Impacts of climate change on Cunningham's skink (*Egernia cunninghami*)

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DECLARATION

I, Benjamin Yeboah Ofori, hereby declare that the work in this thesis entitled "Impacts of Climate Change on Cunningham's skink (*Egernia cunninghami*)" submitted to the Department of Biological Sciences, Macquarie University, Sydney, for the award of a Doctor of Philosophy Degree is my original research work. This work has not been submitted in any other form, for a higher degree at any other university or institution.

Lizard capturing and handling was approved by the Macquarie University Animal Ethics Committee (Protocol number: ARA 2013/015) and was licensed by the Office of Environment & Heritage, NSW National Parks and Wildlife Service (Protocol number: SL101164).

SIGN ……..

BENJAMIN YEBOAH OFORI

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ABSTRACT

Climate change has become a mainstay conservation research topic because of the substantial threat it poses to global biodiversity. The capacity of species to disperse to track the movement of their climate niches, or to adapt *in situ* to novel climates through micro-evolution, will determine their persistence under climate change. Yet, studies assessing the impacts of climate change on biodiversity rarely account for species' dispersal and evolutionary potential. In this thesis, I employ population genomics, and species distribution and landscape connectivity models to assess the potential responses of a philopatric species, Cunningham's skink (*Egernia cunninghami*), to climate change. Genetic data revealed strong population structuring, and different spatial patterns of putatively neutral SNPs versus those under divergent selection. I found a significant positive association between SNPs under divergent selection and temperature. Results suggest that the natural dispersal rate of Cunningham's skink may be insufficient to track shifts in climate zones, irrespective of landscape connectivity. Similar results were obtained by incorporating realistic estimates of dispersal and landscape connectivity into species distribution models, i.e. most populations of *E. cunninghami* may not have adequate dispersal capabilities to track climate change. However, combining measures of exposure, sensitivity and adaptive capacity to assess the vulnerability of *E. cunninghami* and other Australian lizards to climate change revealed that some lizards, including *E. cunninghami*, may have sufficient adaptive potential (micro-evolutionary and plastic responses) to cope with climate change.

CHAPTER DECLARATION

This thesis is structured and written to conform to the "thesis by publication" format. It is organized into seven chapters: an introductory chapter, one review chapter, three data chapters and a general discussion and conclusion chapter. The titles of and my contribution to each chapter are as follows:

Chapter One: Introduction

I reviewed the climate change literature, identified knowledge gaps and did all the writing with feedback from Dr. Linda Beaumont and Prof. Adam Stow.

Chapter Two: Conservation planning under climate change: a need for an integrative modelling approach

I performed the review of the climate change, connectivity, dispersal and species distribution modeling literature and writing of this chapter with feedback from Dr. Linda Beaumont and Prof. Adam Stow.

Chapter Three: Combining dispersal, landscape connectivity and Maxent to assess climate-induced changes in the distribution of Cunningham's skinks

The research idea was perceived by myself and Dr. Linda Beaumont with input from Prof. Adam Stow. I did all the dispersal and landscape connectivity modeling with feedback from Dr. Linda Beaumont and Prof. Adam Stow. The custom R script for the species distribution modeling was designed and written by John

Baumgartner. I wrote the chapter with feedback from Dr. Linda Beaumont, Prof. Adam Stow and John Baumgartner.

Chapter Four: Cunningham's skinks show low genetic connectivity and signatures of divergent selection across its distribution

The research idea and sampling sites were designed by myself, Prof. Adam Stow and Dr. Linda Beaumont. I completed all permit preparation with feedback from Prof. Adam Stow. I did > 95% of the fieldwork and data collection, 100% of the DNA extraction and analysis of SNPs data with some guidance and support from Prof. Adam Stow. I wrote the chapter with feedback from Prof. Adam Stow and Dr. Linda Beaumont.

Chapter Five: Adaptive capacity influence the outcome of climate change vulnerability assessment

I perceived, designed and wrote this chapter with feedback from Dr. Linda Beaumont, Prof. Adam Stow and John Baumgartner. The custom R script for the species distribution modeling was designed and written by John Baumgartner.

Chapter Six: Discussion and conclusion

I organized and wrote this chapter with feedback from Dr. Linda Beaumont and Prof. Adam Stow.

Appendix One: Small mammal study

This describes additional work, unrelated to, and not part of, my thesis that I undertook during my candidature. I led the field work and completed the manuscript preparation with feedback from Professor Daniel Attuquayefio and Professor Yaa Ntiamoa-Baidu. This paper was published in *Environmental Monitoring and Assessment.*

Appendix Two: Community-based nature conservation and biodiversity management

This describes additional work, unrelated to, and not part of, my thesis that I undertook during my candidature. I led the field work and completed the manuscript preparation with feedback from Professor Daniel Attuquayefio and Dr. Erasmus Owusu. This paper was published in *African Journal of Ecology*.

Appendix Three: Certificate of Animal Research Ethics

I attended a workshop Animal Research Ethics and completed all the necessary documents with feedback from Prof. Adam Stow.

Appendix Four: Environment & Heritage, NSW National Parks and Wildlife Service Certificate

I completed all the necessary documents with feedback from Prof. Adam Stow.

ACKNOWLEDGEMENTS

The success of the long-term, multidisciplinary research that formed this thesis relied on the guidance of my supervisors and contributions of the many volunteers that participated in the field work, interviews, data analyses and reviews of the manuscripts that make up the chapters of the thesis. I am immensely indebted to Dr. Linda Beaumont, my principal supervisor, for believing in me and giving me the opportunity to pursue a PhD in Terrestrial Biodiversity Adaptation and Climate Change at the Department of Biological Sciences, Macquarie University. Prior to this study, I had no knowledge of species distribution and landscape connectivity modeling and only a very basic understanding of conservation genetics. Combining these three fields of study into one research project therefore presented an enormous challenge and steep learning for me. But thanks to Dr. Linda Beaumont who constantly reassured me of my capabilities and instilled in me self-belief and confidence when the going was tough. Thank you Linda!

I sincerely thank my associate supervisor Prof. Adam Stow for his continued expertise, enthusiasm, constructive critique, endless patience and support throughout my candidateship, particularly during periods of frustration when things were not going as planned. A special thanks go to Prof. Mariella Herberstein for endorsing the application that brought me here to study at the Macquarie University.

I wish to thank Nicholas Powell, Rafael Alvarez and Steve McAlpin for assisting with fieldwork, Paulo Momigliano, Siobhan Dennison, Rafael de Fraga, Vincenzo Repaci and Joseph Maina for assisting with laboratory work and data analysis, and John Baumgartner for designing and writing the custom R script for the species distribution modeling.

Finally, I thank David Nipperess, Michael Kearney, Steve McAlpin, David Chapple, Harold Heatwole, Jonathan Webb and Richard Shine for their participation in the Dephi process, Michael Gillings and Robert Harcourt for reviewing and providing feedback on sections of the thesis, and all my lab mates, Mohasin Haque, Anindita Roy, Manuel Esperou-Rodriguez and Sabira Sultana for their useful comments on parts of the thesis.

DEDICATION

To my wife Adelaide Ofori, my kids Gloria Oforiwaa Yeboah and John Noble Ofori-Yeboah and all my friends and loved ones.

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CHAPTER ONE

Introduction

Background

Climate change presents a serious threat to global biodiversity, and the ecosystem functions and services upon which humans depend (Chapin III *et al.*, 2000; Sala *et al.*, 2000; Rosenzweig *et al.*, 2008; Warren *et al.*, 2013). Its impacts may be even more profound when coupled with habitat loss and fragmentation (Pimm *et al.*, 2006; Brook *et al.*, 2008; Ackerly *et al.*, 2010; Bancroft *et al.*, 2016). Although the exact pathways and extent to which different organisms will be affected remain yet unclear, ample and widespread evidence suggests that climate change has already caused, and will continue to cause, changes in species distribution (Parmesan & Yohe, 2003; Chen *et al.*, 2011; VanDerWal *et al.*, 2013), alterations in phenology (Cleland *et al.*, 2007; Parmesan, 2007; Singer & Parmesan, 2010; Thackeray *et al.*, 2010; Cleland *et al.*, 2012; Beaumont *et al.*, 2015), physiology (Rosenzweig *et al.*, 2008), morphology (Ruiz-Navarro *et al.*, 2016; Walsh *et al.*, 2016), demography, community compositions (Moritz *et al.*, 2008; Walther, 2010; Bellard *et al.*, 2012) and the nature of ecological interactions (Walther *et al.*, 2002; Parmesan, 2006). Species level extinctions have also been reported (Pounds *et al.*, 1999; Sinervo *et al.*, 2010), with rates of extinction projected to accelerate as climate change intensifies (Thomas *et al.*, 2004; Parry, 2007; Sinervo *et al.*, 2010; Şekercioğlu *et al.*, 2012; Urban, 2015).

The Earth's climate has warmed by ~ 0.74 ^{o}C over the past century, and it is projected that global mean temperatures will increase by 4.3 ^{o}C by 2100, if current trend in greenhouse

gas emissions continues unabated (Stocker *et al.*, 2013). Atmospheric carbon dioxide concentrations have increased by over 40% since the industrial revolution (Pachauri *et al.*, 2014). Climate change may be irreversible and there is a lag response of species to changes in their environment (Menéndez *et al.*, 2006). For this reason, some species will still be threatened by climate change even when or if current greenhouse gas emission levels are reduced through policy interventions. Consequently, it is important for conservation biologists, planners and practitioners to manage species and populations in a manner that increases their resilience and adaptation to climate change (Pressey *et al.*, 2007; Thuiller *et al.*, 2008). Although existing conventional conservation strategies will play a significant role in managing biodiversity (Hunter Jr *et al.*, 2010), they may require improvement and the development of new approaches may be necessary to adequately address the threats of climate change (Heller & Zavaleta, 2009).

To do this effectively requires a better understanding of the interactions between climate change and biodiversity. A crucial ecological and conservation research programme in the 21st Century therefore, is to understand the biological consequences of climate change (Parmesan, 2006; Wiens *et al.*, 2009; Burrows *et al.*, 2011; Gotelli & Stanton-Geddes, 2015). There is considerable variation in the way organisms will response to climate change, but theoretical and empirical evidence suggests that they may disperse to track shifts in their climate niches (Vos *et al.*, 2008; Santos *et al.*, 2009) or adapt through micro-evolution (Bell & Gonzalez, 2009, 2011; Hoffmann & Sgro, 2011; Sgro *et al.*, 2011) or physiological, behavioural or phenological plasticity (Pigliucci, 2005; Fuller *et al.*, 2010; Reed *et al.*, 2011). A more holistic understanding of the impacts of climate change on biodiversity, therefore must consider species' dispersal capacity and adaptive potential against the pace of shifting climate, which averages 6.1 km/decade for terrestrial

communities and from 1.4 to 28 km/decade for marine communities (Burrows *et al.*, 2011). Yet, rarely has any single study assessing the implications of climate change on biodiversity investigated species' dispersal capacity and evolutionary potential simultaneously.

Species distribution models (SDMs) have become a widely used tool for assessing the potential impacts of climate change on biodiversity (Araújo *et al.*, 2006; Elith & Leathwick, 2009b; VanDerWal *et al.*, 2009; Austin & Van Niel, 2011). SDMs analyze the statistical relationship between the current locations of a species and the environmental characteristics (predominantly climate parameters) of those locations. The model can be used to identify potential areas with suitable environmental conditions for the focal species now and in the future (Elith & Graham, 2009; Elith & Leathwick, 2009b; Austin & Van Niel, 2011). The overarching principle here is that species are more likely to persist or establish new populations in areas with suitable environmental conditions. SDMs rely on the assumptions that (i) species occurrences and predictor variables are in equilibrium, (ii) current climatic and geographic constraints that define a species distribution reflects its biophysical limits and (iii) species niches are conserved over space and time (Hannah *et al.*, 2007a; Ashcroft *et al.*, 2009; Elith & Leathwick, 2009b; Franklin, 2010; Thom *et al.*, 2016).

SDMs have been used extensively to project climate-driven range shifts in a multitude of terrestrial, marine and freshwater species (Chen *et al.*, 2011; Urban, 2015), inform the design of surveys seeking populations of rare species (Raxworthy *et al.*, 2003), management of invasive species (Beaumont *et al.*, 2009; Baxter & Possingham, 2011; Beaumont *et al.*, 2014) and delineation of future reserves (Guisan *et al.*, 2006; Hannah *et*

al., 2007b; Keppel *et al.*, 2012), biodiversity hotspots (Thom *et al.*, 2016) and climate refugia (Ashcroft, 2010; Shoo *et al.*, 2011). Yet, some have questioned the accuracy and reliability of outputs of SDMs for conservation planning on the grounds of the numerous uncertainties and discrepancies inherent in climate models (Beaumont *et al.*, 2008) and SDM algorithms (Elith & Leathwick, 2009a; Willis & Bhagwat, 2009; Sinclair *et al.*, 2010; Van der Putten *et al.*, 2010). The tenability of their underlying assumptions under novel climate has also been questioned (Kearney *et al.*, 2010).

To date, most SDMs do not explicitly account for dispersal, biotic interactions and/or demographic and evolutionary processes. However, advances have seen genuine attempts made to account for these processes that determine the presence or absence of species at the local scale and their extinction risks to climate change (Iverson *et al.*, 2004; Midgley *et al.*, 2006; Keith *et al.*, 2008; Engler *et al.*, 2009; Fordham *et al.*, 2012; Harris *et al.*, 2012; Meineri *et al.*, 2012). Nonetheless, given the increasing influence of SDMs on spatial conservation planning, further improvements are required to enhance their predictive capacity.

The role of evolutionary adaptation to populations and species persistence in marginal and changing environments has long been recognized, and several studies have characterized the genetic structure of species across their distributional ranges to inform their management. Patterns of genetic structure are typically characterized using neutral markers, such as microsatellite genotypes which can reveal patterns of gene flow and reproductively isolated populations (Frankham *et al.*, 2002). However, because they are selectively neutral (Nosil *et al.*, 2009; Lowe & Allendorf, 2010), these markers do not

reveal geographical patterns of population divergence at adaptive genetic variation and the extent of local adaptation (Allendorf *et al.*, 2010; Sheth & Angert, 2016).

Recent advances in next-generation sequencing technologies have increased the availability of genomic data for non-model species, making it possible to identify loci that are putatively adaptive, i.e., either under divergent selection or physically linked to regions of the genome that are under divergent selection (Nosil *et al.*, 2009; Allendorf *et al.*, 2010; Hess *et al.*, 2013). Studies using genome scanning have highlighted the spatial patterns of adaptive genetic variation and local adaptations associated with selection in non-model species (Schweizer *et al.*, 2015; Forester *et al.*, 2016). Such knowledge can highlight the potential benefits and risks of enhancing gene flow between populations from dissimilar environments and inform conservation actions under rapid climate change.

Reptiles are a diverse group of vertebrates that live in terrestrial, freshwater and marine habitats (Böhm *et al.*, 2013). As prey, predators, grazers and seed dispersers, they play important roles in energy flow and material recycling and hence, influence the structure and composition of their ecosystems. Like most ectotherms, the abundance, distribution and other life-history traits of reptiles are strongly tied to temperature and rainfall patterns, making them vulnerable to climate change (Huey *et al.*, 2009; Bickford *et al.*, 2010; Sinervo *et al.*, 2010). In Australia, reptiles are particularly diverse, accounting for about 11% of all known reptiles on earth (Brooks *et al.*, 2006). Ninety-three percent of Australia's reptiles are endemic to the continent, with many having restricted ranges and narrow niche requirements (Chapman, 2009). These characteristics likely make them susceptible to climate change (Araújo *et al.*, 2006; Huey *et al.*, 2009). Yet, like those of other regions, Australian reptiles have received proportionately less attention in the climate

change literature compared to birds, mammals and plants (Cabrelli *et al.*, 2014). This necessitates the need to investigate the implications of climate change for as many reptilian species as possible in order to develop and, if necessary, implement effective and targeted conservation intervention to increase their resilience and adaptive capacity to climate change (Franklin, 2010).

Main objectives

In this thesis, I investigate the impacts of climate change on Australian lizards using Cunningham's skink (*Egernia Cunninghami*) as a model species. Further, given the potential vulnerability of Australian lizards to climate change, it is imperative to understand if their dispersal capacity is adequate to facilitate range shifts, or whether they possess sufficient genetic variation to enable adaptation to climate change in situ. It is also important to identify which species may be most vulnerable to climate change, and the factors contributing to their vulnerability, in order to choose the appropriate and cost-effective management strategies. Therefore, the main objectives of my candidature were as follows:

(i) To assess whether Cunningham's skink has adequate dispersal capacity to undertake climate-driven range shifts, and whether increasing habitat connectivity may increase the likelihood that this species will be able to successfully track spatial shifts in its climate niche;

(ii) To characterize the spatial pattern of neutral and adaptive genetic variation of Cunningham's skink and evaluate implications for conservation and management of the species under climate change; and

(iii) To identify Australian lizards vulnerable to climate change and the factors that contribute most to their vulnerability.

Structure and format of thesis

I have organized this thesis into six chapters, and have written and structured it to comply with the format of "thesis by publication". As a result, Chapters 2 – 5 are written as stand-alone chapters, with each structured to conform to the format of the potential journal to which it will be or was submitted. The titles of the chapters are:

Chapter One: *Introduction*

Chapter Two: *Conservation planning under climate change: a need for an integrative modelling approach*

Chapter Three: *Combining dispersal, landscape connectivity and Maxent to assess climate-induced changes in the distribution of Cunningham's skinks*

Chapter Four: *Cunningham's skinks show low genetic connectivity and signatures of divergent selection across its distribution (**this chapter is published in its current form in Ecology and Evolution**)*

Chapter Five: *Adaptive capacity influences the output of climate change vulnerability assessment (**this chapter has been submitted for consideration for publication in Scientific Reports and is currently under review**)*

Chapter Six: *Discussion and Conclusion*

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CHAPTER TWO

Conservation planning under climate change: a need for an integrative modelling approach

Abstract

Effective conservation planning under climate change requires the synthesis of multiple approaches, including species distribution modeling, realistic estimates of dispersal and functional connectivity of landscapes. Species distribution models (SDMs) have been used extensively to assess changes in habitat suitability under climate change. However, the ability of a species to spread across landscapes is often not considered. Whether species are capable of colonizing new habitat and realizing projected range shifts depends, in part, on their dispersal capacity and the connectivity of the intervening landscape matrix. Landscape connectivity models (LCMs) can provide insights into how structures and features of the landscape facilitate or impede the movement of organisms. However, rarely have SDMs and LCMs been combined to assess species responses to climate change. Yet these are complementary tools, and integrating the output of SDMs with LCMs will likely provide a more rigorous approach to spatial conservation planning under climate change. Challenges remain, however, particularly limitations associated with current PC platform and software environments in modeling fine-scale connectivity over a wide geographic region, and in our ability to collate and synthesize data from diverse fields.

Introduction

Globally, biodiversity is being lost at unprecedented rates, driven mainly by habitat loss and fragmentation, invasive alien species, overexploitation and anthropogenic climate change (Brook *et al.*, 2008; Butchart *et al.*, 2010). Mounting evidence suggests that rates of species extinction will increase as the century progresses, due to climate and other environmental changes (Sinervo *et al.*, 2010; Chen *et al.*, 2011; Urban, 2015; Bancroft *et al.*, 2016). Ameliorating the negative impacts of these changes requires more effective conservation planning (Pressey *et al.*, 2007; Brooke, 2008; Thuiller *et al.*, 2008). This calls for an increased capacity to pre-empt biological responses to these changes (Carvajal-Rodríguez, 2010; Kearney *et al.*, 2010; Dawson *et al.*, 2011).

Species distribution models (SDMs), also known as habitat suitability models or environmental niche models, are tools commonly used for assessing climate-induced changes in the distribution of habitat suitable for the target species (Elith & Leathwick, 2009). However, most SDMs do not account for important mechanisms such as dispersal, biotic interactions, evolutionary processes and demography that determine the presence of species at the local scale, extinction risks and colonization potential (Araujo & Guisan, 2006; Araújo & Luoto, 2007; Van der Putten *et al.*, 2010; Travis *et al.*, 2013). As climate changes, the ability of species to locate suitable habitats will depend on their capacity to move across landscapes as well as the connectivity and permeability of the landscape (Taylor *et al.*, 1993; Broennimann *et al.*, 2006; Baguette *et al.*, 2013; Fordham *et al.*, 2014). While some studies have incorporated dispersal into SDMs, fewer have attempted to address the impact of landscape structure and features on the movement of organisms (but see Fordham *et al.*, 2014). Contemporary landscapes are fragmented and dominated by human activities (Cushman, 2006), and this can dramatically affect the movement of

individuals (Trakhtenbrot *et al.*, 2005; Etherington & Holland, 2013; Palmer *et al.*, 2014). Consequently, ignoring the connectivity of the landscape matrix and its effect on dispersal may have considerable implications for spatial conservation planning that utilizes the output of SDMs.

Indeed, for most species the lack of data on dispersal and the influence of landscape heterogeneity on movement makes it difficult to integrate these elements into SDMs. However, recent technological and conceptual advances in ecology, landscape genetics, computer and space science have revolutionized dispersal studies (Hussey *et al.*, 2015; Kays *et al.*, 2015). In parallel, advances in landscape connectivity modeling are providing insights into how landscape features impede or facilitate the movement of organisms (Etherington *et al.*, 2014; Lechner *et al.*, 2015a). Landscape connectivity models (LCMs) are used to identify barriers to dispersal and the corridors that enhance movement and colonization of suitable habitats. LCMs can also be used to predict how landscape features may influence dispersal in novel environments (Zeller *et al.*, 2012). Hence, combining SDMs and LCMs with target species' dispersal rates will promote a deeper understanding of their capacity to respond to climate change via range shifts.

Here, we provide an overview of SDMs, LCMs and the approaches used for gathering empirical dispersal data, and their associated limitations. We then highlight the value of combining these tools, and discuss challenges and future perspectives. For species distribution modeling, we will focus our attention on correlative environmental niche models because they are easy to parameterize and are the most frequently used SDMs (Dormann *et al.*, 2012; Meineri *et al.*, 2015; Pacifici *et al.*, 2015).

Methods for gathering dispersal data

Dispersal is a key life-history trait that mediates exchange of individuals and genes among geographically-isolated populations and colonization of suitable habitats (Trakhtenbrot *et al.*, 2005; Clobert *et al.*, 2009; Taylor *et al.*, 2012; Groó *et al.*, 2013; Driscoll *et al.*, 2014). It thus has ecological and evolutionary consequences for the distribution of species and the spatial structure, dynamics and persistence of populations (McMahon *et al.*, 2013). This is particularly true in changing environments, making dispersal topical and an important prerequisite for spatial conservation planning and effective biodiversity management under climate change (Kokko & López-Sepulcre, 2006; Travis *et al.*, 2013).

A wide variety of approaches have been used to measure dispersal directly. The most basic approach is direct observation of individuals in the field, which provides accurate measures of their dispersal distance, movement patterns, behaviour, and interactions with the environment. However, this can be very challenging when monitoring large populations and small-bodied organisms over broad geographic scales (Watts *et al.*, 2007; Griesser *et al.*, 2014). Alternatively, individuals may be captured, marked then released and recaptured for mark identification (Gibbons & Andrews, 2004). Indeed, capture-mark-recapture (CMR) is the primary means of estimating dispersal and its effect on population dynamics and vital rates (Webster *et al.*, 2002; Peery *et al.*, 2006; Griesser *et al.*, 2014). For organisms that are too small to carry physical tags (e.g., larvae and juveniles of fish and aquatic invertebrates) chemical or fluorescent marking can be used (Thorrold *et al.*, 2007; Liu *et al.*, 2009).

More advanced direct methods operate on the principles of telemetry, whereby a transmitter tag affixed to an organism enables it to be tracked remotely (Cooke *et al.*,

2013). The extension of earth-based radio transmitters to satellite-based and global positioning systems (GPS), as well as development of automated miniature transmitters with built-in computers and animal-borne imaging systems, enables monitoring and mapping of animal movement in near-real-time (Bridge *et al.*, 2011; Kissling *et al.*, 2014). This can help secure vast quantities of accurate dispersal data from local to global scales, including cues for dispersal, settlement and breeding site selections, and the complex relationships between organisms and their environment (Wilson *et al.*, 2009; Hebblewhite & Haydon, 2010; Cooke *et al.*, 2013; Hussey *et al.*, 2015). Multi-sensor acoustic tags (i.e., archival tags combined with other sensors, such as hydrophones, magnetometers and accelerometers), also provide information on the movement patterns, feeding and social behaviour, as well as predator-prey interactions, of marine organisms at high resolution (Goldbogen *et al.*, 2013; Hussey *et al.*, 2015).

Indirect approaches, such as biogeochemical and genetic markers, eliminate the need to artificially tag individuals (Rubenstein & Hobson, 2004; Cowen & Sponaugle, 2009). Biogeochemical markers, typically stable isotopes or elemental ratios, have been used to study the dispersal of plants and animals (insects, mollusks, fish, amphibians, reptiles, birds and mammals) in different environments and at varied spatial and temporal scales (Levin, 2006; Studds *et al.*, 2012; Ethier *et al.*, 2013). The techniques work on the principle that naturally-occurring elements and stable isotope concentrations (Mg/Ca, Mn/Ca, and Sr/Ca, $\delta^{2}H$, $\delta^{15}N$, $\delta^{18}O$, and $\delta^{34}S$) in the environment are distinct and spatially variable (Wunder, 2012). The presence of such markers in an organisms' tissue (e.g., otoliths in fishes, shells and statoliths in mollusks, and keratin from feathers, hair, claws, skin, nails, horn and baleen) reflects the geographical origin of the organism (Militao *et al.*, 2013; Zenteno *et al.*, 2013). Accurate assignment of individuals to their natal sites,

however, requires good knowledge of the origin and abundance of the stable isotope or trace elemental markers, and the temporal scale over which they remain stable (Rubenstein & Hobson, 2004; Pauli *et al.*, 2012; McMahon *et al.*, 2013; Zenteno *et al.*, 2013).

The last few decades have seen a dramatic increase in the use of genetic techniques for estimating dispersal. Two primary analytical approaches are isolation-by-distance (IBD) and assignment test techniques. In IBD, researchers correlate estimates of genetic and geographic distances between populations. Assignment tests typically use allele frequencies and genotype likelihoods to assign individuals to parents or populations of origin (Manel *et al.*, 2005). Genetic approaches are robust, and have been particularly successful for estimating dispersal of animals (mammals, birds, reptiles, amphibians, fish, insects) and plants in various environments. Indirect approaches provide estimates of dispersal over multiple generations and can reveal rare long-distance dispersal. However, they may not reveal the behaviour, movement patterns, and performance of dispersers and their interactions with the environment in real-time (Table 1).

Species distribution modeling

Species distribution models (SDMs) establish a statistical relationship between records of the occurrences of a species and the environmental characteristics of those locations. This relationship is can then be projected onto alternate climate scenarios to identify the distribution of suitable habitat in the future (or the past) (Elith & Leathwick, 2009; Williams *et al.*, 2013; Burrows *et al.*, 2014; Beaumont *et al.*, 2016). SDMs are commonly used to assess the potential impacts of climate and other environmental changes on species

distributions (Elith & Leathwick, 2009; Dormann *et al.*, 2012). They have also been used to identify biodiversity hotspots, areas of endemism, climate refugia (Ashcroft, 2010; Shoo *et al.*, 2011; Thom *et al.*, 2016) and potential invasion by native and non-native species (Beaumont *et al.*, 2009; Baxter & Possingham, 2011; Beaumont *et al.*, 2014). In addition, these tools can inform the design of surveys seeking populations of rare species (Raxworthy *et al.*, 2003) and the prioritization of reserve systems (Guisan *et al.*, 2006; Hannah *et al.*, 2007; Keppel *et al.*, 2012).

However, the usefulness and validity of SDMs, particularly from a conservation perspective, has been criticized. This is because SDMs tend to ignore important ecological processes, such as dispersal, biotic interactions, evolutionary adaptation and demography that determine the distribution of species, colonization potential and extinction risks at local scales (Araujo & Guisan, 2006; Araújo & Luoto, 2007; Thuiller *et al.*, 2008; Kearney *et al.*, 2010; Van der Putten *et al.*, 2010; Travis *et al.*, 2013).

A number of attempts have been made to integrate eco-evolutionary processes into SDMs. For example, Midgley *et al.* (2006) included measures of dispersal in their SDM analysis of potential climate-induced range shifts among the Cape Proteaceae. They estimated that by 2050, mean species range size could reduce by 29% under an unlimited dispersal scenario, 75% under a no dispersal scenario, and 58% when a more realistic estimate of dispersal was utilised. Duckett *et al.* (2013) coupled a genetic estimate of dispersal with an SDM to assess the impacts of climate change on an Australian gecko (*Gehyra variegate*), and found that 17% to 41% of the current habitat of the species may become unsuitable by 2070. Biotic interactions influence species distributions at both local and regional levels (Wisz *et al.*, 2013). Accounting for these interactions within an SDM was found to

significantly influence the potential distribution of European butterfly species at large geographic scales (Araújo & Luoto, 2007).

Keith *et al.* (2008) combined SDMs with stochastic population models to explore the viability of plant populations under climate change. They found that species extinction risks were reduced by complex interactions between life history, disturbance regime and distribution pattern. Dullinger *et al.* (2012) coupled an SDM with demography and seed dispersal models to project spatio-temporal dynamics of mountain plants across the European Alps. They found that ~ 40% of species ranges will become unsuitable by end of the century and that population dynamics will lag behind climate trends, creating an extinction debt. Species endemic to the Alps were projected to experience the greatest range losses. SDMs have also been coupled with metapopulations and source-sink dynamics models to evaluate the effect of climate change and prey availability on the persistence of species (Fordham *et al.*, 2013). Such combinations of models indicated that climate change will dramatically decrease the abundance of Iberian lynx (*Lynx pardinus*) and could cause its extinction in the wild within the next 50 years. It also indicated that accounting for the impacts of climate change, prey abundance and habitat connectivity in a well-planned reintroduction program could avert extinction of the lynx within this century (Fordham *et al.*, 2013).

The above examples suggest that incorporating eco-evolutionary mechanisms into SDMs when modelling the potential impacts of climate change on species distributions may alter predictions of range dynamics and extinction risks. However, the influence of landscape structure and features on dispersal, population dynamics and gene flow has rarely been

included in these studies. Yet, the degree to which landscapes are connected can dramatically impact the spread of organisms (Fordham *et al.*, 2014).

Landscape connectivity modeling

Landscape connectivity is important for maintaining broad-scale eco-evolutionary processes such as dispersal, gene flow and source-sink population dynamics, and ultimately species distribution and persistence (Kool *et al.*, 2013). It is therefore a crucial focus of spatial conservation planning (Lechner *et al.*, 2015b). Several approaches have been used to measure connectivity and to identify corridors that enhance movement or act as barriers to dispersal. Direct field observations, capture-mark-recapture, telemetry and population genetics have provided direct measures and estimates of movement patterns, behaviour and interactions of organisms with their environment. However, gathering high resolution data at large spatial and temporal scales can be very difficult and expensive (Kool *et al.*, 2013). For this reason, researchers have resorted to models, which can be fitted with movement data from known environments and then projected into novel environments and future time-scales (Zeller *et al.*, 2012).

In this regard, several models have been developed, including matrix theory, graph theory, circuit theory and least-cost paths (LCP), with the last two being the most widely used (Zeller *et al.*, 2012). LCP analysis uses simple raster-based algorithms that weight the minimum distance between a source and target cells based on species-specific resistance values of the intervening landscape matrix (Zeller *et al.*, 2012; Etherington & Holland, 2013). For a given source cell, LCP estimates the route of maximum efficiency from the

start cell (source) to the destination cell as a function of the distance travelled and the ecological costs of traversing the landscape (Etherington *et al.*, 2014). Advances in LCP algorithms now allow various categories of cost-paths (least-cost corridors) that better depict habitat heterogeneity and its varying role in dispersal (Chan *et al.*, 2011). LCP models have been used extensively for connectivity analysis because they are relatively easy to run.

Circuitscape uses connections between random and electrical circuit theories to model landscape connectivity. It treats the landscape as a conductive surface within an electrical circuit, with individual movements analogous to current flow and different land cover types providing resistance to movement (McRae *et al.*, 2008; Shah & McRae, 2008). Like LCPs, grid cells representing different vegetation cover types and habitats with varying qualities are assigned resistance (or conductance) values representing the energetic costs, or mortality risk, of traversing these areas. The main advantage of circuitscape over LCP models is that it incorporates multiple dispersal pathways into analyses and creates voltage maps that can be used to identify barriers and restoration opportunities (McRae & Beier, 2007; Shah & McRae, 2008).

Effective implementation of LCP and circuit theory models depends largely on assigning appropriate resistance (or conductance) values to the various land cover types, but this remains a challenge (Spear *et al.*, 2010). Movement data from direct observations, CMR, telemetry and global positioning systems (GPS) technology have been used in some studies (Spear *et al.*, 2010; Harju *et al.*, 2013; Stevenson *et al.*, 2013; Stevenson-Holt *et al.*, 2014). Here, landscape features avoided by moving individuals are given higher resistance scores, while the cover types that most individuals traverse are awarded lower resistance scores

(Cushman *et al.*, 2010; Trainor *et al.*, 2013; Vasudev & Fletcher, 2015). Genetically-derived cost surfaces have also been used (McRae & Beier, 2007; Shah & McRae, 2008; Cushman *et al.*, 2009; Landguth *et al.*, 2010), while expert opinion has been sought to assign costs to resistance surfaces. Although the latter approach is highly subjective and error-prone, it is the most frequently used because empirically-derived movement and genetic data are unavailable for most species (Spear *et al.*, 2010; Zeller *et al.*, 2012).

Combining SDMs, LCMs and dispersal rates

Several approaches have been used to incorporate dispersal into SDMs in an ecologically realistic manner and these could be extended to accommodate measures of landscape connectivity. The basic methods use colonization potential based on "nearest-neighbour" approaches, where grid cells that become climatically suitable can be colonized only if a neighboring cell is already occupied (Bateman *et al.*, 2013). This has been implemented in software packages such as SHIFT (Iverson *et al.*, 2004), BioMove (Midgley *et al.*, 2010) and MigClim (Engler & Guisan, 2009). Other studies have applied Euclidean distance that is equal to the average dispersal distance of the focal species to buffer its current range. Grid cells beyond the buffered cells are presumed to be unreachable by the species (Midgley *et al.*, 2006; Duckett *et al.*, 2013). Because inter-individual variability in dispersal behaviours influence connectivity estimates, some studies have combined spatially explicit metapopulation and individual-based models with the outputs of SDMs (Lawson *et al.*, 2010; Fordham *et al.*, 2012). Combining measures of connectivity and dispersal rates with the output of SDMs is based on the same underlying ecological principles. Broadly, this framework follows a four-step process: (i) projection of climate-

driven changes in the distribution of suitable habitat for the target species; (ii) obtaining realistic estimates of dispersal rate; (iii) connectivity analysis of the landscape matrix across current and future time periods; and (iv) overlaying the dispersal rate with the cost-distances between the current and future distributions to evaluate future suitable areas that can be located by the target species.

Step 1: Species distribution modeling

Given the uncertainties in the output of different SDM algorithms and climate models (Beaumont *et al.*, 2008; Beaumont *et al.*, 2016), the best practice is to use several algorithms and climate models simultaneously (Marmion *et al.*, 2009; Thuiller *et al.*, 2009; Garcia *et al.*, 2012). Reporting the uncertainties associated with SDMs and climate scenarios can help conservation planners and practitioners to make more informed decisions. Linking the output of global climate models with temporally explicit local weather data has been shown to perform better than down-scaled global and regional climate data (Reside *et al.*, 2010). In addition, modeling at fine-spatial scale, for example 1 km × 1 km or finer resolution, may provide better output than modeling at coarse scale (e.g., 50 × 50 km), especially when local climate data is used. Projecting future habitat suitability onto multiple time slices at short time intervals (e.g.10 years) is recommended, as this can provide a more complete picture of fluctuations in habitat suitability over time (Reside *et al.*, 2010).

Step 2: Obtaining realistic estimates of species' dispersal rates

Dispersal distances and rates can be obtained empirically using direct observation, CMR, telemetry, genetics or biogeochemical approaches. Normally the direct approach may fail to measure rare long-distance dispersals that are crucial for range expansion and colonization of new habitats (Trakhtenbrot *et al.*, 2005; Taylor *et al.*, 2012; Viana *et al.*, 2013). It may therefore be useful to combine direct and indirect methods where such data are available or could be obtained. Ideally, dispersal rates should be measured across the entire landscape in order to capture the difference in the rates of movement of organisms in different habitats and land cover types, but in reality, such an approach may not be feasible. Indeed, dispersal data is unavailable for a majority of species and can be expensive and effort-demanding to obtain empirically (Nathan, 2001; Nathan *et al.*, 2008). In most instances therefore, generalizing data across a taxonomic group and habitat types might be necessary. A dispersal kernel could also be fitted from empirically-obtained dispersal distances and rates to account for uncertainties in species' colonization potential (Kool *et al.*, 2013).

Step 3: Landscape connectivity modeling

This requires the identification of key ecological connectivity parameters (including land cover types and geographical features of the landscape) and their influence on dispersal (Etherington & Holland, 2013; Etherington *et al.*, 2014). Connectivity parameters are then assigned values representing their effects on the movement of individuals based on the empirical data (Driezen *et al.*, 2007). Where this is unavailable, expert opinion could be used (Zeller *et al.*, 2012). The spatial data based on this is processed, and a cost-surface

(friction surface or resistance map) of the intervening landscape matrix is produced. This can be created using, for instance, the Resistance and Habitat Calculator in the Gnarly Landscape Utilities ArcGIS toolbox (McRae *et al.*, 2008).

The connectivity of the intervening matrix, i.e., least-cost paths and corridor between occupied grid cells that are projected to become unsuitable and the nearest suitable grid cells, is then modelled using the resistance map and the SDM output as input files. This can be done using the SDMtoolbox package (Brown, 2014) implemented in ArcGIS (ESRI Inc., Redlands CA, USA, 2013), or the CircuitScape software (McRae *et al.*, 2008; Shah & McRae, 2008). It has been argued that LCP models out-perform circuit theory models when modeling connectivity at regional to continental scales, while the latter performs better at local scale (McRae *et al.*, 2008; Shah & McRae, 2008). Therefore, depending on the geographic extent of the study, combining the two models to account for the spatial scale of study might be necessary (Lechner *et al.*, 2015b).

Step 4: Overlaying dispersal rate and measures of connectivity with SDM output

The simplest way to combine SDM and LCM outputs with dispersal rate is to directly compare the least-cost distance between suitable and unsuitable grid cells with the species' dispersal distance over a given time scale. Extant populations identified to occupy grid cells that are projected to become unsuitable in the future could be considered capable of tracking their climate niche if the LCP distance to the nearest suitable location is less than or equal to the dispersal rate of the species (see Chapter 3). This approach can be undertake using standard GIS techniques.

Challenges and future outlook

Since conservation management and prioritization often occur over relatively large areas, models to assist spatial conservation planning need to simultaneously incorporate fine-resolution spatial data over large spatial scales. Unfortunately, such data may be too large to be effectively handled by current LCM software packages and desktop PC platforms (Lechner *et al.*, 2015b). Computational limitations may require compromise solutions. The large and diverse data sets required for connectivity modeling also present substantial data management challenges. Collaborative research groups are emerging to facilitate sharing of equipment and expertise as well as movement and environmental data (Hussey *et al.*, 2015). Web-based infrastructure systems, such as the GenBank, Movebank, Map of Life, Ocean Biogeographic Information System-Spatial Ecological analysis of Megavertebrate Populations, continue to increase the accessibility, standardization and integration of large movement data sets (Hussey *et al.*, 2015; Kays *et al.*, 2015).

Although advances in telemetry provide insights into movements of organisms across broad spatial and temporal scales, not all organisms are amenable to tagging. The implementation costs of telemetry may limit the number of individuals that can be tracked simultaneously (Table 1). Development of cheaper, smaller and lighter transmitters with almost-unlimited lifespans and greater detection ranges will allow near-lifetime tracking of several organisms simultaneously (Cooke *et al.*, 2013; Crossin *et al.*, 2014). Ongoing development of new multi-constellation Global Navigation Satellite Systems (GNSS), such as GLONASS, Gallileo, BeiDou and GPS and the International Cooperation for Animal Research Using Space (ICARUS) are emerging (Tomkiewicz *et al.*, 2010; Crossin *et al.*, 2014). To date, 70 of the over 120 satellites expected to be deployed by GLONASS, Galileo, BeiDou and GPS are in view. The remainder are anticipated to be fully available

in by the end of 2017 (Li *et al.*, 2015). GNSS and miniature ICARUS radio chips have great potential to dramatically reduce the cost of studying organisms from space, and broaden the range of species that can be tracked by satellite and GPS telemetry.

The limitations and uncertainties associated with SDMs have received extensive reviews (Araujo & Guisan, 2006; Pearson *et al.*, 2006; Wiens *et al.*, 2009; Sinclair *et al.*, 2010). Although efforts are being made to incorporate eco-evolutionary processes, there remains the need to develop tactile SDM algorithms that are sufficiently flexible to allow these processes to be incorporated. Currently, we are not aware of a unified model and software package that enables SDMs, LCMs and dispersal rates to be combined in a single run. Development of simple, easy-to-use unified software with graphical user interfaces (GUI) will be useful in facilitating more spatially-explicit conservation planning under climate and other environmental changes.

Presently, the land-cover/land-use and vegetation maps used to create resistance surfaces are mostly static, but in reality these are temporally and spatially dynamic (Sinha *et al.*, 2014). For this reason, functional connectivity of landscapes will change with time and this ought to be accounted for in the modeling process. However, projecting future changes in land-cover in itself, is a huge challenge (Sinha *et al.*, 2014).

Conclusion

Conservation decision-making is about prioritizing actions to address conservation objectives for target species and ecosystems. In an era of rapid climate and environmental changes, the importance of incorporating accurate measures of dispersal rates and

connectivity into conservation planning and population management cannot be overemphasized. We have highlighted the benefits of combining SDMs, LCMs and realistic estimates of dispersal rate to guide conservation planning and have explored how such an integrative approach could be achieved. We also discussed the challenges that arise and how they could be addressed in the near future. Improvements to available software and increases in computational capacity are crucial to realize the full potential of the framework. More than ever, there is a need for multi-disciplinary collaborative research and data sharing at local, regional and international levels, if we are to make conservation planning spatially explicit to accommodate the impacts of global climate change.

Table 1: Strengths and limitations of direct and indirect methods

METHOD	Cost	Accessibility	Labor/skill required	Information gathered	Accuracy
Direct					
Capture-mark-recapture (banding/clipping)	Plastic and metal bands are cheap. Price of aluminum bands cost US$100 – 800 per 1000 bands; Coloured Plastic leg bands cost US$50 – 250 per 1000 bands	Plastic and metal bands come in different sizes and readily available	Tracking can be labor-intensive, very time-consuming especially for large number of individuals over broad spatial extent; less skill required than other methods	Dispersal distance, rate in ecological time-scales; dispersal onset; movement patterns; habitat association, barriers to dispersal, interactions with habitat features, other species	Can accurately determine position of study organism, may not capture rare long-distance dispersal when only few individuals are tagged. May underestimate dispersal when animal moves beyond study area
Radio and acoustic telemetry	Tags are expensive; US$ 100-300 per transmitter	Radio and acoustic units are readily available	Tracking organisms with hand-held antennae is laborious; some level of skill is require for tagging and tracking organisms	Dispersal distance, rate in ecological time-scales; dispersal onset; movement patterns; habitat association; impacts on population growth and vital rates; physical barriers to dispersal	Can accurately determine position of study organism, but may not capture rare long-distance dispersal when only few individuals are tagged

Satellite and GPS telemetry	Tags are very expensive. Typical Satellite and GPS transmitters cost US$ 1000 per tag, plus additional $1000 - 4000 data access cost	Satellite and GPS units are not as readily available as radio and acoustic tags	Attaching tag to individuals requires considerable skill, but once fitted organisms can be tracked remotely with less labour	Contemporary dispersal distances and rates, onset of dispersal; movement pattern; When coupled with bio-loggers and animal-borne videos, information on behaviour, performance, physiology, interactions with other individuals, landscape features	GPS transmitters have very low position errors (≤5 m); satellite tags have min. error margins of 100 – 150 m. GPS also provide accurate time stamping of a position
Indirect				**Indirect**	
Biogeochemical approaches	Establishing maps for markers can initially be expensive	Not yet readily available, but becoming more accessible with advances in technology	Capturing animals for tissue samples can be laborious. Lab analysis of elements/isotopes in tissue require substantial skills	Dispersal distance in ecological and evolutionary time-scale; episodic long-distance dispersal	Can be very accurate when distinct environmental gradient of biogeochemical markers exist
Genetic approaches	Sample collection and DNA extraction and analysis can be expensive, but cheaper compared to telemetry	Becoming more accessible with advances in technology	Dispersal is simple to compute, but requires high level of knowledge. Field work and DNA extraction can be laborious	Dispersal distance and rate in evolutionary time-scale; assignment test can delineate dispersal in ecological time scale; identify physical and ecological barriers to dispersal; episodic long-distance dispersal; effect of dispersal on population genetic structure	Accuracy increases with the degree of genetic differentiation. Assignment test can be very accurate when parents are included in the sample

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CHAPTER THREE

Combining dispersal, landscape connectivity and Maxent to assess climate-induced changes in the distribution of Cunningham's skinks

Abstract

The ability of species to track their climate niche is dependent on their dispersal potential and the connectivity of the landscape matrix linking current and future suitable habitat. However, studies modeling climate-driven range shifts rarely address the movement of species across landscapes realistically, often assuming "unlimited" or "no" dispersal. Here, we incorporate dispersal rate and landscape connectivity with a species distribution model (Maxent) to assess the extent to which Cunningham's skink (*Egernia cunninghami*) may be capable of tracking spatial shifts in suitable habitat as climate changes. Our model was projected onto four contrasting, but equally plausible, scenarios describing futures that are (relative to now) hot/wet, warm/dry, warm/with similar precipitation and warm/wet, at six time horizons with decadal intervals (2020-2070) and at two spatial resolutions: 1 km × 1 km and 250 m × 250 m. The size of suitable habitat was projected to decline 22.5-63.3% at 1 km × 1 km and 25.7-64% at 250 m × 250 m, by 2070. Combining Maxent output with the dispersal rate of the species and connectivity of the intervening landscape matrix showed that most current populations in regions projected to become unsuitable in the medium to long term, will be unable to shift the distance necessary to reach suitable habitat. In particular, numerous populations currently inhabiting the trailing edge of the species' range are highly unlikely to be able to disperse fast enough to track climate change. Unless these populations are capable of adaptation they are likely to be extirpated.

We note, however, that the core of the species distribution remains suitable across the broad spectrum of climate scenarios considered. Our findings highlight challenges faced by philopatric species and the importance of adaptation for the persistence of peripheral populations under climate change.

Introduction

Climate change presents a major threat to global biodiversity and ecosystem services, upon which humans depend (Rosenzweig *et al.*, 2008; Warren *et al.*, 2013). Widespread evidence suggests that climate change has already and will continue to cause changes in species' distributions (Chen *et al.*, 2011; Parmesan & Yohe, 2003; VanDerWal *et al.*, 2013), alterations in phenology (Beaumont *et al.*, 2015; Cleland *et al.*, 2012; Cleland *et al.*, 2007; Parmesan, 2007; Singer & Parmesan, 2010; Thackeray *et al.*, 2010), physiology (Rosenzweig *et al.*, 2008), morphology (Ruiz-Navarro *et al.*, 2016; Walsh *et al.*, 2016), demography and community composition (Bellard *et al.*, 2012; Moritz *et al.*, 2008; Walther, 2010), and the nature of ecological interactions (Parmesan, 2006; Walther *et al.*, 2002). Species level extinctions have been reported (Pounds *et al.*, 1999; Sinervo *et al.*, 2010), with rates of extinction projected to accelerate as climate change intensifies (Parry, 2007; Şekercioğlu *et al.*, 2012; Sinervo *et al.*, 2010; Thomas *et al.*, 2004; Urban, 2015). To minimize the loss of global biodiversity, it is important that conservation practitioners, resource managers and decision-makers adapt their management practices and environmental policies towards amelioration of the impacts of climate change (Brooke, 2008; Pressey *et al.*, 2007; Thuiller *et al.*, 2008). To do this effectively, a greater capacity

to model the impacts of climate change on species distributions is needed (Dawson *et al.*, 2011; Kearney *et al.*, 2010).

Correlative species distribution models (SDMs) have become mainstream tools for projecting climate-driven range changes (Elith & Leathwick, 2009). These tools are used to estimate the statistical relationship between environmental characteristics and species' occurrence patterns, and identify suitable habitats under future (or past) climate scenarios (Austin & Van Niel, 2011; Elith & Leathwick, 2009). SDMs have been used to assess potential climate-driven range shifts and extinction risks in many terrestrial and aquatic invertebrates, vertebrates and plants (Araújo *et al.*, 2011; Araújo *et al.*, 2006; Botkin *et al.*, 2007; Penman *et al.*, 2010; Peterson, 2003; Peterson *et al.*, 2004; Thomas *et al.*, 2004; Thomas *et al.*, 2006a; Thuiller *et al.*, 2005; Thuiller *et al.*, 2006; Van der Putten *et al.*, 2010).

The capacity of organisms to move across landscapes is critical in determining their ability to locate suitable habitats (Pacifici *et al.*, 2015; Travis *et al.*, 2013). Yet, many SDM studies do not account for dispersal, and those that do frequently assume that species have either "unlimited" or "no" dispersal (Guisan & Thuiller, 2005; Pearson, 2006; Thomas *et al.*, 2004). Some studies have, however, used alternate approaches to incorporate more realistic estimates of dispersal (Bateman *et al.*, 2013). The most straight-forward of these approaches adopts a colonization potential based on the "nearest-neighbour" concept, where grid cells that become climatically suitable can be colonized only if a neighboring cell is already occupied (Engler *et al.*, 2009; Iverson *et al.*, 2004; Midgley *et al.*, 2006). Others have applied a Euclidean distance equal to the average dispersal distance of the study species, to create buffers around the current distribution. Projected suitable habitat

outside the buffer zone is presumed to be unreachable by the species (Duckett *et al.*, 2013; Midgley *et al.*, 2006). In contrast, relatively more-complex models fit statistical functions, such as dispersal kernels (Schurr *et al.*, 2012) and spatially explicit metapopulation models (Keith *et al.*, 2008).

Although these approaches have made substantial contributions towards incorporating realistic estimates of dispersal into the output of SDMs, they do not address the effects of landscape structure and features on the behaviour and movement rates of organisms (Taylor & Fahrig; Taylor *et al.*, 1993). Landscapes are spatially heterogeneous, and their degradation and fragmentation, due to human activities (Cushman, 2006), can dramatically impede the spread of organisms (Baguette *et al.*, 2013; Broennimann *et al.*, 2006; Fordham *et al.*, 2014; Taylor *et al.*, 1993). Consequently, the output of SDMs may be misleading if landscape connectivity and its effects on dispersal are ignored. This can have considerable implications for spatial conservation planning and prioritization.

To address this discrepancy, we combine dispersal rates and a landscape connectivity model that accounts for fine-scale habitat heterogeneity and barriers to movement, with the output from an SDM to assess climate-induced range shifts for Cunningham's skink (*Egernia cunninghami*). We used a genetic isolation-by-distance model to obtain an estimate of dispersal and a least-cost path (LCPs) analysis to model the functional connectivity of the intervening landscape matrix. LCPs use algorithms within a geographical information system (GIS) to identify landscape features and cover types that a moving organism prefers or avoids, to locate the route that provides the lowest cumulative resistance between source and destination (Stevenson-Holt *et al.*, 2014). LCPs have been used extensively for spatial conservation planning because they require

relatively less data than other connectivity models and are easy to run (Zeller *et al.*, 2012). Specifically, we asked the following questions:

- To what extent may the distribution of suitable habitat be altered under different future climate trajectories?
- To what extent will suitable habitat be located within protected areas in the future?
- What are the effects of spatial resolution on the size and configuration of future suitable habitat?
- What proportion of populations inhabiting areas projected to become unsuitable in the future may be able to track shifts in suitable habitat, given the species' dispersal rate and landscape connectivity?

Methodology

Species occurrence data

Cunningham's skink (*Egernia cunninghami*) is a common and widespread scincid lizard endemic to southeastern Australia. Its distribution extends from south-east Queensland through New South Wales to the Great Dividing Range in northeastern Victoria, with disjunct populations in the Mount Lofty Ranges in South Australia. The species uses open and sun-exposed granite rock outcrops with relatively large crevices as retreat sites (Langkilde & Shine, 2004; Stow *et al.*, 2001). Occurrence records were obtained from the Global Biodiversity Information Facility (www.gbif.org, accessed 5 March 2014). A total

852 unique occurrence points were available for modeling after removing duplicate and spatially questionable records.

Bioclimatic data

Current and future climate data were obtained from the NSW and ACT Regional Climate Modelling (NARCliM) project (Evans *et al.*, 2014). The projections were generated by four global climate models (GCMs): MIROC3.2-medres (K-I Model Developers, 2004), ECHAM5/MPI-OM (Jungclaus *et al.*, 2006), CGCM3.1-T47 (Flato, 2005) and CSIRO-Mk3.0 (Gordon *et al.*, 2002). These were dynamically downscaled by Evans & Ji (2012) for south-eastern Australia using the Weather and Research Forecasting (WRF) Regional Climate Model. Three alternate parameterizations of the WRF model (hereafter R1, R2, and R3), were used for the downscaling, resulting in 12 future climate scenarios. The NARCliM project assumed the A2 emissions scenario (Nakicenovic *et al.*, 2000), which approximates the relative forcing and mean temperature trajectories of the RCP8.5 scenario (Stocker *et al.*, 2014). In general, CGCM3.1 is a hot/wet scenario, MIROC3.2 is a warm/wet scenario, ECHAM5 is a hot/similar precipitation scenario, and CSIRO-Mk3.0 is a warm/dry scenario, relative to the period 1990-2009 (Evans & Ji, 2012). These products were created for 1990–2009 (current, i.e., “2000”), 2020–2039 (i.e., “2030”), and 2060–2079 (i.e., “2070”). As part of NARCliM, climate projections were further downscaled to spatial resolutions of 0.01° and 0.0025° using ANUSPLIN version 4.4 (Hutchinson & Xu, 2013). Climate predictor variables were derived using ANUCLIM version 6.1.1 (Xu & Hutchinson, 2011).

We projected the above current and future climate data to the Australian Albers Equal Area coordinate system at resolutions of 1 km (for 0.01° data) and 250 m (for 0.0025° data), with standard parallels chosen to minimize distortion across the study area (Snyder, 1987). Since NARCliM was restricted to the time periods centered on 2000, 2030 and 2070, we calculated data for the intervening decades (i.e. 2010, 2020, 2040, 2050, 2060) via linear interpolation using R v.3.12 (R Development CoreTeam, 2014).

We used a suite of five predictor variables that have been shown to model the distribution of reptiles adequately (Araújo *et al.*, 2006). These included (i) annual mean temperature, (ii) temperature seasonality, (iii) maximum temperature of the warmest month, (iv) minimum temperature of the coldest month and (v) annual precipitation. Cunningham's skink dwells in crevices of granite rock outcrops, which provide thermal buffering at fine spatial scales (Scheffers *et al.*, 2013; Scheffers *et al.*, 2014). Hence, we included an index of rock cover (Weathering Intensity Index) (Wilford, 2012) as a static predictor variable. We consider this an important addition because the presence of rock-outcrops with suitable crevices will largely determine range filling under climate change.

Species distribution modeling

The distribution of current and future habitat were projected using Maxent run in R v.3.12 (R Development CoreTeam, 2014). Maxent is a machine learning program that estimates species-environment relationships from spatial environmental data and species' occurrence records (Phillips & Dudík, 2008; Phillips *et al.*, 2009). Because of its high predictive performance, computational efficiency and ease of use, Maxent is a commonly used correlative SDM (Phillips & Dudík, 2008; Phillips *et al.*, 2009). We fitted the model using

different combinations of the linear, quadratic, product, threshold and hinge features, and regularization multipliers to control how tightly the model fitted the given occurrence points. Response curves were visually inspected to ensure that the estimated relationships were ecologically realistic. The most realistic model settings (determined by the smoothness of the response curve) for Cunningham's skink were the linear, product and quadratic features with a regularization multiplier of 1.5. To reduce over-prediction, background records were sampled from grid cells within 100 kilometers of occurrence localities.

Model performance was evaluated using the Area under the Receiver Operating Characteristic Curve (AUC) and the True Skill Statistic (TSS) using 10-fold cross-validation. AUC scores range from 0 to 1. Values of 1 indicate perfect model accuracy while 0.5 suggests that model performance is no better than random. TSS scores range from -1 to 1, with values close to -1 indicating no skill and 1 a perfect ability to distinguish positive and false scores (Allouche *et al.*, 2006). Variable predictive ability and importance to the model were assessed by percentage contribution and jack-knifing. At both spatial resolutions (1 km and 250 m), the final model was fitted using all occurrence data, and habitat suitability maps were generated by projecting these models onto predictor data for the current and six future time slices (2020, 2030, 2040, 2050, 2060 and 2070). Future projections were constrained using a buffer of 300 km around the species current distribution. This buffer ensured that the model did not predict climatically suitable habitats in areas that Cunningham's skink could not reach unaided. The projected continuous habitat suitability maps were transformed into binary suitable and unsuitable habitat using the maximum training sensitivity and specificity logistic threshold (Jiménez-Valverde & Lobo, 2007; Liu *et al.*, 2005).

We calculated the change in climatically suitable habitat between the current and future climate scenarios as the percentage change in the number of suitable grid cells. We also calculated the percentage overlap between the current and future suitable habitat and the percentage of suitable habitat lost or gained within protected areas. For the latter, we obtained a GIS layer of the Australian Protected Area network from the Collaborative Australian Protected Area Database (CAPAD; available at www.environment.gov.au/parks/science/capad).

Estimating annual dispersal distance

Previous capture-mark-recapture (CMR) studies of Cunningham's skink recorded 70.1 m as the longest dispersal distance over four years (Barwick, 1965). Although dispersal in skinks is generally limited, this measure may be an underestimate of the species' dispersal capacity because of its life-history (i.e. high retreat site fidelity) and the limitation of CMR in capturing long-distance dispersal events relevant for colonization of new habitats (Griesser *et al.*, 2014). For this reason, we estimated annual dispersal distance using the genetic isolation-by-distance (IBD) model which relates matrices of genetic distance between individuals to matrices of geographical distance (Manel *et al.*, 2005; Wright, 1943). According to Wright (1943), the "neighbourhood" is defined by the average distance between the natal and breeding sites of the study species. The neighbourhood encompasses the spatial extent within which gene flow is random. In two-dimensional space, the neighbourhood size (NS) is equal to $4\pi\rho\sigma^2$, which is equal to the inverse of the regression slope between a multilocus estimator of individual pairwise genetic distances [$F_{ST}/(1-F_{ST})$] and geographic distance, where ρ is the population density, σ^2 is variance

dispersal per generation and F_{ST} is the pairwise genetic distance between individuals (Rousset, 2000).

We estimated annual dispersal distance (variance) using genetic data from a population of *E. cunninghami* sampled from Armidale, New South Wales (30° 32´ S, 151° 51´ E) (Ofori *et al.*, 2017). We used a generation time of five years and population density of 120 individuals per km^2, as recorded by previous studies (Barwick, 1965; Chapple, 2003).

Modeling functional connectivity

We created a resistance map of the study area using the most recent land-use/cover raster map of Australia *(Land Use of Australia, Version 4, 2005-06*) at 1 × 1 km resolution. Resistance values of each cover type were based on expert knowledge. We applied the Delphi method (Hsu & Sandford, 2007) to calibrate the cost-surface representation of the landscape. We identified a group of 10 experts with substantial knowledge of the ecology of Australian reptiles, and asked them to rank the different land cover types in our study area based on potential cost to the movement of Cunningham's skink. Cover types likely to be avoided by the species because they impede movement, are a total barrier to movement, or expose the species to danger, were given higher cost values than those that facilitate movement. Cover types considered as total barriers were awarded a resistance score of 100, while those through which the species readily moves were awarded a score of 1 (Supporting Information Table S1). Of the 10 experts consulted, seven responded (see acknowledgements). Originally, the collated results were to be returned anonymously to each expert, then ranked a second time. However, because the scores from the experts were

very similar, we used the mean scores from the first iteration to create the resistance surface.

The resistance map was created using the Resistance and Habitat Calculator in the Gnarly Landscape Utilities ArcGIS toolbox (McRae *et al.*, 2008). Least-cost paths among occupied cells that were projected to become unsuitable and the nearest cells that became or remained suitable in the subsequent time horizon were modelled using the landscape connectivity model in the SDMtoolbox package (Brown, 2014) implemented in ArcGIS v10.2.1 (ESRI Inc., Redlands CA, USA, 2013). Given that current connectivity software packages and desktop PC platforms are unable to effectively handle fine-resolution spatial data over large spatial scales, we modeled landscape connectivity at 1 × 1 km only.

Ideally, we would compute LCPs for each grid cell that currently contains a population of Cunningham's skink *and* is projected to become unsuitable under any of the 12 climate scenarios, for a given time period. Because of computational limitations, for each decade we restricted this analysis to only those grid cells that currently contain a population and are projected to be unsuitable under *all* climate scenarios for that decade. We suggest this to be a reasonable approach as a) all future scenarios are currently equally plausible and b) populations projected to have no suitable habitat under all 12 scenarios will be the populations most vulnerable to climate change.

Evaluation of the capacity of Cunningham's skink to track its climate niche

Extant populations identified to occupy grid cells that are projected to become unsuitable in future were considered capable of tracking their climate niche if the least-cost path

distance to the nearest suitable location was less or equal to the dispersal rate of the species.

Results

Distribution of current suitable habitat

Models had high predictive capacity at both spatial resolutions, with an average AUC of 0.818 and 0.793 and TSS of 0.492 and 0.451 for the 1 × 1 km and 250 × 250 m, respectively. The amount of currently suitable habitat projected at 1 × 1 km (15,951,800 ha) was higher than that projected at 250 × 250 m (14,267,150 ha). Generally, the projected current distribution of suitable habitat was consistent with the species' known range. However, the range margin of the projected distribution was slightly further north of populations in southern Queensland. Also, areas in southeastern New South Wales (NSW) and some regions in Southern Australia where the species has not been recorded were projected to be highly suitable (Figure 1). After transforming the projected current suitability map into binary suitable and unsuitable habitat using the maximum training sensitivity and specificity logistic threshold, 74.2% (632 of 852) of the occurrence points were within suitable habitat at 1 × 1 km and 72% (613 of 852) at 250 × 250 m. Maximum temperature of the warmest month contributed most (45.0% for the 1 × 1 km and 46.9% for the 250 × 250 m resolutions) to the models of habitat suitability.

Projected changes in climatically suitable habitat

Climatically suitable habitat for Cunningham's skink was projected to decline by 22.5-63.3% for the 1 × 1 km and 25.7-64.0% for 250 × 250 m resolutions, depending on the climate trajectory and time horizon (Figure 2). In general, suitable habitat was progressively lost over time, at both spatial resolutions and under most climate scenarios. The exception was the warm/similar precipitation scenario, where the proportion of suitable habitat projected to be lost was highest in 2030 then declined (Figure 2). Under all the climate trajectories, the projected percentage loss of suitable habitat at 1 × 1 km and 250 × 250 m for the respective time periods was not significantly different (Fishers Exact Test: df =198; $p > 0.1$).

Under all climate scenarios, habitat was progressively lost from the northern range margins in southeastern Queensland and northeastern NSW, and the western margins toward southeastern NSW, although the core of the skinks' range was projected to remain stable. Under all scenarios, new habitat was gained around the southern region of South Australia and some regions in southeastern NSW, particularly from 2050 to 2070 (Supporting Information Figure S1).

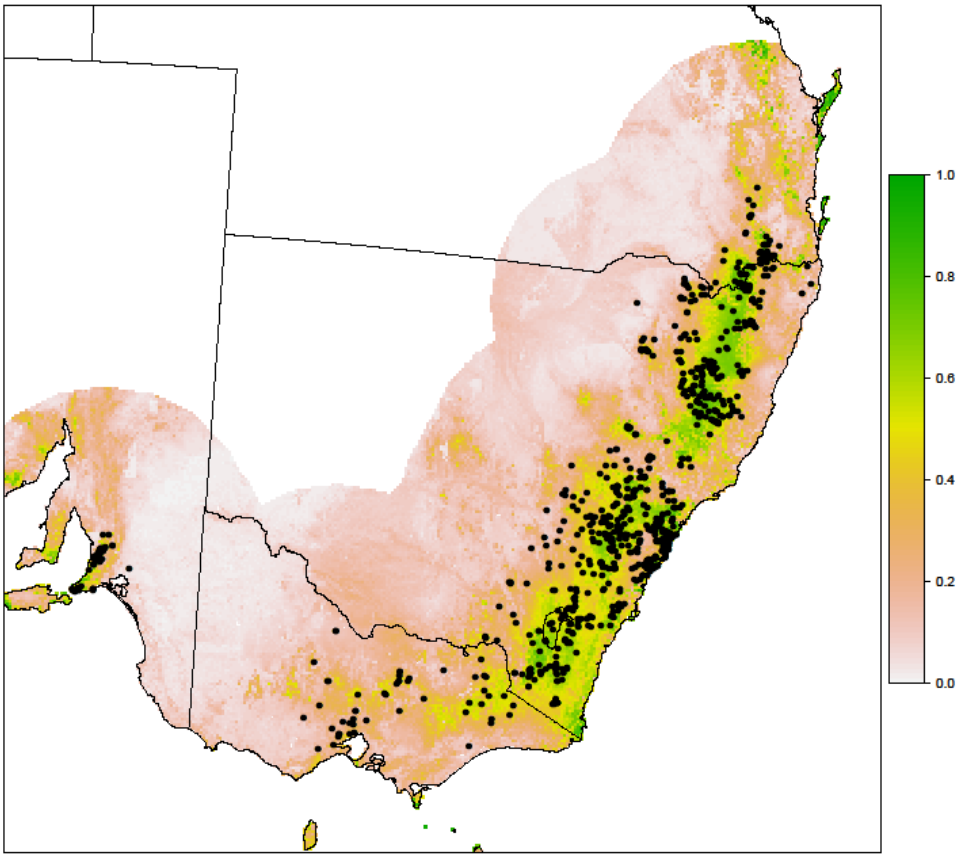

Figure 1: Projected current habitat suitability for Cunningham's skink modelled using Maxent. Suitability ranges from 0 (least suitable) to 1 (most suitable). Black points indicate species occurrence records.

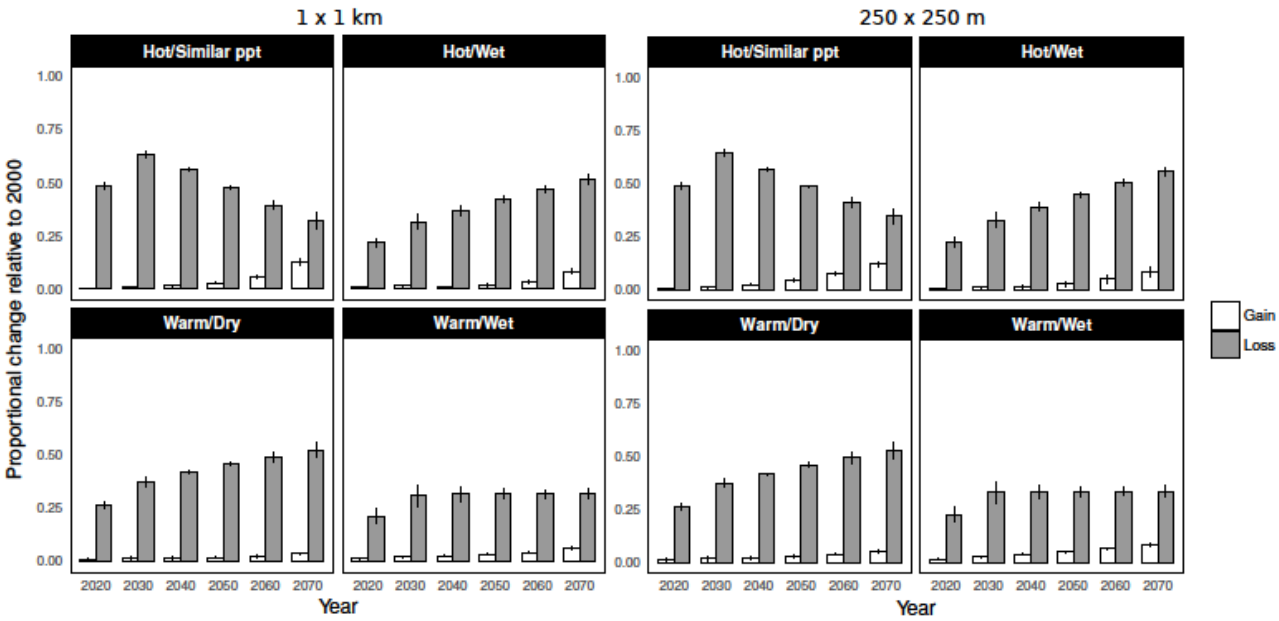

Figure 2: Proportional gain and loss in climatically suitable habitat of Cunningham's skink projected at 1 × 1 km and 250 × 250 m under four contrasting but equally plausible future climate scenarios (hot/wet, warm/dry, hot/similar precipitation and warm/wet) over six time horizons with decadal intervals (2020-2070). Each climate scenario was parameterized using three alternatives of the Weather and Research (WRF) Regional Climate model (R1, R2 and R3), hence values of vertical bars represent average gain/loss, with vertical lines representing standard deviations.

Changes in suitable habitat within protected areas

The area of current suitable habitat projected to be within protected areas at 1 × 1 km and 250 × 250 m resolutions was 4,696,500 and 4,226,777 hectares, respectively. At both spatial resolutions, the projected loss of suitable habitat (relative to 2000) increased slightly over time under the hot/wet and warm/dry scenarios, but declined from 2030

onwards under the warm/similar precipitation and warm/wet scenario (Figure 3). At 250 × 250 m resolution, the loss in suitable habitat ranged from 27.7% (SD = 3%) by 2030, to 34.1% (SD = 6%) by 2070 under the hot/wet condition, and from 23.5% (SD = 5%) to 31.7% (SD = 10%) under the warm/dry scenario. Under the warm/similar precipitation scenario, the highest projected loss of suitable habitat within PAs at both spatial resolutions (57.9% at 250 × 250 m and 54.7% at 1 × 1 km) occurred by 2030, and the lowest (6.3% at 250 × 250 m and 9.0% at 1 × 1 km) by 2070. Similarly, under the warm/wet condition, the area projected to become unsuitable was highest (22.3% at 250 × 250 m and 20.9% at 1 × 1 km) by 2030, and lowest (14.1% at 250 × 250 m and 16.0% at 1 × 1 km) by 2070. Again, the percentage loss of suitable habitat within PAs projected at 1 × 1 km and 250 × 250 m for the respective time periods under all the climate trajectories was not significantly different (Fishers Exact Test: df = 198; $p > 0.1$).

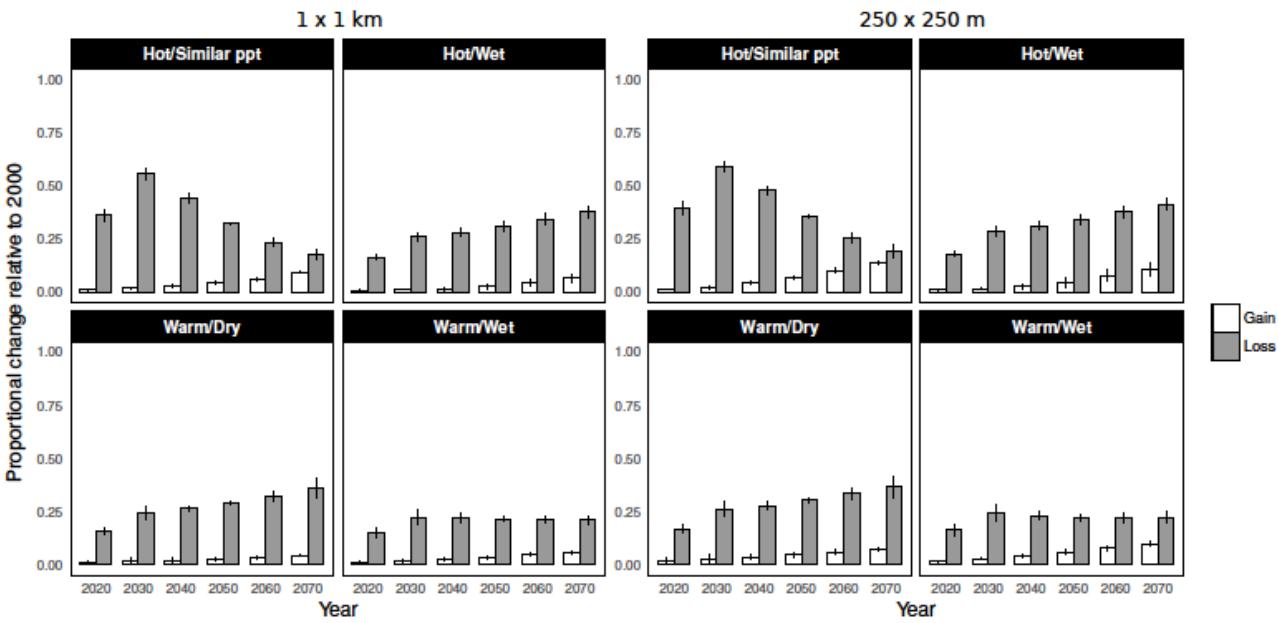

Figure 3: Proportional gain and loss in climatically suitable habitat of Cunningham's skink within protected areas projected at 1 × 1 km and 250 × 250 m under four contrasting but equally plausible future climate scenarios (hot/wet, warm/dry, hot/similar precipitation and warm/wet) over six time horizons with decadal intervals (2020-2070). Each climate scenario was parameterized using three alternatives of the Weather and Research (WRF) Regional Climate model (R1, R2 and R3), hence values of vertical bars represent average gain/loss, with vertical lines representing standard deviations.

Dispersal rate and ability of the species to track its climate niche

Using a population density of 120 individuals per km^2, the isolation-by-distance model estimated the dispersal rate of Cunningham's skink to be 4.3 km per generation (i.e. 5 years). Hence, a population inhabiting an area that is projected to become unsuitable in the next decade is considered capable of tracking spatial shifts in its climate niche if the nearest suitable location (i.e., destination cell), as measured by the cost-distance, is ≤ 8.6 km.

By 2070, 63 (10%) of the 632 occurrence points ('populations') that were located within suitable grid cells were projected to become unsuitable under *all* climate trajectories considered. Eight occupied grid cells were consistently projected to be unsuitable by 2020. As the cost distance between these cells and the nearest cells suitable by 2030 exceed the skink's dispersal rate by 1 – 35.5 km (see Supporting Information Table S2), it is unlikely that any of these eight populations will be able to track their climate niche. By 2030, an additional 16 grid cells currently containing populations of Cunningham's skink were projected to become unsuitable, only five of these will have suitable habitat within the

dispersal distance of the skink. By 2040, 2050 and 2060, an additional 23, 12 and eight grid cells, respectively, with current populations were projected to be unsuitable. For all of these, cells with suitable habitat are at a distance greatly exceeding the skink's capacity for dispersal (17.6-92.3 km) (Supporting Information Table S1). By 2070, no additional occupied grid cell was projected to lose its suitability under all the climate trajectories used. Thus, of the 63 populations in locations projected to be unsuitable under all climate scenarios for 2070, 58 (92%) will be unable to track their climate niche. Hence, we estimate that of the 852 extant populations, at least 6.8% will be extirpated if they are unable to adapt to climate change.

Discussion

Our projections show that climate change could cause substantial declines in the spatial extent of suitable habitat for Cunningham's skink, with range margins progressively retracting towards the core of its current distribution along the Great Dividing Range (GDR) in New South Wales (NSW). Critically, numerous populations currently inhabiting the trailing edge of the species' range are highly unlikely to be able to disperse fast enough to track range shifts. Suitable habitats within protected areas, particularly those located along the species' range periphery are projected to decline over time. However, core areas of the species distribution along the GDR retained their suitability across a broad spectrum of plausible climate scenarios (spanning futures described as warm/wet, warm/dry, hot/wet, hot/similar precipitation, relative to 2000).

Whilst the size of suitable habitat is projected to decline under all future climate scenarios considered, the most severe decline (of 63.3%) was projected to occur under the hot/similar precipitation scenario by 2030. Under this scenario, the lowest range of decline was projected for the decade 2060-2070 (22.5%), primarily due to gains in suitable habitat after 2030 in areas around the Mount Lofty in Southern Australia and regions in north-western NSW.

We estimate that 63 of the 632 populations (defined as the number of 1 km grid cell with at least one occurrence record) will have no suitable habitat in any of the 12 climate scenarios. Of these, only five populations were situated near suitable habitat within the dispersal distance of the species. Our data suggest that the skink's dispersal rate (8.6 km per decade) is insufficient for most (92.1%) populations inhabiting locations projected to become unsuitable to track their climate niche. This is particularly true for populations inhabiting the range margins, suggesting that climate-induced decadal shifts in the species' range will outpace its dispersal capacity. This highlights the challenge faced by Cunningham's skink, and other philopatric species under climate change.

The modeled current distribution of suitable habitat corresponded well with the actual distribution of the species, providing strong support for the Maxent model and the choice of predictors. Projected current habitat was, however, slightly farther north than the known range margin, and some areas within southeastern NSW where the species has not been recorded were also projected to be suitable. This indicates that factors other than climate, such as dispersal and biotic interactions (e.g. competition, predation and parasitism) may be preventing the species from attaining its full potential distribution (Gillingham *et al.*, 2012b; Pearson & Dawson, 2003). The incomplete range filling could also indicate that the

species may not be in equilibrium with the current climate throughout its range (Araújo *et al.*, 2006; Svenning & Skov, 2004). If this is the case, then future range contraction may be more severe than projected here.

Our results are consistent with previous studies assessing the potential impacts of climate change on Australian reptiles. For example, future declines in suitable habitat have been projected for the endangered Australian broad-headed snake, *Hoplocephalus bungaroides* (Penman *et al.*, 2010). Under a hot/dry scenario, the species is projected to lose over 80% of its suitable habitat by 2070 (Penman *et al.*, 2010). Fifty-three Australian elapid snakes and 275 skinks have also been projected to experience range contractions by 2050, with some of these species projected to lose their entire range under hot/dry conditions (Cabrelli & Hughes, 2015; Cabrelli *et al.*, 2014). Similar results have been reported for European species. For example, in the Iberian Peninsula, the ranges of many reptiles have been projected to contract by 2050 and 2080, with more severe declines projected under hot/dry conditions (Araújo *et al.*, 2006; Carvalho *et al.*, 2010).

The spatial resolution at which species distributions are modeled can affect estimated declines or gains in climatically suitable habitat (Austin & Van Niel, 2011; Broennimann *et al.*, 2006; Guisan & Thuiller, 2005). Coarse resolution grid cells may contain a wide range of environments and microclimates, some of which might be suitable for species at their thermal margins (Ashcroft *et al.*, 2009; Gillingham *et al.*, 2012a). Thus, models fitted with predictors scaled at a coarse resolution may not reflect locally suitable microclimates under which species live at their range margins (Gillingham *et al.*, 2012a; Guisan *et al.*, 2007). Bias in model fitting could lead to over- or under-estimation of species' suitable habitat. Fitting SDMs with fine-resolution predictor variables may be more accurate than

modeling at coarse-resolution depending on the species (Seo *et al.*, 2009). For instance, Gillingham *et al.* (2012a) noted that models fitted with coarse-resolution predictors were associated with higher prediction errors. They also found that the spatial extent of areas projected to remain or become suitable in future varied across different resolutions. Similarly, higher rates of retraction at range margins were found when habitat suitability was modeled at 1 km^2 compared to 100 km^2 (Thomas *et al.*, 2006b). In the present study, greater declines in the area of future suitable habitat were recorded when modeled at a resolution of 1 km × 1 km than when modeled at 250 m × 250 m. What is worth noting, however, is that the proportional change (i.e., the ratio of the amount of future suitable habitat to the amount of current suitable habitat) and the spatial distribution of future suitable habitats were comparable for both resolutions.

Assigning appropriate resistance values to the different cover types and landscape features is crucial in connectivity modeling. We employed expert opinion to estimate resistance values because of a lack of empirical data on the species movements, such as travel path, relocation or adequate genetic data from most of the species range. Our approach is therefore subjective and might not necessarily reflect how the species views the landscape (Zeller *et al.*, 2012). Nonetheless, expert opinion provides a good approximation of the resistance values of environmental variables and is the only option until empirical data becomes available (Zeller *et al.*, 2012).

Our results show that most populations occupying the range margins and other locations projected to become unsuitable in the future may not be able to move to suitable locations. This result is supported by recent genetic studies of the skink, which concluded that its dispersal rate is insufficient to track its climate niche, irrespective of landscape

connectivity (Ofori *et al.*, 2017). If our findings hold true for lizards and reptiles in general, then this has dire consequences for conservation. Further research is needed to ascertain the generality of our results and to determine whether lizards have sufficient variation in adaptive traits to enable them evolutionarily adapt to climate change.

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Supplementary Information

Table S1: Mean resistance scores for the land-use and land cover types in the study area as perceived by seven herpetologists (experts). Scores are based-on the tendency of and ease with which Cunningham's skinks will move through the different cover types.

Class ID	Class Description	Resistance score
1	Nature conservation	10
2	other protected areas	10
3	Minimal use	12
4	Grazing native vegetation	15
5	Production forestry	15
6	Grazing modified pastures	25
7	Plantation forestry	15
8	Dryland cropping	25
9	Dryland horticulture	25
10	Land in transition	25
11	Irrigation pasture	30
12	Irrigation cropping	25
13	Irrigation horticulture	25
14	Urban intensive uses including highways	82
15	Intensive anima land/plant production	38
16	Rural residential and farm infrastructure	43
17	mining and waste site	66
18	Large inland bodies	77

Table S2: Least-cost distance (in meters) between occupied suitable grid cells and the nearest suitable location for each decadal time horizon

2020-2030	**2030-2040**	**2040-2050**	**2050-2060**	**2060-2070**
9,576	4,748	17,583	21,883	12,166
13,123	6,085	21,932	25,689	17,353
16,656	6,125	24,005	42,243	24,070
19,700	7,238	24,442	42,747	31,758
24,585	7,893	25,899	51,733	45,057
26,207	9,511	31,785	68,580	59,960
30,353	9,727	36,557	69,560	88,594
44,110	10,002	38,183	88,849	92,257
	11,866	74,564	109,658	
	12,034	86,260	140,983	
	12,102	96,132	169,001	
	25,223	99,100	199,745	
	30,874	143,888		
	33,121	168,963		
	78,441			
	80,957			

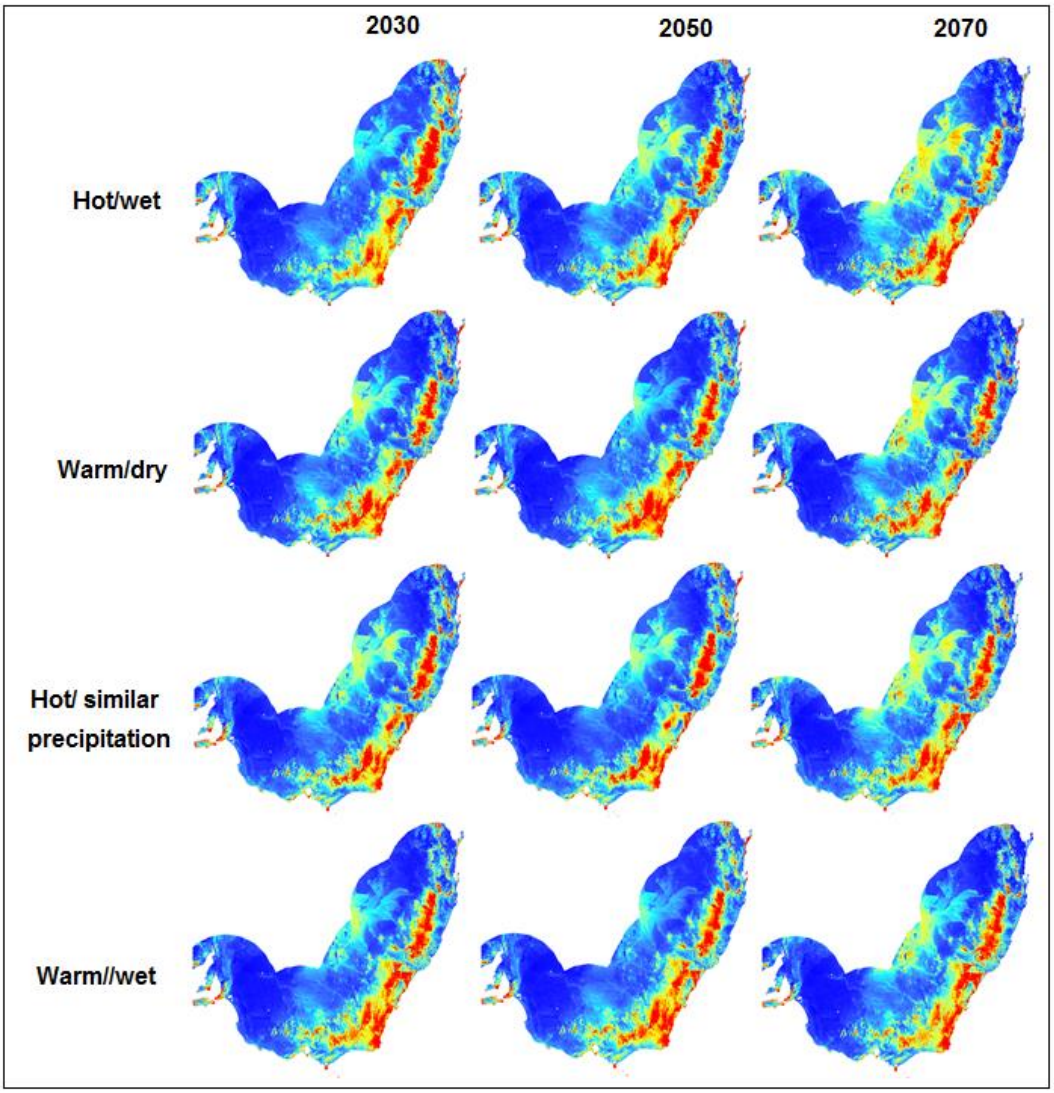

Figure S1: Changes in climatically suitable habitat of Cunningham's skink over time projected (using Maxent) at 1 km × 1 km resolution under the different climate trajectories.

CHAPTER FOUR

Cunningham's skinks show low genetic connectivity and signatures of divergent selection across its distribution

Abstract

Establishing corridors of connecting habitat has become a mainstay conservation strategy to maintain gene flow and facilitate climate-driven range shifts. Yet, little attention has been given to ascertaining the extent to which corridors will benefit philopatric species, which might exhibit localized adaptation. Measures of genetic connectivity and adaptive genetic variation across species' ranges can help fill this knowledge gap. Here, we characterized the spatial genetic structure of Cunningham's skink (*Egernia cunninghami*), a philopatric species distributed along Australia's Great Dividing Range, and assessed evidence of localized adaptation. Analysis of 4,274 SNPs from 94 individuals sampled at four localities spanning 500 km and 4° of latitude revealed strong genetic structuring at neutral loci (mean $F_{ST} \pm SD = 0.603 \pm 0.237$) among the localities. Putatively neutral SNPs and those under divergent selection yielded contrasting spatial patterns, with the latter identifying two genetically distinct clusters. Given low genetic connectivity of the four localities, we suggest that the natural movement rate of this species is insufficient to keep pace with spatial shifts to its climate envelope, irrespective of habitat availability. In addition, our finding of localized adaptation highlights the risk of outbreeding depression should the translocation of individuals be adopted as a conservation management strategy.

Introduction

The threat of climate change to global biodiversity is a major focus of conservation based research and management (Loss *et al.*, 2011). Mountain ecosystems have received particular attention because they harbour higher proportions of endemic species, and these species face increased risk of extinction because of their narrow thermal tolerance and elevational ranges (Bell *et al.*, 2014; Frei *et al.*, 2014; Elsen & Tingley, 2015). The persistence of montane species as climate changes depends on their ability to shift their ranges to higher latitudes and altitudes (Chen *et al.*, 2011), or adapt to future climatic conditions (Hoffmann & Sgrò, 2011). However, altitudinal range shifts may be constrained by limited upslope area and movement restrictions imposed by topography and habitat fragmentation (Bell *et al.*, 2014; Elsen & Tingley, 2015). Further, because montane species typically have small, multiple disjunct populations (Sgro *et al.*, 2011; Huntley & Barnard, 2012), they may lack the capacity to adapt rapidly enough to counter the speed and magnitude of contemporary climate change. Therefore, these species may require management to increase their resilience and adaptive capacity.

Creating and maintaining habitat corridors is one of the most appealing and politically favoured strategies for conserving montane species (Pulsford *et al.*, 2013). The rationale behind this strategy is that increasing habitat connectivity along mountain ranges facilitates range shifts by enabling individuals to track the movement of their climatic envelope, thereby enhancing exchange of individuals and genes among metapopulations, increasing effective population sizes and adaptive potential (Steffen *et al.*, 2009). Corridors could help mediate the ecological and evolutionary processes necessary to sustain communities under changing environments (Doerr *et al.*, 2011).

While the importance of corridors has been demonstrated for wide-ranging and highly mobile species (Heller & Zavaleta, 2009; Sharma *et al.*, 2013), their capacity to facilitate range shifts and enhance the adaptive potential of philopatric species is debatable (Beier & Noss, 1998; Hodgson *et al.*, 2009). Species with low vagility may be unable to undertake the rapid long-distance dispersal necessary to accommodate climate change (Broquet & Petit, 2009). However, it is generally agreed that corridors can provide stepping stones of high quality breeding habitat for philopatric species. This should allow them to undertake multi-generational range shifts, with potential for localized gene flow (Hodgson *et al.*, 2009). The extent to which this is the case in montane ecosystems, where suitable habitat is often highly fragmented, remains unclear.

Limited gene flow between localities, in addition to the effects of drift and selection, will lead to strong genetic differentiation and, potentially, local adaptation (Nosil *et al.*, 2009). Facilitating gene flow between species with high genetic structuring and divergence may be problematic as this can lead to disruption of locally adapted gene complexes and result in outbreeding depression (Slatkin, 1987; Frankham *et al.*, 2011; Sexton *et al.*, 2011). Other non-adaptive genetic processes, such as chromosomal rearrangements can also contribute to outbreeding depression (Frankham *et al.*, 2011). Thus, it is important to identify reproductively isolated and locally adapted populations in order to delineate conservation units for effective management (Moore *et al.*, 2014). In this regard, measures of genetic variation at both neutral and loci associated with adaptation are required.

For most conservation-oriented studies, patterns of genetic structure and local adaptations have been characterized using neutral markers. Markers such as microsatellite genotypes can reveal the patterns of gene flow and reproductively isolated populations. However,

because they are selectively neutral (Nosil *et al.*, 2009; Lowe & Allendorf, 2010), they do not reveal geographical patterns of adaptive genetic variation or the scale of local adaption (Allendorf *et al.*, 2010; Sheth & Angert, 2016). Although neutral and adaptive genetic variation may sometimes show similar spatial patterns (Moore *et al.*, 2014), divergence at neutral and adaptive loci arises principally from different processes. Divergence at neutral loci arises from limited dispersal and gene flow, and genetic drift, whereas adaptive divergence arises from selective sweeps which rapidly increase the frequency of a favoured allele due to directional selection pressures (Slatkin, 1987; Frankham *et al.*, 2002; Nosil *et al.*, 2009; Lowe & Allendorf, 2010; Sexton *et al.*, 2011).

In a homogeneous environment, species with limited dispersal capacity and small population sizes may show considerable genetic partitioning at neutral loci, but may not be differentiated at adaptive loci (Sexton *et al.*, 2014). In a heterogeneous environment, spatial patterns of neutral and adaptive genetic variation may vary depending on the limits of dispersal, and the strength and spatial gradient of selection pressures (Manel & Holderegger, 2013; Forester *et al.*, 2016). As a result, spatial patterns of neutral genetic variation may not be an adequate proxy for adaptive genetic variation and local adaptation, necessitating the need to investigate the spatial patterns of both types of genetic variations.

Recent advances in next-generation sequencing technologies have increased the availability of genomic data in non-model species, making it possible to identify loci that are under divergent selection or are physically linked to regions of the genome that are under divergent selection (Nosil *et al.*, 2009; Allendorf *et al.*, 2010; Hess *et al.*, 2013). Genome scanning has highlighted the spatial patterns of adaptive genetic variation and local adaptations associated with selection in non-model species (Schweizer *et al.*, 2015;

Forester *et al.*, 2016). Such knowledge can highlight the potential benefits and risks of enhancing gene flow between populations from dissimilar environments and inform conservation actions under rapid climate change.

The Great Dividing Range (GDR) of Australia is a key conservation area, and harbours globally endemic and endangered species (Steffen *et al.*, 2009). This mountain range traverses almost 3,500 km of the Australian continent, running from the Alps in southeast Victorian to Atherton in northeast Queensland (Pepper *et al.*, 2014). In 2007, the Australian Government, through the Environment Heritage and Protection Council (EPHC), announced plans to create a connectivity corridor along the GDR to enhance species' range shifts and resilience to climate change (Worboys & Pulsford, 2011).

Similar large-scale conservation corridors have also been established elsewhere, such as the Yellowstone to Yukon project (Y2Y) in North America. This connects the northern Rocky Mountains of the USA and Canada (Graumlich *et al.*, 2010). Other examples include the Albertine Rift connectivity in Africa that runs through DR Congo, Rwanda and Uganda (Plumptre *et al.*, 2007), the Condor Biosphere reserve connectivity in the Ecuadorian Andes (Benitez & Cuesta, 2004), and the Catalonia area of north-east Spain and connectivity to the European Alps (Rafa, 2004). However, the Australian GDR remains the first continental-scale corridor (Worboys & Pulsford, 2011).

Here we use Cunningham's skink (*Egernia cunninghami*) as a model philopatric species to describe spatial patterns of neutral and adaptive genetic variation along the GDR. Reptiles in general have received less attention in the climate change literature, despite being relatively more sensitive to climate change than other vertebrate taxa, such as birds and mammals (Sinervo *et al.*, 2010; Cabrelli *et al.*, 2014). In Australia and within the GDR,

reptiles are the most diverse and dominant vertebrates, and about 7 % of them are listed as threatened under State Acts (Chapman, 2009; Steffen *et al.*, 2009). *Egernia cunninghami* is a common scincid lizard distributed along the GDR and coastal strips to the east. The species is protected throughout it distribution and is declared as threatened in Southern Australia, where some isolated populations have gone locally extinct. Typical of philopatric species, it shows localized movement and high retreat-site fidelity (Stow & Sunnucks, 2004), and its ecology and basic biology are well researched (Brown, 1991; Stow *et al.*, 2001; Chapple, 2003; Bickford *et al.*, 2010; Kearney *et al.*, 2013).

Our main goals are to assess the levels of gene flow and evidence for selection among four populations of Cunningham's skink, that are separated by ~ 100 - 500 km. Specifically, we as: (1) Is localised philopatry in *E. cunninghami* reflected by strong genetic partitioning among regions? (2) Is genetic structure at neutral loci a good proxy for adaptive variation? We discuss the implications of our results for mitigating negative impacts of climate change on this species.

Materials and Methods

Tissue sample collection and DNA extraction

Tail-tip muscle tissue samples of Cunningham's skink were collected from 94 individuals at four localities across the GDR within New South Wales, Australia (Fig. 1). We sampled 18 individuals at Sydney (33°39´ S, 151° 12´), 27 at Armidale (30° 32´ S, 151° 51´ E) in the Northern Tablelands, 27 at Bathurst (33° 33´ S, 149° 24´ E) and 22 at Crookwell (34° 23´S, 149° 22´) in the Central Tablelands. The Euclidean distance between pairs of

localities ranged from 96 km (Bathurst vs. Crookwell) to 500 km (Armidale vs. Crookwell) (Supporting Information Table S1).

Individuals were captured using Elliott live-traps and by hand. Captured individuals were measured and released at the point of capture after a small terminal portion of the tail was removed. The exact locations where samples were taken were marked using a global positioning system (GPS) unit (Garmin GPSmap 62). Tissue samples were kept in 97% ethanol at room temperature prior to laboratory analysis. Lizard capturing and handling followed Macquarie University Animal Ethics Committee recommendations (ARA 2013/015), and was licensed by the Office of Environment & Heritage, NSW National Parks and Wildlife Service (SL101164).

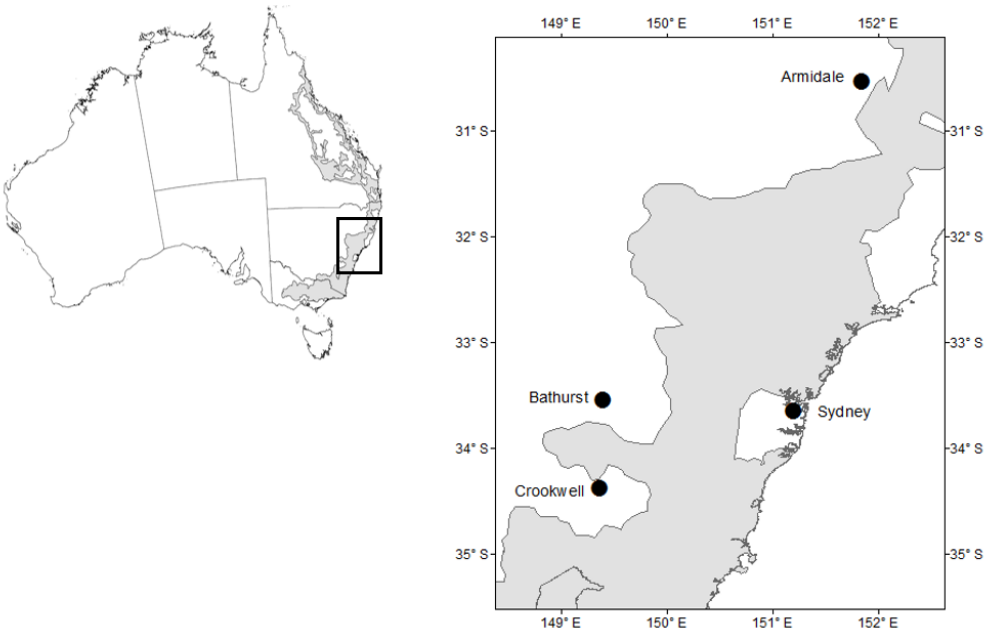

Figure 1: Sampling localities of Cunningham's skink (*Egernia cunninghami*) along the Great Dividing Range, south-eastern Australia. The Great Eastern Range Connectivity Corridor is highlighted in grey.

DNA extraction, SNP discovery and screening

Genomic DNA was extracted from tissue using a commercially available spin-column kit (GenCatch^{TM} Blood & Tissue Genomic DNA Extraction Mini-Prep Kit, Epoch Life Science, Inc.) following manufacturer's protocols. SNP discovery and genotyping were performed at Diversity Arrays Technology Pty. Ltd. (Canberra, Australia) using standard DartSeq^{TM} protocol (for details of the SNPs discovery and screening protocol, see Supporting Information Text File 1). Discovered SNPs were called only if they were present in both homozygous and heterozygous forms.

To ensure the quality of individual samples, all duplicate markers and those with minor allele frequencies < 5% (MAF < 0.05) across all populations were removed. We also removed markers with average read depth < 10 or > 45 for both alleles; individuals genotyped at < 100% call rate (CR: proportion of genotyped SNPs); < 94% reproducibility and two or more SNPs that occurred on one sequence read to avoid physical linkage. DArT-Sequencing returned a total of 81,732 SNPs, of which 4,274 were retained for downstream analyses after secondary filtering. DNA sequences and statistics (i.e., call rate, polymorphic information content, heterozygosity, read depth and reproducibility for all loci and individuals) are accessible from the Dryad Digital Repository (http://dx.doi.org/10.5061/dryad.ko1kj) and Diversity Array Technology Pty. Ltd., Canberra, Australia (Report-DEgs14-1547).

Detection of SNPs under divergent selection (putatively adaptive SNPs)

We used three alternative methods to identify loci putatively under divergent selection from the 4,274 unique SNPs retained for analysis. These approaches are based on outlier loci, defining loci under divergent selection as those with greater than the expected levels of divergence among regional groups, and loci under balancing selection as those with smaller than expected levels of divergence (F_{ST}) among regional groups (Moore *et al.*, 2014). First, we used BAYESCAN, a Bayesian approach that estimates the posterior probability of a given locus being under selection (Foll & Gaggiotti, 2008). We ran BAYESCAN using the default settings as test runs with longer chain parameters gave identical results. Loci under divergent selection were defined as those with greater F_{ST} than the mean among the group and α-values significantly greater than 0. Loci with F_{ST} smaller than expected among the group and α-values significantly less than 0 were considered as balancing selection. All other loci were considered putatively neutral.

Second, we used the hierarchical island model implemented in Arlequin v.3.5 (Excoffier & Lischer, 2010). This method allows lower migration rates among groups to be compared to within groups, and has been shown to reduce the prevalence of false positive (Excoffier & Lischer, 2010). We ran 20,000 simulations with 100 demes per group for 10 groups. Loci with F_{ST} significantly ($p \leq 0.01$) higher than the mean were considered candidates for divergent selection and those with F_{ST} significantly less than the mean among groups were considered candidates for balancing selection. Finally, we ran LOSITAN (Antao *et al.*, 2008) using parameter settings of 50,000 simulations, confidence interval of 0.99, FDR of 0.1 and subsample size of 49. Again, we identified loci under divergent selection as those with significantly greater F_{ST} than the among group mean F_{ST} and balancing selection as loci with F_{ST} significantly smaller than this mean.

To examine gene ontology annotation terms associated with the SNPs under divergent selection, we BLASTed the trimmed sequences for all SNPs identified as candidates for divergent selection against the UNI-PROT/SWISS-PROT and NCBI nonredundant nucleotide database (Altschul *et al.*, 1997). We set the BLAST *e*-value acceptance threshold as 1×10^{-6} with a sequence homology of more than 70% (Benestan *et al.*, 2016).

Summary statistics

We tested for deviation from Hardy-Weinberg equilibrium (HWE) at each sampling locality, and computed levels of expected (He) and observed (Ho) heterozygosity (Nei, 1987) and inbreeding (F_{IS}) on neutral loci using Arlequin 3.5 (Excoffier & Lischer, 2010), GENEPOP 4.3 (Rousset, 2008) and GenAlEx 6.5 (Peakall & Smouse, 2012). We calculated pairwise and overall genetic differentiation (F_{ST}) values (Weir & Cockerham, 1984) and levels of genetic variance between and among localities using the analysis of molecular variance (AMOVA) implemented in GENEPOP 4.3. The significance of these were tested using 1,000 and 999 random permutations in GENEPOP 4.3 and GenAlEx 6.5, respectively. All *P*-values were adjusted for multiple comparisons test using the FDR method in the function 'p.adjust' implemented in R v.2.15.2 with an experiment-wide $\alpha = 0.01$.

Identification of genetic clusters and localities under divergent selection

We identified genetically distinct groups of individuals (i.e., discrete populations) for putatively neutral SNPs and those under divergent selection using three methods, (i)

Bayesian clustering (ii) Discriminant analysis of principal component (DAPC) and (iii) Neighbourhood-joining phylogenetic tree. The Bayesian clustering approach implemented in STRUCTURE (Pritchard *et al.*, 2000) identifies groups of individuals corresponding to the uppermost hierarchical level, and has been shown to perform well with codominant markers such as SNPs. We used the correlated allele frequency and the admixture ancestry models without prior population information to assess values of *K* from 1-5. We performed 20 independent runs for 10,000 generations and 10,000 MCMC iterations for each value of *K*. The preferred value of *K* was determined using the change in the second order of likelihood, ΔK (Evanno *et al.*, 2005) in Structure Harvester webserver (Earl, 2012). Discriminant analysis of principal component (DAPC) was carried out using the adegenet package v.1.4-0 (Jombart, 2008) implemented in the R v.2.15.2. We ran DAPC for SNPs under neutral and divergent selection separately using the function "find.clusters". We retained 80 and 20 principal components (PCs) for neutral and SNPs under divergent selection, respectively, as these explained the vast majority of genetic variation (Fig S3, Supporting information). Finally, we constructed neighbourhood-joining (NJ) phylogenetic trees on the putatively neutral SNPs and those under divergent selection using MEGA6 (Tamura *et al.*, 2013). Simulations were performed based on Reynold's distance (Reynolds *et al.*, 1983) and bootstrapping of 10,000 replications over all loci.

Spatial patterns of divergent selection were inferred from the Neighbourhood-joining tree constructed using SNPs under divergent selection. Divergent selection creates a heterogeneous genomic differentiation by fixing adaptive traits, resulting in accentuated genetic divergence between locations affected by selection (Renaut *et al.*, 2011). Genetic subdivision resulting from divergent selection will also show lower genetic variation between individuals within locations, than those locations under no selection (Renaut *et*

al., 2011). Consequently, genetic subdivisions under strong divergent selection will yield on average an NJ-tree with shorter and more-uniform terminal branches and smaller overall length compared to those experiencing no or less selection pressures.

Results

Detection of loci under divergent selection

Among the three methods used, 138 (3.2%) loci were identified as candidates for divergent selection, 36 (0.84%) as under balancing selection and the rest as putatively neutral. Fifty-four of the loci under divergent selection were common to all three methods (Arlequin, Bayescan and Lositan). Given that false positives are often associated with the outlier loci, we conservatively considered only these 54 loci for downstream analyses of adaptive genetic structure. Alignment of the trimmed sequences of the 54 SNPs (Supporting Information Table S2) to the list of nonredundant nucleotides in the UNI-PROT/SWISS-PROT and NCBI database provided a total of four hits with an *e*-value less the 10^{-6}. Of these, three carried a nonsynonymous SNP (Table 1). The SNP*3129* and SNP3*136* are situated in the gene NOS1, which encodes nitric oxide synthase 1, an enzyme that mediates biological processes, such as neurotransmission, antimicrobial and antitumoral activities. In the central and peripheral nervous system, it is involved in neurotransmission (Hall *et al.*, 1994). The SNP*3130* is situated in the FOXP2 gene, which encodes the Forkhead box protein P2 (Morgan *et al.*, 2016), the function of which is unknown in squamates. The SNP*3134* is situated in the MYH gene, which encodes the myosin heavy chain II isoform-contractile proteins that modulate muscle contraction, cytokinesis and phagocytosis (De La Cruz & Ostap, 2004).

Genetic diversity and differentiation

Of the 4,100 putatively neutral loci, 357 (8.7%) deviated significantly ($P < 0.01$) from HWE, but only 115 (2.8%) remained significant after adjusting for FDR at $\alpha = 0.01$. Expected heterozygosity (He) varied across localities, ranging from 0.056 ± 0.002 at Sydney to 0.202 ± 0.03 at Armidale (mean ± s.e). In general, He was not significantly different from the corresponding observed heterozygosity (Ho), suggesting that the observed deviation from HWE was an artefact of sampling. Fixation index (Fis) was small and non-significant, except for samples from Sydney (Fis = 0.263, $P < 0.001$) that were a combination of individuals from two isolated sites: Barrenjoey headland (33° 32’ S, 151° 20’ E) in the Kur-ring-gai Chase National Park and Box Head (33° 32’ S, 151° 19’ E) in Bouddi National Park (Table 2). Separate analysis of samples from these two sites showed no heterozygote deficit (Supporting Information Table S3), indicating that the high Fis observed when the samples were pooled is a Wahlund effect owing to genetic structure (Frankham *et al.*, 2002).

Table 1: Characterization of high-quality BLAST matches of four sequences of SNPs under divergent selection with nonredundant nucleotides in the NCBI database.

SNP ID	TRIMMED SEQUENCE	GENE	SPECIES	E-VALUE	HIT LENGTH	IDENTITY	SEQUENCE ID	Gene ontology
SNP*3129*	CTGCAGGCTGGATTGGGGGTCTCTGCGGGCCACAAATGGCCCCCAGGCCAGGGTTTGCCCACCCATGCTC	NOS1	*Mabuya perrotetii*	6.00E-14	489	90%	KJ574789.1	Encodes the enzyme nitric oxide synthase 1, which acts as a biologic mediator in several processes including neurotransmission, antimicrobial and antitumoral activities.
SNP*3130*	CTGCAGCCCCAAGGTAAGGGAACAAATGCTCCCATACCTTGAGGAGGTGTCTGTGACTACCTCCCAACCA	FOXP2	*Mabuya sp.*	2.00E-07	845	81%	KJ574491.1	Unknown in squamates.
SNP*3134*	CTGCAGCCCCAAGGTAAAGGAACAAATGTTCCCATACCATAAGGAGGCCTCTGGGACTGCTGCCCCACCA	MYH	*Mabuya sp.*	2.00E-06	920	80%	DQ239423.1	Contains the ATPase activity providing energy that is the driving force for cytokinesis, phagocytosis, and muscle contraction.

SNP*3136*	CTGCAGGATGCAGCA CACGGCCCATTGGCA CCGCTATGCCAGTGC TGGAAAGGAGTGTGC CCTAACAGTG	NOS1	*Eutropis novemcarinata*	2.00E-08	715	88%	KJ574776.1	Encodes the enzyme nitric oxide synthase 1, which acts as a biologic mediator in several processes including neurotransmission, antimicrobial and antitumoral activities.

3

Genetic differentiation among all pairs of localities (i.e., pairwise F_{ST}) was high and significantly different from zero in each case ($P < 0.01$), ranging from 0.126 (Bathurst vs. Crookwell) to 0.742 (Sydney vs. Crookwell) and averaging 0.542 over all populations and loci (Table 3). Analyses of molecular variance (AMOVA) indicated that genetic variation among populations accounted for 65% of population differentiation, while variation within individuals and between individuals accounted for 33% and 2%, respectively.

Table 2: Summary statistics (Sample size N, mean ± standard error for observed [Ho] and expected [He] heterozygosity, inbreeding coefficient Fis) on neutral loci for the four sampling localities.

Locality	**N**	**Ho**	**He**	**Fis (*P*-value)**
Armidale	27	0.192±0.003	0.201±0.003	0.0609 (0.046)
Bathurst	27	0.129±0.003	0.130±0.003	0.0163 (0.208)
Crookwell	22	0.126±0.003	0.126±0.003	0.0147 (0.361)
Sydney	18	0.042±0.001	0.056±0.002	0.2631 (< 0.001)

Table 3: Pairwise population differentiation (F_{ST}) for neutral SNP's (values below diagonal). Probability (*P*-value) based on 9,999 permutations is shown above diagonal.

Neutral Loci				
Locality	Armidale	Bathurst	Crookwell	Sydney
Armidale	0.000	0.001	0.001	0.001
Bathurst	0.644	0.000	0.001	0.001
Crookwell	0.655	0.126	0.000	0.001
Sydney	0.725	0.726	0.742	0.000

Delimitation of genetic clusters

Bayesian clustering in STRUCTURE without prior locality information yielded a best-fit value of $K = 3$ on putatively neutral loci. This was overwhelmingly supported by DAPC and NJ-trees (Fig. 2). Both DAPC and NJ-trees identified samples from Armidale and Sydney as singletons (i.e., discrete populations that did not overlap with the other sampled populations) and those from Bathurst and Crookwell as overlapping clusters. For SNPs under divergent selection, two clusters were identified - Armidale as a singleton and Sydney, Bathurst and Crookwell as the other (Fig. 2), with strong fixation of alleles between these two clusters. Interestingly, all 4,274 SNPs (neutral plus outlier loci) identified patterns similar to the 3,851 putatively neutral SNPs, whereas all the SNPs identified as being under divergent selection by the individual methods showed similar spatial patterns as the 54 candidate SNPs for divergent selection that were common to all four outlier methods. This suggests that false positives had no significant influence on the results.

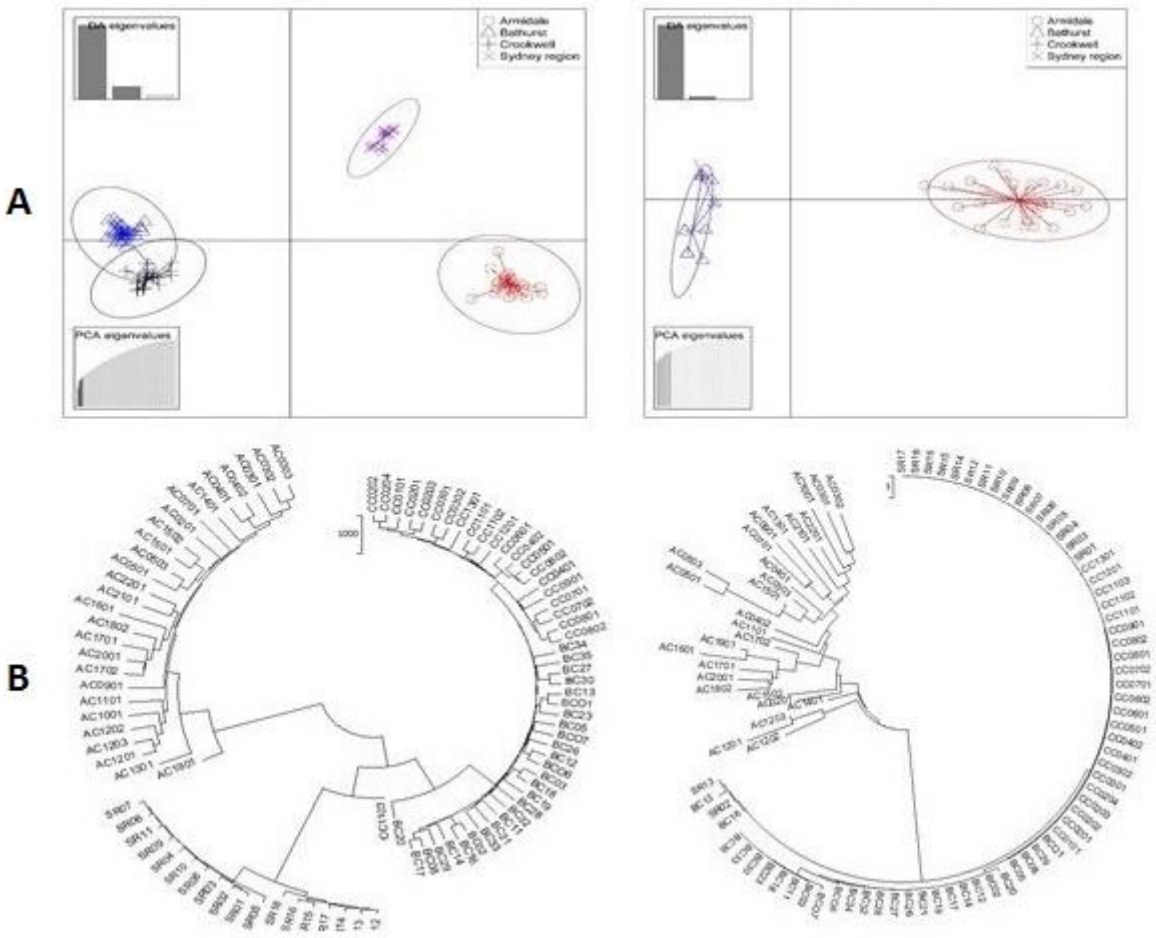

Fig 2: (**A**) Discriminant Analyses of Principal Component (DAPC) on putatively neutral (left) and SNPs under divergent selection (right) showing three and two distinct population clusters, respectively; (**B**) Neighbourhood-joining tree (NJ) for putatively neutral (left) and SNPs under divergent selection (right) based on Reynold's distance and bootstrap simulations of 10,000 replications in MEGA6 software. The scale bar shows Reynold's distance between samples.

The NJ-tree on SNPs under divergent selection showed uniform and short branch lengths for populations at Bathurst, Crookwell and Sydney compared to those at Armidale. This suggested that these three populations experience stronger selection pressures than at Armidale.

Discussion

Our analysis of genetic structure in Cunningham's skink along the Great Dividing Range (GDR) in south-eastern Australia revealed strong genetic partitioning and signatures of selection. Genetic structure at neutral SNPs and those under divergent selection yielded contrasting spatial patterns, showing that in this species, neutral genetic variation is not necessarily a good proxy for adaptive variation. At neutral loci, the genetic distances between each of the four localities analysed were high, with a relatively high proportion of unique alleles at Armidale. SNPs putatively under divergent selection clustered into two groups (Armidale versus Sydney-Bathurst-Crookwell).

The level of genetic differentiation at neutral SNPs among individuals at Bathurst/Crookwell, Sydney and Armidale locations was high ($F_{ST} \geq 0.644$). This level of genetic partitioning is substantially above the F_{ST} level of 0.35, which is approximately the point at which the spread of advantageous alleles across a species' range is prevented (Lowe & Allendorf, 2010). The levels of genetic divergence suggest that individuals at our study localities have long been isolated. Given the low movement rates characterised by this species (Stow & Sunnucks, 2004) and fragmentation of suitable rocky habitat across the study area, such high levels of genetic partitioning were anticipated.

While gene flow can aid the spread of advantageous alleles, high levels of gene flow can also stall local adaptations (Slatkin, 1987; Sexton *et al.*, 2011). However, recent studies demonstrate that beneficial alleles can be maintained, favoured and established, even under high gene flow (Sexton *et al.*, 2014; Schweizer *et al.*, 2015). Thus, neutral and adaptive genetic variation could show different spatial patterns even in highly dispersed species. For example, in the Atlantic herring (*Clupea harengus*) (André *et al.*, 2011) and Atlantic cod (*Gadus morhua*) (Hemmer-Hansen *et al.*, 2013) neutral SNPs and those under divergent selection showed contrasting spatial patterns despite high gene flow.

In a heterogeneous and complex landscape, such as the GDR, species with low dispersal and gene flow among populations may show concordance between patterns of neutral and adaptive variation, if the limits of dispersal corresponds with clines in the environmental drivers of selection (Sexton *et al.*, 2014). For example, in the relative philopatric anadromous Atlantic salmon (*Salmo salar*), similar spatial patterns at neutral and adaptive genetic variations have been reported (Moore *et al.*, 2014). However, despite the limited gene flow and very high genetic structuring at neutral loci in Cunningham's skink, the neutral and adaptive genetic variations showed contrasting spatial patterns. While the neutral SNPs identified three clusters (Bathurst-Crookwell, Sydney and Armidale), the putatively adaptive SNPs clustered into two groups (Armidale versus the other three localities). Although Sydney experiences different environmental conditions, and presumably different selection pressures from Bathurst and Crookwell, this was not detected in our data set. This suggests that lizards at Armidale have been under different selection pressures of a greater magnitude.

We successfully aligned sequences of four of the SNPs identified to be under divergent selection with genes of known identity and function. This strongly supports the claim that these SNPs are located within a functional part of the genome. However, the F_{ST} outlier tests we used to identify loci under divergent selection are designed to detect 'hard' selective sweeps that rapidly fix favourable alleles (Pritchard & Di Rienzo, 2010; Pritchard *et al.*, 2010). As a result, 'soft' selection sweeps, which involve relatively small changes in allele frequencies at a large number of loci underlying the selected trait, may not have been identified (Pritchard & Di Rienzo, 2010; Pritchard *et al.*, 2010; Brauer *et al.*, 2016). Ample evidence suggests that local adaptation to environmental change is largely via polygenic 'soft' selection sweeps, i.e., simultaneous selection acting on variants at many loci of small effects (Pritchard & Di Rienzo, 2010; Pritchard *et al.*, 2010).

Our results have conservation implications under contemporary climate change. Shifts in climate could necessitate shifts in the distribution of the species and also change the locations where particular adaptive genes might be advantageous (Hannah, 2008). Historically, the level of connectivity ($F_{ST} \geq 0.644$) is unlikely to allow for spread of favourable alleles (Lowe & Allendorf, 2010). The high F_{ST} values observed in our data also suggests that connectivity of populations may not be established given the rapid pace of climate change. If this is the case, the alternatives are *in situ* adaptation or localized extinctions.

Like all lizards, Cunningham's skinks are heliotherms, and to avoid overheating and death the lizards must reduce their activity and retreat to cool refuges, reducing foraging time and constraining growth, maintenance, and reproduction (Sinervo *et al.*, 2010). In addition to behavioural adaptation, lizards might be able to evolve a higher optimum body

temperature, but this increases the risk of overheating as the optimum nears the critical maximum temperature (Sinervo *et al.*, 2010). The constraint on thermal adaptation suggests that adaptation alone might not be enough to rescue some lizards from climate-induced extinctions. For example, a positive correlation between the rate of increase in maximum air temperature of the coldest month and local extinctions has been reported among Mexican lizards (Sinervo *et al.*, 2010).

Strong genetic structuring in Cunningham's skink complements similar findings reported in phylogeographic studies of other lizards, mammals, birds and invertebrates inhabiting the GDR (Chapple *et al.*, 2011; Pepper *et al.*, 2014). For instance, the mean F_{ST} for geographic groups of two skink species was 0.96 for mtDNA and 0.89 for nuDNA in *Lampropholis robertsi*, and 0.70 for mtDNA and 0.8 for nuDNA in *L. coggeri* (Bell et al. 2010). Species distribution modelling under representative palaeoclimates suggested that these two species have existed along the GDR in multiple isolated populations throughout the climate cycles of the Pleistocene (Bell *et al.*, 2010). Phylogenetic analysis of the common froglet, *Crinia signifera*, identified three geographically divergent lineages along the GDR that were separated during the late Miocene (~9 million years ago) (Symula *et al.*, 2008). Three geographically separated clades of the lace monitor, *Varanus varius*, have also been identified, with divergences estimated to have occurred during the Pleistocene (Smissen *et al.*, 2013). The high levels of population structuring for multiple taxa distributed along the GDR indicate a general pattern of long-term isolation, predating recent anthropogenic habitat loss. This therefore suggests that habitat corridors may not be a universal solution for species needing to shift their distributions under climate change.

We provide the first genetic evidence for different selection pressures along the GDR for a vertebrate. The presence of divergent selection raises some concerns for alternative management strategies. Translocation is often proposed as a means to rescue species from potential extinction, particularly where the current range becomes unsuitable and there is little or no overlap between this and areas projected to be suitable in the future. Initiating gene flow raises the potential risk of outbreeding depression (Frankham *et al.*, 2011), which can be the result of several factors, including genetic incompatibilities and disruption of co-evolved gene complexes (Frankham *et al.*, 2002). The presence of localized adaptation in Cunningham's skink highlights the potential for outbreeding depression to occur.

Unless climate change forces unprecedented levels of movement in Cunningham's skink, our data suggests that gene flow will be insufficient to spread advantageous alleles in the future. Knowledge of areas where divergent selection is associated with differences in climate can potentially be used to select areas for assisted migration purposes. However, studies on genetic structure based on neutral markers, such as those using microsatellites, may not be informative in this respect, because, as we have shown, patterns of variation at selected parts of the genome may not be concordant (Hemmer-Hansen *et al.*, 2013). In the case of the GDR, if translocation is to be adopted as a management tool, further knowledge on localized adaptation from other taxa will help evaluate whether patterns identified in this study are more general. Knowledge of the concordant patterns of selection across divergent taxa are likely to be crucial for the success of species-recovery programs, if resources are not available for the genetic assessment of individual species.

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SUPPLEMENTARY INFORMATION

Text file 1: SNP discovery and screening

SNPs discovery and genotyping were performed at Diversity Arrays Technology Pty. Ltd. (Canberra, Australia) using standard DartSeq™ protocol as follows:

First, 0.5 µL template DNA was incubated in a 1X solution of Multi-Core™ restriction enzyme buffer (Promega) at 37°C for 2 hours to remove any nucleases present. The DNA was then run on a 0.8% agarose gel pre-stained with GelRed™ at 120V for 20 minutes and checked visually for quality and quantity. Following the quality check, about 100 ng of each sample was transferred to a digestion and ligation reactor. Each sample was digested using a combination of *PstI* and *SphI* restriction enzymes and ligated with unique barcoded adapters (P1 adapter). Barcodes were designed to alter the enzyme recognition sites so that heat killing of enzyme was not required.

Digested and ligated samples were cleaned using a spin-column Qiagen PCR clean up kit and then amplified using PCR with barcode- and adapter-specific primers. Cleaned PCR product was then ran on 0.8% agarose gel to check that digest fell within the standard range. Equimolar amounts of amplified samples from each individual was pooled into a single tube, diluted and denatured using NaOH and then hybridized to the flow cell. The library was then sequenced with Illumina HiSeq2500 (Illumina) for 77 cycles, resulting in fragments of 77 bp long. To assess the reproducibility of SNPs calls, ≥ 15% random replicates were carried through the protocol pipeline. Once sequencing was completed, raw sequenced data were converted to .fastq files using the Illumina HiSeq2500 software.

Sequences from each sample were collected, separated by individuals, stripped of barcodes, cleaned and filtered to include only those with a Phred score ≥ 25. SNPs were identified and called following standard protocols in DArTSoft14™ (Diversity Arrays Technology). Initial alignment to existing sequences in the Dart database from similar organisms was performed to identify any contamination. Alignments to viral and bacterial sequences were also performed to further identify contamination. All monomorphic sequence clusters were removed and SNPs were called only if they were present in both homozygous and heterozygous forms.

Table S1: Matrix of average pairwise geographic distance (km) between sampled localities.

Locality	Armidale	Bathurst	Crookwell	Sydney
Armidale	0			
Bathurst	380	0		
Crookwell	460	96	0	
Sydney	310	192	212	0

Table S2: Sequence of the 54 SNPs identified by all three genome scan methods to be candidates for divergent selection

SNP ID	SEQUENCE
SNP3117	CTGCAGTTTTTCCCTTTACTGTTTTTCAAAGGAACAATGTGCATG
SNP3118	CTGCAGGCTCCACATGATTGGGGTCCCCTGTTCTATAGCATG
SNP3119	CTGCAGTCCAAAGGCCTTGTGAGCGTGCAGAAGATCTGCATG
SNP3120	CTGCAGTGGCTCTGAAGGAGCGGGGAAAGGGCCGCTTGCATG
SNP3121	CTGCAGTCCTCACCCACTTTCCAGAGAGTAAGCCCCTTGGGCGATAATGGGGGCTTGCTTCTGATGGGGC
SNP3122	CTGCAGCGACAACATGCAGAACATGGCTGCCAACACAAAAGACTGGTGAGGGTGCGTGCATG
SNP3123	CTGCAGGACTGTCTTGCAATACCACCCTGAATCCAAGCCAAGTAATAGAGTAGGAACCCAATCCTATGTT
SNP3124	CTGCAGAGGCTTGTTCTCAACAGTGGTATGCAGTGTGGCACAGGTGCTGCTGGTGAGAGAGTGGAATTCT
SNP3125	CTGCAGGTCGCTATGTGTGCGCGCATG
SNP3126	CTGCAGCCTCTACTTGCACAGCAAGGAAGCTGATGGAGGTGAAGAATAAGCAAGGGCTGCATGAGATCGG
SNP3127	CTGCAGCTAGAGGGGACAACTCAGGTAATGTTAACATGAAGCAGGAAGCACATTTGCTGCCTGCATGAGA
SNP3128	CTGCAGCTCCCCAGCTCTGGATATTTTCTTCCTAATCTTGAGTTATCAGTGGGGCAAATCAACTTGCAAA
SNP3129*	CTGCAGGCTGGATTGGGGGTCTCTGCGGGCCACAAATGGCCCCCAGGCCAGGGTTTGCCCACCCATGCTC
SNP3130*	CTGCAGCCCCAAGGTAAGGGAACAAATGCTCCCATACCTTGAGGAGGTGTCTGTGACTACCTCCCAACCA
SNP3131	CTGCAGTGCTACCATTTGTTTCTTGATTCCTTTAGCACCAGCATTACACAGAAATAGCTTTACCCGTCTT
SNP3132	CTGCAGGGTACACTATGACTCGTGCCTTCAGTCGCAGGGTCGCTGACTTGTGACTTGACTTGGGAGACAG
SNP3133	CTGCAGGGAAGCCATCCTTCCCTGTGGGCCAAACTGCACTTTGGCCTGCCACTTCCTTGTTCCATTGCCC
SNP3134*	CTGCAGCCCCAAGGTAAAGGAACAAATGTTCCCATACCATAAGGAGGCCTCTGGGACTGCTGCCCCACCA
SNP3135	CTGCAGTAGTGAGTCTTGTGATCTGCTGCCGTAAGACCAGTTATGGTGCACAAAAGGTGCACTTCCATTG
SNP3136*	CTGCAGGATGCAGCACACGGCCCATTGGCACCGCTATGCCAGTGCTGGAAAGGAGTGTGCCCTAACAGTG
SNP3137	CTGCAGCTCTCAGGAACCATTTCCTGTACCTAAGCCACAGTAGGAAAAGCTGGGAAATCTCATTTGGGAA

SNP3138	CTGCAGCTGCAATGGGTCAAATCAGACCTGTGCCGACTCTATAGCTGGCACAAGTCTGTGTTGATCTGTG
SNP3139	CTGCAGGTGTGCCTTGGGAGTTTGGGGAATGGTCATTTATTAATAGGGCCATTGGGGAATGTGAGCTAGC
SNP3140	CTGCAGTCTATTCTTGTAATGAAAATAGAAGTTTTCACTTTTCTTCTCTGACACGTGAGGAAAAAACAGA
SNP3141	CTGCAGCCACCTCTGCACTTTGTTTAACCCTGTTGTCTATTTCTGGGCATGGGGTCTAGTATAGTTTCAC
SNP3142	CTGCAGTGATATGAGAAATGGCACCTGGTAGAATGTTCACTTCCATGTGCATCTCAAGGTACAGGAACTC
SNP3143	CTGCAGCAACTCTCCCCAGAGTAAGGGGAAGTGATTCCCCTTGCCCTGGGCTGAACCGCAACTAGCCCCA
SNP3144	CTGCAGGTTGGGGGCTGTATGTTAGAATGTTCCACCAGGTAAAGAAGTCTCCCTGCATGTAGGCAAGTAG
SNP3145	CTGCAGATTTTCACCCTGGTCATTCAGTACAACTTGTGCCCACCTAGCTACTAACAGAGCAGGCATGAGA
SNP3146	CTGCAGTCCCACGCACTGGGAAGCTCAGGATTGGGCTGCCCATCAGCTAGGGAGATACATGTGAAGAAAC
SNP3147	CTGCAGTGTTAGGAACTTGGCAGCATG
SNP3148	CTGCAGGAAGAGGGGTTATCTGTTCAAATGCTTCTGCCTACCCACTGATCCAGCTGGCCACATGCATGAG
SNP3149	CTGCAGGATTAGTATGTGGATTTTTATAATGGCACACGCACATTATATATGCATG
SNP3150	CTGCAGCAGGAATTATTAAGGGGAAAGACCATGGCCCAGTGACGTATGGCTCTTGTGCTTTGCATGAGAT
SNP3151	CTGCAGACACTGGACTGTATGTGCATAGGTTGTATTTAAGCTTTATGTTCCTGGGTGGACTGAGAGACGT
SNP3152	CTGCAGTTGTATCAAGCCGTTCATGGTTTTTGTAGTCTTTTGGCTGTCCTTGGTAATATGGTATCAGGAT
SNP3153	CTGCAGGCCCCTAGTCTTAGCAGTAAGTCTTTGATGTTGCTGATGTTTTGTGCCAGTGGCTCAGAAATGG
SNP3154	CTGCAGTGAGGTGGCCTGAGGCCCGGGACATAGAGCCTGCTCTCGTTCCTTCCACTGTGTCATAGCAATT
SNP3155	CTGCAGTGGAGGGACTGTCTGGAGGCCTCCTTGAGATAAGGGAACTTTCATTCCCTTACCCTGGGGAAAG
SNP3156	CTGCAGAAATTATAGTTGCCTCTTTACTCAGTTAATTAGTAGATAACTCAAGCAAGCCATCAGGAAATAC
SNP3157	CTGCAGCAAAATGGACCCAGGTGATTCCGTAAAATTGGCTGTACAGCTCTGAGTGCTCTCTTAAGAGATG
SNP3158	CTGCAGCACAAGGTAGATCGTGGCATGGGCAAGAGTGGGCACAAGAGGATGTGCTCTAATTGCTTCCCCA
SNP3159	CTGCAGTCTATAGACTAGTTAATATATCCCCGTGGTGGCTTCAGTCTGGGCCATAAAGTGCGAAGTGGGG
SNP3160	CTGCAGGGAGAAGTTTCACAACTAGCCAGCCAGCATGTCACTCAGTCAGGCACGAAGGCTGCCGCTGGGT
SNP3161	CTGCAGCAGTCAGATACATGCACACATATGACAGACTGGCACTGCGATGCACCTTACACCACATGCACAC
SNP3162	CTGCAGCCTTGCACACAATCACTAAAGACTGTGCGTGTGCAGGATGACTGTTATAGCCATTCCAGTGCAA
SNP3163	CTGCAGGTCAGCCAGACAGCATGGGACATTGGAAATGGCCGGTAATTGGCTCTGCTCTGTGAGTAGAGCT
SNP3164	CTGCAGCCTCACATGGCAGTTTTGCTGTTGGCCAGCAGGCAGCCCACACTGCCCCACAGAGTACCTCGTA
SNP3165	CTGCAGAACAAATCCAGTGTTTTGTACTGGTCAGTGACTGTAATAAAAGATTCTTCAATTCAATCCAGTG
SNP3166	CTGCAGTGGGTGGGGAGGCAGAGCTTCTTCACTGGAGTCCTTCAAAAACTGCTGCTGCTATGTGAGGCAC
SNP3167	CTGCAGCATTAGAATATTTAGTTCAACCGTTTTCAGACTGAGAAATATGTACAGATCTGGTGGGAGAAGC
SNP3168	CTGCAGAGCTTCTGGTGTGTGTTCTAGGATACAAATTTGGTTCATGTGGAGCACAGACCTGTTGACCCTT
SNP3169	CTGCAGTTCAGTTTTAGTTAAAACAGTGAAAAGGTGACTTTTTGAGACATGTCTTTTGAGGGTGGCTGCA
SNP3170	CTGCAGACCACTGGGACATATTTGGATTGGCGCATAAGTTATTTGATTCTTAAGCAAGAAATTAGCAATA

Table S3: Summary of F statistics (Sample size N, mean ± standard error observed heterozygosity Ho, expected heterozygosity He, inbreeding coefficient Fis) on neutral loci for Sydney Barrenjoey Headlands (BJ) and Box Head (BH).

Locality	**N**	**Ho**	**He**	**Fis (*P*-value)**
Sydney BJ	11	0.039±0.003	0.036±0.003	- 0.0269 (0.706)
Sydney BH	7	0.048±0.003	0.041±0.003	-0.0119 (0.947)

CHAPTER FIVE

Adaptive capacity influences the outcome of climate change vulnerability assessment

Abstract

Climate change vulnerability assessment (CCVA) has become a mainstay conservation decision support tool. CCVAs are recommended to incorporate three elements of vulnerability – exposure, sensitivity and adaptive capacity – yet, lack of data frequently leads to the latter being excluded. Further, weighted or unweighted scoring schemes, based on expert opinion, may be applied. Comparisons of these approaches are rare. We show that, for 17 Australian lizard species, membership within three vulnerability categories (low, medium and high) generally remained similar regardless of the framework or scoring scheme. There was one exception however, where, under the warm/dry scenario for 2070, including adaptive capacity lead to five fewer species being classified as highly vulnerable. Two species, *Eulamprus leuraensis* and *E. kosciuskoi*, were consistently ranked the most vulnerable, primarily due to projected losses in climatically suitable habitat, narrow thermal tolerance and specialist habitat requirements. Our findings provide relevant information for prioritizing target species for conservation and choosing appropriate conservation actions. We conclude that for the species included in this study the framework and scoring scheme used had little impact on the identification of the most vulnerable species. We caution, however, that this outcome may not apply to other taxa or regions.

Introduction

Climate change poses a substantial threat to global biodiversity. Prioritizing conservation actions to ameliorate the impacts of climate change requires that we assess the vulnerability of species to climate change and identify which traits or characteristics drive their vulnerability (Williams *et al.*, 2008; Carvalho *et al.*, 2010; Foden *et al.*, 2013). To this end, climate change vulnerability assessment (CCVA) has become a mainstay conservation decision support tool (Rowland *et al.*, 2011; Small-Lorenz *et al.*, 2013; Lankford *et al.*, 2014; Pearson *et al.*, 2014; Butt *et al.*, 2016). However, most do not assess all the elements of vulnerability and hence paint an incomplete picture of a species' vulnerability to climate change (Pacifici *et al.*, 2015; Butt *et al.*, 2016).

The vulnerability of a population, species or community is considered a function of three elements: exposure, sensitivity and adaptive capacity (Dawson *et al.*, 2011; Foden *et al.*, 2013; Small-Lorenz *et al.*, 2013). Exposure is the magnitude of climate change likely to be experienced by a species across its range, and depends on the rate and magnitude of climate change (Dawson *et al.*, 2011). It is typically quantified using species distribution models (SDMs) fitted with climate variables, and projected onto downscaled output from regional or global circulation models (RCMs, GCMs) (Dawson *et al.*, 2011; Thomas *et al.*, 2011). Most studies have measured exposure using projected loss or contraction of a species' climatically suitable habitat, overlap between the current and future suitable habitat and projected loss of suitable habitat within protected areas (Heikkinen *et al.*, 2010; Araújo *et al.*, 2011; Cabrelli *et al.*, 2014; Cabrelli & Hughes, 2015). Other studies have also included changes in food availability, extreme weather and sea level (Gardali *et al.*, 2012; Bush *et al.*, 2014).

Sensitivity is the degree to which the performance, survival and persistence of species is affected by climate change (Dawson *et al.*, 2011). Most CCVAs have assessed sensitivity using life-history traits, including physiological, behavioural or ecological traits, such as tolerance to temperature or hydrological regimes, habitat specificity and dietary specialization, occupied area, population size, reproductive rate, temperature-dependent sex determination, clutch size, growth rate, generation length, and life span (Heikkinen *et al.*, 2010; Dawson *et al.*, 2011; Thomas *et al.*, 2011; Foden *et al.*, 2013; Pearson *et al.*, 2014; Cabrelli & Hughes, 2015; Tuberville *et al.*, 2015). In general, the number and combination of life-history traits employed in CCVAs varies with the study species, their habitats and data availability (Lankford *et al.*, 2014).

Adaptive capacity is the potential for species or populations to tolerate or adapt to climate change (Dawson *et al.*, 2011). Like sensitivity, adaptive capacity is governed by intrinsic traits, but can be influenced by extrinsic traits such as habitat loss and fragmentation. Although the distinction between sensitivity and adaptive capacity is somewhat ambiguous, dispersal and colonization ability, microevolution and phenotypic plasticity are generally regarded as the components of adaptive capacity (Dawson *et al.*, 2011; Nicotra *et al.*, 2015). Dispersal allows organisms to move to regions with suitable habitat (Trakhtenbrot *et al.*, 2005; Taylor *et al.*, 2012). It also promotes gene flow that increases genetic diversity, fitness and evolutionary potential of geographically isolated populations (Sexton *et al.*, 2011). However, it is unclear whether the natural dispersal rates of species, particularly philopatric species, will be sufficient to track the movement of climate zones (Shaw & Etterson, 2012; Niculae *et al.*, 2016).

Evolutionary adaptive capacity is the ability for species or populations to adapt in situ through micro-evolution (Hoffmann & Sgro, 2011). Evolution is a change in allele frequency, and thus requires adequate heritable genetic variation in populations (Ghalambor *et al.*, 2007; Bell & Gonzalez, 2011). Although the rate of evolutionary adaptation varies among species and populations, and in space and time (Hoffmann & Sgro, 2011), it occurs faster in species with high genetic diversity, large population size, high fecundity and short generation time (Gomulkiewicz & Houle, 2009). For many species, it remains unclear if they can adapt at a sufficient speed to counter the projected rate of climate change. Recent studies, however, have suggested that microevolution may be more rapid than previously thought (Hoffmann & Sgro, 2011; Sgro *et al.*, 2011).

In addition to evolutionary adaptation, species may exhibit phenotypic plasticity, whereby individuals change their phenology, physiology or morphology without undergoing changes in their genetic makeup (Pigliucci, 2005). Individuals have greater fitness when their phenotypes suit the environment (Kingsolver *et al.*, 2002; Reed *et al.*, 2011), yet as climate changes, the phenotype and phenology of populations may no longer confer high fitness (Fuller *et al.*, 2010; Reed *et al.*, 2011). Although phenotypic plasticity alone may not be sufficient for the long-term persistence of species under rapid climate change, it can increase the rate of evolution or buy time for evolutionary adaption (Reed *et al.*, 2011).

The components of adaptive capacity can be assessed by empirical, observational and modelling studies (Dawson *et al.*, 2011). Yet, for most species, there is very little available information on dispersal rates, evolutionary capacity and phenotypic plasticity, or the thresholds at which they are considered adequate to counter the impacts of climate change (Nicotra *et al.*, 2015). Therefore, like sensitivity, adaptive capacity is relative and a better

understanding of the contributions of its components to a species' resilience and resistance to climate change is crucial for advancing its quantification (Foden *et al.*, 2013).

A robust CCVA should account for all three elements, thereby facilitating identification of the most vulnerable species and the characteristics that determine their vulnerability (Dawson *et al.*, 2011; Butt *et al.*, 2016). However, recent reviews indicate that CCVAs are commonly based on sensitivity and exposure (Pacifici *et al.*, 2015; Willis *et al.*, 2015). It has been suggested that assessments that fail to account for any of the three elements may be incomplete and produce biased outcomes, thereby rendering them less reliable for guiding conservation decisions (Heikkinen *et al.*, 2010; Small-Lorenz *et al.*, 2013; Butt *et al.*, 2016).

Another difference in the approach to CCVA is whether all traits incorporated into the analysis contribute equally to a species' vulnerability score. Both unweighted and weighted scoring schemes (where the latter attempts to capture the perceived relative contribution of the various traits to vulnerability) have been used (e.g., Heikkinen *et al.*, 2010; Moyle *et al.*, 2013; Cabrelli *et al.*, 2014; Cabrelli & Hughes, 2015) but the outcome of these scoring systems have been rarely compared.

Here, we explored different approaches to undertaking CCVAs. Our main objective was to assess the relative vulnerability of 17 lizard species distributed along the Great Dividing Range of southeastern Australia, and the factors that make them susceptible to climate change. In doing so, we evaluated the extent to which the omission of adaptive capacity in CCVA, and the weighting of scoring schemes, influences the assessment outcome. Specifically, we asked the following questions: (i) Which species are most vulnerable to climate change and what factors are responsible for their vulnerability? (ii) Is there a strong

positive correlation between vulnerability scores based on all three elements of vulnerability and those that use only exposure and sensitivity? (iii) What effect does the system of scoring vulnerability (unweighted and weighted) have on the outcome of CCVAs? (iv) Are the same species consistently identified as vulnerable, irrespective of the framework used?

Materials and Methods

Study area and species

We assessed the vulnerability of lizards distributed along the Great Dividing Range (GDR) in southeastern Australia to climate change. The GDR traverses almost 3,500 km of the Australian continent, running from the Alps in southeast Victoria to Atherton in northeast Queensland (Pepper *et al.*, 2014). The GDR is a key conservation area because it harbours globally endemic and endangered species (Steffen *et al.*, 2009). As a result, it has been earmarked for the creation of a connectivity corridor to enhance species' mobility and capacity to adapt to climate change (Worboys & Pulsford, 2011).

To demonstrate the generality and transferability of our framework, we selected lizards with a broad spectrum of natural history traits (e.g., body size, reproductive mode, thermal tolerance, habitat association) and for which data on life-history traits, ecology, genetics and occurrence records are readily available. We restricted our analysis to species whose entire distributional range fell within the boundary of the climate data used in this study (approx. 135.7–153.7°E, 23.6–39.5°S). Overall, 17 species, belonging to the families Scincidae, Agamidae and Varanidae, were analyzed.

Assessing exposure

We used Maxent (version 3.3.3k) (Phillips *et al.*, 2004; Phillips *et al.*, 2006) to model the current and future distribution of suitable habitat for the 17 lizard species. Maxent is one of the most frequently used correlative SDMs because of its high predictive performance, computational efficiency and ease of use (Elith et al. 2006; Phillips and Dudik, 2008; Phillips et al. 2009). We obtained species occurrence records from the Atlas of Living Australia (ALA; www.ala.org.au). We removed duplicate and questionable records (i.e., records that fell outside the species' known range) and those that were collected before 1950. Overall, we included more than 31,000 unique occurrence points for the 17 species.

Current and future climate data, at a spatial resolution of 1 × 1 km, were derived from projections developed for the NSW and ACT Regional Climate Modelling (NARCliM) project (Evans *et al.*, 2014). Projections correspond to future climates simulated by four global climate models (GCMs): MIROC3.2-medres (K-I Model Developers, 2004), ECHAM5/MPI-OM (Jungclaus *et al.*, 2006), CGCM3.1-T47 (Flato, 2005) and CSIRO-Mk3.0 (Gordon *et al.*, 2002), dynamically downscaled for south-eastern Australia using the Weather and Research Forecasting (WRF) Regional Climate Model. Three alternate parameterizations of the WRF model (hereafter R1, R2, and R3), were used for downscaling, resulting in 12 future climate scenarios. The NARCliM project assumed the A2 emissions scenario (Nakicenovic *et al.*, 2000), which approximates the relative forcing and mean temperature trajectories of the RCP8.5 scenario (Stocker *et al.*, 2014). In general, CGCM3.1 is a relatively hot/wet scenario, MIROC3.2 is a warm/wet scenario, CSIRO-Mk3.0 is a warm/dry scenario, while ECHAM5 projects major increases in temperature but little change in rainfall (hereafter: hot/similar precipitation scenario) (Evans & Ji, 2012).

We use a suite of five predictor climatic variables that have been shown to predict the distribution of reptiles very well (Araújo *et al.*, 2006). These included annual mean temperature, temperature seasonality, maximum temperature of the warmest month, minimum temperature of the coldest month and annual precipitation. Because microhabitats have been shown to play a significant role in thermal buffering and determining the presence of species at fine spatial resolutions (Scheffers *et al.*, 2013; Scheffers *et al.*, 2014), and given that the selected species dwell in crevices of granite rock outcrops, we included an index of rock cover (Weathering Intensity Index) (Wilford, 2012) as a static predictor variable. We consider this to be an important addition because the presence of rock outcrops with suitable crevices will largely determine range filling under climate change.

We fitted the model using different combinations of Maxent features (i.e., linear, quadratic, product, threshold and hinge features), and varying levels of regularization, to control how tightly the model fitted the given occurrence points. The most realistic model settings as assessed by the smoothness of the response curves for our modelled species were linear, product, quadratic features, and a regularization multiplier of 1.5. To reduce over-prediction, background points were sampled from areas within 100 kilometers of occurrence localities. The fitted model was projected onto the current (20-year time period centered on 2000) and three future time slices (2030, 2050 and 2070). Future projections were constrained using a buffer of 300 km around the current distribution to prevent the model predicting climatically suitable habitats in areas too far beyond the species' range.

Model performance was evaluated using the area under the receiver operating characteristic curve (AUC) and the True Skill Statistic (TSS) based on 10-fold cross-

validation. AUC scores range from 0 to 1, with values of 1 indicating perfect binary classifier accuracy and 0.5 suggesting that model performance is no better than random. TSS scores range from -1 to 1, where 1 indicates perfect agreement between test data and model predictions, and scores of 0 or less indicate performance no better than random (Allouche *et al.*, 2006). Variables' predictive ability and importance to the model were assessed by referring to their percentage contribution, and to the impacts of jack-knifing on model performance. A final model was fitted using all occurrence data, and habitat suitability maps were generated by projecting these models to current and future predictor data. The projected continuous habitat suitability maps were transformed into climatically suitable and unsuitable habitat using the equal training sensitivity and specificity logistic threshold (Liu *et al.*, 2005; Jiménez-Valverde & Lobo, 2007).

Analyses of model output

For each GCM, we computed the change in climatically suitable habitat between the current and future projections as the percentage change in the number of suitable grid cells. We also calculated the percentage of overlap between current and future suitable habitat and the percentage of suitable habitat lost or gained within protected areas. For the latter, we obtained a GIS layer of the Australian protected area network from the Collaborative Australian Protected Area Database (CAPAD; available at www.environment.gov.au/parks/science/capad). We assigned higher exposure scores to species projected to lose a higher proportion of their range and suitable habitat within protected areas, and to those with no overlap between current and future suitable habitat (Supporting Information Table S1, S2 & S3).

Assessing sensitivity

We undertook an intensive survey of the published literature to compile values for 11 traits that capture the sensitivity of each species to climate change. As described below, sensitivity was based on: narrow thermal tolerance (Deutsch *et al.*, 2008; Foden *et al.*, 2013); geographically localized or restricted to a single climatic zone (Heikkinen *et al.*, 2010); specialized habitat (Heikkinen *et al.*, 2010; Dawson *et al.*, 2011) or dietary requirements (Foden *et al.*, 2013), slow reproductive rate (Moyle *et al.*, 2013); temperature-dependent sex determination or small clutches (Cabrelli & Hughes, 2015); low rate of offspring survival; and long generation length (Pearson *et al.*, 2014) or life span (Moyle *et al.*, 2013). Unless otherwise stated, values for the above traits were obtained from Chapple (2003) and Greer (1980). We assessed each trait as follows (see also Supporting Information Table 4):

1. Physiological thermal tolerance: The critical thermal maximum temperature (CT_{max}), defined as the body temperature at which an animal loses the ability to right itself when stimulated (Greer, 1980; Lutterschmidt & Hutchison, 1997), is strongly correlated with thermal tolerance (Huey *et al.*, 2009; Diamond *et al.*, 2012). As some species may already occur in regions where environmental temperature is relatively close to their CT_{max} (Huey *et al.*, 2009; Diamond *et al.*, 2012; Clusella-Trullas & Chown, 2014), we used the ratio of CT_{max} to the median temperature across the species' range as a proxy for physiological thermal tolerance. The median temperature each species may be exposed to in the future was calculated by overlaying occurrence records with data describing future scenarios of mean annual temperature in southeastern Australia (Evans *et al.*, 2014). Species with a relatively lower ratio of CT_{max} to median temperature were given higher sensitivity scores than those with a higher ratio.

2. Range size: We estimated each species' range size using the number of 100 × 100 km grid cells currently occupied. Species with relatively large range sizes were given higher sensitivity scores than those with smaller ranges.

3. Climatic zone: To obtain the number of climatic zones occupied by our study species, we overlaid their occurrence records with Koppen's climate classification of Australia (Greer, 1980). Species that occurred in multiple climatic zones were given lower sensitivity scores than those that occurred in only one zone.

4. Habitat requirements: Species restricted to a single habitat type (habitat specialists) were given higher sensitivity scores than those that occurred in multiple habitats.

5. Dietary requirements: Cabrelli &Hughes (2015) classified Australian skinks as specialists, borderline specialists and generalists based on the breadth of their prey types. We adopted this classification and gave diet specialists higher sensitivity scores than generalists.

6. Reproductive rate: Species that reproduce once or more within a year were given lower sensitivity scores than those that reproduce less frequently.

7. Reproductive mode: Species that give birth to live-young were given lower scores than those that lay eggs.

8. Number of offspring: Species producing five or more offspring per reproductive event were given a lower sensitivity score than those that have fewer offspring per event.

9. Offspring survival: Species with less than 50% of their offspring dying before reaching sexual maturity were given higher sensitivity scores than those with more than 50% of their offspring reaching sexual maturity.

10. Generation length: Species reaching sexual maturity within two years were given lower sensitivity scores than those with longer juvenile stages.

11. Life span: Species that live for 10 years or more were given higher sensitivity scores than those with shorter lifespans.

Assessing adaptive capacity

Although the theoretical basis of adaptive capacity is well understood, its quantification remains difficult and little information and guidance exists to inform its objective assessments (Gardali *et al.*, 2012; Nicotra *et al.*, 2015). We used four measures of adaptive capacity: genetic diversity; body size; habitat fragmentation; and microhabitat buffering (Supporting Information Table S5).

1. Genetic diversity: Given that evolutionary adaptation and plastic responses to climate change depend on the extent of genetic variation within species and among populations (Sgro *et al.*, 2011), we used measures of genetic diversity as a proxy for adaptive potential. Expected heterozygosity (He) for the lizards (measured by microsatellite markers) were obtained from the published literature (for references see Supporting Information Table S5). In principle, species with relatively high genetic diversity are expected to have greater

adaptive potential, hence we assigned higher adaptive capacity scores to species with mean He > 0.8.

2. Dispersal capacity: Empirical data on the dispersal of most lizards is rare. However, given their strong correlation, we used body size as a surrogate for dispersal capacity (Sutherland *et al.*, 2000). In general, the larger the organism, the more mobile it is, hence larger lizards (measured by snout-vent length, SVL) were assigned relatively higher dispersal capacity, and thus adaptive capacity, than smaller ones.

3. Habitat fragmentation: The degree of connectivity of the landscape can impede or enhance movement of organisms, thereby influencing their response to climate change (Broennimann *et al.*, 2006; Heikkinen *et al.*, 2010; Baguette *et al.*, 2013). To assess the degree of habitat fragmentation for individual species, we overlaid species' current range maps with a GIS layer of the land use/land cover of Australia (Australian Land Use and Management [ALUM] Classification, version 7, May 2010, available at www.abs.gov.au). For each species, we calculated the percentage of occupied grid cells that fell within pasture, crop and modified lands. We assigned a higher adaptive capacity score to species with more than 40% of their occupied grid cells within pasture, crop and modified lands, and a lower score to those with less than 10% of the occupied grid cells within these land cover types.

4. *Microhabitat buffering:* The use of microhabitat features that moderate temperature and extreme weather conditions can influence the capacity of species to cope with climate change (Scheffers *et al.*, 2013; Scheffers *et al.*, 2014). Hence, species that used rock crevices and tree hollows as retreat sites were given higher adaptive capacity scores than those that used leaf litter or bare ground.

Vulnerability framework and scoring

We scored the variables of the three elements of vulnerability on an ordinal scale using two scoring schemes: unweighted and weighted (Table 1). In the unweighted scoring scheme, we considered the variables within each element as equally important and were awarded a maximum score of three points and a minimum score of one point (Gardali *et al.*, 2012). In the weighted scheme, the variables within each element were ranked according to their perceived relative contribution to vulnerability (Cabrelli *et al.*, 2014; Cabrelli & Hughes, 2015). Higher maximum scores were awarded to the variables that contributed more to climate vulnerability, with categories within variables awarded a minimum score of one and a median score of half the maximum score (Cabrelli *et al.*, 2014; Cabrelli & Hughes, 2015). For example, of the 11 sensitivity traits used in this study, thermal tolerance was regarded the most important trait and so it was awarded the highest maximum score of 11 for species with narrow thermal tolerance, a score of 5.5 for species with moderate tolerance, and a score of one for species with wide tolerance. Life span was regarded the least important of the traits and was therefore awarded the lowest maximum score of three for short-lived species, a score of two for species with moderate life-spans, and a score of one for long-lived species (Table 1).

Table 1: Description of the variable categories and their scores for the three elements of climate change vulnerability as applied to assess the vulnerability of 17 lizards along the Great Dividing Range of Australia (for references see Supporting Information Table S4 and S5). For geographic range size, N refers to the number of 100 × 100 km grid cells occupied by the species.

Variable	Category (description)	Unweighted score	Weighted score
EXPOSURE			
Change in area of current climatically suitable habitat	Increase or little change (i.e. < 10% decrease)	1	1
	10–50% decrease	2	2
	> 50% decrease	3	4
Overlap between current and future suitable habitat	> 50%	1	1
	10–50%	2	2.5
	< 10%	3	5
Suitable habitat within protected areas	> 50%	1	1
	10–50%	2	1.5
	< 10%	3	3
SENSITIVITY			
Physiological tolerance	Wide (CT_{max}:median temp > 3 °C)	1	1
	Moderate (CT_{max}:median temp = 1.5–3 °C)	2	5.5
	Narrow (CT_{max}:median temp < 1.5 °C)	3	11
Geographic range size	Large (N ≥ 50)	1	1
	Moderate (25 ≤ N < 50)	2	5
	Small (N < 25)	3	10
Climatic zones	Multiregional (> 3 climate regions)	1	1
	Moderate (2–3 climate regions)	2	4.5
	Narrow (1 climate region)	3	9
Habitat requirement	Generalist (> 3 habitat types)	1	1
	Moderate (2–3 habitat types)	2	4
	Specialist (1 habitat type only)	3	8
Dietary requirement	Generalists (omnivore, or exploits a wide variety of food)	1	1
	Moderate (able to tolerate some variety of food)	2	3.5
	Specialist (restricted to a particular food item)	3	7

Reproduction rate	Perennial	1	1
	Annual	2	3
	Biennial	3	6
Reproduction mode	Viviparous	1	1
	Ovoviviparous	2	3
	Oviparous/temperature dependent sex	3	6
Mean Clutch size	Large (≥ 5)	1	1
	Moderate (= 3–4)	2	2.5
	Small (2)	3	5
Offspring survival rate	> 80% of offspring reach sexual maturity	1	1
	50–80% of offspring reach sexual maturity	2	2.5
	< 50% of offspring reach sexual maturity	3	5
Generation length	Short (< 2 years)	1	1
	Moderate (3–4 years)	2	2
	Long (5 years)	3	4
Life span	Long-lived (> 10 years)	1	1
	Moderate (5–10 years)	2	2
	Short-lived (< 5 years)	3	3
ADAPTIVE CAPACITY			
Dispersal capacity	Low (SVL < 100 mm)	1	1
	Moderate (100 mm < SVL < 200 mm)	2	3
	high (SVL > 200 mm)	3	6
Genetic variability and evolutionary potential	Low (He > 0.6)	1	1
	Moderate (0.6 < He < 0.8)	2	2.5
	high (He > 0.8)	3	5
Habitat fragmentation or barriers to dispersal	high (> 50% of range within pasture, crop and modified lands [PCMLs])	1	1
	Moderate (10–50% of range within PCMLs)	2	2
	Low (< 10% of range within PCMLs)	3	4
Microhabitat buffer	Uses open ground only	1	1
	Uses ground litter cover and tree bark	2	2
	Uses deep rock crevices, burrows, under rocks and holes in logs	3	3

Climate vulnerability score and ranking threshold

To generate a climate change vulnerability score (*Vs*), we first divided the sum of the scores for each of the three elements of vulnerability by their respective potential maximum score to generate exposure score (*Es*), sensitivity score (*Ss*) and adaptive capacity score (*As*). We then computed *Vs* as (*Es* + *Ss*) – *As*. Where only exposure and sensitivity were used, *Vs* equalled the mean of *Es* and *Ss* (Gardali *et al.*, 2012; Cabrelli & Hughes, 2015).The *Vs* ranged from zero to 100; species with *Vs* ≥ 66 were ranked as high vulnerability, those with Vs from 33 to 66 were ranked as moderate vulnerability and those with Vs less than 33 were classified as low vulnerability. We evaluated the relationship between the two assessment methods (i.e., with and without considering adaptive capacity) and scoring schemes (i.e., unweighted and weighted) using the Spearman's rank correlation coefficient and analysed the difference between them using the Fisher's exact test.

Results

Exposure

Loss of suitable habitat varied across climate trajectories and time horizons, with up to 15 lizards (88%) projected to lose portions of their climatically suitable habitat by 2070 (Supporting Information Table S1). Seven species (41%), including *Eulamprus leuraensis*, *Eulamprus kosciuskoi*, *Eulamprus heatwolei*, *Eulamprus tympanum*, *Egernia frerei*, *Egernia kingii* and *Egernia cunninghami* were projected to lose at least 50% of their current suitable habitat by 2070. *Lissolepis coventryi* was the only species projected to gain

(25.5%-135.9%) climatically suitable habitat under all climate scenarios and time horizons considered (Supporting Information Table S1). The proportion of species assigned to the three exposure categories also varied with climate trajectory and time horizon. In general, most species were assigned to the moderate and low exposure categories (Figure 1), with no significant difference between the weighted and unweighted scoring schemes (Fisher's exact test: df = 32; $p > 0.05$). *Eulamprus leuraensis* was the only species assigned to the high exposure category under all the climate trajectories and time horizons considered.

Sensitivity

Two species were categorised as having high sensitivity to climate change: *E. leuraensis* and *L. coventryi*, both of which are habitat specialists, have small population sizes and narrow geographic range sizes. The remaining species were assigned to the moderate sensitivity category, with scores between 54.5-66.7 for the unweighted score and 39.9-63.8 for the weighted score. Sensitivity scores for the two scoring schemes were strongly correlated (Spearman's correlation, $r_s = 0.91$, $df = 32$, $p < 0.01$), and although the unweighted scores were higher than the weighted scores (Figure 2) this had no effect on the proportion and identity of the species assigned to the various sensitivity categories.

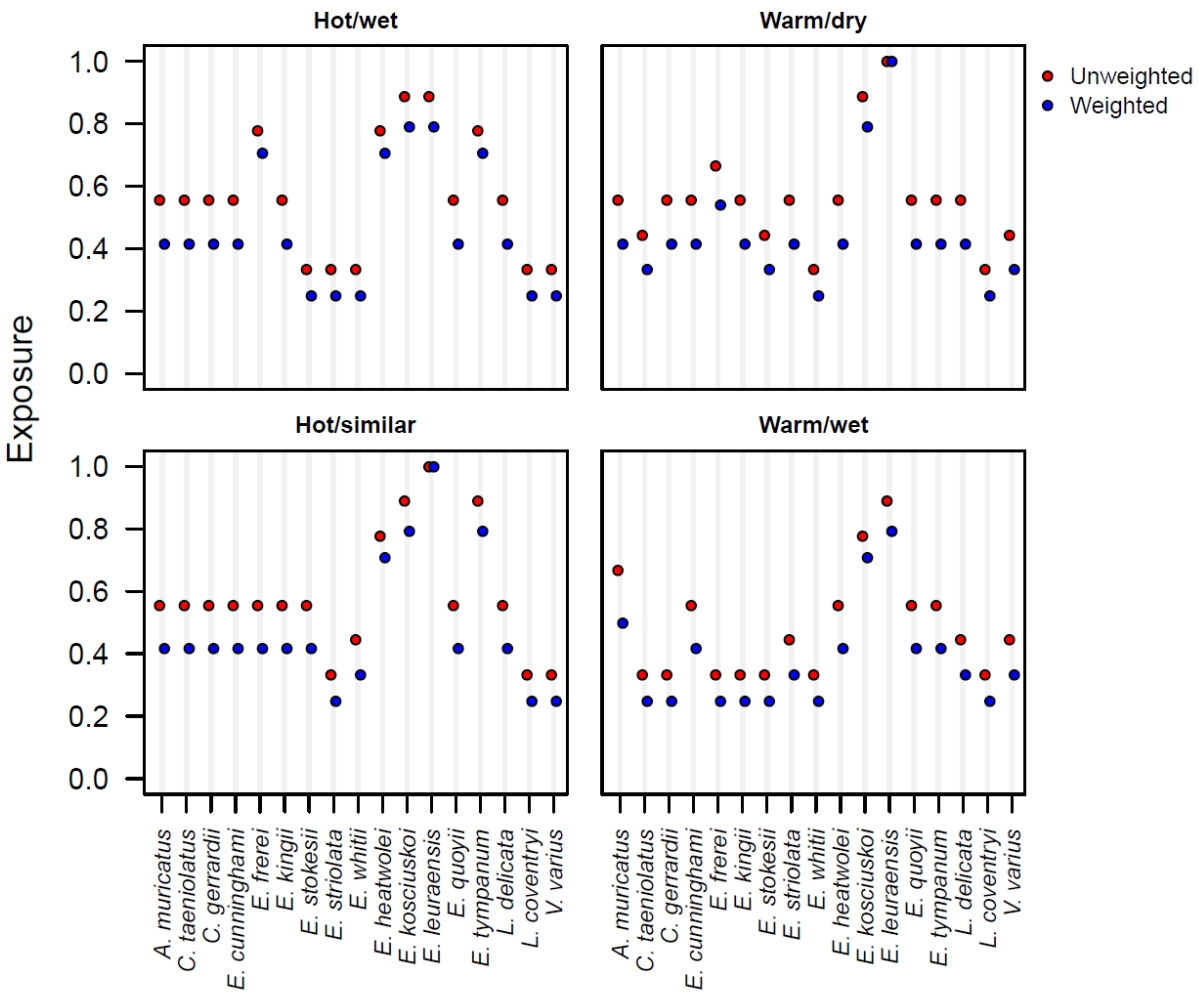

Figure 1: Weighted and unweighted exposure scores for 17 Australian lizards under projected climate change by 2050**.** Exposure was assessed using four contrasting future climate scenarios that are equally plausible: hot/wet; warm/dry; hot/similar precipitation; and warm/ wet scenarios. Score > 0.67 is high, from 0.33 to 0.67 is moderate and < 0.33 is low. See Supporting Information Figure S1 and S2 for exposure scores at 2030 and 2070.

Adaptive capacity

None of the 17 species were classified as having low adaptive capacity (Ac), and those with high Ac were characterized by high genetic diversity and dispersal capacity. Depending upon the scoring scheme and time period, up to 76% of the species were assigned to the moderate Ac category. Six species, *Cyclodomorphus gerrardii*, *Varanus varius*, *Egernia striolata*, *E. cunninghami*, *E. kingii* and *E. frerei* were classified as having high Ac under the unweighted scoring scheme. Four of these (excluding *E. frerei* and *E. striolata*) were also assigned to the high Ac category by the weighted scoring scheme.

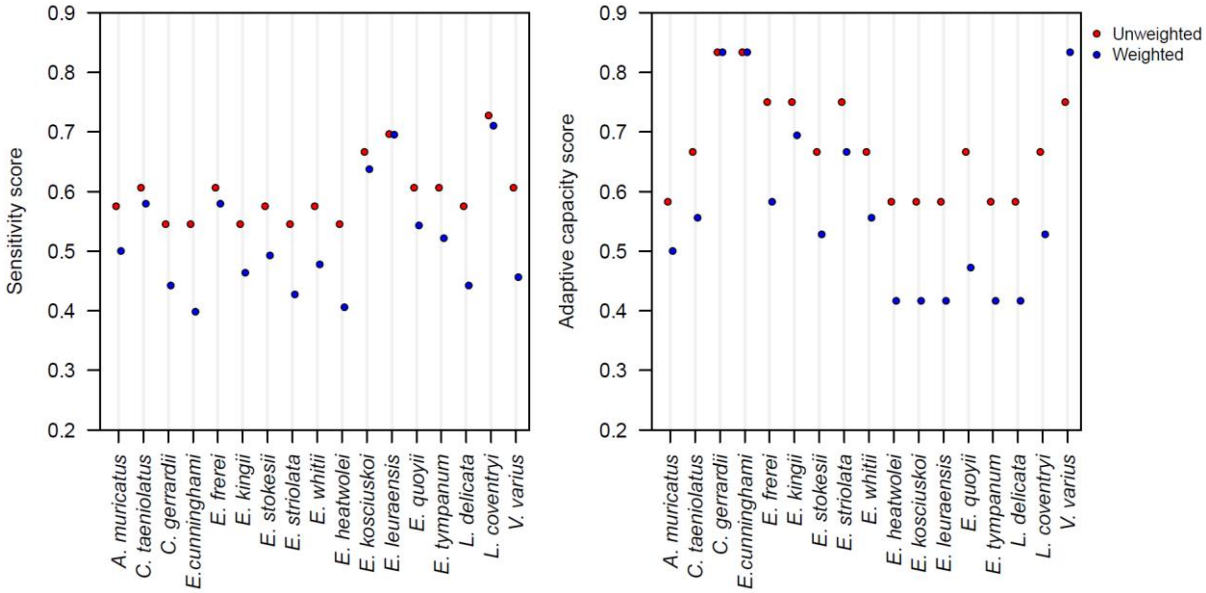

Figure 2: Weighted and unweighted scores of sensitivity and adaptive capacity of the 17 Australian lizard species to climate change. Score > 0.67 is high, from 0.33 to 0.67 is moderate and < 0.33 is low.

Overall vulnerability

Accounting for exposure, sensitivity and adaptive capacity

Although the vulnerability scores for individual species varied across the four climate scenarios and three time horizons (Supporting Information Table S6), membership within the three vulnerability categories remained relatively similar. Generally, there were no significant differences between the two scoring schemes or between the ES and ESA frameworks (Fisher's exact test: df = 32, $p > 0.05$) (Fig. 3). There was an exception, however. In the unweighted scoring scheme, under the warm/dry scenario for 2070, omitting adaptive capacity led to five additional species being classified as highly vulnerable, compared to the two (*E. leuraensis* and *E. kosciuskoi*) included in the ESA framework. Indeed, *E. leuraensis* and *E. kosciuskoi* were classified as highly vulnerable in both frameworks and scoring schemes, across most of the climate scenarios and time horizons.

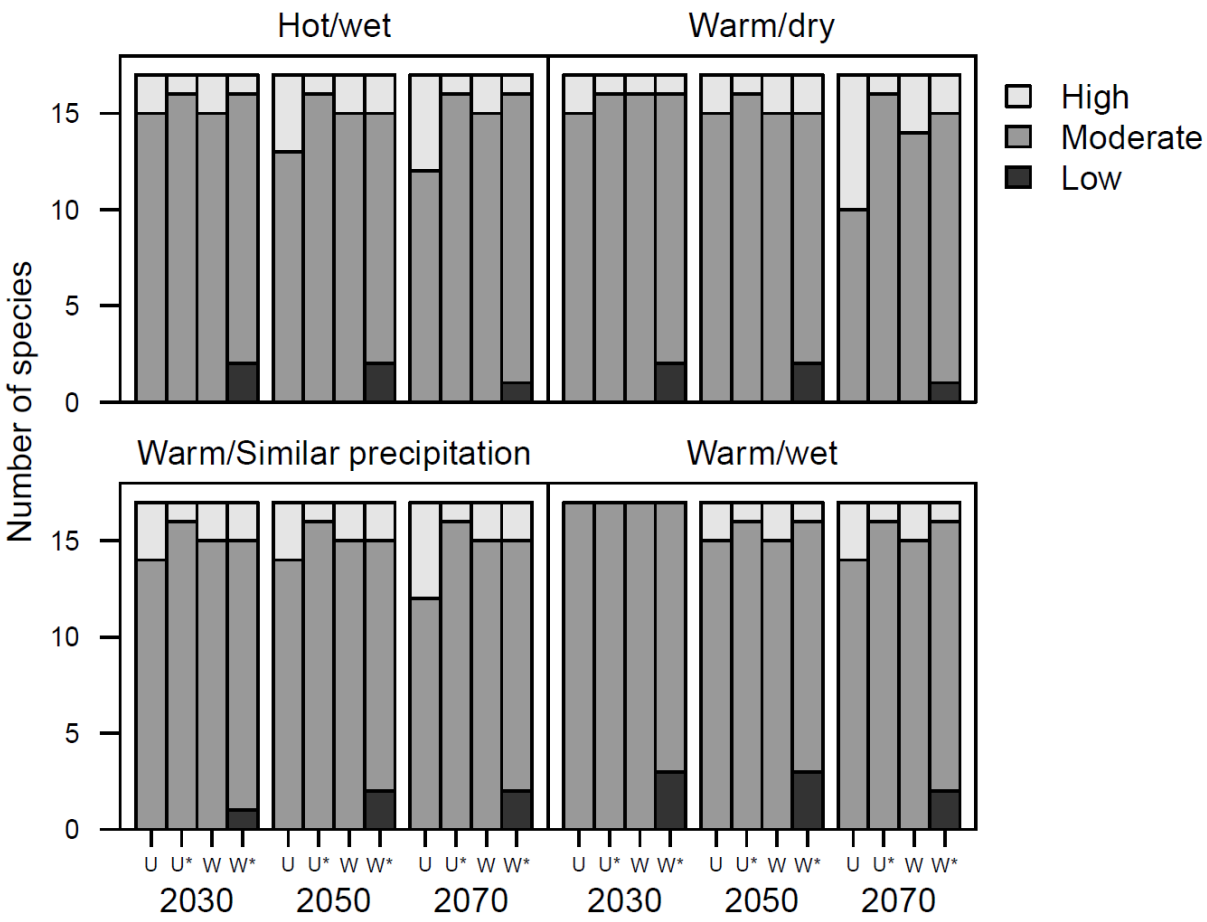

Figure 3: Number of species assigned to the three climate change vulnerability rankings for the 17 lizards, according to the unweighted (U) and weighted (W) scoring schemes. Asterisks (*) indicate that analyses considered adaptive capacity in addition to exposure and sensitivity.

Discussion

In this era of rapid climate change, making informed decisions about where and how to allocate resources for conservation is crucial (Ferraro & Pattanayak, 2006; Butt *et al.*, 2016). Here, we applied a CCVA framework that integrates species' exposure, sensitivity and capacity for adapting to climate change, to 17 lizard species distributed across the

Great Dividing Range of Australia. We found that incorporating adaptive capacity into a CCVA may influence the composition of species assigned to the various vulnerability categories. Our results also highlighted how the degree of exposure to climate change is temporally dynamic, and ought to be assessed over multiple time horizons to facilitate informed, species-specific management decisions. Our findings provide relevant information to guide conservation strategies for Australian lizards under climate change.

Unweighted vs. weighted schemes

When all three elements of vulnerability were integrated, the difference between the number and composition of species within the various vulnerability categories under the weighted and unweighted schemes were not significant (Fisher's exact test: df = 32; $p > 0.05$). The majority (≥ 59%) of lizard species were classified as moderately vulnerable under both schemes, with only one to two assigned to the high vulnerability category (weighted and unweighted schemes, respectively). These two species, *E. leuraensis* and *E. kosciuskoi*, should be priorities for conservation management. The key contributors to their vulnerability were substantial losses in the spatial extent of climatically suitable habitat, narrow thermal tolerance, small geographic range, and low dispersal capacity. However, it has been suggested that species assigned to a high vulnerability category may persist if they are able to adapt to the novel future climate (Dawson *et al.*, 2011; Foden *et al.*, 2013). Although both *E. leuraensis* and *E. kosciuskoi* have moderate adaptive capacity, this measure is relative and does not highlight a species' true capacity to adapt to changes in climate (Nicotra *et al.*, 2015). As such, active monitoring and management of these species might be necessary to prevent climate-driven extinction. Actions should be aimed at

reducing their sensitivity to climate change; external stressors, such as habitat loss and degradation, predation by feral cats, and competition with invasive species should be managed. Where there is evidence that their populations are declining over time, assisted migration may be necessary to safeguard the species from extinction.

The species that are not currently at risk from climate change could also be categorized as being potential adapters, potential persisters, or as having high latent risk, depending on their exposure, sensitivity and adaptive capacity rankings. Each of these classes has particular implications for conservation management (Foden *et al.*, 2013). Potential adapters are the species that are highly exposed and sensitive to climate change, but have high capacity to adapt and tolerate the impacts of the change (Dawson *et al.*, 2011; Foden *et al.*, 2013). Potential persisters are species that are highly exposed and have low adaptive capacity, but are not sensitive to climate change (Dawson *et al.*, 2011; Foden *et al.*, 2013). Species in this class may be able to tolerate changes in climate conditions. Species with high latent risk are those with high sensitivity and low adaptive capacity, but are currently not highly exposed to climate change. These species are not of immediate management concern, but could become highly vulnerable if exposed beyond the modelled time frame (Dawson *et al.*, 2011; Foden *et al.*, 2013).

According to the unweighted scheme, *E. frerei*, *E. cunninghami* and *E. kingii* are highly exposed under at least one climate scenario and time slice, and have high adaptive capacity, but moderate sensitivity to climate change. These species are therefore borderline potential adapters and must be monitored to ensure they retain stable populations over time. Under both schemes, *Lissolepis coventryi* has low exposure, high sensitivity and moderate adaptive capacity across all the climate scenarios and at least two time slices.

This species lies at the border of high latent risk and not of immediate conservation concern. Species that are highly exposed, but have moderate sensitivity and adaptive capacity are also not of immediate concern, but represent new priorities for conservation. Changes to external stressors that increase their sensitivity and decrease their adaptive capacity may result in these species becoming more vulnerable to climate change.

The species assigned to the high exposure category are projected to experience greater losses in climatically suitable habitat than those assigned to the moderate and low categories. This supports the findings of other studies on Australian reptiles (Cabrelli *et al.*, 2014; Cabrelli & Hughes, 2015) and suggests that loss in climatically suitable habitat will be a key driver of the vulnerability of lizards in Australia. For species with sufficient dispersal capabilities, creating and maintaining connectivity between current and future habitat may be necessary to facilitate their movement across the landscape (Crooks & Sanjayan, 2006; Doerr *et al.*, 2011). Connecting populations that are in close proximity, but are separated by physical barriers, could also enhance gene flow, genetic diversity and the capacity of species to adapt to climate change.

Omission of adaptive capacity

A frequent challenge to CCVAs has been the lack of data on adaptive capacity (Nicotra *et al.*, 2015; Butt *et al.*, 2016). Yet, we demonstrate that ignoring adaptive capacity can influence the results; more species were classified as highly vulnerable, especially under the weighted scheme. This may impede reliable identification of conservation priorities, leading to suboptimal use of limited conservation resources. This emphasizes the need to

comprehensively assess all three elements of vulnerability where such data are available, as advocated by recent studies (Foden *et al.*, 2013; Butt *et al.*, 2016).

Caveats

Our study identified only two species as highly vulnerable to climate change. However, these results should be interpreted with caution, because we only considered 17 species in our analysis, and it is possible that we excluded several species that are highly vulnerable to climate change. For example, the montane specialist skink *Lampropholis robertsi* and its congener *L. coggeri* are endemic to rainforests of northeast Australia, have relatively narrow distributions, occur within a narrow climatic zone, and have relatively low dispersal capacity. These characteristics suggest they might be highly vulnerable to climate change, but they were not included in our analysis because their occurrence records were too few to allow for reliable models.

We point out that the adaptive capacity scores used in this study are relative, and may not reflect true capacities of the study species. Our study lizards have ample genetic diversity that could enable them to adapt to climate change (Supporting Information Table S5). However, neutral genetic diversity as used in this study does not have any direct influence on fitness, and it is unclear if it is a good proxy for variation under natural selection (Holderegger *et al.*, 2006). Recent technological advances in next-generation sequencing show promise in identifying genetic markers for traits that confer thermal tolerance (Manel & Holderegger, 2013). These markers could be useful to forecast adaptive responses of species to climate change (Sunday *et al.*, 2014).

We ranked the dispersal capacity of lizards based on their body size, however, in general, lizards have limited dispersal capacity compared to large mammals and most birds. As yet, it is unclear if the localized mobility of lizards is sufficient to keep up with the pace of climate change (Araújo *et al.*, 2011; Huntley & Barnard, 2012; Shaw & Etterson, 2012). Genetic characterization of Cunningham's skink showed strong population differentiation that suggests that the species is unlikely to track its climate envelope even where habitats are contiguous (Ofori *et al.*, 2016). Moreover, the use of species distribution models to project changes in climatically suitable habitat has its own limitations that have been well documented elsewhere (Pearson et al. 2006; Wiens et al. 2009; Sinclair et al. 2010). Species distribution models are sensitive to the choice of modelling algorithm (Pearson, 2006; Elith & Graham, 2009; Beaumont *et al.*, 2016) and climate trajectory (Beaumont *et al.*, 2008). Therefore, different algorithms, and future changes in climate that do not conform to the climate trajectories used in the present study, could provide dramatically different exposure estimates and hence species vulnerability rankings.

Other external stressors that were not accounted for, such as predation, competition and invasion, and potential disease outbreaks could substantially influence vulnerability to climate change (Brook *et al.*, 2008).

Conclusion

We have shown that the choice of CCVA frameworks and scoring schemes can influence the proportion and composition of species assigned to the different vulnerability categories. Sensitivity, exposure and adaptive capacity traits are unlikely to contribute equally to

scores of species vulnerability to climate change (Cabrelli *et al.*, 2014; Cabrelli & Hughes, 2015), and intuitively, weighted scores may provide a more realistic assessment. However, given the lack of empirical evidence to support vulnerability trait scores, it remains difficult to select an appropriate weighting scheme (Foden *et al.*, 2013; Lankford *et al.*, 2014). This is further complicated by the large number of variables that may be relevant for different taxonomic groups. Our study suggests that there is greater congruence between species' vulnerability rankings according to the weighted and unweighted schemes when all three elements of vulnerability are integrated. This suggests that, under such a framework, the unweighted scheme may provide similar information with respect to species' vulnerabilities and their associated traits.

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SUPPLEMETARY INFORMATION

Table S1: Percentage change in climatically suitable habitat for 17 Australian lizard species under four climate scenarios, for 2030, 2050 and 2070 and time horizons. Habitat suitability was modelled using Maxent. Figures with "+" indicate gains in the size of suitable habitat.

Climate change scenario	**Hot/wet**			**Warm/dry**			**Hot/similar precipitation**			**Warm/wet**		
Species/ Time	**2030**	**2050**	**2070**	**2030**	**2050**	**2070**	**2030**	**2050**	**2070**	**2030**	**2050**	**2070**
Amphibolurus muricatus	20.0	31.6	41.8	24.3	35.3	45.5	39.9	38.9	39.5	13.5	21.1	28.6
Ctenotus taeniolatus	23.4	28.1	32.2	12.1	13.6	15.1	45.6	28.3	8.0	8.3	2.2	11.5
Cyclodomorphus gerrardii	23.7	34.4	42.3	27.9	37.4	47.8	32.9	30.5	26.5	1.4+	13.0+	26.2+
Egernia cunninghami	30.7	41.4	47.4	36.7	44.9	50.8	63.3	46.2	22.5	29.5	30.0	27.2
Egernia frerei	38.4	52.6	64.5	45.6	61.6	73.4	46.0	48.4	51.3	0.9	11.1+	16.8+
Egernia kingii	32.9	43.8	52.5	29.7	45.7	58.0	33.4	34.8	35.6	0.4	3.4+	8.1+
Egernia stokesii	1.5	11.5+	61.7+	21.4	28.8	35.6	46.9	17.4	149.7+	13.2	8.3	74.0+
Egernia striolata	18.0+	4.1+	9.7	29.7	19.3	11.1+	45.6+	2.7.0+	24.3	12.0+	12.4	28.7
Egernia whitii	6.1	11.9+	34.4+	11.5+	26.7+	43.6+	12.4	14.4+	50.0+	11.3+	44.3+	88.5+
Eulamprus heatwolei	33.6	50.0	64.9	29.3	46.2	61.2	52.6	57.5	63.1	21.2	31.5	42.6

Eulamprus kosciuskoi	54.5	71.4	82.7	48.0	65.6	77.0	76.2	79.6	82.6	38.1	50.2	60.7
Eulamprus leuraensis	70.6	97.0	99.9	62.1	97.3	99.9	90.4	99.9	100.0	27.2	63.8	79.5
Eulamprus quoyii	21.3	27.6	32.6	17.8	24.5	29.9	32.1	30.4	28.3	12.4	16.2	20.0
Eulamprus tympanum	34.4	56.8	74.8	29.1	49.5	67.1	49.5	62.2	74.0	21.0	36.7	51.4
Lampropholis delicata	23.1	37.4	50.1	30.7	44.9	58.2	44.5	42.6	42.1	12.3	18.5	25.5
Lissolepis coventryi	25.6+	66.2+	106.9+	27.5+	45.0+	58.7+	25.5+	79.1+	135.9+	37.2+	76.6+	119.6+
Varanus varius	19.0+	30.1+	51.0+	7.3	4.8	2.1	2.8	11.1+	32.2+	29.6+	78.9+	127.8+

Table S2: Percentage overlap between current and future climatically suitable habitat for 17 Australian lizard species under four contrasting but equally plausible climate scenarios: hot/wet; warm/dry; hot/similar precipitation; and warm/ wet scenarios by 2030, 2050 and 2070. Habitat suitability was modelled at 1 km x 1 km resolution using Maxent.

Climate change scenario	**Hot/wet**			**Warm/dry**			**Hot/similar precipitation**			**Warm/wet**		
Species/ Time	**2030**	**2050**	**2070**	**2030**	**2050**	**2070**	**2030**	**2050**	**2070**	**2030**	**2050**	**2070**
Amphibolurus muricatus	79.9	68.4	58.0	75.6	64.6	54.3	60.1	60.9	60.3	86.3	78.6	71.0
Ctenotus taeniolatus	76.5	71.0	63.4	84.8	81.0	75.9	54.4	71.2	83.1	85.6	89.8	88.0
Cyclodomorphus gerrardii	75.9	65.5	57.4	71.9	62.2	51.5	67.1	69.3	71.3	94.9	92.6	87.3
Egernia cunninghami	68.3	57.6	48.2	62.4	54.1	47.4	36.6	52.3	67.8	68.9	68.1	68.1
Egernia frerei	60.6	47.3	35.5	54.4	38.4	26.6	54.0	51.6	48.7	91.3	95.8	92.2
Egernia kingii	67.1	56.2	45.7	70.2	54.3	42.0	66.5	65.2	64.1	92.5	94.5	93.9
Egernia stokesii	87.1	87.2	85.6	75.4	66.0	57.6	51.1	65.3	85.4	81.6	80.9	81.5
Egernia striolata	94.2	88.8	77.4	68.6	75.0	83.2	99.9	83.6	62.5	98.3	80.0	64.0
Egernia whitii	91.2	93.7	93.7	96.3	95.8	95.1	85.0	92.2	93.7	96.5	96.6	96.3
Eulamprus heatwolei	66.3	49.7	34.7	70.3	53.3	38.2	47.4	42.2	36.5	78.0	67.7	56.3
Eulamprus kosciuskoi	45.5	28.6	17.3	25.0	34.4	23.0	23.8	20.4	17.4	61.9	49.8	39.3
Eulamprus leuraensis	30.0	29.8	0.0	37.0	2.6	0.1	9.6	0.1	0.0	63.6	25.4	6.3
Eulamprus quoyii	78.7	72.0	67.4	81.8	75.5	70.1	67.9	69.6	71.7	87.0	83.5	80.0

Eulamprus tympanum	65.6	43.2	25.2	70.8	50.5	32.9	50.5	37.8	26.0	78.5	62.8	47.7
Lampropholis delicata	76.7	62.4	49.7	69.3	55.0	41.6	55.4	57.2	57.7	87.3	81.2	74.1
Lissolepis coventryi	98.9	99.1	98.7	99.5	98.5	97.4	98.9	99.7	99.9	99.1	98.7	98.1
Varanus varius	95.8	92.3	87.2	85.5	81.6	77.0	90.9	89.4	86.2	99.9	98.4	94.9

Table S3: Percentage change in climatically suitable habitat within Protected Areas for 17 Australian lizard species under four contrasting but equally plausible climate scenarios: hot/wet; warm/dry; hot/similar precipitation; and warm/ wet scenarios by 2030, 2050 and 2070. Habitat suitability was modelled at 1 km x 1 km resolution using Maxent. Figures with "+" indicate gains in suitable habitat.

Climate change scenario	**Hot/wet**			**Warm/dry**			**Hot/similar precipitation**			**Warm/wet**		
Species/ Time	**2030**	**2050**	**2070**	**2030**	**2050**	**2070**	**2030**	**2050**	**2070**	**2030**	**2050**	**2070**
Amphibolurus muricatus	7.9	16.1	25.2	10.5	18.4	26.7	19.4	20.2	22.6	5.1	84.9	12.5
Ctenotus taeniolatus	19.5	21.7	24.4	6.9	4.4	3.1	43.5	21.5	1.8	6.4	6.0	15.0
Cyclodomorphus gerrardii	21.4	27.7	35.9	20.9	29.9	40.5	32.5	27.1	20.7	0.4	15.9+	33.6+
Egernia cunninghami	25.0	29.1	33.2	22.9	27.1	32.9	54.7	29.2	9.0	20.9	18.6	16.0
Egernia frerei	30.5	43.9	56.7	36.5	54.2	68.3	39.1	42.2	45.6	0.5+	7.1+	9.3+
Egernia kingii	32.2	41.7	49.2	24.2	38.2	50.7	34.3	33.8	33.1	7.0	2.8	2.4+
Egernia stokesii	0.8	0.4	100+	3.5	3.8	3.2	44.8	21.9	299.7+	21.0	2.8	284.8
Egernia striolata	38.9+	30.8+	23.3+	31.7	22.1	43.4+	69.3+	38.7+	15.6+	18.3+	6.4+	3.5
Egernia whitii	13.7	7.3	1.7+	2.3	4.7+	13.6+	25.4	10.4	9.7+	1.4+	19.8+	42.3+
Eulamprus heatwolei	28.0	41.5	54.7	22.5	36.7	50.6	45.5	48.4	53.1	16.8	24.5	33.8
Eulamprus kosciuskoi	43.4	60.4	74.0	36.9	53.8	66.6	70.5	72.9	75.6	29.0	39.4	49.0
Eulamprus leuraensis	60.6	94.5	99.9	59.0	95.2	99.8	88.1	99.8	100.0	35.6	67.0	73.8
Eulamprus quoyii	10.6	16.6	21.3	10.3	15.2	18.9	18.9	17.9	17.4	7.7	10.2	12.6

Eulamprus tympanum	26.1	43.3	59.7	22.6	38.8	53.2	45.8	53.5	61.8	12.2	21.5	31.3
Lampropholis delicata	12.3	22.3	34.0	18.2	29.4	42.4	34.1	30.0	28.5	6.8	8.4	12.4
Lissolepis coventryi	20.7+	43.1+	68.1+	18.4+	28.5+	35.4+	17.9+	48.1+	81.1+	26.5+	50.9+	82.1+
Varanus varius	13.6+	28.4+	43+	0.4	10.1	19.4	0.7+	20.7+	39.3+	21.2+	50.3	73.2

Table S4: Sensitivity traits for 17 Australian lizard species. Ctmax/median temp represents physiological thermal tolerance, calculated as the ratio of critical maximum temperature (CT_{max}) to the median temperature across the species' range. Geographic range size is the number (N) of 100 x 100 km grid cells that have occurrence records: Large is N ≥50; Moderate is 25 ≤ N < 50; Small is N < 25. Habitat requirements: Specialists are species that are restricted to only one habitat type; Generalists occur in more than three habitat types. Dietary requirements: Specialists are species that restricted to a particular food item; Generalists exploits a wide variety of food items. Climate zone: Multiregional species occur within more than three climate regions; Moderate occur within two to three climate regions; Narrow occur in only one climate region.

SPECIES	**Ctmax/median temp**	**Geographic range size**	**Habitat requirement**	**Dietary requirement**	**Climatic zone**	**Reproduction rate**	**Reproduction mode**
Amphibolurus muricatus	1.54	Large (99)	Specialist	Generalist	Multiregion	Annual	Oviparous
Ctenotus taeniolatus	1.40	Moderate (42)	Specialist	Generalist	Multiregion	Annual	Viviparous
Cyclodomorphus gerrardii	1.51	Large (53)	Generalist	Specialist	Moderate	Annual	Viviparous
Egernia cunninghami	1.53	Large (50)	Generalist	Generalist	Moderate	Annual	Viviparous
Egernia frerei	1.40	Moderate (26)	Specialist	Generalist	Multiregion	Annual	Viviparous
Egernia kingii	1.22	Large (152)	Generalist	Generalist	Multiregion	Annual	Viviparous
Egernia stokesii	1.15	Moderate (36)	Generalist	Generalist	Multiregion	Annual	Viviparous
Egernia striolata	1.34	Large 167)	Generalist	Generalist	Multiregion	Annual	Viviparous

Egernia whitii	1.60	Small (20)	Generalist	Generalist	Multiregion	Annual	Viviparous
Eulamprus heatwolei	1.58	Moderate (43)	Generalist	Generalist	Multiregion	Annual	Viviparous
Eulamprus kosciuskoi	1.78	Small (8)	Specialist	Generalist	Moderate	Annual	Viviparous
Eulamprus leuraensis	1.62	Small (2)	Specialist	Generalist	very Narrow	Annual	Viviparous
Eulamprus quoyii	1.44	Large (250)	Specialist	Generalist	Multiregion	Biannual	Viviparous
Eulamprus tympanum	1.62	Small (22)	Generalist	Generalist	Moderate	Annual	Viviparous
Lampropholis delicata	1.39	Large (127)	Generalist	Generalist	Multiregion	Annual	Viviparous
Lissolepis coventryi	1.58	Small (13)	Specialist	Generalist	Narrow	Annual	Viviparous
Varanus varius	1.52	Large (53)	Generalist	Generalist	Multiregion	Annual	Oviparous

Table S4: Continued

Species	**Mean Clutch size**	**Offspring survival**	**Maturation length (years)**	**Life span (years)**	**References**
Amphibolurus muricatus	6	<50%	1 to 2	> 10	Greer [1,]Light, et al. [2]
Ctenotus taeniolatus	10	<50%	1 to 2	4 to 6	Greer [1,]Chapple [3,]Greer [4]
Cyclodomorphus gerrardii	20	<50%	2	> 10	Greer [1,]Chapple [3,]Greer [4]

Egernia cunninghami	6	<50%	5	> 10	Greer [1],Chapple [3],Greer [4],Barwick and Bryant [5],Barwick [6],Stow, et al. [7],Fraser [8]
Egernia frerei	7	<50%	4	> 10	Chapple [3],Greer [4],O'Connor and Moritz [9]
Egernia kingii	6	<50%	3	> 10	Greer [1],Chapple [3],Greer [4],Arena and Wooller [10]
Egernia stokesii	5	<50%	5	> 10	Greer [1],Light, et al. [2],Chapple [3],Greer [4]
Egernia striolata	3	<50%	2 to 3	8 to 10	Greer [1],Chapple [3],Greer [4]
Egernia whitii	3	<50%	2 to 3	>8.5	Greer [1],Chapple [3],Greer [4]
Eulamprus heatwolei	4	<50%	2 to 3	> 10	Greer [1],Chapple [3],Greer [4]
Eulamprus kosciuskoi	3	<50%	2 to 3	> 10	Greer [1],Chapple [3],Greer [4]
Eulamprus leuraensis	3	<50%	3	> 10	Greer [1],Chapple [3],Greer [4],O'Connor and Moritz [9],Dubey, et al. [11]
Eulamprus quoyii	4	<50%	2 to 3	> 10	Greer [1],Chapple [3],Greer [4],O'Connor and Moritz [9]
Eulamprus tympanum	3	<50%	2 to 3	> 10	Greer [1],Chapple [3],Greer [4],O'Connor and Moritz [9],Doughty and Shine [12]
Lampropholis delicata	4	<50%	2	8 to 10	Greer [1],Greer [4]
Lissolepis coventryi	3	<50%	2	> 8	Greer [1],Chapple [3],Greer [4],Clemann, et al. [13]
Varanus varius	9	<50%	3 to 4	> 10	Greer [1],Light, et al. [2]

Table S5: Adaptive capacity traits for 17 Australian lizard species sourced from the published literature. Body-size was used as proxy for dispersal capacity. In general, species with relatively large body size are presumed to have higher dispersal rate. Also, species with higher neutral genetic diversity are presumed to have relatively higher adaptive potential.

SPECIES	**Body-size (SVL in mm)**	**Genetic diversity (mean He)**	**Habitat fragmentation**	**Microhabitat buffer**	**References**
Amphibolurus muricatus	39-125	0.856 (0.232 - 0.964)	>50%	OR,OL	Greer [1,]Michael, et al. [14,]Schwartz, et al. [15,]Pepper, et al. [16,]Hitchen, et al. [17,]Hitchen, et al. [18]
Ctenotus taeniolatus	80	0.8138 (0.649 - 0.887)	>50%	UL,UR	Michael, et al. [14,]Cogger [19,]Harradine, et al. [20,]Dennison, et al. [21]
Cyclodomorphus gerrardii	255	0.817 (0.54 - 0.95)	>50%	UL,UR	Cogger [19,]Koumoundouros, et al. [22] Fuller et al. 2005
Egernia cunninghami	230-250	0.862 (0.516 - 0.955)	>50%	UR,UL	Barwick [6,]Stow, et al. [7,]Michael, et al. [14,]Langkilde, et al. [23]
Egernia frerei	180-200	0.66	10%-50%	UL	Chapple [3,]Cogger [19,]Fuller, et al. [24]
Egernia kingii	200-230	0.798	>50%	UR,BW	Chapple [3,]Cogger [19]
Egernia stokesii	155-190	0.68 (0.1 - 0.9)	>50%	UR,BW, TH	Gardner, et al. [25,]Gardner, et al. [26]
Egernia striolata	100-199	0.875 (0.763-0.915)	>50%	UR,UL	Cogger [19,]Michael, et al. [27,]Duckett, et al. [28]
Egernia whitii	75-110	0.9145 (0.874 - 0.933)	>50%	UR	Chapple [3,]Michael, et al. [14,]Cogger [19,]Chapple [29,]Chapple and Keogh [30]

Eulamprus heatwolei	80	0.68 (0.314 - 0.909)	>50%	UR	Cogger [19], Langkilde, et al. [23], Morrison, et al. [31]
Eulamprus kosciuskoi	80	0.643 (0.271 - 0.898)	>50%	UR,BW	Cogger [19], Scott, et al. [32]
Eulamprus leuraensis	80 - 85	0.7 (0.32 - 0.81)	>50%	DGT	Cogger [19], Dubey and Shine [33]
Eulamprus quoyii	90 - 118	0.674	10%-50%	UR,UL	Michael, et al. [14], Cogger [19], Noble, et al. [34]
Eulamprus tympanum	80-96	0.674	>50%	UR,UL	Cogger [19], Langkilde, et al. [23], Blomberg and Shine [35]
Lampropholis delicata	34-46	0.701 (0.114 - 0.959)	>50%	LL,UB,UR	Michael, et al. [14], Cogger [19], Chapple and Thompson [36]
Lissolepis coventryi	100-130	0.668 (0.216 - 0.817)	>50%	UL,BW,UR	Greer [1], Clemann, et al. [13]
Varanus varius	200-2000	0.934 (0.882 - 0.963)	>50%	LL,OR	Michael, et al. [14], Guarino [37], Weavers [38]

Table S6: Unweighted (I) and weighted (II) vulnerability scores for 17 Australian lizards under projected climate change by 2030, 2050 and 2070. Vulnerability was assessed using four contrasting future climate scenarios that are equally plausible: hot/wet; warm/dry; hot/similar precipitation; and warm/ wet scenarios. Analysis was done using all three elements of vulnerability (ESA): exposure, sensitivity and adaptive capacity and using exposure and sensitivity only (ES). Score > 0.67 is high, from 0.33 to 0.67 is moderate and < 0.33 is low.

Hot/wet	**2030**		**2050**		**2070**		**2030**		**2050**		**2070**	
Species	**ES I**	**ESA I**	**ES I**	**ESA I**	**ES I**	**ESA I**	**ES II**	**ESA II**	**ES II**	**ESA II**	**ES II**	**ESA II**
Amphibolurus muricatus	0.51	0.48	0.56	0.52	0.57	0.52	0.42	0.44	0.46	0.47	0.46	0.47
Ctenotus taeniolatus	0.58	0.5	0.58	0.50	0.58	0.50	0.50	0.48	0.50	0.48	0.50	0.48
Cyclodomorphus gerrardii	0.55	0.42	0.55	0.42	0.55	0.42	0.43	0.34	0.43	0.34	0.43	0.34
Egernia cunninghami	0.55	0.42	0.55	0.42	0.61	0.46	0.41	0.33	0.41	0.33	0.45	0.36
Egernia frerei	0.58	0.47	0.69	0.54	0.75	0.58	0.50	0.47	0.64	0.57	0.66	0.58
Egernia kingii	0.55	0.45	0.55	0.45	0.66	0.52	0.44	0.40	0.44	0.40	0.57	0.48
Egernia stokesii	0.51	0.45	0.45	0.41	0.51	0.45	0.41	0.43	0.37	0.40	0.41	0.43
Egernia striolata	0.49	0.41	0.44	0.38	0.44	0.38	0.38	0.36	0.34	0.34	0.34	0.34
Egernia whitii	0.57	0.49	0.45	0.41	0.45	0.41	0.45	0.45	0.36	0.39	0.36	0.39
Eulamprus heatwolei	0.55	0.51	0.66	0.58	0.72	0.62	0.41	0.47	0.56	0.57	0.58	0.58
Eulamprus kosciuskoi	0.72	0.62	0.78	0.66	0.78	0.66	0.67	0.64	0.71	0.67	0.69	0.66
Eulamprus leuraensis	0.79	0.67	0.79	0.67	0.79	0.67	0.74	0.69	0.74	0.69	0.72	0.68

Eulamprus quoyii	0.58	0.5	0.58	0.50	0.58	0.50	0.48	0.50	0.48	0.50	0.48	0.50
Eulamprus tympanum	0.58	0.53	0.69	0.60	0.75	0.64	0.47	0.51	0.62	0.60	0.64	0.62
Lampropholis delicata	0.57	0.52	0.57	0.52	0.62	0.55	0.43	0.48	0.43	0.48	0.51	0.54
Lissolepis coventryi	0.53	0.46	0.53	0.46	0.53	0.46	0.48	0.48	0.48	0.48	0.48	0.48
Varanus varius	0.47	0.4	0.47	0.40	0.47	0.40	0.35	0.29	0.35	0.29	0.35	0.29

Table S6: Continues

Warm/dry	**2030**		**2050**		**2070**		**2030**		**2050**		**2070**	
Species	**ES I**	**ESA I**	**ES I**	**ESA I**	**ES I**	**ESA I**	**ES II**	**ESA II**	**ES II**	**ESA II**	**ES II**	**ESA II**
Amphibolurus muricatus	0.57	0.52	0.57	0.52	0.57	0.52	0.46	0.47	0.46	0.47	0.46	0.47
Ctenotus taeniolatus	0.53	0.46	0.53	0.46	0.53	0.46	0.46	0.45	0.46	0.45	0.46	0.45
Cyclodomorphus gerrardii	0.55	0.42	0.55	0.42	0.55	0.42	0.43	0.34	0.43	0.34	0.43	0.34
Egernia cunninghami	0.55	0.42	0.55	0.42	0.66	0.50	0.41	0.33	0.41	0.33	0.55	0.42
Egernia frerei	0.58	0.47	0.64	0.51	0.75	0.58	0.50	0.47	0.56	0.51	0.69	0.60
Egernia kingii	0.55	0.45	0.55	0.45	0.72	0.56	0.44	0.40	0.44	0.40	0.63	0.52
Egernia stokesii	0.51	0.45	0.51	0.45	0.51	0.45	0.41	0.43	0.41	0.43	0.41	0.43
Egernia striolata	0.49	0.41	0.55	0.45	0.44	0.38	0.38	0.36	0.42	0.39	0.34	0.34
Egernia whitii	0.45	0.41	0.45	0.41	0.45	0.41	0.36	0.39	0.36	0.39	0.36	0.39

Eulamprus heatwolei	0.55	0.51	0.55	0.51	0.72	0.62	0.41	0.47	0.41	0.47	0.60	0.59
Eulamprus kosciuskoi	0.67	0.58	0.78	0.66	0.78	0.66	0.59	0.59	0.71	0.67	0.71	0.67
Eulamprus leuraensis	0.79	0.67	0.85	0.70	0.85	0.70	0.74	0.69	0.85	0.76	0.85	0.76
Eulamprus quoyii	0.58	0.50	0.58	0.50	0.58	0.50	0.48	0.50	0.48	0.50	0.48	0.50
Eulamprus tympanum	0.58	0.53	0.58	0.53	0.75	0.64	0.47	0.51	0.47	0.51	0.62	0.60
Lampropholis delicata	0.57	0.52	0.57	0.52	0.68	0.59	0.43	0.48	0.43	0.48	0.53	0.55
Lissolepis coventryi	0.59	0.50	0.53	0.46	0.53	0.46	0.52	0.51	0.48	0.48	0.48	0.48
Varanus varius	0.47	0.40	0.53	0.43	0.53	0.43	0.35	0.29	0.39	0.32	0.39	0.32

Table S6: Continues

Hot/similar precipitation	**2030**		**2050**		**2070**		**2030**		**2050**		**2070**	
Species	**ES I**	**ESA I**	**ES I**	**ESA I**	**ES I**	**ESA I**	**ES II**	**ESA II**	**ES II**	**ESA II**	**ES II**	**ESA II**
Amphibolurus muricatus	0.57	0.52	0.57	0.52	0.57	0.52	0.46	0.47	0.46	0.47	0.46	0.47
Ctenotus taeniolatus	0.58	0.50	0.58	0.50	0.47	0.42	0.50	0.48	0.50	0.48	0.41	0.42
Cyclodomorphus gerrardii	0.55	0.42	0.55	0.42	0.55	0.42	0.43	0.34	0.43	0.34	0.43	0.34
Egernia cunninghami	0.72	0.53	0.55	0.42	0.49	0.39	0.60	0.45	0.41	0.33	0.37	0.30
Egernia frerei	0.58	0.47	0.58	0.47	0.69	0.54	0.50	0.47	0.50	0.47	0.64	0.57
Egernia kingii	0.55	0.45	0.55	0.45	0.55	0.45	0.44	0.40	0.44	0.40	0.44	0.40

Egernia stokesii	0.57	0.49	0.57	0.49	0.45	0.41	0.45	0.46	0.45	0.46	0.37	0.40
Egernia striolata	0.44	0.38	0.44	0.38	0.49	0.41	0.34	0.34	0.34	0.34	0.38	0.36
Egernia whitii	0.57	0.49	0.51	0.45	0.45	0.41	0.45	0.45	0.41	0.42	0.36	0.39
Eulamprus heatwolei	0.66	0.58	0.66	0.58	0.72	0.62	0.56	0.57	0.56	0.57	0.60	0.59
Eulamprus kosciuskoi	0.78	0.66	0.78	0.66	0.78	0.66	0.71	0.67	0.71	0.67	0.71	0.67
Eulamprus leuraensis	0.85	0.70	0.85	0.70	0.85	0.70	0.85	0.76	0.85	0.76	0.85	0.76
Eulamprus quoyii	0.58	0.50	0.58	0.50	0.58	0.50	0.48	0.50	0.48	0.50	0.48	0.50
Eulamprus tympanum	0.58	0.53	0.75	0.64	0.75	0.64	0.47	0.51	0.66	0.63	0.66	0.63
Lampropholis delicata	0.57	0.52	0.57	0.52	0.57	0.52	0.43	0.48	0.43	0.48	0.43	0.48
Lissolepis coventryi	0.53	0.46	0.53	0.46	0.53	0.46	0.48	0.48	0.48	0.48	0.48	0.48
Varanus varius	0.47	0.40	0.47	0.40	0.47	0.40	0.35	0.29	0.35	0.29	0.35	0.29

Table S6: Continues

Warm/wet	**2030**		**2050**		**2070**		**2030**		**2050**		**2070**	
Species	**ES I**	**ESA I**	**ES I**	**ESA I**	**ES I**	**ESA I**	**ES II**	**ESA II**	**ES II**	**ESA II**	**ES II**	**ESA II**
Amphibolurus muricatus	0.51	0.48	0.62	0.55	0.57	0.52	0.42	0.44	0.50	0.50	0.46	0.47
Ctenotus taeniolatus	0.47	0.42	0.47	0.42	0.57	0.49	0.41	0.42	0.41	0.42	0.50	0.48
Cyclodomorphus gerrardii	0.44	0.35	0.44	0.35	0.45	0.36	0.35	0.29	0.35	0.29	0.35	0.29

Egernia cunninghami	0.55	0.42	0.55	0.42	0.55	0.42	0.41	0.33	0.41	0.33	0.41	0.33
Egernia frerei	0.47	0.40	0.47	0.40	0.48	0.41	0.41	0.42	0.41	0.42	0.41	0.42
Egernia kingii	0.44	0.38	0.44	0.38	0.44	0.38	0.36	0.34	0.36	0.34	0.36	0.34
Egernia stokesii	0.57	0.49	0.45	0.41	0.44	0.40	0.45	0.46	0.37	0.40	0.37	0.40
Egernia striolata	0.44	0.38	0.49	0.41	0.49	0.41	0.34	0.34	0.38	0.36	0.38	0.36
Egernia whitii	0.45	0.41	0.45	0.41	0.42	0.39	0.36	0.39	0.36	0.39	0.36	0.39
Eulamprus heatwolei	0.55	0.51	0.55	0.51	0.54	0.50	0.41	0.47	0.41	0.47	0.41	0.47
Eulamprus kosciuskoi	0.61	0.55	0.72	0.62	0.72	0.62	0.53	0.55	0.67	0.64	0.67	0.64
Eulamprus leuraensis	0.63	0.56	0.79	0.67	0.85	0.70	0.56	0.57	0.74	0.69	0.85	0.76
Eulamprus quoyii	0.53	0.46	0.58	0.50	0.58	0.50	0.44	0.47	0.48	0.50	0.48	0.50
Eulamprus tympanum	0.58	0.53	0.58	0.53	0.68	0.59	0.47	0.51	0.47	0.51	0.62	0.60
Lampropholis delicata	0.51	0.48	0.51	0.48	0.57	0.52	0.39	0.45	0.39	0.45	0.43	0.48
Lissolepis coventryi	0.53	0.46	0.53	0.46	0.53	0.46	0.48	0.48	0.48	0.48	0.48	0.48
Varanus varius	0.47	0.40	0.53	0.43	0.58	0.47	0.35	0.29	0.39	0.32	0.44	0.35

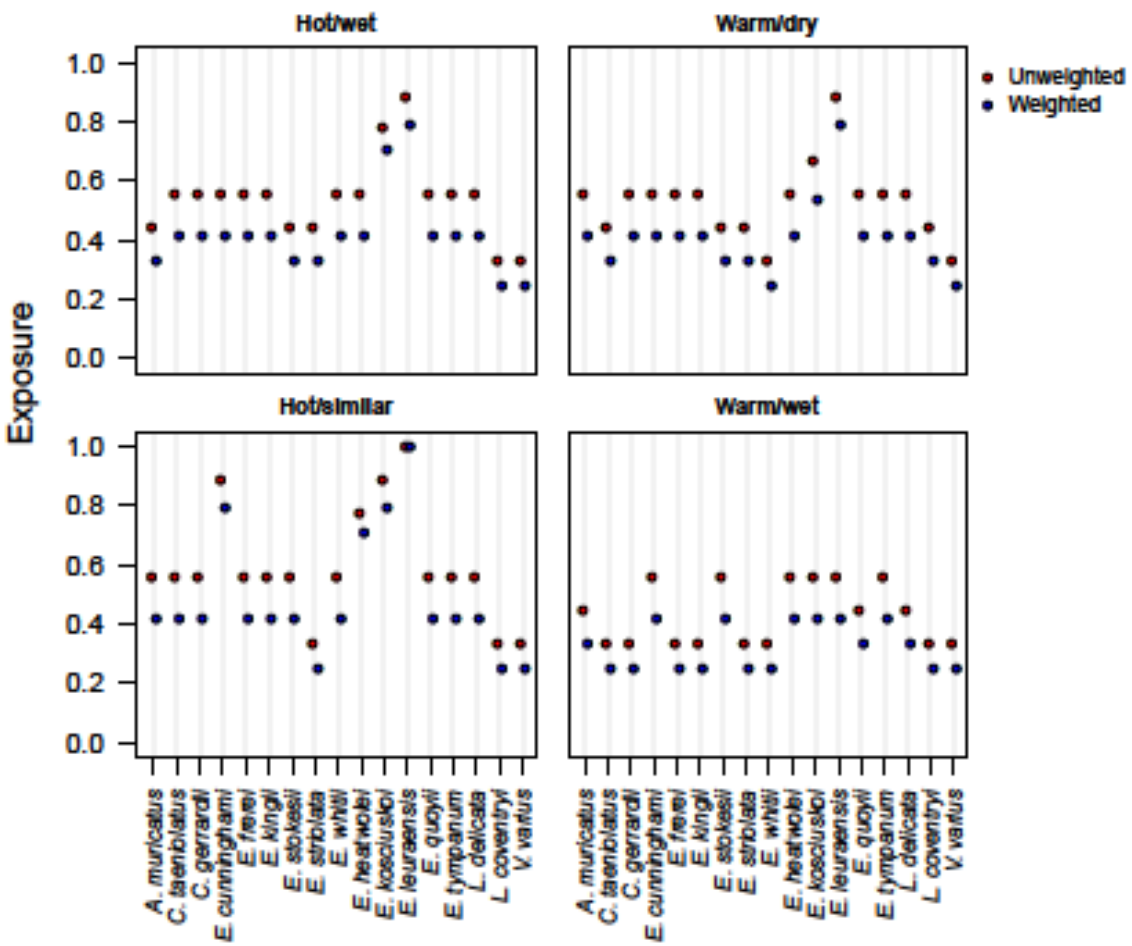

Figure S1: Weighted and unweighted exposure scores for 17 Australian lizards under projected climate change by 2030**.** Exposure was assessed using four contrasting future climate scenarios that are equally plausible: hot/wet; warm/dry; hot/similar precipitation; and warm/ wet scenarios. Score > 0.67 is high, from 0.33 to 0.67 is moderate and < 0.33 is low.

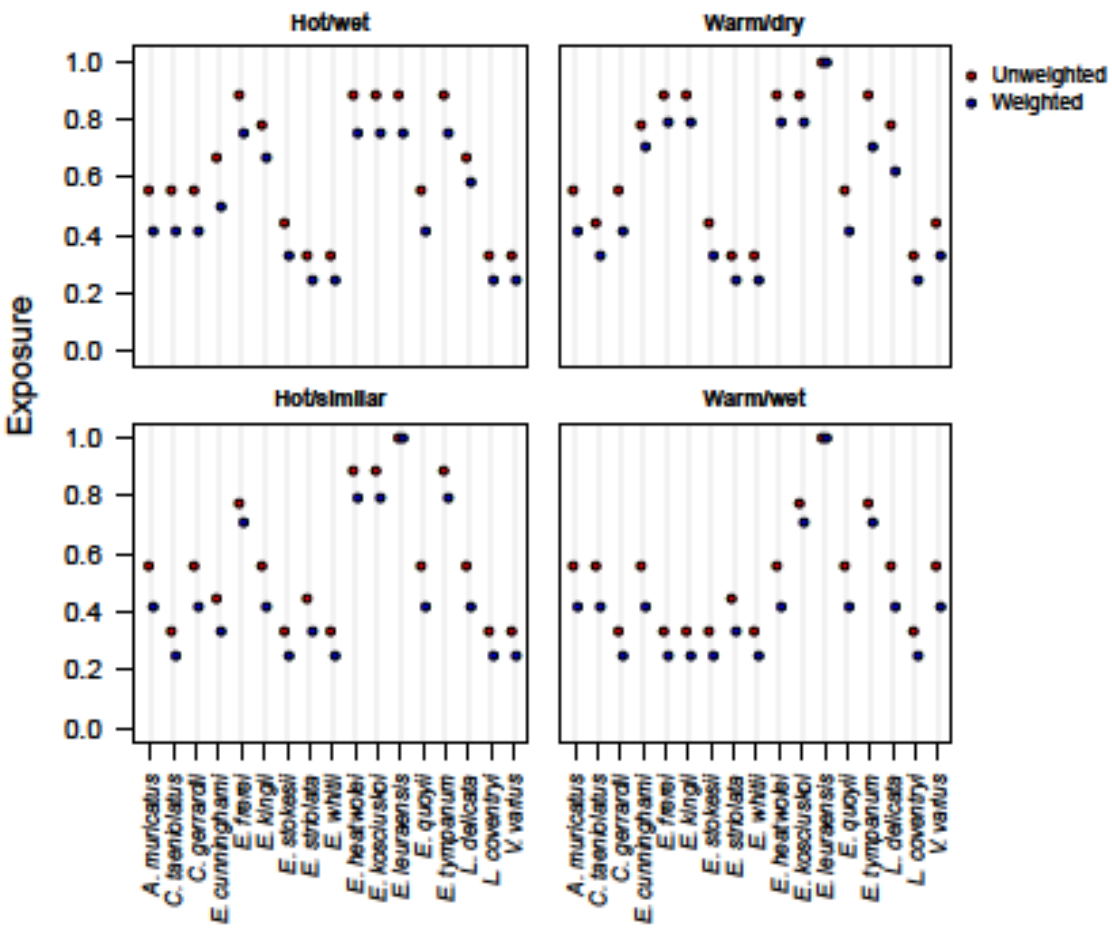

Figure S2: Weighted and unweighted exposure scores for 17 Australian lizards under projected climate change by 2070**.** Exposure was assessed using four contrasting future climate scenarios that are equally plausible: hot/wet; warm/dry; hot/similar precipitation; and warm/ wet scenarios. Score > 0.67 is high, from 0.33 to 0.67 is moderate and < 0.33 is low.

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CHAPTER SIX

Discussion

Introduction

Biodiversity faces continuing threats from climate change, with reptiles considered particularly at risk because their life-history is inextricably linked to climate (Mitchell & Janzen, 2010; Urban *et al.*, 2014). Some reptile populations have already experienced climate-induced declines and extinctions (Parmesan & Yohe, 2003; Sinervo *et al.*, 2010), and several others are living under conditions close to their thermal tolerance (Huey *et al.*, 2009). As temperatures continue to rise throughout the century, more reptile species, particularly those in tropical regions, will be vulnerable to extinction (Carvalho *et al.*, 2010; Sinervo *et al.*, 2010). To minimise the effects of climate change on reptiles, conservation planners and practitioners must adapt their management actions to increase the adaptive capacity of species (Brooke, 2008; Kearney *et al.*, 2010; Groves *et al.*, 2012). To do this effectively requires a better capacity to predict the response of species to climate change (Kearney *et al.*, 2010).

Reptiles may respond to climate change by tracking their thermal niches across landscapes, or via adaptation (Hoffmann & Sgro, 2011; Sgro *et al.*, 2011; Urban *et al.*, 2014). It remains unclear, however, whether their dispersal rate is adequate to track the pace of climate change. Also unclear, is whether reptiles have sufficient genetic variation to enable adaptation to occur. An additional consideration is that the magnitude of climate change will vary spatially and temporally, with species responding idiosyncratically to these changes (Cabrelli & Hughes,

2015). Hence, assessing the potential impacts on multiple species in multiple regions is imperative to obtain deeper insights into species-specific responses, and identify the characteristics of those species most vulnerable to climate change. This approach can provide the requisite information for conservation planners and practitioners to prioritize conservation targets and adapt their management plans accordingly.

In this thesis, I highlighted the importance of combining output of species distribution models (SDMs) with species' dispersal rate and landscape connectivity to inform conservation planning under climate change (Chapter 2). I then combined a genetic estimate of dispersal, and landscape connectivity, with Maxent to assess the impacts of climate change on the distribution of Cunningham's skink (*Egernia cunninghami*) (Chapter 3). I also characterized the spatial patterns of genetic variation and signatures of divergent selection in populations at four localities, using over 4,200 SNPs (Chapter 4). Finally, I assessed the vulnerability of 17 lizards species, distributed along the Great Dividing Range of Australia, to climate change using a framework that incorporated all the three elements of vulnerability: exposure, sensitivity and adaptive capacity (Chapter 5).

Here, I present a summary of the main findings and discuss their implications for the conservation of Australian lizards, in particular, and reptiles in general. I then discuss the strengths and limitations of my research methodology and make recommendations for improvement and future research.

Summary of main findings

Good forecasts of the responses of species to climate change are important for effective conservation planning. In Chapter 2, I reviewed species distribution and landscape connectivity models and their applications, as well as approaches for gathering dispersal data. Relatively few studies have incorporated realistic estimates of dispersal into species distribution modelling, and none of these have considered the effect of landscape connectivity on the movement of organisms. Landscape connectivity models (LCMs) have provided useful insights into the connectivity of landscapes and likely corridors that can facilitate the exchange of individuals and genes between geographically-isolated populations, and the potential colonization of suitable habitats. SDMs and LCMs provide complementary information to guide spatial conservation planning, but their outputs have rarely been combined with dispersal data. Chapter 2, thus, highlighted the importance of combining outputs of SDMs and LCMs with dispersal data. This intuitively provides deeper insights into the potential impacts of climate change on the availability of suitable habitat for the target species, and offers more spatially explicit information to guide conservation planning.

In Chapter 3, I combined dispersal rate, landscape connectivity and Maxent to assess the impacts of climate change on Cunningham's skinks (*Egernia cunninghami*) and the capacity of this species to track its climate niche across 12 future climate scenarios. Using Maxent, climatically suitable habitat for the skink was projected to decline 22% to 63% by 2070, depending upon the climate scenario. Similar results were found when modeling at two spatial resolutions - 1 km × 1 km and 250 m × 250 m. My findings were consistent with previous studies on reptiles in Australia and Europe. For example, climatically suitable habitats of most Australian elapid

snakes and skinks were projected to contract by 2050 (Cabrelli *et al.*, 2014; Cabrelli & Hughes, 2015). Similarly, ~ 50% of reptiles in the Iberian Peninsula were projected to experience contractions in their suitable habitat (Carvalho *et al.*, 2010), while 35% of reptiles in continental Europe were projected to lose substantial portions of their ranges by the end of the century (Araújo *et al.*, 2006).

Using the genetic isolation-by-distance model, I estimated the annual dispersal rate of Cunningham's skink to be 8.6 km per decade. Combining the output of Maxent with the dispersal rate of the species and permeability of the landscape matrix, indicated that at least 6.4% of populations of the species would not be unable to track shifts in their climate niche.

Adaptive responses (evolutionary adaptation and phenotypic plasticity) of species to climate change will depend on genetic variation among populations (Sgro *et al.*, 2011). In Chapter 4, I characterized the spatial patterns of genetic variation of Cunningham's skinks and investigated signatures of divergent selection across four localities, spanning 500 km and 4° latitude, using over 4,200 SNPs. The results showed low genetic connectivity and signatures of divergent selection between these populations. The level of genetic partitioning was substantially above the F_{ST} level of 0.35, which is the point at which the spread of advantageous alleles across a species' range is prevented (Lowe & Allendorf, 2010). This indicates historical isolation of lizard populations at our study localities, and supports the finding in Chapter 3 that the natural movement rate of the species is insufficient to keep pace with spatial shifts to its climate niche.

Neutral and putatively adaptive genetic variation yielded contrasting spatial patterns. As far as I am aware, this is the first evidence of a signature of selection among a species within the Great

Dividing Range (GDR). A preliminary evaluation of the environmental correlates of selection showed strong association (Z-score > 4, DIC = 7709, $P < 0.001$) between SNPs under selection and temperature. This indicates that adaptation to climatic differences may have occurred. The influence of climate on the genetic structure of populations across the species' range has been shown in several species (Hand *et al.*, 2016; Sexton *et al.*, 2016). Spatial variation in adaptation to thermal environments has been reported in *Anolis* lizards (Hertz & Huey, 1981; Wang *et al.*, 2013). In North American grey wolves (*Canis lupus*), variation in allele frequencies of several candidate genes for selection, such as *LEPR*, *TYR* and *SLC14A2*, were strongly associated with temperature and precipitation (Schweizer *et al.*, 2015). *LEPR* plays a functional role in cold tolerance and cold adaptation and the SNP tagging *LEPR* was highly associated with the minimum temperature of the coldest month (Schweizer *et al.*, 2015).

Climate change vulnerability assessment (CCVA) has become a major conservation decision support tool, but for many species a lack of data can prevent adaptive capacity being included. In Chapter 5, I used a framework that comprehensively accounts for exposure, sensitivity and adaptive capacity. I applied it in an assessment of 17 lizard species distributed along the GDR in southeastern Australia, to assess their respective vulnerabilities to climate change and to identify traits that are associated with their vulnerability. The data showed that exposure to climate change varied across species, climate trajectories and time horizons, highlighting the importance of conducting CCVAs over multiple future time-scales and climate scenarios. Sensitivity and exposure or adaptive capacity scores were not strongly correlated, suggesting that each element of vulnerability is unique and ought to be included in the analysis. Species' vulnerability rankings were influenced by the omission of adaptive capacity, particularly under

the unweighted scheme in the analysis, and the relative contribution of the various traits included in the framework. This emphasized the need to incorporate adaptive capacity into CCVAs.

Conservation implications of my main findings

A number of strategies have been used to manage biodiversity under climate and other environmental changes. These include the creation of new protected areas and expansion of existing ones, increasing the area and quality of habitats, assisted migration, translocation, and *ex situ* conservation (Adger *et al.*, 2005; Lindenmayer *et al.*, 2010; Hannah, 2011). Recently, however, increasing the connectivity of habitats has gained popularity and political support as the most efficient strategy to enhance the adaptive capacity of species to climate change (Crooks & Sanjayan, 2006; Heller & Zavaleta, 2009; Worboys *et al.*, 2010; Doerr *et al.*, 2011). Conservation biologists, planners and practitioners generally agree that increasing ecological connectivity enhances population persistence by facilitating dispersal, exchange of individuals and genes, and colonization of suitable habitats (Heller & Zavaleta, 2009; Krosby *et al.*, 2010). This may be particularly important in the context of climate change, where species' climate niches are shifting (Chen *et al.*, 2011). Consequently, efforts are being made to create and maintain large-scale connectivity to enable species to track climate-driven range shifts (Krosby *et al.*, 2010; Worboys *et al.*, 2010).

The Great Dividing Range (GDR), which stretches almost 3,500 km along the eastern margins of Australia (Pepper *et al.*, 2014), has been earmarked for the creation of a connectivity corridor. This continental-scale corridor will facilitate range shifts across many taxa from diverse

environments (Worboys & Pulsford, 2011). Indeed species with high dispersal and migratory capacity, such as most birds and large mammals, have been shown to benefit from large-scale connectivity (Minor & Lookingbill, 2010; Sharma *et al.*, 2013; Niculae *et al.*, 2016). However, the main results of my research suggest that large-scale corridors may not be a universal solution for species needing to shift their distributions under climate change.

The strong population genetic structuring for Cunningham's skinks and other lizards found in the GDR (e.g., see Bell & Gonzalez, 2011; Chapple *et al.*, 2011) indicate a general pattern of long-term isolation, predating recent anthropogenic habitat loss. This finding, coupled with the SDM results in Chapter 3 suggest that the dispersal rates of these lizards might be insufficient for them to track their climate niches, irrespective of habitat availability and connectivity. Climatically suitable habitats for 17 lizards distributed across the GDR were projected to contract (Chapter 5) rather than shift to new geographic regions. Consequently, these species might benefit more from increasing the spatial extent and quality of habitats, particularly in the core areas of the range that are projected to retain favourable climates. Species inhabiting areas of the range periphery that will become unsuitable in future will have to adapt to novel conditions if they are to persist. For Cunningham's skink, I found strong genetic differentiation and signatures of divergent selection, which means that the species to some extent might be able to adapt. Management strategies should be aimed at enhancing the species' adaptive capacity or reducing their sensitivity to climate change. Actions such as minimizing external threats like wildfires, predation pressure from feral cats, competition from invasive species and restoration of degraded habitats may be useful in this regard.

The species *Eulamprus leurensis and E. kosciuskoi* identified as highly vulnerable to climate change (Chapter 5) must be prioritized for conservation. Their responses to climate change should be monitored, and the interventions needed to support them must be assessed and carefully selected. Where ample evidence indicates that populations are declining over time, a translocation program might be necessary. Translocation of species to more favourable locations has become a viable solution towards salvaging species from extinction (Hoegh-Guldberg *et al.*, 2008; Vitt *et al.*, 2009; Seddon, 2010). Although the benefits of translocation are theoretically grounded (Lunt *et al.*, 2013), risks may be involved (Seddon *et al.*, 2009; Weeks *et al.*, 2011). The genetic study of Cunningham's skink (Chapter 4) indicates that isolated populations can be strongly structured and might show signatures of selection and adaptation to their local environment. Therefore, to avoid the risk of outbreeding depression that can reduce the fitness of individuals, translocation programs might benefit from genetic studies of the vulnerable species.

Methodological strength and weakness

By combining a realistic estimate of dispersal and landscape connectivity with a correlative SDM, my research adds to the growing body of literature on impacts of climate change on global biodiversity, and extends previous approaches. Moreover, the incorporation of dispersal and adaptive potential into climate change vulnerability assessment is a substantial improvement on previous CCVA frameworks for this taxa. As far as I am aware, my CCVA is the first on reptiles to explicitly account for adaptive capacity. Furthermore, my research is the first to characterize

the spatial patterns of adaptive and neutral genetic variation of a vertebrate species across the Great Dividing Range of Australia. Although the demand for projections of future species distribution has triggered an upsurge in the use of SDMs, few other studies have integrated eco-evolutionary processes to assess the impacts of climate change on reptiles.

Although my research has immediate application and can better inform biodiversity conservation in the face of ongoing climate change, there were some methodological limitations. I discussed these below to inform conservation planners and practitioners about the uncertainties associated with my findings in order for them to make informed decisions.

Uncertainties in climate and species distribution models

Correlative SDMs are frequently used to assess the impacts of climate change on species because, relative to mechanistic models, they require less data, are easy to implement and can be applied to a wide range of organisms simultaneously (Dormann *et al.*, 2012; Meineri *et al.*, 2015; Pacifici *et al.*, 2015). These models provide a useful way of incorporating future conditions into conservation planning (Syphard & Franklin, 2009; Wiens *et al.*, 2009), but the accuracy and reliability of their outputs have been questioned because of uncertainties inherent in both climate models and SDM algorithms (Thuiller *et al.*, 2013). Future projections of climate change by different Global Circulation Models can vary considerably (Beaumont *et al.*, 2008). Similarly, different SDM algorithms can project contrasting changes in future climatically suitable habitat, even when fitted with the same set of variables and when predictive performance is similar (Elith & Leathwick, 2009; Willis & Bhagwat, 2009; Sinclair *et al.*, 2010; Van der Putten *et al.*, 2010; Beaumont *et al.*, 2016). To address these discrepancies, it has been

proposed that several SDMs and climate models should be used simultaneously (i.e., in 'ensembles') (Beaumont *et al.*, 2008; Beaumont *et al.*, 2009; Marmion *et al.*, 2009; Thuiller *et al.*, 2009; Beaumont *et al.*, 2016).

In this research, I applied four different climate models and three parameterizations that capture probable future climate scenarios, but only one SDM, Maxent, was used (Chapters 3 and 5). Although Maxent has been shown to have high predictive performance and is easy to use (Phillips & Dudík, 2008; Phillips *et al.*, 2009), its transferability in space and time may be poor (Rotenberry & Wiens, 2009). Recently, the model has been shown to be less likely than alternate algorithms to predict future habitat completely disjunct from current habitat (Beaumont *et al.*, 2016). Indeed, a completely different vulnerability score is expected when projected suitable habitat for a species lies beyond its current habitat.

The choice of climatic variables used to fit models can also influence the accuracy of projections of future climatically suitable habitat. In this thesis (Chapters 3 and 5), I used a set of five abiotic predictors that have previously been shown to explain the distributions of reptiles in Australia (Cabrelli *et al.*, 2014; Cabrelli & Hughes, 2015) and Europe (Araújo *et al.*, 2006; Carvalho *et al.*, 2010). However, the small set of variables might only explain coarse differences in climatic suitability for species across space (Garcia *et al.*, 2016). Although it is difficult to measure all the variables that determine a species' niche, parameterising a model with a larger set of predictors is more likely to capture most of the niche dimensions that account for observed species distributions (Wiens *et al.*, 2009). The disadvantage in using a large set of predictors, however, is the intricate balance between complexity and tractability. While a smaller set of predictors may not capture all the important niche dimensions that determine the distribution of

species, using a larger set of predictors may lead to model over-fitting. Identifying the relative importance of predictors to minimize the number of parameters remains a challenge since it is unclear if such importance will change under a novel environment in time and space.

Biotic interactions, particularly interspecific competition, have been shown to influence the distribution of species at local (Pearson & Dawson, 2003; Suttle *et al.*, 2007; Van der Putten *et al.*, 2010) and macroecological (Araújo & Luoto, 2007) scales. Species may be absent from some regions with climatically suitable habitat because of strong competition, predation and parasitism. In general, climate change could alter species interactions, such as competition and predation. For example, climate change could expose species to increased competition from warm-adapted species and hence limit their distribution (Huey *et al.*, 2009). Faster population growth of warm-adapted predator species can dramatically reduce prey populations, thereby affecting their migratory capacity (Thuiller *et al.*, 2013). Thus, incorporating biotic interactions into SDMs offers more predictive insight into future species distributions under climate change (Araújo & Luoto, 2007; Van der Putten *et al.*, 2010; Wisz *et al.*, 2013), but this remains a challenge. Incorporating biotic interactions in this study could reduce the amount of suitable habitat available for the study species (Chapter 3), in turn increasing the vulnerability of prey and competitively inferior species (Chapter 5).

Dispersal modeling

Dispersal plays a fundamental role in the distribution of species, as well as the structure and dynamics of populations and ecosystems (Clobert *et al.*, 2009). Under climate change,

colonization of locations projected to become suitable will depend on the dispersal ability of individuals and the permeability of the intervening landscape matrix (Wiens *et al.*, 2009; Travis *et al.*, 2013; Palmer *et al.*, 2014). Here, I used the genetic isolation-by-distance model to estimate the average distance and rate of dispersal of Cunningham's skinks, and combined it with landscape connectivity and the output of Maxent to evaluate the ability of the species to track its climate niche (Chapter 3). Average dispersal distances and rates can be helpful in predicting how species will spread across landscapes. However, the existence of large between-individual variation in dispersal capacity means that the possible outcomes can vary considerably (Palmer *et al.*, 2014).

Colonization of suitable habitat may predominantly be mediated by long-distance dispersal (Trakhtenbrot *et al.*, 2005). Indeed, it has been shown that the probability of successful migration across fragmented landscapes is high among long-distance dispersers (Higgins & Richardson, 1999; Pearson & Dawson, 2005). Using long-distance dispersal values rather than average dispersal distance would increase the likelihood that populations facing unsuitable conditions in the future would be able to shift to suitable areas (Chapter 3). Yet, measuring long-distance dispersal events is difficult and given the lack of information about long-distance dispersal for Cunningham's skinks, I was restricted to using the average dispersal distance.

Landscape connectivity modeling

Resistance analysis is the foundation for landscape connectivity modeling. One of the most critical steps in connectivity modeling is the development of rigorous species-specific landscape

resistance maps or cost surfaces. Assignment of inappropriate resistance values to land cover types and landscape features will lead to misleading conclusions. Yet, assigning appropriate resistance values remains a major challenge. Several approaches have been shown to be effective in identifying factors that influence the movement of individuals and the spatial scale at which these factors operate (Cushman *et al.*, 2010). Landscape genetics has been used to assess the effect of landscape structure and processes on gene flow and population structure by correlating genetic distances to landscape distances reflecting resistance to movement (McRae & Beier, 2007; Luque *et al.*, 2012).

However, gene flow and population differentiation measure dispersal over historic time scales, which may not be the most important parameter in contemporary conservation planning (Cushman *et al.*, 2010; Cushman & Lewis, 2010). Recent advances have resulted in attempts to remove history from usual measures of gene flow by integrating demographic parameters (Landguth *et al.*, 2010; Landguth & Cushman, 2010; Cushman *et al.*, 2012; Landguth & Schwartz, 2014). Indeed, for conservation planning under climate change, movement of organisms may matter more than the movement of genes (Cushman *et al.*, 2010). To directly capture the landscape features that influence movement of organisms in real time, cost surfaces have been parameterized using direct observation, capture-mark-recapture and telemetry data (Zeller *et al.*, 2012). Arguably, this holds the most promise because it allows information on the movement of individuals to be gathered directly in a spatially explicit manner (Cushman *et al.*, 2010). However, such individual-based data are lacking for most species, and difficult and expensive to obtain (Zeller *et al.*, 2012).

In this study, I sought expert opinion to estimate resistance values for Cunningham's skinks because of a lack of empirical information on the movement of this species. Expert-based opinion is a cost-effective approach, easy to apply and often provides a good approximation of the resistance values, although it can be subjective (Zeller *et al.*, 2012). However, the Delphi method has been shown to increase consensus among expert opinions (Hsu & Sandford, 2007). The resistance values provided by the panel of experts consulted for this study were consistent in the first round, so I did not ask them to award resistance values to various landscape features for the second time.

Another methodological limitation associated with connectivity derives from the current land-use/cover map for Australia used to create the landscape resistance map. Given that ecosystems and landscape processes are dynamic and constantly changing, a resistance map based on a static landscape structure is unlikely to reflect future conditions. The present findings may, therefore, be different from what will prevail in future. Accounting for future land-use/cover change or updating the landscape resistance map as more data becomes available could circumvent this problem.

Genetic data and analysis

Sampling

In Chapter 4, I characterized the spatial genetic structure of Cunningham's skinks and assessed evidence of localised adaptation. I analysed over 4,000 SNPs from 94 individuals sampled across four localities. The number of individuals sampled per location and SNPs analysed were

sufficient to address my research questions. However, the sample localities were too few to provide a more complete picture of the spatial pattern of neutral and adaptive genetic variation. Although I expect strong population differentiation across the entire GDR, my results do not highlight how populations located between and beyond the sampled localities will relate to the others. The putatively adaptive SNPs delineated two clusters: Armidale and the rest (Bathurst, Crookwell and Sydney). It will be interesting to know the spatial limit of these clusters as this has conservation implications.

Identification of outlier loci

I used three alternative genome scan methods, (i) BAYESCAN (Foll & Gaggiotti, 2008), (ii) the hierarchical island model implemented in Arlequin v.3.5 (Excoffier & Lischer, 2010) and (iii) LOSITAN (Antao *et al.*, 2008) to identify loci under divergent selection (putatively adaptive loci). These approaches are based on outlier loci, and hence define loci under divergent selection as those with greater than expected levels of divergence among regional groups (Moore *et al.*, 2014), i.e. those with F_{ST} > than the mean among the group and α-values significantly > than 0.

Although these methods have been shown to be effective in detecting loci under selection, they are designed to detect 'hard' selective sweeps that rapidly fix favourable alleles (Pritchard & Di Rienzo, 2010; Pritchard *et al.*, 2010). Consequently, they may fail to detect 'soft' selection sweeps, which involve relatively small changes in allele frequencies at a large number of loci underlying selected traits (Pritchard & Di Rienzo, 2010; Pritchard *et al.*, 2010; Brauer *et al.*,

2016). Mounting evidence suggests that local adaptation to environmental change is largely achieved through simultaneous selection acting on variants at many loci of small effects (i.e., polygenic 'soft' selection sweeps) (Pritchard & Di Rienzo, 2010; Pritchard *et al.*, 2010). 'Soft' selection sweeps can be detected by spatially explicit genotype-environmental association analyses in which the effects of landscape structure and shared population history are accounted for (Brauer *et al.*, 2016).

This study could have benefitted from such analysis, but the few, geographically distant sample locations flag the risk of autocorrelation. This is because geographic distance and any other covariates characterising climatic conditions are bound to be correlated given that we sampled at only four locations with no replications. Because climate at the four locations is different, searching for loci under selection and then finding that these loci also incidentally are associated with climatic differences is circular.

Vulnerability Framework

Climate change vulnerability is a function of exposure, sensitivity and adaptive capacity, but it is unlikely that these elements and their variables will contribute equally to species vulnerability in space and time. Therefore, ranking them in order of their contribution to vulnerability intuitively will lead to a realistic result. However, empirical data on the level of influence of each element, and the variables within elements, on a species' vulnerability are unavailable due to the difficulty in measuring them in the field or controlled experiments. Also, it is unknown whether the contribution of the variables will change with community composition or across

geographic areas. I sought expert opinion in ranking the importance of the variables of exposure, sensitivity and adaptive capacity. As discussed previously, expert opinion can be subjective and may be inaccurate irrespective of the number of experts involved and rigorousness of the survey method.

The lizard species used in the vulnerability assessment had sufficient neutral genetic diversity, but neutral genetic diversity has no direct effect on fitness (Holderegger *et al.*, 2006), and as yet it unclear whether this is a good proxy for adaptive genetic variation (Holderegger *et al.*, 2006). The adaptive capacity scores used in this study are relative, and may not reflect the true measure of the capacity of the study species to adapt to climate change. Recent technological advances in next-generation sequencing show promise in identifying genetic markers for traits that confer adaptation to climate (Manel & Holderegger, 2013). These markers could be useful in forecasting adaptive response of species to climate change (Sunday *et al.*, 2014).

I ranked the dispersal capacity of lizards based on their body size, but this does not reflect the true movement ability of the individual species. In general, lizards have limited dispersal capacity compared to large mammals and most birds, and it is unclear if the localized mobility of lizards is sufficient for them to keep pace with climate change (Araújo *et al.*, 2011; Huntley & Barnard, 2012; Shaw & Etterson, 2012). For instance, genetic characterization of Cunningham's skink showed strong population differentiation that suggests this species is unlikely to track its climate envelope even where habitats are continuous (Ofori *et al.*, 2017). Also, other external stressors that were not accounted for, such as predation, competition, potential disease outbreaks and wildfire could substantially influence dispersal and evolutionary capacity, and hence the vulnerability of the species to climate change (Brook *et al.*, 2008).

Recommendations for future research

The findings and methodological limitations of this thesis underscore fundamental knowledge gaps and research questions that ought to be addressed in order to make predictions more relevant to guide effective conservation management. Given the established theoretical and conceptual basis of species distributions, the question arises why integrated modeling frameworks do not yet account for the fundamental processes and their interplay. A fundamental determinant of a species distribution is the interaction between dispersal, biotic interactions and evolutionary adaptation, and how these vary across landscapes. Yet, there is lack of data on dispersal, evolutionary adaptation and important species interactions for a majority of species (Thuiller *et al.*, 2013). Also lacking is an understanding of the interplay between these, and how they vary spatially and temporally. There is, therefore, an urgent need to intensify efforts to conduct basic ecological studies to provide the valuable data required to parameterize predictive models.

More field observations and laboratory-based experiments are needed to ascertain the relative importance of climate-sensitive traits and how they interact with each other and with the environment. The advances in next-generation sequencing have enabled researchers to study biological systems at levels never before possible. Genome scans have revolutionized the study of population diversity and helped us to better understand the genetic basis of adaptation. Already, some studies have combined genomic and phenotypic information to provide deeper insights into evolutionary processes and speciation (e.g., Bernatchez *et al.*, 2016; Günther *et al.*, 2016; Shu *et al.*, 2016). As the field advances, studies should identify candidate genes that confer tolerance to environmental change and the contribution of various adaptive genes to

climate change adaptation across species' ranges. This would allow for definitive measures of adaptive potential of species across space and time.

Gathering and accumulating information on the movement of organisms and frequency of long-distance dispersal in different landscapes is of particular importance for conservation planning under climate change. A wide variety of approaches have been used to directly measure dispersal. Direct observation of individuals in the field is the most basic approach, providing accurate measures of their dispersal distance, movement patterns, behaviour, and interactions with the environment. Recent advances in telemetry technologies and automated systems have revolutionized the type, amount and quality of data that can be collected on moving organisms in near real-time (Wilson *et al.*, 2009; Cooke *et al.*, 2013; Hussey *et al.*, 2015; Kays *et al.*, 2015). Movement data can be coupled with demographic data and detailed environmental layers into a spatially-explicit individual-based model. This can provide a cutting-edge opportunity to elucidate how organisms respond to changes in habitat quality, productivity and resource availability. It can also be used to project how species will respond to future habitat fragmentation, climate change, or other environmental alterations with little data availability.

More efficient approaches for storage, analysis and data sharing among ecologists, conservation biologists, planners and practitioners and policy-makers are needed. Software packages that allow integration of the different and large data sets required to model the distribution and vulnerability of species to climatic and other environmental changes must be developed. These should be freely accessible and easy to use. Currently, the R-platform is an excellent example.

Conclusion

Climate change is expected to exert considerable pressure on global biodiversity and ecosystem services upon which humans depend, over this century and beyond. Safeguarding biodiversity from extinction will require conservation efforts that increase their resilience and resistance to climate change. This in turn requires a better understanding of the response of species to climate. This thesis (i) combined landscape connectivity and correlative species distribution models with a realistic estimate of dispersal to assess the impacts of climate change on Cunningham's skinks, (ii) characterized the spatial patterns of genetic variation and evaluated signatures of divergent selection across the species' range, and (iii) utilised a framework that integrates exposure, sensitivity and adaptive capacity to climate change and applied it to assess the vulnerability of 17 lizard species distributed in the Great Dividing Range of Australia.

I found that climatically-suitable habitat of Cunningham's skinks will contract over time and that the dispersal rate of the species will not be sufficient for it to track its climate niche, irrespective of habitat connectivity. I also found that *Eulamprus leurensis* and *E. kosciuskoi* are highly vulnerable to climate change. My results have important implications for conservation of Australian lizards and provide necessary information for prioritizing conservation targets and guiding appropriate strategies. The framework applied in this thesis is generic and can be extended to other regions and taxonomic groups with little modification, depending on data requirement. It can also be updated as additional data become available.

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APPENDIX ONE

Spatio-temporal variation in small mammal species richness, relative abundance and body-mass reveal changes in a coastal wetland ecosystem in Ghana

Abstract

Coastal wetlands in Ghana are under severe threat of anthropogenic drivers of habitat degradation and climate change, thereby increasing the need for assessment and monitoring to inform targeted and effective conservation of these ecosystems. Here, we assess small mammal species richness, relative abundance and body-mass in three habitats at the Muni-Pomadze Ramsar site of Ghana, and compare these to baseline data gathered in 1997 to evaluate changes in the wetland ecosystem. Small mammals were live-trapped using Sherman collapsible and pitfall traps. We recorded 84 individuals of 10 species in 1,485 trap-nights, whereas the baseline study recorded 45 individuals of seven species in 986 trap-nights. The overall trap-success was therefore greater in the present study (5.66%) than the baseline study (4.56%). The species richness increased from one to four in the forest, and from zero to eight in the thicket, but decreased from six to four in the grassland. The total number of individuals increased in all habitats, with the dominant species in the grassland shifting from *Lemniscomys striatus* to *Mastomys erythroleucus*. Three species, *Malacomys edwardsi*, *Grammomys poensis* and *Praomys tullbergi* are the first records for the Muni-Pomadze Ramsar site. Generally, the average body-mass of individual species in the grassland was lower in the present study. The

considerable changes in small mammal community structure suggest changes in the wetland ecosystem. The conservation implications of our findings are discussed.

Introduction

Assessment and monitoring of ecosystem health is of fundamental importance for environmental policy, biodiversity conservation and management of natural resources (Corona *et al*., 2011). Concerns about the rapid loss of global biodiversity due to habitat loss and degradation, and anthropogenic climate change have intensified the need to assess and monitor biodiversity, particularly in regions where these threats are most pervasive (Magurran and Henderson, 2003). Knowledge of the rate and extent of environmental change in time and space, the causes of the change, and its impact on species and populations is vital for devising effective and targeted conservation management (Cohen *et al*., 2003). For this reason, the international community has proposed strategies for intensive biodiversity assessment and monitoring. For example, international conventions such as the FAO Global Forest Resources Assessment, the Kyoto Protocol, the United Nations Convention on Biological Diversity, the Ministerial Conference for the Protection of Forests (MCPFE-Forest Europe), and the Montreal Process, have made it mandatory for signatory countries to assess, monitor and report on the status of their biodiversity (Corona *et al*., 2011).

A range of methods, indicators and indices have been developed to assess the health and ecological status of terrestrial and aquatic ecosystems. Algorithms for modelling the physical, chemical and biological relationships within ecosystems and their changes over space and time

in response to external stressors are most ideal for assessing the health of ecosystems (Ferretti, 1997). However, these models are difficult to parameterize and to validate because of the complexity of the relationships that maintain ecosystem structure and function (Ferretti, 1997). Comprehensive, well-designed repeated surveys have thus been used most frequently to provide ecological and environmental data that inform changes in ecosystem health (Corona *et al*., 2011).

Ecological communities are often not randomly composed, and population sizes are influenced by birth, death, immigration and emigration rates (Volkov *et al.*, 2003). These, in turn, are affected by habitat quality, ecosystem productivity, and availability and distribution of resources in space and time (Avenant, 2011). Due to differences in species habitat and resource requirements, a few species in a community are often exceptionally abundant, while most occur in low numbers. Core species are often present in high numbers because they are able to maximize available resources and compete better than occasional species (Magurran and Henderson, 2003). However, if conditions in an ecosystem alter sufficiently to favour occasional species, new core species drawn from the pool of occasional species can replace the existing ones. Thus, changes in species assemblages can indicate disturbance regimes, or subtle changes in ecosystems health (Sullivan and Sullivan, 2001).

The Muni-Pomadze Ramsar site in the Central Region of Ghana provides a critical interface between aquatic and terrestrial ecosystems, harbouring unique biodiversity and maintaining gene flow and energy and nutrient flows across this ecotone (Gordon and Cobblah, 2000). This coastal wetland is located about 55 km west of Accra, and covers an area of 90 km^2 and is one of five coastal wetlands designated as Ramsar sites in 1992 on the basis of its

international importance as habitat for migratory waterbirds (Ntiamoa-Baidu, 1991, 2000; Gordon *et al*., 2000). The site also has cultural and spiritual significance to the local Efutu people, as a traditional hunting ground and home of gods and ancestral spirits. Asafo Companies compete annually to capture a live bushbuck at the site during the "Aboakyir" festival of the local people (Ryan and Attuquayefio, 2000). Successful capture of this symbolic animal signifies a state of peace, harmony and goodwill, and acceptance by the gods and ancestral spirits of the local peoples' request to celebrate their annual festival. Grasscutters *(Thryonomys swinderianus)*, royal antelopes *(Neotragus pygmaeus)*, duikers *(Cephalophus* sp.) and some medium-sized reptiles like monitor lizards *(Varanus* sp.) at the site are also hunted for food (Ryan and Attuquayefio, 2000).

Small mammals are important components of the Ramsar site, playing vital ecological roles that maintain the structure and composition of the wetland's ecosystems. They serve as important seed, seedling and fungal spore consumers and dispersers (Angelici and Luiselli, 2005). They also serve as prey for a wide variety of first-level avian, reptilian and mammalian predators (Habtamu and Bekele, 2012), making them important for the health and proper functioning of the wetland ecosystem. Changes in the ecological structure of the wetland, in turn, may affect the small mammal community because of their rapid turnover, high reproductive capacity and sensitivity to changes in their environment. Changes in small mammal abundance, species composition and body-mass can thus be used as a measure of disturbance of their environment (Avenant, 2011). For this reason, assessment and monitoring of small mammal populations has become an integral part of environmental impact assessment (EIA) programmes.

We assessed the species richness, relative abundance and body-mass of small mammals at the Muni-Pomadze Ramsar site, and compare these to the findings from a baseline study in 1997 to evaluate ecological changes in the wetland ecosystem over the past decade. We discuss the implications of our findings for management of the Ramsar site.

Materials and methods

Study site selection for previous and current study

The study area (Fig. 1) has been described in detail elsewhere (Gordon *et al.*, 2000; Attuquayefio and Ryan, 2006). During the baseline study in 1997 (Ryan and Attuquayefio, 2000), three main habitat types: (i) forest (Yenku Forest Reserve Block A, (ii) savanna grassland and (iii) dense continuous thicket (Yenku Forest Reserve Block B) were selected and demarcated for small mammal sampling. These sites were maintained for the current survey for uniformity and ease of comparison of results. The geographical coordinates and dominant plant species at the different habitat are presented in Table 1.

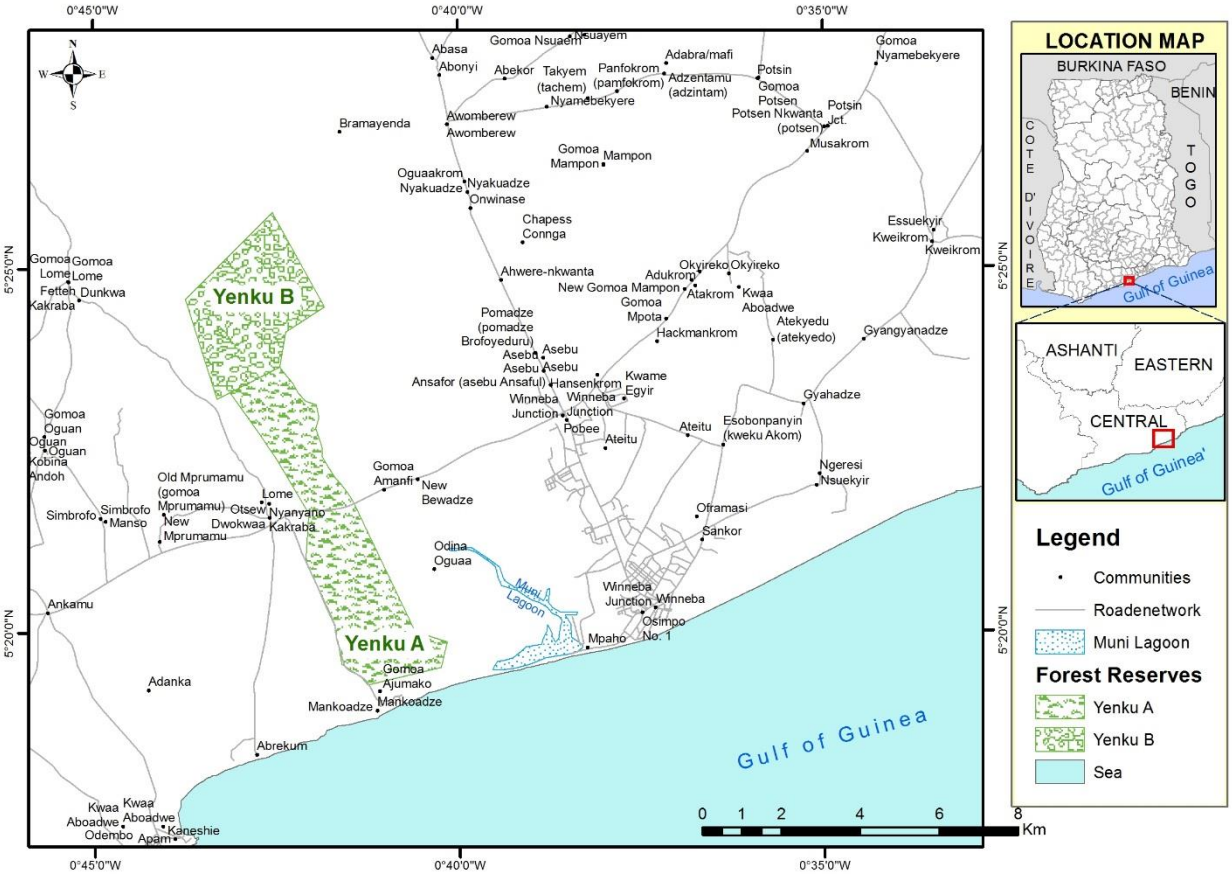

Figure 1: Map of the Muni-Pomadze Ramsar site showing the sampling sites (Yenku Block A and Yenku Block B).

Table 1: Description of Muni-Pomadze Ramsar site and the sampling locations

Study site	Coordinates	Habitat type (common plant species)
Yenku Block 'A'	N05o 22.679' W00o 42.194'	Old-growth secondary forest (mixed natural growth, Eucalyptus and Teak plantations, Cassia sp.
Yenku Block 'B'	N05o 19.789' W00o 41.637'	Thicket (Herbs- Aspilia africana, Abutilon mauritianum, Chromolaena odorata; shrubs- Securinega virosa, Lantana camara, Clausena anisata; Small trees- Azadirachta indica, Zanthoxylon xantholoides, Ficus congensis)
	N05o 19.899' W00o 41.615'	Savanna grassland (Common species include Sporobolus pyramidalis, Panicum maximum, Vertiveriafulvibarbis, Heteropogon contortus, Andropogon gayanus, Setaria pallid-fusca)

Live-trapping and handling of small mammals

Sherman and National live traps were used to capture small mammals in the baseline study (carried out in July, 1997). Trap were baited with a fresh mixture of peanut butter, maize flour and fish oil and placed along transects established in each habitat for three to five consecutive nights. Trap-lines consisted of 50 Sherman live traps and eight National live traps, or 100 Sherman traps and 16 National traps per transect. Sherman traps were spaced about 10 m apart, whereas National traps were spaced about 60 m. Overall there was a total of 174 trap-

nights in the forest, 232 trap-nights in the thicket and 580 trap-nights in the grassland (Ryan and Attuquayefio, 2000).

However, in the present study (undertaken in 2012), we used Sherman live traps and pitfall traps with drift fences. Two Sherman trap-lines, each comprising of 20 trap-stations placed at 10-metre intervals, and one pitfall trap-line of 15 buckets spaced at 5 m intervals was established in each habitat, giving a total of 55 trap units per habitat. Sherman traps were baited with a mixture of maize flour and peanut butter. Traps were set during the day and checked the following morning for three consecutive nights per trapping session. There was a trapping session each in the dry season (January), and major (June) and minor (August) wet seasons, totaling 495 trap-nights in each habitat. As in the baseline study, captured individuals were identified on the spot, sexed, weighed, marked and released at the point of capture. Small mammal trapping and handling complied with recommended guidelines and standard methods for mammal fieldwork (Sikes *et al*., 2011), and taxonomy followed Wilson and Reeder (2005).

Data analysis

We considered the species richness to be the number of individual species captured in a particular habitat. Because the species accumulation curve did not plateau, we estimated the potential number of species in a habitat using the Chao1, Chao2, bootstrap and Jacknife1 implemented in the program EstimateS version 9.0 (Colwell et al., 2012). The relative abundance of individual species was computed as the ratio of the number of a particular species to the total number of all individuals captured in a habitat. Trap-success was calculated

as the ratio of the number of individuals captured to the total trap-nights in a habitat multiplied by 100%. We also estimated species diversity and evenness using the Shannon-Wiener (H') and Pielou's (J') indices, respectively, implemented in EstimateS. Using a two-tailed *t* test at $\alpha = 0.05$, we tested the significance of the difference between mean body-mass of individuals of the different species captured in the present and baseline studies.

Results

Changes in species composition, abundance and body mass

We captured 84 individuals belonging to nine rodent and one shrew species in 1,485 trap-nights in the present study, giving an overall trap-success of 5.66% for the study area. Twenty individuals from eight species were captured in the thicket in 495 trap-nights (trap-success = 4%), 14 individuals from four species in the forest in 495 trap-nights (trap-success = 2.8%) and 50 individuals from four species in the grassland in 495 trap-nights (trap-success = 10.1%) (Table 2). Species diversity was highest (H' = 1.61) in the thicket and lowest (H' = 0.84) in the grassland, but evenness of species was greater (J' = 0.89) in the forest (Table 3).

Table 2: Number and relative abundance (in parentheses) and composition of small mammal species recorded during the 1997 baseline and present (2012) studies in the different habitats

Small Mammals	**Locality/Habitat**					
	Yenku Block A		**Yenku Block B**			
	Forest		**Grassland**		**Thicket**	
Species	**2012**	**1997**	**2012**	**1997**	**2012**	**1997**
Hylomyscus alleni	6(43%)	1(100%)	0	0	0	0
Grammomys poensis	1(7%)	0	0	0	0	0
Lemniscomys barbarus	0	0	0	6(13%)	1(5%)	0
Lemniscomys striatus	0	0	5(10%)	23(51%)	3(15%)	0
Malacomys edwardsi	0	0	0	0	1(5%)	0
Mastomys erythroleucus	4(29%)	0	36(72%)	2(4%)	10(50%)	0
Praomys tullbergi	0	0	0	0	2(10%)	0
Gerbilliscus kempi	0	0	8(16%)	6(13%)	1(5%)	0
Uranomys ruddi	0	0	1(2%)	5(11%)	1(5%)	0
Crocidura olivieri	3(21%)	0	0	3(7%)	1(5%)	0
Total no. of individuals	**14**	**1**	**50**	**45**	**20**	**0**
Total no. of species	**4**	**1**	**4**	**6**	**8**	**0**
Total no. of trap-nights	**495**	**174**	**495**	**580**	**495**	**232**
Trap-success	**2.8**	**0.14**	**10.1**	**4.6**	**4.0**	**0.0**

Species accumulation curves showed no distinct plateau for all the habitats (Fig. 2), suggesting that more species could be recorded with increasing trapping effort. In the baseline study, 45 individuals from seven species were recorded in 986 trap-nights (overall trap-success = 4.56%). Forty-four individuals from six species were captured in the grassland in 580 trap-nights (7.6%), only one individual in the forest in 174 trap-nights (trap-success = 0.14%), and no individual in the thicket in 232 trap-nights (Table 2).

Table 3: Species diversity estimated using the Shannon Weiner index and richness estimated using the Chao, Jacknife and Bootstrap.

HABITAT	J'	H'	Chao1	Chao2	Jacknife1	Jacknife2	Bootstrap
Forest	0.894	1.24	4	4	4.889	5.667	4.404
Thicket	0.774	1.61	20.5	8	13.333	18	10.105
Grassland	0.605	0.838	4	4	4.889	5.667	4.347

H' = Shannon-Wiener's index (- Σ pi ln(pi)), **J'** = Pielou's evenness (H'/ln(S)), where S is species richness and pi is the proportion of individuals in the *i*th species.

Table 4: Morphometrics (mean and range) of small mammals at the Muni-Pomadze Ramsar site

Species	N	WT	TL	HBL	HFL	EL
Hylomyscus alleni	5	32.8(21-40)	141.6(108-159)	110.5(107-143)	25	16.6(15-19)
Praomys tullbergi	2	21.5(19-24)	110	92.5(90-95)	25	15
Lemniscomys barbarus	1	20	109	89	25	14
Lemniscomys striatus	5	34.4(19-58)	105.8(68-123)	108.8(98-120)	25	15
Malacomys edwardsi	1	110	142	140	35	21
Mastomys erythroleucus	50	41.9 (22-70)	119.8(105-134)	119.3(105-134)	24.4(24-25)	14.7(14-16)
Grammomys poensis	1	54	110	138	25	15
Gerbilliscus kempi	7	71(53-80)	149(139-170)	134(130-137)	26.9(26-28)	19.4(18-20)
Uranomys ruddi	1	37	-	110	15	10
Crocidura olivieri	4	27.8 (21-32)	72.5(70-80)	111.3 (100-115)	20.3(20-21)	10

Legend: WT = weight in grams; TOTL = total length of the body and tail; TL = tail length; HBL = total length of head and body; HFL = hind foot length; EL = ear length

The small mammals recorded from thicket and forest in this study included three species, *Malacomys edwardsi*, *Grammomys poensis* and *Praomys tullbergi* that were not previously recorded at the Muni-Pomadze Ramsar site. The species we recorded from grassland were common to those of the baseline study, but two species *Lemniscomys. barbarus* and *Crocidura olivieri* which were recorded in the baseline study were missing from the present species list in this habitat (Table 2). *Lemniscomys striatus* was the dominant species (53.5%) in grassland during the baseline study, but the current study recorded *Mastomys erythroleucus* as the most dominant species (72%) in grassland.

The average body mass of individual species ranged from 27.8 g (*C. olivieri*) to 54 g (*G. poensis*) in the forest, 20 g (*Lemnyscomys. barbarus*) to 110 g (*Malacomy edwardsi*) in the thicket and 34.4 g (*L. striatus*) to 71 g (*Gerbilliscus kempi*) in the grassland (Table 4). In general, the average body masses of individual species in the grassland were lower in the present study compared to those of the baseline study (Figure 3), but this difference was significant for *G. kempi* only ($t_{0.025,}$ df = 10, $P < 0.05$). All the rodent species showed signs of breeding activity during the major and minor rainy seasons. For *M. erythroleucus*, breeding activity continued into the dry season, but the number of males with scrotal testes declined by half (97% in the rainy season and 45% in the dry season). Slightly fewer female rodents were captured in all three habitats, but overall rodent sex-ratio for the study area was about ♂1:♀1. Generally, sex ratio, and timing and duration of breeding activity of individual species in the current study were similar to those in the baseline study.

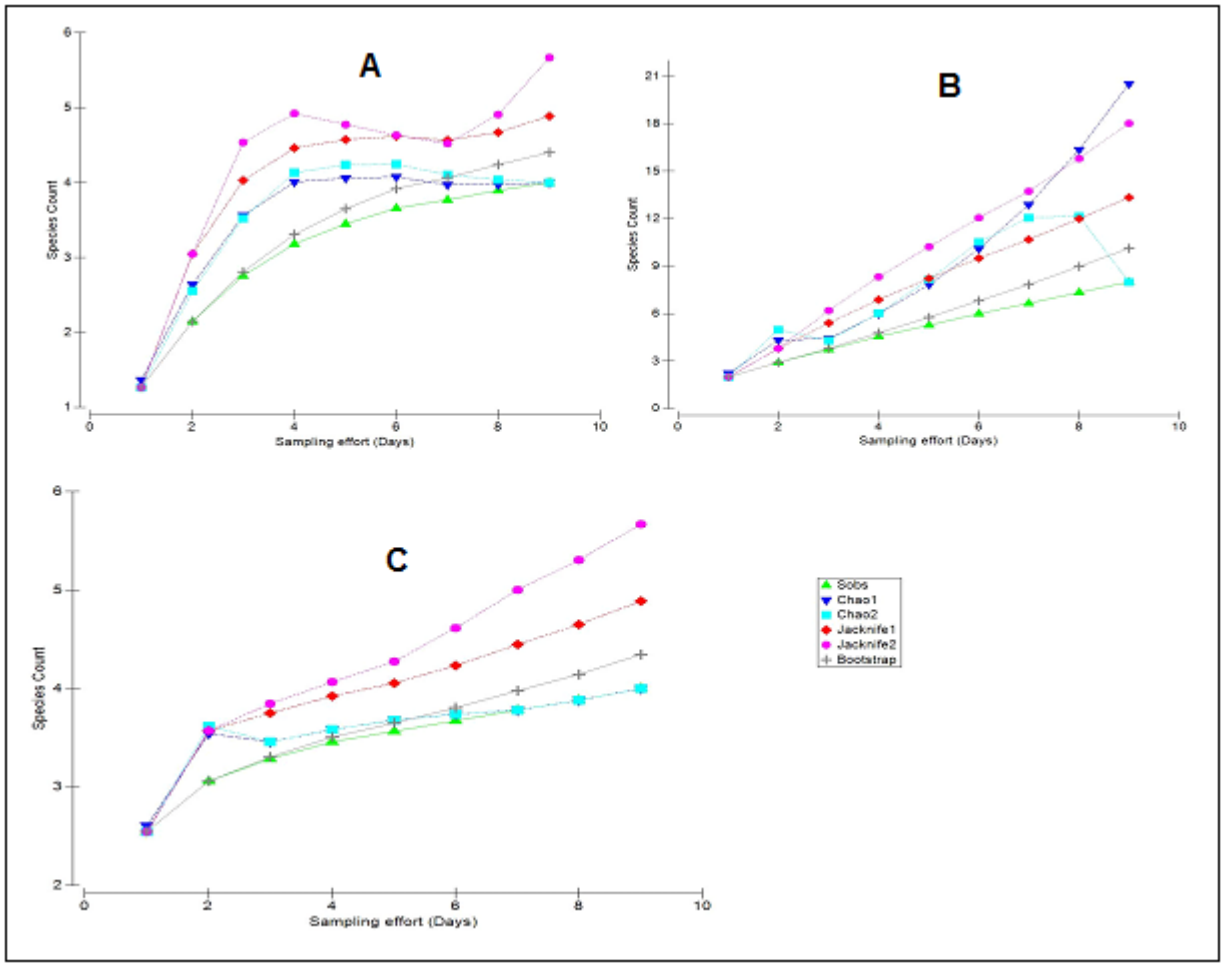

Figure 2: Species accumulation curve for the forest (A), thicket (B) and grassland (C) obtained using Sobs, Chao, Jackknife and Bootstrap estimators.

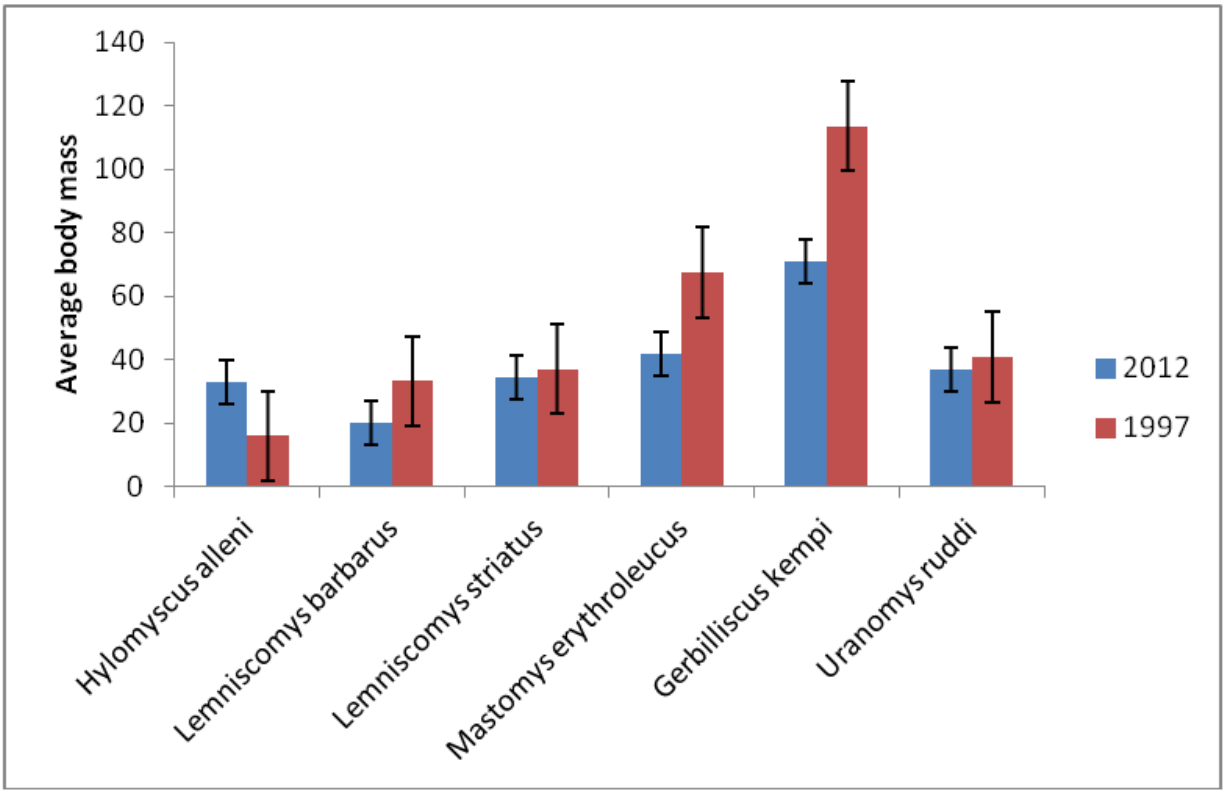

Figure 3: Average body-mass (Biomass) of small mammals at the Muni-Pomadze Ramsar site

Discussion

The abundance and distribution of small mammals vary spatio-temporally depending on the structural complexity of the vegetation cover, and availability and distribution of valuable resources (Blaum *et al*., 2007), as well as the extent to which individuals can tolerate biotic (e.g., competition and predation) and abiotic (e.g., climate) conditions (Avenant, 2011). This study revealed significant changes in small mammal species richness, abundance and body-mass at the Muni-Pomadze Ramsar site, suggesting changes in the wetland ecosystem over the

past 15 years. The increase in the species richness and relative abundance in the forest and thicket indicated improvement in the vegetation cover and the overall structure of these habitats. The current dense vegetation cover of the thicket and forest may be offering more diverse microhabitats, microclimatic heterogeneity, high quality food, nesting materials and protection for small mammals (Fichet-Calvet *et al*., 2009; Makundi *et al*., 2009).

Other factors, such as reduced predation pressures and higher trapping effort in the present study might also have contributed to this outcome. During the baseline survey, high numbers of mongooses, which are known predators of small mammals, were encountered in the thicket and forest. However, in the present study we encountered only a few in the forest and none in the thicket. Hunting by local people might have caused the decline of mongooses in the study area. Generally, it takes greater trapping effort to capture rare species, particularly in forest ecosystems (Nicolas and Colyn, 2003). By definition, rare species are uncommon and occur in low numbers and hence, encounter traps less often. Fewer traps set for fewer nights are therefore less likely to capture rare species (Fichet-Calvet *et al*., 2009).

Contrary to the forest and thicket where there was considerable increase in the species richness compared to the baseline data, the number of species in the grassland decreased. The average body-mass of individual species also decreased, with a shift from *L. striatus* to *M. erythroleucus* as the dominant species. This, and possibly the reduced number of *Uranomys ruddi* caught, a very patchily distributed species across West Africa, may suggest deteriorating conditions (e.g., lower quality and quantity of food and other vital resources) in this habitat. *Mastomys erythroleucus* is a typical grassland species, important pest of agriculture and an opportunistic species known to invade and proliferate in human-modified landscapes and

degrading habitats (Habtamu and Bekele, 2012). The lower species richness recorded in the grassland may also be due to the lower trapping effort in this study (495 trap-nights) compared to the baseline study (580 trap-nights). The disproportionate relative abundance of *M. erythroleucus* contributed greatly to the relative abundance of small mammals recorded in the grassland.

The species composition in the grassland, thicket and forest were typical of these habitats, except for *M. erythroleucus* captured at the edges of the forest abutting maize and cassava farms. This opportunistic grassland species is known to seek refuge in forest edges from where they invade nearby farms (Decher and Bahian, 1999). The species captured in the thicket comprised forest and grassland species as expected. This habitat is a transition between forest and grassland, and has different forms and species of plants that provide greater structural complexity in the vegetation and more diverse niches for more species to coexist. The species accumulation curves did not plateau for the forest and thicket (Fig. 2), suggesting that increased trapping effort will increase species richness in these habitats. This is supported by the species richness estimators used; Chao1, Chao2 and Bootstrap supported 4 species each in the forest and grassland, but Jacknife1 estimated 5 species each. There was however great discrepancy in the expected number of species in the thicket among estimators. Whereas Chao2 gave eight species, Bootstrap 10, and Jacknife1 13, Chao1 estimated 21 species in this habitat (Table 3). Chao1 uses abundance data and Chao2 occurrence records from multiple samples in aggregation to estimate species richness (Chao 1987). The wide variation in the estimates of species richness could be due to differences in estimator algorithms and the low

sample sizes of our data. Bootstrap, for example, is generally regarded as a poor estimator of species richness (Chazdon et al., 1998).

The incomplete sampling of species at the wetland is not only due to the low trapping effort, but is also due to shortcomings in our sampling protocol. Most forest-obligate small mammals are arboreal, and are more likely to be captured by traps placed high up in tree branches and in the forest canopy (Nicolas and Colyn, 2003). Placing traps on the ground only, therefore reduced the likelihood of capturing these species, which form the majority of small mammals in the forest and arguably thickets. Moreover, the bait used in traps might have influenced the species captured, especially the shrews. Only *C. olivieri* was reported for the wetland, but studies in similar habitats elsewhere in the country, such as the Accra Plains and the Volta Region, reported more species of shrews including *C. buettikoferi and C. grandiceps* that are listed as Near Threatened by the IUCN Red List (Decher and Bahien, 1999; Decher and Abedi-Lartey, 2002).

The breeding pattern of rodents in the study area was seasonal and related to the rainfall pattern. This observation is consistent with reports from previous small mammal studies, and is probably because the abundance of protein-rich diets like foliage, seedlings and insects, and lush vegetation cover during the wet season provide adequate security for lactating females and their offspring (Attuquayefio and Wuver, 2003; Nicolas and Colyn, 2003; Makundi *et al.*, 2009; Fichet-Calvet *et al.*, 2009; Habtamu and Bekele, 2012). Breeding activity of *M. erythroleucus* continued during the dry season probably indicating a year-round breeding pattern in this species (Fichet-Calvet *et al.*, 2009). Although more males were captured than females, the male:female ratio of rodents was not significantly different from unity. Dispersal

in rodents is generally male-biased, reflecting in males encountering traps more frequently than females (Nicolas and Colyn, 2003).

Given that the present and baseline studies suffer from the same shortcomings, it is reasonable to attribute the changes in species richness, composition and biomass to changes in the wetland. The main threats to the Ramsar site include bushfires, clearing of the vegetation for crop farming, firewood harvesting, grazing and hunting of small and large mammals, birds and reptiles like the monitor lizards, tortoises and pythons (Wuver and Attuquayefio, 2006). Portions of the forest have been cut down and converted into corn and cassava farms, whereas the grassland has been reduced and degraded by rampant and indiscriminate bushfires deliberately set by hunters, or resulting from uncontrolled burning by farmers during the clearance and preparation of their farmlands within and close to the Ramsar site. Hunting in the wetland directly kills and reduces abundance and diversity of its wildlife, while firewood harvesting and clearing of the vegetation for crop farming destroys their habitats. Annual and occasional bushfires, particularly in grassland habitats is good for its maintenance. However, frequent and indiscriminate burning of this vegetation by hunters and via uncontrolled burning by farmers during clearing and preparation of farms adjacent to the wetland directly kills the wildlife and destroys their habitats.

Although threats facing the wetland have long existed, its biodiversity has recently become easy target for human over-exploitation due to the burgeoning human population in the communities surrounding the wetland. General lack of formal education, entrenched poverty and the quest for survival as a result of the ever-growing human population has eroded the practice of sustainable traditional hunting, agriculture, limitation of land use to a relatively

smaller segment of the population using simple tools on smaller land areas (Wuver and Attuquayefio, 2006). Thus, the environmentally-friendly traditional and cultural practices and belief systems that conserved the wetland's ecosystem are no more effective. Therefore, to improve the current status of the wetland's ecosystem management should encourage local participation in the conservation of the site. Public education and conservation awareness creation and the introduction of alternative forms of livelihood and biomass energy remain essential to the conservation of the wetland. Given the cultural and socio-economic significance of the site, integrating traditional and modern knowledge system of biodiversity conservation is more likely to be embraced by the local people.

Conclusion

We found changes in the small mammal species richness, abundance and body-mass at the Muni-Pomadze Ramsar site over the past 15 years, suggesting changes in the coastal wetland during this period. Our findings suggested a deteriorating condition in the grassland habitat. Whiles there was visible evidence that portions of the forest has been cleared and converted into maize and cassava farms has attracted opportunistic grassland species like *M. erythroleucus*, the presence of forest obligate species such as *H. alleni* and *G. poensis* suggested that the untouched portion of the forest is in good ecological health. Management of the Muni-Pomadze Ramsar site need to focus more on curtailing the threats facing the wetland, particularly the grassland. Further cutting down of the forest for crop farming should be stopped through the introduction of legal and incentive systems. Education and

involvement of the local communities in the management of the wetland remains critical for conserving its biodiversity and the ecological and socioeconomic services they provide.

Acknowledgements

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This paper study is published ***Ofori, B. Y***., *Attuquayefio, D. K., Owusu, E. H., Musah, Y., & Ntiamoa-Baidu, Y. (2016). Spatio-temporal variation in small mammal species richness, relative abundance and body mass reveal changes in a coastal wetland ecosystem in Ghana. Environmental Monitoring and Assessment, 188(6), 1-10.*

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APPENDIX TWO

Ecological Status of the Mount Afadjato-Agumatsa Range in Ghana after a Decade of Local Community Management

Introduction

Over the past few decades, the world community have recognized the need to involve local people in the management of conservation areas (CAs) (Ferraro, 2006). This paradigm shift from the old state-centred "fences and fines" management to a community-based management (CBM) approach empowers local people to play much more active roles (Balint, 2006). The underlying principle of the CBM concept is that local people are more inclined to implement any management decisions for which they had provided some input, and given sufficient technical support they can determine for themselves appropriate conservation solutions (Shackleton *et al*., 2002). However, the ability of local communities to effectively manage CAs is being debated, despite recent successes. Indeed, available empirical evidence suggests that community-managed forests are more effective in reducing forests loss than strictly protected areas in the tropics (Africa, Asia, South and North Americas) (Porter-Bolland et al., 2012).

The different purposes for which CAs are established, and variations in their tenure regimes, socio-economic and cultural contexts make it difficult to generalize the performance of CAs across regions, and warrants evaluation of individual CAs. A number of methods have been developed for assessing the ecological status and management effectiveness of CAs, but

currently there is no globally-sanctioned metric because of the aforesaid reasons (Chape et al. 2005). Although remotely-sensed data are useful for monitoring trends in forest cover extent, they have rarely been used to evaluate the performance of CAs in Ghana and Africa. Here, we used Landsat images and questionnaires to assess the ecological status of Mount Afadjato-Agumatsa Range (MAAR), a community-managed CA in Ghana. The specific objectives were to assess the changes in forest cover and threat status of the MAAR over the past decade.

Materials and Methods

Study Area

Mount Afadjato and part of the Agumatsa range (0º 15'- 0º 45'E; 6º 45'- 7º 15'N) with an area of about 12 km^2 (Fig. 1) is managed by the Gbledi and Fodome-Ahor traditional authorities in the Hohoe District of the Volta Region of Ghana (Owusu *et al*., 2005). Rainfall is single-peak between April and October, with higher precipitation in June, September and October (mean rainfall = 1,650 mm, range = 1,594.8 mm - 1,762.2 mm). Annual temperature ranges from 19ºC to 29ºC and average relative humidity is 90% (Hawthorne & Abu-Juam, 1993). The vegetation follows a characteristic pattern of relief and exposure, with Dry Semi-deciduous forest occupying the western slopes, and savanna grassland dominating the eastern side (Hall & Swaine, 1993). About 2,098 people live in six fringe communities (Gbledi-Gbogame, Kyebi, Togodo, Woti, Dzigbodi and Fodome-Ando), with an annual population growth rate of 2.4%. Farming is the main economic activity, involving crops like cassava, maize, yam, rice, plantain, cocoa, coffee and oil palm (GWS, 2007).

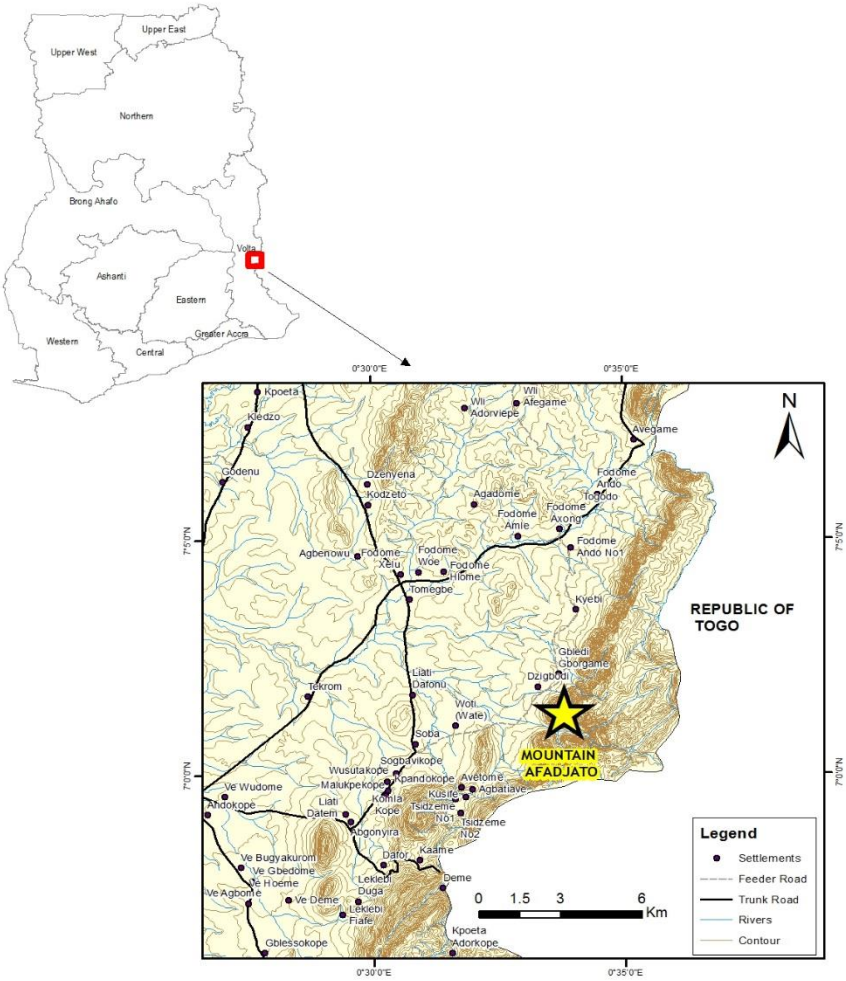

Figure 1: Map of the Mount Afadjato-Agumatsa Range (MAAR) of Ghana showing fringe communities (Gbledi Gbogame, Kyebi, Togodo, Woti, Dzigbodi and Fodome Ando)

Methods

Satellite Imagery

Post-classification comparison and combination of normalized difference vegetation index (NDVI) and image differencing were used on LANDSAT ETM+ images of December 1998, 2003 and 2008 (Fig. 2) to determine and quantify land cover changes that have occurred in the study area. The use of classified multi-temporal NDVIs derived from LANDSAT images is a standard procedure for analyzing land cover changes (Attua and Fisher, 2011).

Questionnaires and Interviews

Information on the prevalence and severity of past and current threats was obtained using questionnaires and interviews of 12 respondents selected *a priori*, notably the site manager, liaison officer, six rangers, two community wardens, and two long-serving volunteers. Each respondent was provided with a checklist of the known common threats to most conservation areas in Ghana (Ofori and Attuquayefio, 2012), and was required to identify and tick on a list, all threats to management of MAAR before 1998. Each respondent was also required to rank each threat factor on the basis of its prevalence and degree of impact on the integrity of the MAAR forest ecosystem. The ranking was based on an ordinal scale of 0 to 5, with 0 = *non-existent*, and 1, 2, 3, 4, and 5 representing *very low*, *low*, *moderate*, *high* and *very high* prevalence/severity, respectively. This protocol was repeated for all the threats currently facing the MAAR (2008).

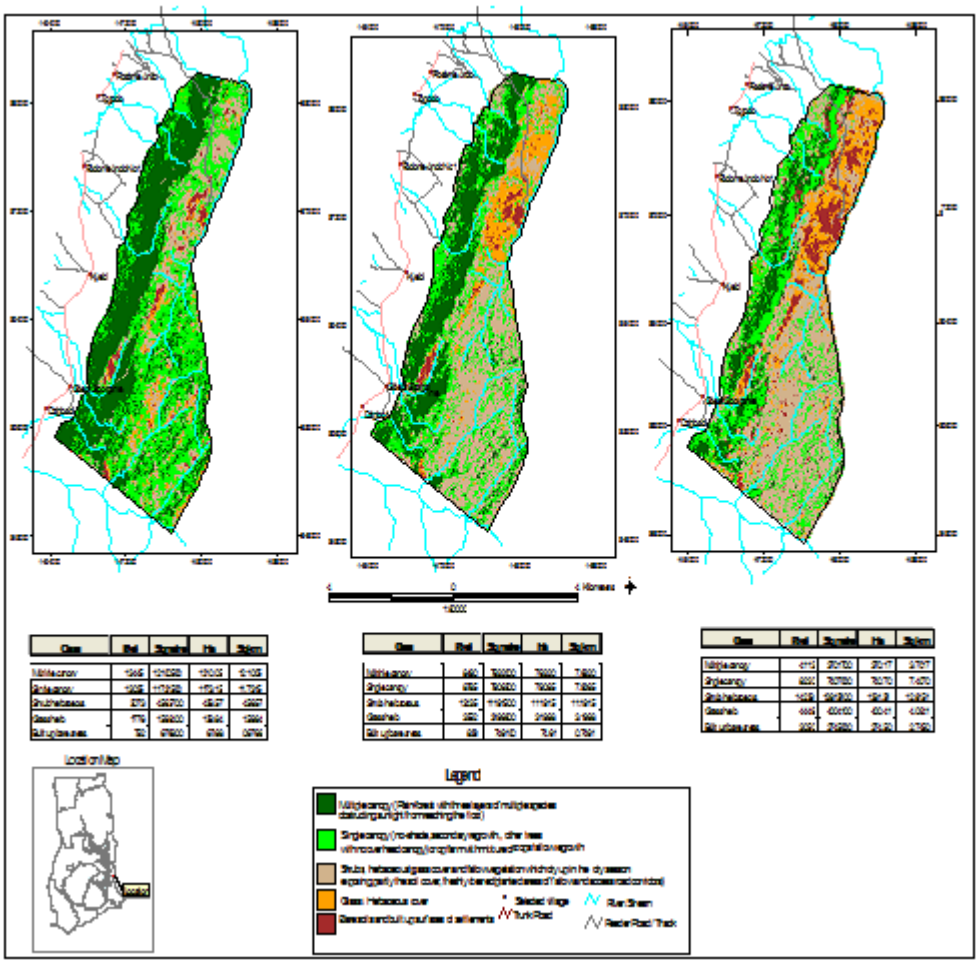

Figure 2: Time-series satellite images of the Mount Afadjato-Agumatsa Range showing land-cover changes over 10 years period (extreme right image = 1998, middle image = 2003 and extreme left image = 2008). Source: CERSGIS, University of Ghana, Legon.

Results and Discussion

Changes in Forest and other Cover Types

Land cover statistics from classified images showed that the extent of forest with two or three vertical canopy strata (multiple canopy) more than doubled, whereas the forest with single canopy stratum increased by ~7% by the end of the fifth year of conservation intervention. After 10 years, multiple and single canopy forests increased by 227% and 58%, respectively, giving an overall increase of 115% at the MAAR. Shrub, grass and built-up areas decreased by 64.4%, 60.1% and 75.3%, respectively by the end of the tenth year (Table 1). The results suggest rapid forest restoration and a move toward a more mature forest structure.

In the past, six threat factors, notably hunting, farm encroachment, logging, bushfires, as well as harvesting of firewood and non-timber forest products (NTFPs) were highly prevalent and severe. Except for logging, which has ceased, all the other threats are still present in the MAAR, but with drastically-reduced prevalence and severity rom 'moderate' to 'very low' (Fig. 3). Conservation initiatives like planting of indigenous trees in degraded areas, firebelt creation and conservation education seem to be yielding positive results. The active involvement of the youth might have also played a significant role, as they had been offered alternative livelihoods to illegal hunting and logging at the site. Incentives in the form of allowances paid from funds generated from ecotourism could be important motivation for the youth to work hard to protect the MAAR (Forgie *et al*., 2001). Changes in household economies and decreased population due to rural-urban migration, although not covered by this study, might have contributed to the positive results (Brooks et al., 2012). Our results, which are supported by findings from Ethiopia (Takahashi and Todo, 2012), Tanzania

(Blomley et al., 2008), Nepal (Nagendra et al., 2005) and Mexico (Ellis and Porte-Bolland, 2008), suggest that local communities can manage important biodiversity areas given sufficient technical support.

Table 1: Changes in forest and other cover types at the MAAR. The percentage change in each vegetation cover type was estimated as TA – IA)*/IA x 100 %,* where TA = Total area covered by a vegetation cover type under the year under consideration, IA = Initial area covered by that cover type. A negative value means the area covered decreased over the time under consideration).

Cover type	**Total area covered**			**Percentage change**	
	1998	**2003**	**2008**	**1998-2003**	**1998-2008**
Multiple canopy	3.7017	7.632	12.1005	106.2%	226.9%
Single canopy	7.407	7.9065	11.7315	6.7%	58.4%
Shrub	12.8151	11.1915	4.5657	-12.7%	-64.4%
Grass	4.0041	3.1968	1.5984	-20.2%	-60.1%
Bare areas	2.745	0.7461	0.6768	-72.8%	-75.3%

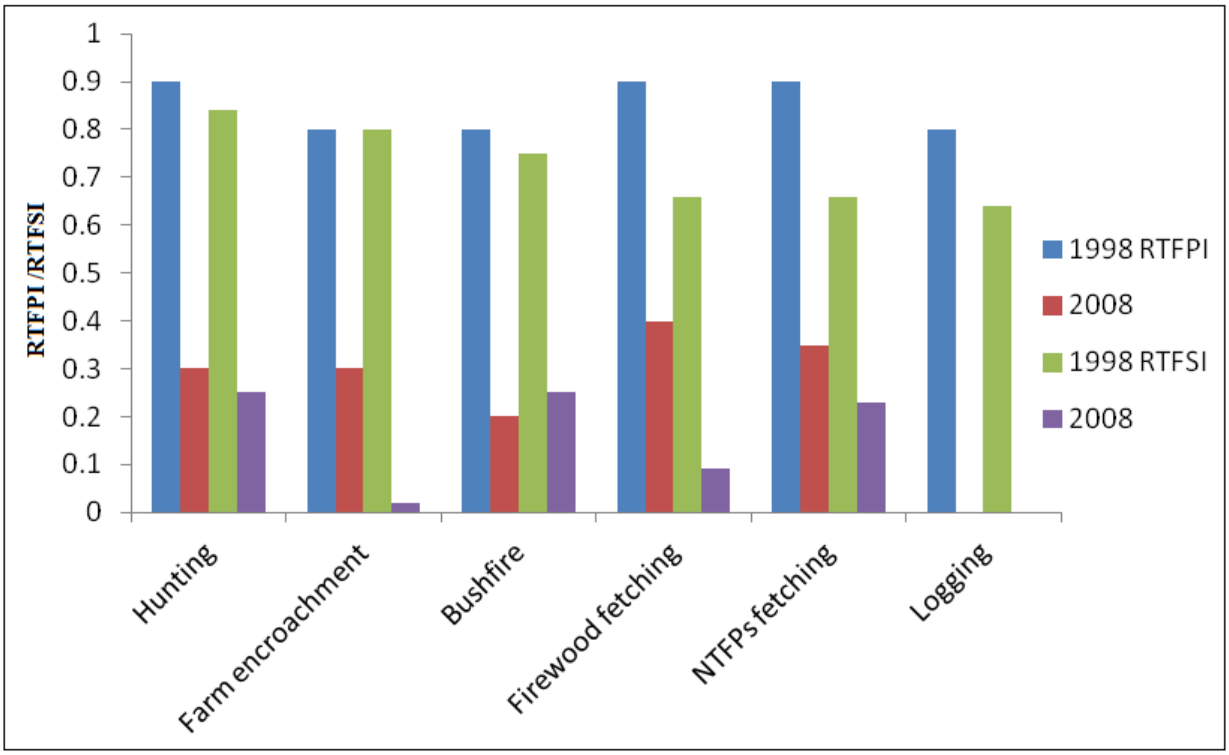

Figure 3: Relative threat factor prevalence (RTFPI) and severity (RTFSI) indices for the MAAR in 1998 and 2008. (RTFPI = MTFPS/S_{max}; RTFSI = MTFSS/ S_{max}; MTFPS = Total score of respondents for the prevalence of a particular threat divided by the number of respondents; MTFSS = Total score of respondents for the severity of a particular threat divided by the number of respondents, and S_{max} is the maximum possible score of a threat factor = 5. The RTFPI and RTFSI can take any value (score) ranging from 0 to 1, with RTFPI or RTFSI value of 0 (zero) meaning that threat factor is non-existent. The scores of RTFPI and RTFSI were interpreted as: > 0.9 = Very high prevalence/severity; 0.7-0.9 = High prevalence/severity; 0.35-0.69 = Moderate prevalence/severity; 0.15-0.34 = Low prevalence/severity; < 0.15 = Very low prevalence/severity).

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APPENDIX THREE

Animal Research Ethics Certificate

MACQUARIE UNIVERSITY

ANIMAL RESEARCH AUTHORITY (ARA)

AEC Reference No.: 2013/015 **Date of Expiry:** 31 August 2014

Full Approval Duration: 1 September 2013 to 31 August 2016 (36 Months)

This ARA commences on the 1 September 2013 until the Date of Expiry (unless suspended, cancelled or surrendered) and will only be renewed upon receipt of a satisfactory Progress Report before expiry (see Approval email for submission details).

Principal Investigator:
A/Prof Adam Stow
Biological Sciences
Macquarie University, NSW 2109
adam.stow@mq.edu.au
0452 636 800

Associate Investigators:
Benjamin Y. Ofori 0420 587 125

In case of emergency, please contact:
the Principal Investigator / Associate Investigator named above, or
Animal Welfare Officer - 9850 7758 / 0439 497 383

The above-named are authorised by MACQUARIE UNIVERSITY ANIMAL ETHICS COMMITTEE to conduct the following research:

Title of the project: **Functional Diversity and Potential Impacts of Climate Change on Cunningham's skink Egernia cunninghami**

Purpose: 7 - Research: Environmental Study

Aims: **To determine the functional diversity of different populations along altitudinal gradient.**
To correlate the present distribution with current climate and biotic variables to predict future distributions and shifts
To produce a framework to enhance connectivity of current and future distributional areas

Surgical Procedures category: 1 - Observation Involving Minor Interference

All procedures must be performed as per the AEC-approved protocol, unless stated otherwise by the AEC and/or AWO.

Maximum numbers approved (for the Full Approval Duration):

Species	Strain	Age/Sex/Weight	Total	Supplier/Source
27	Cunningham skinks (Egernia cunninghami)	Any	180	wild
		TOTAL	180	

Location of research:

Location	*Full street address*
Kaputar National Park	Kaputar, NSW, 2390 Australia
New England National Park	Armidale, Northern Tablelands, NSW, 2358, Australia
Willis Reserve	Crookwell, Southern Tablelands, NSW, 2583, Australia

Amendments approved by the AEC since initial approval: N/A

Conditions of Approval: N/A

Being animal research carried out in accordance with the Code of Practice for a recognised research purpose and in connection with animals (other than exempt animals) that have been obtained from the holder of an animal suppliers licence.

Professor Mark Connor (Chair, Animal Ethics Committee) **Approval Date: 16 May 2013**

Adapted from Form C (issued under part IV of the Animal Research Act, 1985)

APPENDIX FOUR

Environment and Heritage, NSW Parks and Wildlife Services Certificate

Office of Environment & Heritage
NSW National Parks & Wildlife Service

SCIENTIFIC LICENCE
NATIONAL PARKS & WILDLIFE ACT, 1974
Section 132c

Name and postal address of principal licensee	Nominated premises (where appropriate)
Mr Benjamin Ofori Macquarie University U 5 142 Herring Rd MACQUARIE PARK NSW 2113	

Your licence number is: SL101164

This licence is valid from: 17 May 2013

This licence will expire on: 28 February 2015

Additional authorisations:

Project Title: Adaptive Capacity and Potential Impacts of Climate Change on Cunningham's skinks

This licence authorises the following activities: Harm, trap, capture, measure, collect tail tips for DNA analysis, release Cunningham's skinks.

This licence authorises the principal licensee and any associates named in **Attachment A** to conduct those activities authorised above, to those species, communities or materials listed in **Attachment B**, at the locations specified in **Attachment C** of this licence.

This licence also authorises the principal licensee to import or export those species, or materials listed in **Attachment B** interstate as provided under s126 of the *National Parks and Wildlife Act 1974* (NPW Act) and to conduct research on park under clause 23 of the *National Parks and Wildlife Regulation 2009* (NPW Reg), where this forms part of a project approved by a delegated officer of OEH.

This licence is issued subject to the provisions of NPW Act, NPW Reg, the general conditions listed below, any special conditions as may be notified in writing to the licensee by the Chief Executive of OEH ("the Chief Executive") or a 'delegated officer' of OEH ("delegated officer") and the OEH "Scientific Licensing" policy.

Signature of Delegated Officer	**Signature of Principal Licensee***
Date: 20 May 2013	Date:.....

* This licence is not valid unless it is signed by the principal licensee. By signing this licence the licensee agrees that they have read, understood and agree to comply with all of the conditions listed on the licence.

Page 1 of 6 SL101164 Issued on 17 May 2013