularly in a climate change context, for a number of reasons. They circumvent the need for comprehensive distribution data which are lacking for many species, they can be applied rapidly to large numbers of species, and they are able to generate projections of species potential distributions under future climates. A variety of techniques exist that enable users to minimise some of the uncertainties outlined above: using multiple

algorithms to project onto the climate surfaces produced by multiple GCMs, for instance, reduces the predictive uncertainty of single-algorithm and single-GCM approaches by combining their forecasts (Araújo and New 2007). Technical advances that enable key ecological processes, such as dispersal and *in situ* adaptation, to be explicitly considered in the modelling process will enhance their utility as conservation planning tools even further.

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CHAPTER 8

Discussion

INTRODUCTION

Climate change is expected to exert considerable pressure on the Earth's biodiversity over the course of the 21st century and beyond (Thomas *et al.* 2004; Steffen *et al.* 2009; Maclean and Wilson 2011). Limiting the severity of its impacts will require conservation efforts that are focused at the level of ecosystems and landscapes. Complimenting these ecosystem-based approaches are those that focus on individual species, in which the species most in need of conservation attention are identified, and appropriate management strategies are developed. In this thesis, a species-based approach was adopted to investigate the climate change vulnerability of one particular taxonomic group, the Australian reptiles. Using a variety of techniques, including environmental niche modelling, risk assessment and protected area planning, I identified which species may be particularly vulnerable to climate change in the future, and highlighted areas that appear important for reptile conservation, are robust to climate change, and may be valuable additions to the existing National Reserve System (NRS). In this discussion, I review the principal findings of the preceding chapters, highlight some of the strengths and limitations of the approaches adopted in this work, and make suggestions for management and research directions that warrant further attention.

SUMMARY OF MAIN FINDINGS

Many aspects of reptilian biology are linked closely to climate, raising concerns that reptiles could be particularly vulnerable to the negative impacts of climate change (Mitchell and Janzen 2010; Sinervo *et al.* 2010; Micheli-Campbell *et al.* 2011). In Chapters

2 and 3, I summarised the mounting empirical evidence to support these concerns, describing shifts in phenology and behaviours among some reptile species in response to changes in climate, both in Australia and elsewhere. The finding that species are already responding to climate change suggests future impacts on this taxonomic group could be severe, yet predictions of potential range contractions and population declines over the 21st century are lacking for the vast majority of Australia's reptile species.

A primary aim of this thesis was to address this knowledge gap by identifying which species may be particularly vulnerable to future climate change. To achieve this, I first used environmental niche models (ENMs) to project species climatic ranges into the future. To my knowledge, this work provides the most comprehensive assessment of potential range shifts among reptiles anywhere in the world, in terms of the total number of species modelled. The models projected climatic range contractions by 2050 for 71.5% of all species included in Chapters 4-6 (Table 1). This finding is broadly consistent with similar assessments of reptiles in Europe, which also forecast range contractions for a large number of species over the course of the 21st century (Araújo *et al.* 2006; Carvalho *et al.* 2010). However, my results revealed a considerably higher proportion of species projected to undergo future range contractions than these European assessments: Araújo *et al.* (2006), for example, projected range contractions for only 35% of species by 2050 in a continent-wide analysis, and Carvalho *et al.* (2010) projected range contractions for 50% of species in a finer-scale analysis of the Iberian Peninsula. These differences may be the result of variations in the modelling procedures used, or of the high percentage of endemic species in Australia (93% compared with 48% in Europe), which generally possess more specialised ecological niches and are therefore more susceptible to contractions in their climatic envelope.

Table 1. The number of species projected to undergo future range contractions, the number of species projected to lose all climatically suitable area, and the average change in climatic range size across all species included in Chapters 4-6.

Group	No. of species modelled	No. of species projected to lose climatically suitable area by 2050	No. of species projected to lose all climatically suitable area by 2050	Mean % change in climatic range size by 2050	Median % change in climatic range size by 2050
<i>Elapids</i>	81	57 (70.4%)	1 (1.2%)	-12.66	-26.06
<i>Skinks</i>	315	223 (70.8%)	21 (6.7%)	-13.89	-27.62
<i>Freshwater turtles</i>	32	26 (81.3%)	7 (21.9%)	-38.75	-63.04
All	428	306 (71.5%)	29 (6.8%)	-15.51	-28.83

Australia's freshwater turtles fared worse than the elapids and skinks with regard to the model projections, with the greatest average reduction in climatic range size of all three groups (Table 1). The turtles also had the highest percentage of species expected to experience climatic range contractions by 2050 (81.3%), which is consistent with a global analysis of freshwater turtles that projected range contractions for 86% of modelled species by 2080 (Ihlow *et al.* 2012). These results may reflect the relative dependence of freshwater turtles on water availability compared to terrestrial species, or it may be a consequence of slight differences in the modelling procedures used. For example, I used a minimum of 10 occurrence records as a criterion for inclusion in the freshwater turtle assessment (Chapter 6), because this threshold has been used successfully in other studies modelling climate change impacts on turtle distributions (Ihlow *et al.* 2012). This was less than the threshold I used for the elapid snakes and skinks in Chapters 4 and 5 respectively (15 records), and the inclusion of rarer species in the turtle assessment may have

contributed to the marked range contractions projected for many turtle species in Chapter 6.

In Chapters 4-6, I argued that model projections should not be used as the sole means of assessing species vulnerability to climate change. This is because ENMs project shifts in suitable habitat, rather than shifts in the distributions of species. Some species, for instance, may possess certain traits that allow them to remain in areas that become climatically unfavourable, whereas others may possess traits that prevent them from moving into new suitable areas. Generating a more comprehensive assessment of species vulnerability to climate change therefore requires a combination of model projections with information on species traits. Accordingly, I designed three novel assessment frameworks that explicitly incorporated these two sets of information. Applying these frameworks to the elapids, skinks and freshwater turtles, I found that vulnerability scores varied widely among species from all three groups, indicating that species responses to climate change will be idiosyncratic. Phylogenetic patterns in vulnerability were generally absent among all three groups. Some biogeographic patterns were present but these were weak and inconsistent. Broadly, arid and temperate reptiles appeared most vulnerable to climate change overall, possibly reflecting the higher levels of warming projected in the arid zone and the oceanic barrier preventing southwards shifts of species climatic ranges in the temperate zone. Among all three groups, multiregional species appeared least vulnerable overall as a consequence of their generalist habits and wide climatic niches.

In Chapter 7, I coupled the output of ENMs with a site prioritisation tool to evaluate the effectiveness of the existing NRS at protecting Australia's reptiles under climate change, and to identify currently unprotected areas that may be valuable additions to the network. I

found that the representation of most species climatic ranges in the NRS would decrease under future climate change. I also found that few areas maintained their importance for reptile conservation across all four time periods (current, 2030, 2050 and 2070), as a consequence of species climatic range shifts. Those that did, however, may be particularly valuable additions to the NRS because they are likely to offer the greatest return in conservation investment.

METHODOLOGICAL STRENGTHS AND WEAKNESSES

In this thesis, I employed a number of techniques, including environmental niche modelling, vulnerability assessment, and protected area planning using MARXAN. While the main strengths and limitations of these approaches have already been discussed in detail (Chapters 4-7), here I highlight some additional factors that should be considered when interpreting the results of the preceding chapters.

Environmental niche modelling

Correlative environmental niche models (ENMs) use a set of environmental variables to characterise the places where a species occurs (or does not occur). These models can then be projected onto other areas, or other time periods, to determine where environmental conditions are most suitable for that species (Guisan and Zimmermann 2000; Franklin 2009). ENMs have been used extensively to derive estimates of species range shifts under future climate change because of their ease of use and low data requirements compared to

mechanistic approaches. However, enthusiasm for their use is not universal due to the uncertainties and assumptions associated with their output. While these limitations have been reviewed in other studies (e.g. Heikkinen *et al.* 2006; Wiens *et al.* 2009; Sinclair *et al.* 2010), I would like to highlight one particular issue that has specific relevance to my work.

ENMs assume that a species current distribution is in equilibrium with climate, and that the species therefore inhabits all areas that are environmentally suitable. This may not be true if factors other than climate, such as the presence of a predator or geographic barrier, limit the distribution of a species in some areas. In Spain, for instance, the northern range boundaries of several reptile species have expanded northwards over the last few decades in line with recent warming, but the southern boundaries have remained relatively stable, suggesting that species are not limited by climate in the southern parts of their ranges (Moreno-Rueda *et al.* 2012). This is also likely to be true for Australian species because Australia is an island, and oceanic barriers are therefore likely to play an important role in limiting the range boundaries of some species. Barriers of unfavourable habitat are also likely to limit the ranges of many species, particularly in Queensland where rates of land clearing are highest (DERS 2010). In these cases, ENMs will be prone to omission errors which reduce their accuracy. Throughout this thesis, I have assumed that the ENM projections map species climatic ranges, rather than their actual ranges. Nevertheless, caution should be applied when interpreting the model projections presented here, particularly with respect to those species whose range boundaries are unlikely to be limited by climate.

Vulnerability assessments

Because conservation resources are invariably in short supply, identifying which species are likely to be at greatest risk of population declines and extinction is a primary goal of conservation management. Qualitative vulnerability assessments are popular tools by which this can be achieved. In Chapters 4-6 I developed novel assessment frameworks based on a points system that awarded points to species for a number of different variables. Species were then assigned to various vulnerability categories depending on their overall points score across all variables. This method is in contrast to rule-based systems, such as that employed by the IUCN, in which species are assigned to vulnerability categories determined by whether or not they satisfy one of several criteria (IUCN 2001). Both points-based and rule-based systems are generally considered preferable to qualitative assessments because of their transparency and repeatability (Todd and Burgman 1998; Burgman *et al.* 1999), and have consequently been used extensively to assess priorities for conservation action (e.g. Millsap *et al.* 1990; Lunney *et al.* 1997; Pheloung *et al.* 1999).

The principal disadvantages of points-based approaches have been outlined in Chapter 4. The main criticism is that the way in which the variables are combined to generate an index of vulnerability is essentially arbitrary. Additive assessments, in which the points awarded for each variable are summed to produce an overall vulnerability score, are particularly problematic because they imply the variables are in some way substitutable (McCarthy *et al.* 2004). In this thesis, I addressed these problems in two ways: 1) I used expert opinion to rank the variables in order of importance so they could be weighted more objectively than if I had attempted this myself, and 2) I designed the frameworks to incorporate the results of a multiplicative assessment, which implies imperfect

substitutability, alongside an additive one. Nevertheless, it is essential that the results derived from the assessments presented here are seen as a preliminary step only towards understanding the vulnerability of species to climate change. More comprehensive assessments of the species identified as being most vulnerable, using expert opinion or mechanistic models for instance, would be a logical next step.

Online questionnaires and the Delphi technique

In Chapters 4 and 5, I used a questionnaire to elicit the opinions of a group of experts on the relative importance of the variables used in the vulnerability assessments. A questionnaire was considered appropriate for this goal because all communication with participants could be done via email, without the need for face-to-face meetings which are costly and time consuming to organise. The simplicity of questionnaires also means they are repeatable, which is a distinct advantage in the context of climate change because future projections are regularly updated.

The questionnaires were distributed over two rounds, and interspersed with feedback in the form of a group summary, following the Delphi technique (Hsu and Sandford 2007).

Studies have shown that the Delphi technique not only increases consensus among panels of experts, but that this consensus is often more accurate than the opinions of the individual participants (Rowe and Wright 1999). I found that the range of responses following the second questionnaire round varied less than those following the first round, but only for the particularly important and unimportant variables. This suggests that some variables were clearly more important than others, but that the ‘moderately important’ variables were

exceedingly difficult to rank. It would be interesting to investigate whether the experts' opinions regarding these moderately important variables converged over subsequent rounds, however this would need to be balanced by the increased time and risk of participant withdrawals that would be involved.

Conservation planning with MARXAN

MARXAN is one of the most widely used conservation planning tools, both in Australia and elsewhere, and is therefore a well-known and understood method among scientists and practitioners (Ball *et al.* 2009). Its advantages include its ease and speed of use, its ability to incorporate costs and its flexibility to be applied to a multitude of different systems. Nevertheless, MARXAN is often criticised for oversimplifying the implementation process by assuming that every important factor can be included as either a feature or a cost, and by incorporating only a very basic assessment of connectivity (Wintle 2008). It is therefore important that the priority areas identified in Chapter 7 are seen as possibilities only that should then be taken to stakeholder groups for further scrutiny.

RECOMMENDATIONS FOR FUTURE RESEARCH

The results of this thesis raise several interesting questions. Addressing these questions would further our understanding of the vulnerability of reptiles to climate change, and assist in the design of better policies and management strategies. These questions include:

1. Are the results presented in this thesis corroborated by other approaches to vulnerability assessment?

More detailed assessments using other approaches should be used to corroborate (or refute) the species ranks, and thereby test the robustness of the frameworks presented in this thesis. These approaches may include qualitative assessments based on expert elicitation, mechanistic modelling (where sufficient data are available), and empirical testing. A long-term dataset of reptile population dynamics, for instance, could be used to test the hypothesis that species assigned to the higher vulnerability categories would respond more strongly to climatic perturbations (droughts, El Niño years etc.) than species in the lower vulnerability categories, assuming that these climatic events are a reasonable proxy for climate change.

2. Can the results of this thesis be converted into estimates of extinction risk?

Translating the results of this thesis into estimates of extinction risk would provide useful, additional information to conservation managers. The ENM projections could be converted into predicted changes in abundance using a species-area curve, and then expressed in terms of extinction risk using IUCN Red List criteria. This is because the threshold values used to determine the IUCN categories on the basis of population declines are linearly related to the logit transform of threshold extinction risk values (Maclean and Wilson 2011). The trait information could then be used to describe the uncertainty associated with the extinction estimates derived from the ENMs. For example, a species might be found to be at high risk of extinction because its climatic range is projected to disappear by 2050,

but this estimate could then be deemed very uncertain if the species possesses traits that may allow it to persist in areas that become climatically unsuitable.

3. Does the loss of species under climate change translate into a loss of functional diversity?

The results of this thesis show that large numbers of Australia's reptiles may be lost under future climate change, but whether this would translate into a loss of functional diversity has yet to be explored. The loss of a species from an area may only have minimal impact on the functioning of a community if other species possessing similar traits are able to persist. In contrast, the loss of a species may have a much more significant impact if the combination of traits that it possesses is unique. Such an assessment would provide a valuable insight into how the redundancy among species traits may buffer reptile communities against a loss of function under climate change (Thuiller *et al.* 2006; Gallagher *et al.* in press).

4. How can the results of this thesis, in combination with other assessments, contribute towards a climate change adaptation plan for Australia's reptiles?

In this thesis, I have concentrated on the value of the NRS at protecting Australia's reptiles under future climate change (Chapter 7). However, it is widely agreed that the effective conservation of species under climate change will need to extend beyond the use of protected areas (Heller and Zavaleta 2009). Indeed, there are a number of other conservation-based strategies that are likely to be vital additions to a climate change adaptation plan for Australia's reptiles, as well as for other groups. These include:

i) Species-specific action plans for the most vulnerable species

Species-specific action plans should be developed to outline adaptation strategies aimed at protecting the most vulnerable species against the impacts of climate change. Ideally, these action plans should be integrated with assessments of vulnerability to other threatening processes, such as habitat degradation and invasive species, although further research is required to establish how best to achieve this. These action plans could draw heavily on the results reported in this thesis. For example, one strategy that has received considerable attention in the climate change literature is the translocation of species to cooler areas, and decisions on where and when to move a species could be informed by the model projections – sites with stable or improving climate suitability could represent possible target areas for translocation, whereas those with decreasing climatic suitability could represent possible source populations (Fouquet *et al.* 2010; Thomas 2011). However, translocations for conservation purposes entail significant risks and are by no means a guaranteed success – a recent review of reptile translocations found a success rate of only 35% (Germano and Bishop 2009). Nevertheless, translocations are considered by many researchers to have merit for some species, namely those with limited dispersal capabilities, specialised habitat requirements and highly fragmented populations (Fordham *et al.* in press). The pygmy blue-tongue lizard (*Tiliqua adelaidensis*) and the Western swamp turtle (*Pseudemydura umbrina*), which were both allocated to the highest vulnerability categories in Chapters 5 and 6 respectively, have already been identified as potential candidates for translocation (Burbidge *et al.* 2011; Fordham *et al.* in press). Ideally, these action plans should be integrated with assessments of vulnerability to other threatening processes, and further research is required to establish how best this can be achieved.

ii) Species monitoring

The results from this thesis suggest that many reptile species are likely to benefit from climate change. The yellow-faced whipsnake (*Demansia psammophis*), the broad-banded sand swimmer (*Eremiascincus richardsonii*), the narrow-banded sand swimmer (*Eremiascincus fasciolatus*) and the common sawshelled turtle (*Myuchelys latisternum*), for instance, were all projected to experience expansions in their climatic ranges and possess traits that may allow them to exploit these increases in climate space. Monitoring will be needed to see if these species do expand their ranges under climate change and become more abundant, as this may result in the displacement of other species that are unable to compete. It has been suggested that these indirect biotic impacts may be more harmful to many species than the direct impacts of climate change (Steffen *et al.* 2009).

iii) Increasing connectivity between protected areas

Maximising connectivity through the effective management of lands outside protected areas is widely held to be an important adjunct to expanding the existing NRS for the protection of species under climate change (Hannah *et al.* 2002; Heller and Zavaleta 2009), and many initiatives are already underway (Whitten *et al.* 2011). Off-reserve conservation will be particularly beneficial for species with poor dispersal capabilities, such as many reptiles, especially those with little overlap between their current and future climatic ranges, by increasing the likelihood species will be able to disperse between protected areas.

Dispersal corridors of native vegetation are ideally situated along the strongest climatic gradients which provide numerous climatic niches in close proximity, allowing species to track shifts in their preferred climate over short distances. In Australia, these typically run from inland areas towards the coast, in contrast to regions in the northern hemisphere where climatic gradients are generally strongest in a north-south direction. The ENM projections of several species support the suggestion that the contraction of species climatic ranges is likely to occur in a longitudinal, rather than a latitudinal, direction (Fig. 1). Coupling the model projections of multiple taxa with detailed vegetation maps may help identify possible dispersal corridors that would be particularly beneficial to species under climate change.

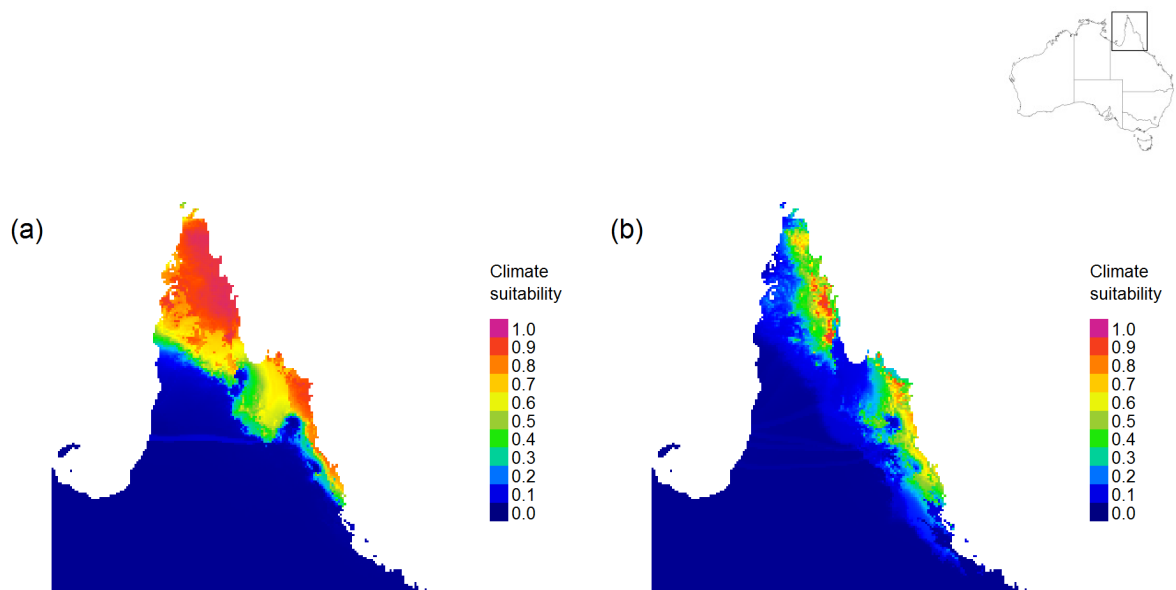


Figure 1. The (a) current and (b) 2050 climatic ranges of the brown-headed snake (*Furina tristis*), illustrating a range contraction towards the coast rather than a shift southwards.

CONCLUSION

In this thesis, I investigated the documented and predicted impacts of climate change on Australia's reptiles. I found that some species are already responding to the relatively modest climatic changes that have occurred to date, and that many more are likely to become susceptible to range contractions and population declines over the next few decades. These findings have important implications for conservation. Expansions of Australia's NRS are challenging given the dynamics of species range shifts projected under climate change, and other strategies, such as off-reserve conservation and translocation, may become increasingly necessary. Protecting Australia's reptiles under climate change therefore requires both the identification of the most vulnerable species and an assessment of appropriate management strategies. To this end, this thesis provides a wealth of information on which managers can draw.

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SUPPLEMENTARY
INFORMATION

The supplementary information associated with Chapters 4 – 7 can be found on the accompanying CD. This CD contains the following files.

Chapter	Description	Filename
4	Supplementary table 1	<i>Chapter_4/Supplementary_table_1.pdf</i>
4	Supplementary table 2	<i>Chapter_4/Supplementary_table_2.xls</i>
4	Maps of species current and 2050 climatic ranges	<i>Chapter_4/Elapid_species_maps.pdf</i>
5	Supplementary table 1	<i>Chapter_5/Supplementary_table_1.pdf</i>
5	Supplementary table 2	<i>Chapter_5/Supplementary_table_2.xls</i>
5	Supplementary table 3	<i>Chapter_5/Supplementary_table_3.pdf</i>
5	Maps of species current and 2050 climatic ranges	<i>Chapter_5/Skink_species_maps.pdf</i>
6	Supplementary table 1	<i>Chapter_6/Supplementary_table_1.pdf</i>
6	Supplementary table 2	<i>Chapter_6/Supplementary_table_2.xls</i>
6	Supplementary table 3	<i>Chapter_6/Supplementary_table_3.pdf</i>
6	Maps of species current and 2050 climatic ranges	<i>Chapter_6/Turtle_species_maps.pdf</i>
7	Supplementary table 1	<i>Chapter_7/Supplementary_table_1.pdf</i>
7	Maps of species current, 2030, 2050 and 2070 climatic ranges	<i>Chapter_7/Species_maps.pdf</i>

Ethics application reference-5201001302 - Final approval

Ethics Secretariat< ethics.secretariat@mq.edu.au> Tue, Nov 2, 2010 at 11:58 AM
To: Prof Lesley Hughes <lesley.hughes@mq.edu.au>
Cc: Miss Abigail Cabrelli <abigail.cabrelli@mq.edu.au>

Dear Prof Hughes,

Re: "The impact of climate change on Australia's reptiles" (Ref: 5201001302)

The above application was reviewed by the Human Research Ethics Committee. Final Approval of the above application is granted, effective 02 November 2010, and you may now commence your research.

The following personnel are authorised to conduct this research:

Prof Lesley Hughes- Chief Investigator/Supervisor
Miss Abigail Cabrelli- Co-Investigator

Please note the following standard requirements of approval:

1. The approval of this project is conditional upon your continuing compliance with the National Statement on Ethical Conduct in Human Research (2007).
2. Approval will be for a period of five (5) years subject to the provision of annual reports. Your first progress report is due on 2 November 2011.

If you complete the work earlier than you had planned you must submit a Final Report as soon as the work is completed. If the project has been discontinued or not commenced for any reason, you are also required to submit a Final Report for the project.

Progress reports and Final Reports are available at the following website:

http://www.research.mq.edu.au/for/researchers/how_to_obtain_ethics_approval/human_research_ethics/forms

3. If the project has run for more than five (5) years you cannot renew approval for the project. You will need to complete and submit a Final Report and submit a new application for the project. (The five year limit on renewal of approvals allows the Committee to fully re-review research in an environment where legislation, guidelines and requirements are continually changing, for example, new child protection and privacy laws).

4. All amendments to the project must be reviewed and approved by the Committee before implementation. Please complete and submit a Request for Amendment Form available at the following website:

http://www.research.mq.edu.au/for/researchers/how_to_obtain_ethics_approval/human_research_ethics/forms

5. Please notify the Committee immediately in the event of any adverse effects on participants or of any unforeseen events that affect the continued ethical acceptability of the project.

6. At all times you are responsible for the ethical conduct of your research in accordance with the guidelines established by the University. This information is available at the following websites:

<http://www.mq.edu.au/policy/>

http://www.research.mq.edu.au/for/researchers/how_to_obtain_ethics_approval/human_research_ethics/policy

If you will be applying for or have applied for internal or external funding for the above project it is your responsibility to provide the Macquarie University's Research Grants Management Assistant with a copy of this email as soon as possible. Internal and External funding agencies will not be informed that you have final approval for your project and funds will not be released until the Research Grants Management Assistant has received a copy of this email.

If you need to provide a hard copy letter of Final Approval to an external organisation as evidence that you have Final Approval, please do not hesitate to contact the Ethics Secretariat at the address below.

Please retain a copy of this email as this is your official notification of final ethics approval.

Yours sincerely

Dr Karolyn White

Director of Research Ethics

Chair, Human Research Ethics Committee