

THE IMPACTS OF CLIMATE CHANGE ON AN AUSTRALIAN
ARID ZONE GECKO SPECIES (*Gehyra variegata*)

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Bachelor of Science (Honours)

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This thesis is presented for the degree of Doctor of Philosophy

March 2013



DECLARATION

The work described in this thesis was carried out in the Conservation Genetic Lab at Macquarie University. All work described in this thesis is original and has not been submitted, in any other form, for a higher degree at any other institution.

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March 2013

Throw up a handful of feathers, and all must fall to the ground according to definite laws; but how simple is this problem compared to the action and reaction of the innumerable plants and animals which have determined, in the course of centuries, the proportional numbers and kinds of trees now growing on the old Indian ruins.

Charles Darwin (1859)

ABSTRACT

In 1859 Charles Darwin acknowledged the difficulty in predicting the likely impact of environmental change to biodiversity. During this century rapid global climate change (GCC) is likely to have a profound effect on the distribution and evolutionary fate of biodiversity. Thus predicting how species will respond to climatic fluctuations is one of the most important contemporary questions in conservation biology. Here, I explored the impact of past, present and future climates on a widely distributed Australian gecko, *Gehyra variegata*, using an interdisciplinary approach. To make more realistic estimates of a species' likely future distribution I incorporated a genetic estimate of dispersal into species distribution models (SDM). The data suggested a large proportion of the current distribution will fail to colonise the predicted future distribution, and will result in a significant reduction to current levels of genetic diversity. Phylogeographical analysis suggested that higher levels of genetic diversity for this species have been associated with the channel country in arid Australia since the Pleistocene. This region has the highest water run-off throughout the arid biome and has been an important environmental feature to help the species persist through past unfavourable climatic conditions. However, it is unlikely to maintain favourable conditions in the near future due to increasing aridity. Corridors of natural habitat are often considered a conservation solution to help species disperse between habitat patches and maintain gene flow, although natural habitat can also experience structural changes over space and time which may influence connectivity. I revealed that structural changes reduced the number of retreat sites for this species, which influenced levels of dispersal and rates of predation. My data suggests the evolutionary fate of this species is likely under threat in the near future and careful consideration needs to be given to future land usage if we wish to protect biodiversity.

CHAPTER DECLARATIONS

Chapter One: Introduction

I performed the review of literature and writing of this chapter.

Chapter Two: Rapid isolation and characterisation of microsatellite loci from a widespread Australian gecko, the Tree Dtella, *Gehyra variegata*

I performed all aspects of the work required for this paper including the sampling, DNA extraction, microsatellite primer design, primer testing, polymerase chain reactions (PCR), fragment analysis, and statistical analysis. I wrote the manuscript with feedback provided by my supervisor Associate Professor Adam Stow. This chapter has been published in Conservation Genetic Resources under the same title.

Chapter Three: Keeping up with the neighbours: Using a genetic measurement of dispersal and species distribution modelling to assess the impact of climate change on an Australian arid zone gecko (*Gehyra variegata*)

The research idea was designed by myself and approved by Associate Professor Adam Stow. I completed all permit preparation, the selection of sampling sites, the sampling of geckos (with assistance from Abigail Cabrelli and field volunteers from Macquarie University), DNA extractions, PCR, and fragment analysis myself. The custom R script to model the dispersal dilation between the present and future predicted species distribution was designed in conjunction with, and coded by, Dr Peter Wilson (Macquarie University). I completed all statistical analyses and wrote the manuscript with feedback provided by my supervisor

Associate Professor Adam Stow and Dr Peter Wilson. This chapter has been published in Diversity and Distributions under the same title.

Chapter Four: Predicting impacts of global climate change on intraspecific genetic diversity needs realistic dispersal estimates

The research idea was designed by myself and approved by Associate Professor Adam Stow. I completed all permit preparation, the selection of sampling sites, the sampling of geckos (with assistance from Abigail Cabrelli and field volunteers from Macquarie University), DNA extractions, PCR, fragment analysis, and statistical analysis myself. I wrote the manuscript with feedback provided by my supervisor Associate Professor Adam Stow. This chapter is currently under review.

Chapter Five: Higher genetic diversity and historical refugia are associated with stable water sources for a gecko with a wide distribution in arid Australia

The research idea was equally designed with Associate Professor Adam Stow. I completed all permit preparation, the selection of sampling sites, the sampling of geckos (with assistance from Abigail Cabrelli and field volunteers from Macquarie University), DNA extractions, PCR, fragment analysis, and statistical analysis myself. I wrote the manuscript with feedback provided by my supervisor Associate Professor Adam Stow. This chapter has been published in Diversity and Distributions under the same title.

Chapter Six: Levels of dispersal and tail loss in an Australian gecko (*Gehyra variegata*) are associated with differences in forest structure

I performed all aspects of this work myself including the research idea, study design, permit preparation, the selection of sampling sites, the sampling of geckos (with assistance from Abigail Cabrelli and field volunteers from Macquarie University), DNA extractions, PCR, fragment analysis, and statistical analysis. I wrote the manuscript with feedback provided by my supervisor Associate Professor Adam Stow. This chapter has been published in Australian Journal of Zoology under the same title.

Chapter Seven: Conclusions

I summarised the findings of my thesis by outlining the major implications for the conservation of arid zone ecosystems in Australia, and suggest future research applications.

Appendices

1. *Liopholis kintorei* study - I completed all of the molecular work and fragment analysis and contributed with regards to manuscript preparation. This paper was published in *PLoS ONE*.
2. *Egernia striolata* study - I completed all aspect of the research and wrote the manuscript with feedback provided by my supervisor Associate Professor Adam Stow. This paper was published in *Copeia*.
3. Host tree modelling - I performed all aspects for the host tree species distribution modelling and analysis.

4. *Gehyra variegata* fecundity study - I completed all aspect of the research and wrote the manuscript with feedback provided by my supervisor Associate professor Adam Stow.

PERSONAL ACKNOWLEDGEMENTS

When I first made the decision to change careers from a computer engineer to a scientist, I knew the journey would be long, but the satisfaction I now receive from studying and working in a career that I am now passionate about has exceeded all my expectations. Therefore, I must first acknowledge and thank with all sincerity Associate Professor Mariella Herberstein. You were the first person I had the pleasure of meeting at Macquarie University when I walked into your office almost 8 years ago. Your unrivalled enthusiasm and welcoming nature instantly reassured me that all my goals were achievable, without the confidence you initially gave me I doubt whether I would be presenting this thesis today. To my supervisors and mentors – Associate Professor Adam Stow and Professor Michael Gillings, I thank you for your continued expertise, support, and enthusiasm. I would also like to especially thank Associate Professor Adam Stow for his endless patience throughout my undergraduate and postgraduate studies. Whilst my experimental design, fieldwork, laboratory, creative, and analytical science skills have developed well over the last four years, I sincerely appreciate the extra time, dedication, and supervision you provided in helping develop my science writing skills. Whilst these are far from being perfected, it is probably with a sense of relief that you are finally relieved from this responsibility.

When I began my PhD, I was exceptionally fortunate to work within the Conservation Genetics Lab at Macquarie University. I would specifically like to thank Shannon Smith, Vincenzo Repaci, Stephen Hoggard, Jessica Boomer, Heidi Ahonen, Kate Umbers, Chris Turnball, and Andrew Beattie for accepting and welcoming me into the CGL team, both professionally and socially I owe something to you all for helping me through this thesis. Also, I thank all postgraduate members of the STOW and EMMA Lab (Heather Baldwin, Maria Asmyhr, Paolo Momigliano, Jake Coates, Miranda Christopher, and Liette Vandine)

for the professional, supportive, and humorous atmosphere you were all able to create and maintain over the last 4 years. I would also like to give special thanks to my long-time friends Igor Kan and Bonnie Dalrymple for your friendship and calming influence throughout both my undergraduate and postgraduate studies. The times we spent together were a much needed distraction from the pressure of postgraduate life; I hope that our friendships continue into the next stage of my science career.

To my family, I am indebted for everything you have given me over the years. I thank you all for my strength of character, independence, freedom, and the love you continually give whilst we live many miles apart. Mum, you have always given me the confidence that anything I wanted to achieve in life, no matter how impossible it may seem, is achievable. Dad, I thank you for your mischievous, curious, and analytical nature, which has driven my passion for life and the natural world. Both of you still claim I inherited my intelligence from your side of the family, although I am not prepared to settle that debate here today. To my sister Joanne, thank you for being the best sister an annoying little brother could ever wish for, and for continually inspiring me with your determination. To my nephew Thomas, the fun and laughter I have when I'm in your presence I hope to repay by inspiring you to live your life and help realise your dreams.

And finally and most importantly, to my partner Andrea Croy, your beauty, endless support, and unquestionable love are the main reasons I am 'happily' completing this thesis today. You have helped me through the most difficult times in my life and have helped me create my most treasured memories. I offer you my most sincere love and hugs, and look forward to taking many more special journeys with you in the next step of our lives.

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CHAPTER ONE

This thesis aims to provide insights into the likely impacts of climate change (past, present and future) for an Australian arid zone gecko (*Gehyra variegata*), with comment on the significance of these findings for the future conservation management practices of woodland species in this region. To allow my approaches and conclusions to be critically evaluated and perhaps appreciated, the first chapter will provide background information on the arid zone of Australia (including its biodiversity and paleoclimate), the refugia hypothesis, global climate changes (including predicted impacts and the limitations to current assessment methods), and the species I adopted for this study.

Introduction

Biodiversity

The biodiversity present today amongst the world's flora and fauna has resulted from billions of years of evolution, and can be found throughout all of the major biomes of the world.

Biodiversity can be broken down into three distinct levels, including ecosystem diversity (the variety of habitats and processes), species diversity (the variety of species and taxa), and genetic diversity (the levels of genetic variation within a single species or population). At all levels biodiversity does not remain static and is constantly changing in response to evolutionary processes, natural environmental fluctuations, and external threats such as human impact. Because human disturbance can have a comparatively larger negative impact, it is vital to protect biodiversity against these threats. This is important because biodiversity represents an integral component to the biological systems that support life on Earth.

Throughout the world only seventeen countries have been classified by Conservation International (1998) as 'mega-diverse countries', meaning those countries with exceptionally high levels of biodiversity. The concept was first developed to help prioritise conservation efforts worldwide. Collectively, the seventeen mega-diverse countries account for approximately two thirds of the world's biodiversity, yet only cover 10% of the global surface (Groombridge, 1992). Australia is one of those mega-diverse countries. More specifically, in comparison to the number of published species worldwide, Australia can account for a large percentage of species within the chordates (12.5 %), invertebrates (7.3 %), plants (7.1 %), fungi (11.9 %), and lichen (20.6 %); (all species 7.8 %). At a lower taxonomic level, high percentages of the world's species are found in the Australian reptile (10.5 %), fishes (16.0 %), cephalochordata (24.2 %), tunicata (27.4 %), hemichordata (15.7 %), echinodermata (21.1 %), pycnogonida (16.0 %), crustacea (15.5 %), onychophora (43.0 %), mollusca (10.2 %), annelida (13.1 %), cnidaria (17.4 %), porifera (24.6 %), bryophyta (11.4 %), and

gymnosperms (11.7 %). Additionally, exceptionally high levels of endemism have been found in Australian species of vascular plant (92 %), amphibian (93 %), reptile (89 - 93 %), bird (45 %), and mammal (83 - 87 %). In summary, Australia's status as a mega-diverse country is justified because it contains more species of vascular plants, amphibians, birds and mammals than 79 - 95 % of countries on earth, and more reptiles than any other country (Groombridge, 1992; Beattie, 1995; Mittermeier *et al.*, 1997; Mittermeier *et al.*, 1998; WCMC, 1998; Australian-Government, 2001; Commonwealth, 2001; Brooks *et al.*, 2006).

Within the seventeen mega-diverse countries, Australia is the only country which spans an entire continent and is considered to be a developed nation with a low population density. This privileged status would seemingly provide the country with the economic viability and space to adequately protect biodiversity without compromising land use for its growing population. Unfortunately, Australia does not have a good record for the conservation of its own biodiversity. In total, there are 46 countries listed by the World Conservation Monitoring Centre (WCMC) that protect a greater proportion of their land in reserve systems than Australia. This complacency has likely contributed to the 110 plant and animal species that have become extinct in Australia since European settlement (ANBG, 1998; Commonwealth, 2001). This number includes more extinctions of plant (60) and mammal (50) species than any other country in the world.

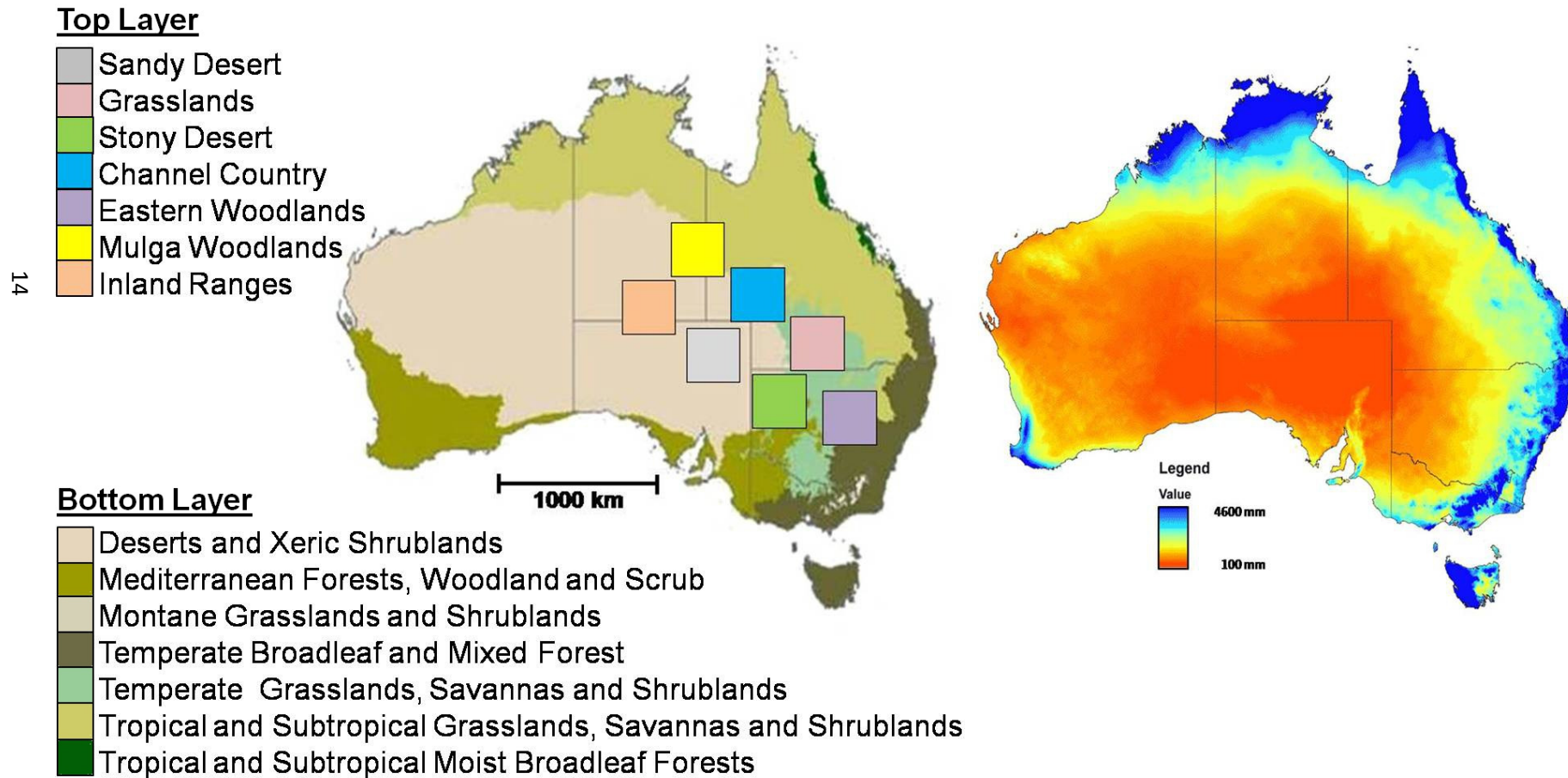
Australia's arid climate

A considerable proportion of Australia's exceptional biodiversity is located in the arid and semi-arid zone of inland Australia, which includes the inland ranges, grassland, woodlands, sandy desert, channel country, and stony desert habitats. This region is generally defined as having a moisture index of < 0.4 (mean annual rainfall divided by evaporation), and is typically of low relief and low in human population. The arid and semi arid zones throughout

the world represent more than one third of the earth's land surface area, yet in Australia it accounts for ~ 70 % of the continents 7.7 million km² terrestrial surface (Greer, 1989). The biome is Australia's largest, in addition to being one of the largest desert ecosystems in the world. Although unlike many of the other desert biomes around the world, the majority of the Australian arid zone is a sparse mosaic of vegetation with contrasting landscape types (Fig. 1.1). Here, adjacent geographical regions can have very disparate landscape features, yet with very similar temperature and precipitation values. For example, the Simpson Desert borders the channel country region in south-west Queensland. The former consisting of an extremely high, long and wide parallel dune system and the latter displays low relief and widespread ephemeral flooding, yet climatic conditions are almost undistinguishable. Additionally, similar soils do not always produce the same landscape features. Here, both flat sandy deserts and sand dune systems can be found.

Figure 1.1 Habitats and rainfall

The approximate locations of the primary arid landscapes and habitat coverage distributed throughout the arid zones of central and eastern Australia (Left) , and the mean annual rainfall (mm) (Right) (Source: Department of Agriculture, Fisheries and Forestry - <http://www.daff.gov.au>).



The low rainfall and aridity of the Australian climate is associated with the continent's latitude. The continent is located across the Tropic of Capricorn which has a high pressure subtropical atmospheric belt. Warm and dry tropical airs leaving the equatorial regions descend onto the continent, and any moisture received via the south-easterly Pacific Ocean trade winds are commonly deposited on the eastern coastal fringe due to the Great Dividing Range's cooling effect. Therefore, stable pressure systems must be disrupted for the arid zone to receive rains, which is an unusual event.

The Australian climate is highly variable from year to year and can suffer from extreme weather events. For example, within the last decade the country has experienced rainfall which more than doubled the annual average, causing floods spanning ~1 million km², and extreme droughts which culminated in widespread fire events. The variability of the Australian climate is attributed to major atmospheric fluctuations of air pressure and rainfall patterns, called the Southern Oscillation. In Australia, the Southern Oscillation Index calculates the difference in monthly mean air pressure between Tahiti and Darwin, which reveals the strength and phase of the Southern Oscillation. Deviations from a long term average state (typical Walker Circulation); can result in El Niño and La Niña events. El Niño events in Australia are commonly characterised by a higher probability of dry conditions, the greatest impact from which is usually over the inland arid regions. These events are often accompanied by warmer temperatures during the winter and spring seasons, which exacerbate the lower than average rainfall by increasing evaporation. Whereas, La Niña events often bring cooler than average temperature and increased rainfall.

The paleoclimate of Australia

Despite the size of the Australian arid biome it has a relatively young origin in the late Pliocene to Mid - Pleistocene (~3 - 1.2 mya), in comparison to the smaller mesic coastline

which originated from Mesozoic Gondwanan forests (~251 - 65 mya) (Fujioka *et al.*, 2005; Byrne *et al.*, 2008). Therefore, the continent has not always been dominated by an arid landscape. During the Palaeocene (~66 - 55 mya), the only hints of aridity were in the North West. Largely conditions were warm and humid and the landscape was dominated by rainforests and swamp (Apthorpe, 1988; Martin, 2006). By the Eocene (~55 - 33 mya) we see the first evidence for a dry season in central Australia (Martin, 2006), and although the rainforests still dominated in the warm and humid conditions some sclerophyllous vegetation had appeared (Hill, 1998). This was followed by cool wetter periods in the Oligocene (~33 - 23 mya) (Feary *et al.*, 1991). The Miocene (~23 - 5 mya) is the first time in Australia we see major evidence for progression towards an arid landscape (Kershaw *et al.*, 1994). The rainforests became highly fragmented and only persisted in small remnants, and the inland forests began to diversify as the region increased in aridity. Additionally, regular water flows throughout the vast paleodrainage channels in Western Australia began to dry up (Martin, 2006). Although the Pliocene (~5 - 2.5 mya) began with a short wetter period, the general trend was for increasing aridity across the continent (Quilty, 1994). The vegetation had now transitioned to a more familiar and quintessentially Australian landscape, largely consisting of woodlands, arid shrub-lands and grasslands. The Pleistocene climate, ~ 2,588,000 - 11,700 years before present (bp) (Gibbard *et al.*, 2010), oscillated dramatically between dry and wetter phases, which corresponded to the glacial and interglacial cycles of the Northern Hemisphere respectively. Despite an almost lack of glaciation events in mainland Australia, glacial cycles resulted in reduced vegetative cover and the expansion of the inland deserts. Although inter-glacial phases were much wetter, the common pattern throughout the Pleistocene was for decreasing levels of precipitation and the transition to an arid climate and landscape that Australia is familiar with today (Martin, 2006).

Refugia hypothesis

The extensive and almost constant climatic oscillations during the Pleistocene involved rapid changes in both temperature, rainfall and CO₂ concentrations (Davis & Shaw, 2001), which must have had a profound effect on the Australian flora and fauna. According to niche theory, a species can respond to climatic fluctuations in one of four non-mutually exclusive ways (Jackson & Overpeck, 2000):

- Toleration - physiological or behavioural plasticity
- Adaptation - behavioural or evolutionary
- Migration - moving to areas which maintain favourable conditions
- Extinction - being unable to do any of the above.

The Pleistocene, and the subsequent response of species to the climatic oscillations, have been intensely studied over the last few decades (Bennett *et al.*, 1991; Hewitt, 1996, 1999, 2000; Byrne *et al.*, 2008). Fossil evidence indicates that species experienced extensive shifts in distribution in response to changes in climate (Brewer *et al.*, 2002). At the initiation of the last glacial maxima (LGM), species unable to tolerate or adapt to the drier phases were likely forced into extinction (Ferris *et al.*, 1999). However, for many species favourable conditions did not totally disappear, and some were able to persist in small remnants. During the wetter phases, when the environmental conditions became more favourable, species returned and expanded their range. The location of these refuges in times of harsh climatic conditions, are known as refugia in the literature (Keppel *et al.*, 2012), and are a very valuable conservation commodity, because without them many of Australia's present day biota would have gone extinct.

The Earth has experienced multiple glacial cycles in the past which have been frequently associated with the fragmentation of species ranges and their current phylogeographical patterns (Kilpatrick & Fowler, 1998). The last glacial cycle commenced approximately

135,000 bp during the Pleistocene, where species presumably contracted into remnant habitat, and finally gave way to the present interglacial cycle after 117,000 years (Hewitt, 1996).

Thus, it is often suggested these observed patterns within species are a result of them expanding to occupy their former ranges (McGlone, 1985). Glacial refugia in Australia for species associated with vegetation can be thought of as those areas where vegetation persisted yet experienced expansion and contraction events as the climate oscillated between very dry and wetter conditions (Grivet & Petit, 2002).

The rates of contraction and expansion events are likely to be different for woodland fauna in comparison to the flora. During the expansion events, the dispersal of faunal species that are strongly dependent on vegetation for retreat sites, thermoregulation, or foraging for example, is limited to the dispersal ability and establishment success of the vegetation (Comes & Kadereit, 1998; Austerlitz *et al.*, 2000). Whereas, the rate of contraction for woodland fauna is determined by their dispersal ability across an inhospitable matrix, as the vegetation dies in-situ from the impact of unfavourable climatic conditions (Ferris *et al.*, 1999). The dispersal ability into refugial areas during arid climate phases is therefore important to understand for the conservation of woodland fauna in the future.

The Pleistocene glacial and interglacial cycles have differed significantly between the Northern and Southern Hemispheres, thus refugial characteristics may also differ considerably. In the Northern Hemisphere the expansion of Pleistocene glacial ice sheets resulted in the broad-scale contraction of species into southern refugia (towards the equator), yet it is unclear whether expanding ice sheets were analogous to the expansion of Australian inland deserts within the Southern Hemisphere (Byrne *et al.*, 2008). Here, it has been suggested that broad-scale Pleistocene refugia may be associated with the inland ranges or the mesic east (both on the periphery of the expanding desert), which may have provided a buffer to the hyper-aridity of glacial conditions (Byrne *et al.*, 2008). Alternatively, if woodland

vegetation persisted in some areas, due to a buffering effect from local environmental features, refugia may also have existed in-situ at finer spatial and temporal scales. These areas are often referred to as cryptic- or micro-glacial refugia, and may explain the phylogeography of species populations that persist in a mosaic of habitat throughout the Australian arid zone (Stewart & Lister, 2001).

Several methods exist to help identify past refugial areas, which each differ in the availability and resolution of applicable data and the accuracy of the predictions that can be inferred. Pollen records can be utilised to discern the locality of some plant species (Huntley & Birks, 1983), although it becomes a limited approach when the number of individuals in a population is small, or when the species reproduces vegetatively or via wind pollination (Birks, 1989; Willis *et al.*, 2000). Fossils provide the potential for some of the most direct evidence for detecting the presence of refugia, by radio-dating fossils and identifying them at the species level (Field *et al.*, 2000). Unfortunately, fossil records are very sparse and finding sites of this nature is an extremely rare event (Rowell *et al.*, 2001). Species distribution models (SDM) are another tool that has been adopted to locate those regions that remained stable across multiple climatic conditions, for both individual species and habitats (Graham *et al.*, 2006; Moussalli *et al.*, 2009). Although, this approach is rarely used in isolation and is often combined with other methodologies to test for congruency between the findings (Scoble & Lowe, 2010).

In recent years molecular techniques have become a popular choice to explore and date the demographic history of species, due to their increased accessibility and continued reduction in cost of implementation. Species within arid regions have often been characterised with intra-specific genetic diversity (Pepper *et al.*, 2006). Thus, exploring these patterns of genetic variation can reveal the fragmentation of species ranges during past climates. By utilising these approaches numerous studies have suggested the location of refugia based on regions

with the highest genetic diversity and / or inferring the demographic history of a population (Hewitt, 1996; King & Ferris, 1998). These techniques can be applied at a range of spatial scales where sampling density permits, and can therefore be utilised to test for distinct genetic differences among and within potential regions of refugia (Stewart & Lister, 2001).

Sequencing regions of organelle DNA is amongst one of the most useful molecular markers for phylogeographical studies, and they have several benefits in comparison to nuclear markers (Ennos *et al.*, 1999). Firstly, due to the maternal inheritance of chloroplast and mitochondrial DNA, the retention of historical genetic structure is higher than biparentally inherited nuclear markers which are shuffled at each generation. Furthermore, organelle DNA is haploid which reduces the effective population size by half and increases the likelihood of genetic drift. This can increase the probability of intra-specific differentiation, which facilitates interpretations of the species phylogeographical history and subsequent identification of refugia (Petit *et al.*, 1997). Additionally, organelle DNA can be utilised as a molecular evolutionary clock to determine divergence dates between the branches of a species phylogeny (Ferris *et al.*, 1999). These times can then be correlated with both geological and climatic events to determine under what conditions the refugial regions were beneficial to species persistence. However, the mutation rate for many regions of DNA cannot be reliably quantified, as it is highly dependent upon reliable fossil record calibration points, which do not exist for most species (Heads, 2005; Ho & Phillips, 2009). Despite this limitation it is commonly accepted that at least broad-scale estimates can be made by adopting this approach (Byrne *et al.*, 2008).

Previously, molecular studies were restricted in the number of samples they could use due to cost limitations, which severely reduced the chance of sampling rarer haplotypes across broad geographic regions (Freeman *et al.*, 2001). Yet in the last five to ten years it has become relatively cheap to produce large molecular datasets, which can improve the accuracy of

inferences on the demographic history of species. In combination with other lines of research, molecular techniques have become a very powerful research tool.

How increasing aridity has impacted the Australian flora and fauna

Whilst the northern hemisphere experienced numerous and substantial glaciation events in the past, Australia was largely free from glacial impacts. For example, during the Pleistocene only 0.5 % of mainland Australia was glaciated (Williams, 2000). Although, the documented increasing aridity throughout these periods has resulted in two clear phylogenetic and phylogeographical patterns of diversity across the continent's arid biota.

The first pattern relates to the origins and diversification of the Australian arid zone lineages. Here, molecular phylogenies from several plant (Mummenhoff et al., 2001; Shepherd et al., 2004; Crayn et al., 2006; Watanabe et al., 2006), reptile (Chapple & Keogh, 2004; Hugall et al., 2008), insect (Leys et al., 2003; Cooper et al., 2007), and bird species (Joseph et al., 2006) have provided evidence for a single origin from a mesic ancestor. In contrast, other plant (Murphy et al., 2003; Ariati et al., 2006), marsupial (Krajewski et al., 2000; Crowther & Blackett, 2003), and reptile (Rabosky, 2006) species' phylogenies suggest in situ adaptive diversification from multiple central locations (Byrne et al., 2008). Both scenarios indicated that the ancestral origins pre-dated the Pleistocene.

The second pattern revealed the maintenance of intra-specific diversity was congruent with Pleistocene climatic cycling (Byrne et al., 2008). This qualitative evaluation suggested finer scale geographically structured intra-specific lineages are common in Australian arid species across multiple taxa with lower dispersal capabilities. These included plant, insect, amphibian, reptile, mammal, fish, mollusc, and crustacean species (Blackett et al., 2001; Byrne et al., 2002; Byrne et al., 2003; Sanetra & Crozier, 2003; Byrne & Hines, 2004; Carini

& Hughes, 2004; Chapple & Keogh, 2004; Hughes et al., 2004; Hughes & Hillyer, 2006; Kearney et al., 2006; Edwards, 2007). Where highly localised Pleistocene refugia could be identified in the northern hemisphere, the species within these Australian studies all displayed multiple clades which lacked the molecular signature of recent expansion events. Here, the high diversity and deep divergences amongst lineages indicated multiple localised refugia throughout the species' ranges (Byrne et al., 2008). In these locations where populations persisted, lineage divergence are thought to have accumulated through the cyclical expansion and contraction of habitat which mirrored climatic fluctuations.

Global climate change

Knowledge on the location of past refugia and the environmental features they may have been associated with, has become increasingly valuable information for conservation when considering the likely impact rapid global climate change (GCC) will have on biodiversity in the near future (Thomas *et al.*, 2004).

Past climatic changes were the result of natural fluctuations caused by variation in the Earth's orbit or the volcanic output of carbon dioxide (CO₂) into the atmosphere (Root & Schneider, 2006). However, more recently global climates have been substantially influenced by human activities (IPCC, 1996). Unfortunately, the atmosphere has become the dumping ground for human gaseous waste. This practice has resulted in an increased concentration of atmospheric greenhouse gases, which has been firmly established beyond all reasonable doubt to contribute to global climate change beyond background rates (Hughes, 2003), and will likely contribute 1.5°- 6 °C to global temperatures in the next century (IPCC, 2001). Global trends indicate that the current rate of global warming exceeds any period of time in the last 1000 years, with both changes in temperature and precipitation that exceed both natural decadal and century scale variability (IPCC, 2001). Since 1900 the Earth's global average surface

temperature has already increased by 0.6 ± 0.2 °C, and there is substantial evidence suggesting this has already resulted in negative impacts for species and ecosystems throughout the world (Hughes, 2003; Thuiller *et al.*, 2005; IPCC, 2007).

In Australia, changes in climatic variables over recent decades have been consistent with global trends. The continent's average temperature has been rapidly increasing since 1910, with decadal increments of 0.1- 0.2 °C since 1951 (Suppiah *et al.*, 2001). These temperature increases are not uniformly distributed across the continent or seasons, with the greatest warming having occurred over the inland arid regions during the winter and spring seasons (Hulme & Sheard, 1999). The average temperature increases have also been associated with the increased frequency of extreme warm events, decreased frequency of cold events, increased frequency of El Niño events, and the decreased frequency of La Niña events. All of these changes to climatic conditions have contributed to the increasing aridity of the Australian continent.

Over the past century regions of Australia have experienced increased rainfall, yet due to high inter-annual variability this is not a significant increase on a continent wide scale (Hennessy *et al.*, 1999). This variability can also be problematic. The little annual rain that the arid regions do receive can either fall all in one day or not at all. So it would take a substantial increase in rainfall to be of greater benefit to biodiversity in the region, especially when you consider that falls of less than 6 mm disappear before they can be absorbed (Martin, 2006). Thus, due to the simultaneous increase in temperatures and rate of evaporation, little (if any) of the rainfall increases will be available to the continent's flora and fauna (Hughes, 2003).

Australian climate projections for the near future predict a similar pattern to what has been experienced over the last few decades. Relative to 1990, annual average temperatures are predicted to increase by 0.4 - 2.0 °C by 2030, 1.0 - 6.0 °C by 2070, and with an increased frequency of extreme temperatures (Hughes, 2003). It would seem that average annual rainfall

is more difficult to project, and often different models do not concur in their estimations, which is likely due to their inability to accurately simulate El Niño Southern Oscillation events (IPCC, 2001). Despite this uncertainty, modelling predicts that every 1.0 °C of warming will be accompanied by an 8 % increase in evaporation and the intensification of droughts during El Niño years. The overall scenario, once all variables are accounted for, will see a decrease in the moisture balance of ~40 - 120 mm per degree of temperature. This represents a decrease of 15 - 160 mm by 2030, 40 - 500 mm by 2070, and decreases in water run-off throughout continental Australia (Arnell, 1999; Hughes, 2003).

Predicted impacts from global climate change

Contemporary research and the fossil record clearly outlines the impacts that past GCC had on the abundance and distribution of species, which will continue to be impacted in similar ways in the future (Hughes, 2000; Walther *et al.*, 2002; Thomas *et al.*, 2004; Thuiller *et al.*, 2005; IPCC, 2007). The utility of SDM has been the principal method to determine regions of favourable climatic conditions for species past, present and future; from which the species distribution is inferred. The consistent message suggests that GCC will cause the majority of species distributions to contract, shift to higher latitudes and / or altitudes, and become increasingly fragmented (Hughes, 2003).

It has been suggested that the impact of near future GCC scenarios will likely result in the local extinction or displacement of Australian plant species because most are constrained within a narrow geographic and climatic range (Pouliquen-Young & Newman, 2000). For example, of the 819 Eucalypt species throughout the Australian landscape 53 % have current distributions spanning < 3 °C of mean annual temperature (Hughes *et al.*, 1996). Furthermore, it was predicted that 59 % of 27 Acacia species would disappear with a 1 °C increase in mean annual temperature and those remaining would suffer a 75 % decline in their present

distribution (Pouliquen-Young & Newman, 2000). It has been shown in controlled experiments that when temperature changes are accompanied by elevated concentrations of atmospheric CO₂, plant growth will often be enhanced due to the CO₂ fertilization effect (Bazzaz & Fajer, 1992). However, it must be noted that in these experiments plants were provided with optimal growing conditions, including water and nutrient availability, yet the Australian continent is already nutrient poor and the climate is projected to increase in aridity (Hughes, 2003). In general, the Australian tree flora which are known to provide habitat for a large number of species across a range of taxa (Gibbons & Lindenmayer, 2000), are likely to experience substantial changes in the future.

Understanding the impact of near future GCC on invertebrates in Australia has received less attention, yet is important because invertebrates provide many ecosystem services and are often an integral component of the vertebrate diet. One modelling study of 77 Australian butterfly species, (Beaumont & Hughes, 2002) indicated that even when species displayed a wide climatic range the impacts from GCC were likely to be negative. For example, with a temperature increase of 2.1 - 3.9 °C by 2050, up to 92 % of the species' favourable climatic regions were predicted to decrease by at least 50 %. Despite the limitation of research in this area, the negative impact to vegetation is likely to be mirrored in those invertebrates that depend on the vegetation for their survival.

Substantially more GCC impact assessments for vertebrate species have been made in Australia, although the findings paint a similar negative picture. In separate studies, across 99 threatened species, ~ 80 % of species were predicted to lose 80 - 100 % of their current favourable climatic conditions, using likely temperature increases and rainfall scenarios (Brereton *et al.*, 1995; Dexter *et al.*, 1995). Species with a non threatened conservation status are predicted to be equally at threat. For example, across 345 Australian reptile species (including the terrestrial elapid snakes, skinks and freshwater turtles) 87 % are predicted to

suffer range contractions by 2050 under the A2 emissions scenario (Cabrelli Unpublished PhD Thesis); (A2 = likely future which describes an increasing population, technology, and CO₂ emissions, where economic growth is favoured over environmental concerns). In addition to the predicted response from changes in climatic variables, some vertebrate species will be indirectly affected by the negative changes in distribution from their host vegetation and sources of prey.

Limitations of species distribution modelling

Correlative modelling approaches are a powerful predictive tool to assess the impact of GCC to species. Although, careful consideration needs to be given to ensure variable choice and model parameterization are appropriate for the species in question (Synes & Osborne, 2011). Making arbitrary choices during the model-building process may result in reducing a models predictive ability and / or increasing uncertainty. Here, there are clearly defined procedures to help circumvent these types of issues which include; removing auto-correlated variables or those with low predictive ability to avoid over-fitting the model, selecting future climate models appropriate for the region, and utilising fine scale grids for climate layers if a sufficiently high number of evenly distributed species occurrence records exist. Modelling parameters are then often determined by the number and location of species occurrence records, and whether climate variables in the projected distribution fall within the range covered in the training data. Furthermore, the databases where occurrence records are sourced from (i.e. The Global Biodiversity Information Facility - GBIF), can have errors. Thus, the recorded points need to be manually checked to ensure that they do not occur outside of the species known distribution and / or is not likely to represent a second species. Failing to exclude erroneous records will result in an over-estimation of the species climatic envelope, and any subsequent projections made from the data.

Even when robust model-building processes have been adopted it does have several limitations. First, the number and distribution of occurrence records used to estimate the bioclimatic conditions that the species currently occupies can have a large influence on predictions (Costa *et al.*, 2010). For example, if known occurrence records do not represent the species geographic range, then the species climate tolerance may be underestimated. This can be avoided by obtaining numerous records that are not clustered in a single geographic eco-region. Second, the models assume a species to be in equilibrium with its present climate (O'Connor, 2001). Unfortunately, testing this assumption is something that can only be achieved retrospectively, and is of greater concern for invasive species in a state of spread (Elith *et al.*, 2010). Finally, the models commonly make predictions based on abiotic variables (such as climate, soil, aspect, slope etc), thus assuming they are the primary factors influencing a species distribution. Whilst this correlative approach may capture some biotic processes implicitly (Davis *et al.*, 2005; Kearney & Porter, 2009), predation, competition and dispersal ability are not directly incorporated within current models. Although there seem to be no obvious approaches to test for present distribution equilibrium, or to incorporate the complexity of species interactions into modelling, opportunities to incorporate dispersal characteristics do exist.

What determines the distribution of a species is a fundamental question in ecology. Dispersal ability is likely to be a key variable which influences a species geographic range, and could provide more realistic projections, yet is rarely incorporated. One of the major problems is obtaining measures of dispersal at the landscape scale. Options may include capture-mark-recapture, radio tracking of tagged individuals or genetic estimates of dispersal. Genetic approaches offer the greatest potential because they only require a single sampling effort of individuals. Additionally, genetic methods target the dispersal of breeders over multiple generations, which the other two approaches fail to achieve. This is even more applicable

considering SDM projections are often made over timescales greater than the generation length of the species in question.

Study species

The selection of a representative arid zone woodland species that had the appropriate ecological characteristics to facilitate research at the required temporal and spatial scales was critical for this study. Furthermore, a comprehensive understanding of the selected species' ecology and life history would help plan research, sampling design, and develop evolutionary theory. Due to the size of the Australian arid zone, a common species with a wide distribution that encompassed all the arid zone habitats under study was required. The species also needed to have relatively low vagility, because high dispersal ability could dilute the genetic signals of population structure over both spatial and temporal scales. Finally, the species also needed to be strongly associated with arid woodlands for its preferential habitat, because it has already been firmly established that climatic fluctuations influence the distribution of native vegetation (Hughes, 2003).

One of the most ubiquitous taxa within arid zone Australia is the squamate reptiles which contain several major evolutionary lineages, each with many species and genera (Donnellan *et al.*, 1999). In comparison to other vertebrate species they are often more accessible and easier to sample (Hibbits *et al.*, 2005), and for this reason have become the focus of intense ecological research. Findings suggest that reptile distributional patterns are controlled by habitats fluctuating throughout space and time (Pianka, 1972), and the primary factor determining geographic range is habitat continuity (King, 1979), which are strongly influenced by climatic conditions. Geckos represent one of the largest lizard families with species numbers exceeding 850 worldwide, and one species from the Australian arid zone has

become relatively well known - *Gehyra variegata* (Bustard, 1969; Pianka & Pianka, 1976; Moritz, 1987; Henle, 1990).

Gehyra variegata is a tree dwelling, nocturnal and moderately sized gecko that is widely distributed throughout the arid and semi arid regions of Australia. There is no evidence to suggest *G. variegata* has ever been of conservation concern and is not currently listed in the IUCN Red List of Threatened Species (as of June 2012). Throughout the 1960s, this species was intensely studied (Bustard, 1967, 1968a, b, 1969, 1970) and it is from this time that our in-depth understanding of the species' ecology and life history traits have been recorded. This initial work then facilitated progressive studies throughout the last four decades (King, 1979; Moritz, 1987; Kitchener *et al.*, 1988; Henle, 1990; Moritz, 1992; Sarre *et al.*, 1995; Sarre, 1998; Sistrom *et al.*, 2009).

Although *G. variegata* is widely distributed throughout the arid regions of Australia, in the 1970's it was found to contain three distinct chromosomal races ($2n = 40a$, $40b$, and 44) (King, 1979). Of these races two are rock dwellers ($2n = 40b$ and 44) (Kitchener *et al.*, 1988; Sarre, 1998), from which the $2n = 44$ race was recently described as a distinct species (*Gehyra lazelli*) (Sistrom *et al.*, 2009). Although the $2n = 44$ race is sympatric with the $2n = 40a$ race in some areas, they can be distinguished by using morphological characteristics (Sistrom *et al.*, 2009). Additionally, the $2n = 40a$ is more widely distributed and predominately retreats beneath exfoliating bark and tree debris (Bustard, 1968a; Henle, 1990; Duckett & Stow, 2012).

The literature supports varying rates of dispersal for *G. variegata*, which can be explained if dispersal rates vary with habitat, between chromosome races, and / or if capture-mark-recapture methodologies underestimate true rates of dispersal. For example, annual movements have been recorded that vary from 5 to 150 metres (Bustard, 1969; Moritz, 1987; Henle, 1990; Sarre *et al.*, 1995). More recently, fine scale genetic approaches suggest regular

dispersal occurs between fragments of up to one kilometre (Hoehn *et al.*, 2007). Sarre (1998) also revealed that *G. variegata* could rapidly colonise new habitats where vegetation was continuous, yet this seems unlikely to occur in fragmented habitat due to high predation pressure from numerous mammals, bird and larger reptiles (Bustard, 1969).

Gehyra variegata is dependent upon the woodland habitat not only to facilitate its dispersal, but it is also very important for many stages of its life history (Bustard, 1968a). The species is commonly found underneath exfoliating bark, within woody crevices of its host trees, or within woody tree debris that has fallen to the ground. First, these woody retreat sites lower predation risk substantially from a plethora of predators, in comparison to when *G. variegata* is moving through open spaces (Gruber & Henle, 2008). In fact, arboreality is believed to have evolved in response to higher predation risk at ground level (Henle, 1990). Second, woody retreat sites are vital for thermoregulation, because reptile physiology and behaviour is influenced by body temperature and has direct and indirect consequences to an individual's fitness. For example, body temperature can regulate auditory and locomotor performance, which facilitates predator avoidance, prey capture and prey handling. Body temperature also impacts the rate at which processes such as growth, reproduction and metabolism occurs (Werner, 1976; Bennett, 1980; Goode & Duvall, 1989; Van Damme *et al.*, 1991; Angilletta & Werner, 1998). Conducting thermoregulation whilst in woody crevices allows *G. variegata* to avoid extreme day- and night-time temperatures. Third, the woody retreat sites are utilised by invertebrate species for similar reasons, so the majority of *G. variegata* foraging activities are also conducted here. Finally, woody retreat sites are utilised for both reproduction and the incubation of eggs, which again provides protection from both temperature fluctuations and predatory events. In most locations, the absence of woody retreat sites would negatively impact the health of individuals due to the increased exposure to the desert elements, and / or death from increased exposure to predators.

Summary

To effectively assess the vulnerability of species from the impact of GCC requires knowledge in multiple biological disciplines (Williams *et al.*, 2008); including ecology, physiology, genetic diversity, adaptive capacity, resilience and sensitivity to change, and changes to intra- and interspecific processes. The resulting suite of information may then be used to assess whether the species is likely to be of conservation concern in the near future. In the chapters to follow I utilise *G. variegata*^{40a} as my study species and focus on a few key areas.

This small Australian gecko is a non endangered species with a wide distribution throughout the arid regions of Australia. The species is highly dependent upon the woody vegetation for its retreat sites, facilitation of dispersal, and also for many stages of its life history. Thus, a genetic estimate of dispersal was of greatest importance to understanding the likely impacts of changes to vegetative structure and climate (past, present, and future) for this species. This will likely further our knowledge on the environmental features that promote population persistence for other arid woodland biota, and the actions we can take in the future to conserve Australia's biodiversity in the region. A measure of genetic variation before and after the impact has been included, because the conservation of genetic biodiversity is mandated by the International Convention on Biological Diversity (www.cbd.int), and is recognised by the International Union for Conservation of Nature (www.iucn.org) as one of three forms of biodiversity deserving conservation.

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CHAPTER TWO: DESIGNING MOLECULAR TOOLS

In a preliminary study (unpublished data) I tested the cross amplification success for a set of microsatellite markers that were designed for the Western Australian *Gehyra variegata*^{40b} chromosome race. Due to the poor success rate, I decided to design a new set of microsatellite markers specifically for *Gehyra variegata*^{40a}. These new markers would supplement those that were found to be useable to provide greater statistical power at finer spatial scales of analysis. This chapter was successfully published in Conservation Genetic Resources.

Duckett, P.E., & Stow, A. (2010) Rapid isolation and characterisation of microsatellite loci from a widespread Australian gecko, the Tree Dtella, *Gehyra variegata*. Conservation Genetics Resources, 2, 349-351.

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CHAPTER THREE: DISPERSAL AND SPECIES DISTRIBUTION MODELLING

In this chapter I utilise the new microsatellite markers to obtain estimates of dispersal for *Gehyra variegata*^{40a} at the landscape scale, dispersal estimates are then incorporated into the species distribution modelling process. This allowed me to quantify the regions of the current distribution that are capable of reaching the predicted future distribution, and those areas of the future distribution that are likely to be colonised. This chapter has been published in Diversity and Distributions.

Duckett, P.E., Wilson, P.D. & Stow, A. (2013) Keeping up with the neighbours: Using a genetic measurement of dispersal and species distribution modelling to assess the impact of climate change on an Australian arid zone gecko (*Gehyra variegata*^{40a}). Diversity and Distributions. 10.1111/ddi.12071.

Keeping up with the neighbours: Using a genetic measurement of dispersal and species distribution modelling to assess the impact of climate change on an Australian arid zone gecko (*Gehyra variegata*^{40a})

Abstract

Aim During this century, rapid climate change will have a profound effect on global biodiversity, and species survival will be contingent on their ability to adapt or disperse. Species distribution models are a popular tool for gauging how the distribution of favourable climate may change over space and time. Evaluating the level of dispersal between the current distribution and potential future distribution of a species is key to predicting their survival, but rarely estimated. Here we applied species distribution models and a genetic estimate of dispersal to quantitatively assess dispersal to new distributions in the timescale imposed by future climate change.

Location / Methods We sampled 635 adult *Gehyra variegata*^{40a} throughout central and eastern Australia, encompassing much of the recorded distribution for this gecko. We genotyped all individuals at 16 microsatellite loci, from which we estimated mean annual dispersal distance using Wright's neighbourhood size. Species distribution modelling predicted the current and future distribution of the species, and we used annual dispersal distances to evaluate whether the species could keep up with shifts in the range of their favourable climatic conditions.

Results Our estimates of mean dispersal show that 17 - 41 % of the current *G. variegata*^{40a} distribution is unlikely to contribute to their future distribution given the timescale imposed by future global climate change.

Main Conclusions Our approach can make further use of molecular and occurrence record data sets to answer whether a species has the capacity to reach future areas of favourable climate and the extent to which the current distribution will contribute to this process.

Keywords: Climate Change, Conservation, Dispersal, Genetics, Neighbourhood, Species Distribution Modelling.

Introduction

It is common knowledge that global climates have influenced the natural distribution of biodiversity. Evidence from both contemporary observations (Hughes, 2000; Walther *et al.*, 2002; Thuiller *et al.*, 2005) and the fossil record (Davis & Shaw, 2001) demonstrate the influence changing climates exert on species distributions. Atmospheric greenhouse gases are certain to increase in the future and Global Climate Models (GCMs) predict global warming in the range of 1.1 – 6.4 °C by the year 2100 relative to 1990 (IPCC, 2007). This unprecedented rate of change in the world's climate is expected to result in numerous extinctions (Thomas *et al.*, 2004). For example, across lizard taxa it is predicted that an appropriate thermal niche will not be retained in-situ, and that climate change has already resulted in 12 % of local populations becoming extinct across 48 species of Mexican lizard since 1975 (Sinervo *et al.*, 2010). In order to survive, species may adapt to climate change either through plasticity or evolutionary adaptation, but this might not be possible within the timescales imposed by global climate change (Gienapp *et al.*, 2008; Visser, 2008), or when the conditions have not been experienced in their evolutionary history (Ghalambor *et al.*, 2007). The alternative to adaptation is relocation, the success of which is contingent on the dispersal ability of the organism in question and the scales at which new favourable areas are located (Gaston & Blackburn, 2002; Thomas *et al.*, 2004).

Species distribution modelling (SDM) is a well established technique used to predict species distributions under various climate scenarios. The technique correlates species occurrence records with climate variables to model the environmental requirements, which are then used to predict species distribution patterns. SDMs have shown how species ranges may shift in response to climatic changes, thus revealing any loss or gain in the areas with favourable conditions (Cordellier & Pfenninger, 2009; Fouquet *et al.*, 2010). Predictions from SDMs have been coupled with genetic techniques to infer the process of past divergences and the

locality of refugia (Knowles *et al.*, 2007; Waltari *et al.*, 2007). A problem with SDM is that this correlative approach predicts a species distribution without explicitly incorporating processes that potentially limit its range (Kearney & Porter, 2004; Guisan *et al.*, 2006; Heikkinen *et al.*, 2007; Morin & Thuiller, 2009). To provide greater confidence in projections of species future distribution, consideration needs to be given to mechanistic variables including physiological traits, biotic interactions and dispersal characteristics (Davis *et al.*, 2005; Kearney & Porter, 2009).

Dispersal is likely to be among the most important mechanistic factors influencing species ranges, and may therefore be a key variable for predicting future distributions following climate change. The need to consider dispersal when predicting changes in species distributions has been recognised many times throughout the last two decades (Pitelka *et al.*, 1997; Cain *et al.*, 1998; Cain *et al.*, 2000; Nathan & Muller-Landau, 2000; Araújo & Guisan, 2006). However, the few SDM studies that have incorporated dispersal to gauge the effect of climate change are plant studies (Ostendorf *et al.*, 2001; Iverson *et al.*, 2004; Engler & Guisan, 2009). Additionally, some have simulated dispersal rates (Pagel & Schurr 2012), but to our knowledge none have used a genetic estimate of dispersal, which is important when considering dispersal over multiple generations. A major impediment to predicting future distributions is obtaining measures of dispersal at the landscape scale.

In the last decade genetic techniques have been utilised across many taxa to indirectly measure dispersal (Stow *et al.*, 2001; Sumner *et al.*, 2001; Watts *et al.*, 2007; Pinsky *et al.*, 2010; Duckett & Stow, 2012). Genetic estimates of dispersal could be combined with SDMs to better assess the likelihood of species reaching potential future distributions within the required timescale. SDM first predicts the current and future distribution of species using a correlative approach with presence data and environmental variables. Then, using a dispersal estimate inferred from the genetic data we can evaluate whether a species is likely to keep

pace with their predicted range shift. This interdisciplinary approach incorporates both correlative and mechanistic variables that limit species distributions to quantitatively assess the proportion of a current species distribution that can feasibly reach their future distribution. Increasing the capacity to predict a species response to climate change will help improve the uncertainty in this field (Heller & Zavaleta, 2009).

In this study we investigate the impact of climate change on an Australian arid zone gecko. The Australian arid zone represents the country's largest biome which houses exceptional levels of biodiversity including a diverse and endemic lizard fauna (Cogger, 2000; Byrne *et al.*, 2008). The arid zone spans approximately 70% of continental Australia and is characterised by annual climatic variation, some topographical heterogeneity, ephemeral river systems, and a sparse mosaic of vegetation (James & Shine, 2000; Martin, 2006). We use microsatellite markers to estimate levels of dispersal and annual dispersal distances for a small tree dwelling gecko (*Gehyra variegata*^{40a}) across the major landscape features in arid Australia. We then couple these estimates with SDMs to determine if the species is capable of reaching new distributions imposed by future climate change. Because of the speed at which the climate is expected to change, we predict that a proportion of this species current distribution will be too far away from its predicted future distribution, which will result in isolation from favourable climatic conditions. We also predict that a proportion of the area that is suitable for *G. variegata*^{40a} in the future is unlikely to be colonised over the next 70 years. If either of the predictions is confirmed we will identify and quantify those areas.

Methods

Study species and sampling strategy

Gehyra variegata is a small gecko that is widely distributed throughout the arid regions of Australia and has three distinct chromosomal races ($2n = 40a$, $40b$, and 44) (King, 1979). The rock dwelling $2n = 44$ race was recently described as a distinct species (*Gehyra lazelli*) (Sistrom *et al.*, 2009). The $2n = 40b$ variant may also utilise rocky outcrops as retreat sites (Hoehn *et al.*, 1996; Sarre, 2007) and the $2n = 40a$ variant predominately retreats beneath exfoliating bark and tree debris (Bustard, 1968; Henle, 1990; Duckett & Stow, 2012). We sampled the most widely distributed tree dwelling $2n = 40a$ variant which is found throughout central and eastern Australia. Because the $2n = 44$ is sympatric with the $2n = 40a$ variant in some areas, we used morphological characteristics to avoid misidentification (Sistrom *et al.*, 2009). Sequence data from the ND4 region of the mitochondrial genome was collected for each individual and confirms the presence of a single species (unpublished data). Our study sites were located throughout the arid and semi-arid zones of central and eastern Australia, which closely matches the complete distribution of *G. variegata*^{40a} (King, 1979).

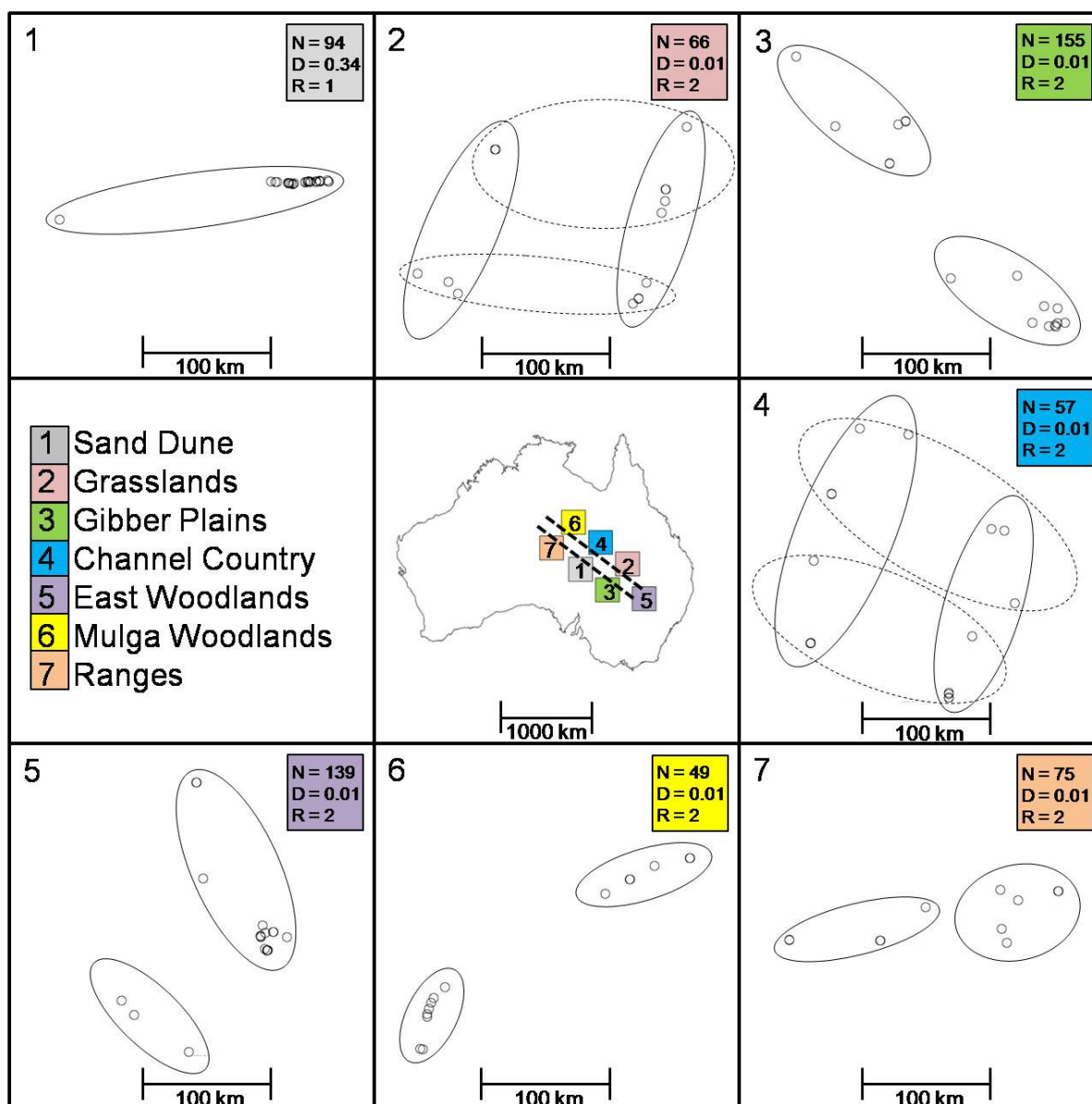
The distribution of *G. variegata*^{40a} throughout arid zone Australia was broadly categorised by habitat type and landscape features: mulga woodlands (sparse woody vegetation), eastern woodlands (denser woody vegetation), Mitchell grasslands (predominantly tussock grass), the channel country (sprawling riverbeds with ephemeral flooding events), gibber plains (stony deserts with sparse woody vegetation), sandy deserts (sparse woody vegetation and dune fields), and MacDonnell Ranges (regions of higher relief); which we now refer to as 'landscapes' (Figure 3.1). *Acacia aneura* (mulga) and *Acacia cambagei* (stinking gidgee or wattle) dominates the woody vegetation in most of these landscapes, with the exception of the eastern woodlands which are commonly comprised of the genera *Eucalyptus* and *Callitris*. *G. variegata*^{40a} was collected from each of these landscapes to evaluate variation in dispersal,

assuming that dispersal characteristics will differ among landscapes. We could have evaluated the relationship of dispersal with environmental gradients, such as that represented by the climatic data or soil type. However, in arid Australia, distinctive and adjacent landscapes often have very similar climatic conditions and a single soil classification can be found in contrasting landscapes (e.g. sandy plains versus sand-dune formations). On a broader scale, understanding how landscape features influence genetic structure has been a major goal of landscape genetics in the last decade (Storfer *et al.*, 2010), and dispersal resistance is often categorised by broad landscape features and characteristics (Spear *et al.*, 2010). Our sampling covered a large proportion of this species distribution and spanned much of the rainfall and temperature gradients experienced in arid Australia along with most of the soil types (ANRA 2001). We therefore expect that our sampling captured much of the variability in dispersal that may be present throughout the distribution of *G. variegata*^{40a}.

Samples were collected from two large-scale transects (~1700 km) designed to include the majority of landscapes inhabited by *G. variegata*^{40a} (Figure 3.1). Here, the intention was not to replicate the landscape types within each transect, but allowed a measure of dispersal to be taken at the largest geographic scale within the species known distribution. Within each landscape type, smaller replicate areas were sampled to allow dispersal to be compared between landscapes, and with larger geographic scales (Figure 3.1). Sampling effort within each replicate landscape was similar, yielded a varying number of individuals and encompassed a mean area of (mean 4900 km² ± 3500). The wide variation in the area from where individuals were sampled at different locations is largely due to the harsh environmental conditions within the Simpson Desert, where only a single transect was possible. Here, individuals were only located in a small geographic range ~275 km² (Figure 3.1).

Figure 3.1 Sampling design

The sampling design: landscape type can be identified by matching the colours and / or the numbers shown in the key. Within each landscape the number of samples (N), samples per km² (D), number of replicate sampling areas (R), individuals within each replicate (solid line), and individuals within each replicate for across catchment comparisons (broken line) are given. Localities where *G. variegata*^{40a} was captured are marked by an open circle. Broken lines on the map (figure centre) represent the two large scale transects.



During 2009 and 2010 we captured 635 individual adults by searching potential retreat sites across the largest of the *G. variegata* chromosomal races (2n 40a) (King, 1979), with very few exceptions, individuals were found in retreat sites associated with woody vegetation. The time period of collection coincided with the end of an El Niño-southern oscillation event that had created a long dry period, therefore dispersal estimates are likely to be associated with these conditions. Adult geckos were classified by using the minimum snout-vent length of a gravid female (Kitchener *et al.*, 1988), or if male, by visual recognition of the obvious bulges, just distal to the cloaca, which contain their hemipenes. The location of each tree on which individuals were captured was recorded using GPS. The distances between capture locations within each landscape ranged from 0 to 300 km, and prior to release a tail-tip tissue biopsy was taken and stored in 95 % ethanol for analysis back in the laboratory.

Laboratory procedures

We extracted total DNA using a modified salting-out protocol (Sunnucks & Hales, 1996) and genotyped all 635 individuals at 16 microsatellite loci by Polymerase Chain Reaction (PCR) (Table 3.1). The final reagent concentrations and the thermocycling conditions for PCR are outlined elsewhere (Hoehn & Sarre, 2006; Duckett & Stow, 2010). To test our data quality we reanalysed five percent of individuals at all loci and identical genotypes were obtained for each of these individuals in both runs.

Table 3.1 Summary statistics

Observed (H_O) and expected (H_E) heterozygosity for 16 microsatellites across the 635 individual *G. variegata*^{40a} samples. F_{IS} values marked * showed significant deviation from Hardy-Weinberg Equilibrium after adjustment for multiple tests ($\alpha < 0.05$).

<i>Locus</i>	<i>N</i>	<i>N_A</i>	<i>Range</i>	<i>H_E</i>	<i>H_O</i>	<i>F_{IS}</i>
GVVSN	620	45	168-400	0.877	0.742	0.155*
GV4B6	600	44	304-516	0.954	0.767	0.197*
GV92I	622	16	96-168	0.847	0.619	0.270*
GV1C10	620	38	292-480	0.943	0.827	0.123*
GVMJA	621	15	224-296	0.817	0.763	0.067*
GVYR7	612	25	272-488	0.901	0.779	0.136*
GV3C6	618	10	164-232	0.229	0.189	0.173*
GVVVF	607	29	316-532	0.888	0.713	0.197*
GVWD8	614	29	156-268	0.905	0.832	0.081*
GV4C9	608	38	204-504	0.911	0.775	0.150*
GVGVB	621	25	128-240	0.906	0.847	0.066*
GV3E10	615	36	208-364	0.950	0.777	0.183*
GVN6E	624	13	228-276	0.861	0.796	0.076*
GV17E	616	26	324-464	0.897	0.851	0.052*
GV56J	626	25	128-268	0.882	0.832	0.057*
GVT64	610	52	336-608	0.942	0.854	0.094*
Mean		29.15		0.857	0.748	0.128*

Summary genetic data

We calculated summary data including number of alleles (N_A), observed heterozygosity (H_O), and expected heterozygosity (H_E) using GENALEX v6.0 (Peakall & Smouse, 2006).

Measurements of F_{IS} , linkage disequilibrium, and the significance of any deviation from Hardy-Weinberg equilibrium (HWE) was calculated with FSTAT v2.9.3 with corrections for multiple tests (Goudet, 2001).

Characterising dispersal by analysis of relatedness

We assessed the geographic distribution of pairwise genetic similarity for adult individuals within the replicate areas of each landscape by spatial autocorrelation using GENALEX v6.0 (Peakall & Smouse, 2006). The GENALEX software calculates a spatial autocorrelation coefficient (r), which is commonly referred to as relatedness (Repaci *et al.*, 2006; Colson *et al.*, 2012). Significantly higher relatedness at close geographic scales infers that dispersal is limited at the spatial scales being examined. Because ephemeral river systems are common features in some regions within the Australian arid zone, we assessed if rivers were associated with higher or lower levels of dispersal as these may potentially influence the precision of our estimates of average dispersal distance. We analysed the distribution of relatedness across- and along-river systems in the channel country and Mitchell grassland landscape. For all analysis we used the single population option with distance categories defined to maximise the number of pairwise comparisons, and where possible to allow for comparisons across landscapes at similar spatial scales. The 95 % confidence intervals around mean relatedness (r) within each distance category were estimated by bootstrapping 9999 times, and the 95 % confidence intervals around a random distribution (mean $r = 0$) was determined by 9999 permutations.

Calculating annual dispersal distance

Following Wright, the ‘neighbourhood’ is a unit of genetic structure that reflects the average distance between the natal and breeding site of the organism in question (Wright, 1943; Slatkin & Barton, 1989). Using a method based on the neighbourhood, we indirectly estimated annual dispersal distance by approximating the neighbourhood size. Neighbourhood size (NS) can be estimated from the inverse of a regression slope between a multi locus estimator of individual pairwise genetic distances ($F_{ST} / (1 - F_{ST})$) regressed on geographic distance (Rousset, 1997, 2000). This relationship can be biased by very small spatial scales, thus we exclude comparisons where individuals occur at the same GPS point (same tree), and regress the logarithm of geographic distance against the $\hat{\theta}$ estimator of genetic distance using GENEPOP3.2a (Raymond & Rousset, 1995). The regression method has been demonstrated to provide good levels of congruency between direct and indirect estimates of NS (Sumner *et al.*, 2001), and remains robust to low rates of long distance dispersal, when isolation by distance (IBD) is measured in non linear habitats, when IBD is weak, or from higher sampling variance (Watts *et al.*, 2007).

Neighbourhood size is equal to $4\pi D\sigma^2$, where D is the population density and σ^2 is the variance of per generation dispersal. This facilitates either the evaluation of density if dispersal is known ($D = NS / 4\pi\sigma^2$), or dispersal if density is known ($\sigma^2 = NS / 4\pi D$). From this two dimensional estimate of dispersal area between parent and offspring we calculated a linear estimate of annual dispersal per individual by considering the species' generation length of 2 years (Bustard, 1969). In each replicate area within landscapes we estimated the effective density (D_E) by dividing the effective population (N_E) by the area occupied by those samples (length multiplied by the width of the furthest points). Various methods exist for calculating N_E from multi-locus datasets, which vary from short term methods to those that account for

long term variation (Leberg, 2005; Wang, 2005). Although coalescent-based approaches, which may consider longer term variation in allele frequencies, have been used with some success, incomplete sampling can confound results, and so these methods remain more applicable to systems where sampling is known to be complete (Slatkin, 2005). The benefit of using a contemporary estimate of N_E in this study ensured that dispersal estimates were conservative and not confounded by historical gene-flow, which seems appropriate when rare events over evolutionary timescales may be irrelevant to current ecological processes in arid Australia (Pinsky *et al.*, 2010). Therefore, we adopted the sib-ship assignment method using a single sample of multi-locus genotypes as implemented by COLONYv2.0.1.1 (Jones & Wang, 2010). In simulation studies this method has outperformed the heterozygote excess, linkage disequilibrium, and temporal methods and does not require the assumption of random mating (Wang, 2009). For our analysis we used a full-likelihood approach with a long-run and medium-likelihood precision, no sib-ship prior, and a standard genotyping error rate of 2 %.

These estimates of dispersal can be potentially biased by the scale of analysis as genetic structure may change with scale (Ruckelshaus, 1998). We evaluated the effect of scale by applying this method to each replicate within each landscape, and also to each of the large-scale sampling transects. For the method to be applied there needed to be no significant difference in average dispersal estimates calculated at the different geographic scales.

Inferring current and future species distributions from species distribution modelling

Using available occurrence data for *G. variegata*^{40a}, we modelled environmental suitability using MAXENT 3.3.1. The resulting models were utilised to predict areas of climatic suitability to 2030 and 2070 using four Global Circulation Models with the A2 scenario. See 'Supplementary Information' for a full explanation and justification of model building and modelling procedures.

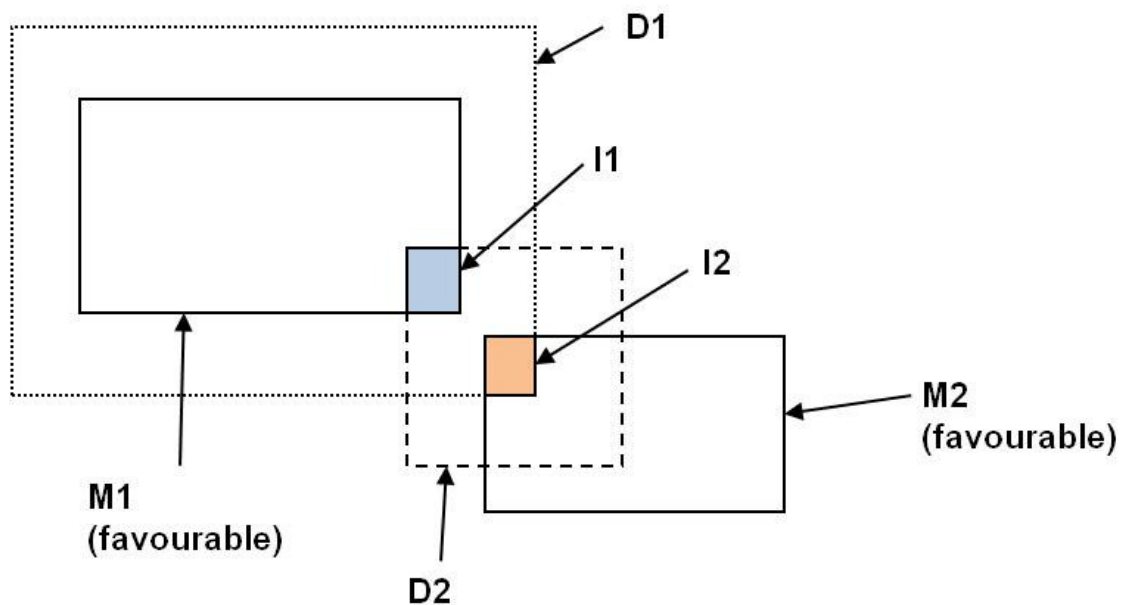
Quantitatively assessing the future species distributions

We designed R scripts (Supplementary Information Scripts 3.1 and 3.2) to identify the proportion of the current distribution which could feasibly contribute to areas within the future distribution, and the proportion of the future distribution reachable within the measured timescale. We estimated these proportions based on mean annual dispersal distance (± 1 sd), calculated across all landscapes, and using the minimum and maximum annual dispersal distance identified when comparing all landscape types. The three key components of the script involve dilation (which modelled dispersion), boundary detection, and intersection of the presence-absence maps (Figure 3.2). More information on these image processing and analysis techniques for binary images is available from Russ, (1995), and from James, (1987) whose BASIC functions were adapted for the first two components.

Finally we assessed how much of the predicted distribution populated by *G. variegata*^{40a} will overlap with agricultural and urbanised environments using land-use GIS data (Australian-Government, 2006). Future projections of land use in Australia are currently unavailable at sufficient quality for the present study, thus we assumed land use remains static until 2070.

Figure 3.2 Dilation model

The approach used to model dispersal processes begins with the presence-absence forms of current (M1) and future (M2) distributions of favourable climate conditions produced by the species distribution model. Dilating M1 with a dilation radius equal to (mean annual dispersal distance * (years between M1 and M2)) produces a map (D1) of maximum reachable area. The intersection between D1 and M2 identifies grid cells of the future distribution reachable from the current distribution (I1). Dilating I1 with the same dilation radius = (D2). The intersection between D2 and M1 identifies grid cells from the current distribution that can supply organisms to grid cells within the reachable future distribution.



Results

Summary statistics for the genetic data

The 16 primer pairs successfully amplified polymorphic loci with unambiguous alleles (Table 3.1), and revealed high levels of polymorphism, with $N_A = 10 - 52$, $H_O = 0.189 - 0.854$, $H_E = 0.229 - 0.954$. All loci showed a significant homozygote excess across the complete dataset. However, analysis at finer spatial scales (within 4 km²) rarely showed significant deviation from HWE. This indicates that the homozygote excess apparent when all samples are pooled is a Wahlund effect owing to genetic structure (Wahlund, 1928). There was no evidence for linkage disequilibrium, and our high rate of amplification success indicates that null alleles were absent or at a very low frequency.

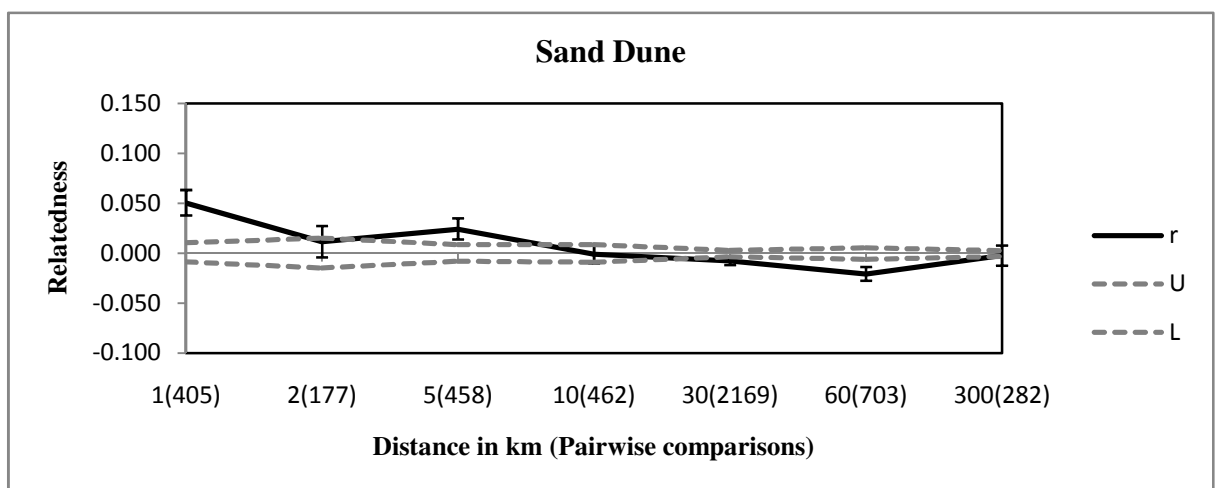
Inferring dispersal patterns from genotypic structure within each landscape

From the spatial distribution of relatedness we inferred that the level of dispersal differs considerably across the landscapes (Figure 3.3 A - I). Dispersal in landscapes A to D is generally at shorter distances in comparison to those in landscapes E to I. We show significantly higher levels of relatedness among individuals at close distances to each other ($r = 0.02 - 0.09$) within the sand dune (A), mulga woodlands (B), gibber plains (C), and eastern woodlands (D) landscapes. Relatedness did not differ from random expectations at any distance within the channel country (E-F), Mitchell grasslands (G-H), MacDonnell Ranges (I), or within and across catchments, thus suggesting higher levels of dispersal in these landscapes.

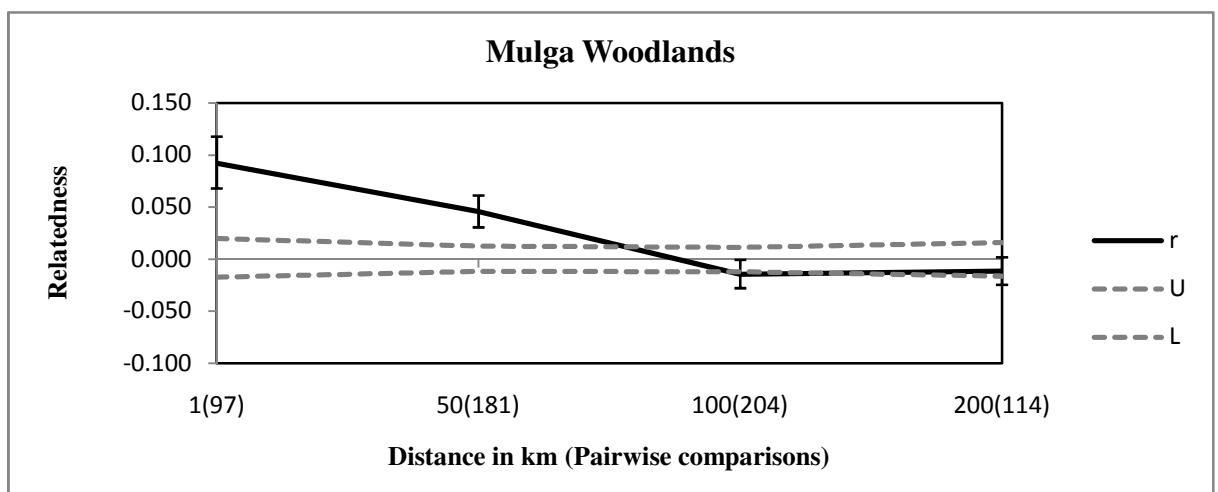
Figure 3.3 Spatial auto-correlations

The spatial distribution of relatedness varies considerably between landscapes. Data was pooled across two replicate sampling areas (Fig. 3.1) to generate the spatial correlogram for each landscape. An exception was the sand dune habitat which consisted of samples from a single area. The solid line tracks relatedness, dashed lines represent the upper (U) and lower (L) 95 % confidence interval around random expectations while bars around relatedness values show the 95 % confidence determined by bootstrapping.

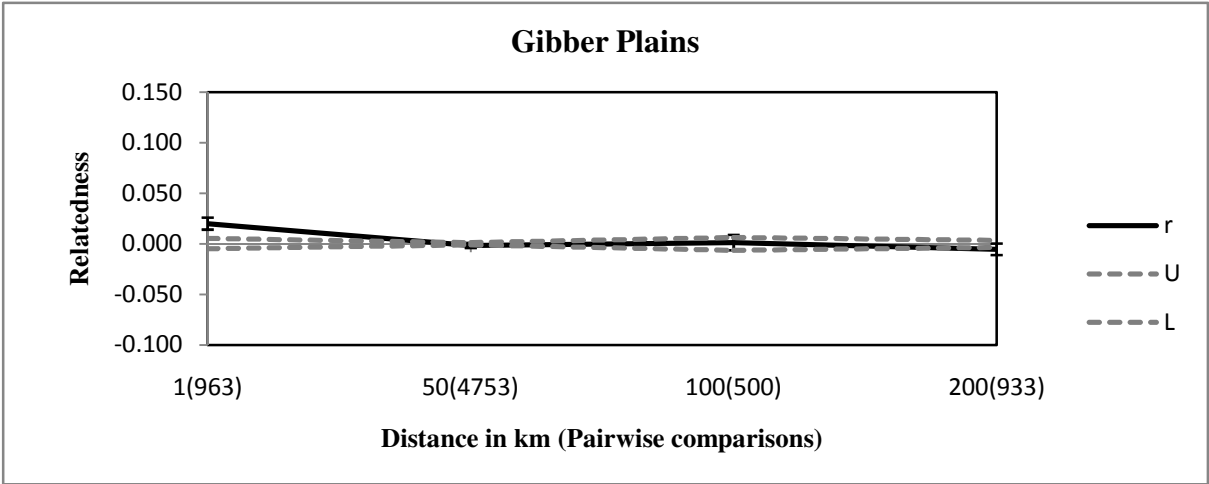
(A)



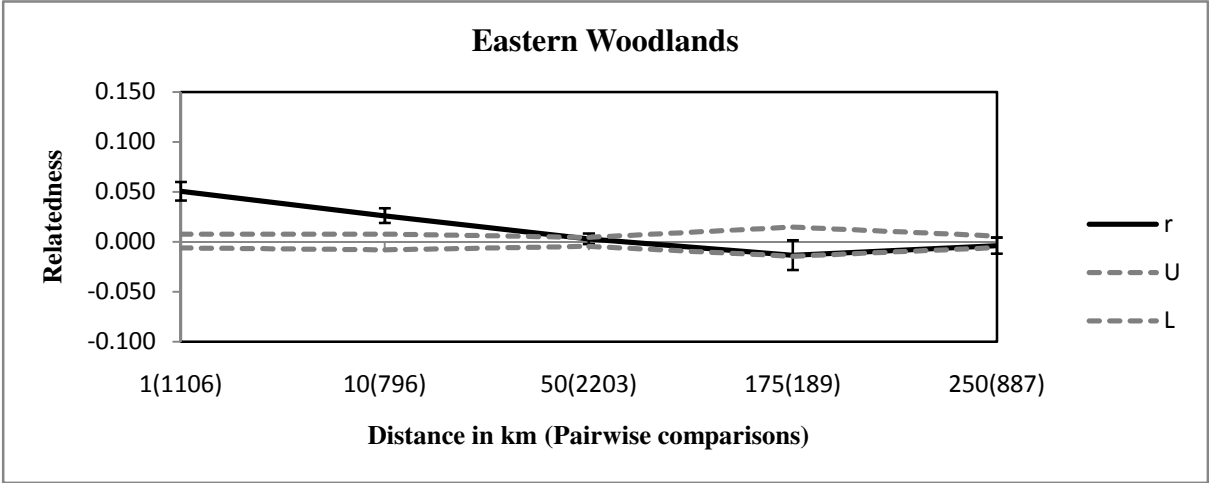
(B)



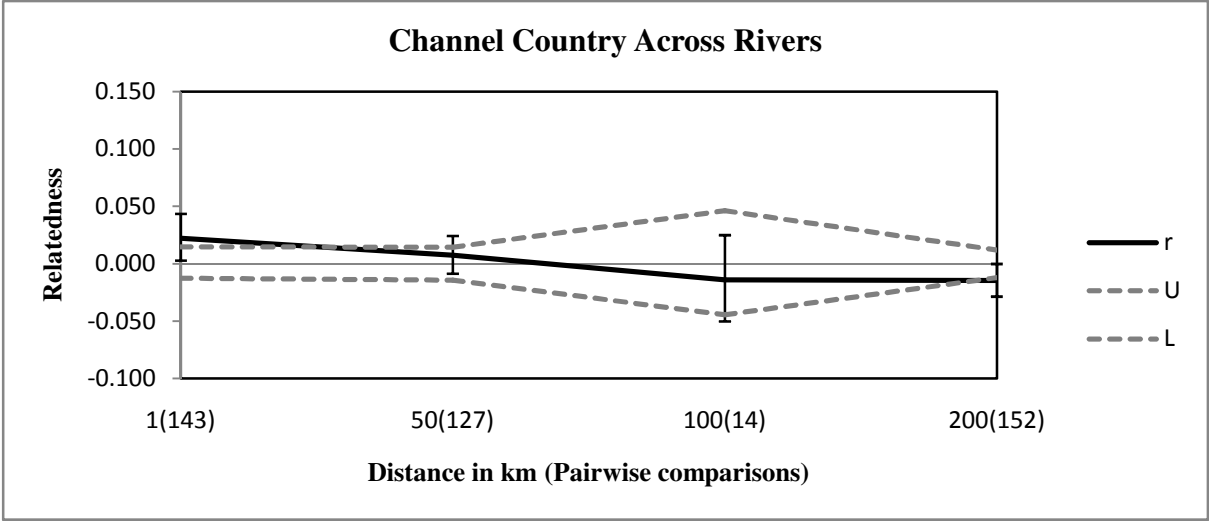
(C)



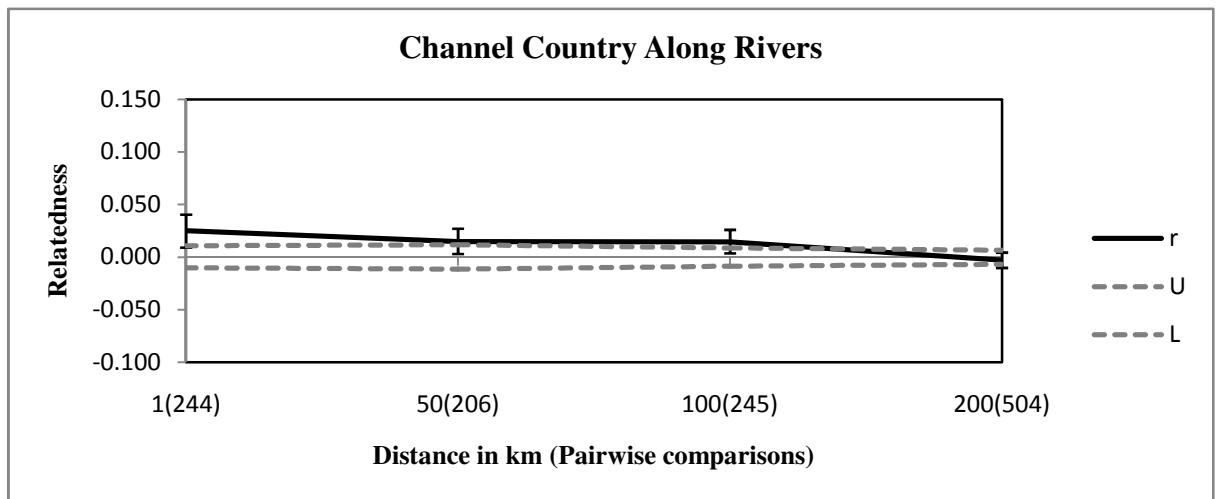
(D)



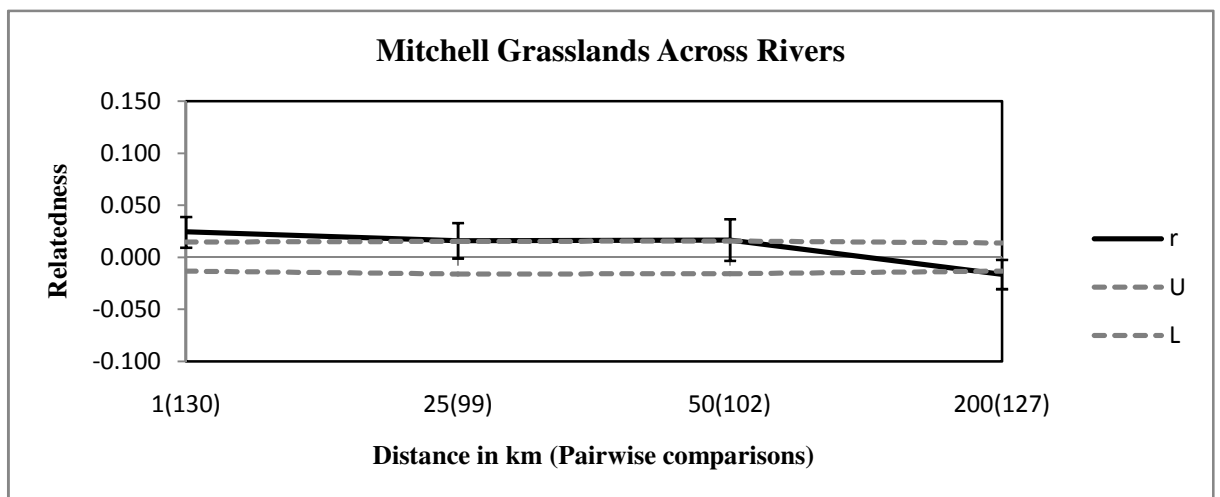
(E)



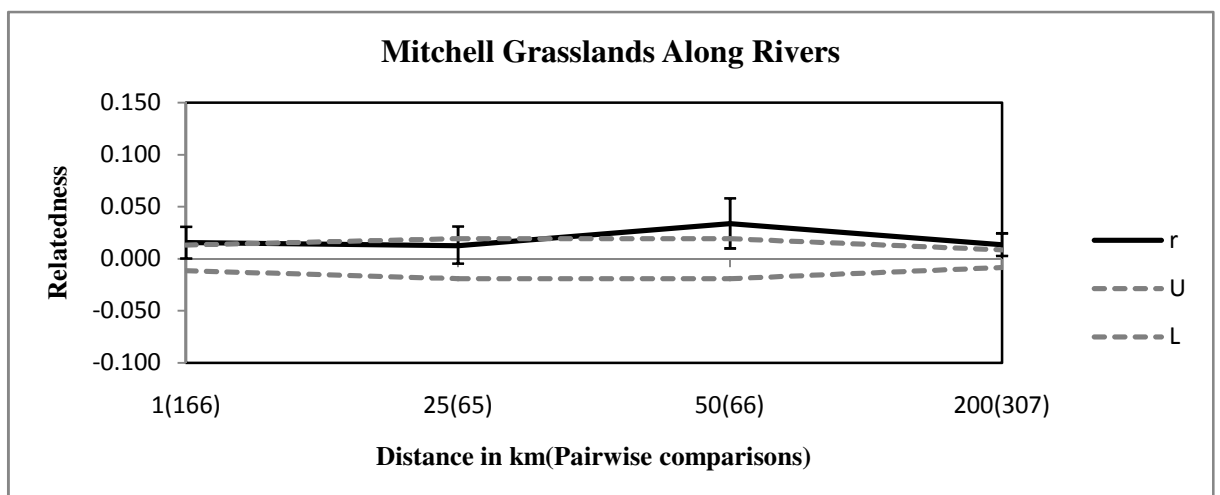
(F)



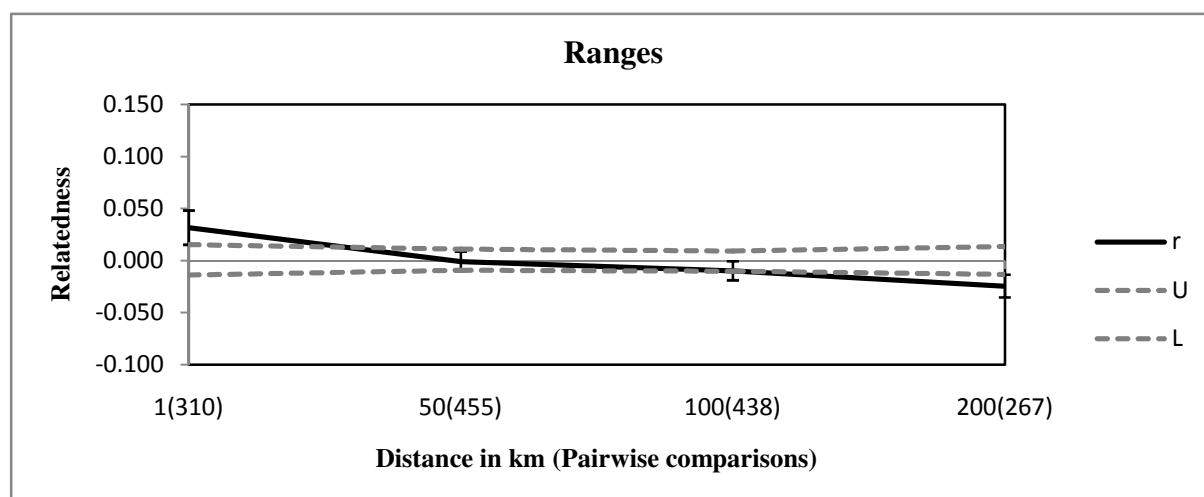
(G)



(H)



(I)



Annual dispersal distances

The annual dispersal distance estimated from neighbourhood sizes in each landscape largely supports the levels of dispersal inferred from the spatial autocorrelation of relatedness. Annual dispersal distance is lower within the sand dune, mulga woodlands, and gibber plains in comparison to channel country, grasslands, and MacDonnell Ranges (Table 3.2). Annual dispersal distance for the eastern woodlands was also estimated to be high, despite the significant genotypic structure at small spatial scales. The minimum and maximum annual dispersal distances were calculated from individuals sampled within the Simpson Desert (1.69 km / yr) and the channel country (7.59 km / yr) landscapes. The mean annual dispersal distance calculated from our large-scale transects fell within the range of landscape dispersal estimates, and was not significantly different to the mean annual dispersal distance calculated across all landscapes (Table 3.2; $t = -0.59$, $df = 9$, p (two-tailed) = 0.57). We therefore used the mean annual dispersal distance pooled across landscapes (4.85 km / yr \pm 1.73) to predict the connectivity from the current distribution to the future distribution. This was the lower of the two estimates and was selected for a conservative assessment.

Table 3.2 Landscapes and dispersal

The mean (\pm sd) of our neighbourhood size (NS), effective density (D_E), and dispersal rate estimates for each landscape, and for each broad scale transect.

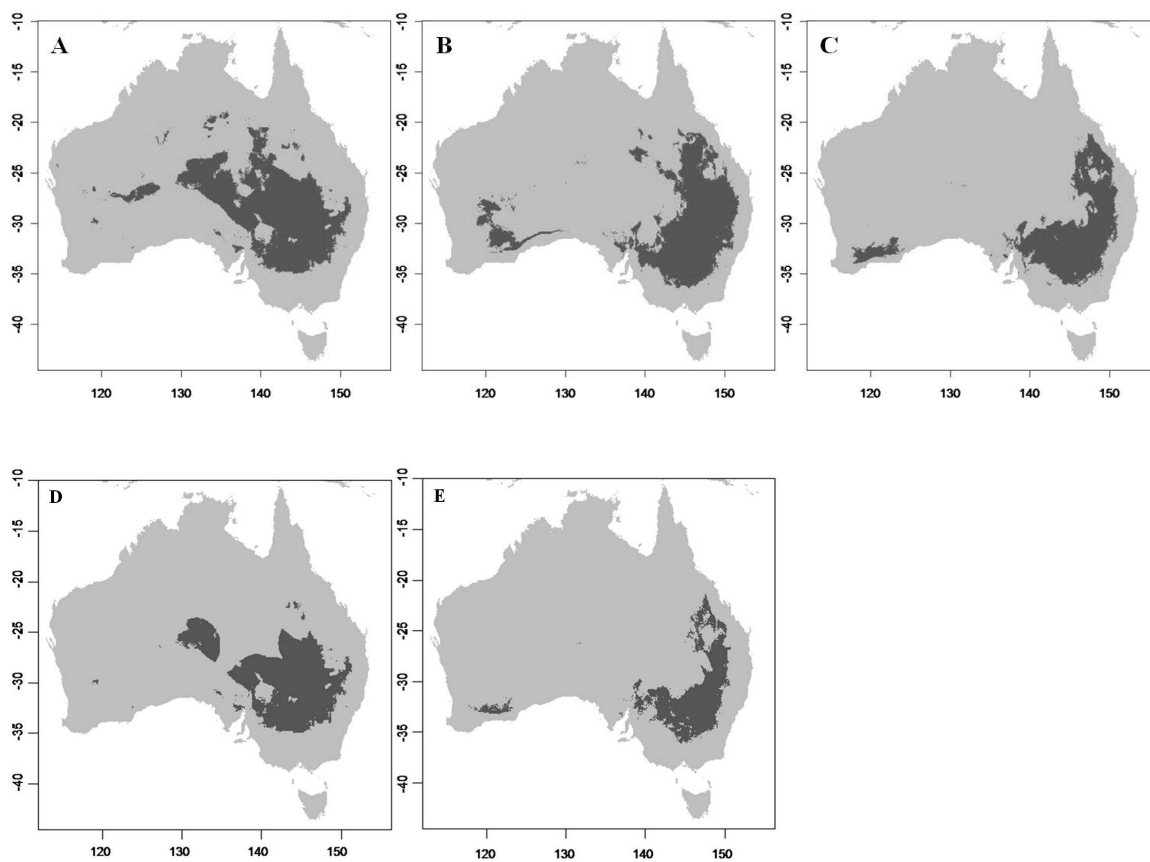
Landscape	NS	D_E	Dispersal rate (km/yr)
Sand dune (Single sample area)	139	1.09	1.69
Mulga woodland	136 ± 75	0.05 ± 0.02	2.96 ± 0.68
Channel country across catchment	614 ± 145	$0.24 \pm <0.01$	3.21 ± 0.91
Grassland across catchment	586 ± 493	$0.04 \pm <0.01$	4.54 ± 1.20
Gibber plains	413 ± 155	$0.03 \pm <0.01$	4.62 ± 0.74
Channel Country within catchment	807 ± 752	0.03 ± 0.02	5.70 ± 2.67
Grasslands within catchment	1126 ± 89	$0.03 \pm <0.01$	5.86 ± 0.80
Eastern woodland	251 ± 173	$<0.01 \pm <0.01$	6.23 ± 1.05
MacDonnell Ranges	715 ± 318	$0.01 \pm <0.01$	6.26 ± 0.18
Mean			4.85 ± 1.73
<hr/>			
All Samples			
Transect 1	52	<0.01	5.05
Transect 2	56	<0.01	5.50
Mean			5.28 ± 0.32

Predicted distributions from species distribution models

The *G. variegata*^{40a} SDM AUC scores were high (0.873 ± 0.005), thus the presence records contained in the test sample of the data were predicted reliably between runs which provided strong support for the MAXENT model. This suggested sampling bias was not a concern and the variables selected were a good fit. The predicted current range (1.39 ± 0.15 million / km²) closely resembles the known current range for *G. variegata*^{40a} (Figure 3.4 A) (King, 1979; Cogger, 2000). The current range of *G. variegata*^{40a} is predicted to decline by 2030 (0.87 ± 0.25 million / km²), and further by 2070, (0.62 ± 0.24 million / km²) (Figure 3.4 B-C), with a general shift in distribution towards the southeast and eastern areas of Australia. The area of suitability in the south-west region is predicted to increase, and most of this is currently not occupied by the species. Highly localised refugia are predicted to persist in central Australia.

Figure 3.4 *Gehyra variegata*^{40a} distribution models

Presence-absence maps for the predicted distributions of *G. variegata*^{40a}. Suitable areas are shown in dark grey and unsuitable areas in light grey. The following distributions are presented: A = the present; B = the year 2030; C = the year 2070; D = the areas that are capable of supplying individuals to the 2070 distribution; E = the area that can be reached by 2070 based on our genetic estimates of dispersal.



Quantitative assessment of the future distribution

Using mean annual dispersal ± 1 sd, we show that *G. variegata*^{40a} can populate between 86 to 99 % of its predicted future distribution that has favourable conditions, and this is achieved by dispersal of individuals originating from 59 to 83 % of the current distribution. From this we infer that 17 to 41 % of the species' current distribution will not be able to keep up with its predicted range shift (Figure 3.4 D-E). Furthermore, the percentage of the predicted *G. variegata*^{40a} distribution that overlaps with areas occupied by agricultural and urbanised areas increases from 4.7 % (current) to 29.1 % (2070). Using maximum annual dispersal estimates resulted in complete connectivity between the current and future distributions. Using minimum annual dispersal results in the species populating 82 % of the predicted future distribution and this is achieved from individuals occupying 48 % of the predicted current distribution.

Discussion

Knowledge of the dispersal capacity of a species will help refine predictions made of the impact of future climate change. Dispersal is also among the most difficult traits to measure, with genetic approaches showing most promise at the landscape scale (Segelbacher *et al.*, 2010). The levels of dispersal that we inferred using two different analytical approaches (spatial patterns of relatedness and Wright's neighbourhood size), were largely consistent with each other. The annual dispersal distances we revealed seem reasonable given that dispersal characteristics are known to vary between habitats in this species (Bustard, 1969; Moritz, 1992). Also the highest levels of dispersal we discovered in the MacDonnell Ranges are congruent with previous studies, where little population structure across distances up to 100 km has been measured (Moritz, 1992). Although recapture studies suggest much lower dispersal distances than characterised here, Moritz (1987) found rapid recolonisation events

occurred at larger spatial scales, and recapture methods are likely to strongly underestimate true dispersal distances (Shreeve, 1995; Pike *et al.*, 2008).

By estimating average dispersal distances, and the areas favourable for *G. variegata*^{40a} following climate change, we calculated that up to 41% of the current distribution will not contribute towards the colonisation of areas with favourable climate by 2070. Furthermore up to 14 % of those favourable areas cannot be populated because the extent of the range shift exceeds the distance the species are expected to cover within the timescales imposed by climate change. These estimates changed considerably when either maximum or minimum annual dispersal distances were applied to the model. This highlights the value in obtaining realistic dispersal estimates across a species' geographic range, and to consider how these contemporary rates are likely to reflect future dispersal rates under realistic climate change scenarios. Nonetheless, this approach can potentially take advantage of molecular and occurrence record datasets to provide dispersal estimates for use with assessment of the impact of future climate change.

Our genetic estimates of annual dispersal rates have to be based on past conditions and it is conceivable that dispersal characteristics might change according to the prevailing weather conditions. Therefore when estimating our dispersal distance from neighbourhood size we carefully considered how N_E was calculated. Methods were available that estimated contemporary or historical N_E (Leberg, 2005; Wang, 2005). We adopted a contemporary method because the *G. variegata*^{40a} we sampled were captured towards the end of an El Niño-southern oscillation event. Hence dispersal estimates would be representative of drier rather than wetter conditions. This is preferable because the Australian climate is largely predicted to experience increasing aridity in the near future (IPCC 2007; Suppiah *et al.*, 2007; Timbal & Jones, 2008).

During future changes in distribution highly dispersive individuals may bias the leading edge of the range shift in each area. This new concept of spatial sorting has been demonstrated within the rapidly expanding populations of the invasive cane toad in Australia (Shine *et al.*, 2011). We have no information on whether dispersal characteristics would be selected for in this study. However, the approach we adopted (Roussett's 1997) measures the 'variance' of dispersal not 'mean' dispersal. Therefore information from individuals dispersing greater distances than the mean value was incorporated. Furthermore, modelling changes in distribution using minimum, mean and maximum dispersal rates can help assess the influences of highly dispersive individuals. Under favourable conditions the colonisation of new habitat may be dominated by the highest dispersers, justifying the use of the maximum dispersal rates in our model. However, favourable conditions seem unlikely in the near future due to the negative impacts of rising temperatures, increasing aridity, and vegetation declines within inland Australia (Hughes, 2003; IPCC 2007). Lower levels of dispersal under these conditions are supported by our lowest dispersal estimates occurring in our driest location, the sand dune landscape (Figure 3.3). Thus, the mean annual dispersal distance provided us with a conservative and perhaps more realistic estimate than applying the maximum dispersal rate.

How global climate change will influence biotic interactions, which may subsequently increase or decrease dispersal rates, is unknown for most species (Callaway *et al.*, 2004). Recent studies suggest when species are temporarily released from pathogenic or predation pressure dispersal rates can increase (Van Grunsven *et al.*, 2007; Murrell & Barraquand, 2012). Further, the type and magnitude of competition for resources can also influence dispersal (McCarthy, 1997). Experiments manipulating competition for resources have shown that a reduction in nutrition for gravid lizards decreases the dispersal of their offspring (Massot & Clobert, 1995). Nonetheless, our mean estimate of dispersal was derived from observations collected across a large area, consisting of several distinct landscapes and presumably, varying biotic interactions. Therefore our sampling strategy is likely to account

for contemporary levels of variation in dispersal. Finally, behavioural plasticity or evolutionary in-situ adaptation to climatic changes may negate the need to disperse altogether, for at least some individuals. In Australia, nesting lizards (*Bassiana duperreyi*) have adjusted nest depth and the timing of oviposition in response to rising temperatures, allowing them to temporarily remain in-situ (Telemeco *et al.*, 2009). However, long term persistence becomes less probable with increasing rates of climatic change, exemplified by the localised extinction of several lizard species in the last decade (Sinervo *et al.*, 2010).

Our SDM projections may have been influenced by our assumption that the distribution of *G. variegata*^{40a} was in equilibrium with current climate. The influence of assuming equilibrium is shown by Elith *et al.*, (2010), where they adjust models to better predict the distribution of cane toads in Australia. The cane toad is a vagile invasive species lacking any predator control, and has been spreading since its introduction. Correlative based predictions assuming equilibrium, combined with presence records that are unlikely to have adequately sampled future environmental conditions, were shown to provide inaccurate predictions. These same issues are less likely for the widely distributed and native *G. variegata*^{40a} (Bustard, 1968; Arnold & Poinar, 2008). Currently, *G. variegata*^{40a} is almost certainly much closer to its distribution equilibrium, rather than a state of spread. Additionally, we sampled over an extensive geographic and climatic range, including some of the driest and hottest locations within Australia, therefore a number of our presence records are likely to reflect future conditions. This was demonstrated with our extremely low 'clamping' estimates due to the overwhelming majority of projected regions falling within the range covered in the SDM training data (Supplementary Information).

If our estimates of mean annual dispersal distance are representative of future dispersal rates, then our quantitative modelling approach predicts that rapid climate change will relocate and reduce the distribution of *G. variegata*^{40a}. For those stranded in small areas of suitable

climate, or areas with less than optimal climatic conditions, there may be detrimental consequences of isolation and small population sizes (Cushman, 2006). Although some may persist through environmental stochastic challenges for some time, population viability may be compromised in the long term by inbreeding and the random accumulation of deleterious alleles or loss of beneficial ones (Lande, 1993; Frankham, 1998; Frankham *et al.*, 2004). These processes have been demonstrated to reduce fitness and increase extinction risk in a range of organisms including reptiles, birds, mammals, and fish (Gilpin & Soulé, 1986; Hanski, 2011). Alternatively, the impact of climatic change in these regions may be buffered to some degree by the persistence of microhabitat, which may have enabled persistence during the climatic fluctuations of the Pleistocene (Duckett and Stow, 2013). In addition, human land use may potentially fragment distributions and exacerbate the problems of climate change for *G. variegata*^{40a}. In 2070 the distribution of *G. variegata*^{40a} is predicted to have a substantial portion overlapping with agricultural and urbanised areas (Australian Government 2006). In Western Australia both *G. variegata*^{40b} and the similar-sized *Oedura reticulata* suffered reduced genetic diversity and increased genetic structure where their natural habitat was fragmented by agriculture (Hoehn *et al.*, 2007). On the other hand, *G. variegata*^{40a} are often located in human impacted environments (Cogger, 2000; Personal Observation), therefore it remains unclear the degree to which land use practices may fragment the distribution of *G. variegata*^{40a}.

Coupling both SDMs and genetic estimates of dispersal will assist with predicting a species response to climate change. As we have shown, this approach incorporates both correlative and mechanistic variables to quantitatively identify areas of the current distribution of *G. variegata*^{40a} that are likely to become isolated and areas of the predicted future distributions that cannot be colonised. Further advances may come from simultaneously incorporating other variables into models such as multi-species interactions or the changes in vegetative cover through time (Hampe, 2004). Nonetheless, we show that available molecular and

occurrence record datasets may be amenable to assess and help prioritise those species which will be most vulnerable to the impacts of climate change.

Acknowledgements

This work was supported by Macquarie University and the Wildlife Preservation Society of Australia Limited. Lizards were handled in accordance with Macquarie University and South Australian Animal Ethics committee recommendations. Tissue collection was licensed by the New South Wales National Parks and Wildlife Service (S12353), Northern Territory Parks and Wildlife Commission (33155), Queensland Environment Protection Agency (WITK04616407), and South Australia Department of the Environment and Natural Resources (Z25499-4). We thank Macquarie University volunteers for their assistance during field collections and A. Cabrelli for assistance in basic SDM techniques.

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Supplementary information

Inferring current and future species distributions from species distribution modelling

Input datasets

We supplemented our field observations with data from the Global Biodiversity Information Facility (GBIF - www.gbif.org) to provide ~3000 unique widely distributed occurrence records. With a large number of records distributed throughout the species known range, sampling bias is less likely to produce false negative results (Costa *et al.*, 2010). All data was manually checked to remove both obvious errors (oceanic occurrences), and records matched by their geographic location to represent the 2n = 40b and 2n = 44 chromosomal races of this species (King, 1979).

Observed baseline climate data was provided by the WorldClim data set (Hijmans *et al.*, 2005) at a grid resolution of 2.5 arc minutes. These data are monthly mean maximum and minimum temperatures and monthly precipitation averaged over the years 1960 to 1990. These data were used to compute 19 bioclimatic variables defined by (Nix, 1986) and (Busby, 1991); (See Table 3.3 for details of the 19 bioclimatic variables). An important source of uncertainty when projecting SDMs onto future climate is the variation in predicted climate across General Circulation Models (GCMs) (Beaumont *et al.*, 2008; Fordham *et al.*, 2011). We used four GCMs developed for the IPCC Fourth Assessment Report (Soloman *et al.*, 2007), which (Suppiah *et al.*, 2007) showed higher overall skill in representing 20th Century climate in the Australian region, and which provided the necessary monthly temperature and precipitation data. They were: BCCR, CSIRO Mark 3.5, INMCM3 and MIROC 3.2.2 medres. Details of each GCM are provided in Table 3.4. Data for each GCM was obtained from the Climate Model Inter-comparison Project (CMIP) website (www-pcmdi.llnl.gov/ipcc/about_ipcc.php last accessed 12 February 2012).

The method used to generate future climate data was the anomaly method used by Hijmans *et al.* (2005). The following sequence of operations was applied to data for each GCM: (a) Baseline mean monthly maximum and minimum temperature, and monthly precipitation, was computed for a single climate of the 20th Century model run. Monthly averages were made over the period 1960 to 1990 to match the WorldClim data; (b) The resulting 36 GIS grids (12 months x 3 variables) were interpolated from the coarse GCM grids to the WorldClim 2.5 arc minute grid using bicubic spline interpolation (Press *et al.*, 2002); (c) We also computed decadal mean monthly temperature and precipitation data for a decade centred on 2030 for a single model run giving a set of 36 future decade files which were then interpolated to the WorldClim 2.5 arc minute grid as described earlier; (d) A monthly anomaly grid was then produced for maximum and minimum temperatures and precipitation storing the difference between the GCM's baseline and decadal data; and (e) For each month and each variable (i.e. maximum and minimum temperature and precipitation) the anomaly grid was then added to the observed baseline grid to produce an adjusted observed climate for 2030. This procedure was repeated for the decade centred on 2070. Future climate data were examined for 2030 and 2070 based on the A2 greenhouse gas scenario. This model was selected because of its 'business as usual' characteristics, which describe an increasing population, technology, and CO₂ emissions, where economic growth is favoured over environmental concerns; hence it represents a likely future.

Model building and modelling

We modelled environmental suitability for the occurrence data using MAXENT 3.3.1 (Phillips *et al.*, 2006; Phillips & Dudík, 2008); this method has been validated with multiple species worldwide. The extent of the climate data were longitude 111.975 to 156.275 / latitude -9.975 to -44.525, this includes the whole of continental Australia including

Tasmania. A mask was applied to all climate data layers ensuring their identical configuration and exclusion of non Australian and oceanic grid cells (and hence contain no data), and inclusion of Australian land based grid cells (with data). When modelling species specific responses to global climate change, Beaumont *et al.*, (2005) recommends reducing the number of parameters within the model; which has since become common practice in many studies (Synes & Osborne, 2011). This is shown to help circumvent the likelihood of co-linearity and over-fitting problems, which may otherwise lead to the misrepresentation of a species range or the loss of biological relevance. We therefore reduced the number of bioclimatic variables from 19 to 8 (Bio 1, 4, 5, 6, 8, 9, 16, 17 - Table 3.3), by excluding those which displayed high correlation to each other (> 0.8 Pearson Correlation), and / or low predictive ability in the model. Variable predictive ability and importance to the model was assessed by percent contribution and jack-knifing in MAXENT. We used the area under the receiver operating characteristic curve (AUC) (Manel *et al.*, 2001) and cross validation to evaluate model robustness and any sampling bias that may be present. In each of our 10 replicate runs MAXENT randomly set aside 25 % of the occurrence records as test data, this allows the program to build the model from the remaining occurrence records (training data) and then test predictive accuracy against the test data. We used the MAXENT linear, product, quadratic, hinge and threshold features to fit the model with an expanded set of changes on the original covariates. This approach provides more flexibility when modelling species with non-linear responses to change (Huff et al., 2012), and is considered optimal when a large presence dataset, which increases model complexity, is utilised (Papes et al., 2012). We ran multiple preliminary MAXENT models with varying levels of regularisation. Model performance declined with increasing regularisation, therefore we proceeded to use the MAXENT regularisation default (Regularisation = 1) (Brooke et al., 2012; Kuemmerle et al., 2012). Lastly, SDM with MAXENT assumes that each variable in the projected distribution falls within the range covered in the training data, and employs 'clamping' to limit variables to

this range. Predictions based on models with high levels of clamping can be difficult to interpret and trust (Elith et al., 2010). Using the MAXENT clamping tools we found extremely low levels of clamping across our four future GCM projections (< 0.01 clamping for > 99.81 % of the dataset), indicating clamping was not impacting our projections and neither variable fell outside the range present in our training data.

We utilised the resulting MAXENT model to predict areas of climatic suitability (mean \pm 1 sd) to 2030 and 2070 using the four GCM with the A2 scenario. We averaged the four GCM results for each decade, and both current and future predictions were transformed into presence-absence predictions based on the equal test sensitivity and specificity logistic threshold (0.46 ± 0.01) (Liu *et al.*, 2005). This was the more conservative and precise option in comparison to the Maximum test sensitivity plus specificity logistic threshold (0.40 ± 0.05) (Liu *et al.*, 2005), and ensures that the reduction in climatically favourable areas was not overestimated.

Table 3.3 Bio / Worldclim variables

The 19 bioclimatic variables: temperatures are in Celsius / precipitations are in millimetres.

Variable name	Abbreviation	Definition
bio1	AnnTemp	Mean annual temperature (mean across 12 months of the year)
bio2	MeanMonTempRange	Mean monthly temperature range
bio3	Isothermality	Ratio bio2/bio7
bio4	TempSeason	Temperature seasonality = Coeff. of variation mean monthly temperature throughout the year
bio5	MaxTemp	Maximum mean monthly temperature over 12 months
bio6	MinTemp	Minimum mean monthly temperature over 12 months
bio7	AnnTempRange	bio5 – bio6
bio8	MeanTempWetQtr	Mean temperature for the wettest consecutive 3 months
bio9	MeanTempDriestQtr	Mean temperature for the driest consecutive 3 months
bio10	MeanTempWarmQtr	Mean temperature of the warmest consecutive 3 months
bio11	MeanTempColdQtr	Mean temperature of the coldest consecutive 3 months
bio12	AnnPrecip	Sum of monthly precipitation values
bio13	PrecipWettestMon	Precipitation of the wettest month
bio14	PrecipDriestMon	Precipitation of the driest month
bio15	PrecipSeason	Precipitation seasonality = Coeff. of variation mean monthly precipitation throughout the year
bio16	PrecipWettestQtr	Precipitation of the wettest consecutive 3 months
bio17	PrecipDriestQtr	Precipitation of the driest consecutive 3 months
bio18	PrecipWarmQtr	Precipitation of the warmest consecutive 3 months
bio19	PrecipColdQtr	Precipitation of the coldest consecutive 3 months

Table 3.4 Global circulation models

Details of the four General Circulation Models (GCMs): Precipitation and temperature skill rankings are based on scores listed in Table 2 of Suppiah *et al.* (2007) who evaluated the performance of all IPCC Fourth Assessment Report GCMs in simulating observed climate in the Australian region over the period 1961 to 1990.

Originating Group(s)	CMIP3 I.D.	Grid cell size (lat x long degrees)	Calendar	Precipitation skill	Temperature skill
Bjerknes Centre for Climate Research	BCCR-BCM2.0	~2.8 x 2.8	Gregorian, days since 1800-1-1	Moderate	Excellent
CSIRO Atmospheric Research	CSIRO-Mk3.5	~1.875 x 1.875	365-day, days since 0000-01-01	Very good	Very good
Institute for Numerical Mathematics	INM-CM3.0	~4 x 5	365-day, days since 2001-1-1	Good	Good
Centre for Climate System Research (The University of Tokyo), National Institute for Environmental Studies, and Frontier Research Centre for Global Change (JAMSTEC)	MIROC3.2 (medres)	~2.8 x 2.8	Gregorian, days since 1850-01-01	Very good	Excellent

Source: Suppiah, R., Hennessy, K. J., Whetton, P. H., McInnes, K., Macadam, I., Bathols, J., Ricketts, J. & Page, C. M. (2007) Australian climate change projections derived from simulations performed for the IPCC 4th Assessment Report. *Australian Meteorological Magazine*, 56, 131-152.

Supplementary Information

Script 3.1 R Script for dilation model part A

Test script for DispDist Function

PDW 17 May 2011

Change the following path to point to the location of the script

DispDistFunction.R

source("C:/Users/timebombtd/Documents/uni/PhD/Script/DispDistFunction.R")

The function DispDist is called as follows:

#

DispDist(M1,M2, MeanDistance)

#

In the function call, replace the two paths to current (M1) and future

(M2) files with paths to the files you wish to analyse.

#

NOTE: The function is rather naive (i.e. a philistine) when it comes to

writing output files. IT WILL OVERWRITE existing files without warning. It

writes output files to the folder in which M1 is located. I suggest putting

copies of M1 and M2 in a folder created to hold the analysis for those two

maps.

#

The value MeanDistance in the function call represents the TOTAL dispersal

distance expected for the time between the M1 and M2 maps. So, if you have an

estimate for the mean annual rate (in km/year) then the dispersal distance

required for the computations = number_of_years * mean_annual_rate. Naturally,

in the example function call below one replaces "200" with this value.

#

Four maps are written to the output folder: D1.asc, D2.asc, I1.asc, and I2.asc

corresponding to the eponymous definitions in the notes.

Test average dispersal across all habitats i.e $4.84\text{km} * 60 \text{ years} = 290.4$.

DispDist("C:/Users/timebombtd/Documents/uni/PhD/Script/Current8varequal.asc",

"C:/Users/timebombtd/Documents/uni/PhD/Script/20708varequal.asc",

396

Supplementary Information

Script 3.2 R Script for dilation model part B

```
# Explore the use of binary image morphology operators e.g. boundary detection
```

```
# PDW 1 & 13 May 2011
```

```
# 2 Jun 2011: Patched bug in call to DilateMap: needed CellSize parameter
```

```
# Some important constants:
```

```
Earth_radius <- 6371.1 # mean earth radius in km
```

```
degtorad <- pi/180
```

```
radtodeg <- 180/pi
```

```
####
```

```
GCD.deg <- function (deglat1,deglong1,deglat2,deglong2)
```

```
{
```

```
  lat1 <- degtorad*deglat1
```

```
  long1 <- degtorad*deglong1
```

```
  lat2 <- degtorad*deglat2
```

```
  long2 <- degtorad*deglong2
```

```
  z <- acos(sin(lat1)*sin(lat2)+cos(lat1)*cos(lat2)*cos(long2-long1))
```

```
return(Earth_radius*z)
```

```
}
```

```
####
```

```
EndLatLong <- function (dist,bearing,lat1,long1)
```

```
{
```

```
  lat2 <- asin(sin(lat1)*cos(dist/Earth_radius) +  
cos(lat1)*sin(dist/Earth_radius)*cos(bearing))
```

```
  long2 <- long1 + atan2(sin(bearing)*sin(dist/Earth_radius)*cos(lat1),cos(dist/Earth_radius)-  
sin(lat1)*sin(lat2))
```

```
  return (c(lat2=lat2,long2=long2))
```

```
}
```

```
####
```

```
FindBoundary <- function (bi)
```

```
{
```

```
  nr <- nrow(bi)
```

```
  nc <- ncol(bi)
```

```
  obi <- matrix(0,nr,nc)
```

```

for (r in 2:(nr-1))

{

  for (c in 2:(nc-1))

  {

    bh <- (bi[r-1,c]==0) || (bi[r+1,c]==0) || (bi[r,c-1]==0) || (bi[r,c+1]==0)

    bd <- (bi[r-1,c-1]==0) || (bi[r-1,c+1]==0) || (bi[r+1,c-1]==0) || (bi[r+1,c+1]==0)

    b <- bh || bd

    obi[r,c] <- b && bi[r,c]

  }

}

return(obi)

}

####

EdgeDetection <- function (map)

{

  nr <- nrow(map)

```

```

nc <- ncol(map)

edges <- matrix(0,nr,nc)


for (r in 2:(nr-1))

{

  for (c in 2:(nc-1))

  {

    bh <- (map[r-1,c]==0) || (map[r+1,c]==0) || (map[r,c-1]==0) || (map[r,c+1]==0)

    bd <- (map[r-1,c-1]==0) || (map[r-1,c+1]==0) || (map[r+1,c-1]==0) || (map[r+1,c+1]==0)

    b <- bh || bd

    edges[r,c] <- b && map[r,c]

  }

}

edgelist <- which(edges==1,arr.ind = T)


return(edgelist)

}

```

```

DilateMap <- function
(dilated_map,edgelist,dist,mask,Yul.centre,Xll.centre,CellSize,NumCols,NumRows)

{

  #write("Dump of dilation function
processing:","/home/peterw/Documents/DilationPuzzle1.txt")

  npts <- nrow(edgelist)

  for (i in 1:npts)

  {

    # Compute cell-centre lat/long for the current point in the edgelist

    lat1 <- Yul.centre - (edgelist[i,"row"] - 1)*CellSize

    long1 <- Xll.centre + (edgelist[i,"col"] - 1)*CellSize


    # leftcol, rightcol, toprow, botrow

    endpt <- EndLatLong(dist,3*pi/2,degtorad*lat1,degtorad*long1)

    leftcol <- trunc((radtodeg*endpt[2] - Xll.centre+CellSize/2)/CellSize)

    if (leftcol < 1) { leftcol <- 1 }

    if (leftcol > NumCols) { leftcol <- NumCols }


    endpt <- EndLatLong(dist,pi/2,degtorad*lat1,degtorad*long1)

```

```

rightcol <- trunc((radtodeg*endpt[2] - Xll.centre+CellSize/2)/CellSize)

if (rightcol < 1) { rightcol <- 1 }

if (rightcol > NumCols) { rightcol <- NumCols }


endpt <- EndLatLong(dist,0,degtorad*lat1,degtorad*long1)

toprow <- trunc((Yul.centre - radtodeg*endpt[1])/CellSize) + 1

if (toprow < 1) { toprow <- 1 }

if (toprow > NumRows) { toprow <- NumRows }


endpt <- EndLatLong(dist,pi,degtorad*lat1,degtorad*long1)

botrow <- trunc((Yul.centre - radtodeg*endpt[1])/CellSize) + 1

if (botrow < 1) { botrow <- 1 }

if (botrow > NumRows) { botrow <- NumRows }


for (r in toprow:botrow)

{

  for (c in leftcol:rightcol)

  {

    if ((dilated_map[r,c] != 1) && (mask[r,c] != 1))

```

```

{

  #write(paste("Row =",r," Col =",c," dilated_map[r,c]
=",dilated_map[r,c]),"/home/peterw/Documents/DilationPuzzle1.txt",append=T)

  lat2 <- Yul.centre - (r - 1)*CellSize

  long2 <- Xll.centre + (c - 1)*CellSize

  if (GCD.deg(lat1,long1,lat2,long2) <= dist)

  {

    dilated_map[r,c] <- 1

  }

}

}

}

}

}

}

#dilated_map[mask] <- 0

return(dilated_map) #[mask] <- 0)

}

```



```

SaveASC <- function
(theMap,nRows,nCols,Xll_corner,Yll_corner,Cell_size,NoData_value,fname)

{

write(paste("ncols      ",nCols,sep=""),fname)

write(paste("nrows      ",nRows,sep=""),fname,append=T)

write(paste("xllcorner   ",Xll_corner,sep=""),fname,append=T)

write(paste("yllcorner   ",Yll_corner,sep=""),fname,append=T)

write(paste("cellsize    ",Cell_size,sep=""),fname,append=T)

write(paste("NODATA_value ",NoData_value,sep=""),fname,append=T)

write.table(theMap,fname,quote=F,sep=" ",row.names=F,col.names=F,append=T)

}

```

```

DispDist <- function (path_M1,path_M2,dispdist)

```

```

{

Start <- Sys.time()

###par(mfrow=c(2,3))

###dispdist <- 200

```

```

###path_M1 <- "/home/peterw/Documents/Dispersal distance functions/Test
maps/OZ_Barleria_prionitis_Current_mean_t.asc"

basePath <- dirname(path_M1)


map.hdr <- scan(path_M1,nlines=6,what="character")


# Set basic grid parameters as global values that can be used in functions

NumCols <- as.numeric(map.hdr[2])

NumRows <- as.numeric(map.hdr[4])

Xll <- as.numeric(map.hdr[6])

Yll <- as.numeric(map.hdr[8])

CellSize <- as.numeric(map.hdr[10])

NoData <- as.numeric(map.hdr[12])

rm(map.hdr)

Yul.centre <- Yll + (NumRows-1)*CellSize + CellSize/2

Xll.centre <- Xll + CellSize/2

```

```

M1 <-
matrix(as.numeric(scan(path_M1,skip=6,what="integer")),nrow=NumRows,ncol=NumCols,b
yrow=T)

nd_list <- which(M1==NoData,arr.ind = T)

M1[nd_list] <- 0


nd_mask <- matrix(0,NumRows,NumCols)

nd_mask[nd_list] <- 1


###image(map1,main="Map 1")


edgelist1 <- EdgeDetection(M1)

D1 <-
DilateMap(M1,edgelist1,dispdist,nd_mask,Yul.centre,Xll.centre,CellSize,NumCols,NumRow
s)


###image(output_map1,main="Output_Map 1")

D1_out <- D1

D1_out[nd_list] <- NoData

```

```
SaveASC(D1_out,NumRows,NumCols,Xll,Yll,CellSize,NoData,paste(basePath,"/D1.asc",sep
=""))
```

```
rm(D1_out)
```

```
###path_M2 <- "/home/peterw/Documents/Dispersal distance functions/Test
maps/OZ_Barleria_prionitis_Mean_AR4_Decade2050_mean_t.asc"
```

```
M2 <-
matrix(as.numeric(scan(path_M2,skip=6,what="integer")),nrow=NumRows,ncol=NumCols,b
yrow=T)
```

```
M2[nd_list] <- 0
```

```
###image(map2,main="Map 2")
```

```
# Make intersection between dilated M1 (= D1) and M2
```

```
I2 <- D1 + M2
```

```
I2 <- ifelse(I2 < 2,0,1)
```

```
if (sum(I2) > 0)
```

```
{
```

```

###image(I1,main="I1")

I2_out <- I2

I2_out[nd_list] <- NoData

SaveASC(I2_out,NumRows,NumCols,Xll,Yll,CellSize,NoData,paste(basePath,"/I2.asc",sep=
""))

rm(I2_out)

edgelist2 <- EdgeDetection(I2)

D2 <-

DilateMap(I2,edgelist2,dispdist,nd_mask,Yul.centre,Xll.centre,CellSize,NumCols,NumRows)

if (length(which(I2 == M2)) != NumRows*NumCols)

{

###image(output_map2,main="Output_Map2")

D2_out <- D2

D2_out[nd_list] <- NoData

SaveASC(D2_out,NumRows,NumCols,Xll,Yll,CellSize,NoData,paste(basePath,"/D2.asc",sep
=""))

rm(D2_out)

```

```

I1 <- D2 + M1

I1 <- ifelse(I1 < 2,0,1)


if (sum(I1) > 0)

{

  ###image(I2,main="I2")

  I1_out <- I1

  I1_out[nd_list] <- NoData


SaveASC(I1_out,NumRows,NumCols,Xll,Yll,CellSize,NoData,paste(basePath,"/I1.asc",sep=
""))

  rm(I1_out)

  ###print(sum(I1))

  ###print(sum(I2))

} else

{

  cat("*** Map1 and I2 do not intersect!\n")

}

} else

{

```

```
cat("Map2 is entirely within Map1, so there is no range shift only shrinkage.\n")

}

} else { cat("*** Map2 and I1 do not intersect!\n")}

Finish <- Sys.time()

(ElapsedTime <- Finish - Start)

}
```

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CHAPTER FOUR: ESTIMATING GENETIC LOSS

In this chapter I utilise the quantified measure of dispersal and new modelling approach to estimate losses to genetic diversity in *Gehyra variegata*^{40a} due to the impacts from future climate change. This chapter is currently under review.

Duckett, P.E., & Stow, A. (In Review) Predicting impacts of global climate change on intraspecific genetic diversity needs realistic dispersal estimates.

Predicting impacts of global climate change on intraspecific genetic diversity benefits from realistic dispersal estimates.

Abstract

Species distributions are significantly influenced by global climate change (GCC), and the current rate of change is predicted to severely impact biodiversity throughout the next century. Knowledge of dispersal characteristics is needed to more accurately predict the areas which species are capable of reaching in the timescales imposed by GCC, and to estimate losses to genetic diversity. Previously, dispersal capabilities have been assumed, which overestimate (no dispersal) or underestimate (unlimited dispersal) losses to genetic diversity. Here we utilised a recent approach which combined a quantified measure of dispersal with species distribution models (SDM), to then estimate losses to genetic diversity to an extensively sampled Australian gecko. We revealed future range contractions are likely to result in substantial losses to current levels of genetic diversity. This interdisciplinary approach can realistically quantify losses to genetic diversity, identify parts of the distribution requiring translocation, prioritise areas for conservation management and facilitate the development of conservation policy.

Keywords: Climate Change, Conservation, Dispersal, Genetic Diversity, Modelling.

Introduction

It is commonly accepted that global climates have continually influenced the distribution of species throughout all of the world's ecosystems (Davis & Shaw, 2001; Strasburg & Kearney 2005; Thuiller *et al.*, 2005). This has been demonstrated in both arid and wet tropical regions of Australia to have resulted in fluctuations to species genetic diversity (Hewitt, 1996; Schneider *et al.*, 1998). Whilst past climates have changed over geological timescales, the current rate of warming is faster than any conditions experienced by the world's biota in the last 1000 years (IPCC, 2001). For this reason understanding the impact of GCC to biodiversity in the near future has become one of the greatest challenges for conservation biology. In the last few decades the extent to which GCC will impact the distribution of species has been estimated numerous times using SDM (Guisan & Thuiller, 2005; Kearney *et al.*, 2010). Because many species show some degree of genetic structuring throughout their range (Bohonak, 1999), changes in the favourable climate for less mobile species in the near future is likely to be associated with losses of genetic variation.

Rarely has the impact of GCC to intraspecific genetic diversity been estimated. Gaining this knowledge is valuable for conservation because higher levels of genetic variation may increase the adaptive potential of a species to changing environmental conditions, and buffer species against stochastic events (Frankham *et al.*, 2004). For these reasons genetic diversity is recognised by the International Union for Conservation of Nature (www.iucn.org) as one of three forms of biodiversity deserving conservation. Subsequently, the conservation of genetic biodiversity is mandated by international conventions and national legislature including, the International Convention on Biological Diversity (CBD, 1992), the Habitats Directive of the European Union (Directive 92/43/EEC 1992), and the National Strategy for the Conservation of Australia's Biological Diversity (Department of the Environment, Water, Heritage and the Arts 1996, 2010 - 2030), amongst others.

In order to comply with current policy and conserve current levels of intraspecific genetic diversity, we need to adopt methods which quantify and identify those locations within a species current distribution that are likely to reach their predicted future distribution. This requires approaches which incorporate realistic estimates of dispersal capabilities into SDM, which has proven difficult (Franklin, 2010). The lack of information on species dispersal abilities to help achieve this has often resulted with studies assuming dispersal to be unlimited or zero. Thus, the predicted future levels of genetic diversity will be a product from either all individuals or only those that overlap with the current distribution and both scenarios are clearly unrealistic for many species. However, the true level of dispersal, and hence genetic diversity, will fall somewhere in-between (Balint *et al.*, 2011).

Here we utilise a widely applicable method (Duckett *et al.*, 2013), which combined genetic estimates of dispersal and SDM to assess which parts of a species current distribution are likely to contribute towards colonising areas that are climatically suitable in the future. We then identify evolutionary clades for this species, and quantify losses to genetic diversity due to GCC induced range shifts. We hypothesise that when species with low vagility experience distributional shifts over a relatively short period of time they will also suffer losses to current levels of genetic diversity. We demonstrate that combining SDM with unrealistic dispersal assumptions results in substantial differences in estimates of genetic loss. Ultimately these unrealistic assumptions will either fail to provide information relevant to help conserve genetic biodiversity, or waste precious conservation resources.

Methods

Sampling and summary genetic data analysis

To test our hypothesis, we used data collected from 740 *Gehyra variegata*^{40a} individuals (Chapter 3 samples have been supplemented with an additional 105 individuals). Sampling procedures are detailed in Duckett *et al.*, (2013). Briefly, tissue samples were obtained from *G. variegata*^{40a} throughout the arid regions of central and eastern Australia where the species uses exfoliating bark and tree debris as retreat sites (Bustard, 1968; Henle, 1990; Duckett & Stow, 2012). We extracted DNA and genotyped all individuals at 16 microsatellite loci (Hoehn & Sarre, 2006; Duckett & Stow, 2010), and we calculated summary statistics for each locus using GENALEX v6.0 (Peakall & Smouse, 2006). The significance of any deviation from Hardy-Weinberg equilibrium (HWE) was calculated with FSTAT v2.9.3 with corrections for multiple tests (Goudet, 2001) (Table 4.1). We sequenced the mtDNA ND4 region for each individual (Forstner *et al.*, 1995). The 740 individual mtDNA sequences were aligned and summary statistics were produced using MEGA v5 (Tamura *et al.*, 2011) (Table 4.2).

Table 4.1 Summary statistics

Observed (H_O) and expected (H_E) heterozygosity for 16 microsatellites across all *G.*

variegata^{40a} samples ($N = 740$). F_{IS} values marked * showed significant deviation from Hardy

Weinberg Equilibrium which is indicative of a spatial Wahlund effect owing to genetic

structure (Wahlund, 1928) ($\alpha < 0.05$ after adjustments for multiple tests)

<i>Locus</i>	<i>N</i>	<i>N_A</i>	<i>Range</i>	<i>H_E</i>	<i>H_O</i>	<i>F_{IS}</i>
GVVSN	730	43	168-400	0.87	0.74	0.15*
GV4B6	715	48	280-516	0.95	0.76	0.20*
GV92I	735	17	96-172	0.87	0.65	0.25*
GV1C10	733	41	288-480	0.94	0.83	0.12*
GVMJA	732	16	224-296	0.81	0.76	0.07*
GVYR7	713	25	272-488	0.90	0.79	0.12*
GV3C6	732	8	164-212	0.24	0.20	0.17*
GVVVF	718	29	340-532	0.90	0.74	0.18*
GVWD8	725	29	156-268	0.90	0.83	0.08*
GV4C9	724	35	204-504	0.91	0.77	0.15*
GVGVB	735	26	128-244	0.91	0.86	0.05*
GV3E10	729	39	208-364	0.95	0.78	0.18*
GVN6E	736	14	224-276	0.86	0.80	0.07*
GV17E	725	30	324-464	0.90	0.85	0.06*
GV56J	738	26	128-268	0.88	0.85	0.04
GVT64	724	54	336-608	0.94	0.85	0.10*
Mean		30		0.86	0.75	0.12*

***Note: 635 samples were sourced from Chapter 3 and supplemented with an additional 105 samples.**

Table 4.2 **Summary statistics**

Summary statistics for 740 *G. variegata*^{40a} mtDNA ND4 sequences.

<i>G. variegata</i> ^{40a}	<i>x</i>
Base Pairs	541
Haplotypes	199
Haplotype Diversity	0.97
Conserved Sites	274
Variable Sites	267
Parsimony Informative Sites	251
Singleton Sites	16
Alignment Gaps / Missing Data	2
G+C / A+C Content	0.46 / 0.54
Transition / Transversion Bias (R)	5.16

Identifying evolutionary clades

We used MODELTEST v3.7 (Posada & Crandall, 1998) to determine the best-fit model of DNA substitution across 88 models for tree construction. Each model was assessed using the Akaike, Corrected Akaike, or Bayesian Information Criterion likelihood scores. Utilising all sequences, both distance based and bayesian methods were adopted to construct trees and compare the distribution of haplotypes without phylogenetic inferences. In MEGA v5, we used 10 000 bootstrap replicates to generate neighbour-joining and maximum parsimony, trees. In MrBayes (Ronquist & Huelsenbeck, 2003) we used two runs, each with one cold and three heated chains for 2×10^7 generations, and with the sampling of likelihood parameters taken every 100th generation. The convergence of the chains was confirmed by analysis of the log likelihoods similarity, potential scale reduction factor (1.00 to < 1.01), and the standard deviation of split frequencies (≤ 0.01). The first 1×10^6 trees were discarded as burn-in, and those remaining were used to construct a majority rule consensus tree. We delineated clades by reciprocal monophyly (Moritz, 1994) based on a minimum of 2 % sequence divergence using MEGA v5. We also considered whether this method was likely to reflect clades based on ecological in-exchangeability due to differences in localised environmental conditions, by visualising the spatial distribution of the clades (Crandall *et al.*, 2000).

Species distribution modelling and connectivity assessments

The presence / absence datasets which predicted the range of favourable climatic conditions for *G. variegata*^{40a}, during 2010 and 2070 were sourced from Chapter 3 / Duckett *et al.*, (2013). Their substantial occurrence record dataset was distributed throughout the species known range, thus sampling bias was unlikely to be problematic (Costa *et al.*, 2010). Their future projections to 2070 used the ensemble forecasting framework (Thuiller *et al.*, 2005; Araújo & New, 2007), which considers the central trend from several SDMs and is

preferential amongst modellers due to the improved accuracy and robustness of these forecasts (Araújo & New, 2007; Marmion *et al.*, 2009; Grenouillet *et al.*, 2011; Oppel *et al.*, 2011). Future predictions were based on the A2 (business as usual) emissions scenario (IPCC, 2007), which is considered to be by far the most realistic scenario due to projected population growth and rising CO₂ emissions (Tol, 2005).

We identified the individuals from each clade within the current distribution which could feasibly colonise the future distribution based on zero, minimum, mean, maximum, and unlimited dispersal scenarios (Duckett *et al.*, 2013). The Duckett *et al.* Dilation Model suggested mean dispersal (4.85 km / yr \pm 1.73) was preferential in comparison to the maximum rate (7.59 km / yr), because, in the region under consideration, future climates are predicted to increase in aridity (Hughes, 2003) and *G. variegata*^{40a} dispersal rates were substantially lower in the driest regions (1.69 km / yr). The model also assumed random dispersal in all directions, which is preferential when considering both coastal and inland areas are potential future refugia (Byrne, 2008). This also simplifies the model assumptions and ensures conservative projections (Gustafson *et al.*, 2006). Ideally spatial and temporal vegetation layers would be beneficial to the model, allowing for the assignment of dynamic dispersal rates, yet this information is not currently available for the Australian continent at the appropriate scales. Please see Duckett *et al.* (2013, Supplementary Information) for detailed methods on the SDM and connectivity assessments.

Quantifying the levels of current genetic diversity retained in the future

Using our microsatellite and mitochondrial sequence datasets we quantified the levels of genetic diversity lost within each clade between the present and 2070 for each of our dispersal scenarios. After establishing baseline measures, for each dispersal scenario we then removed all individuals from the locations that could not contribute to the predicted future distribution

within the timescale imposed by GCC (Duckett *et al.*, 2013). We accounted for differing clade membership size by using rarefaction to the minimum number of individuals across the scenarios ($N = 4$). We calculated microsatellite diversity (referred to as Allelic Richness - A_R) in FSTAT v2.9.3, and Haplotype Richness (Inverse of Simpson's Index of Diversity - H_R), and Phylogenetic Diversity (P_D) in R v2.14.0 with the Picante and Vegan libraries. To compare if the predicted losses significantly differed between dispersal scenarios we used a Wilcoxon Signed Rank Test.

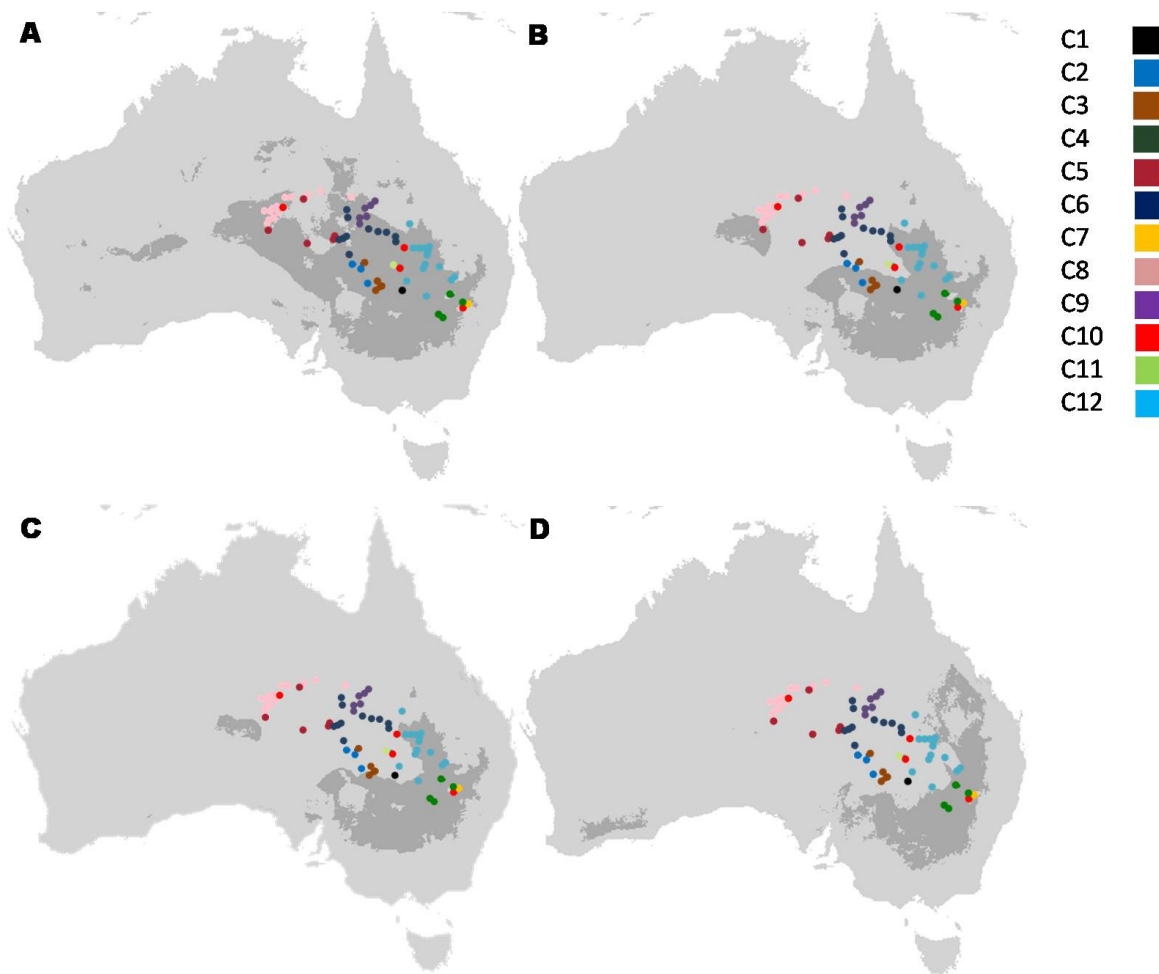
Results

Modelling

The SDM results for *G. variegata*^{40a} (Chapter 3) predicted a substantial reduction in climatically favourable areas (2010 ~1.39 km² / 2070 ~0.62 million km²) and a broad scale range shift in an approximate south east direction under the IPCC A2 climate scenario to 2070. The loss of favourable areas is greatest throughout the central regions of Australia, where only two very small refugia are predicted to persist (Fig. 4.1). These central areas are known to house an exceptionally diverse and largely endemic lizard fauna (Cogger, 2000).

Figure 4.1 *Gehyra variegata*^{40a} distribution models with clades

Presence-absence maps for the predicted current (A) and future (D) distributions of *G. variegata*^{40a}. Suitable areas are shown in dark grey and unsuitable areas in light grey. Also the following distributions show the areas that are capable of supplying individuals to the 2070 distribution using (A) unlimited / maximum, (B) mean, (C) minimum, and (D) no dispersal. Each coloured dot represents the present location of sampled individuals and the evolutionary clade (C) they belong to (Please view Figure 4.2 for *G. variegata*^{40a} phylogeny).



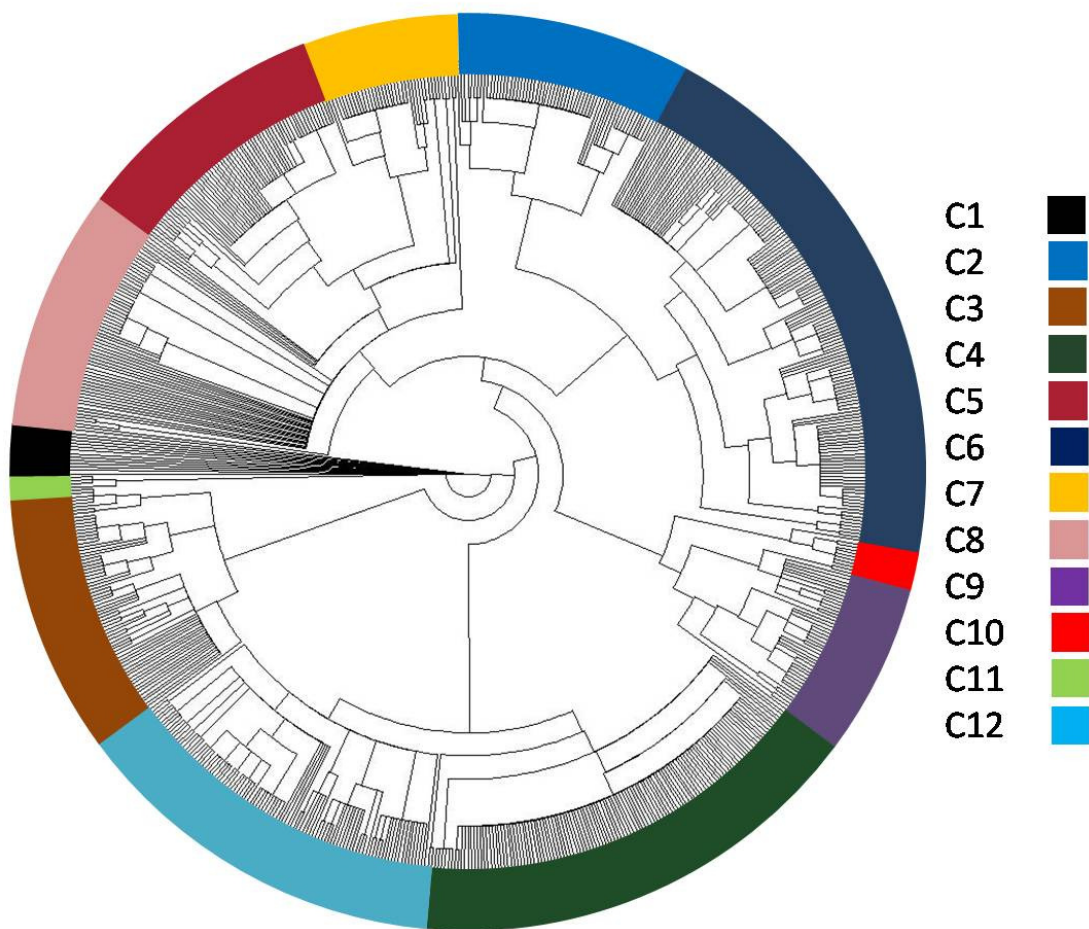
Evolutionary clades

We found strong support for the generalised time-reversible mode of evolution with a gamma distribution and a proportion of invariant sites (GTR+G+I) (Tavare, 1986). All tree construction algorithms consistently clustered individuals on the same branches, and allowed the identification of 12 clades based on 2 % sequence divergence between reciprocally monophyletic groups. In most cases the clades clustered broadly with geographic sampling and possibly reflect sections of the *G. variegata*^{40a} distribution that are adapted to different environmental conditions (Fig. 4.2). Whilst climatic envelopes vary little between adjacent clades, the density of vegetation and landscape features varied among clades considerably (ranges, sandy desert, stony deserts, channel country, and woodlands).

Figure 4.2 Bayesian consensus cladogram

Shown is a consensus Bayesian cladogram based on 541bp of mtDNA ND4 sequence data.

The 740 individual *G. variegata*^{40a} samples have been delineated into 12 evolutionary clades (C) by reciprocal monophyly.



Dispersal scenarios and connectivity

There were dramatic differences in the proportion of each clade predicted to persist into the future depending on whether dispersal was quantitatively assessed, or whether unlimited or no dispersal was assumed (Fig. 4.1). For those parts of the distribution that remain in climatically unsuitable areas there are only two eventualities, adaptation or localised extinction. Unlimited dispersal obviously resulted in all individuals within each clade being retained, which is an unrealistic outcome (Engler & Guisan, 2009). If the contemporary maximum dispersal rate is used, which seems unrealistic when considering the arid biome is predicted to increase in aridity, then again all individuals within each clade would be retained. The other extreme, which assumed no dispersal, resulted in all individuals from 9 of the 12 clades being stranded in areas with an unfavourable climate, thus necessitating rapid adaptation to unfavourable conditions to avoid localised extinction. Furthermore, a proportion of individuals from the other 3 clades are predicted to be similarly impacted. Minimum dispersal rates (i.e. those calculated from sand-dune landscapes) result in 6 of 12 clades retained in areas without favourable climatic conditions. However, because there is no reason to expect large areas of inland Australia to transform into 'sandy desert' these dispersal estimates are likely to be too low. When mean estimates of dispersal were incorporated only 3 entire clades, and a proportion of individuals from 8 clades were predicted to be stranded in areas with an unfavourable climate. In this case, incorporating more realistic dispersal estimates strongly influenced predictions for the proportion of each clade likely to have connectivity to future areas of climatic suitability. This is likely to be the case for most organisms.

Impact to current levels of genetic diversity

Our analysis of the highly variable microsatellite and mtDNA sequence datasets (Table 4.1 and 2), revealed that when mean estimates of dispersal are incorporated, intraspecific genetic

diversity will be reduced in 11 of the 12 clades by 2070 under our GCC projections (Table 4.3). Across these 11 clade we show that allelic richness (A_R) significantly declines by 13.4 ± 27.6 % (mean \pm 1 sd; $p < 0.01$), haplotype richness (H_R) significantly declines by 33.5 ± 36.9 % ($p < 0.01$) and phylogenetic diversity (P_D) significantly declines by 53.7 ± 44.2 % ($p < 0.01$). In comparison, an unlimited or maximum dispersal model resulted in no change to current levels of genetic diversity between the present and 2070, substantially underestimating losses relative to a dispersal model. In comparison, a no or minimum dispersal model displays substantially greater losses to current levels of genetic diversity, overestimating losses relative to a mean dispersal model. See Table 4.3 for details of genetic diversity in each clade across the varying dispersal scenarios.

Using the mean dispersal model, the areas where we quantified the greatest losses to intraspecific genetic diversity were located within clades throughout the central regions of arid zone Australia. Clades 9 and 11, located within the ephemeral river systems of the Channel Country and north-west New South Wales, are projected to become extinct. Additionally clades 5 and 6, located within the Central Ranges and Simpson Desert, are predicted to experience substantial losses to genetic diversity. Thus some of the most highly diverse and temporally stable clades will be negatively impacted by the effects of GCC (Duckett *et al.*, 2013). In contrast, the clades within the arid areas of eastern Australia will suffer comparatively lower losses to genetic diversity.

Table 4.3 Measure of genetic diversity

Standardised measures of genetic diversity within *G. variegata*^{40a} clades (C) at 2010 and 2070 using mean- (Me), min- (Mi), and no- dispersal (No) scenarios include: microsatellite variation (Allelic Richness - A_R), and mtDNA variation (Haplotype Richness - H_R and Phylogenetic Diversity - P_D); number of individuals (N). All comparisons significantly differed ($p < 0.01$). *Assuming unlimited or maximum dispersal results in no change in genetic variation from 2010 levels.

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	2010*				2070 _{Me}				2070 _{Mi}				2070 _{No}			
C	N	A_R	H_R	P_D	N	A_R	H_R	P_D	N	A_R	H_R	P_D	N	A_R	H_R	P_D
1	15	5.313	1.000	0.001	10	5.089	1.000	<0.001	0	0	0	0	0	0	0	0
2	61	5.312	2.984	0.010	47	5.278	1.967	0.008	5	4.804	1.471	0.001	0	0	0	0
3	71	5.418	16.313	0.013	70	5.406	15.909	0.013	62	5.378	14.029	0.012	0	0	0	0
4	123	4.749	1.365	0.012	123	4.749	1.365	0.012	123	4.749	1.365	0.012	115	4.681	1.197	0.001
5	66	5.271	5.642	0.014	6	4.271	3.571	<0.001	0	0	0	0	0	0	0	0
6	148	5.509	13.100	0.035	16	5.197	3.368	0.002	0	0	0	0	0	0	0	0
7	30	4.008	1.982	0.009	25	3.722	1.404	0.008	25	3.722	1.404	0.008	21	3.560	1.348	0.003
8	71	4.992	7.446	0.013	17	4.766	6.721	0.003	0	0	0	0	0	0	0	0
9	46	5.484	12.302	0.011	0	0	0	0	0	0	0	0	0	0	0	0
10	9	4.979	1.976	0.003	7	4.700	1.324	<0.001	6	4.553	1.000	<0.001	6	4.553	1.000	<0.001
11	4	4.875	2.667	0.001	0	0	0	0	0	0	0	0	0	0	0	0
12	97	5.461	19.808	0.016	93	5.446	18.441	0.016	87	5.443	16.783	0.014	0	0	0	0
Mean	62	5.114	7.215	0.012	34	4.052	4.589	0.005	26	2.387	3.004	0.004	11	1.066	0.295	<0.001

Discussion

Incorporating dispersal capabilities into SDM is necessary to help quantify the impact of GCC to current levels of genetic diversity. Understanding where the greatest losses will occur is important for the conservation of species, because it is genetic diversity that provides the evolutionary potential for species to respond to change. We adopted the Duckett *et al.*, (2013) Dilation Method which demonstrated that the pace of shifting favourable climatic conditions exceeded the generational dispersal capacity of *G. variegata*^{40a}. Similar to past climatic change within Australian ecosystems (Hewitt, 1996; Schneider *et al.*, 1998), we show the species range contractions and shifts in distribution are likely to result in losses to current levels of genetic diversity. However, this loss is substantial to the majority of the clades identified due to the rate of climatic change in the near future. Thus, the evolutionary potential of *G. variegata*^{40a} may be impacted by GCC in the near future. This approach could be applied to identify and prioritise those species, or parts of a species distribution requiring intervention throughout the next century.

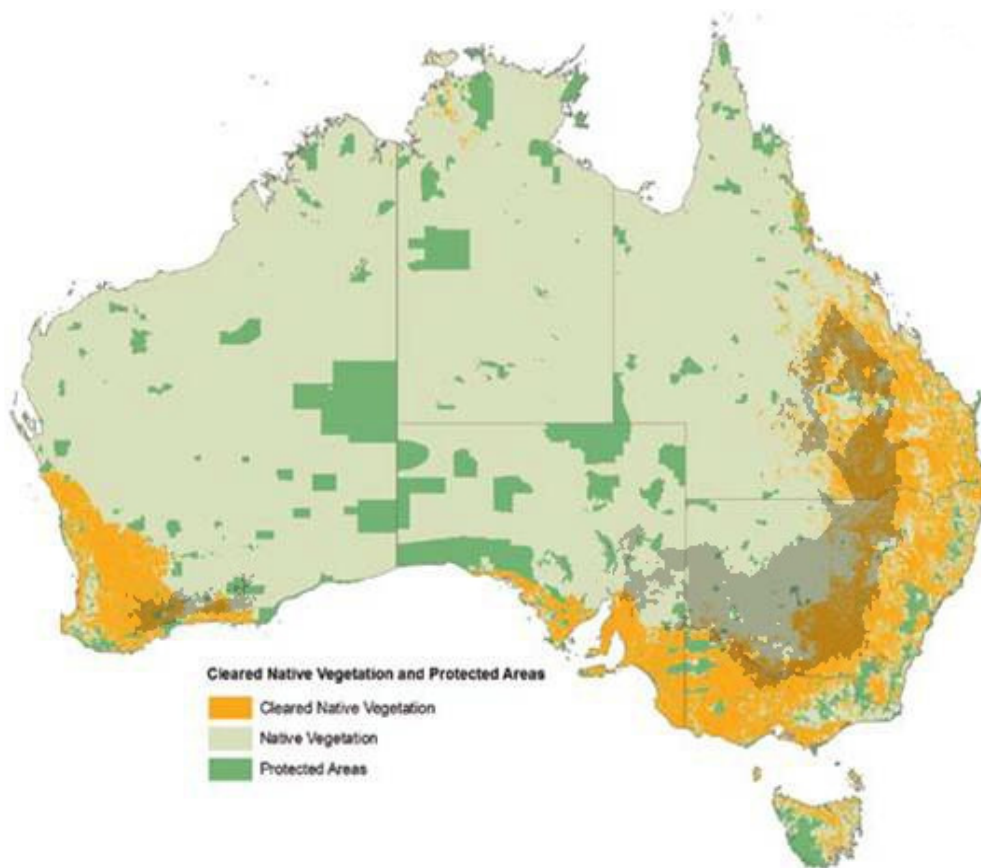
We utilised molecular markers that are considered to be almost selectively neutral, and thus may only loosely reflect genetic variation at functional components of the genome (Reed & Frankham, 2001). Here, higher precision and confidence could be achieved by genotyping individuals at many more loci or targeting functional regions (Hoffmann & Willi, 2008). However, it is commonly accepted that reductions in genetic diversity are directly related to increased inbreeding and declining effective population sizes (Wright, 1969; Frankham *et al.*, 2004). Small population sizes have been clearly linked with reductions in species fitness and their future adaptability to changing environments (Frankham, 1996). Thus, neutral markers are a useful surrogate and have been used extensively in conservation studies as they have been shown to display positive and significant correlations with population fitness, explaining between 15 - 20 % of its variation (18 animal / 16 plant species) (Reed & Frankham, 2003).

For example, in *Rana temporaria* (European Common Frog), small isolated populations displayed lower microsatellite heterozygosity which was associated with reduced variation in quantitative genetic traits and higher mortality in comparison to populations in undisturbed habitat (Johansson *et al.*, 2007). Similar findings were reported within *Rana sylvatica* (Wood Frog) (Halverson *et al.*, 2006).

Our approach and results can improve conservation policy and strategy on topics including reserve design, habitat restoration, habitat corridors and translocations. For our model species, *G. variegata*^{40a}, approximately 29% of the predicted future distribution that can feasibly be colonised have already been cleared of native vegetation (Fig. 4.3). This provides useful spatial information to identify and, if necessary, restore areas of natural habitat which can contribute to the National Reserve System (Taylor & Figgis, 2007). This level of information, for multiple woodland species with varying natural history traits, would provide valuable information to construct a broader conservation policy for arid woodland fauna. Further, one of the most cited solutions to assist dispersal in response to GCC are conservation corridors (Heller & Zavaleta, 2009). Here, our findings can help design corridors of natural habitat to promote connectivity to and among localities predicted to be refugia in the future (Beier & Gregory, 2012).

Figure 4.3 Vegetation status and protected areas

Shown are the areas of native vegetation, protected areas and areas that have been cleared of native vegetation throughout Australia. The future distribution of *G. variegata*^{40a} is predicted to overlap substantially with those areas that have been previously cleared (Opaque greyscale). (Source: Australia's Biodiversity Conservation Strategy 2010–2020 - Department of the Environment, Water, Heritage and the Arts).



Where conservation corridors are unlikely to succeed, either because of the absence of suitable habitat or the distances involved are simply too large, translocations may become necessary to retain current levels of genetic diversity, which may otherwise only be replaced by the longer term process of mutation (Moritz, 1999). However, using translocation as a conservation strategy needs careful consideration. The clear benefit of moving individuals from clades that are likely to become extinct to those regions where persistence is likely, is that current levels of genetic diversity can be maintained (Weeks *et al.*, 2011). Yet, incorrectly identifying those clades requiring intervention may unnecessarily increase the risk of deleterious effects to the source and / or host population and waste precious conservation resources. Where only a proportion of a clade requires the translocation of individuals, our approach can ensure they are only translocated to future areas that other members of the same clade can successfully colonise (i.e. clades 5 and 6). Also, for those clades predicted to face localised extinction our approach can identify suitable habitat with consideration for the risk of outbreeding depression (Frankham *et al.*, 2011; Weeks *et al.*, 2011). For example, the utility of the decision tree from Frankham *et al.*, (2011) may suggest that clades 9 and 11 could be translocated to clades 1 and 10 respectively, because these geographically adjacent clades are both reciprocally monophyletic and have similar climatic envelopes. This will ultimately help the management and conservation of biodiversity by prioritising efforts and minimising the risk of disrupting adaptive gene complexes that may be beneficial for species in the near future.

While Duckett *et al.*, (2013) and our study indicates the usefulness of combining dispersal and SDM to quantitatively predict levels of genetic diversity in the future, the SDM still makes several assumptions that are yet to be fully addressed in this field. The modelling still does not account for whether the species' current distribution is in equilibrium with the climate, or whether biotic interactions have a limiting effect. A further problem when modelling species over large spatial scales is the coarse resolution of the climate data and its inability to detect

micro-refugia, where small pockets of favourable microclimate conditions may persist (Byrne, 2008). Additionally we assumed that individuals will go extinct when they became geographically isolated in unsuitable climatic conditions. Yet our understanding of behavioural and / or physiological responses, or which functional genes will be selected for from the varying climatic conditions is unknown for most species (Gienapp *et al.*, 2008). Therefore the likelihood of in-situ adaptation within each clade cannot be calculated, although it seems unlikely based on recent documented localised extinctions of several lizard species (Sinervo *et al.*, 2010). For example, Reid's paradox suggests that dispersal is likely to be an evolutionary dynamic trait, after showing that cane toads (*Bufo marinus*) increased their dispersal rates on the expanding front. However, we had no information on the likelihood of selection for dispersal characteristics across the *G. variegata*^{40a} distribution. Therefore, we cannot comment on whether dispersal capabilities above the mean value will be more likely when ranges contract under GCC scenarios. All these areas of uncertainty need to be progressively incorporated into SDM to test the accuracy and precision of predictions further, which is likely to benefit and progress this field further.

Conclusion

Under an increasingly variable climate, genetic diversity will become a progressively more valuable commodity to aid the survival of species. Therefore quantitatively assessing potential losses to intraspecific genetic diversity is a key challenge in conservation biology.

Furthermore this needs to be achieved rapidly to assess the impact of current GCC for numerous species worldwide. Despite the inherent uncertainty that still exists within the modelling field, our approach to making these assessments is not based on unrealistic dispersal assumptions, which is a useful progression. The implementation of our approach adds value to large molecular and occurrence record datasets that exist for a range of taxa and

species. Incorporating estimates of dispersal will improve predicting the impact of GCC to genetic diversity and provide critical information for conserving biodiversity into the future.

Acknowledgements

This work was supported by Macquarie University. Lizards were handled in accordance with Macquarie University and South Australian Animal Ethics committee recommendations. Tissue collection was licensed by the New South Wales National Parks and Wildlife Service (S12353), Northern Territory Parks and Wildlife Commission (33155), Queensland Environment Protection Agency (WITK04616407), and South Australia Department of the Environment and Natural Resources (Z25499-4). We thank Macquarie University volunteers for their assistance during field collections.

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CHAPTER FIVE: PHYLOGEOGRAPHY AND REFUGIA

In this chapter I explored the phylogeographic and demographic history of *Gehyra variegata*^{40a} throughout arid zone Australia. I identified the likely location and environmental features that were associated with historical refugia at both broad and smaller spatial scales, with comment on the likely impact of near future climate change. This chapter has been published in Diversity and Distributions.

Duckett, P.E., & Stow, A. (2013) Higher genetic diversity is associated with stable water refugia for a gecko with a wide distribution in arid Australia. Diversity and Distributions, xx, xxx-xxx.

Higher genetic diversity is associated with stable water refugia for a gecko with a wide distribution in arid Australia

Abstract

Aim Those locations and features providing refugia for species during unfavourable climatic phases may be important to identify and conserve to help protect biodiversity in the near future. During the Pleistocene, climates oscillated between glacial and inter-glacial periods. In the Northern Hemisphere, the impact from glacial ice sheets caused species to disperse to warmer southern refugia, but less is known about changes to species distributions during these periods in the Southern Hemisphere.

Location In Australia, the climate alternated between highly arid and wetter periods during the Pleistocene. It has been proposed that inland refugia during arid phases may be associated with the inland ranges (areas of higher relief), the mesic east, or areas that maintained favourable species-specific ecological conditions. We test these hypotheses by carrying out a phylogeographical analysis of a widely distributed tree-dwelling gecko, *Gehyra variegata*^{40a}, throughout the central and eastern regions of arid Australia.

Methods We utilised a mtDNA sequence and microsatellite dataset for 740 *G. variegata*^{40a} throughout its known distribution. We also use species distribution modelling to predict the species likely past, present and future distribution.

Results The majority of *G. variegata*^{40a} lineages diverged during the Pleistocene, and those located in regions of arid Australia where mean annual water run-off is highest, displayed higher levels of genetic diversity in comparison to geckos from locations with lower runoff. We also show that genetic diversity increased with proximity to water sources.

Main Conclusions It is likely that *G. variegata*^{40a} contracted to refugia associated with stable water sources during Pleistocene arid phases. However, modelling suggests that unfavourable

climate conditions will be present in this region by 2070. Therefore Pleistocene refugia for *G. variegata*^{40a} are unlikely to be refugia in the future. More generally, our results suggest that water runoff could be a useful predictor to identify favourable conditions for some arid species.

Keywords: Arid, Australia, Conservation, Genetic Diversity, Phylogeography, Species Distribution Modelling, Refugia, Vegetation, Water

Introduction

Global climate change (GCC) has profoundly affected the natural distribution and abundance of biological diversity (Hughes, 2000; Walther *et al.*, 2002; Thuiller *et al.*, 2005). With global temperatures now increasing at unprecedented rates, the natural distribution of species is expected to be severely impacted (Thomas *et al.*, 2004; IPCC, 2007). In recognition of this threat, conservation programs are beginning to value and utilise the growing body of climate change literature to facilitate the preservation of biodiversity (Rouget *et al.*, 2006; Vos *et al.*, 2008). One important approach to help reduce the future impact on biodiversity is knowledge of historical processes that have influenced the evolutionary and colonisation histories of species (Byrne *et al.*, 2008). Molecular data can provide useful indications of historical processes because demographic change will be reflected in the distribution and abundance of genetic diversity. These processes are likely to have influenced connectivity, created population bottlenecks and / or opened up new ecological niches across a species distribution. Thus, throughout a species' distribution there is likely to be varying amounts of genetic diversity resulting from differences in demographic history. Identifying and conserving the locations of high intraspecific genetic diversity is one strategy needed to ensure that the evolutionary potential of a species is preserved for the future (Scoble & Lowe, 2010).

During the Pleistocene epoch, ~ 2,588,000 - 11,700 years bp (Gibbard *et al.*, 2010), climatic conditions oscillated between dry and wet phases. How these conditions impacted on species throughout this period has been speculated since the 19th century (Darwin, 1859). In the last three decades molecular techniques have become another valuable tool in biogeographical studies, and have provided important insights into the origins and assembly of the world's biomes (Crisp, 2006). For example, evidence from the Northern Hemisphere, where most research has been conducted (Beheregaray, 2008), suggests that Pleistocene glacial oscillations caused the distribution of species to change considerably (Avise, 2000), and may

have been responsible for the decline and extinction of many species (Guthrie, 2003). Those species surviving the glaciations responded by contracting into remnant habitat (refugia) during glacial maxima, and expanding during the inter-glacial periods that followed (Hewitt, 1996). This repeating pattern of range contractions and expansions, which mirrored the Pleistocene climate, has shaped the genetic structure of numerous species (Hewitt, 1996, 1999; Avise, 2000).

In the Southern Hemisphere, the Australian arid biome (defined by a moisture index of ≤ 0.4), has received relatively little phylogeographical analysis and a number of questions relating to the diversification and the location of refugia for biodiversity in this biome remain unresolved (Byrne *et al.*, 2008). The desertification of Australia began towards the end of the Miocene (~23 - 5mya) (Bowler *et al.*, 2006), but the arid regions currently present in Australia have a much younger origin around the Pliocene (~ 3 mya) (Fujioka *et al.*, 2005; Fujioka *et al.*, 2009). Despite the recent origin, the arid biome is Australia's largest, in addition to being among the largest desert systems in the world, covering approximately 70 % of mainland Australia (~7.5 million km²). Although the biome displays relative topographic homogeneity, habitat heterogeneity exists at both broader and smaller spatial scales. Species' richness and ecological processes have been well described in arid Australia (Barker & Greenslade, 1982; Stafford Smith & Morton, 1990), and the region houses a rich and largely endemic lizard fauna (Cogger, 2000).

In Australia the climatic oscillations during the Pleistocene did not result in substantial glacial and inter-glacial cycles, instead most regions experienced hyper aridity interspersed with more humid phases. This resulted in the formation of extensive dune fields during the hyper-arid periods, which created an inhospitable environment for most species due to the disappearance of water and vegetation. Some suggest that the waxing and waning between vegetative and desert landscapes in Australia were analogous to movements of glacial ice in

the Northern Hemisphere, whereby biota contracted into large scale refugia (Hewitt 2001; Byrne *et al.*, 2008). However, the response varies amongst taxa, where both large scale expansion and contraction events and more localised responses have been discovered (Byrne *et al.*, 2008). As the climatic conditions in Australia continue to change, the location of past arid zone refugia are important areas to identify for conservation programs. Potentially, these areas may be refugia again in the future. Furthermore, parts of a species distribution in close proximity to refugia typically contain the highest levels of genetic diversity, and this diversity may be needed to maintain the evolutionary potential of species during periods of rapid change. Levels of genetic variation reflect effective population sizes and isolated parts of a species distribution with few individuals, or recently founded areas, will have relatively low effective population sizes. Therefore, we predict that areas where a species has persisted over historical time scales (refugia) will have consistently higher effective population sizes and as a consequence, higher levels of genetic variation.

In this study we investigate the demographic history for the *Gehyra variegata*^{40a} chromosomal race, a small gecko with an extensive distribution throughout the Australian arid zone. The species is commonly found within woodland habitats, underneath the exfoliating bark and woody crevices of its host trees, which it utilises for thermoregulation, predator avoidance, egg incubation and foraging (Bustard, 1968). Due to this species' dependence on vegetation (and indirectly the water that supports it), we hypothesise that the Pleistocene climate strongly influenced its distribution. We test whether levels of genetic variation are associated with environmental features in the Australian arid zone and whether lineage divergence in *G. variegata*^{40a} corresponded with the Pleistocene period.

The inland MacDonnell ranges and mesic east have been proposed as potential refugia during the Pleistocene (Byrne *et al.*, 2008). Additionally the channel country, a large area (~300,000 km²) located in the central to eastern arid zone of Australia, may have also provided refugia

for species during drier periods. Localised rainfall within arid Australia can be highly variable and sometimes lacking entirely, whereas water run-off is more stable (ABS, 2012). The channel country regions receive the majority of their water via run-off, where rainfall in northern Queensland flows south-west until it reaches Lake Eyre in South Australia. This paleodrainage channel has been a permanent feature of the arid zone for at least 60,000 years (Magee & Miller, 1998). We predict that historical refugia will contain higher genetic variation and / or demographic signatures of population stability. The environmental features that we evaluate as potential refugia are the MacDonnell Ranges in central Australia, the mesic east and channel country. We also test whether water sources are associated with genetic variation at smaller spatial scales. We then use species distribution modelling (SDM) to assess whether conclusions drawn for our genetic data are congruent with the predicted distribution during the last glacial maxima (LGM), and to predict whether the historical refugia we identified are likely to represent future refugia for *G. variegata*^{40a}.

Methods

Study species and sampling strategy

(Source Chapter 3): *Gehyra variegata* is a gecko with three distinct chromosome races ($2n = 40a$, $40b$, and 44), and is widely distributed throughout the arid regions of Australia (King, 1979). Both the $2n = 44$ and $2n = 40b$ races are rock dwellers (Hoehn *et al.*, 2007; Sarre, 1996), of which the former has recently been described as a distinct species (*Gehyra lazelli*) (Sistrom *et al.*, 2009). Here, we focus on the most widely distributed tree dwelling $2n = 40a$ race from the central and eastern arid regions of Australia, this race favours exfoliating bark and tree debris for diurnal retreat sites (Bustard, 1968; Henle, 1990; Duckett & Stow, 2012). We used morphological characteristics to avoid misidentification with *G. lazelli* which is

sympatric with *G. variegata*^{40a} in some areas (Sistrom *et al.*, 2009). ND4 mitochondrial sequence data from each individual also confirmed the presence of a single species.

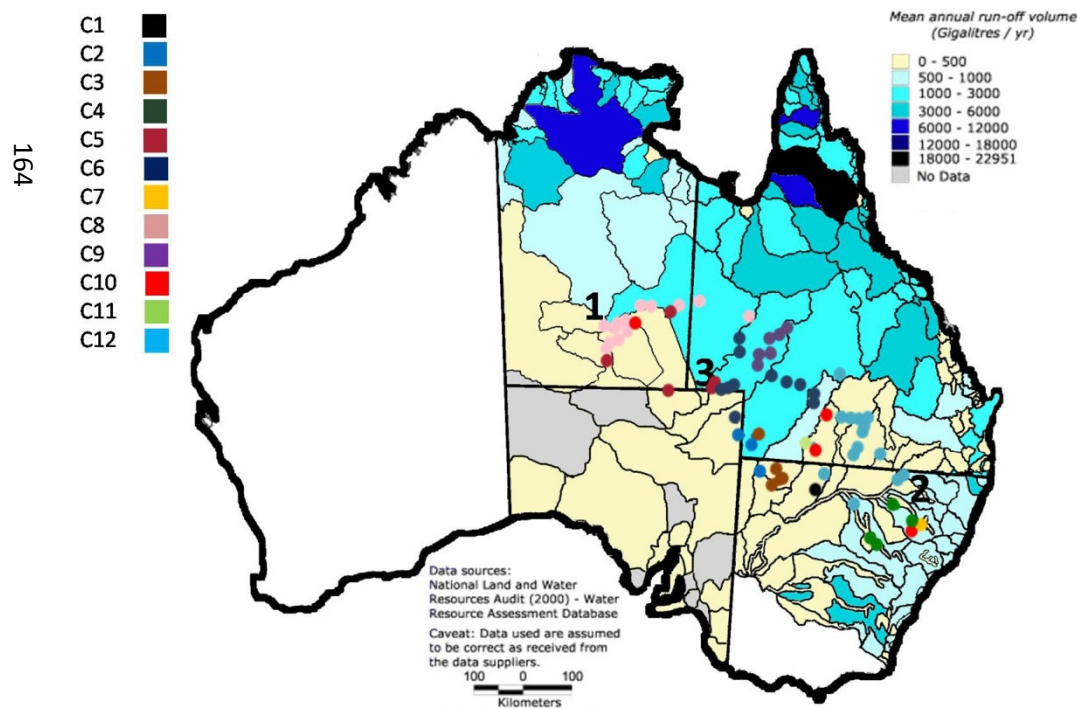
Our study sites were located throughout the arid and semi-arid zones of central and eastern Australia (Fig. 5.1), which closely matches the complete distribution of *G. variegata*^{40a} (King, 1979). The arid zones were broadly categorised to allow patterns of genetic diversity to be associated with broad scale environmental features across the species distribution, including the inland ranges (greatest elevation), the mesic east (densest vegetation), and channel country (largest catchment). These features largely correspond to the MacDonnell Ranges, Brigalow Belt, and Channel Country respectively (Australian-Government 2012). The woody vegetation in most of these landscapes are dominated by *Acacia aneura* (mulga) and *Acacia cambagei* (stinking gidgee or wattle), with the exception of the eastern regions where woodland is typically comprised of the genera *Eucalyptus* and *Callitris*. Between 2009 and 2011 we extensively sampled throughout the species known distribution (King, 1979), and successfully captured 740 individual geckos across the three arid zone features by searching potential retreat sites. Capture locations were recorded using GPS, and prior to release a tail-tip tissue biopsy was taken and stored in 95 % ethanol for analysis back in the laboratory.

We obtained the mean annual surface water run-off statistics for multiple regions within each of the states and territories covered by this study from the Australian Government Natural Resources Atlas, National Land and Water Resource Audit 2000 (www.anra.gov.au) (Fig. 5.1). Historical measures were not available for Australia; therefore contemporary measures may not reflect those of the Pleistocene period. However, a paleodrainage channel has persisted in this region for at least 60,000 years (Magee & Miller, 1998).

Figure 5.1 Sampling strategy and water run-off

The mean annual run off for the Australian states and territories, and sampling localities in this study (colour coded to their designated clade). Numbers 1, 2, and 3 mark the location of the MacDonnell Inland ranges, Mesic east, and the Simpson Desert respectively. The highest levels of genetic variation were associated with the channel country where mean annual run off is also higher (C3, 6, 9, and 12). C2, 4, and 7 represent likely suture zones.

*Modified from source - Australian Government Natural Resources Atlas, National Land and Water Resource Audit 2000 (www.anra.gov.au).



Laboratory procedures

Total DNA was extracted using a modified salting-out protocol (Sunnucks & Hales, 1996). All 740 individuals were genotyped at 16 microsatellite loci (Table 5.1), and sequences for the mtDNA ND4 region were obtained by Polymerase Chain Reaction (PCR). The final reagent concentrations and the thermocycling conditions for PCR are outlined elsewhere (Forstner *et al.*, 1995; Hoehn & Sarre, 2006; Duckett & Stow, 2010). To test our data quality we re-genotyped and sequenced five percent of our sample. Individuals were randomly selected, genotyped at each microsatellite locus and re-sequenced at ND4. After ascribing genotypes and sequences to individuals these data were then compared to the previously collected data to estimate error rates.

Table 5.1 Summary statistics

Observed (H_O) and expected (H_E) heterozygosity for 16 microsatellites (Hoehn & Sarre, 2006; Duckett & Stow, 2010) across 740 individual *G. variegata*^{40a} samples. F_{IS} values marked * showed significant deviation from Hardy-Weinberg Equilibrium after adjustment for multiple tests ($\alpha < 0.05$). Source: Chapter 4 / Table 4.1.

<i>Locus</i>	<i>N</i>	<i>N_A</i>	<i>Range</i>	<i>H_E</i>	<i>H_O</i>	<i>F_{IS}</i>
GVVSN	730	43	168-400	0.87	0.74	0.15*
GV4B6	715	48	280-516	0.95	0.76	0.20*
GV92I	735	17	96-172	0.87	0.65	0.25*
GV1C10	733	41	288-480	0.94	0.83	0.12*
GVMJA	732	16	224-296	0.81	0.76	0.07*
GVYR7	713	25	272-488	0.90	0.79	0.12*
GV3C6	732	8	164-212	0.24	0.20	0.17*
GVVVF	718	29	340-532	0.90	0.74	0.18*
GVWD8	725	29	156-268	0.90	0.83	0.08*
GV4C9	724	35	204-504	0.91	0.77	0.15*
GVGVB	735	26	128-244	0.91	0.86	0.05*
GV3E10	729	39	208-364	0.95	0.78	0.18*
GVN6E	736	14	224-276	0.86	0.80	0.07*
GV17E	725	30	324-464	0.90	0.85	0.06*
GV56J	738	26	128-268	0.88	0.85	0.04
GVT64	724	54	336-608	0.94	0.85	0.10*
Mean		30		0.86	0.75	0.12*

Summary genetic data

For the microsatellite dataset, we calculated summary statistics including number of alleles (N_A), observed heterozygosity (H_O), and expected heterozygosity (H_E) using GENALEX v6.0 (Peakall & Smouse, 2006). Measurements of F_{IS} , linkage disequilibrium, and the significance of any deviation from Hardy-Weinberg equilibrium (HWE) were calculated with FSTAT v2.9.3, correcting for multiple tests (Goudet, 2001). The null allele frequency for each locus was estimated using the Expectation Maximization (EM) algorithm (Dempster *et al.*, 1977) using FREENA (Chapius and Estoup, 2007). The sequence alignment and summary statistics for the mtDNA dataset were produced using MEGA v5 (Tamura *et al.*, 2011) (Table 5.2).

Table 5.2 **Summary statistics**

Summary statistics for 740 *G. variegata*^{40a} mtDNA ND4 sequences. Source: Chapter 4 / Table 4.2.

<i>Gehyra variegata</i> ^{40a}	<i>x</i>
Base Pairs	541
Haplotypes	199
Haplotype Diversity	0.97
Conserved Sites	274
Variable Sites	267
Parsimony Informative Sites	251
Singleton Sites	16
Alignment Gaps / Missing Data	2
G+C / A+C Content	0.46 / 0.54
Transition / Transversion Bias (R)	5.16

Phylogenetic analyses

We used MODELTEST v3.7 (Posada & Crandall, 1998) to determine the best-fit model of DNA substitution among 88 tree construction models. Each model was assessed using the Akaike, Corrected Akaike, or Bayesian Information Criterion likelihood scores. Utilising all sequences, both distance based and Bayesian methods were adopted to construct trees and compare the distribution of haplotypes without phylogenetic inferences. In MEGA v5, we used 10,000 bootstrap replicates to generate neighbour-joining and maximum parsimony trees. In MrBayes (Ronquist & Huelsenbeck, 2003) we used two runs, each with one cold and three heated chains for 2×10^7 generations, and with the sampling of likelihood parameters taken every 1×10^2 generation. The convergence of the chains was confirmed by analysis of the log likelihoods similarity, potential scale reduction factor (1.00 to < 1.01), and the standard deviation of split frequencies (≤ 0.01). The first 10 % of trees were discarded as burn-in, and those remaining were used to construct a majority rule consensus tree. We identified and make reference to well supported mtDNA clades that exhibited reciprocal monophyly (Moritz, 1994) (Source Chapter 4). Sequence divergence was quantified using MEGA v5, and consideration was given as to whether these clades represented individuals from discrete parts of the distribution (Ryder, 1986).

Divergence dating

It has become common practice in phylogenetics to date divergence events. To achieve absolute dating requires reliable calibration points from the fossil record (Ho & Phillips, 2009), which are rare for most data sets (Heads, 2005). However, it is widely accepted that reasonable approximations can be generated (Byrne *et al.*, 2008). In this study we estimate the divergence among lineages of *G. variegata*^{40a} using BEAST v1.5.2 (Drummond & Rambaut, 2007). The calibration point for the Time to Most Recent Common Ancestor (TMRCA) for

all our samples was adopted from a phylogeny of 35 *Gehyra* species throughout Oceania, which dated species divergences based on fossil record calibration and ND2 sequence data (Arnold & Poinar, 2008; Heinicke *et al.*, 2011). For each clade we used the mtDNA sequences for each unique haplotype and defined taxon sets that were reciprocally monophyletic based on the MrBayes phylogeny. We used the best-fit substitution model inferred from MODELTEST (General Time Reversible + Gamma / Invariant Sites), with an uncorrelated lognormal relaxed clock model with an estimate clock rate to allow for rate heterogeneity among lineages (Drummond *et al.*, 2006). We used a coalescent tree prior, because all individuals were of the same species, and the choice of constant population size model was based on the results from Bayesian Skyline Plots (not shown). For the TMRCA prior we specified a normal distribution with a mean \pm sd of 8 ± 3 Ma, corresponding to the estimated time when *G. variegata* first diverged from its closest relative (Heinicke *et al.*, 2011). Posterior estimates of parameters were obtained from two independent runs, each with 7.5×10^8 iterations with parameters taken every 1×10^3 iterations, with the first 20 % discarded as burn-in. The convergence of the stationary distribution was assessed by analysing the posterior samples in Tracer v1.5 to ensure all ESS parameters were > 200 (Rambaut & Drummond, 2007). We consider the time estimates approximate, with our primary objective being to determine if divergences correspond with the Pleistocene period.

Demographic history

We analysed mismatch distributions to infer the demographic history for each of the clades we identified by testing if the mtDNA sequence data deviated from neutral expectations. Multi-modal distributions suggest historically stable or amalgamated populations, in comparison to uni-modal populations which suggest expanding populations (Slater, 1987; Rogers & Harpending, 1992). We performed Tajima's D and Fu's F_s to test for recent

directional selection (Tajima, 1989; Fu, 1997), and the McDonald-Kreitman Test to test for natural selection (McDonald and Kreitman 1991). Tajima's D is used to detect changes in population size or selection, where significantly negative values suggest expanding populations or positive selection, and positive values indicate contracting populations or balancing selection. Fu's F_s is used to detect population expansion or genetic hitchhiking. In both tests, where values approach zero, populations are inferred to be stable. We then tested for deviations from a sudden expansion model using Harpending's Raggedness Index, where significant values indicate population stability (Harpending, 1994). We also tested for evidence of recent admixture within each clade, where a significant result may indicate past suture zones (Chakraborty, 1990). The significance of each test was assessed with 1×10^4 parametric bootstraps using Arlequin v3.11 (Excoffier *et al.*, 2005). To visualise the distribution and frequency of mtDNA haplotypes for each clade we used TCS v1.21 (Clement *et al.*, 2000).

Measures of genetic diversity

To quantify and compare the levels of genetic diversity within each clade we used our microsatellite and mtDNA sequence datasets. Because larger sample sizes are expected to contain more genetic diversity, in each test we account for differing sample sizes by using rarefaction to the minimum number of individuals within a clade ($N = 4$). Standardised microsatellite diversity, referred to as Allelic Richness (A_R), was calculated in FSTAT v2.9.3 (Goudet, 2001). Haplotype Richness (H_R), based on the inverse of Simpson's Index of Diversity, and Phylogenetic Distance (P_D) was calculated in R v2.14.0 (RCDT 2011) with the Picante and Vegan libraries. To test whether higher genetic diversity was associated with broad scale environmental features, for each clade we estimated genetic diversity (P_D , H_R , and A_R) and regressed these measures against the geographic distance from the landscape features

being tested as potential refugia. To test any association between genetic variation and proximity to the MacDonnell ranges and the mesic east, geographic distances were measured from the central point of each clade to either the central point of the MacDonnell Ranges or the nearest point of contact with the mesic east bioregion. Mean annual run-off was also regressed against measures of genetic variation. Regressions were carried out using *vassarstats* (<http://vassarstats.net>). Our prediction was that genetic diversity will increase with proximity to locations that have acted as historical refugia.

Testing whether higher genetic diversity is associated with proximity to water

To test whether higher genetic diversity was associated with proximity to a water source over smaller distances (within a single 'landscape' type), we regressed standardised measures of genetic diversity generated from a total of 102 individuals with linear geographic distance from water sources in the Simpson Desert. The Simpson Desert covers a region with the lowest average annual rainfall totals in Australia, and may approximate what were more widespread conditions during dryer phases of the Pleistocene. At this location we sampled individuals in six separate areas ($< 3 \text{ km}^2$) to a maximum distance of $\sim 26 \text{ km}$ from a single water source, Eyre Creek and Lake Nappanerica. Each of these locations contained a sufficient number of individuals to capture common alleles ($> 5 \%$). Regression and significance testing used *vassarstats*.

Species distribution modelling - past, present, and future

If the highest levels of genetic diversity represent Pleistocene arid zone refugia for *G. variegata*^{40a}, then these areas should be congruent with their predicted LGM distribution. We performed SDM with MAXENT 3.3.1 (Phillips *et al.*, 2006; Phillips & Dudík, 2008). We

modelled the likely present and past environmental suitability for *G. variegata*^{40a} using a substantial occurrence record dataset, and eight climatic variables (Appendix S1) at a 2.5 arc min (~5 km²) resolution obtained from the WorldClim database (www.worldclim.org), (Hijimans *et al.*, 2005). The climatic variables allow the characterisation of the mean and variability of temperature and rainfall throughout the region, and were selected over others due to their higher predictive ability in the model. The past distribution of *G. variegata*^{40a} was projected to the LGM (~21,000 years before present) using the Paleoclimate Modelling Intercomparison Project Phase II (PMIP2) dataset. Future climate projections were sourced from Chapter 3 / Duckett *et al.* (2013). All predicted distributions were transformed into presence-absence maps. See 'Supplementary Information' for a detailed description of the modelling procedure.

Results

Summary statistics for the genetic data

The 16 primer pairs successfully amplified polymorphic loci with unambiguous alleles (Table 5.1), and revealed high levels of allelic variation, with $N_A = 8 - 54$, $H_O = 0.20 - 0.86$, $H_E = 0.24 - 0.95$. Error rates estimated from repeat genotyping and sequencing, and checks of data entry, found errors at a low frequency (< 0.01), and these were corrected. All loci showed a significant homozygote excess across the complete dataset. However, analysis at smaller spatial scales (within 4 km²) rarely showed significant deviation from HWE. This indicates that the homozygote excess apparent when all samples are pooled is a likely Wahlund effect owing to genetic structure (Wahlund, 1928). We had a high rate of amplification success across all loci and null alleles were at a low frequency (mean \pm sd; 0.04 ± 0.02), and there was no evidence for linkage disequilibrium. Following the removal of ambiguously aligned

nucleotides, 740 mtDNA ND4 sequences were trimmed to 541bp, which revealed high levels of variation among haplotypes (Table 5.2).

Species phylogeny and estimated timing of divergence

All three model evaluation methods provided strong support for the generalised time-reversible mode of evolution with a gamma distribution and a proportion of invariant sites (GTR+G+I) (Tavare, 1986). All tree construction algorithms consistently clustered individuals on the same branches, and allowed the identification of 12 major clades, where a minimum of 2 % sequence divergence between reciprocally monophyletic groups was found. In most cases the clades contained individuals that were sampled from the same geographic region (Fig. 5.2). The basal divergences within our phylogeny pre-date the Pleistocene epoch (7,970,000 - 2,740,000 years bp), whereas the majority of divergences among *G. variegata*^{40a} lineages are congruent with a Pleistocene influence (1,900,000 - 200,000 years bp; Table 5.3).

Figure 5.2 Bayesian consensus cladogram

A consensus Bayesian cladogram based on 541bp of mtDNA ND4 sequence data. The 740 individual *G. variegata*^{40a} samples have been delineated into 12 major clades by reciprocal monophyly. Each line touching the cladogram edge represents a single sample and its designated clade. *Note this type of tree only represents branching patterns and branch lengths do not represent time.

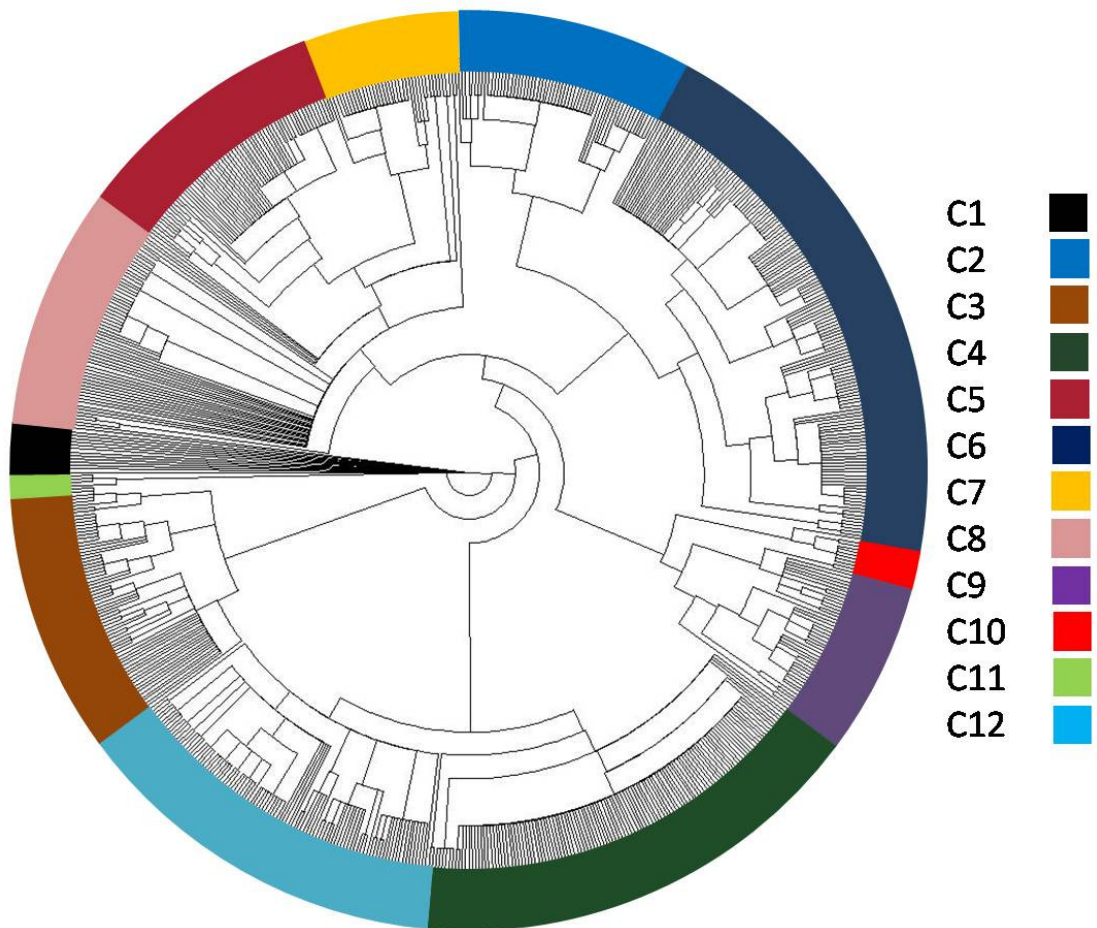


Table 5.3 Demographic histories

Summary statistics exploring the demographic history for each of the *G. variegata*^{40a} clades (C) we identified. Values marked * showed significant deviation from neutral expectations ($P < 0.02$). Statistics are not provided for C1 due to a lack of haplotypic variation.

C	Fu's Fs	p-value	Tajima's D	p-value	Raggedness	p-value	Chakraborty Obs/Exp	p-value	TMRCA (years)
1	-	-	-	-	-	-	-	-	7,970,000
2	8.414	0.975	1.121	0.895	0.168	0.161	12/22.881	0.011*	300,000
3	-5.673	0.078	-0.306	0.443	0.009	0.514	33/22.636	0.203	1,900,000
4	-2.221	0.175	-2.030	0.001*	0.436	0.579	9/5.829	0.001*	600,000
5	4.018	0.893	-0.556	0.330	0.031	0.697	17/23.734	0.063	200,000
6	-1.020	0.458	-1.502	0.034	0.013	0.216	35/31.741	0.227	300,000
7	11.633	0.998	0.504	0.761	0.176	0.999	8/18.080	0.006*	200,000
8	-0.918	0.433	-1.131	0.114	0.259	0.538	22/19.632	0.039	400,000
9	0.774	0.659	0.178	0.645	0.035	0.030	19/19.995	0.755	400,000
10	4.388	0.971	-1.651	0.033	0.518	0.932	3/5.443	0.560	400,000
11	0.134	0.327	-0.780	0.197	0.306	0.603	3/2.567	0.765	2,740,000
12	-7.472	0.057	-0.559	0.333	0.006	0.646	40/26.166	0.321	600,000

Contrasting demographic histories

Analysis of the number of synonymous and non-synonymous substitutions in each clade detected a statistically significant excess of synonymous substitutions in clade 5 ($P < 0.05$), indicating a purifying selection on the ND4 gene. The assumption of neutrality could not be rejected in the other 11 clades. We infer contrasting demographic histories among clades (C1-12) (Table 5.3 and Supplementary Information Figure 5.6). Both clades 3 and 12, located within the channel country, displayed numerous haplotypes separated by relatively few mutational steps. While this might suggest recent population expansion this was not statistically supported with Fu's F_s or Tajima's D . Other channel country clades (C6 and 9) possessed haplotypes with a larger number of mutational steps between them relative to each of the other clades assessed. While these sorts of patterns are indicative of demographic stability, there was no statistical support for this. We found significant evidence for recent admixture in the south channel country, and the east (C2, 4, and 7, $p = < 0.02$). These suture zones do not represent past refugia, and the demographic history for each individual clade can be attributed to previous overlapping of populations from past expansion events with subsequent isolation. We did not infer the demographic history for C1 due to the presence of only a single haplotype.

Higher genetic diversity is associated with the channel country

Our analysis of the microsatellite and mtDNA sequence datasets within C1 - 12 revealed that standardised measures of genetic variation were generally higher within C3, 6, 9, and 12 (Table 5.4). We show that the decline in mtDNA genetic diversity (P_D and H_R) is not strongly associated with increasing distance from either the 'mesic east' ($R^2 = 0.008$ and 0.016 ; $p = 0.388$ and 0.345) or 'inland ranges' ($R^2 = 0.058$ and 0.046 ; $p = 0.223$ and 0.249). Yet a weak association was inferred from the A_R dataset ($R^2 = 0.273$ and 0.245 ; $p = 0.040$ and 0.051).

Here, the association visible in A_R suggest increases in genetic diversity with proximity to the inland ranges, although this is largely driven by one point close to the mesic east. The clades which displayed the highest levels of genetic variation were located within the channel country of arid zone Australia, which is characterised by a higher mean annual run off than any other sampling locality (Fig. 5.1). Across all 12 clades we found a strong association between higher levels of mtDNA genetic diversity (P_D and H_R) and higher mean annual run-off ($R^2 = 0.459$ and 0.546 ; $p = 0.007, 0.003$); a weaker association remained for A_R respectively ($R^2 = 0.230$; $p = 0.057$) (Fig. 5.3).

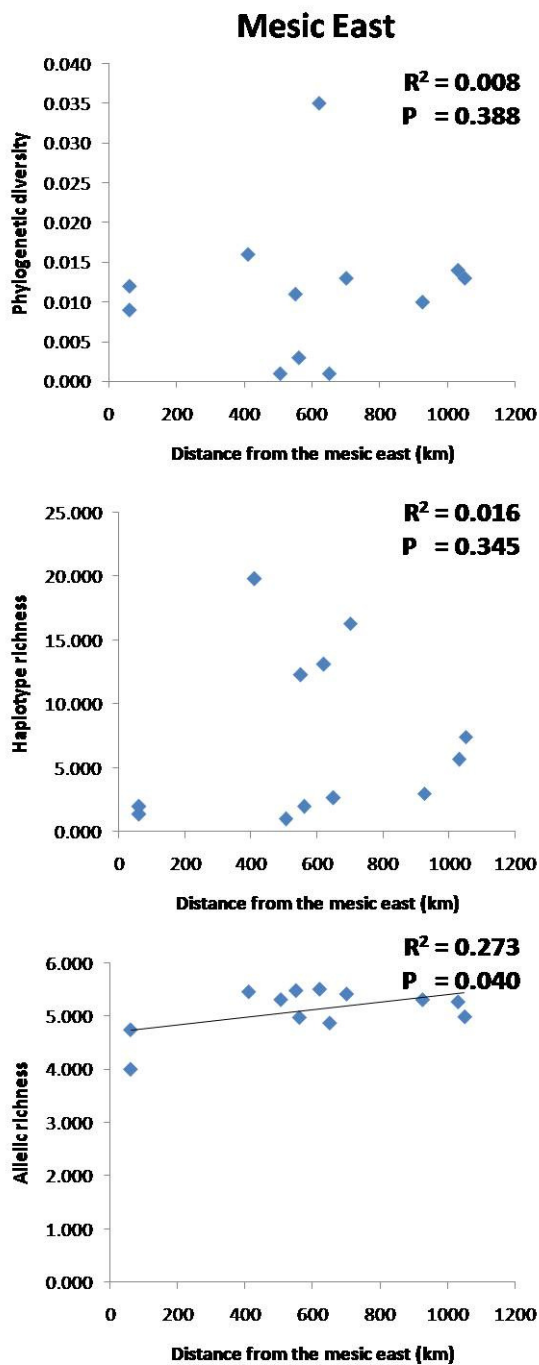
Table 5.4 Measures of genetic diversity

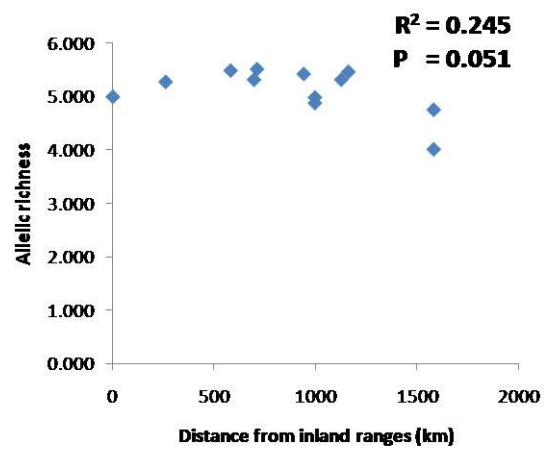
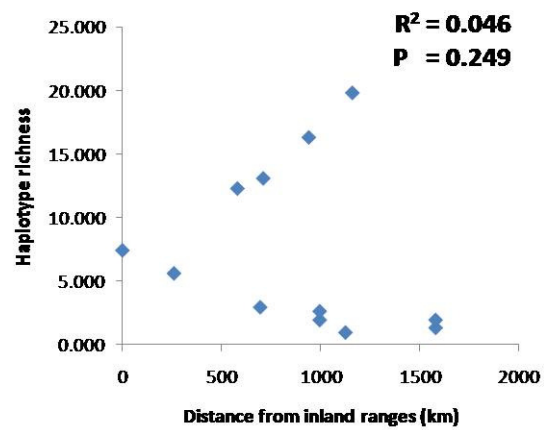
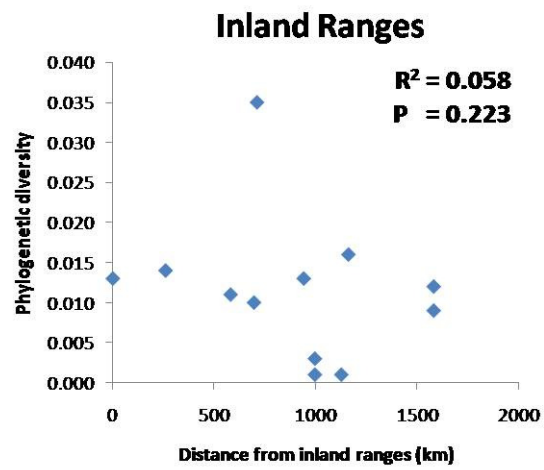
Standardised measures of genetic diversity for *G. variegata*^{40a} include Allelic Richness (A_R) using microsatellite data from (Table 5.1), and Haplotype Richness (H_R), and Phylogenetic Diversity (P_D) using mtDNA ND4 sequence data, across each of the 12 clades (C). Source: Chapter 4 / Subset of Table 4.3.

C	N	A_R	H_R	P_D
1	15	5.313	1.000	0.001
2	61	5.312	2.984	0.010
3	71	5.418	16.313	0.013
4	123	4.749	1.365	0.012
5	66	5.271	5.642	0.014
6	148	5.509	13.100	0.035
7	30	4.008	1.982	0.009
8	71	4.992	7.446	0.013
9	46	5.484	12.302	0.011
10	9	4.979	1.976	0.003
11	4	4.875	2.667	0.001
12	97	5.461	19.808	0.016
Mean	62	5.114	7.215	0.012

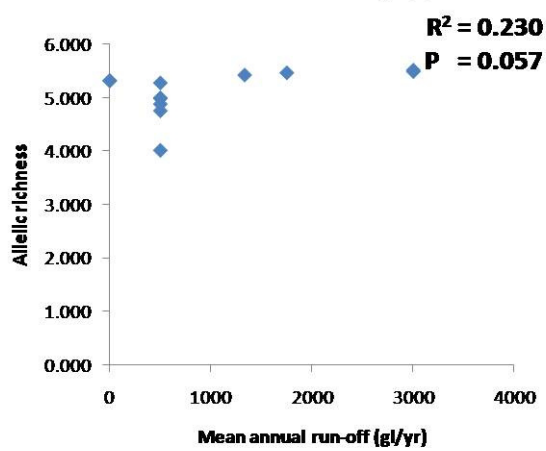
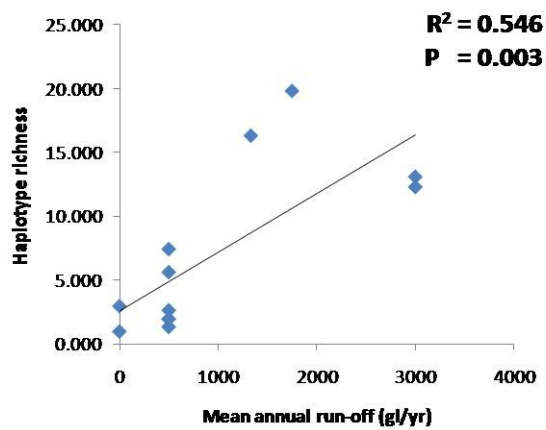
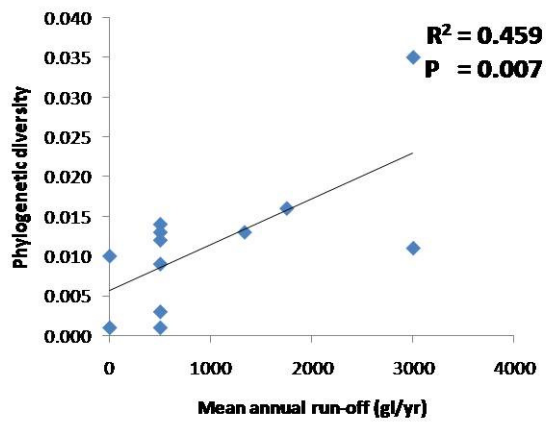
Figure 5.3 Regression analysis

Regressions of standardised measures of genetic variation (P_D , H_R , and A_R) with the geographic distance (km) of collected samples from the Mesic East and MacDonnell Ranges, and with Mean annual run-off (gigalitres per year). The strength (R^2) and significance (P) of each regression is provided, a 'trend' line was included when the relationship was significant.





Water run-off



Higher genetic diversity is associated with localised water sources

The analysis of our Simpson Desert dataset ($n = 102$), shows that genetic diversity (P_D , H_R , and A_R) declines significantly with increasing distance from water sources in this region (Eyres Creek and Lake Nappanerica) ($R^2 = 0.786, 0.623$, and 0.641 ; $p = 0.009, 0.031$, and 0.027 respectively) (Fig. 5.4). Within each of these areas there is a visible increase in the stand size and frequency of *Acacia* species, which provides habitat for *G. variegata*^{40a}. This suggests refugia may be associated with stable water sources which facilitates the persistence of its habitat.

Species distribution modelling

SDM revealed the likely distribution of those areas with favourable climatic conditions for *G. variegata*^{40a} during the LGM, present and future. Modelling for past and present climates suggests the channel country has long been part of this species distribution, which provides support for our genetic data. However, future projections (Chapter 3) suggests that favourable climatic conditions will not be retained in this region, and will contract and shift in an approximate south-east direction (Fig. 5.5).

Figure 5.4 Regression analysis

Regressions of standardised measures of genetic variation with the geographic distance of collected samples from stable water sources found within the Simpson Desert. The strength (R^2) and significance (P) of each regression is provided.

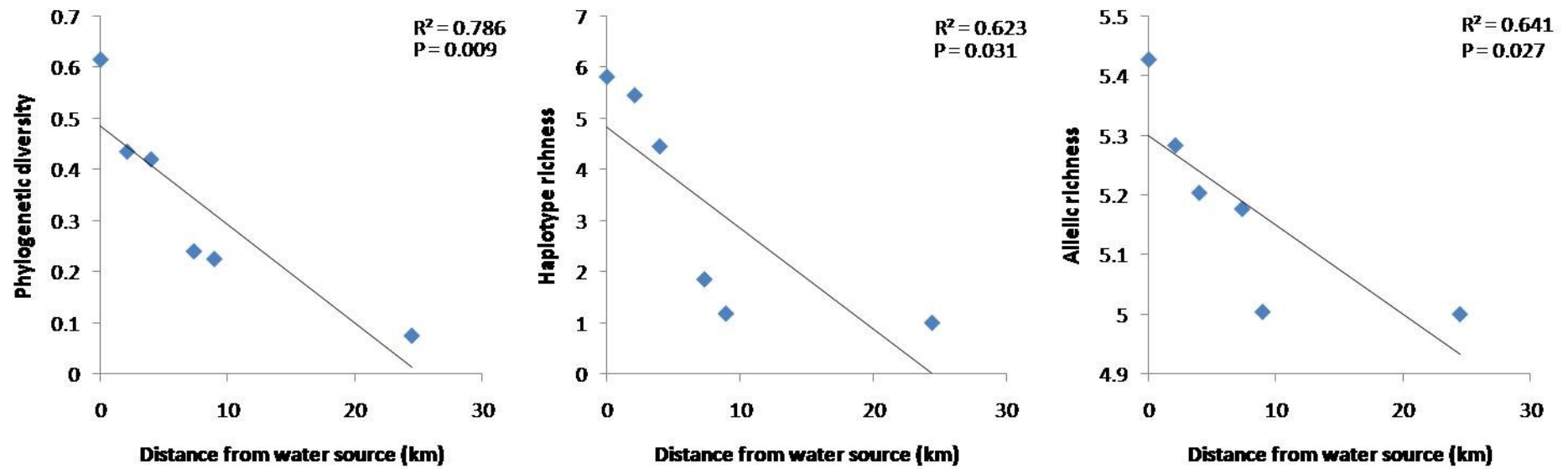
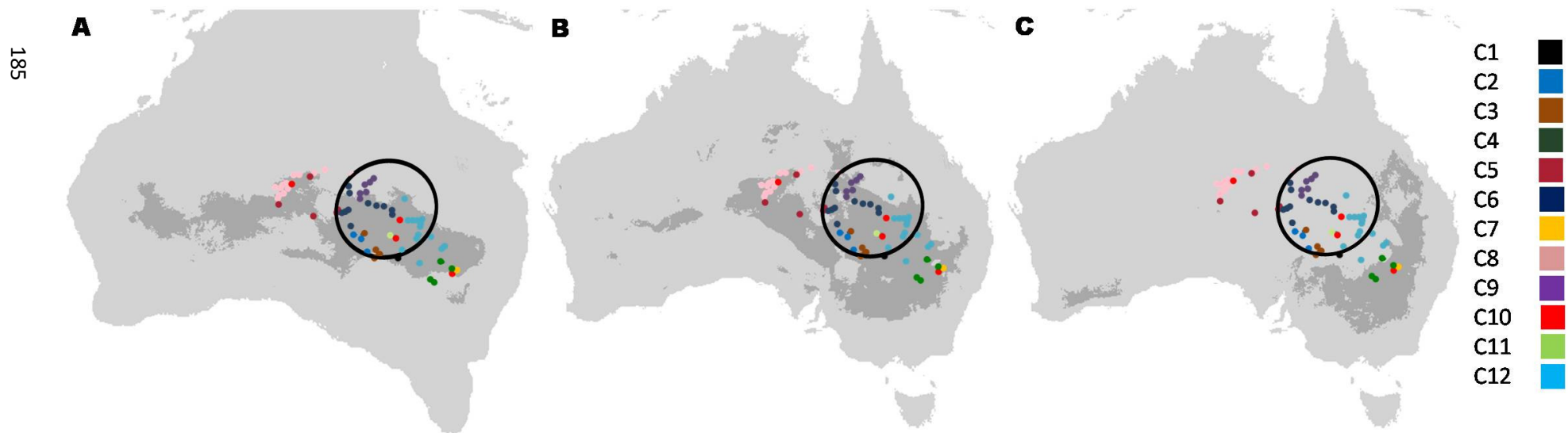


Figure 5.5 *Gehyra variegata*^{40a} distribution maps

Presence-absence maps for the predicted distributions of *G. variegata*^{40a}. Favourable climatic conditions areas are shown in dark grey and unsuitable areas in light grey. The following distributions are presented: A = the past (LGM); B = the present (2010); C = the future (Source: Chapter 3 - 2070 A2 scenario where realistic population and CO₂ increases and economic growth is favoured over environmental concerns). Each coloured dot represents the present location of sampled individuals and the evolutionary clade (C) they belong to. The black circle represents the approximate location of the channel country.



Discussion

Phylogeographic approaches and SDM have rarely been applied to identify historical refugia in arid Australia, despite the power of this interdisciplinary approach being previously demonstrated (Strasburg *et al.*, 2007). Genetic data from *G. variegata*^{40a} sampled from several arid Australian landscapes and SDM indicate long-term persistence of this species in the channel country, a region that indirectly receives more water than other arid regions. The channel country is inferred to have been part of the distribution of this species since at least the LGM, and has maintained high levels of genetic diversity throughout the Pleistocene in comparison to other regions. However, the SDM for *G. variegata*^{40a} did not predict favourable climatic conditions in the channel country in the near future.

Our data shows broad scale geographic structuring of lineages, where the estimated time of genetic divergences for the majority of clades were after the peak in amplitude for Pleistocene climatic oscillations; ~600,000 to 200,000 years bp (Byrne *et al.*, 2008). The Pleistocene period has been associated with lineage splitting for marsupial, acacia, and other lizard species in arid Australia (Blacket *et al.*, 2001; Byrne *et al.*, 2001; Chapple *et al.*, 2004; Strasburg *et al.*, 2007). The survival of *G. variegata*^{40a} throughout hyper-arid Pleistocene events, provides support for the interpretation of our genetic data, suggesting the presence of refugia. Previous studies identified Pleistocene refugia in the northern and western regions for *Heteronotia binoei* (Strasburg *et al.*, 2007). Thus, *G. variegata*^{40a} refugial areas could have been on the periphery of the expanding central Australian deserts. Therefore, the species' current widespread distribution may reflect a major re-colonisation event since the LGM. However, despite the contrasting levels of haplotype richness and, differing demographic histories across the contemporary distribution of *G. variegata*^{40a}, we did not conclusively identify the presence of multiple localised refugia in the past because clades identified were not inferred to be recently expanding.

Higher levels of genetic diversity were inferred for clades located in the channel country, in comparison to those clades from the inland ranges or mesic east. This provided evidence for multiple areas of population persistence during the Pleistocene in the channel country region. Although, the classic signature of past range expansion events out of Pleistocene refugia, which has been revealed for other Australian arid zone geckos (Strasburg *et al.*, 2007), was not identified. However, in the mesic east and the MacDonnell inland ranges, potential locations for refugia (Byrne *et al.*, 2008), we found comparatively lower levels of genetic diversity. This suggests that regions that promoted population persistence throughout the Pleistocene might have been less extensive in these regions compared to the channel country for *G. variegata*^{40a}. The channel country region receives water from monsoonal rains falling in the north of Queensland which then drain throughout (and supply) several hundred thousand square kilometres via an ancient paleodrainage channel towards Lake Eyre in the north-east of South Australia (Fig. 5.1). Outside of this region rainfall predominately flows towards the coast, and sporadic and localised rains supply much of the arid region. Thus, it would seem that local water availability and not rainfall influences persistence. The importance of a stable water supply to *G. variegata*^{40a} is also demonstrated by our genetic data at shorter spatial scales (Fig. 5.4). Here, we found that higher genetic diversity was associated with water presence, suggesting longer term persistence occurs in closer proximity of water. Although again, the water sources are rarely filled by local rains, and receive the vast majority of their water via rainfall in northern locations. During very arid phases suitable vegetation for *G. variegata*^{40a} is likely to be lost in areas other than those with a stable water supply. These data support the notion that water supply is likely to be associated with historical refugia.

The SDM performed in this study still made several commonly made assumptions which are yet to be fully evaluated in this area of research. For example, in some situations, assuming distribution equilibrium has been shown to result to inaccurately predict a species range (Elith

et al., 2010), however, this is more likely to be problematic for invasive species in a state of spread rather than the widely distributed and native *G. variegata*^{40a}. We also assumed that in-situ behavioural and physiological responses to rapid climatic changes were unlikely. There may be some justification for this because the localised extinction of many lizard species has recently been documented (Sinervo *et al.* 2010). Our work also highlights the importance of considering the influence of climate outside the regions being evaluated by SDM. For *G. variegata*^{40a} water availability (run-off) may be an important predictor of species' presence and not localised rainfall per se, which currently is not explicitly captured in the models. This is relevant for many arid regions throughout the world where localised rains are infrequent yet water delivered by run-off is more common. For example the Nile, Colorado and Yellow River all flow through desert ecosystems which themselves experience little rainfall. As climates continue to warm globally, incorporating run-off variables will likely improve the predictive ability of SDM for many species. This may be a necessary approach, given that climate models predict widespread decreases in water run-off throughout many countries in the Americas, Africa, Eurasia, and Australasia (Arnell *et al.* 2011).

The phylogeography of *G. variegata*^{40a} revealed that past refugia may be associated with water supply and not necessarily where rains fall, and this is potentially the case for many other arid species throughout the world. The long-term persistence of stable water supplies in the channel country appear to have provided refugia for several aquatic species (Hamilton *et al.*, 2005), and our data suggests that these regions may also be important for the long term persistence of woodland biodiversity. However, modelling of future climate suggests that the channel country region in Australia may not be suitable for our woodland species by 2070. The predicted increases in temperature and evaporation for the Australian arid regions will result in a reduced moisture index. Therefore, arid ecosystems are likely to change, with potential impacts to the woodland vegetation that *G. variegata*^{40a} and many other species are dependent upon. Greater knowledge of how water run-off has influenced persistence

throughout catchments in arid regions, and how climatic change will impact host-tree species, may improve our ability to predict the impacts of climate change and to identify and protect contemporary reservoirs of genetic variation.

Acknowledgements

This work was supported by Macquarie University. Lizards were handled in accordance with Macquarie University and South Australian Animal Ethics committee recommendations.

Tissue collection was licensed by the New South Wales National Parks and Wildlife Service (S12353), Northern Territory Parks and Wildlife Commission (33155), Queensland Environment Protection Agency (WITK04616407), and South Australia Department of the Environment and Natural Resources (Z25499-4). We thank Abigail Cabrelli and Macquarie University volunteers for their assistance during field collections.

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Supplementary information

Species distribution modelling

Input datasets

We supplemented our field observations with data from the Global Biodiversity Information Facility (GBIF - www.gbif.org) to provide ~3000 unique widely distributed occurrence records. All data was manually checked to remove obvious errors (oceanic occurrences), and records matched by their geographic location to represent the 2n = 40b and 2n = 44 (*Gehyra lazelli*) chromosomal races of this species (King, 1979; Sistrom *et al.*, 2009).

Observed baseline climate data was provided by the WorldClim data set (Hijmans *et al.*, 2005) at a grid resolution of 2.5 arc minutes. These data are monthly mean maximum and minimum temperatures and monthly precipitation averaged over the years 1960 to 1990. These data were used to compute 19 bioclimatic variables defined by Nix (1986) and Busby (1991); (See Table 5.5 for details of the 19 bioclimatic variables).

Model building and modelling

We modelled environmental suitability for the occurrence data using MAXENT 3.3.1 (Phillips *et al.*, 2006; Phillips & Dudík, 2008); this method has been validated with multiple species worldwide. The extent of the climate data were longitude 111.975 to 156.275 / latitude -9.975 to -44.525, this includes the whole of continental Australia including Tasmania. A mask was applied to all climate data layers to ensure that oceanic grid cells (which therefore contain no data), and land based grid cells (with data) were identically configured. When modelling species specific responses to global climate change, Beaumont *et al.*, (2005) recommends reducing the number of parameters within the model; which has since become common practice in many studies (Synes & Osborne, 2011). This is shown to help circumvent the likelihood of co-linearity and over-fitting problems, which may otherwise

lead to the misrepresentation of a species range or the loss of biological relevance. We therefore reduced the number of bioclimatic variables from 19 to 8 (Bio 1, 4, 5, 6, 8, 9, 16, 17 - S1 Table 5.5), by excluding those which displayed high correlation to each other (> 0.8 Pearson Correlation), and/or low predictive ability in the model. Variable predictive ability and importance to the model was assessed by percent contribution and jack-knifing in MAXENT. We used the area under the receiver operating characteristic curve (AUC) (Manel *et al.*, 2001) and cross validation to evaluate model robustness and any sampling bias that may be present. In each of our 10 replicate runs MAXENT randomly set aside 25 % of the occurrence records as test data, this allows the program to build the model from the remaining occurrence records (training data) and then test predictive accuracy against the test data; all other parameters were MAXENT defaults. We utilised the resulting MAXENT model to predict areas of climatic suitability to the LGM using the PMIP2 data. All predictions were transformed into presence-absence predictions based on the 'equal test sensitivity and specificity logistic threshold' (0.46 ± 0.01) (Liu *et al.*, 2005). This was the more conservative and precise option in comparison to the 'maximum test sensitivity plus specificity logistic threshold' (0.40 ± 0.05) (Liu *et al.*, 2005), and ensures that the reduction in climatically favourable areas was not overestimated.

Supplementary Information

Table 5.5 Bio / Worldclim variables

The 19 bioclimatic variables: temperatures are in Celsius / precipitations are in millimetres.

Bioclim and WorldClim name	Abbreviation used in the present study	Definition
bio1	AnnTemp	Mean annual temperature
bio2	MeanMonTempRange	Mean monthly temperature range
bio3	Isothermality	Ratio bio2/bio7
bio4	TempSeason	Temperature seasonality = Coeff. of variation mean monthly temperature throughout the year
bio5	MaxTemp	Maximum mean monthly temperature over 12 mths
bio6	MinTemp	Minimum mean monthly temperature over 12 mths
bio7	AnnTempRange	bio5 – bio7
bio8	MeanTempWetQtr	Mean temperature for the wettest consecutive 3 mths
bio9	MeanTempDriestQtr	Mean temperature for the driest consecutive 3 mths
bio10	MeanTempWarmQtr	Mean temperature of the warmest consecutive 3 mths
bio11	MeanTempColdQtr	Mean temperature of the coldest consecutive 3 mths
bio12	AnnPrecip	Sum of monthly precipitation values
bio13	PrecipWettestMon	Precipitation of the wettest month
bio14	PrecipDriestMon	Precipitation of the driest month
bio15	PrecipSeason	Precipitation seasonality = Coeff. of variation mean monthly precipitation throughout the year
bio16	PrecipWettestQtr	Precipitation of the wettest consecutive 3 months
bio17	PrecipDryestQtr	Precipitation of the driest consecutive 3 months
bio18	PrecipWarmQtr	Precipitation of the warmest consecutive 3 months
bio19	PrecipColdQtr	Precipitation of the coldest consecutive 3 months

Supplementary information literature cited

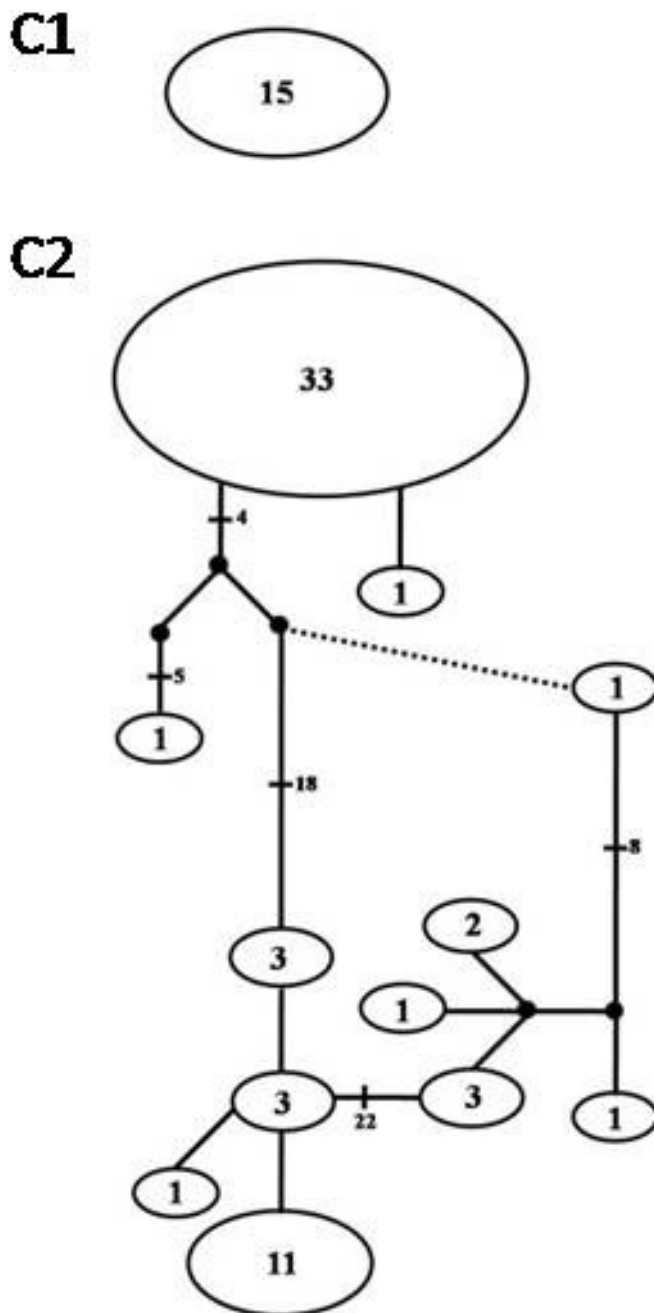
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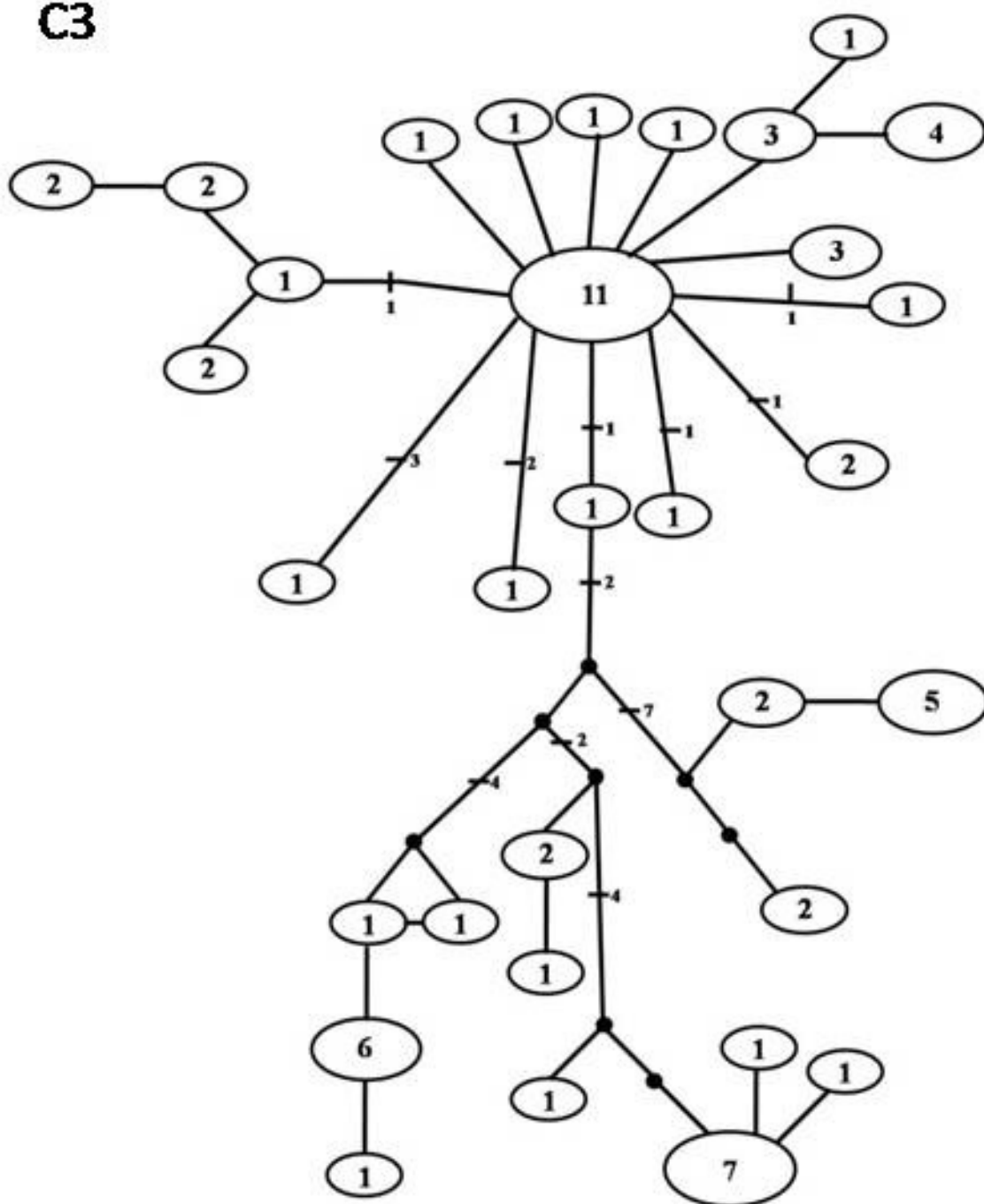
Supplementary Information

Figure 5.6 Haplotype networks

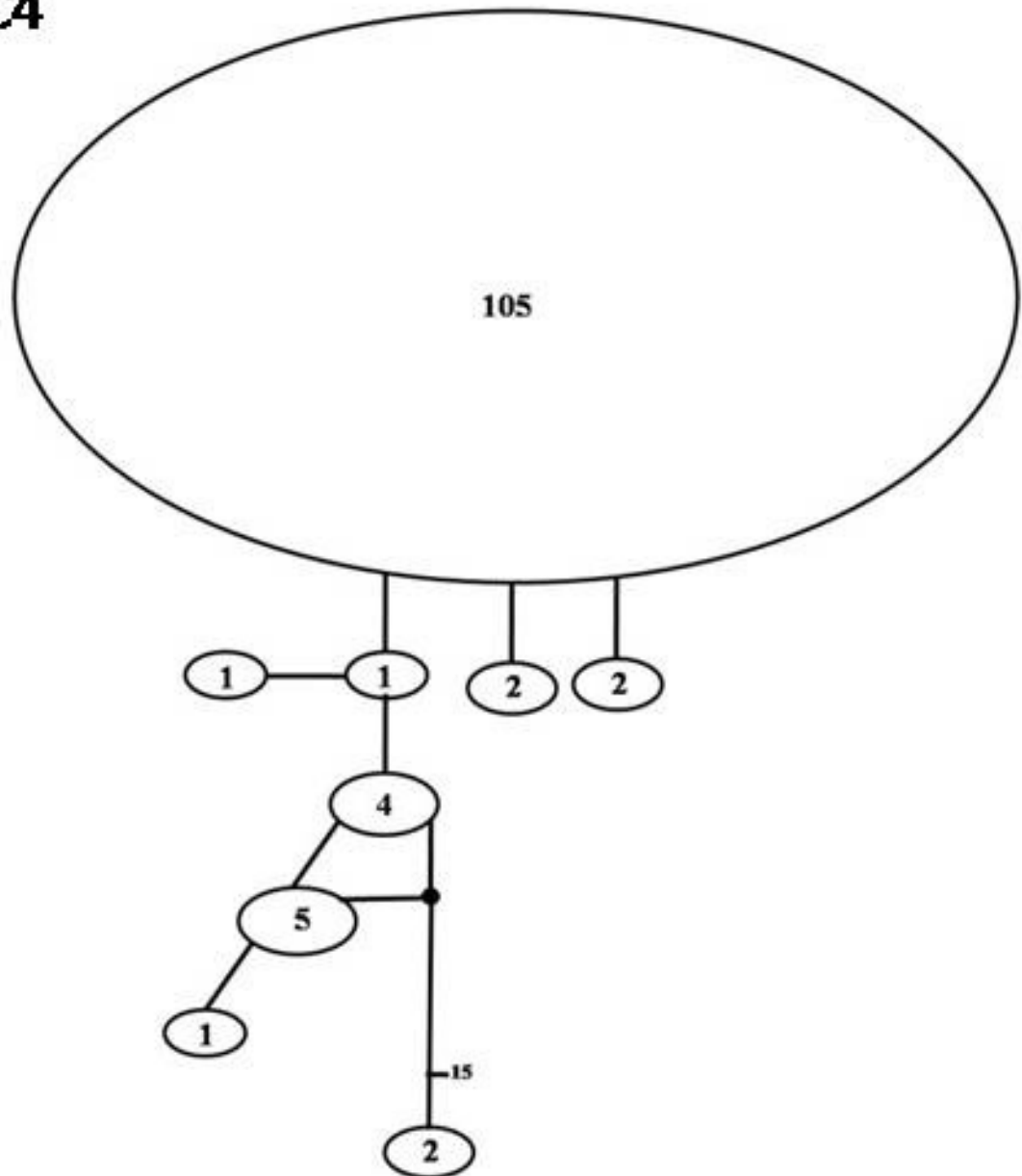
Haplotype networks for *G. variegata*^{40a} Clades (C) 1 - 12 using 541bp of mtDNA ND4 sequence data. Each oval represents a unique haplotype and the size is proportional to the number of individuals found with that haplotype. Each branch represents one inferred mutational step and slashes across branches indicate additional mutations.



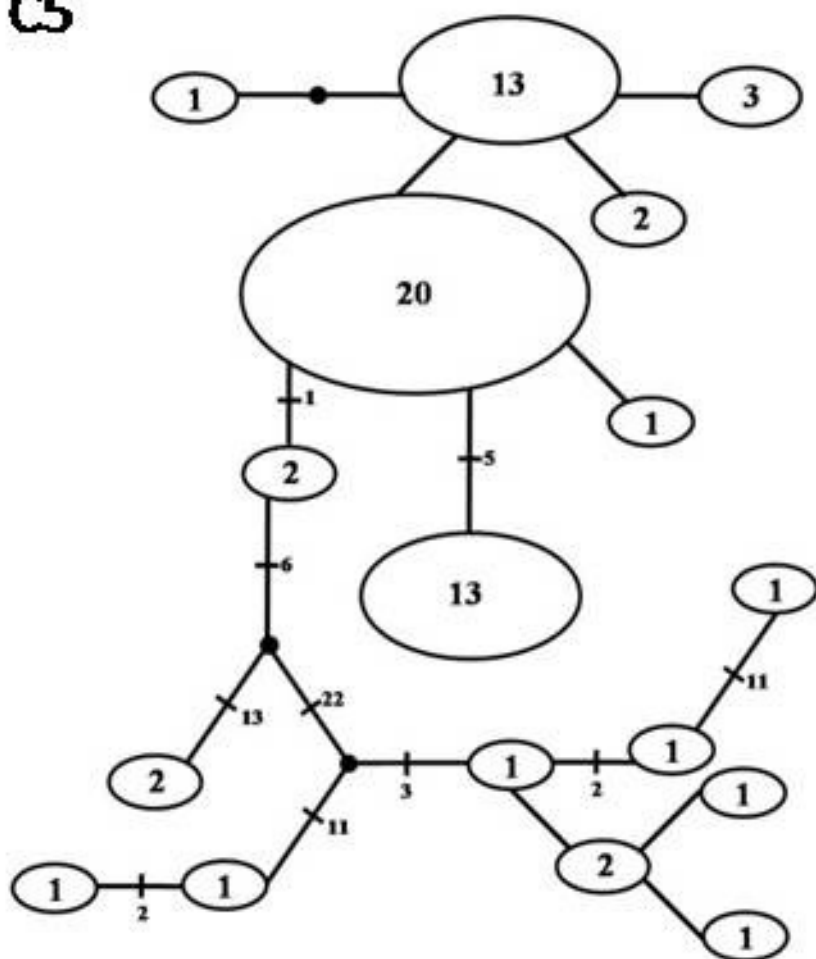
C3



C4

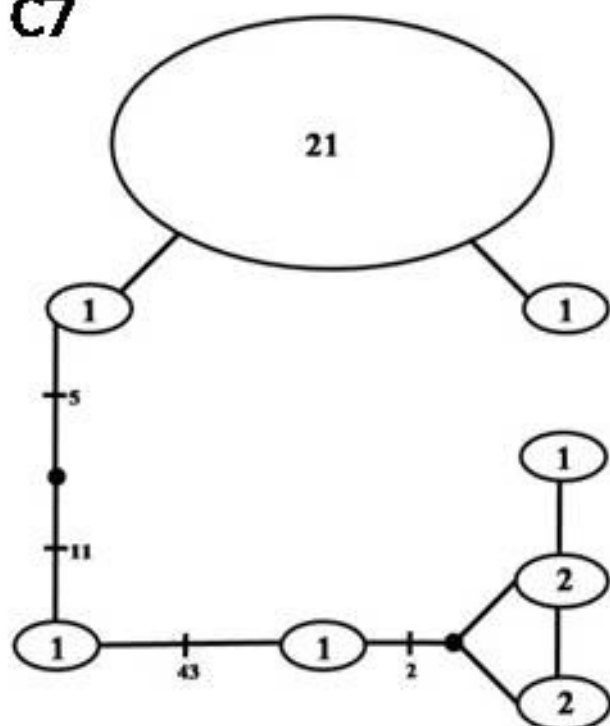


C5

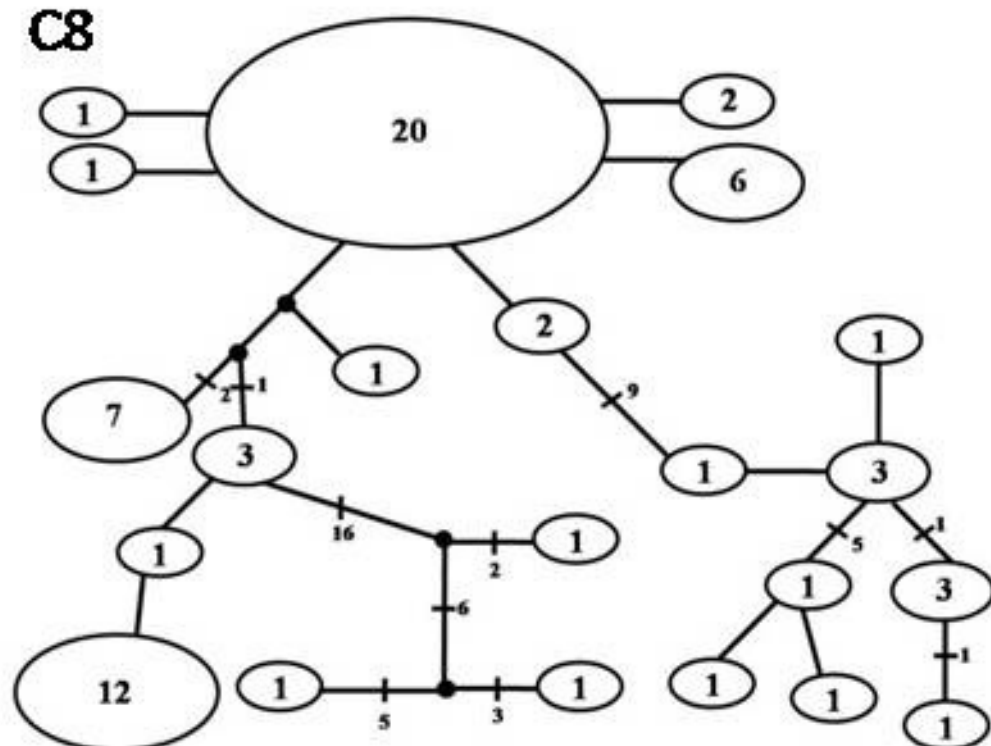


[illegible]

C7



C8

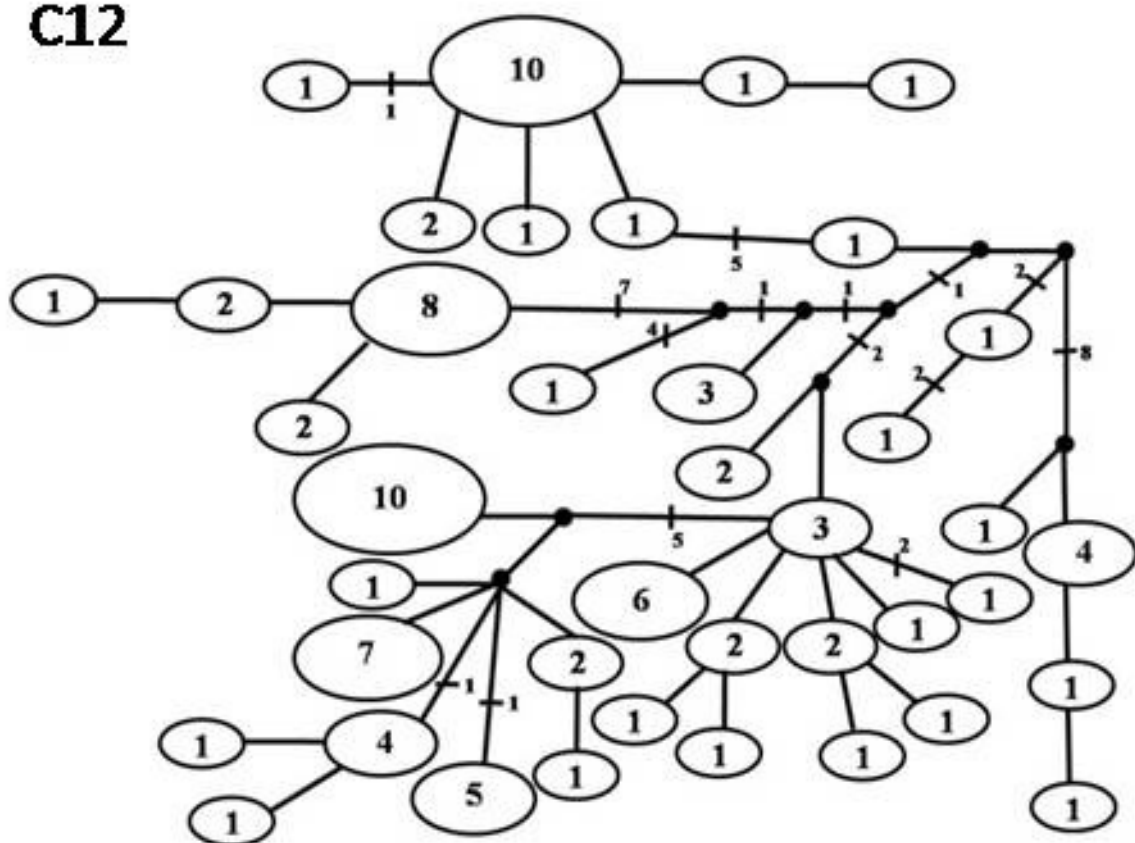


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graph TD
    6((6)) ---|17| 1((1))
    6 --- 2((2))
  
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A tree diagram with root node 2 and two child nodes 1.

C12



CHAPTER 6: FOREST STRUCTURE AND DISPERSAL CHARACTERISTICS

In this chapter I explored if differences in forest structure were associated with levels of dispersal, by conducting a fine scale comparative study between *G. variegata*^{40a} in conservation areas versus adjacent state forest areas. This chapter was successfully published in the Australian Journal of Zoology.

Duckett, P.E., & Stow, A. (2012) Levels of dispersal and tail loss in an Australian gecko (*Gehyra variegata*) are associated with differences in forest structure. Australian Journal of Zoology, 59, 170-176.

Chapter 6 of this thesis has been removed due to copyright reasons

CHAPTER SEVEN

Extending as far back as to the inception of evolutionary theory it was suggested that the distribution of most species cannot be accounted for solely by climatic conditions (Darwin, 1859). Subsequently, the other factors that may influence the ranges of species throughout the world has intrigued scientists for over a century, and has remained one of ecology's most fundamental questions. Yet the answer remains unknown for the vast majority of species. Despite our knowledge and technology having increased substantially since Darwin's time, the majority of our projections on the future distribution of species are still based on climate variables alone. This presented interesting research opportunities to improve upon current modelling techniques by incorporating the effects of additional ecological variables.

This chapter discusses the main findings from the experimental chapters whilst exploring their implications in the near future. Primarily, I focus on the impacts near future climate change will have on the biodiversity of Australia. I also suggest how these problems may be exacerbated in the near future due to increasing demand for the conversion of natural habitat into agricultural, urban and commercial areas throughout the region.

Final discussion

Despite Australia releasing some of the highest levels of greenhouse gases on a per capita basis, in comparison to global production the continent is only responsible for 1% of the world's greenhouse gas emissions (ABS, 2010). In the unlikely event that Australia could substantially reduce its emissions in the very near future, it would only have a minor impact to the global average. Therefore, regardless of any future local emissions policy we can expect global climate change to be one of the factors to profoundly influence the distribution of Australia's flora and fauna over the next century. For this reason understanding the impact and likely changes to species is equally as important as fixing the root cause (Hughes, 2003), to ensure that the high levels of biodiversity and unique behaviours displayed by some of the Australian fauna is conserved (Groombridge, 1992; McAlpin *et al.*, 2011; Duckett *et al.*, 2012) / (Appendix 1 and 2).

In the context of a rapidly changing environment, such as the impacts of global climate change, understanding species' dispersal characteristics is a high priority for conservation. This is because dispersal plays a crucial role in species tracking their favourite environmental conditions throughout both space and time (Polechová *et al.*, 2009). Therefore, for one of the focal points of this thesis, I investigated how to incorporate a genetic estimate of dispersal into species distribution modelling which intuitively will increase the accuracy of projections. However, although our work is a useful progression, like other modelling techniques it still makes several assumptions. Primarily, the projections were based on random dispersal in all directions using the mean annual dispersal ability of *G. variegata*^{40a}, which we believed was justifiable for the following reasons:

First, contemporary annual dispersal distances differed between the habitats under study, whilst this suggested that dispersal characteristics were not random per se, it does not suggest a preference for dispersal direction. Here, we found that the most arid environment (Simpson

Desert) produced the smallest annual dispersal distance (Chapter 3). IPCC projections for the Australian climate in the near future suggest that despite small increases in localised rainfall, the continent will experience a decreased moisture index due to increasing mean annual temperatures, higher evaporation, an increase in intensity and duration of extreme droughts, and an increase in frequency of El Niño events (Hughes, 2003). This suggests that annual dispersal distance is likely to be lower in the future in comparison to contemporary rates. Second, increasing aridity will also negatively impact arid zone vegetation including tree species that are currently used by *G. variegata*^{40a} (Appendix 3). The removal of host trees throughout the species' current distribution will likely increase the fragmentation of native habitat and impede dispersal distances in the future (Hoehn *et al.*, 2007). Subsequently, with a reduction in available retreat sites individuals may suffer from increased exposure to detrimental environmental conditions and predation events (Chapter 6). Third, as the predicted species' distribution shifts towards the eastern coastline of Australia it will become increasingly fragmented due to overlapping agricultural, urbanised and commercial environments (Chapter 3), which may impede dispersal further. Finally, species distributions are highly influenced by biotic interactions which are considered to be more influential at smaller spatial scales in comparison to continent wide distributions (Morin *et al.*, 2007). Thus, as species' ranges contract and fragment in the future, biotic interactions may have a greater impact on dispersal rates than the present time (Case *et al.*, 2005). For example, when environmental conditions change at local scales, spatially defined simulations suggest that competition can control the rate of species' immigration and restrict their ability to track favourable climatic conditions through space and time (Brooker *et al.*, 2007). Additionally models and empirical evidence also suggest predators can have a similar impact on the rates of range shifts of their prey (Bruehlheide & Scheidel, 1999; Lavergne *et al.*, 2010).

In summary, although the colonisation success of the future distribution will be determined by individuals with the maximum annual dispersal distance, the contemporary rates we estimated

(Chapter 3) are likely to decline in the future due to changes in climatic conditions and the subsequent effects from the reduction of habitat. We suggest a mean annual dispersal distance would be more realistic while still providing a conservative estimate of the realised future distribution. Random dispersal in all directions was also a necessary assumption to simplify the model and maintain conservative projections, and because refugia have been projected and hypothesised to exist within both inland and coastal Australia (Chapter 5) / (Byrne *et al.*, 2008).

The impact of global climate change

Although *G. variegata*^{40a} is capable of rapid population expansion and colonisation of vacant habitat when environmental conditions are favourable (Appendix 4) / (Moritz, 1987), our near future climate change projections suggest worryingly negative impacts. The species distribution modelling we completed is congruent with the findings from many studies over the last decade, which suggest that in response to near future climate change, species ranges will contract and shift to higher altitudes or latitudes. In the case of *G. variegata*^{40a}, its range is predicted to shift in an approximate south-east direction and be reduced by $\sim 0.77 \pm 0.24$ million / km² by 2070 (Chapter 3). Large areas of arid Australia, such as the channel country, that facilitated population persistence and stability during the Pleistocene until the present day, are no longer predicted to provide favourable environmental conditions in the near future (Chapter 5). In addition, this region contained some of the highest levels of genetic variation.

When dispersal was incorporated into those climate projections we were able to quantify and identify regions of greatest conservation concern and those areas that would be important in the future. We identified that up to 41 % of the current distribution was too far away from its predicted future distribution, suggesting climate induced range shifts would be accompanied by substantial losses to genetic variation by 2070 (Chapter 4), potentially reducing the

population fitness and adaptive potential of *G. variegata*^{40a}. Furthermore we were able to identify the 86 % of the predicted future distribution that was likely to be colonised.

Unfortunately, the location of the predicted future distribution of favourable climatic conditions overlapped with current agricultural and urbanised areas. This is problematic when natural habitat needs to be preserved and restored if we are to conserve arid woodland species in the near future, but the demand for the continued conversion of natural habitat into areas appropriate for human use will continue as populations continue to grow. Thus, habitat fragmentation is likely to be of greater concern in the future in comparison to the present day.

Habitat fragmentation

Over the next century habitat fragmentation due to climate induced range shifts will have a major impact on the performance and survival of *G. variegata*^{40a}, which is likely to be the case for other arid woodland species. When habitats become fragmented the smaller species populations they contain are affected by demographic processes, which can detrimentally impact population dynamics, their genetic composition and ultimately their persistence (Cole, 1954). For example, small populations may experience the 'Allee effect' (Stephens & Sutherland, 1999; Stephens *et al.*, 1999), where a species or localised population suffer reproductive failure through low mate availability. Additionally, as populations are reduced in number their buffering capacity against environmental and demographic stochasticity is simultaneously reduced, which increases the probability of localised extinction from random events (Lande, 1993; Massot *et al.*, 2008). However, the genetic characteristics of small fragmented populations are suggested to have a greater effect on a population's viability than are stochastic events (Frankham, 1995; Frankham, 1998b; Frankham, 1998a, 2005). Inbreeding depression is more likely to occur in small populations due to the repetitious crossing of related individuals which increase the risk of reduced heterozygosity and the

fixation of deleterious alleles in the next generation. Numerous examples highlight that these negative outcomes of inbreeding are intrinsically linked to offspring and ultimately population fitness (Charlesworth & Charlesworth, 1987; Eldridge *et al.*, 1999; Reed & Frankham, 2003; Leimu *et al.*, 2006).

This problem will be exacerbated by continued land clearing practices which will force species into a mosaic of smaller and smaller areas of native habitat. Since European settlement in the 1830s, the majority of Australia's native vegetation has been cleared or modified by humans. The rate of land clearing in Australia (~ 600,000 ha / year) is one of the highest in the world (only exceeded by Brazil, Indonesia, Congo and Bolivia), and the majority of this has occurred since 1945. While the clearance of native vegetation has been steadily declining from 1990 (561,000 ha) to 2008 (216,500 ha), the rate of clearance still exceeds the rate of replenishment and only a small percentage of the land is being reserved for the conservation of biodiversity (ABS, 2010).

As arid woodland species are forced towards the east coast of Australia one ecosystem that may have great conservation value in the near future is the Brigalow Belt. This region receives its name from a species of silvery wattle, known as 'Brigalow' (*Acacia harpophylla*), although species of Belah, Gidgee, Lancewood and Bendee are the dominant trees in the region (Australian-Government, 2001). This extensive ecosystem covers approximately 6 million hectares from Townsville in Northern Queensland to northern New South Wales, yet only 2 % of the Brigalow Belt is protected within conservation reserves. Yet again the major threat to the Brigalow Belt ecosystem has been extensive land clearing and modification, which still continues. The impacts to the region's biodiversity has already been extensive with several animal species becoming totally extinct (*Psephotus pulcherrimus*, *Conilurus albipes*, *Bettongia penicillata* and *Notomys mordax* / Paradise Parrot, White-footed Rabbit-rat, Brush-tailed Bettong and the Darling Downs Hopping-mouse) and locally extinct (*Macrotis lagotis*,

Dasyurus viverrinus, and *Perameles nasuta* / Bilby, Eastern Quoll and Long-nosed Bandicoot) (Australian-Government, 2011). Recovery plans are currently being developed and implemented to help reduce the threat of land clearing to the Brigalow Belt ecosystem, yet opportunities may also exist in this region to help protect arid woodland species migrating to the area in the near future.

Research applications

My research contributes to a growing body of literature on the evolutionary processes which have driven the diversification and maintenance of Australian arid zone species. Here, my findings were congruent with past studies, where the ancestral clades of *G. variegata*^{40a} predated the Pleistocene. Furthermore, clades displayed high levels of genetic diversity which lacked the signature of a recent expansion event (Byrne *et al.*, 2008). Overall, this supported the notion that Australian arid species were able to persist throughout the arid phases of the Pleistocene within multiple localised regions. Additionally, this research has immediate application to assist the conservation of biodiversity from the impacts of global climate change. We were able to identify the proportion of each *G. variegata*^{40a} clade that was unable to colonise the predicted future distribution, and determine how this would impact the genetic composition of each clade in the future (Chapter 3 and 4). In the absence of unlimited time and monetary resources this helps prioritise conservation efforts to those clades of greatest conservation concern and / or to those that will provide the species with the greatest fitness benefit in the long term. Solutions may include restoring or conserving areas of natural vegetation that will act as conservation corridors and stimulate higher dispersal rates. In this instance our approach can be adopted to designate the most appropriate location for corridors and to provide those clades at risk with connectivity to future regions of favourable

conditions. However, this solution will be unfeasible for some clades as they are simply too far away. The alternate solution is to translocate individuals from at risk clades.

The translocation of species to more favourable habitat is becoming a viable solution to help preserve and restore biodiversity, especially for those species that cannot disperse the required distance in the timescales imposed by global climate change (Hoegh-Guldberg *et al.*, 2008). Despite the theoretical benefits, translocations can be risky without careful consideration and their success is often highly variable (Manchester & Bullock, 2000). Within Australia, there are several areas where improvements to existing translocation policy and practices have been urgently requested before they are utilised more frequently (Burbidge *et al.*, 2011). Here, our approach can provide relevant information to help manage the genetic basis of the translocation. It can assist in helping to identify the future location of appropriate climatic conditions and which environmental features are desirable to promote clade persistence (Chapter 3 and 5). Knowledge of the genetic composition of clades (Chapter 4) could be utilised to avoid overlapping clade membership, thus reducing the risk of outbreeding depression (Frankham *et al.*, 2011). Also, this approach can help source which populations to translocate to maximise effective population sizes and genetic diversity.

Identifying the areas of the predicted future distribution that are likely to be colonised provides several clear benefits for conservation planning. The Brigalow Belt is one ecosystem overlapping with the projected future distribution, but has previously suffered from substantial land clearing. Our approach can help make informed decisions with regards to the preferred locations for the reservation or restoration of the Brigalow Belt ecosystem in the future for the national reserve system (Chapter 3). Additionally, the Brigalow Belt regions of the predicted future distribution that are too far away and unlikely to be colonised may be ideal regions to consider for the translocation of those clades requiring intervention.

Additionally, if the restoration of natural habitat is a feasible strategy within the Brigalow Belt to help accommodate the conservation of woodland species, we suggest that careful consideration is required with regards to the frequency of retreat sites (Chapter 6). Woody retreat sites are utilised by numerous species for predator avoidance, thermoregulation, foraging, and reproduction (Gibbons & Lindenmayer, 2000). Thus, the structure and frequency of these finer-scale features within woodland habitats may have important implications for population fitness and persistence. Here, to effectively restore the Brigalow ecosystem and improve the probability of translocation success for *G. variegata*^{40a}, an understanding of climate change impacts to the host tree species is also required. In the event that the host trees that provide retreat sites are declining themselves, adopting a pull assisted colonisation strategy would help determine which tree species could regionally persist to provide appropriate habitat for a variety of fauna (Lunt *et al.*, 2013).

Future directions

It is vital to understand the additional factors which are likely to influence the probability of a species realising its predicted future distribution for conservation management practices to be effective. Currently, most models are based on static variables between a few points in time, to either simplify model assumptions or through a lack of available data. Yet each variable is likely to be more dynamic and fluctuate considerably through both space and time. We were able to quantify different dispersal distances of *G. variegata*^{40a} within the different habitats it currently occupied. Ideally, we would have liked to incorporate these findings into the species distribution modelling (SDM), so that dispersal rates could be assigned dynamically depending on an individual's location at any point in space and time.

Here, I must acknowledge that other methods in landscape genetics do currently exist in order to understand how landscape features influence connectivity. These new approaches are based

on 'Isolation By Resistance' models (IBR) ,which attempt to account for the spatial heterogeneity within landscapes, and are suggested to be more robust than Euclidean distance measures (McRae, 2006). A typical resistance surface is calculated within a raster GIS environment, and applied as a spatial layer to assign a value to each position within a landscape, which represents how that position may facilitate or impede connectivity for a given organism. This has recently been applied to help predict species' distributions and assess how their genetic composition is likely to change, using applications such as CDPOP; amongst others (Compton et al., 2007; Cushman & Lewis 2010; Landguth & Cushman 2010; Segelbacher et al., 2010; Shirk et al., 2010). The greatest drawback with this approach is that it requires the assignment of resistance values to every point in the landscape under analysis, yet the actual resistance for the majority of landscape features throughout the world, at a sufficiently high resolution, are commonly unknown (Spear et al., 2010). Active consideration needs to be given to this problem because the numerous confounding variables and uncertainties inherent in this process can result in a lack of confidence in any subsequent projections (Beier et al., 2008).

Errors in assigning resistance values to landscape surfaces will lead to misleading conclusions. To overcome this challenge researchers are adopting parameterisation data from the field, expert opinion, and model optimization processes (Spear et al., 2010). The main criticism of the field data approach is that the data is often sourced from experimental studies, which increases the cost substantially. Whilst manipulative studies can provide an adequate control for confounding variables, and focus on the resistance of interest, this may not provide realistic data about behaviour and dispersal in natural conditions. Expert opinion is clearly a cost effective alternative, yet can easily be inaccurate and struggles to assign specific resistances that are relative to each other (Clevenger et al., 2002). Here, the relationship of resistance between landscape features may or may not be linear as critical thresholds can exist (With & Crist, 1995; Brouquet et al., 2006). Model optimisation approaches seek to test the

multiple resistance surfaces against each other, in order to determine their relationship and to confirm which have the greatest explanatory power (Cushman et al., 2006). However, the success of model optimisation is highly dependent on variable selection and the starting point in the simulation, both of which are selected by the researcher and obviously subject to the same problems as the expert opinion approach (Spear et al., 2010).

If resistance values can be assigned reliably to landscape surfaces, there are still many challenges which need to be overcome which relate to model algorithms, variable weighting, and scale. The least cost path algorithm (Adriaensen et al., 2003) assumes that dispersal direction is not random, and that all dispersing individuals have perfect knowledge about the landscapes resistance, which will allow them to make perfect decisions to achieve the optimal route. Alternatively, the circuit theory based algorithm (McRae et al., 2008) assumes that all potential pathways influence movement / gene flow to some degree. Neither algorithm choice is considered to be correct in isolation (Spear et al., 2010). Variable weighting is considered to be one of the most difficult hurdles. Univariate resistant surfaces are clearly unrealistic, because the connectivity between natural populations will rarely be determined by one factor. In comparison, multivariate resistant surface value assignment has greater biological relevance, but are extremely complex to calibrate with confidence because the relative weight of each resistance is often unclear (Spear et al., 2010). Finally, the application of resistance surface based modelling has only been applied to studies at a relatively small geographic scale (< 15,000 km²) (Cushman & Lewis, 2010; Cushman & Landguth, 2010), therefore there predictive ability at larger spatial scales is unknown.

Presently, a definitive method to assign resistant surfaces to models is not obvious and the use of these types of models in the literature, whilst increasing in popularity, have been implemented with relative simplicity and may lack biological relevance. Further consideration is also needed to establish the impact biotic interactions may have on resistant values, such as

predation, competition, and density dependant factors. For this reason informative projections with regards to genetic forecasting are not available.

However, the primary reason resistant surfaces could not be implemented within the thesis is because it would have required continent wide data on the vegetative state and composition for Australia at annual increments between 2010 - 2070 with a 2.5 arc minute resolution. At this present date (March 2013), this data was not available although would make a very useful progression for this field in the near future. Temporal raster layers at such a granular resolution would facilitate the implementation of biologically relevant dispersal rates to known landscape features, ultimately providing a greater level of realism in connectivity assessments. Also, understanding the likely path an organism will choose to utilise will provide extremely valuable information to facilitate corridor or reserve design, and predict the risk of secondary contact between genetically divergent clades.

In Chapter 5, I suggested that species distributions may be influenced by geographically disparate climatic conditions, such as rainfall events in one location that deliver water to another area via water run-off. Variables of this nature are currently not explicitly captured with SDMs, yet their utility could have international significance for conservation assessments. My final suggestion applies to the assisted colonisation debate, our understanding of the complexities and intricate co-dependent relationships that persist within ecosystems are likely to be of paramount importance for the successful restoration of habitat and species. Whilst, bet-hedging approaches have been advocated in the literature to move multiple taxa and genotypes given the uncertainties about of their future performance in differing climatic envelopes (Beale *et al.*, 2008). It would be of greater benefit to understand how, where, and when biotic interactions between dependent species will breakdown due to climate impacts, and whether useful surrogates can be adopted.

Conclusions

The exceptional levels of biodiversity within the Australian arid biome are of paramount importance for the continued health and existence of humanity. Where biodiversity is depleted it often leads to environmental and economic collapse. Thus, a major challenge over the next century is to consider how to achieve sustainable human development, whilst conserving native habitat in the right way and in the right areas to prevent further loss to biodiversity. In addition, this needs to be achieved while the continent faces rapid climatic changes that are also likely to negatively impact a large number of its species. Despite the limitations inherent within the field of SDM, incorporating a genetic estimate of dispersal to improve their usefulness was a worthy progression and is immediately applicable to other arid woodland species. Furthermore, this approach can be rapidly applied to assess the impact of near future global climate change for any species where both molecular and occurrence record datasets are available. These types of impact assessment are becoming increasingly urgent for species worldwide, yet the timescale within which to complete them is quickly reducing.

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APPENDICES

Appendix 1

This study was successfully published in PLoS ONE:

McAlpin, S., Duckett, P. & Stow, A. (2011) Lizards Cooperatively Tunnel to Construct a Long-Term Home for Family Members. PLoS ONE, 6, e19041.

Lizards cooperatively tunnel to construct a long-term home for family members

Abstract

Constructing a home to protect offspring while they mature is common in many vertebrate groups, but has not previously been reported in lizards. Here we provide the first example of a lizard that constructs a long-term home for family members, and a rare case of lizards behaving cooperatively. The great desert skink, *Liopholis kintorei* from Central Australia, constructs an elaborate multi-tunnelled burrow that can be continuously occupied for up to 7 years. Multiple generations participate in construction and maintenance of burrows. Parental assignments based on DNA analysis show that immature individuals within the same burrow were mostly full siblings, even when several age cohorts were present. Parents were always captured at burrows containing their offspring, and females were only detected breeding with the same male both within- and across seasons. Consequently, the individual investments made to construct or maintain a burrow system benefit their own offspring, or siblings, over several breeding seasons.

Introduction

Cooperative behaviour and social aggregations are relatively common in many animal groups, but rare in lizards, a large and otherwise behaviourally diverse group (Pianka & Vitt, 2003). Mate fidelity is another trait that is uncommon in lizards (Chapple, 2003). Within social groups, cooperation is widely considered to be facilitated by genetic relatedness, and as such thought to have evolved in groups of related individuals (Clutton-Brock, 2009). In addition, breeding males are expected to invest more in their offspring as their certainty of paternity increases (Emlen, 1995). These predictions may explain the rarity of cooperative behaviours in lizards and their lack of investment in long-term home construction for groups of individuals.

Several lizard species belonging to the closely allied *Egernia* and *Liopholis* genera have kin-based sociality, a trait that is considered pleisomorphic to the group (Gardner *et al.*, 2008). The only other lizard demonstrated to live in groups of related individuals is *Xantusia vigilis* (Davis *et al.*, 2010). Within the *Liopholis* and *Egernia* genera, species that form long-term groups tend to aggregate in pre-existing retreat sites, mostly rock crevices (Chapple, 2003). Although these species are characterised by groups that consist of close kin levels of polygamy vary both within and across species (Chapple, 2003; While *et al.*, 2009). One species, *Liopholis kintorei* constructs and maintains an interconnected network of tunnels within which it aggregates (Chapple, 2003). We have measured these spanning 13 meters across and with up to 20 entrances. Groups of individuals living within these consist of adults and immature lizards with overlapping generations. *Liopholis kintorei* is viviparous with 1–7 offspring produced annually (Chapple, 2003). The tunnels provide protection from predators and the extreme thermal environment in the region (Chapple, 2003) and construction and regular maintenance must require a large investment of time and energy.

Here we evaluate the longevity of these burrow systems, whether multiple individuals construct and share tunnels, the relatedness among group members and their dispersal characteristics. Because kin-based sociality is an ancestral trait (Gardner *et al.*, 2008), cooperation among close kin would suggest that in this case inclusive fitness benefits have led to this behaviour. Furthermore, this would provide the first example of lizards constructing a long-term home for family members.

Methods

Field collections

The study was conducted at Uluru – Kata Tjuta National Park, Northern Territory, Australia. From 1999 to 2009 monitoring was carried out once a year between September and April when lizards are most active. Monitoring consisted of searching for new burrow systems and inspecting all previously located burrow systems. For each burrow system the number of entrances and spatial organisation were recorded. Activity levels were noted by recording track activity and the presence of any fresh adult and immature lizard scats in their latrine area. Thirty hours of observations were carried out September to December 1996 within a raised hide located 8 meters from a burrow system containing an adult pair and 4 immature lizards. During this time burrowing activity, lizard locations and interactions were recorded. Trapping was undertaken during the summer activity periods at spatially discrete burrow systems distributed across 45 km². Tissue biopsies were taken from the tail tips of 31 adult and 89 juveniles, with groups of individuals (mean group size \pm SD; 4.19 ± 1.67) sampled from 26 burrow systems. Sexing of adult individuals was carried out by visual appraisal. All methods involving *L. kintorei* were carried out in accordance with a protocol considered and approved by Parks Australia and the Macquarie University Ethics Committee under the Animal Research Authority 2008/025.

Genotyping

Total DNA was extracted from 120 tissue samples using a salting-out protocol (Sunnucks & Hales, 1996) and genotyped by amplifying seven microsatellite loci, ECU1, 2, 3 (Stow, 2002) and EST 1, 2, 9, 12 (Gardner *et al.*, 1999). Numbers of alleles at these loci ranged from 8 to 24 and analysis of data from adults using the software GENEPOP 3.0.1 (Raymond & Rousset, 1995) showed that none of the loci significantly deviated from Hardy-Weinberg or linkage equilibrium. The combined non-exclusion probability for siblings was 0.0004, calculated using CERVUS 3.0.3 (Marshall *et al.*, 1998).

Analysis of relatedness

The maximum likelihood method of CERVUS 3.0.3 and COLONY 2.0.0.1 were used to assign parents to offspring (Marshall *et al.*, 1998; Wang & Santure, 2009). All adult individuals (>165 mm SVL (Chapple, 2003)) were included as candidate parents. Simulations for CERVUS were run with: 10,000 cycles, 50 % of candidate parents sampled, 100 % of loci typed and a genotyping error rate of 1 %. For our COLONY analysis we carried out a full-likelihood approach and allowed both males and females to be polygamous, and therefore the assignment of half siblings. We carried out a long-run with medium likelihood precision and no sib-ship prior. We used the same error rates as the analysis with CERVUS. Parental assignments were accepted if the candidate was not genetically incompatible at more than one locus and could be the parent with 80 % or 95 % confidence using CERVUS and that these assignments were compatible with those calculated using COLONY at $p > 0.8$. COLONY identified groups of half and full siblings, even if one or both parents were not sampled. These sibling groups were accepted at $p > 0.8$. In addition, the relatedness between individuals was estimated from allele frequency data obtained from all 120 samples. In order to calculate average levels of relatedness for individuals sampled within the same burrow complex we

used a likelihood approach with KINGROUP 2.0 (Konavalov *et al.*, 2004). Dispersal patterns were inferred by examining the geographical structuring of relatedness using spatial autocorrelation analysis. Relatedness estimates calculated in GenAlEx 6.0 (Peakall & Smouse, 2006), were analysed at several distance classes. For each distance class, the significance of any deviation from zero was assessed by 999 permutations (Peakall & Smouse, 2006) and the 95 % confidence intervals around relatedness were obtained via bootstrapping 999 times. Distance bins were chosen to estimate relatedness within a burrow system (distance = 0), among individuals sampled in different burrow systems that were within 0.500 kilometres of each other, and for individuals located between 0.500 and 0.999 kilometres and 1.000 meters to 14.000 kilometres of each other.

Results

Field observations

Adult and immature individuals use, share and maintain more than one tunnel in the system. This was directly observed and was evident from fresh tracks left by different sized individuals at tunnel openings. Tunnels are mostly excavated and maintained by adults and immature lizards contribute small ‘pop’ holes to the network. These are too narrow to be maintained by adult individuals. On average, only 6 % of tunnels within a burrow system became disused each year. From the first record of the 26 burrow systems, the average (\pm s.d.) period of continuous occupancy in years is 4.04 ± 1.43 (Fig. 8.1), each of these burrow systems had annual breeding success, so this time period represents 4 age cohorts of offspring. High philopatry of immature lizards to their natal burrow system was demonstrated by the genetic data.

Parentage and relatedness analysis

Polygynous males were detected with 40 % of the male parents siring offspring to different females, and these were each located in different burrow clusters (separated by 18 – 179 meters). Juveniles from a single breeding season that were assigned the same mother show an absence of multiple paternity, and all females for which more than one age cohort of offspring were identified had bred with the same male across more than one breeding season. Only a single female was located in a different burrow system to one of its offspring (67 meters separate). As a consequence, groups of immature lizards only contained full siblings in 18 of 24 burrow systems where more than one immature lizard was sampled, and 12 of these contained siblings of more than one age cohort (Fig. 8.1). A low level of dispersing immature lizards is also demonstrated by the spatial distribution of relatedness. Levels of relatedness among immature lizards sharing the same tunnel system was high (mean relatedness \pm s.d.; 0.446 ± 0.123) and significantly greater than the relatedness among lizards located in different tunnel systems, even those located within 500 meters of each other (Fig. 8.2). Parents were always captured in a burrow containing their offspring and burrows in relatively close proximity (0 - 500 meters) could contain immature lizards that shared the same father.

Figure 8.1 Measures of relatedness

Relatedness composition within burrow systems. For each of 26 burrow systems two sets of relatedness data (R) are given, the average $R \pm 1$ s.d between all lizards captured at that burrow and, in the next column to the right, $R \pm 1$ s.d between the immature lizards. The average relatedness among all 120 genotyped individuals is shown by the lower horizontal line ($R = 0.021$), the upper horizontal line shows the average within-group relatedness ($R = 0.371$). Along the x-axis, for each group a series of numbers are given separated by commas. From bottom to top these are; the number of adults, age cohorts of immature lizards, total group size of sampled individuals and the minimum number of years for which the burrow has been continuously occupied.

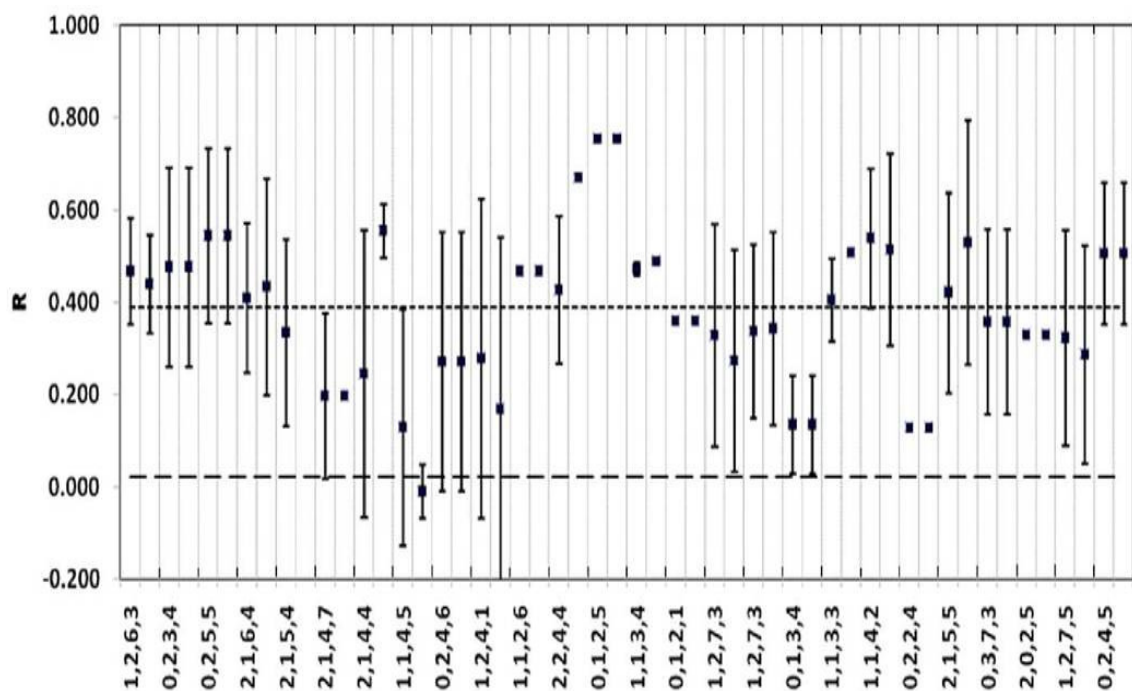
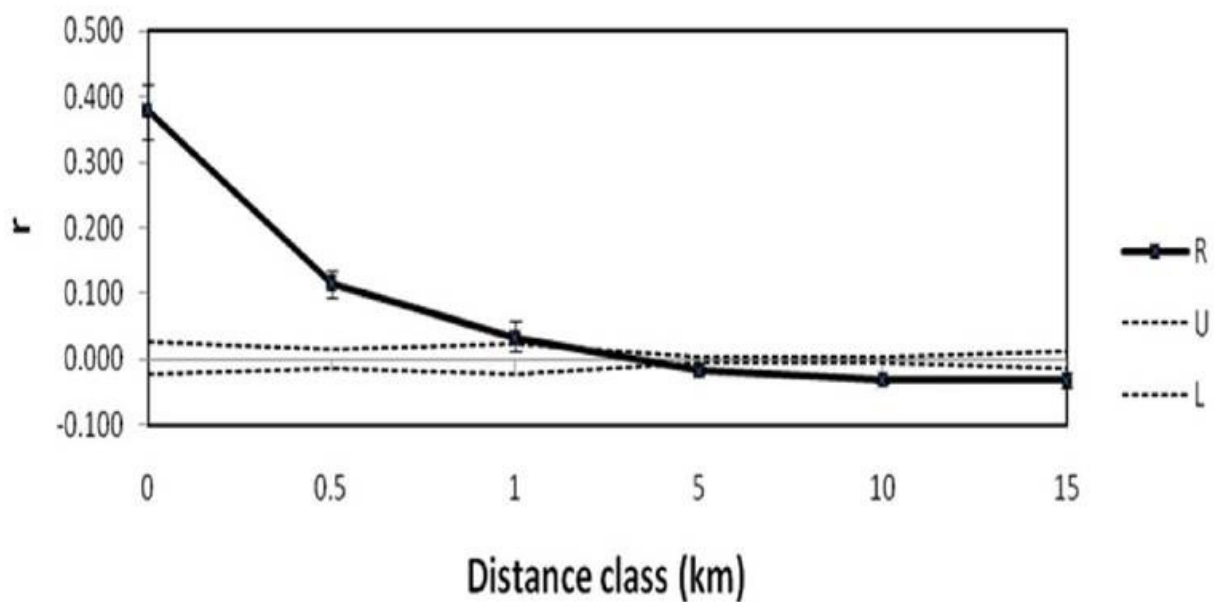


Figure 8.2 Spatial autocorrelation

The distribution of genotypic similarity (r) with geographic distance (kilometres) for immature lizards. The solid line tracks relatedness, dashed lines represent the upper (U) and lower (L) 95 % confidence interval around random expectations while bars around R show the 95 % confidence interval around this estimate determined by bootstrapping. The distance class of 0 kilometres contains the r estimate among individuals sharing the same burrow system.



Discussion

Liopholis kintorei cooperates to construct a burrow system that houses close kin (Fig. 8.1).

Furthermore, the investment in time and energy that adult *L. kintorei* make towards creating this unique and elaborate tunnel system is realized by the high probability that it protects their offspring (Emlen, 1995; While *et al.*, 2009), providing a unique example of parental care in lizards. For *L. kintorei* the relative importance of direct and indirect benefits of tunnel excavation and maintenance have not been estimated. Additionally, low levels of dispersal can increase competition between relatives (Griffin & West, 2002). Nonetheless, in *L. kintorei* there must be a net benefit to these behaviours, because they evolved in groups of close kin (Gardner *et al.*, 2008), this strongly suggests that inclusive fitness advantages played a role.

High natal philopatry of juvenile lizards has been associated with social aggregations of other members of the *Liopholis* and *Egernia* groups, and more recently, the unrelated lizard *Xantusia vigilis* (Chapple, 2003; Davis *et al.*, 2010). Indirect parental care in the form of reduced intraspecific aggression may offer a selective advantage to low juvenile dispersal (O'Connor & Shine, 2003; Davis *et al.*, 2010). Our data on *L. kintorei* suggest that whatever the benefits of low juvenile dispersal are, they have driven the provisioning of an extensive burrow system in the absence of other retreat sites. Interestingly, two sympatric congeners *L. inornata* and *L. striata* appear to have lost their sociality and are largely solitary burrowers (Chapple, 2003; Gardner *et al.*, 2008).

For long-term social aggregations home sites need to be defensible and within foraging distance of a reliable food source (Nowak *et al.*, 2010). The long-term stability of burrow systems constructed by *L. kintorei* implies that they may defend their home. The principle food source for *L. kintorei* is the termite *Drepanotermes perniger* (McAlpin, 2001) which has a naturally patchy distribution and burrow systems appear to be constructed in close proximity to the termite mounds. While the presence of a reliable food source in this arid

environment seems necessary to support social aggregations of *L. kintorei*, it is unlikely to explain the evolution of these social groupings.

In mole rats the food aridity hypothesis proposes that less rainfall is associated with increasing sociality because food resources become patchier (Jarvis *et al.*, 1994). Patchy food resources may select for individuals to aggregate close to food resources and cooperate because of the costs involved with dispersal and burrowing. However, the origin of the *Liopholis* lineage in mesic regions (Chapple & Keogh, 2004) and apparent loss of sociality for several species of *Liopholis* that occupy arid areas suggests that the food aridity hypothesis may not explain social aggregations in *L. kintorei*. Furthermore, there are several *Egernia* species in arid regions that are primarily rock-dwelling (e.g. *E. stokesii*) and therefore have less choice when it comes to the location of their housing but still live in large kin-based social groups (Chapple, 2003). Nonetheless, the distribution and abundance of the primary food source for *L. kintorei* may influence aspects of their sociality. For example, it would be of interest to explore whether the proximity and longevity of termite colonies are associated with group sizes of *L. kintorei* and the length of time for which they occupy their tunnel systems.

The construction and maintenance of a long-term family home occurs in many other taxa, in vertebrates there are examples from most phyla, though it appears most prevalent in birds and mammals (Emlen, 1995). However, this form of parental care and cooperation to construct housing where one's offspring and siblings mature was, until now, unknown among lizards, a group containing at least 5000 species (Chapman, 2009). We have identified inclusive fitness benefits of this behaviour in *L. kintorei*, which, given the few examples of sociality in lizards, would also seem to explain its rarity.

Acknowledgements

We thank the Anangu people for their valuable advice and permission to work on their land.

We also thank Shannon Smith and Richard Frankham for comments on earlier drafts of the manuscript.

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Appendix 2 of this thesis has been removed due to copyright reasons

Duckett, P.E., Morgan, M.H. & Stow, A.J. (2012) Tree-Dwelling Populations of the Skink

Egernia striolata Aggregate in Groups of Close Kin. *Copeia*, 2012, 130-134.

Appendix 3

Species distribution modelling for two tree species commonly utilised by *Gehyra variegata*^{40a} throughout arid zone Australia

Introduction

To better judge the future implications of climate change to *G. variegata*^{40a} dispersal, we use species distribution modelling to predict the potential future distributions of two arid woodland tree species commonly inhabited by the species throughout its distribution.

Methods

We modelled environmental suitability for two widely distributed tree species, *A. aneura* (mulga) and *A. cambagei* (gidgee) using MAXENT 3.3.1. GBIF provided the occurrence records for *A. aneura* (612) and *A. cambagei* (170), and the bioclimatic variables with the greatest predictive ability were as follows; *A. aneura* (Bio 3, 8, 9, 10, 15, 16, 18, and 19) and *A. cambagei* (Bio 1, 4, 5, 8, 9, 11, 12, and 17); (Table 8.4).

Results

The current distribution predicted for both tree species (*A. aneura* and *A. cambagei*) closely matches that of *G. variegata*^{40a}, yet the response to future climates for each of these tree species are dramatically different. The predictive ability for the host tree models was exceptionally high (AUC scores for *A. aneura* / *A. cambagei* = 0.894 ± 0.008 / 0.906 ± 0.018). The predicted range of bioclimatically suitable areas for *A. cambagei* increases substantially from its current range (1.17 ± 0.34 million / km²) to its 2030 predicted range (2.73 ± 1.5 million / km²). By 2070 this range contracts in an approximate south easterly

direction, but still remains larger than their current range ($1.56 \pm 0.75 \text{ km}^2$). In comparison, the predicted suitable areas for *A. aneura* almost disappears, the current range (1.3 ± 0.22 million / km^2) rapidly declines by 2030 ($<0.01 \pm <0.01$ million / km^2) and fails to recover by 2070 ($0.00 \pm <0.01$ million / km^2); (Fig. 8.3).

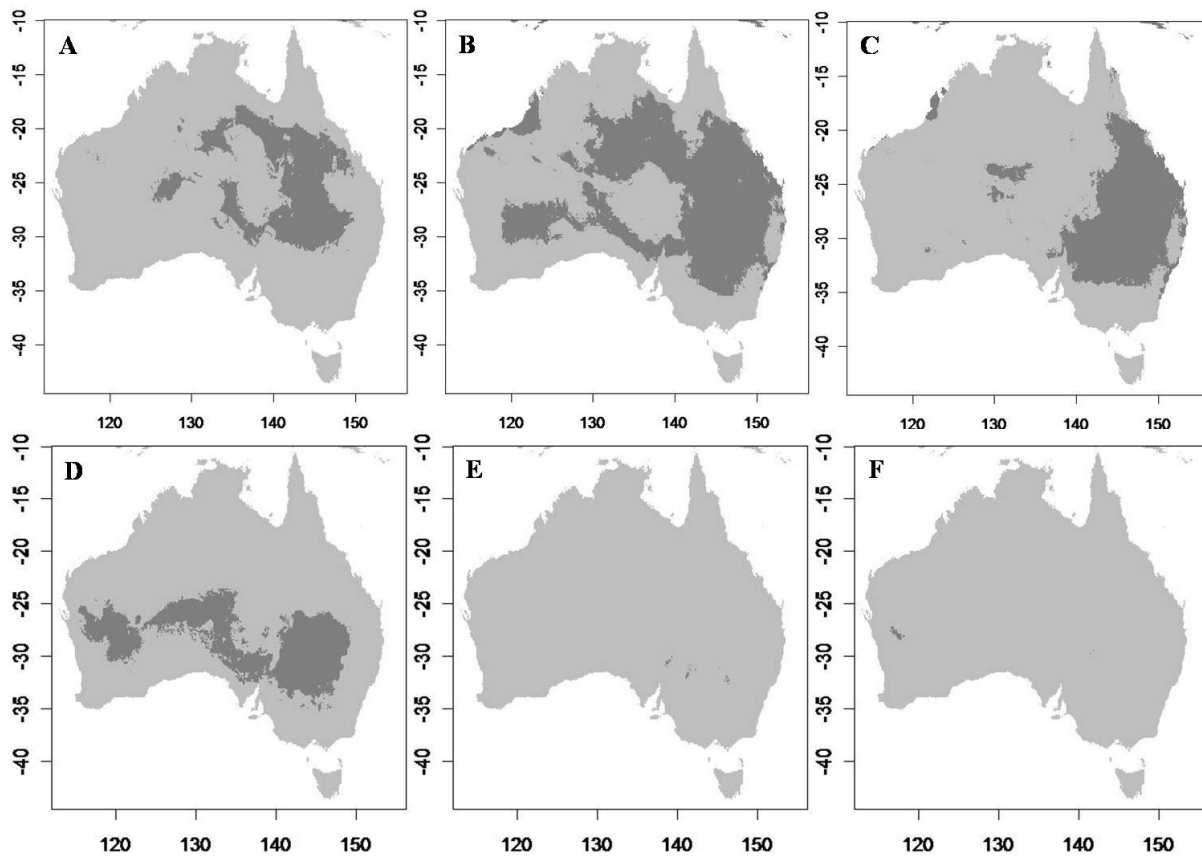
Table 8.4 Bio / Worldclim variables

Bio- / Worldclim variables. Temperatures are in Celsius, precipitations are in millimetres.

Variable name	Abbreviation	Definition
bio1	AnnTemp	Mean annual temperature (mean across 12 months of the year)
bio2	MeanMonTempRange	Mean monthly temperature range
bio3	Isothermality	Ratio bio2/bio7
bio4	TempSeason	Temperature seasonality = Coeff. of variation mean monthly temperature throughout the year
bio5	MaxTemp	Maximum mean monthly temperature over 12 months
bio6	MinTemp	Minimum mean monthly temperature over 12 months
bio7	AnnTempRange	bio5 – bio6
bio8	MeanTempWetQtr	Mean temperature for the wettest consecutive 3 months
bio9	MeanTempDriestQtr	Mean temperature for the driest consecutive 3 months
bio10	MeanTempWarmQtr	Mean temperature of the warmest consecutive 3 months
bio11	MeanTempColdQtr	Mean temperature of the coldest consecutive 3 months
bio12	AnnPrecip	Sum of monthly precipitation values
bio13	PrecipWettestMon	Precipitation of the wettest month
bio14	PrecipDriestMon	Precipitation of the driest month
bio15	PrecipSeason	Precipitation seasonality = Coeff. of variation mean monthly precipitation throughout the year
bio16	PrecipWettestQtr	Precipitation of the wettest consecutive 3 months
bio17	PrecipDriestQtr	Precipitation of the driest consecutive 3 months
bio18	PrecipWarmQtr	Precipitation of the warmest consecutive 3 months
bio19	PrecipColdQtr	Precipitation of the coldest consecutive 3 months

Figure 8.3 Tree species distribution maps

Presence-absence maps for *A. cambagei* and *A. aneura*. Suitable areas are shown in dark grey and unsuitable areas in light grey. The following distributions are presented: A to C, and D to F show the predicted present, 2030 and 2070 distributions for *A. cambagei* and *A. aneura* respectively.



Appendix 4

Multiple clutches in captive *Gehyra variegata*^{40a} demonstrate the potential for faster population growth

Abstract

Arid regions of Australia are characterised by large climatic variability, and during favourable seasons many species have high reproductive outputs. Geckos are a successful group in arid Australia yet are constrained to few eggs per clutch, and some observations suggest few clutches per breeding season. *Gehyra variegata*^{40a} is distributed throughout much of inland Australia, and two single egg clutches per annum has been reported in wild populations in central NSW. This captive breeding study of *G. variegata*^{40a} shows that individuals can lay significantly more eggs per breeding season (mean \pm SD; 5.5 ± 0.5) than previously reported in the literature for wild individuals (mean \pm SD; 1.93 ± 0.4 ; $P < 0.001$). Additionally I demonstrate *G. variegata*^{40a} may have faster population growth than previously expected.

Keywords: Captive Breeding, Fecundity, Population dynamics

Introduction

In Australia, rapid population growth is characteristic of species living in the ‘boom and bust’ environment of central Australia (Kingsford *et al.*, 1999; Byrne *et al.*, 2008). During wet phases some populations will experience increases in habitat availability, which may facilitate population expansion into new areas. The success of a founding population is intrinsically linked to the rate of population growth, as rapid population increase is thought to reduce the probability of localised extinction through stochastic events (Cole, 1954). However gecko species seem to be at odds with this requirement due to limited reproductive output. Across >90 genera, 850 species worldwide, all geckos have a clutch size of 1-2 eggs (Kluge, 1987; Shine & Greer, 1991), yet paradoxically arid zone Australia houses an impressive richness of gecko species, many of which have broad distributions (Cogger, 2000). I now refer to the number of eggs an individual produces within a single breeding season as ‘fecundity’.

Gehyra variegata (Tree Dtella) is abundant throughout its distribution that covers much of mainland Australia (Cogger, 2000). Its ecology has been studied in detail and it possesses the following ecological traits: low fecundity (two single egg clutches per annum), delayed maturity (two years), high egg / juvenile mortality (63 %), moderate adult mortality (20 %), and numerous predators (predation results in tail loss for 8.5 % of adult females which prevents them reproducing in that season) (Bustard, 1967; 1968; 1969; 1970; Henle, 1990).

Whilst these characteristics are not uncommon for small lizards, it seems counterintuitive that this species has been so successful.

In this preliminary study I investigate this paradox by breeding adult *G. variegata*^{40a} in captivity for a single season to assess species' fecundity. Fecundity is a fundamental ecological parameter utilised to calculate population growth, yet is often elusive and difficult to study in wild populations (Gadgil & Solbrig, 1972). First, I assess whether a disparity exists between field observations of fecundity and the potential fecundity of the species.

Second, I demonstrate how a small increase in fecundity may have major consequences for the rate at which populations grow (Oli & Dobson, 2003).

Methods

Animals and their maintenance

I collected two gravid female lizards and one male lizard at the start of the breeding season (Henle, 1990) from Sturt National Park, NSW, Australia. The collection of gravid females ensured that they were sexually mature. Typically a single male occupies a home site with multiple females (Bustard, 1970), and I therefore attempted to simulate this in captivity. All geckos were housed in an enclosure (60 x 45 x 60 cm) with 8 - 10 cm depth of sand, wooden branches and layers of tree bark for shelter. Temperatures replicated optimal breeding temperatures for the duration of the breeding season (Bustard, 1968). Heat was provided using a 40 W incandescent light bulb located above one corner of the enclosure, providing a thermal gradient from 20 - 30 °C for a 12 hour day (0600 - 1800 h), falling to 18 °C overnight. All lizards were supplied with water and crickets (dusted in Exo-terra calcium and multi-vitamin supplements) *ad libitum*.

Egg maintenance

The enclosure was checked daily for eggs from the start of the breeding season until no further eggs were laid. Eggs were relocated into a vermiculite incubator (1.5:1; water:vermiculite by weight), with a constant temperature (28 °C) until all eggs hatched.

Genetic assays

I extracted total DNA from tail tip tissue biopsies taken from each adult female (n = 2) and hatchling (n = 11) using a modified salting-out protocol (Sunnucks & Hales, 1996). I used polymerase chain reaction (PCR) methods to isolate mitochondrial DNA (mtDNA) ND4 haplotypes from all adult females and hatchlings using standard author protocols (Forstner *et al.*, 1995). PCR products were electrophoresed on a 2 % agarose gel to visually assess the quality and quantity of amplicons, and for the absence of excess primer dimer. The resulting amplicons were sequenced using an Applied Biosystems 3130x genetic analyser to identify mother - offspring pairs. The sequences were checked by eye to assess the quality of the results. To ensure data integrity ~10 % of the samples were reanalysed and identical sequences were obtained for each individual in both runs.

Maternal fecundity

To identify mother - offspring pairs, I used 790 bp of mtDNA ND4 sequence data from females and hatchlings to visually match haplotypes after alignment using CLUSTALX v2.0.8 (Thompson *et al.*, 1997). The significance of any difference in mean fecundity between my captive study and that reported in Bustard (1969) and Henle (1990) was tested via a randomization process with 5000 permutations, performed using the sample2 module of RT v2.1 (Manly, 1997).

Estimating population growth

To examine the influence of fecundity on population growth, I designed a simple model using known ecological parameters to compare measures of fecundity from previous mark-recapture studies to my captive breeding study. These ecological parameters for *G. variegata*^{40a} are

incorporated into Equation (1), with an assumed sex ratio at parity (Bustard, 1967; 1968; 1969; 1970; Henle, 1990).

Equation 1.

$$P^{T+1} = \text{Floor} \lambda ([P^T A] + [(P^T - O^{T-1} / 2) R F J])$$

Equation 1: With each model iteration (per season), the population is ‘floored’ so that the result produced is an integer (λ); because part of an individual cannot reproduce. Time (T), population (P), probability of adult survival (A), new offspring (O), probability of females reproducing (R), average fecundity (F), and probability of egg / juvenile survival (J).

Results

Summary data

The two captive female lizards produced eleven eggs (all single egg clutches) in total between November and January; all were successfully incubated and hatched after 40 – 53 days (mean \pm SD; 46 ± 5.5). From the high quality DNA extractions PCR methods successfully isolated the mtDNA ND4 region from each individual.

Females show high levels of fecundity

Each adult female had a unique mitochondrial haplotype, therefore allowing unambiguous assignment of six and five hatchlings to each adult. Average fecundity in this study (mean \pm SD; 5.5 ± 0.5) was significantly higher ($P < 0.001$) than previously observed for this species (mean \pm SD; 1.93 ± 0.4) (Henle, 1990). This indicates *G. variegata*^{40a} may be physiologically capable of higher fecundity when stable conditions are presented.

High potential for population growth

I show a large difference in population estimates between comparisons of fecundity reported in the literature to my captive breeding result (Table 8.5), after applying my simple model (Equation 1) for a relatively short period of time (20 years / 10 generations).

Table 8.5 Fecundity simulation

The model (Equation 1) is simulated for 20 years, starting with a single breeding pair and assuming an equal sex ratio throughout.

	Mean Fecundity	Start Population	End Population
Literature	1.93	2	2
Captive Breeding	5.5	2	294

Discussion

I have provided evidence that *G. variegata*^{40a} has higher fecundity than previously reported in the literature. Until now, all reports of fecundity in this species have been from field studies. This highlights the importance of studying reptile species in captivity whereby reproductive output can be monitored accurately. On the basis of this I tentatively suggest that in stable environmental conditions with abundant resources, the reproductive output of *G. variegata*^{40a} may facilitate rapid population growth.

Both previous reports of fecundity report two single egg clutches during the breeding season: Nov – Jan (Bustard, 1968; 1969; Henle, 1990), which contrasts considerably with my findings. One explanation, which Bustard (1969) suggests, is that observations rely on mark-recapture sampling which can be biased due to incomplete habitat searches and / or the probability of recapture. Additionally, one female in my study oviposited six eggs within ten weeks, and as Bustard (1969) only sampled for a continuous six day period each month, it is possible oviposition occurred during his absence and thus went unrecorded. The removal of nest eggs in some bird species can promote the greater production of eggs (Monaghan *et al.*, 1995), yet has not been documented within reptile species. Another explanation for this disparity is that maximum fecundity is only achieved when conditions are stable, and resources are sufficient.

Under stable environmental conditions, it would seem the reproductive physiology of *G. variegata*^{40a} may facilitate rapid population growth. My simple model shows how a small increase in fecundity (1.93 to 5.5) can cause a difference of two orders of magnitude in population size (2 vs 294); over identical timescales. Note that when using the fecundity estimate from the literature, a single breeding pair would fail to grow in number (see Table 8.5). Ultimately species that are physiologically capable of rapid population expansion are able to reach a viable population size, thus reducing their risk of extinction via stochasticity,

in comparatively less time to populations increasing slowly. This would seem to be the case for *G. variegata*^{40a}.

This study highlights the importance of obtaining realistic estimates of individual ecological parameters. Whilst population dynamics are influenced by a plethora of these characteristics, inaccuracies in a single measurement can cause large disparities in population estimates.

Acknowledgements

This work was supported by a Macquarie University Staff Grant to A Stow. Lizards were handled in accordance with Macquarie University Animal Ethics committee recommendations and tissue collection was licensed by the N.S.W. National Parks and Wildlife Service (S12353). I thank Rizzo, Leia and The Fonz for their active contribution to this project.

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Appendix 5 of this thesis has been removed as it may contain sensitive/confidential content