REFUGIA IN THE AUSTRALIAN MONSOONAL TROPICS

Stability and what it means for northern Australian lizards

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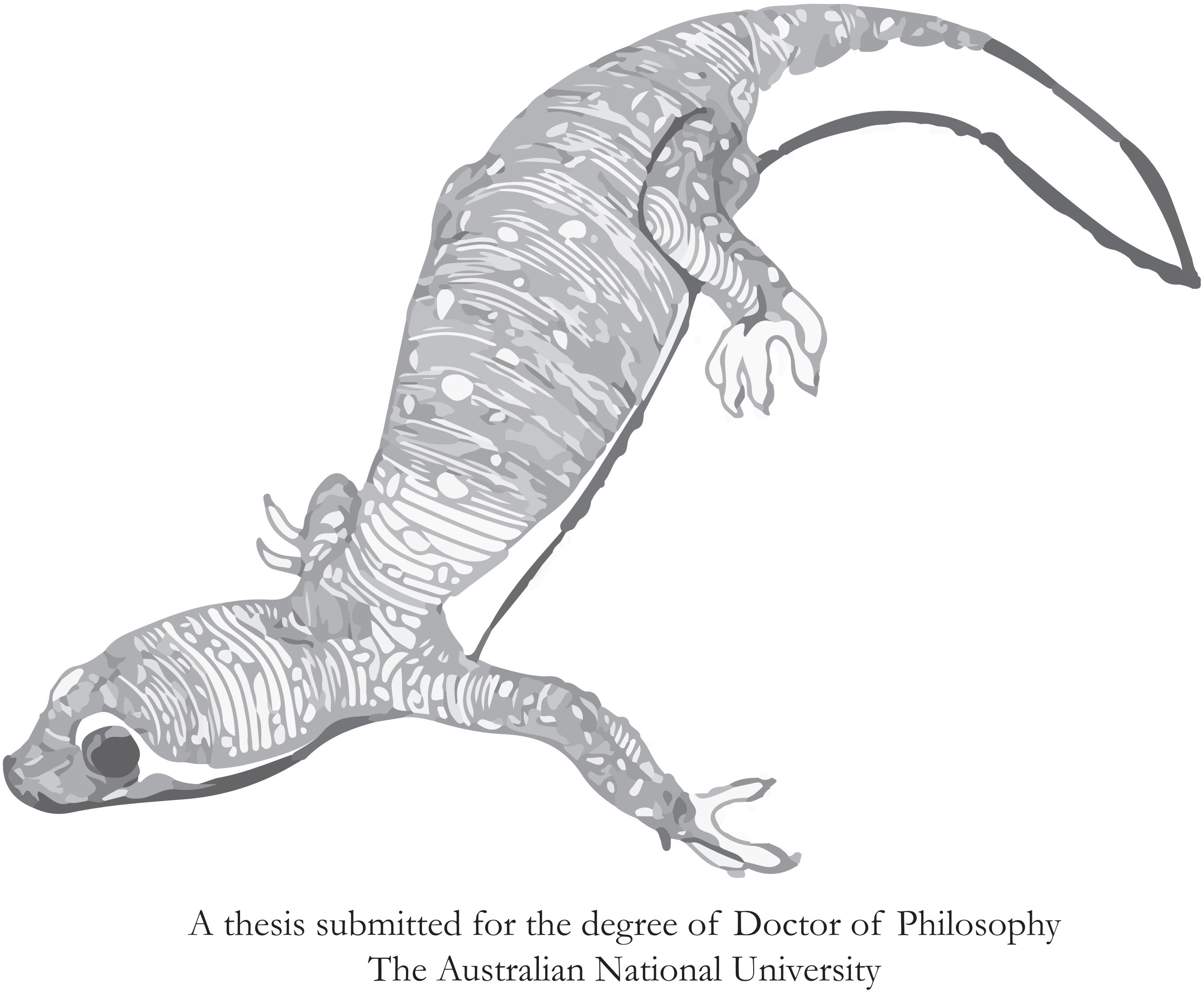

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DECLARATION

The research presented in this thesis is my own original work except where due reference is given. All chapters are co-authored, and the authorship order indicates the intellectual contribution and workload. No part of this thesis has been submitted for any previous degree. This research is supported by an Australian Government Research Training Program (RTP) Scholarship.

CMcDonald

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ABSTRACT

Understanding what has driven the distribution of biodiversity across the world is a central question in biogeography. One possible explanation is the persistence of organisms in refugia, areas of stability that allow taxa to persist during times of unfavourable climate, with the potential to expand from there in later times. In this dissertation, I explore measures of refugia and stability, and the contribution of refugia to the diversity patterns of lizards in the Australian Monsoonal Tropics.

Stability and refugia are widely used concepts in macroecology and biogeography, but their use is not always clearly defined. In Chapter 1 I present a conceptual framework for thinking through concepts of stability, focusing on five key questions. Thinking through these questions provides a clear understanding of any definition of stability, assisting with comparing studies and interpreting the biological implications of their results.

In Chapter 2 I empirically test the importance of using this framework, comparing four different measures of stability to see which best predicts reptile diversity in the Australian Monsoonal Tropics. I find large differences in the performances of the stability measures, demonstrating the importance of carefully considering the biological meaning of stability measures before including them in studies.

Chapter 3 investigates drivers of diversity patterns across the Australian Monsoonal Tropics, including stability as well as current climate, geology and disturbance.

Finally, in the fourth chapter I explore the impact of refugia on the biogeography of lizards in the Kimberley region. I test refugia across different spatial scales (fine and coarse grain) and temporal scales (Holocene and Pleistocene) to examine the drivers of diversity patterns in the region.

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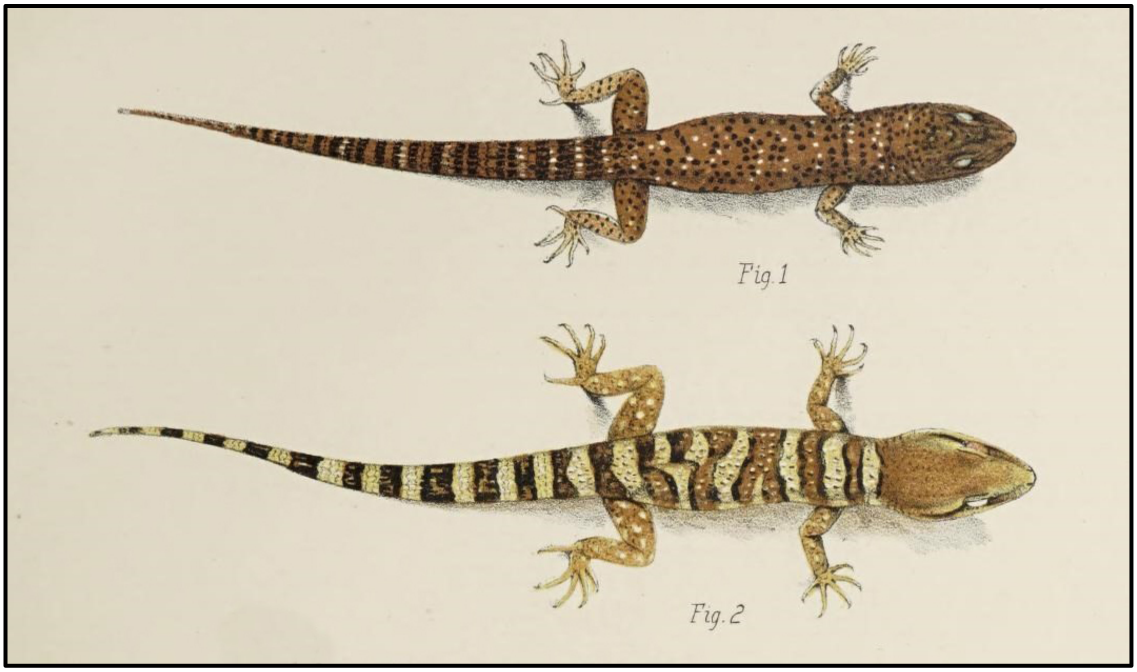
Introduction



Heteronotia bynoei, now *Heteronotia binoei* and *Heteronotia fasciolatus*, from *Report on the work of the Horn Scientific Expedition to Central Australia,* 1896

Introduction

The question of why some areas have more biodiversity than others is a major theme of macroecology. There are many possible drivers of patterns of diversity, including current environment, phylogenetic history and human disturbance. Patterns of diversity are also strongly affected by past environmental conditions. In particular, areas of past stability often harbour high levels of current day diversity. Stability is generally measured by identifying refugia, areas that allow taxa to persist during times of unfavourable climate, with the potential to expand from there in later times (Ashcroft 2010). In my thesis, I seek to explore how refugia are identified and measured, and what impact they have had on the lizard diversity of the Australian Monsoonal Tropics. I focus on environmental changes over the last 80,000 years, which allows an exploration of the impact of glacial cycles on diversity. This introductory chapter contains an overview of the context and background behind my research, followed by a summary of the chapters within this thesis.

REFUGIA

Refugia are areas of stability that allow taxa to remain viable despite regionally unfavourable conditions. They are distinct from refuges, which operate on ecological time scales such as providing shelter from the summer heat, although the two terms are sometimes used interchangeably (Keppel et al. 2012). The term *refugia* was introduced to describe areas where taxa survived during the last glacial period (Bennett and Provan 2008). The term was first used in the 1950s (Heusser 1955), although the concept was used much earlier, for example by Darwin (1859) to explain why there should not have been much evolution as species moved in response to glaciations. Most studies on refugia still focus on Quaternary glaciations in the Northern Hemisphere (Keppel et al. 2012), but the term has been broadened to refer to any period of unsuitable climate on an evolutionary timescale.

The concept of refugia provided a way of thinking about biogeography where species are not in equilibrium with their environment, unlike classical island biogeography for example. This has allowed refugia to be applied to many questions in macroecology. For example, the forest refuge model was the dominant model for vertebrate diversification in the tropics for over 30 years (Moritz et al. 2000). This model held that tropical rainforests retreated to refugia during dry periods of the

Pleistocene, with taxa in the rainforest fragments becoming isolated and evolving independently. Wetter periods then allowed the rainforests to expand and link together, and the new taxa to disperse. While originally developed for the Amazon rainforest (Haffer 1997, Haffer 1969), this model has been tested in biomes across the tropics, including the Atlantic Forest (Leite et al. 2016), savannas (Bueno et al. 2017), the Australian Wet Tropics (Schneider and Moritz 1999), and central African rainforests (Migliore et al. 2018).

Individual refugia exist on a continuum between macrorefugia and microrefugia (Figure 1). Macrorefugia are large areas where the general climate is favourable over time (Rull 2014), providing a large buffer against extinction (Ashcroft 2010). Microrefugia, also known as cryptic refugia, are small pockets of favourable microclimates that exist in a generally unsuitable region, such as deep crevices in a small rocky outcrop (Ashcroft 2010, Ashcroft et al. 2012, Rull 2014) or south-facing slope (Birks and Willis 2008). They have been important in explaining the population genetics in north American red maple and beech trees (McLachlan et al. 2005), while groups of microrefugia have allowed the persistence and speciation of caddisfly in the Balkans (Previsic et al. 2009). Spatial clusters of microrefugia can protect metapopulations, as has occurred for many taxa in the Iberian Peninsula (Gómez and Lunt 2007).

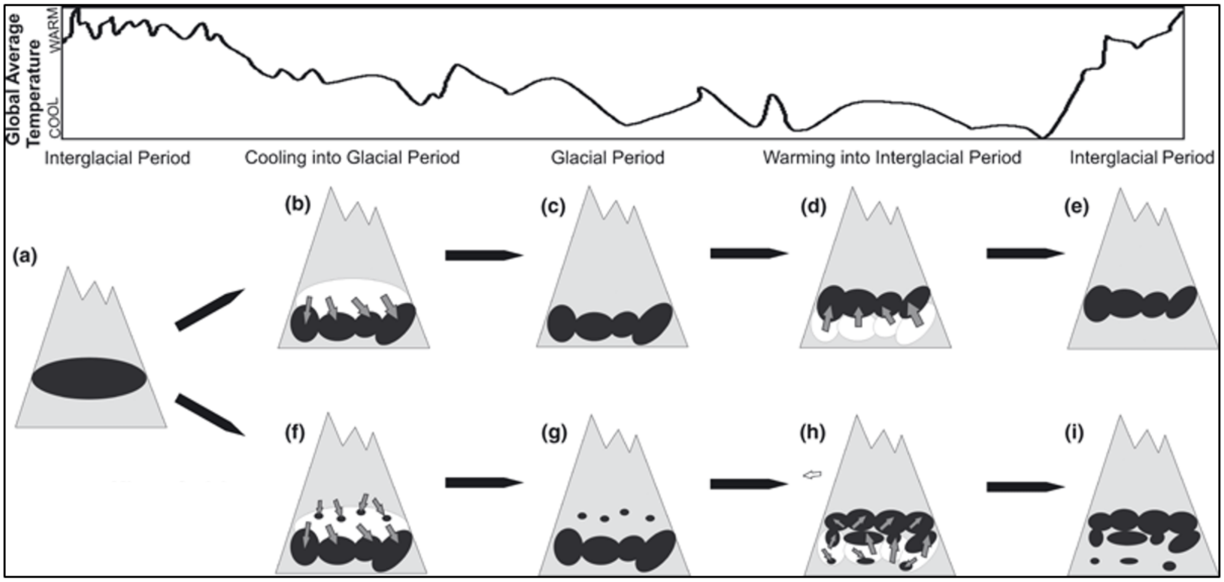


Figure 1. Contrasting population responses of a hypothetical montane species occupying macrorefugia (b)–(e) or microrefugia (f)–(i) to a glacial cycle. The grey polygons represent mountains and the black ovals represent populations, moving up and down the mountain in response to changing climates. Figure reproduced from Mosblech et al. (2011)

Refugia can enable both persistence and isolation, depending on their spatial and temporal scale (Ashcroft et al. 2012). They can promote persistence, buffering populations from climatic variability and providing a haven from extinction. When separated geographically, they can also foster genetic isolation, enhancing evolutionary processes. Past studies have indicated the location of refugia align with other spatial patterns of diversity. For example, studies in the Australian Wet Tropics, which underwent significant expansions and contractions throughout the Pleistocene, showed that climatic suitability during the Last Glacial Maximum was the best predictor of current diversity, outperforming even present day suitability (Boyer et al. 2016, Araújo and Pearson 2005, Graham et al. 2006). Other studies have indicated that refugia are associated with high endemism, species richness (Fordham et al. 2016, Rosauer et al. 2015), phylogenetic endemism (Rosauer et al. 2015), genetic diversity between populations, and low spatial genetic structure within populations (Carnaval et al. 2009, De Lafontaine et al. 2013, Gavin et al. 2014).

Identifying refugia

Refugia can be identified using three main sources of information: fossil records, phylogeography, and distribution and climate models (Gavin et al. 2014).

Fossil records can be used to identify refugia by allowing an insight into the historical presence of taxa in areas, including those outside their current range (Gavin et al. 2014). Fossil pollen is commonly used to identify refugia as it can inform local scale vegetation responses to changing environments through time. The method was developed in Australia (Kershaw and Nix 1988), and is now widely used in identifying glacial refugia. However, fossils are not distributed evenly across taxa, time or space (Ashcroft et al. 2012, Gavin et al. 2014), and are particularly sparse in northern Australia (Bowman et al. 2010), meaning this method can be difficult to use.

Phylogeography involves using genetic information to infer demographic processes and the patterns within and between species, including population size and historical migration (Gavin et al. 2014). Phylogeography has been widely used in studies in South America, Europe and North America, as well as some applications in the Australian Wet Tropics and southern Australia. More recently it has been used in studies across northern Australia (Melville et al. 2016, Pepper et al. 2017, Rosauer et al. 2016, Wadley et al. 2016, Catullo et al. 2014). Phylogeography is increasingly being combined with species distribution models (SDMs) under inferred paleoclimates, with the results of SDMs being used as hypotheses for phylogeography to test (e.g. Hugall et al. 2002, Knowles 2003).

My research focuses on the third source of inference, models of distributions and climate. Climate models can be used to examine environmental fluctuations through time, allowing for the identification of areas of predicted stability. SDMs allow for the prediction of species ranges and community turnover through space and time (Dormann 2007, Gavin et al. 2014). The known distribution of a species is used to calculate an environmental envelope which can then be projected onto an area or time period (Hugall et al. 2002). Other modelling systems, such as generalised dissimilarity modelling (GDM) which models community turnover (Ferrier et al. 2007), which when projected through time can also be used to infer the presence of refugia. Such models are widely used in identifying refugia, including in studies in the Australian Wet Tropics (Boyer et al. 2016, e.g. Graham et al. 2010) and eastern Australian rainforests more generally (Weber et al. 2014).

However, SDMs rely on several key assumptions, including range equilibrium, niche conservatism, and that the current distribution reflects the abiotic limits of the taxa. These are exacerbated when projecting to other time periods to test refugial hypotheses. For example, the models assume that all relationships between taxa and the environment are constant throughout space and time and that the current distribution of taxa reflects the current climate: assumptions that are rarely realistic and do not take into account novel climates that may occur in other time periods (Heikkinen et al. 2006, Guisan and Rahbek 2011, Araújo and Pearson 2005). Additionally, hindcast SDMs rely on accurate paleoclimate proxy data or global circulation models (GCMs), which can be difficult to evaluate. Despite these limitations, SDMs have been shown to be accurate in providing relative measures of suitability for species (e.g. Elith et al. 2006), including through time (Hugall et al. 2002).

THE AUSTRALIAN MONSOONAL TROPICS

The Australian Monsoonal Tropics (AMT) cover 1.4 million km^2 (Bowman et al. 2010) in northern Australia, extending to approximately 20°S (Woinarski et al. 2007). The AMT is characterised by the Asian monsoon climatic pattern (Cook and Heerdegen 2001), where 80-90% of rainfall falls between November and April (Bowman et al. 2010).

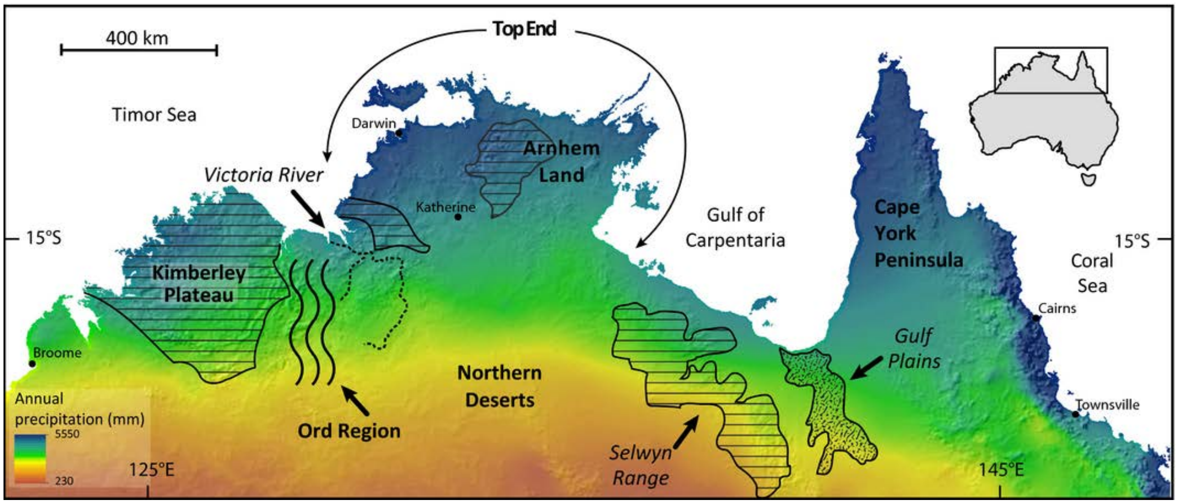


Figure 2. The Australian Monsoonal Tropics. Major areas of raised or dissected terrain are shown with horizontal hatching, rivers are shown with dashed lines, and substrate barriers are shown with mottled lines, with wavy lines for the region of the Ord River and arid intrusion. Colouration shows annual precipitation, with increasing aridity towards the south. Figure from Moritz et al. (Moritz et al. 2016)

The AMT is a highly heterogeneous landscape containing savannas, tropical woodlands and sandstone plateaus (Woinarski et al. 2007), with a strong latitudinal rainfall gradient (Cook and Heerdegen 2001) (Figure 2). Fire plays an important role in shaping the landscape, particularly in the dry season when the AMT is the most fire prone area in Australia (Bowman et al. 2010). Much of the AMT has low topographic relief, although the west Kimberley has the most rugged topography in Australia (Woinarski et al. 2007). There are three major Proterozoic sandstone regions in the AMT – the Kimberley, Arnhem Plateau and parts of Cape York – separated by biogeographical barriers associated with Cretaceous sea floors (Bowman et al. 2010). These sandstone rocks have been deeply weathered, leading to thin and infertile soils across much of the AMT (Woinarski et al. 2007).

Compared to the rest of Australia, the AMT has been relatively undeveloped by Europeans (Woinarski et al. 2007), with Aboriginal people living in the area for at least 65,000 years. It has much lower population density and relatively large areas of intact vegetation (Woinarski 2000), containing a quarter of the world's remaining tropical savanna in good condition (Bowman et al. 2010). Much of it is managed for conservation, including many First Nations-managed Indigenous Protected Areas. However, there is pressure to increase development in the region (Bowman et al.

2010), particularly through agriculture and irrigation projects (Australian Government 2015), making it important to study the biota before further disturbance.

Although understudied by academics, particularly compared to the southern mesic regions of Australia, there has been an increasing interest in the biodiversity of the AMT over the last twenty years, accompanied by greater sampling efforts. Many areas within the region are listed as national biodiversity hotspots, such as the North Kimberley, Cape York Peninsula and the Arnhem Plateau (Woinarski et al. 2007). The biota shows a mix of origins, with old Gondwanan lineages existing alongside newer Asian immigrants (Rowe et al. 2008, Oliver and Hugall 2017). The region has high richness, endemism and phylogenetic endemism in many taxa (Rosauer and Jetz 2015, Rosauer et al. 2016, Crisp et al. 2001, Powney et al. 2010), with many endemic radiations, particularly in the north Kimberley and Arnhem regions, including in land snails, mammals, reptiles and plants (Slatyer et al. 2007, Barrett 2016, Köhler and Criscione 2013, Potter et al. 2014, Palmer et al. 2013, Pepper and Keogh 2014, Oliver and Hugall 2017).

Environmental history of the AMT

The AMT is highly geologically stable, with the last major geologic shifts occurring approximately 80mya (Johnson 2004). There have been large changes in sea level associated with glacial cycles, ranging from 140m below the current sea level to up to 8m above (Hope et al. 2004), with the modern shoreline dating from 6kya (Lees 1992).

The past climate of the region is established by paleoclimate proxies from across Australia and the Asian monsoon region, but also an increasing amount of data from the AMT itself. Although most paleoecological research in northern Australia has focused on the Atherton tableland area of the Australian Wet Tropics (Reeves et al. 2013), recent work has focused on the rest of the region, particularly the Mitchell Plateau in the Kimberley. There are spatial and temporal gaps in the paleoclimate proxy data, however a consistent story emerges across data sources, including speleothems (Denniston, Wyrwoll, et al. 2013, Denniston, Asmerom, et al. 2013, Woodhead et al. 2016), rock art (Goodall et al. 2009), sediment cores from across northern Australia and the surrounding continental shelf (Proske et al. 2014, Field et al. 2017, Konecky et al. 2016, Burrows et al. 2014, Williams et al. 2009), and foraminifera (Christensen et al. 2017, Andrae et al. 2018). Most of this data is for the last 30kya, with particularly good resolution for the Holocene.

The monsoonal climate, part of the larger Asian-Australian monsoon system, originated approximately 30-40mya (Bowman et al. 2010), with the Pliocene dominated by warmer and wetter climates than before (Sniderman et al. 2016) The last 30kya have been characterised by changes in the monsoon intensity (Reeves et al. 2013, Williams et al. 2009) caused by global geological changes and glacial cycles (Bowman et al. 2010), with large oscillations in climate since the Pliocene (Reeves et al. 2013). These changes had large spatial variability in the magnitude and direction of change, and led to long periods of cool dry climate in the early Holocene, with increasing local aridity and variability in the monsoon in the late Holocene (Reeves et al. 2013). There has also been large spatial variation in the climate of the AMT across time. For example, the Top End (Figure 2) has remained relatively mesic through time, with the Kimberley experiencing harsher aridity (Potter et al. 2018). The current monsoon has large inter-annual variation in its length and timing, largely associated with changes in the El Nino-Southern Oscillation and Indian Ocean Dipole (Cook and Heerdegen 2001).

Under future climate change, the Monsoonal North is predicted to become hotter, with more extreme temperatures. Extreme rainfall events are predicted to become more intense, although overall precipitation trends are unclear due to the difficulty of modelling tropical monsoons. Cyclones are likely to become less common but more intense, and sea levels will continue to rise above Holocene levels (Moise et al. 2015).

Refugia in the AMT

Refugia in the AMT appear to be predominately in areas with complex topography. In particular, phylogeographic evidence suggests much of the Top End and Kimberley region have acted as refugia, providing protection from drying for mesic-adapted species (Pepper and Keogh 2014, Byrne et al. 2008). Specific areas within the Kimberley have been proposed as refugia, including the rugged northwest (Fujita et al. 2010, Potter et al. 2014) and northeast (Potter et al. 2014). The Wingate Range, between the Victoria and Daly Rivers, may also have provided a refugia from aridification (Potter et al. 2012), along with the Selwyn Range (Catullo et al. 2014, Noble et al. 2017). The Arnhem Plateau may have acted as a refugia from both climatic changes, with its high topographic complexity providing stable environments, and sea level change, with the surrounding lowlands inundated several times during the Pleistocene (Woinarski et al. 2006).

Other refugia in the region include offshore islands, particularly those off the Kimberley, which have acted as refugia from Holocene sea level changes (Potter et al. 2018, Gibson 2014) and more recent landscape changes associated with European colonisation (e.g. Gibson 2014). At a finer spatial scale boulder escarpments and limestone ridges may act as microrefugia by buffering against climate extremes (Woinarski 2000), with hotspots of endemism found in these areas across groups (Catullo et al. 2014, Potter et al. 2012, Oliver et al. 2017, Criscione et al. 2012, Moritz et al. 2016).

LIZARDS

Squamates, which include lizards, snakes and worm-lizards are the most diverse group of extant reptiles (Evans 2003). Australia is a hotspot for squamates with over 1000 Australian species described, a number that continues to rise with an average of 11 new species described every year (Tingley et al. 2019). Several families are at their most diverse in Australia, including Scincidae (skinks) and Typhlopidae (blind snakes) (Hutchinson and Donnellan 1993). Around 800 of the Australian squamate species are lizards (Tingley et al. 2019).

Lizards have been widely used as model organisms in phylogeographic and speciation studies, due to their abundance and the accumulated knowledge of their physiology, life history and demographics (Camargo et al. 2010). In particular, lizards are an ideal study system for studying refugia. Lizards are unable to internally regulate their temperature, so are dependent on the environment. This means they have a high sensitivity to changes in climate (Deutsch et al. 2008, Sinervo et al. 2010) and to microclimates in the landscape, making them ideal for identifying stable regions of climate. Tropical species are particularly sensitive to climate (Huey et al. 2009, Deutsch et al. 2008), with some hypothesising that the relatively stable climate, at the diurnal and seasonal scale, of the tropics leads to lizards having narrower thermal limits and a higher sensitivity to increases in temperature (Janzen 1967).

Lizards are also low dispersal animals, making them more vulnerable to local adaptation, speciation and extinction. Once a taxon has become locally extinct, the low dispersal abilities means that lizards predominately recolonise areas nearby existing populations. This makes them an ideal study system for studying historical refugia, particularly at fine spatial scales, as their current distributions are strongly influenced by the past.

Lizards in AMT

The AMT has high species richness in lizards, particularly in the Kimberley region (Powney et al. 2010, Woinarski 1992). The amount of spatial and genetic data available for lizards in the AMT has increased dramatically in the last five years, allowing the identification of strong spatial patterns in reptile distribution across the region and sometimes revealing new hotspots of diversity (Oliver et al. 2017). For example, phylogenetic endemism has large variation across the landscape (Rosauer et al. 2016), particularly across rainfall gradients and changes in topographic complexity (Moritz et al. 2016).

Lizards in the AMT also show a large amount of cryptic speciation and intraspecific variation (Laver et al. 2018, Moritz et al. 2016), with much taxonomic work currently underway. This includes *de novo* discovery (Oliver et al. 2014, Doughty et al. 2012), splitting widespread taxa into genetically distinct, short-ranged taxa (Oliver et al. 2020, Doughty et al. 2016), and completely reassembling species boundaries (Melville et al. 2019).

AIMS AND OBJECTIVES OF THE THESIS

Given the rapid rate of climate change, identifying and conserving refugia is critical (Reside et al. 2013). By understanding how refugia and environmental variation have influenced the patterns of diversity we see today, we can model how taxa and biogeographic patterns will change in response to future climates. Most previous studies on refugia have been carried out at global scale, or in relativity simple to model biomes such as rainforest. The AMT is a more challenging environment to model, but its more complex environment could yield more insights into these relationships. Additionally, the increasing pressure to develop the region makes it important to study and conserve the biodiversity in the region. The research within this thesis aims to make a significant contribution to our understanding of refugia and their impact on biogeographic patterns, particularly within the AMT.

This thesis comprises two main parts. The first section explores methodological questions around identifying refugia and measuring stability. The second section applies these techniques to understand the patterns of diversity within the AMT.

Thesis Structure

This thesis expands our understanding of how to measure stability and refugia, and the impacts of them on the biogeography of the AMT. This thesis contains published work and work prepared for publication that has been co-authored with collaborating researchers. As such, these chapters can be read independently, and some duplication of ideas or concepts may arise. All the research presented within this work is original, and the contribution of each co-author is stated below. No part of this thesis has been submitted for any previous degree.

Introduction

Presents the background introduction to material covered within the thesis. I am the sole author of this chapter.

Chapter 1: The importance of defining measures of stability in macroecology and biogeography

In Chapter 1, I provide a conceptual framework for defining measures of stability, allowing for clearer hypotheses, more accurate interpretation of results and easier comparisons across studies.

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CJM formulated the ideas for the framework, collected data and drafted the manuscript. CCM, SF and DFR contributed substantial conceptual and editorial advice. All authors contributed to writing and approved the final manuscript.

Chapter 2: Stability predicts diversity, but what is the best measure of stability?

Chapter 2 examines the impact of choosing different measures of stability on analyses. Within this chapter, I compare four different measures of stability to see which best predicts diversity within the western AMT.

This chapter is under review: McDonald-Spicer, C. J, Moritz, C. C, Ferrier, S., & Rosauer, D. F. (in review). Stability predicts diversity, but what kind of stability? *Ecography.*

CJM led conceptualisation, data analysis and writing. CCM, SF and DFR contributed substantial conceptual and editorial advice. All authors contributed to writing and approved the final manuscript.

Chapter 3: A bioregionalisation of lizard communities in the Australian Monsoonal Tropics

In Chapter 3 I examine the biogeographic regions for lizards in the AMT, and look at the environmental drivers of these regions, including both refugia and other abiotic factors.

The authorship of this chapter will be: McDonald-Spicer, C.J., Moritz, C.C., Harwood, T. & Rosauer, D.F.

CJM led conceptualisation, data analysis and writing. DFR and CCM contributed substantial conceptual and editorial advice. All authors contributed to writing and approved the final manuscript.

Chapter 4: Refugia in the Kimberley across spatial and temporal scales

In Chapter 4, I compare refugia at different spatial and temporal scales to see which best explains diversity in the Kimberley. I test the relative importance of microrefugia and landscape level refugia, from both Holocene drying and Pleistocene glaciation cycles.

The authorship of this chapter will be: McDonald-Spicer, C.J., Moritz, C.C., Harwood, T. & Rosauer, D.F.

CJM led conceptualisation, data analysis and writing. CCM contributed substantial conceptual and editorial advice. All authors contributed to writing and approved the final manuscript.

Synthesis

Finally, I summarise the key points of my thesis chapters, drawing together key themes and elements and placing them into broader context. I am the sole author of this chapter.

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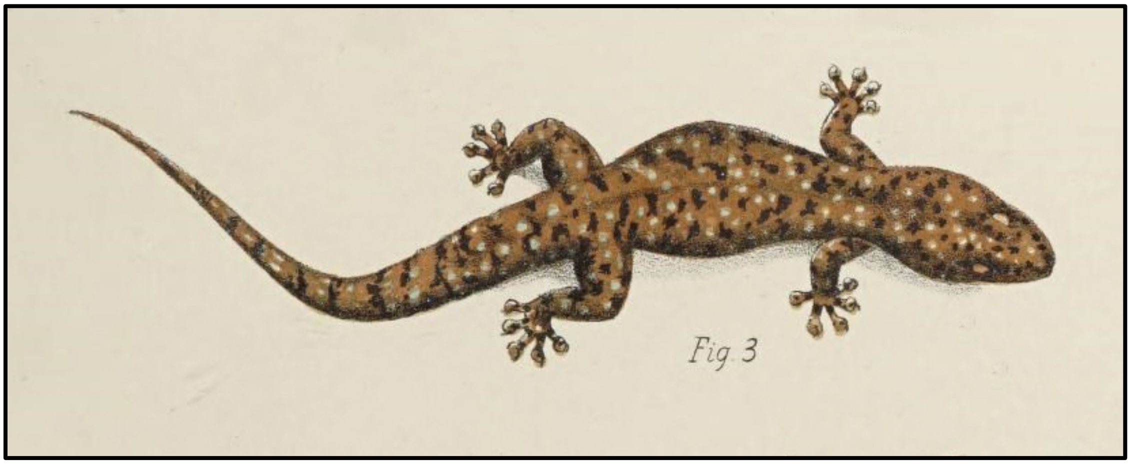
CHAPTER 1

The importance of defining measures of stability in macroecology and biogeography



Gehyra variegata, now *Gehyra moritzi,* from *Report on the work of the Horn Scientific Expedition to Central Australia*, 1896

The importance of defining measures of stability in macroecology and biogeography

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ABSTRACT

Stability, the continuity of environments or habitats through space and time, is a widely used concept in macroecology and biogeography and is often invoked in studies attempting to explain the uneven spatial distribution of biodiversity. Stability can be measured in various ways and at various spatiotemporal scales; however, few studies explicitly define their use of the term. This makes interpreting and comparing studies difficult. We suggest an integrated approach to defining measures of stability in macroecology and biogeography. This approach addresses five key challenges concerning the biological, environmental and spatiotemporal scales at which stability is assessed, and how the complexity of change across time and space is summarised into a metric of stability. Using this approach allows for clarity around the choice, conceptualisation, communication and comparison of measures of stability.

STABILITY IN MACROECOLOGY AND BIOGEOGRAPHY

The term *stability* appears widely, and in many different contexts, across ecology and evolutionary biology (Ives and Carpenter 2007, Grimm and Wissel 1997). In macroecology and biogeography, a wide range of studies have linked stability to the accumulation of biodiversity in specific areas and to processes such as evolution of the abiotic niche. For example, the relative climate stability of an area through time has been linked to high richness and endemism of species and genetic lineages, compared to less stable areas (Carnaval et al. 2009, Gavin et al. 2014, Cowling et al. 2015, Rosauer et al. 2015, Sandel et al. 2016).

In this context, stability is defined broadly as the continuity of environments, habitats, or populations through space and time. For instance, a site where a single habitat has occurred across millennia (e.g., rainforest) would be considered more stable than a site that has experienced multiple habitat switches (such as repeated shifts between rainforest and grassland) (Costa et al. 2018). Within this broad definition, measures of stability can vary in terms of the entity being measured (e.g., climate, species, or habitat), the spatiotemporal scale used (e.g., global studies over millions of years to local interannual studies), and the method of calculating it (e.g., the variance, mean or extremes). However, studies do not always clearly define their measure, leading to ambiguity in the interpretation of results. This is the issue we seek to address. We focus on stability as measured over millennia across regional to landscape scales, a topic of many studies; although the framework we describe can be applied to many different spatial and temporal scales.

Landscapes exhibiting higher stability tend to accumulate more biological diversity than areas with higher stochasticity, suggesting that stability could be a potential cause of diversity. This can occur through processes of speciation (as stability may promote speciation) and persistence (as stability may protect taxa from extinction). Stability can promote speciation over long time scales by allowing taxa more time to adapt to their local environment (Klopfer 1959, Fischer 1960), or by isolating populations in separate stable areas, allowing them to diverge (Haffer 1997). High species and functional diversity can then help to stabilise communities and biomes by buffering against climatic changes over time, for example by increasing resistance as shown by Isbell et al. (2015).

The relatively short time scale of the analyses of stability we consider, typically from the Last Glacial Maximum (LGM, 21kya) or Last Interglacial (LIG, 120kya) to the present, means they are usually focused on persistence rather than speciation. Continuity of environments and habitats can allow diversity to persist by protecting older communities and lineages from extinction whilst they are lost in less stable areas. For example, stable regions in Africa are believed to have protected Gondwanan lineages such as ricinuleid spiders from extinction during the climatic changes following the breakup of Gondwana (Murienne et al. 2013). Persistence can be assessed explicitly, for instance using population genetic tests for sustained high population size or range expansion, often within the context of refugia – climatically stable regions that allow taxa to persist while the climate in surrounding areas is unsuitable (e.g., Carnaval et al. 2009). Such insights may be relevant to deriving recommendations and policies on how to manage ecosystems for resilience to future climate change (Reside et al. 2013), imbuing the assessment of stability with important practical implications. However, it is important to note that attributes such as increased diversity over time may constitute a biological response to stability but are not measures of stability in themselves.

MEASURES OF STABILITY

The broad perspective on stability adopted across macroecology and biogeography still leaves open a vast array of possible measures of stability that can be employed in any given study. Few authors justify their particular measure, and the measures from different studies vary markedly in terms of the attribute of the system for which stability is being assessed (e.g. climate, habitat), the spatial and temporal scales of analysis, and the strategy used to synthesise complex spatiotemporal results into a summary metric. This leads to ambiguity about what is being measured and how to interpret results. For example, terms such as 'climate stability' and 'habitat stability' are often used without definition, and sometimes interchangeably (e.g. Faye et al. 2016). This issue has been identified before in relation to community ecology (e.g. Grimm and Wissel 1997), but no clear solution has emerged. With a rising number of macroecological studies invoking stability in its various forms (Figure 1), it is important to strive for greater clarity around the definition of measures of stability employed in such studies.

Here, we propose a framework for conceptualising stability within the context of particular biogeographic or macroecological hypotheses and for better understanding the choices which need to be made in defining an appropriate measure of stability in any given context. These choices correspond to five questions that must be answered when conceptualising stability:

1. What are we measuring stability of?
2. What is the spatial scale?
3. What is the temporal scale?
4. How is the interaction between space and time addressed?
5. How do we summarise temporal variation into a single measure of stability for a site?

We hope this framework will assist authors in making informed decisions in selecting and defining measures of stability employed in their studies and will allow for more effective comparison of results across the body of research on this topic.

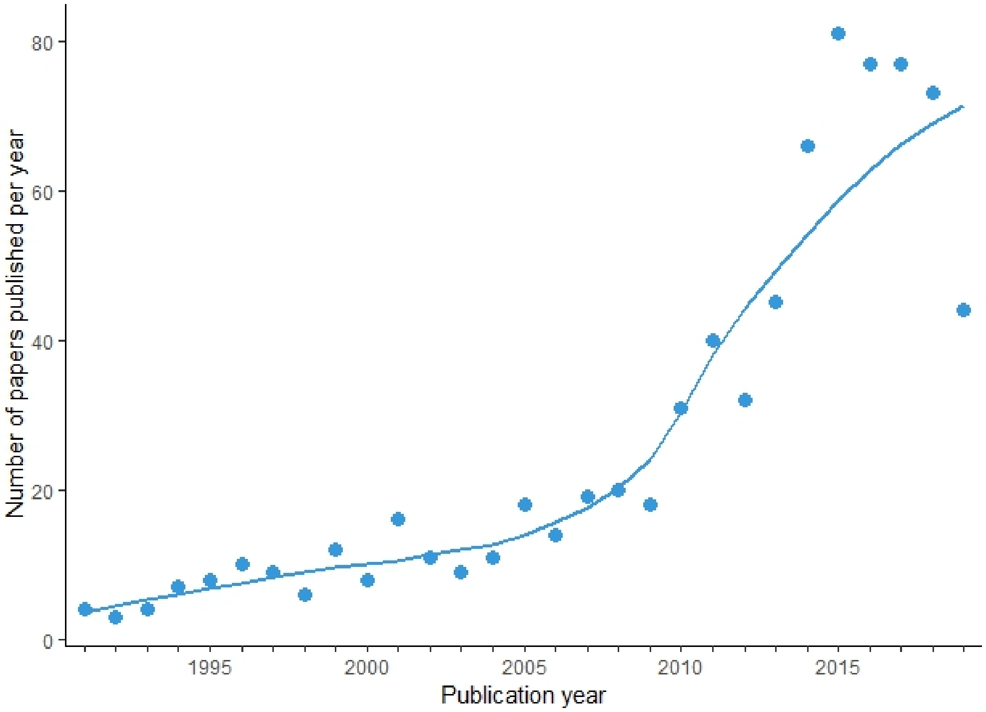

Figure 1. The number of macroecological studies invoking stability is rising. This shows the publication date for papers in Web of Science using the term "stability" and either "macroecolog*" or "biogeograph*" in their title, abstract, or keywords on 13 August 2019. The line depicts the loess regression as a visual aid.

A FRAMEWORK FOR DEFINING MEASURES OF STABILITY

Various authors have acknowledged confusion around the concept of stability (e.g. Pimm 1984, Grimm and Wissel 1997, Donohue et al. 2013), but despite this there is little consistency in how stability is defined and measured.

Our framework focuses on one stability property: spatial continuity through time within geographic or climatic space, as it may be used for predicting alpha and beta diversity at biogeographic scales. It builds on the checklist described by Grimm and Wissel (1997), which sought to help ecologists clarify how the term stability was used. That paper defined three fundamental categories of stability concepts: persistence (persistence through time), resilience (returning to reference state after disturbance), and constancy (staying essentially unchanged). However, we view these as the biological manifestations of a single stability concept, that is, spatial continuity through time. Spatiotemporal continuity is then the driver of other forms of stability.

Additionally, in the two decades since the publication of Grimm and Wissel's (1997) checklist, there have been many studies focusing on the methodology of defining stability. However, this literature has yet to be unified. For example, recent studies have revealed the importance of using fine temporal resolution to capture climate fluctuations (Fordham et al. 2018), and the importance of considering the temporal extent when defining areas of stability (Ashcroft et al. 2012). Other studies have focused on describing metrics for quantifying stability, including climate velocity (Loarie et al. 2009, Brito-Morales et al. 2018) and how the relationship between space and time changes with different metrics (Garcia et al. 2014). Here, we combine each of these components to provide a comprehensive conceptual framework for selecting and defining measures of stability in future studies.

The general concept of stability employed in our framework is illustrated in Figure 2, which shows a variable changing through time, for example species' ranges expanding and contracting through time but maintaining continuity in space. To derive a basic measure of stability for any given point in this region, we can create a line graph showing change over time at that point (Figure 2b). From Figure 2, we can see there are several questions and challenges that arise in relation to key features of any given measure of stability, summarised in Table 1.

Table 1. Challenges in defining measures of stability.

Feature of stability	Checklist question for this feature	Possible options
(1) Ecological attribute	What are we measuring stability of?	Environment, species, assemblage, biome
(2) Spatial scale	What spatial scale is being considered?	Size of the research area (extent), resolution of spatial data (grain)
(3) Temporal scale	What temporal scale is being considered?	Time-period being studied (extent), resolution of time slices (grain)
(4) Interaction between space and time	How is the interaction between space and time addressed?	No interaction (local stability), movement within adjacent regions (neighbourhood stability), dispersal-limited movement (dynamic landscape stability)
(5) Metric	How do we summarise temporal variation into a single measure of stability?	Average, extremes, variance, difference, presence, rate of change

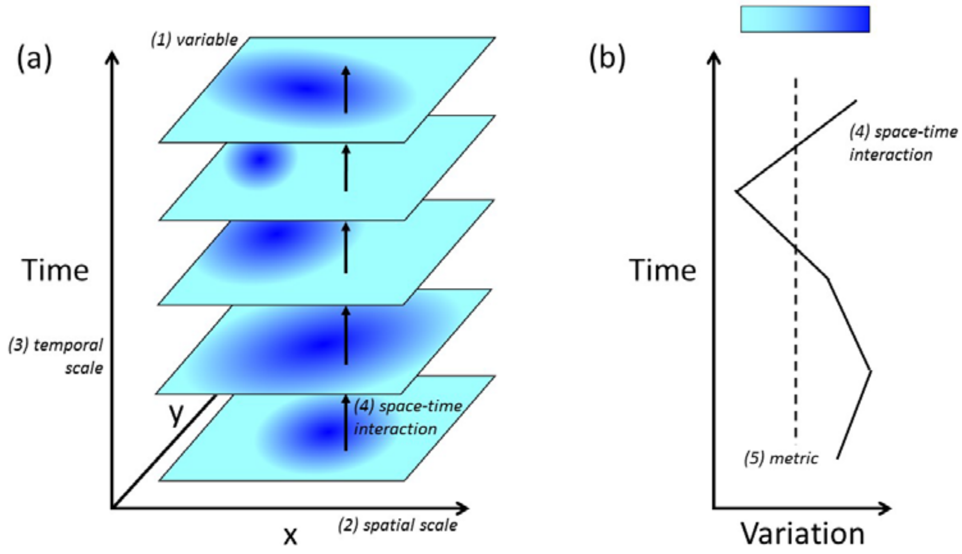

Figure 2. Measuring stability through space and time involves answering several key questions, as discussed in the text. (a) Shows a variable (such as temperature or habitat suitability) changing across space (x and y axes) and through time (vertical axis). The planes show a region at different time points, and the shading represents the variable being measured, for example habitat suitability. The arrows track a single site through time. The choices in metric design are shown in italics. In order to measure stability we need to choose (1) the variable being measured, (2) the spatial scale it is being measured across, (3) the temporal scale being measured across, and (4) the way of measuring the interaction between space and time. (b) Shows stability for the site tracked in (a), summarised into a line graph. To do so, we need to choose (4) the interaction between space and time and (5) the metric used to summarise patterns to a single measure of stability for that site (vertical dashed line), for example the arithmetic mean.

What are we measuring stability of?

Stability can be measured in relation to many different attributes of a system, or of a particular entity within that system. At the scales we are concerned with here, we can measure the variability of an environmental parameter, such as annual mean temperature, or the range of a species, assemblage or biome, measured for example using the bioclimatic envelope.

The simplest way to measure stability, and one of the most commonly used, is to examine it across one or more environmental parameters, such as a measurement of temperature or rainfall. This allows for the measurement of how much, or how fast, the environment has changed over time using measures such as climate velocity (the displacement rate of climate through time divided by the rate through space (Loarie et al. 2009)). Environmental or climate stability therefore refers to continuity in environmental variables at a specific location. For example, southern Africa has high climate stability as the rate of change of mean annual temperature over the last 21ky has been low, while in contrast central Europe has low climate stability, as it has experienced large changes in its temperature since the LGM (Sandel et al. 2016). Measures of environmental stability can be used to encapsulate variation in the past or projected future (Garcia et al. 2014), or novel climates that have arisen, or are expected to arise (Williams et al. 2007). Environmental stability can also be used as a proxy for changes in the potential distribution of species or biomes if there are no distributional data available for the biological group of interest (Garcia et al. 2014).

Models of species-level stability rest on estimates of the changing spatial distribution of a species' abiotic niche over time, or the continuity in the spatial location of a species range through time. For example, desert pupfish have stable ranges because they inhabit a limited number of desert ponds that have moved little (Brown and Feldmeth 1971). This contrasts with species whose ranges are shifting rapidly, either due to direct human intervention (introductions) or to track climate change. Species-level stability can be used to look at questions of extinction or migration under past or future climates (Nogués-Bravo 2009). It is usually measured using correlative ecological niche models (ENMs), which are fitted to the current realised niche then projected into the time periods of interest. There are several issues with this method, including the assumptions that species are in equilibrium with their environment and that a taxon's realised and fundamental niches are equivalent. Correlative ENMs also do not generally account for biotic interactions, non-analogue climates, or niche shifts (e.g. Pearson and Dawson 2003, Nogués-Bravo 2009, Fitzpatrick and Hargrove 2009). Hence, there is strong interest in applying more mechanistic models of species stability (e.g. Fordham et al. 2012, Mathewson et al. 2017), but this approach remains difficult to scale up to large numbers of taxa. For now, it seems that despite their well-known limitations, practicality dictates use of correlative models in most cases (Wiens et al. 2009).

Compositional or assemblage stability relates to changes in community composition (beta diversity) over time. For example, the Serengeti Plains in eastern Africa have high compositional stability as the community has changed little over time, possibly due to the low rainfall and small species pool (Anderson 2008). This contrasts with areas where the community composition has changed rapidly, for example through species introductions or species range shifts associated with climate change. Compositional stability is usually measured using macroecologically constrained 'stacked' species distribution models (Guisan and Rahbek 2011), although distance matrix-based modelling techniques such as generalised dissimilarity models (GDM) (Ferrier et al. 2007) are also used. These models assess the degree to which community composition has been stable over time.

Biome or ecosystem stability is analogous to species stability, but here the goal is to estimate the stability of the range of a biome rather than a species. It is measured with a particular regional assemblage in mind, usually by fitting ENMs to the realised niche of the biome, or sometimes using mechanistic dynamic vegetation models (Thuiller et al. 2008). These methods use models fitted in the present and projected into other time periods to assess the continuity, and hence stability, of the biome or vegetation type (e.g. Costa et al. 2018). Biome stability has been studied in a variety of systems, with clearest results for those with well-defined climatic boundaries such as rainforests (Graham et al. 2010, Rosauer et al. 2015), or regional forest to savannah transitions (Hirota et al. 2011).

These different types of biological stability are interlinked. Compositional stability is impacted by biome stability, as when a biome retreats or expands it affects the community composition at a site. Biome stability is in turn affected by environmental stability, depending on the broadness of the ecosystem's climatic tolerance (West and Salm 2003). This close interaction may explain why many studies looking at climate or habitat stability are unclear about which they are studying, despite the concepts being quite distinct (Ashcroft 2010).

Environmental variables — Most studies of stability include a measure of environment, whether explicitly or in models such as ENMs. The term 'environment' is very broad. For the current purpose, it comprises the abiotic variables describing a region, including its climate, geology, and topography. These variables can be looked at in two ways – as raw or as transformed variables. Raw variables are those directly measured in the environment, for example annual precipitation as measured by a weather stations, or inferred through a model or proxy, such as annual mean temperature derived from a paleoclimate model. Estimating stability using these variables would directly measure changes in the abiotic environment. Alternatively, measures of stability can be derived using environmental variables which have first been statistically transformed to better reflect observed present-day patterns in the turnover of the species composition of communities across these gradients. For example, methods such as GDM and Gradient Forest use available biological data to statistically transform each of a set of raw environmental variables, such that distances within the multivariate space, defined by these transformed variables, correlate as closely as possible with observed dissimilarities in present-day species composition between sampled sites (Ferrier et al. 2007, Ellis et al. 2012). This approach scales the relative effect that changes in different environmental variables are expected to have on compositional turnover (e.g. the relative importance of temperature versus precipitation), and variation in this effect at different points along any given gradient (e.g. a higher rate of turnover per unit change in precipitation at the low versus high end of a precipitation gradient). This scaling of environmental space also allows changes over time to be expressed in terms of the compositional dissimilarity expected between two time points, as a function of changes in multiple environmental variables (Blois et al. 2013).

Using either raw or transformed variables, the variables that are most important will depend on the physiology, niche and ecological interactions of the biological entity of interest (Williams et al. 2012). Regions that are stable for one species or entity may not be stable for another. The best way to identify informative variables, at least for studying single entities, is to include physiological and ecological data, such as those obtained from performance trials and experimental or extensive field studies. However, for many systems these data are not available and are impractical to obtain, such that realised distributions are used as a surrogate. When direct physiological data are not available, data on the ecology of the taxa can be combined with environmental layers and presence/absence data (Williams et al. 2012).

What is the spatial scale?

The issue of scale has been discussed widely in ecological literature since at least the 1970s, with several comprehensive reviews published (e.g. Wiens 1989, Levin 1992, Chave 2013). The importance of conducting studies at an appropriate spatial scale is well-known (e.g. Chase and Leibold 2002, Williams et al. 2002, Cavender-Bares et al. 2006), as processes and correlates that are important at one scale may not be important at others. For example, biotic interactions tend to be important in describing species distributions at local scales, with decreasing importance as the scale increases. In contrast, climate is classically viewed as being an important driver of diversity at a regional scale and above and less so at a local scale. However, recent work has shown the importance of microclimates for environmental filtering at local scales, with the mechanisms by which drivers influence biogeographic patterns also changing with scale (Chase and Leibold 2002, Hortal et al. 2010, D'Amen et al. 2017).

Our framework recognises two major components of spatial scale, extent and resolution, both of which need to be chosen carefully based on the patterns and processes being studied. Spatial resolution, also known as grain or focus, relates to the size of the individual spatial units being analysed (Turner et al. 1989, Whittaker et al. 2001). These may be plots of a few square metres or grid cells of 100 km. As the size of the spatial units increases, variation between cells decreases because more variation is captured in each individual cell (Levin 1992). This means that some patterns, such as micro-refugia, will be more apparent at a fine resolution that captures more variation between cells (e.g. Ashcroft et al. 2012).

Extent refers to the overall size of the analysis region, such as a protected area, biogeographic region, country or global scale (Wiens 1989). A greater extent generally captures more variance between the cells. It is important to note that very few systems are completely closed, so processes and patterns outside the chosen extent may still impact on the results (Wiens 1989). Taxa perceive and interact with their environment at different scales, so using a priori behavioural and ecological data will assist in choosing an appropriate scale (Wiens 1989, Rahbek 2004, Anderson et al. 2010).

What is the temporal scale?

Like the spatial scale, the temporal scale of a study needs to be defined in terms of both extent and resolution. The temporal extent considered will depend largely on the question being considered. For instance, looking at the stability of an area over a month would give a very different response to looking over a millennial timescale, with the location of areas of stability varying based on the timeframe considered (Ashcroft et al. 2012). Without attention to the temporal scale, studies addressing the same question may be mistakenly compared despite measuring very different things. Most studies invoking stability focus on millennial time scales, often since the last interglacial or LGM, although some consider smaller temporal extents, including down to intra-annual time scales (e.g. Martin and Ferrer 2015, Gainsbury and Meiri 2017).

Temporal resolution refers to the number and spacing of time periods considered, represented in Figure 2 by the number of time slices included. A study comparing only the LGM to the present would have a different result to one considering the same temporal extent, but with modelled data for every 100 years, with higher temporal resolution leading to greater accuracy (Fordham et al. 2018). If, for example, the modelled range of a population became regionally extinct at one time but was later re-established, it would not have maintained continuity through time, so would not be considered stable. However, if one considered only two time points, before and after this discontinuity, this break in continuity would not be identified.

Studies at different temporal scales may not be comparable (Wiens 1989). Different processes operate at different scales, with a gradual shift from ecological to evolutionary processes as the temporal extent lengthens (Chave 2013). Yet, there is a link between variation at different scales, such as between annual temperature range and longer term temperature fluctuations (Janzen 1967). Studies at a large spatial scale often (though not always) use a large temporal scale as well (Wiens 1989). This means that the appropriate temporal scale for a study will depend on the processes being studied and the spatial scale chosen, as well as any time lags between the process and response (Anderson et al. 2010) and the generation times of the organisms being studied, if any (Levin 1992).

How is the interaction between space and time addressed?

Another challenge in describing stability in a region is considering how changes over both space and time interact. How can changes through time across the surrounding landscape be addressed in assessing stability for a single site? Three possible ways to address this are local stability, neighbourhood stability, or dynamic landscape stability.

The simplest case is local or static stability, where a single site in a region is compared to itself through time (Graham et al. 2010). A stable area would be one that has remained continuously suitable or similar through time. This approach does not take the conditions in adjacent cells into account, although the spatial scale is still important. Local stability is the most commonly measured type of stability.

Neighbourhood stability considers the spatially dynamic nature of environments, whereby a species or biome may persist by moving locally to track changes in the environment. In neighbourhood stability, a single cell is compared to the surrounding cells in the region, to look for analogous environments. Climate change velocity uses this method, comparing change in climate over time to that over space (Sandel et al. 2011).

In more complex dynamic landscape stability models, entities such as species or biomes can shift to track changes across the landscape through time. The size of the surrounding region considered can be scaled depending on the question and organism of interest. The maximum distance allowed from the original cell of interest to a surrounding analogous cell depends on the capacity of the organism or biome to disperse, being larger for a high-dispersal organism such as a bird compared to a low-dispersal organism such as a lizard (Sandel et al. 2011).

The method chosen to combine space and time will have a significant impact on the final measure of stability, as shown in Figure 3. In this example, a site becomes completely unsuitable at one time, suggesting local extinction using a static stability model. However, when using a dynamic stability model (Graham et al. 2010), which allows species or biomes to track contiguous suitable environments through the landscape, changes are much less pronounced.

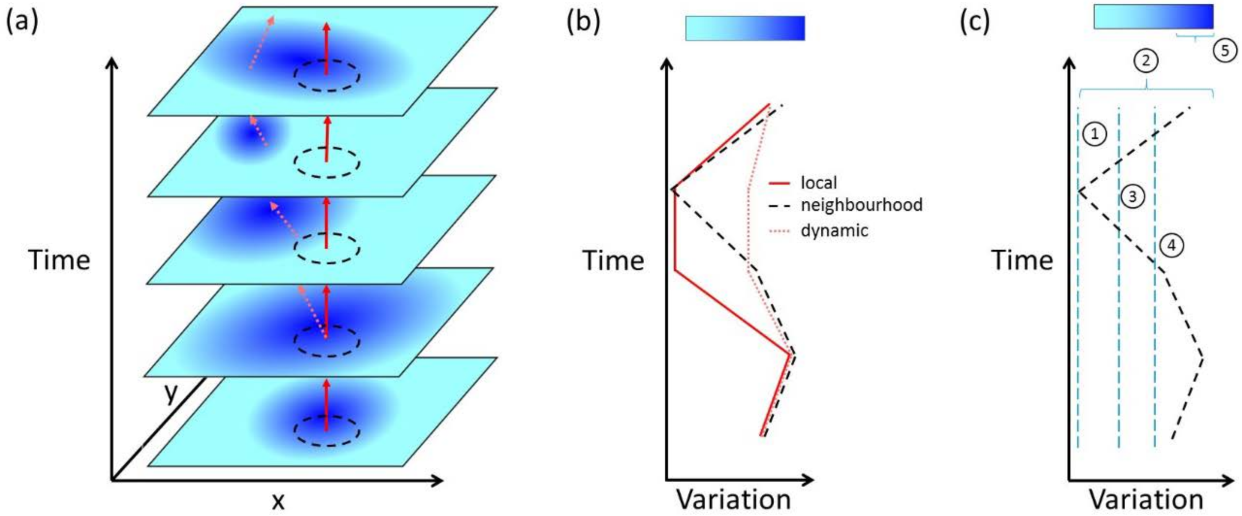

Figure 3. Stability through time for a site: (a) is a variant of Figure 2, showing a variable (for example, habitat suitability for a species) changing over space (x and y axes) and time (vertical axis). Here we show different methods of combining space and time when measuring stability for a site: local stability (red arrow), neighbourhood stability within a radius of the original site (red arrow combined with the circle around the site), and fully dynamic landscape stability allowing for tracking across the landscape (yellow arrow). (b) Shows how stability for that site would be measured across time using all three methods for combining space and time. The shaded bar represents the value of the variable being measured (e.g. habitat suitability for the site), and each line in the plot represents a method of combining space and time. (c) The final step of measuring stability is to obtain a single value for the stability at each site. This illustrates possible metrics for doing this. These include (1) extremes (shown as the minimum), (2) difference or anomalies (shown as the difference between one end of the time series and the extremes), (3) geometric mean, (4) arithmetic mean or (5) percentage of time in a given range of values (with the bracket indicating a hypothetical range of values).

How do we summarise temporal variation into a single measure of stability for a site?

Having resolved the first four challenges, a final decision is choosing a metric to summarise temporal variation for a site into a single measure. There are six commonly used classes of metric (see Table 2): difference between time periods, mean, rate of change, extremes, presence in all time periods, and variance between time periods.

Different metrics emphasise different biological processes, so their choice should be driven by the system and question being studied. For example, extremes such as very low suitability may indicate bottlenecks in a population, while the geometric mean is useful in showing whether a region was continuously suitable through time. Some metrics rely on decisions made in other steps. Climate velocity, for example, is a measure of the rate of change of the environment but assumes some form of dynamic stability (where entities can track changes across the landscape) (Ma et al. 2016).

Table 2. Commonly used metrics for summarising stability. Biological meanings are defined assuming that stability is being measured for climate, but similar interpretations apply for other levels of stability.

Metric	**Definition**	**Examples of specific metrics**	**Biological question**
Difference between time periods	The amount of change that has occurred between time periods.	Climate anomalies (e.g. Sonne et al. 2016)	How similar is the current environment or available niche to environments in other time periods?
Mean	The climate or suitability of a location averaged across time.	Arithmetic mean; geometric mean (e.g. Graham et al. 2010)	What climatic conditions have taxa had to adapt to?
Rate of change of environment	The speed at which the environment has changed over time.	Climate velocity (Ma et al. 2016)	How well can taxa track the changes in climate?
Extremes	The most extreme conditions or suitability experienced over time.	Maximum temperature; minimum suitability	Could taxa have consistently occurred at this location across time?
Presence in all time periods	The predicted presence of the attribute of interest (e.g. climate, biome or taxa) across all time periods.	Percentage of time in which conditions have been similar to the present; presence of a biome/taxa in all time periods (e.g. Terribile et al. 2012)	How well does the current climate represent the conditions taxa have experienced?
Variance	The variance (for example, in suitability or temperature) between time points.	Standard deviation (e.g. Brown et al. 2014)	How much climatic variability have taxa experienced?

IMPLEMENTING THE FRAMEWORK

Together, these five challenges make up a framework for designing and communicating measures of stability at the biogeographic scale. By working through each of these challenges sequentially, a more robust measure of stability that is relevant to the hypothesis being tested will be designed and communicated. Explicitly considering the variable being measured will ensure that the results can be interpreted in a biologically meaningful way. The choice of spatial and temporal scales will affect the drivers and mechanisms that can be tested for. How stability is summarised into a single number for each site – through both the choice of how space and time interact and the choice of metric – will change the biological meaning of the result and which hypotheses can be tested. Figure 4 summarises the challenges and the options available for each.

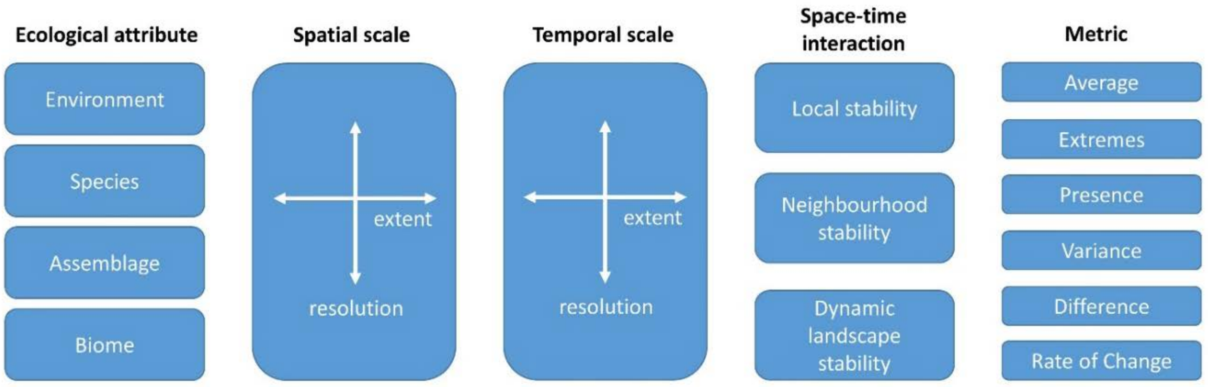

Figure 4. A methodological framework for analysing stability in macroecology and biogeography, showing the five challenges to resolve when defining measures of stability as it relates to diversity at biogeographic scales, and the possible options for each.

Unfortunately, while there have been a few studies measuring the impact of one specific aspect of stability, for example temporal resolution (Fordham et al. 2018) or dynamic and static stability (Graham et al. 2010), there have been no studies systematically altering how stability is measured across the five dimensions of stability. This gap in the literature means that, while explicitly considering how stability is measured is important from a conceptual and communication perspective, it is difficult to know what impact the current lack of clarity has on the results of studies. Future studies systematically investigating this will enable measurement of the impact of consciously choosing a stability measure.

Despite this lack, some insight can be gained in comparing the results of studies investigating the same region but using different measures of stability. For example, there has been a lot of research on stability of the Australian Wet Tropic rainforests, starting with some of the earliest spatial models of paleoclimate (Nix and Switzer 1991). While this is an intensively studied region, with broad patterns of stability well-established from both paleomodeling and paleoecological data (Vanderwal et al. 2009), there is variation in the details of results. Much of this is due to differences in the stability metrics used. For example, using dynamic stability consistently shows greater connectivity between refugial areas, compared to using static stability (Graham et al. 2010, Rosauer et al. 2015). Changing the spatial extent can make a significant difference to predictions of refugia (e.g. Vanderwal et al. 2009). Similarly, the differences in the refugia identified by Bell et al. (2010) and Moussalli et al. (2009) are likely due to a combination of the taxa chosen (widespread versus montane skinks), and the metrics used to summarise across time, specifically the geometric mean versus the product of suitability.

As can be seen in this example and in Box 1, the framework offers a clear foundation for choosing the most appropriate way of measuring stability, based on a given hypothesis. Doing so, and clearly communicating the choices made and reasons behind them, will help to enhance interpretation and comparison across multiple studies in this field, while future research will help clarify the quantitative importance of these decisions.

BOX 1 – AN EXAMPLE OF THE FRAMEWORK

Here, we give two examples of how this framework can be used to determine possible approaches to measuring stability (see Figure 5).

Our first example uses stability to test the hypothesis 'Areas that acted as refugia through the last glacial-interglacial period have shaped patterns of phylogenetic diversity (PD) in the Australian Wet Tropics (AWT) Rainforest'. For testing this hypothesis, the variable being measured would be the biome as a whole, particularly as tropical rainforest as a biome is well-defined climatically and so can be readily modelled using a small number of environmental variables (Hilbert et al. 2007). The spatial scale would ideally be a local to regional resolution, to allow for the identification of fine patterns of PD at the same resolution, with an extent slightly larger than the AWT, including a buffer to allow for past climatic changes and reduce edge effects. The temporal scale would be an extent of the present to the LGM, with as fine a resolution as possible given the available data, and the generation time of the taxa. A common practice is to use only a few time periods – the present, the LGM, and one or two intermediary points in the Holocene, representing the variability observed in pollen records (Kershaw and Nix 1988). While this reduces computation time, having such a low resolution means that key features, such as periods of high velocity, could be missed. Thus, temporal resolution would ideally be of centuries or even decades (e.g. Fordham et al. 2018). Allowing space and time to interact through dynamic landscape stability allows the biome to shift and track suitable climatic conditions (Graham et al. 2010). There are several appropriate metrics that could be used to identify refugia, for example the rate of change (e.g. climate velocity), or the minimum suitability over time. In contrast, the average suitability over time would not be appropriate as areas that have been moderately unsuitable but stable could get the same score as areas that have fluctuated between being highly suitable and highly unsuitable.

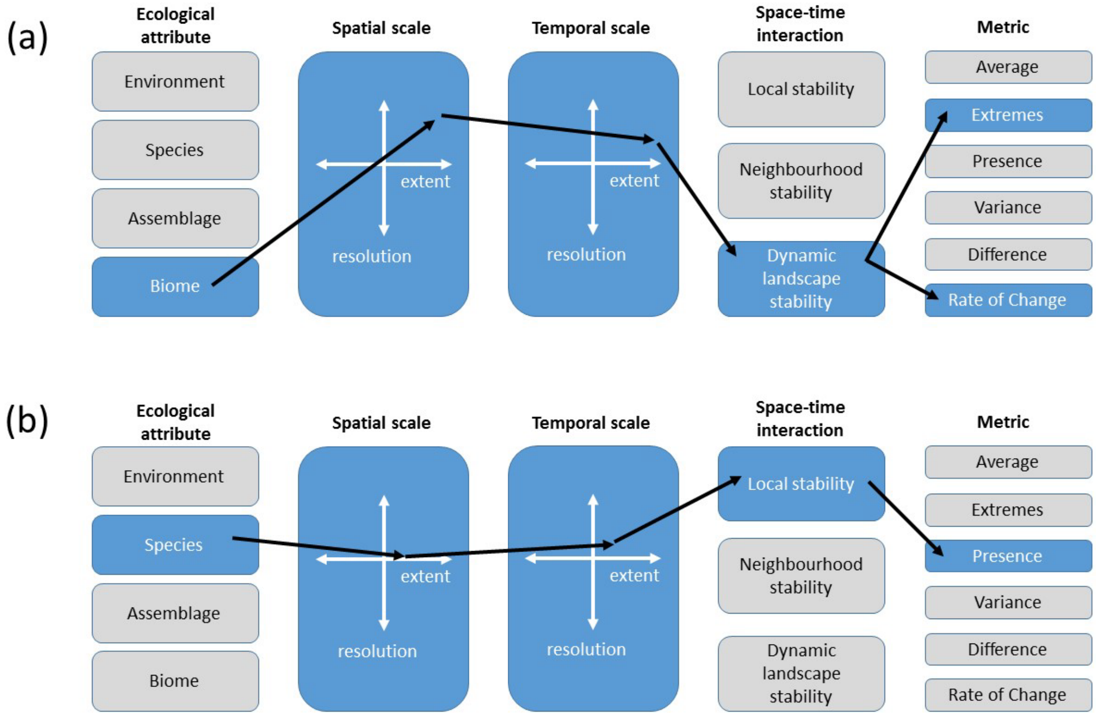

Figure 5. Two examples of how the methodological framework for stability in macroecology and biogeography can be used: (a) Shows appropriate choices for measuring stability when testing the hypothesis 'Areas that acted as refugia through the last glacial-interglacial period have shaped patterns of phylogenetic diversity in the Australian Wet Tropics'. (b) Shows appropriate choices for measuring stability over much smaller spatiotemporal scales, when aiming to identify current microrefugia for an endangered species with a shrinking range.

Our second example uses stability to identify current microrefugia for a low-dispersal endangered species with a shrinking range induced by climate change. Here, the variable being measured is species stability. The spatial scale would be a local extent with fine resolution, in order to incorporate microclimate observations (e.g. Ashcroft et al. 2012). Temporal scale would likely be an extent of 50 to 100 years, possibly including future projections, with a resolution of years (e.g. Cheddadi et al. 2017). Static stability may be appropriate here, as the aim is to identify areas to focus conservation efforts. Finally, the most appropriate metric would likely be the presence of the species at a site in all time periods.

IMPLICATIONS FOR FUTURE PROJECTIONS AND CONSERVATION

While the concept of stability has traditionally been used to study the past, an increasing number of studies use the concept of stability to identify areas that may act as refugia under future climate change. These can then be used to evaluate current reserve systems and incorporated into conservation planning (Reside et al. 2013), with refugia now being considered in the creation of government policy as well. For example, the Australian Government's Biodiversity Conservation Strategy explicitly references the need to "identify and protect climate change refugia" (Natural Resource Management Ministerial Council 2010).

With such direct, practical implications, it is even more vital that stability is clearly defined and that an appropriate measure be used. Multiple studies have shown the identification of future refugia, and, hence, appropriate reserve choices, are heavily dependent on the methodological choices made (Ashcroft et al. 2012, Keppel et al. 2012, Reside et al. 2013). Employing our framework in studies of future climate change will ensure that sound conservation recommendations can be made.

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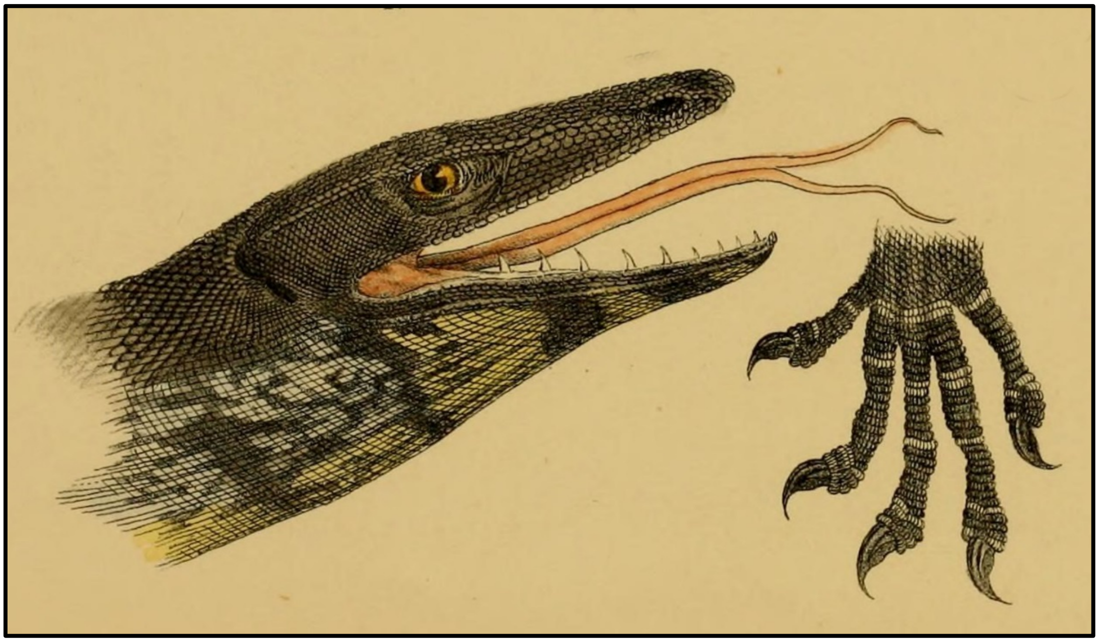
CHAPTER 2

Stability predicts diversity, but what is the best measure of stability?



Hydrosaurus varius, now *Varanus varius,* from *Natural History of Victoria*, 1885

Stability predicts diversity, but what is the best measure of stability?

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ABSTRACT

Many studies in macroecology and biogeography use stability to explain diversity patterns, however there are many measures of stability to choose from. There is currently little empirical data on how the measure of stability used affects the results of a study. We tested four measures of stability to see if there was a difference in how well they predicted diversity across a biologically rich region, the Australian Monsoonal Tropics. We measured stability through time for both habitat suitability (using stacked species distribution models) and community dissimilarity (using generalised dissimilarity modelling), and summarised across time using both mean and standard deviation. We then predicted richness and endemism using these stability models. We found that all measures of stability improved predictions of diversity, compared to models using only current environment. There were large performance differences between the stability measures, and richness and endemism were best predicted by different stability measures. This suggests that comparing multiple stability measures in a single study may enable hypothesis testing of processes that cause diversity patterns. Our results demonstrate the importance of carefully considering the biological application of stability measures before including them in studies.

INTRODUCTION

Stability, or the continuity of environments or ranges through time, is often used to explain patterns of diversity in macroecological and biogeographic studies. Stability has been linked to increased species richness, endemism and lineage endemism (Cowling et al. 2015; Gavin et al. 2014; Sandel et al. 2016; Rosauer et al. 2015), as well as to an increase in some species traits, such as specialisation in seed dispersal methods (Schleuning et al. 2012). Climatically stable regions often function as evolutionary refugia (Ashcroft 2010; Carnaval et al. 2009; Sandel et al. 2011), providing areas for taxa to persist as the climate in surrounding areas changes, and are often linked to the presence of many small-ranged taxa (Harrison & Noss 2017).

Given the wide use of the concept of stability, it is important to examine how it is measured. There are various methods of measuring stability (McDonald-Spicer et al. 2019), and the interpretation of any results depends on the method used. However, while the theoretical importance of clearly defining measures of stability is clear, there is little empirical work examining how the stability measure used affects results, and how this can inform understanding of biogeographic processes.

Stability through time in macroecological studies is usually measured by looking at change in a landscape over a series of points in time (time slices). This change can be across various ecological attributes, including modelled climate, habitat suitability or community turnover, depending on the biological definition of stability required. Change across time slices can then be summarised to a single value of stability for each point in time through a variety of methods, such as the mean, variation or range.

In this paper we compare four different concepts or measures of stability to see which best describes current patterns of squamate diversity in a complex and biologically rich landscape, the Australian Monsoonal Tropics. Our stability models compare two approaches to modelling stability through time for multiple species – a species-level and a community-level approach. The species-level approach models species' ranges independently and then combines the models, using aggregated (stacked) species distribution models (sSDMs), while the community-level approach combines species data first and then models community dissimilarity through time. Each of these approaches use two common metrics of variation across time, standard deviation and mean.

Comparing the explanatory power of these four measures of stability will highlight the importance of choosing appropriate stability methods, and how the measure chosen alters the biological interpretation of the results. Additionally, including multiple measures of stability in a single study may allow for different aspects of biology to be measured, giving greater insight into the drivers of diversity in this region.

MATERIALS AND METHODS

Spatial and taxonomic scope

Our analyses focus on the western Australian Monsoonal Tropics (AMT). This region is a heterogeneous landscape of savannas and tropical woodlands with a strong latitudinal rainfall gradient (Bowman et al. 2010). It has relatively low human population density, and a correspondingly low extent of habitat conversion compared to other tropical savannas (Woinarski et al. 2007) with a substantial part managed for conservation. We define the western AMT as all parts of the AMT biome west of 138°E, including the Top End and Kimberley (Figure 1). This excludes the Carpentarian biogeographic barrier and all areas to the east of this, as these are quite faunistically distinct from the western AMT.

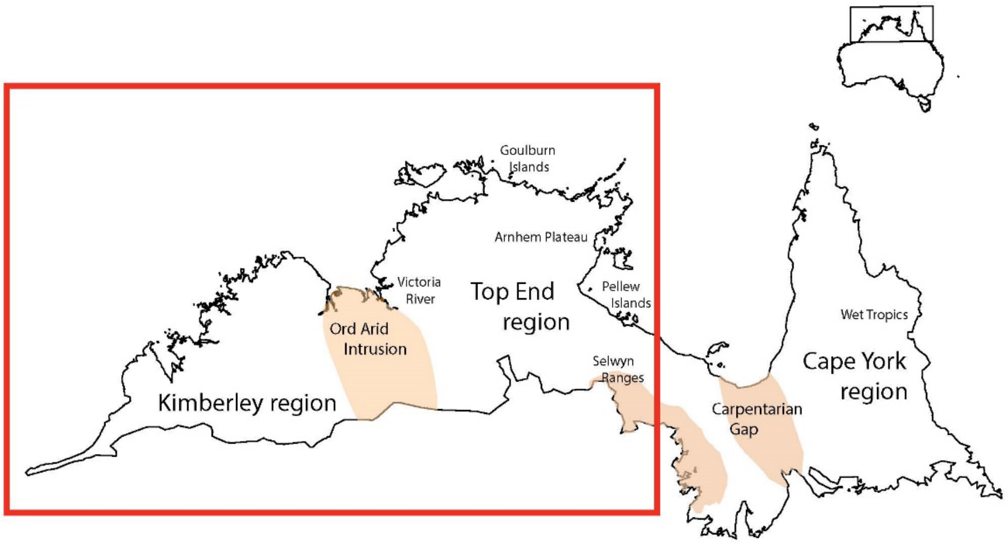

Figure 1. The Australian Monsoonal Tropics, with the study region outlined. Shaded regions are the major biogeographic barriers in the region – the Ord Arid Intrusion between the Kimberley and Top End, and the Carpentarian Gap between the Top End and Cape York.

Squamates are an ideal system for studying the influence of past environment, due to their high sensitivity to changes in climate (Deutsch et al. 2008; Sinervo et al. 2010) and low dispersal abilities. We obtained presence-only occurrence data for species in the Agamidae, Scincidae, Varanidae, Carphodactylidae, Diplodactylidae, Pygopodidae and Gekkonidae families occurring from 9°S to 25°S and 112°E to 156°E from the Atlas of Living Australia (Atlas of Living Australia 2019) and from our own fieldwork. Records from the Atlas of Living Australia are a combination of specimen records from Australian museum collections and observational records. The records were identified to species level and any with missing latitude or longitude details were removed. Species ranges implied by ALA records were compared to field guides to exclude erroneous, outlying locations (Cogger 2014; Wilson & Swan 2013). Only species that occurred within the study region were included but ranges of these taxa that continued outside the region were not truncated. This reduced the impact of edge effects on the analysis. For some taxa which have undergone recent and substantial taxonomic revision it was not possible to assign ALA records to new species, so these records were omitted. As with all studies within northern Australia, records are clustered in more accessible regions, including along roads (Figure 2a). The final dataset comprised 63,888 spatially unique records across 335 species. The number of records per species ranged from a single record for 21 species to 4377 records for *Heteronotia binoei*, with a mean of 191 records per species (Figure 2b).

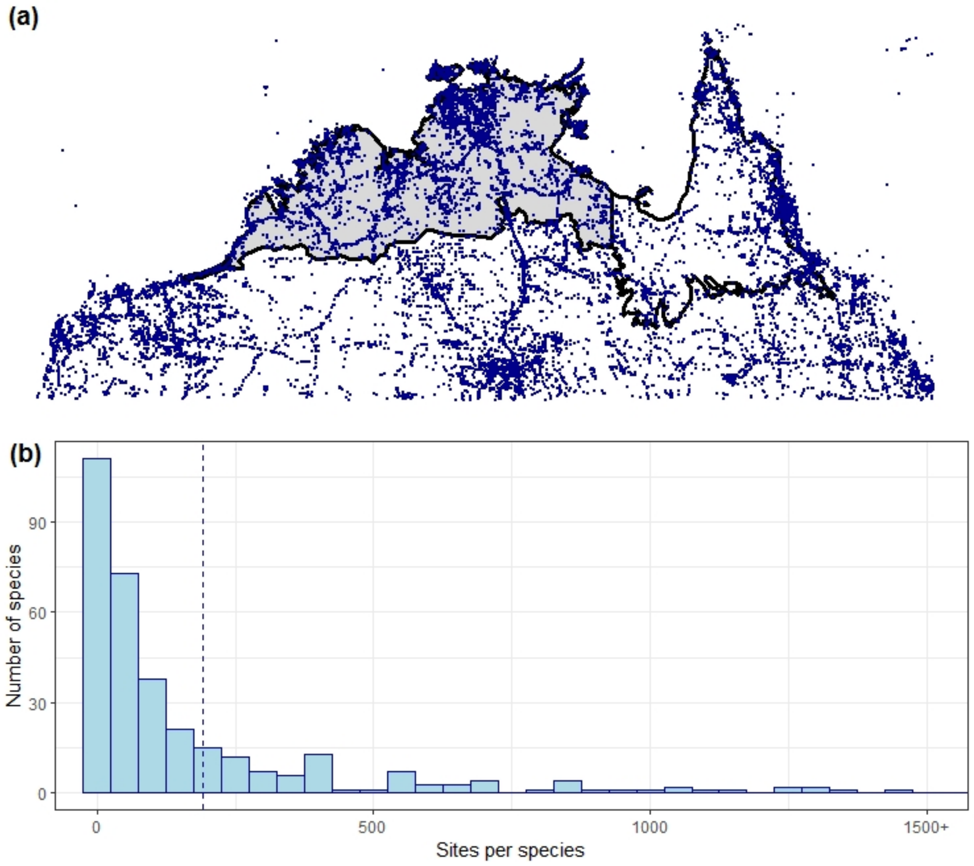

Figure 2. The distribution data used in the analyses. A) Site distribution, with the Australian Monsoonal Tropics outlined and the study region shaded in grey. B) Number of sites per species, with the mean of 191 sites shown by the dotted line.

Environment and paleoclimate variables

For the measures of past stability, we used climatic variables modelled from the present to 80,000 years ago (kya), and eleven soil, geology and topography variables. As the region is highly geologically stable, geology and soil variables were assumed to have been constant over the past 80ky.

We used eight temperature and precipitation variables: annual mean temperature, temperature seasonality, mean temperature of the warmest quarter, mean temperature of the coldest quarter, annual precipitation, precipitation seasonality, precipitation of the wettest quarter, and precipitation of the driest quarter. These were calculated from the HadCM3 Global Climate Model (GCM) (Singarayer & Valdes 2010), found to be the most appropriate GCM for the Asian-Australian monsoon, including when projected to the last glacial maximum (DiNezio & Tierney 2013), and downscaled to a resolution of 2.5 arc minutes (approximately 4.5km) (Rosauer et al. 2015). Analyses using paleoclimate data are more meaningful when multiple time slices, or points in time, are used instead of one or two snapshots (Fordham et al. 2018). Our models used 52 time slices ranging from the present day to 80kya, with time slices every 1,000 years until 22kya, and then every 2,000 years.

The geological and topographic variables used were: calcrete in or below soil profile, solum average median clay content, soils dominated by coarse fragments, solum average median horizon saturated hydraulic connectivity (ASRIS 2011), mean geological age, inherent rock fertility (Geoscience Australia 2012), gravity anomalies (Geoscience Australia 2008), magnetic anomalies (Milligan & Petkovic 2002), topographic relief (Geoscience Australia 2015), and, to capture impact of geographic distance, latitude and longitude. These variables were chosen based on previous literature which found them to be important in predicting compositional turnover (Williams et al. 2012). They were downscaled to match the resolution of the paleoclimate data using the ‘raster’ package in R (Hijmans 2016; R Core Team 2016).

Modelling stability

We measured stability across a large group of species, combining species data using both a species-level approach (stacked species distribution models (Mateo et al. 2012)) and a community-level approach (generalised dissimilarity models (Ferrier et al. 2007)). Each of these approaches was summarised through time using two methods – arithmetic mean and standard deviation – to give a total of four metrics of stability.

Species distribution models

Our first method of modelling stability through time involved species distribution models (SDMs). SDMs were fitted to each species individually using Maxent (Phillips et al. 2017), and then projected back to each of the paleoclimate time slices using the method described in Rosauer et al. (Rosauer et al. 2015) (see Supplementary Material). In order to maintain consistency and comparability to the GDM, all environment and climate variables were available to the models. The models were then aggregated to create a stacked SDM (sSDM) (e.g. Mateo et al. 2012). Nineteen models with an AUC less than 0.7 were excluded from subsequent steps, leaving 316 models (Figure 3a). The majority of the excluded models (15 models) were for species occurring in only one or two sites.

Community dissimilarity model

Our second method of modelling stability through time used community dissimilarity. To model community dissimilarity, we fitted a generalised dissimilarity model (GDM) (Ferrier et al. 2007) for the present day environment within the 'gdm' package in R (Manion et al. 2016). This model predicts compositional turnover or pairwise beta diversity between sites as a function of difference between those sites along environmental gradients. We removed sites with less than six species to reduce the effect of limited sampling (Figure 3b). To select predictor variables, we carried out a model selection test using stepwise backward elimination. This begins with a GDM including all environment and climate variables described above and progressively removes the least effective predictor, one at a time, until all non-significant predictors are removed. The resulting model included geographic distance, temperature seasonality, mean temperature of the warmest quarter, annual precipitation, elevational range, geological age, soil fertility and longitude. The GDM was then used to create transformed environment and climate layers for each time step in the past, which allowed for the prediction of community compositional dissimilarity between any two grid cells at different times and/or locations. See Supplementary Material for more details.

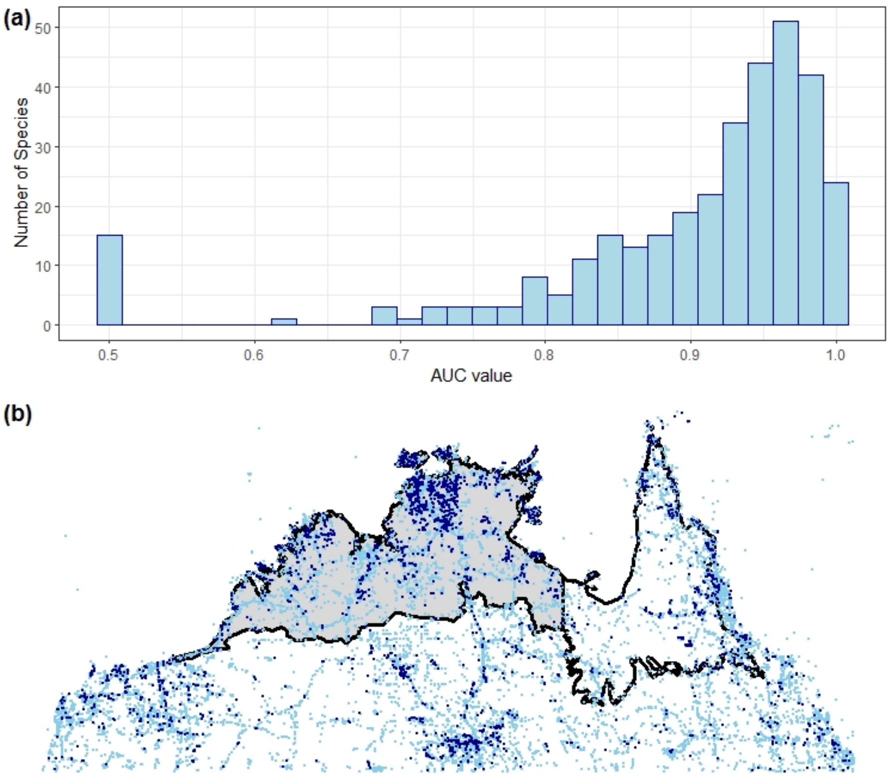

Figure 3. The distribution data used in the stability analyses. a) Histogram of AUC values for species distribution models. Models with an AUC of less than 0.7 were excluded from further analysis. b) Distribution of sites used in GDM analysis, with those sites containing six or more species in dark blue. Sites excluded from the analysis are shown in light blue. The Australian Monsoonal Tropics is outlined and the study region shaded in grey.

Diversity metrics

We used two measures of current species diversity in our models, richness and weighted endemism (Crisp et al. 2001). Weighted endemism weights a grid cell's richness by the inverse of the range size of each species. These diversity measures were calculated using the SDMs in Biodiverse (Laffan et al. 2010) using the current day SDMs for all species, again on a 4.5km grid. Both richness (alpha diversity) and weighted endemism (beta diversity) were log-transformed in the final generalised linear models to make the variables more normally distributed.

Stability metrics

Stability can be measured in a variety of ways, each containing different information about a system's history. To encompass some of this variation, we used four metrics of stability – GDM_{mean}, GDM_{sd}, $\text{sSDM}_{\text{mean}}$, and sSDM_{sd}. These all measure the stability of the environment, with the environmental parameters scaled based on the responses of the biota (species composition or occurrence) as estimated across space in the current environment.

The GDM_{sd} stability metric measures variability of community composition across time. Using this metric, high stability is found in areas where the predicted community assemblage has changed little through time. This metric was calculated by fitting a GDM to the current day and projecting the model into the paleo-environment at each time slice, before estimating the dissimilarity of the species assemblages in each time period to the present. This was summarised across time by calculating the standard deviation of the dissimilarity to the present composition through time for each grid cell.

The GDM_{mean} stability metric looks at community turnover through time. In this metric, high stability is found in areas where the predicted community assemblage through time has been very similar to the present community assemblage. The dissimilarity to the present for each time period was calculated the same way as for the GDM_{sd} metric, and then summarised by taking the arithmetic mean of each grid cell over time.

$sSDM_{sd}$ measures the magnitude of change in species' habitat suitability that has occurred across time. In this metric, areas of high stability are areas where the suitability has not changed much through time. Like the GDM stability metrics, this metric has no concept of 'good' or 'bad' environment, with only the magnitude of change in suitability mattering. It is calculated by taking the standard deviation of the likelihood of occurrence across time for each species, and then averaging it across all species predicted to occur in the cell.

The last stability metric, $sSDM_{mean}$ measures suitability across time for each species, averaged across all species predicted to occur in the cell using the arithmetic mean. Using this metric, areas of highest stability are areas that have been mostly suitable through time across species. It is similar to measures used previously to model continuity of suitable conditions for biomes such as rainforest (Graham et al. 2010; Carnaval et al. 2014; Rosauer et al. 2015). This metric is tied to the current richness and distributions of the taxa more strongly than the other three metrics. It is calculated by taking the arithmetic mean of suitability across time for each species, and then averaging it across all species.

Generalised linear models

Generalised linear models (GLMs) were fitted to explain the two diversity metrics using R. We fitted GLMs using current environment and then added each of the scaled stability metrics. Current environment was described using five variables: annual mean temperature, mean annual precipitation, elevational range, mean geological age and inherent rock fertility.

We also fitted GLMs using current environment, mean current suitability, and each of the stability metrics. Mean current suitability was calculated by taking the arithmetic mean of current day suitability across all species. This was included in the generalised linear models to control both for other elements of current environment not used in the linear models, and for the fact that some stability measures used are more strongly influenced by current suitability due to how they are calculated (for example, $sSDM_{mean}$). Controlling for these allows us to look more clearly at the impact of the past.

Spatial autoregressive models were fitted for each of our GLMs using the 'spdep' package version 0.8-1 (Bivand & Wong 2018) to control for spatial autocorrelation over a 500km radius.

RESULTS

Diversity in the AMT

Endemism hotspots occurred in the western and northern parts of the Kimberley region and on the Arnhem Plateau. Other areas of high endemism include the north east of the Top End and islands off the Kimberley and Top End, as well as the Pellew Islands off the Carpentarian Gap. All locations are shown in Figure 1. Low endemism is found in the more arid regions of the southern AMT, as well as along the eastern edge of the Kimberley Plateau. Richness is concentrated in similar areas to endemism, as well as further across the Arnhem Plateau and in the Victoria River region. Low squamate richness is found primarily in the southern Kimberley Plateau and in arid regions along the southern edge of the AMT (Figure 4).

The current day GDM explained 26% of the deviance in community turnover, with large areas of turnover between the northern and southern Kimberley, and between the Arnhem Plateau and southern Top End. This explanatory power is reasonable for a GDM including presence-only data, with other studies showing similar levels of deviance explained (e.g. Rose et al. 2016). The model fit and non-linear functions fitted to the predictor variables in the GDM are shown in Supplementary Figure 1.

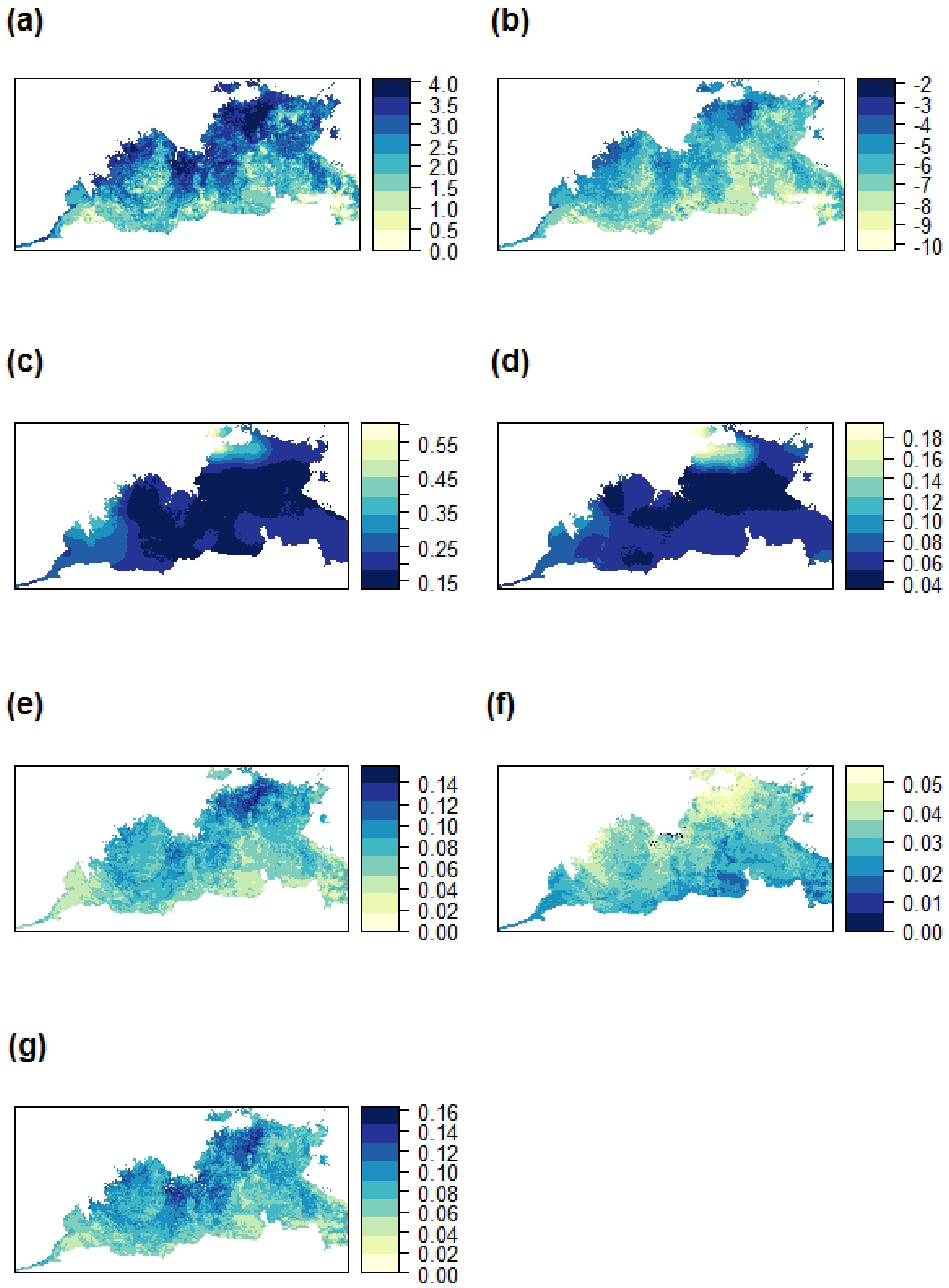

Figure 4. Patterns of diversity and stability in Squamates. a) Richness on a log scale, b) Weighted endemism on a log scale. For both of these, dark blue areas are areas with higher diversity, yellow areas are less diverse.

c) to f) show areas of stability as identified by the four stability measures. In all, dark blue areas are more stable and yellow areas are more unstable through time. c) GDM_{mean} d) GDM_{sd} e) $sSDM_{mean}$ f) $sSDM_{sd}$. g) Mean current suitability, with dark blue areas showing the highest mean suitability and yellow areas showing the lowest.

Stability measures

The two measures of stability based on GDM show broadly similar patterns to each other, with a large band of stability (dark blue in Figure 4) across the centre of the Top End and in the western Kimberley. The GDM_{sd} measure shows overall more instability (yellow in Figure 4), particularly in the north western Top End.

In contrast, $sSDM_{mean}$ and $sSDM_{sd}$ show quite different patterns (Figure 4e and 4f). The Arnhem Plateau and some regions of the Kimberley are highly stable for the $sSDM_{mean}$ stability measure. For $sSDM_{sd}$, the most stable regions are across the southern edge of the AMT, with some highly stable regions along the Kimberley coast. This suggests areas that are mostly suitable through time are not necessarily those areas where suitability has not changed much through time.

Using stability to predict diversity

In all of the fitted linear models, including stability increased the model fit compared to those models including only current environment (Table 1). When including only environmental variables and stability metrics, richness was best predicted by the $sSDM_{mean}$ metric, with an R^2 value of 73%. The positive coefficient for the stability measure means that areas that have been highly suitable for many species through time tend to have higher richness. After including mean current suitability to better control for current environment, the patterns for richness change with the $sSDM_{mean}$ metric performing relatively poorly. Species richness is best predicted by the $sSDM_{sd}$ metric, with an R^2 of 79%, although the differences between models is slight. The negative coefficient means that areas that have had the least change in their suitability tend to have higher species richness.

Endemism showed similar patterns when including only environmental variables and stability metrics, being best predicted by the $sSDM_{mean}$ metric, with an R^2 value of 66% (Table 2). The coefficient is positive indicating that areas with high endemism also tend to have been suitable for many species through time. The positive coefficient means that areas that have had high turnover, i.e., where the community composition has been very different to the current composition, tend to have higher endemism.

Table 1. Results of spatial autoregressive models for species richness. Richness was log-transformed to meet the assumptions of the model. R^2 is the Nagelkerke pseudo-R^2, Coefficient is the coefficient of the stability metric. Change in AIC measures the change against the best model (shown in bold).

	Stability + current environment				*Stability + current environment + mean current suitability*			
Stability metric	AIC	ΔAIC	R^2	Coefficient	AIC	ΔAIC	R^2	Coefficient
No stability measure	49016	6034	0.68335	N/A	33297	1663	0.78407	N/A
GDM (mean)	49017	6035	0.68335	0.0010470	33299	1665	0.78407	-0.000225
GDM (sd)	48927	5945	0.68405	0.023385	33293	1659	0.7841	0.0049342
sSDM (mean)	**42982**	**0**	**0.72663**	**0.30138**	33068	1434	0.78528	-0.073874
sSDM(sd)	46602	3620	0.70144	0.18816	**31634**	**0**	**0.79265**	**-0.16988**

Table 2. Results of spatial autoregressive models for weighted endemism. Endemism was log-transformed to meet the assumptions of the model. R^2 is the Nagelkerke pseudo-R^2, Coefficient is the coefficient of the stability metric. Change in AIC measures the change against the best model (shown in bold).

	Stability + current environment				*Stability + current environment + mean current suitability*			
Stability metric	AIC	ΔAIC	R^2	Coefficient	AIC	ΔAIC	R^2	Coefficient
Current environment only	86231	3326	0.62949	N/A	75772	2898	0.71281	N/A
GDM (mean)	83961	1056	0.64943	0.19233	**72874**	**0**	**0.73239**	**0.19059**
GDM (sd)	83549	644	0.65293	0.19704	73106	232	0.73087	0.17333
sSDM (mean)	**82905**	**0**	**0.65833**	**0.35784**	75255	2381	0.71642	-0.18534
sSDM(sd)	83065	160	0.657	0.33745	75668	2794	0.71355	-0.072595

DISCUSSION

The initial results showed that areas that have been more suitable for species through time tend to have higher species richness, a result supported by many previous studies (e.g. Boyer et al. 2016). However, adding mean current suitability into the model led to quite different results, with richness correlating with low variability in suitability. This suggests squamate species richness in northern Australia develops in areas that have a constant level of suitability, or areas with more stable environment as scaled by species habitat preferences. This reflects findings in other studies, including in the neighbouring Australian Wet Tropics region (e.g. Graham et al. 2006).

This change between the models is likely due to that fact that the $\text{sSDM}_{\text{mean}}$ metric, initially the most important, is closely linked to current species ranges and reflects current suitability.

Including mean current suitability as a predictor allows us to better control for the effect of current environment, and focus on the impact of past stability on current patterns.

The areas of highest endemism also initially correlated with regions that have been more suitable for species through time. After adding mean current suitability into the model, endemism correlated with areas where the current community assemblage is quite different to that in the past. The correlation of endemism with areas where the community assemblage is predicted to have experienced high turnover was an unexpected result, contrasting with previous suggestions that endemism hotspots develop in areas of low change (Sandel et al. 2011; Rosauer et al. 2015; Sandel et al. 2016; Harrison & Noss 2017).

One possible explanation for this is that the relationship between stability and endemism may not be causal at this time scale, with both patterns instead being a reflection of patterns occurring over a longer time scale. Alternatively, it could be a signal of refugia: species ranges expanding and contracting through time with the changing environment, and in the present day contracting into refugia. These refugia would have many short-ranged species, causing a hotspot of endemism. Species in the skink genus *Carlia* in the Top End islands, for example, show a pattern of demographic contraction in the early Holocene, in concert with rising sea levels (Potter et al. 2018). More explicit modelling and testing of these hypotheses, perhaps using population genetics to understand demographic changes (e.g. Carnaval et al. 2009), is needed to fully understand this pattern.

Including multiple measures of stability and diversity allowed us to compare different hypotheses of the drivers for increased diversity. This gave more insight than simply including a single measure of 'stability'. If we had only considered how one measure of stability impacted on diversity, for example $sSDM_{mean}$, the results indicate that richness and endemism show the same patterns, with increased stability leading to higher diversity. Comparing multiple measures of stability and carefully considering the biological meanings of these measures allowed for the differences in patterns between alpha and beta diversity to be identified.

The results of our analyses could be affected by how we measured stability, specifically how we summarised across space and the number of time slices used. Our study used static stability, which looks at stability at a single site, discounting the ability of species to disperse into more favourable surrounding areas. Modelling approaches that explicitly include dispersal, such as

KISSMig (Nobis & Normand 2014), would allow for the calculation of dynamic stability (Graham et al. 2010). Dynamic stability considers the surrounding area and allows species to track suitable habitat across space, and may be a more effective representation of how taxa behave under changing climates. Additionally, our use of presence-only data introduced bias into our modelling, including collection and geographic bias.

Our study used 52 time slices over 80ky, however other studies suggest that even finer scale temporal data is needed to accurately capture past climatic instability (Fordham et al. 2018). Unfortunately, such fine scale data is not currently available for the HadCM3 GCM. Finally, there is wide variation in paleoclimate estimates of the AMT between GCMs (DiNezio & Tierney 2013). In this we chose to use the HadCM3 model alone, based on previous comparisons with paleo-climate proxies across the region (DiNezio & Tierney 2013); however using multiple GCMs may be preferred.

The key finding of this study is that different metrics of stability have different levels of importance when measuring drivers of diversity. This supports previous theoretical work suggesting that it is important to carefully consider how to measure stability (McDonald-Spicer et al. 2019). Additionally, comparing multiple metrics of stability and diversity allowed for greater insight into the processes driving biogeographic patterns in this study region, allowing us to develop hypotheses for further study. This means it is very important to be clear about what each metric of stability is measuring, as the biological implications of 'high stability' vary according to the metric used.

ACKNOWLEDGEMENTS

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Author contributions: CJM led conceptualisation and writing and executed the data analysis. All other authors contributed equally to both conceptualisation and manuscript preparation.

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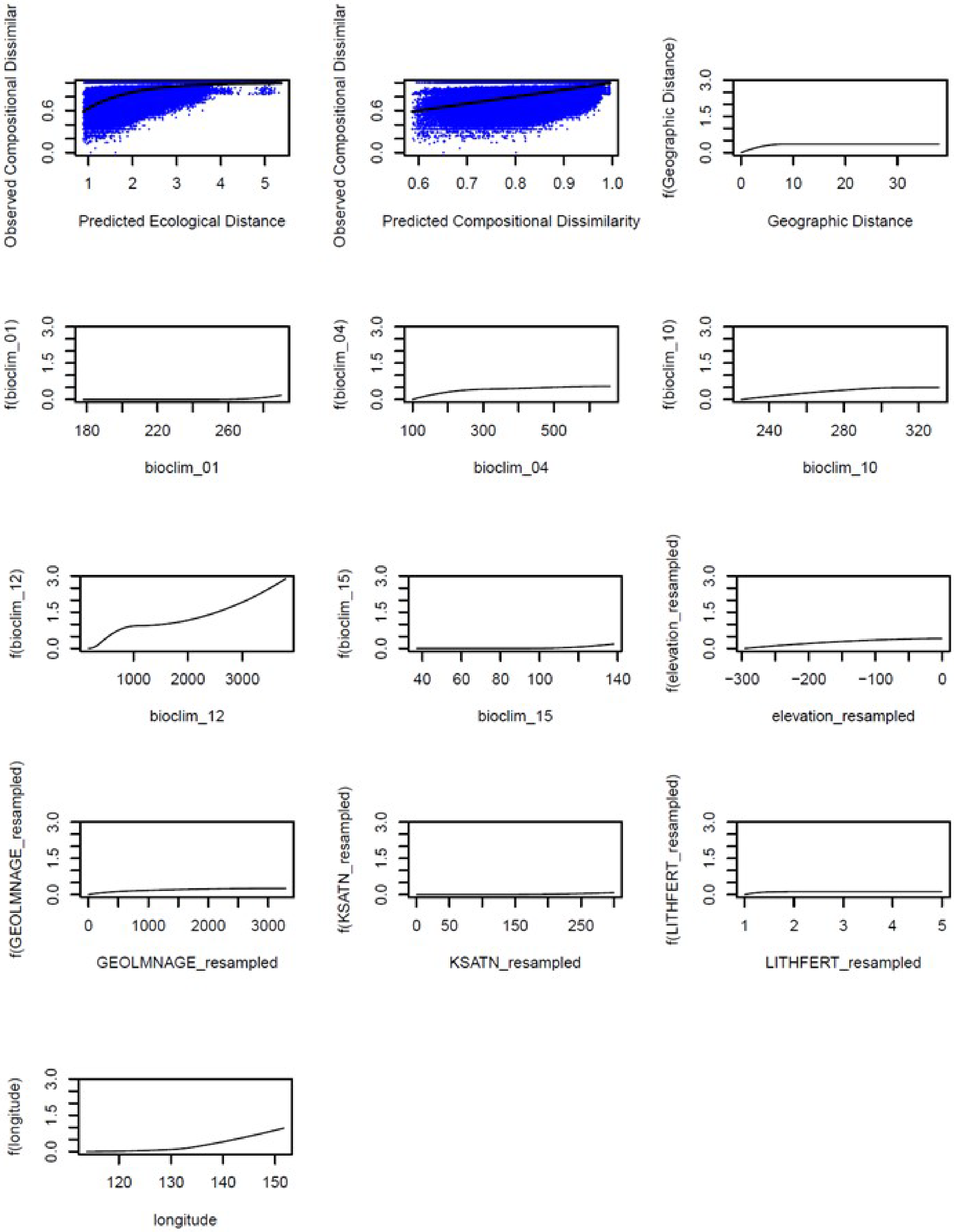
SUPPLEMENTARY MATERIAL



SM Figure 1. Model fit and nonlinear functions fitted to the predictor variables in the GDM.

SM Table 1. Pearson correlation matrix for variables in GLMs.

	Elevation	Temperature	Precipitation	Geologic Age	Rock fertility	Mean current suitability	sSDM_{sd}	$\text{sSDM}_{\text{mean}}$	GDM_{mean}	GDM_{sd}	WE (log)	Richness (log)
Elevation	1											
Temperature	-0.06	1										
Precipitation	-0.17	0.20	1									
Geologic Age	-0.59	-0.05	0.24	1								
Rock fertility	-0.02	0.13	-0.11	0.11	1							
Mean current suitability	-0.51	0.44	0.45	0.50	0.19	1						
sSDM_{sd}	-0.35	0.45	0.66	0.40	0.06	0.83	1					
$\text{sSDM}_{\text{mean}}$	-0.48	0.31	0.55	0.55	0.18	0.89	0.85	1				
GDM_{mean}	0.04	0.25	0.24	-0.07	-0.05	0.09	0.40	0.04	1			
GDM_{sd}	0.08	0.08	0.38	-0.06	-0.04	0.11	0.41	0.13	0.87	1		
WE (log)	-0.36	0.45	0.59	0.36	0.20	0.74	0.69	0.68	0.25	0.29	1	
Richness (log)	-0.31	0.50	0.57	0.26	0.20	0.78	0.69	0.73	0.12	0.19	0.59	1

Detailed Methods – Species Distribution Models

Species distribution models were fitted using Maxent version 3.3.3 (Phillips et al. 2017) through R, following the method described in Rosauer et al. (2015). For each species, 2000 background points were randomly selected from a radius of 2.5 degrees around the location records for each species. This geographic restriction was so that the models would emphasise locally relevant variables. Standard settings were used, including linear models, a prevalence of 0.5 and a regularisation multiplier of 1. In order to maintain consistency and comparability to the GDM, all environment and climate variables were available to the models, and predicted distributions were limited to within 400km of current occurrence points using a convex hull.The models were then projected into each of our time slices, using clamping to limit extrapolation into novel climates.

AUC values for each model were calculated by Maxent. Nineteen models with an AUC less than 0.7 were excluded from subsequent steps, leaving 316 models (Figure 3a). The majority of the excluded models (15 models) were for species occurring in only one or two sites.

The models were then aggregated to create a stacked SDM (sSDM) for each species (e.g. Mateo et al. 2012). All of the projected SDMs for each species were stacked, and then summarised to a single raster layer by taking either the standard deviation (for the sSDM_{sd} measure) or arithmetic mean (for the $\text{sSDM}_{\text{mean}}$ measure) for each cell. These single raster layers were then combined across the species by taking the mean value for each grid cell.

Detailed Methods – Generalised Dissimilarity Models

Our generalised dissimilarity models (GDM) (Ferrier et al. 2007) were fitted using the 'gdm' package version 1.3.11 in R (Manion et al. 2016). As our data is presence only, we assume absence at non-presence sites.

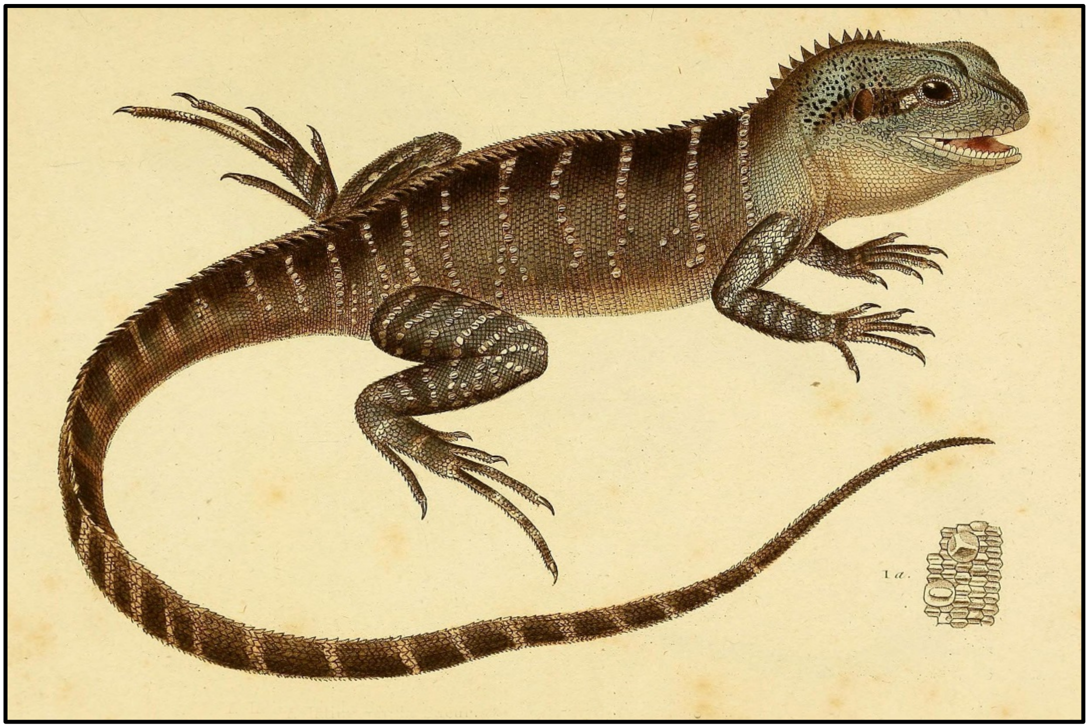
To select predictor variables, we carried out a model selection test using stepwise backward elimination. This begins with a GDM including all environment and climate variables described above and progressively removes the least effective predictor, one at a time, until all non-significant predictors are removed.

Our final GDM was run using four splines and the variables geographic distance, temperature seasonality, mean temperature of the warmest quarter, annual precipitation, elevational range, geological age, soil fertility and longitude.

The GDM was then used to create transformed environment and climate layers for each time step in the past using the gdm.transform function. To calculate the dissimilarity of each time period to the present, the absolute value of the difference between the past and present values for each variable was calculated and then added, before being transformed using the GDM link function. This gives each grid cell a value between 0 (completely similar to the present) and -1 (completely dissimilar to the present). This dissimilarity to the present was then be compared across time periods to calculate our two GDM stability measures.

CHAPTER 3

A bioregionalisation of lizard communities in the Australian Monsoonal Tropics



Istiurus lesueurii, now *Intellagama lesueurii,* from *Erpétologie générale, ou, Histoire naturelle complète des reptiles*, 1834

A bioregionalisation of lizard communities in the Australian Monsoonal Tropics

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ABSTRACT

Biogeographic regionalisations are widely used in macroecology and conservation, however it is important that they are based on accurate information. The Australian Monsoonal Tropics is a highly diverse but understudied region in northern Australia, with increasing taxonomic and survey work being done. Here we conducted a bioregionalisation of lizards in the Australian Monsoonal Tropics. We identified four key biogeographic provinces, with these patterns driven largely by habitat variability and physiologically limiting conditions. We also showed the importance of accurate bioregionalisations when setting conservation priorities, with our bioregionalisation suggesting that the Gulf region is under-conserved.

INTRODUCTION

Bioregionalisation, or the classification of biota into geographical units for analysis, is a central aim in descriptive biogeography. Bioregions are discrete areas of land containing unique assemblages of taxa, climate, and geography, and often reflect species distributions more accurately than climate, vegetation structure or remote sensing alone (e.g. Olson et al. 2001, Särkinen et al. 2011). The methods and taxa used to identify bioregions vary across the world, with Wallace's regions based on animals (Wallace 1876, Holt et al. 2013), the accepted bioregionalisations of Africa and Europe based on plants (White 1993, European Environment Agency 2003), and the Neotropics on a combination of plants and animals (Morrone 2014).

Classifying biota into bioregions allows for a spatially explicit framework for macroecological and conservation assessments. They are often used in exploring patterns of diversity (e.g. Davies et al. 2007, Kreft and Jetz 2007) and historical biogeography (e.g. Matzke 2013), and can be useful in exploring differing impacts of climate change (e.g. Salazar et al. 2007, Knapp and Smith 2001). Bioregions are also incredibly important for conservation, allowing for the protection of ecological processes (e.g. migrations in East Africa), more robust reserve selection, and criteria for conservation organisations to focus their resources (Olson et al. 2001, Myers et al. 2000). For these reasons, they are often required as part of conservation agreements, such as the international Convention on Biological Diversity (1992).

Australia has a long history of bioregionalisations (summarised in Ebach 2012), with two main systems used in policy. The Interim Biogeographic Regionalisation for Australia (IBRA) divides Australia into 89 bioregions, with 419 subregions, based on geology, landforms, climate and flora and fauna (Thackway and Cresswell 1995). The WWF Bioregionalisation is a global bioregionalisation, identifying 867 ecoregions based on communities, climate and geology (Olson et al. 2001). The Australian National Reserve System uses these bioregionalisations to identify and set conservation targets and priorities.

The Australian Monsoonal Tropics comprises the top fifth of Australia and contains a variety of habitats including a quarter of the world's tropical savannas that remain in good ecological condition (Woinarski et al. 2007). Bioregionalisations of the area were first done in the 1990s (Woinarski 1992), with revisions for various taxa recently published (Shelley et al. 2019, Catullo, Lanfear, et al. 2014, Braby et al. 2020), although the IBRA and WWF remain the main bioregions used for conservation. However, the Australian Monsoonal Tropics is understudied compared to the rest of the mesic and arid regions of the continent, meaning that a reassessment of these bioregionalisations using a more comprehensive dataset is due, particularly given increasing development pressure (Australian Government 2015). Lizards have received a large amount of recent taxonomic, genetic and survey work in the Australian Monsoonal Tropics, making them a useful study system for exploring the biogeography of the area. They are also low-dispersal, climate sensitive taxa (Sinervo et al. 2010, Deutsch et al. 2008), so are useful for fine-scale biogeographic analyses.

In this paper we identify the major lizard biogeographic provinces in the Australian Monsoonal Tropics, incorporating the most recent taxonomic and environmental information. We look at the drivers of these provinces, and examine the conservation implications of our new bioregionalisation.

METHODS

Study region

Our analyses focus on the Australian Monsoonal Tropics (AMT) (Figure 1). This region is a heterogeneous landscape of savannas and tropical woodlands with a strong latitudinal rainfall gradient (Bowman et al. 2010). It has relatively low human population density, and a correspondingly low extent of habitat conversion compared to other tropical savannas (Woinarski et al. 2007) with approximately one-quarter managed for conservation. The AMT stretches from Cape York in the east to the Kimberley in the west, excluding the Australian Wet Tropics, and is bounded to the south by the Australian Arid Zone and dispersed sandstone plateaus.

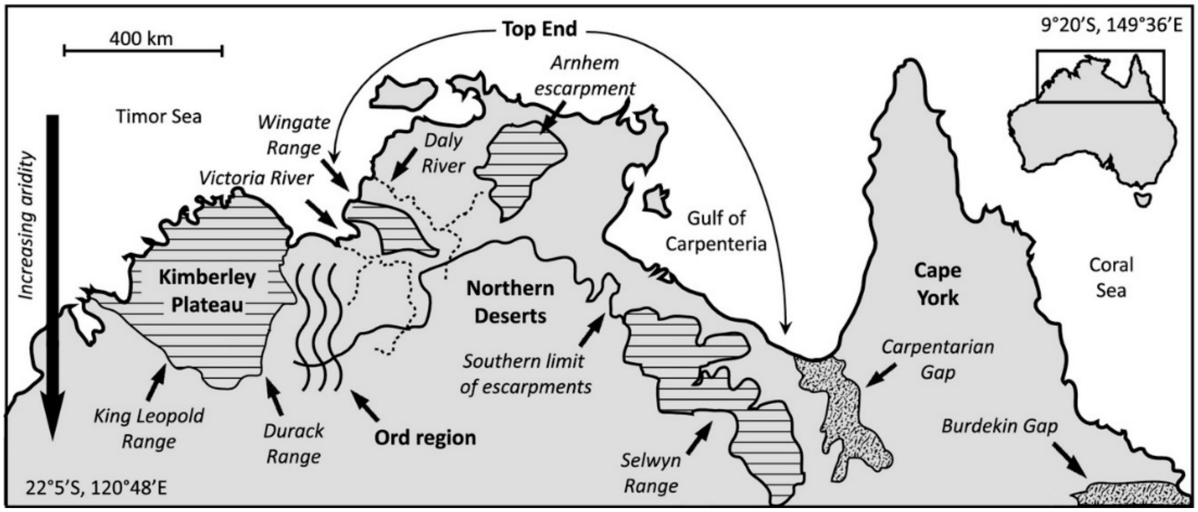

Figure 1. The Australian Monsoonal Tropics. Major areas of raised or dissected terrain are shown with horizontal hatching, rivers are shown with dashed lines, and substrate barriers are shown with mottled lines, with wavy lines for region of the Ord River arid intrusion. Figure from Catullo et al. (2014).

Species data

Low dispersal animals such as lizards provide a good study system for looking at biogeographic patterns. We obtained presence-only occurrence data for lizard species in the Agamidae, Scincidae, Varanidae, Carphodactylidae, Diplodactylidae, Pygopodidae and Gekkonidae families occurring from 9°S to 25°S and 112°E to 156°E from the Atlas of Living Australia (Atlas of Living Australia 2019) and from our own fieldwork, with additional records for Diporiphora (Melville et al. 2019).

The records were identified to species level and any with missing latitude or longitude were removed. Only species that occurred within the study region were included but ranges of these taxa that continued outside the region were included until 25° latitude. This reduced the impact of edge effects on the analysis. The combined dataset was cleaned to remove outlier records and introduced species, and to update taxonomy. We used the Australian Reptile Online Database (Macdonald 2019) to assess species ranges and identify outliers, and updated taxonomy using recent publications (Oliver et al. 2014, Melville et al. 2019, Oliver et al. 2020, Rabosky et al. 2017, Hoskin and Couper 2012).

As with all studies within northern Australia, records are clustered in more accessible regions, including along roads (Figure 2a). The final dataset comprised 59,755 spatially unique records across 350 species. The number of records per species ranged from a single record for 15 species to 7,155 records for *Carlia munda*, with a mean of 170 records per species.

The spatial distribution of record locations (Figure 2a) and the estimated under sampling in areas such as the Gulf and western Cape York (Figure 2b), indicate our dataset is highly spatially biased. One option to control for this is to use a coarse grid resolution, as in some previous assessments (Slatyer et al. 2007, Woinarski 1992). Another is to use discrete areas, such as bioregions (e.g. Olson et al. 2001) or catchments (e.g. Shelley et al. 2019), which reduces sampling bias (Williamson et al. 2011). Using the second method, in our bioregionalisation we assigned each record to an IBRA bioregion, based on the IBRA 7 (Department of the Environment 2012). These IBRA regions were used as the base spatial unit for our analyses, following other studies (e.g. Olson et al. 2001).

Bioregionalisation

We identified provinces based on the similarity of species composition between regions, as used in previous biogeographic work (Shelley et al. 2019). Using the software Biodiverse v3.00 (Laffan et al. 2010), we generated a matrix of species turnover for all pairwise IBRA region combinations using Simpson's beta , or S_2 (Lennon et al. 2002). Simpson's beta was used as it is not inflated by local differences in richness (Lennon et al. 2002), meaning it reduces the effect of unequal sampling (Tuomisto 2010).

It can be calculated as:

$$\beta_{sim} = 1 - \frac{a}{a + \min{(b, c)}}$$

Where *a* is the number of species found in both regions, *b* is the number found only in the first region and *c* is the number unique to the second region. Species richness and endemism were calculated for each IBRA region and each province identified within the AMT. We considered endemism for provinces in relation to the AMT, where a species found outside the AMT may still be considered endemic to a region within it, if this is its sole AMT occurrence.

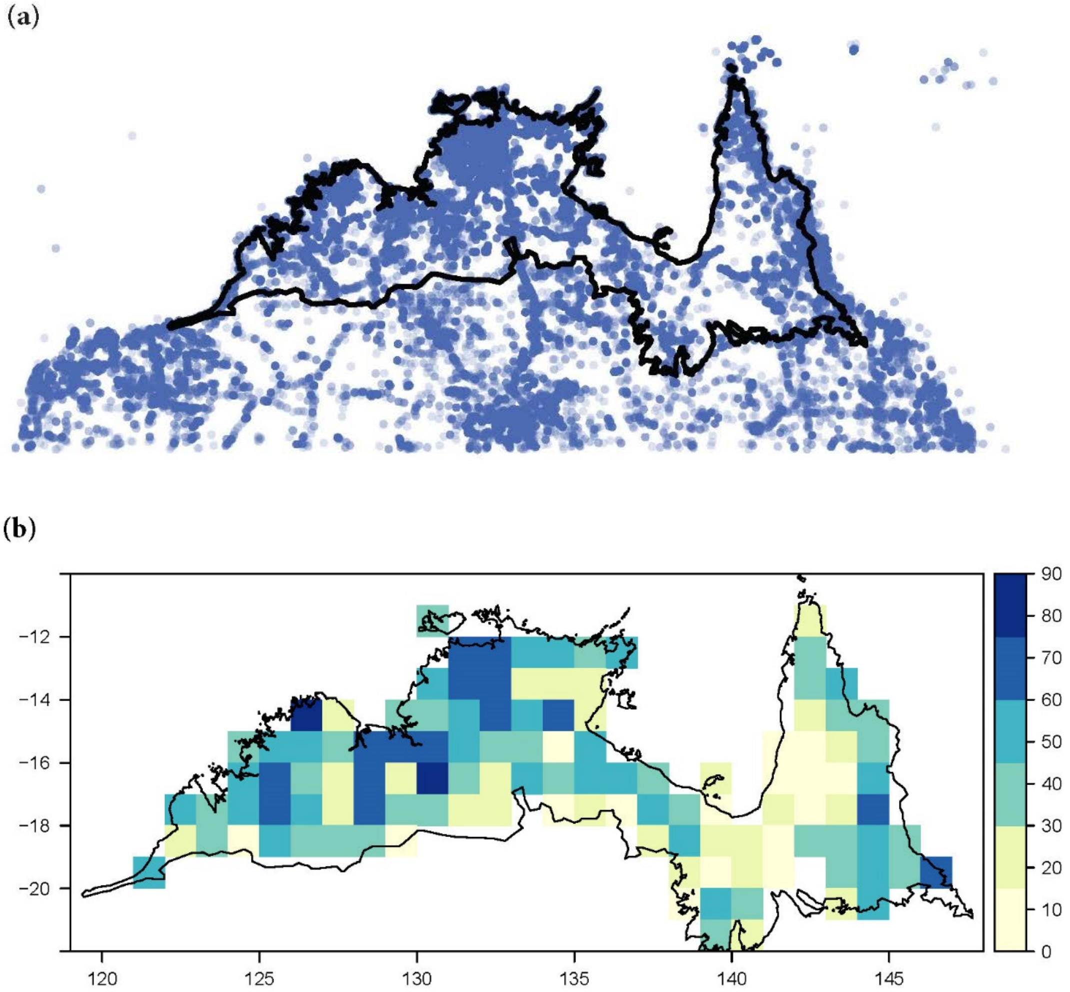

Figure 2. a) Distribution records used in the analyses, with the Australian Monsoonal Tropics outlined in black. b) Chao estimate, calculated in Biodiverse (Laffan et al. 2010), showing estimated regions of undersampling. The scale shows the estimated percentage of species sampled in each grid cell.

Environmental variables for modelling drivers of diversity

We used thirteen environmental variables in our analyses (see Table 1), divided into five categories: data bias, ecological disturbance, habitat variability, limiting conditions, and past conditions. Each variable tests a specific hypothesis relating to diversity in the AMT. The data bias variables test for the impact of sampling methods on our results. Disturbance variables measure the impact of recent habitat disturbance on diversity. Habitat variability tests the importance of variation in the environment, while limiting conditions tests temperature and moisture variables that may provide physiological limitations. Finally, past conditions variables measure the importance of past climate in predicting lizard diversity in the AMT.

All layers were resampled from their original resolution to 0.01 degree using the 'raster' package in R (Hijmans 2016), using bilinear interpolation for continuous variables and nearest neighbor for categorical variables.

We calculated limiting conditions through time using climate data from the HadCM3 paleoclimate model, downscaled to 4.5km resolution (Rosauer et al. 2015). Paleoclimates for 41 time points between the present and 80,000 years ago were used, spaced every 1ky for the first 22kya and then every 2ky. Precipitation variability for each grid cell was measured as the standard deviation of the precipitation of the driest quarter across these time points, meaning a low value would have experienced little change (high stability). Past temperature was measured for the temperature of both the coldest and warmest quarter, summarised across time by taking the most extreme quartile that occurred at a grid cell across time (lower quartile for coldest temperature, upper quartile for warmest temperature). We used quartiles to measure the most extreme conditions, while minimising the effect of any outliers caused by uncertainties in the paleoclimate model.

Finally, we measured collecting bias by calculating the shortest distance from any grid cell to the nearest named locality (town etc.), using the distanceFromPoints function in the 'raster' package and localities from Geoscience Australia (2013).

Table 1. Environmental variables used in our analyses

Variable	**Description**	**Hypothesis**	**Data source**
Data bias			
Distance from towns	Distance to the nearest named locality, a proxy for sampling bias (low value=close to towns, more sampling effort).	Areas near settlements will have higher diversity due to collecting bias (e.g. Schmidt-Lebuhn et al. 2012).	See methods
Region area	Logarithm of the area of the IBRA region (low value=smaller area). Used in linear models only.	Larger areas will have higher diversity, as they will capture more species (leading to higher richness) and a larger proportion of each species' range (leading to higher endemism).	(Department of the Environment 2012)
Disturbance			
Fire frequency	Number of fires affecting the area over 15 years (low value=fire refugia).	Lower fire frequency will be correlated with higher diversity (Andersen et al. 2005).	(Craig et al. 2002). Original raster resolution 0.01°
Land use	Land use of site, ranging from conservation to intensive use (low value=conservation and natural environments).	Areas with less intensive land use will have higher diversity, as they act as refugia from recent changes (Ribeiro et al. 2009).	(Australian Bureau of Agricultural and Resource Economics and Sciences 2011). Original raster resolution 0.01°
Habitat variability			
Geology	Type of geology, including rock type and age (categorical variable). In LMs measured as the number of geology types present in the region (low value=less geologic diversity).	Turnover in geology type will be correlated with species turnover, as some species specialise to specific geology types (Pepper et al. 2008).	(Geoscience Australia 2012)
Elevational range	Range of elevational values occurring in a grid cell (low value=less topographically complex).	High variability in topography will have higher diversity as there are more niches available, more opportunities for isolation between areas, and topographically complex regions act as refugia (Pepper and Keogh 2014, e.g. Powney et al. 2010).	(Hutchinson et al. 2008). Original raster resolution 0.0025°
Limiting conditions			
Aridity	Aridity index, ratio of precipitation to evaporation (low value=very arid).	Low water availability will be correlated with low endemism and high richness (e.g. Powney et al. 2010).	Data downscaled after Reside et al. (2013) to 0.000833° resolution

Soil permeability	Saturated hydraulic conductivity of soil, in mm/h (low value=water moves through soil slowly).	Areas of low soil permeability will have higher diversity, as they hold moisture for lizards to use and supports reproduction through maintaining egg hydration.	(Williams et al. 2012). Original raster resolution 0.01°
Minimum temperature	Monthly minimum temperature (low value=colder temperatures.	Colder temperatures are correlated with lower diversity as species cannot adjust their behaviour to cope with them.	Data downscaled after Reside et al. (2013) to 0.000833° resolution
Maximum temperature	Monthly maximum temperature (low value=cooler temperatures.	Higher temperatures are correlated with lower diversity as they limit activity time.	Data downscaled after Reside et al. (2013) to 0.000833° resolution
Past conditions			
Precipitation variability	Variation in precipitation of the driest quarter over the last 80ky (low value=more stable, less variation).	Areas with low variability in moisture availability through time act as refugia and will have higher endemism.	See methods
Past minimum temperature	Lowest quartile of minimum temperature that has occurred over the last 80ky (low value=colder minimum temperatures).	Areas that have experienced colder temperatures in the past will have less endemism.	See methods
Past maximum temperature	Upper quartile of maximum temperature that has occurred over the last 80ky (low value=cooler minimum temperatures).	Areas that have experienced warmer temperatures in the past will have less endemism.	See methods

Drivers of bioregionalisation

To understand the environmental factors driving our bioregionalisation, we examined community turnover and drivers of alpha and beta diversity in the AMT.

We fitted a generalised dissimilarity model (GDM) to understand drivers of community turnover in the region. GDMs predict compositional turnover or pairwise beta diversity between sites, or record locations, as a function of difference between those sites along environmental gradients, and allow for non-linear relationships (Ferrier et al. 2007). We fitted our GDM using the 'gdm' package in R (Manion et al. 2016) using all variables, with the most parsimonious model identified using backwards elimination.

We calculated corrected weighted endemism (CWE) and species richness for each IBRA region in Biodiverse v3.0, using the presence data (Laffan et al. 2010). CWE is a measure of endemism that corrects for richness, and was calculated for each of the 19 IBRA regions including records and regions from outside the AMT. We also used within-genus phylogenetic endemism (PE) as calculated in Rosauer et al. (2016), averaged across each IBRA region. Due to the lower availability of genetic data, PE was not used for the eastern AMT (Figure 3).

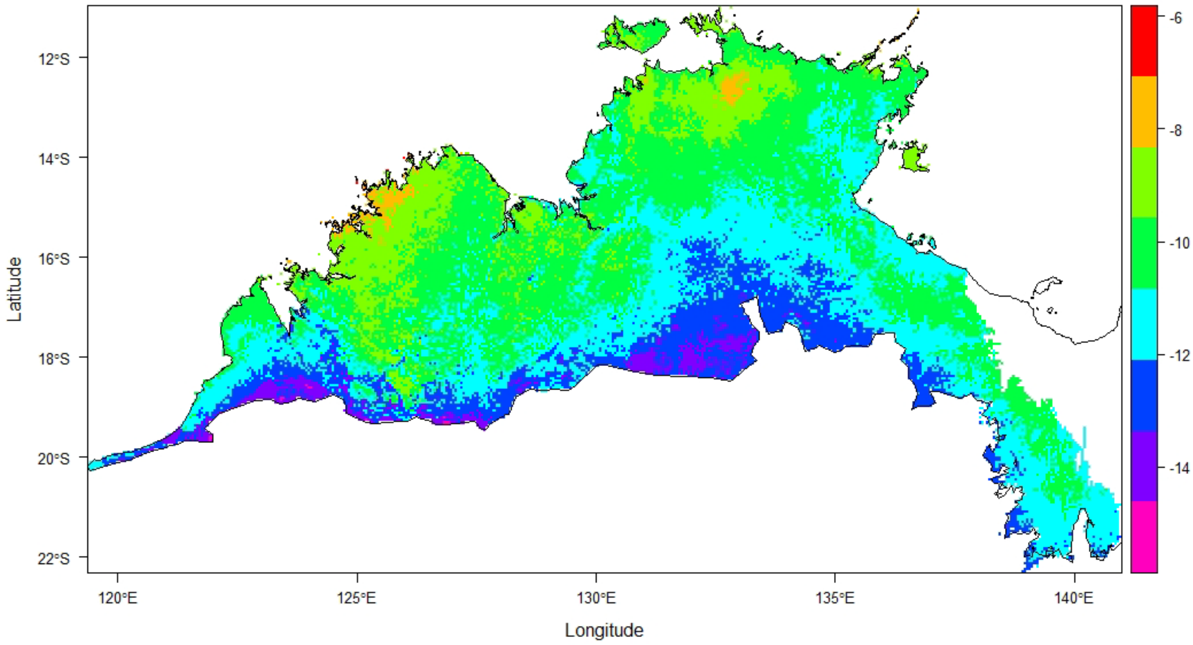

Figure 3. Phylogenetic endemism, as calculated in Rosauer *et al.* (2016). PE is plotted on a log scale, with red showing areas of high PE (for example, in the Kimberley islands). The Australian Monsoonal Tropics is outlined in black.

We then fitted generalised linear models to all three of our diversity metrics across the AMT using the same environmental data used in the GDM fitting, with the best model selected using stepwise model selection by AIC. The linear models were fitted using the 'stats' package in R. Environmental data were averaged across the cells in each IBRA region to get a single value, with the exception of geology type, which was counted to get a measure of geological diversity. The log of the area of each IBRA region was also included as an explanatory variable.

Conservation analysis

Bioregionalisations are important tools for conservation priority setting, with the Australian Government, for example, setting a target that at least 10% of each bioregion be managed for conservation (Natural Resource Management Ministerial Council 2009). To examine the policy and conservation implications of our bioregionalisation, we calculated how much of each province is managed for conservation and compared this to the widely-used WWF bioregionalisation (Olson et al. 2001, also Figure 4). We identified areas managed for conservation using Australian land use data (Australian Bureau of Agricultural and Resource Economics and Sciences 2011), using areas listed as "Nature Conservation" and "Other protected areas including Indigenous uses". As the Mount Isa Inlier IBRA region (MII) is not included in the relevant WWF provinces, we excluded this region from our analyses.

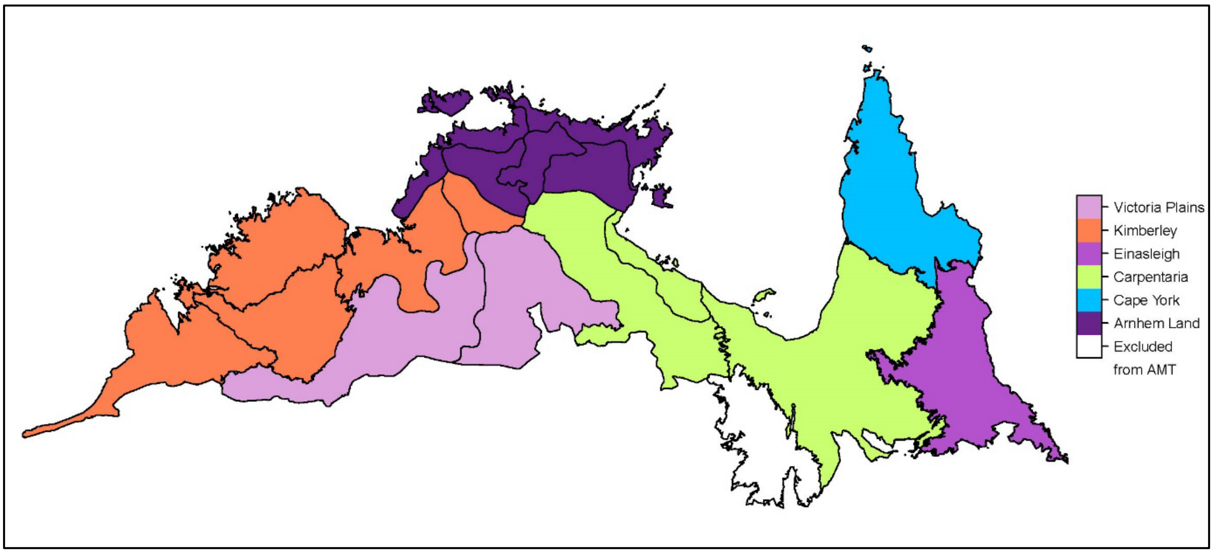

Figure 4. Bioregionalisation of the Australian Monsoonal Tropics used by WWF, as presented in Olson *et al.* (2001).

RESULTS

Bioregionalisation

Based on the distribution of lizard species, we propose four major biogeographic provinces within the AMT, with dendrogram branch lengths showing between 6 and 32% divergence in species composition between them (Figure 5).

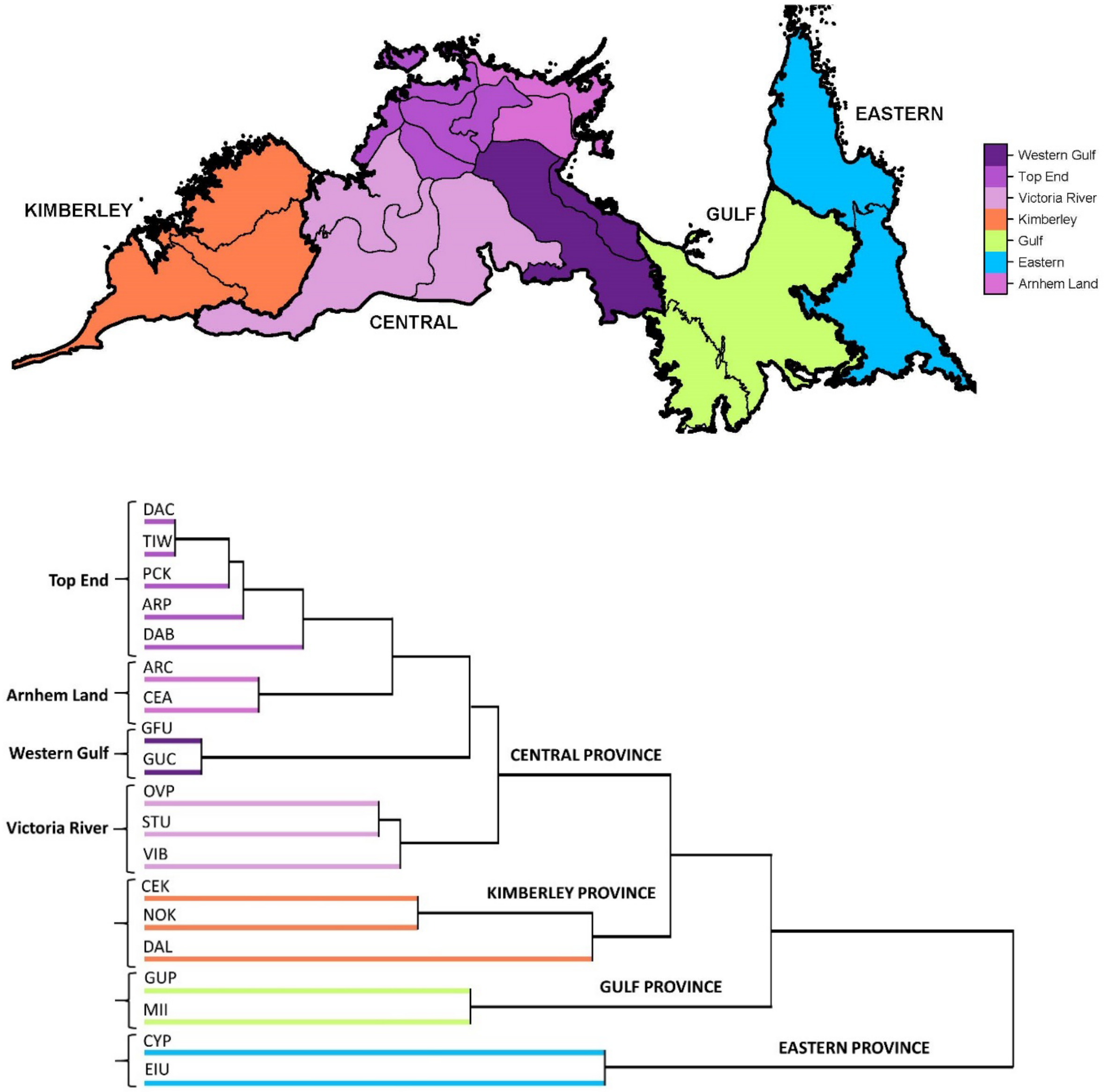

Figure 5. Proposed lizard biogeographic provinces (in capitals) and subprovinces (in lower case) in the Australian Monsoonal Tropics, and the tree based on Simpson's beta dissimilarity matrix the bioregionalisation was based on.

The Eastern province, comprised of the Einasleigh Uplands and Cape York Peninsula IBRA regions, is the most divergent (33%) from the other provinces (node height, Table 2). This is reflected in Table 3, where the highest dissimilarity scores are between Eastern regions and those in other provinces. The Eastern province also contains the highest amount of divergence within a province, with 37% divergence between the two regions. The province comprises 146 species, of which 63 are unique to the province, giving it the second highest endemism score of the four provinces (CWE=0.6). Cape York Peninsula showed the highest endemism of all IBRA regions (CWE=0.5, Figure 6).

The Gulf province has a 24% divergence in species composition from the other provinces, and comprises two IBRA regions with 26% divergence between them. The Mount Isa Inlier and Gulf Plains regions had similarly low endemism scores (CWE=0.2), with the province overall having the lowest richness and endemism scores of the four provinces (richness=120, CWE=0.3).

The Central province comprises four subprovinces that exhibit 7 to 21% divergence from their nearest sister cluster. Overall, the Central province was the most species rich (richness=198) with the highest endemism score (CWE=0.7).

The Victoria River subprovince comprises of the Victoria Bonaparte, Sturt Plateau and Ord Victoria Plain regions. The Victoria River subprovince had the highest species richness of the three subprovinces (richness=150).

The Western Gulf subprovince is quite distinct from the adjacent main Gulf province, with only 60% of its species also occurring in the latter, the majority of these being widespread across the AMT. There are a small number of species restricted to the combined Gulf province and Western Gulf subprovince, mostly geckoes (skinks: *Cryptoblepharus zoticus*, *Ctenotus pulchellus*, *C. striaticeps*; geckoes: *Diplodactylus barraganae*, *Gehyra borroloola*, *G. lauta*, *G. robusta*, and *Oedura bella*). The Western Gulf subprovince comprises two IBRA regions, the Gulf Coastal, and the Gulf Fall and Uplands.

The Arnhem Land and Top End subprovinces are the most closely related. The Arnhem Land subprovince comprises the Central Arnhem and Arnhem Coast IBRA regions, each with 9% divergence. The Top End subprovince comprises five IBRA regions, with 2 to 12% divergence between them. It has the highest endemism score out of the Central Province subregions (CWE=0.5), as well as the highest PE (PE=7.32×10^{-5}). The Top End subprovince comprises Daly Basin, Arnhem Plateau, Pine Creek, Tiwi Cobourg and Darwin Coastal. These were the most similar regions, with the lowest dissimilarity scores between Tiwi Cobourg and the surrounding Top End regions (Table 3).

The Kimberley province comprises the Dampierland, Northern Kimberley and Central Kimberley IBRA regions, with 33 to 35% divergence between them. It contains 150 species, of which 40 are found only in this province. The Kimberley province has the highest PE, particularly the Northern Kimberley region (PE= 1.2 x 10^{-4}).

Table 2. Values of the node height, number of IBRA regions (n), number of unique species (unique), richness, CWE, PE, and approximate area in millions of kilometres^2, for all provinces, subprovinces and regions in the Australian Monsoonal Tropics.

PROVINCES, *subprovinces*		**Node height**	**n**	**Unique**	**Richness**	**CWE**	**PE**	**Area**
Entire AMT			**17**		**348**	**1**	**-**	**1393**
EASTERN		**0.326**	**2**	**63**	**146**	**0.635**	**-**	**238.8**
	EIU	0.367			113	0.184	-	116.3
	CYP	0.367			90	0.272	-	122.6
GULF		**0.239**	**2**	**5**	**120**	**0.335**	**-**	**288.2**
	MII	0.26			77	0.08	1.44 x10^{-5}	67.8
	GUP	0.26			100	0.128	-	220.4
CENTRAL		**0.136**	**12**	**56**	**198**	**0.692**	**3.05x10^{-5}**	**621.6**
Victoria River		0.079	3		150	0.379	1.91x10^{-5}	297
	VIB	0.204			103	0.235	4.08 x10^{-5}	73
	STU	0.187			75	0.065	5.62 x10^{-6}	98.6
	OVP	0.187			122	0.152	1.72 x10^{-5}	125.4
Western Gulf		0.214	2		108	0.211	1.76x10^{-5}	145.6
	GUC	0.045			66	0.085	1.88 x10^{-5}	27.1
	GFU	0.045			105	0.091	1.74 x10^{-5}	118.5
Arnhem Land		0.107	2		74	0.2	3.95x10^{-5}	68
	CEA	0.091			44	0.074	2.58 x10^{-5}	34.6
	ARC	0.091			70	0.109	5.39 x10^{-5}	33.4
Top End		0.071	5		103	0.414	7.32x10^{-5}	111
	DAB	0.127			69	0.071	3.79 x10^{-5}	20.9
	ARP	0.078			75	0.105	9.14 x10^{-5}	23.1
	PCK	0.068			80	0.095	8.54 x10^{-5}	28.5
	TIW	0.024			42	0.063	7.53 x10^{-5}	10.1
	DAC	0.024			84	0.136	7.15 x10^{-5}	28.4
KIMBERLEY		**0.062**	**3**	**40**	**150**	**0.521**	**5.83x10^{-5}**	**244.6**
	DAL	0.357			103	0.148	1.69 x10^{-5}	83.6
	NOK	0.217			100	0.241	1.2 x10^{-4}	84.2
	CEK	0.217			92	0.144	3.61 x10^{-5}	76.8

Table 3. Simpson's beta dissimilarity matrix for IBRA regions in the Australian Monsoonal Tropics. Cells highlighted in purple represent very high values, those with greatest dissimilarity; cells highlighted in yellow indicate very low values, those that are most similar in composition.

	ARC	ARP	CEA	CEK	CYP	DAB	DAC	DAL	EIU	GFU	GUC	GUP	MII	NOK	OVP	PCK	STU	TIW
ARC	-																	
ARP	0.23	-																
CEA	0.09	0.11	-															
CEK	0.51	0.49	0.45	-														
CYP	0.66	0.72	0.66	0.82	-													
DAB	0.30	0.20	0.18	0.39	0.72	-												
DAC	0.23	0.11	0.14	0.5	0.75	0.13	-											
DAL	0.53	0.51	0.45	0.30	0.82	0.41	0.5	-										
EIU	0.64	0.68	0.66	0.78	0.37	0.65	0.70	0.81	-									
GFU	0.19	0.23	0.14	0.43	0.72	0.16	0.29	0.50	0.69	-								
GUC	0.30	0.36	0.25	0.44	0.65	0.36	0.33	0.47	0.61	0.05	-							
GUP	0.53	0.55	0.5	0.62	0.56	0.49	0.56	0.66	0.33	0.43	0.36	-						
MII	0.5	0.52	0.45	0.51	0.69	0.51	0.52	0.51	0.49	0.23	0.36	0.26	-					
NOK	0.46	0.45	0.39	0.22	0.8	0.33	0.49	0.41	0.81	0.51	0.45	0.68	0.57	-				
OVP	0.39	0.36	0.27	0.22	0.79	0.23	0.39	0.24	0.78	0.31	0.30	0.59	0.42	0.35	-			
PCK	0.21	0.08	0.09	0.44	0.76	0.10	0.09	0.48	0.71	0.21	0.32	0.58	0.53	0.44	0.33	-		
STU	0.39	0.39	0.27	0.4	0.76	0.22	0.32	0.36	0.68	0.15	0.35	0.44	0.45	0.4	0.19	0.32	-	
TIW	0.14	0.05	0.33	0.43	0.55	0.07	0.02	0.40	0.57	0.17	0.33	0.45	0.45	0.33	0.26	0.05	0.19	-
VIB	0.29	0.28	0.23	0.22	0.78	0.13	0.29	0.41	0.74	0.30	0.27	0.57	0.43	0.3	0.19	0.24	0.21	0.19

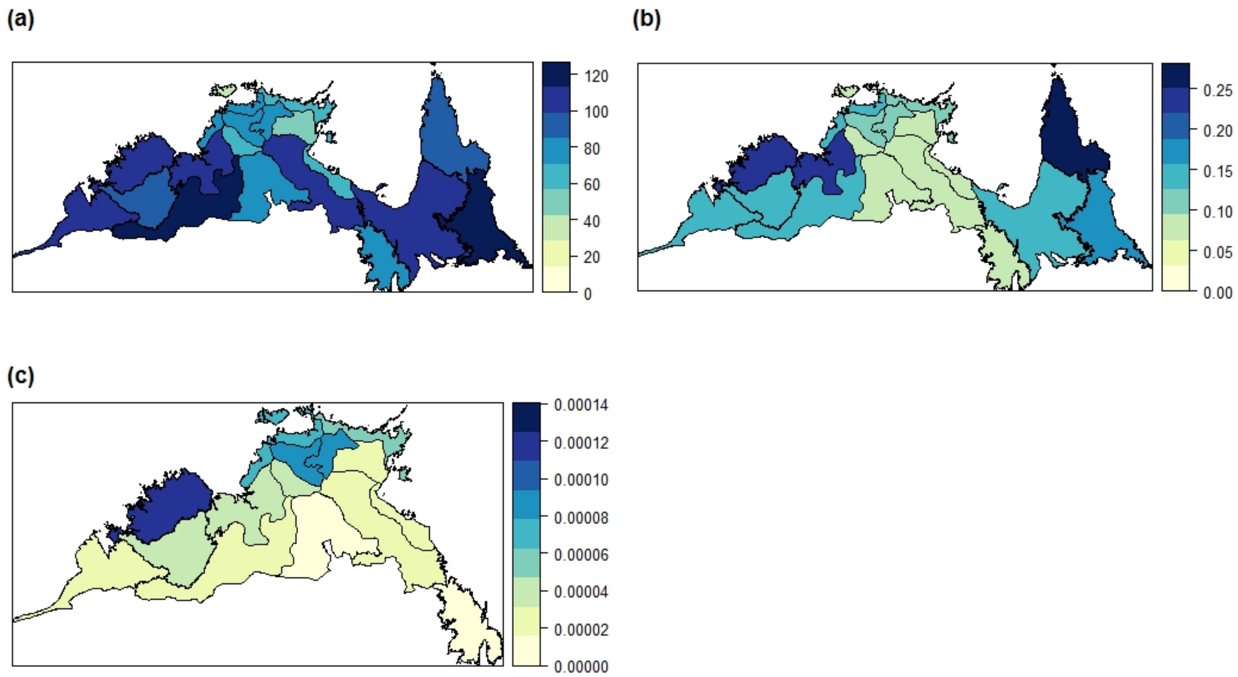

Figure 6. Values for each IBRA region of (a) species richness, (b) corrected weighted endemism and (c) phylogenetic endemism for lizards in the Australian Monsoonal Tropics.

Drivers of bioregionalisation

Our GDM explained 23% of compositional turnover (Figure 7), similar to other studies using GDM on presence-only data (e.g. Rose et al. 2016). Geographic distance was the most important variable, and the discussion hereafter refers to the turnover that was independent of geographic distance.

Compositional turnover was best explained by past minimum temperature, current maximum temperature and elevational range, with distance from towns, fire frequency, and geology type also important (Table 4). The predicted spatial variation broadly aligns with our identified provinces (Figure 7), separating the Kimberley, Central, Gulf and Eastern regions, and indicating the Victoria River and Gulf regions may act as transition zones between biomes. It also identifies similarities in lizard communities between the Top End and Cape York areas, perhaps reflecting past connectivity. These regions were connected as recently as 10,000 years ago, and previous research has indicated that historical connectivity may be more important than current connectivity in explaining divergence patterns (Peñalba et al. 2019).

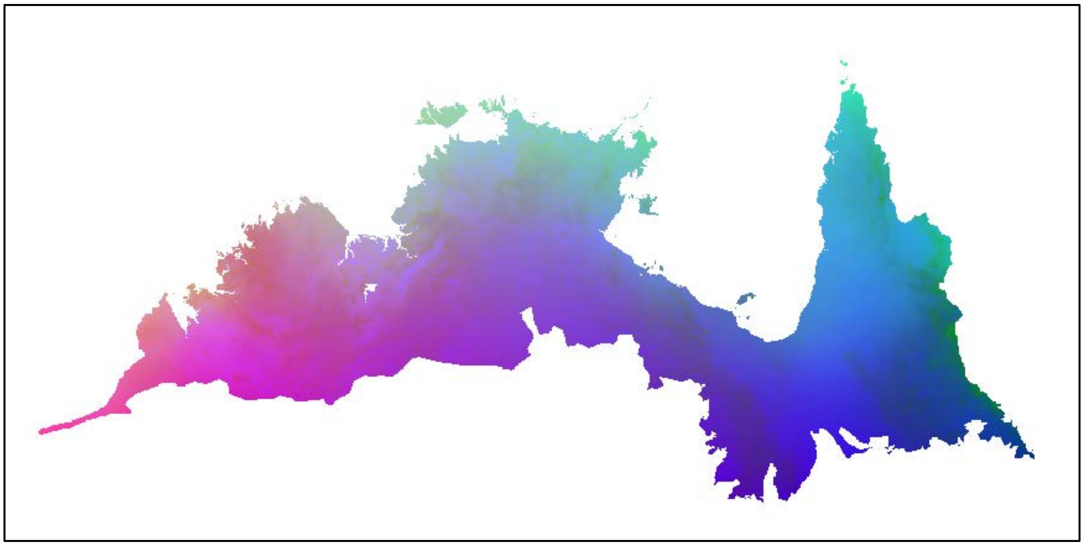

Figure 7. Predicted spatial variation in lizard species composition, calculated from the GDM for the entire AMT. Colours represent gradients in species composition derived from transformed environmental predictors. Locations with similar colours are expected to contain similar lizard communities.

The drivers of alpha and beta diversity differ greatly, with the two measures of beta diversity (CWE and PE) showing more similarity (Table 4).

Table 4. Results for the models exploring the drivers of our bioregionalisation of the AMT. Variables are shown for the best model fitted with all variables available. Brackets indicate the direction of the correlation (for linear models) or the weight of the variable (for GDM); significant variables are denoted by *. Deviance explained is R^2 for linear models.

		Richness	**CWE**	**PE**	**GDM**
Deviance explained best model		**83.38%**	**83.45%**	**86.62%**	**22.83%**
Geographic distance		NA	NA	NA	* (32.1)
Distance from towns	*Data bias*	-	(+)	(+)	* (0.63)
Region area	*Data bias*	-	* (+)		-
Fire frequency	*Disturbance*	-	-	(+)	* (0.22)
Land use	*Disturbance*	-	* (+)		-
Geology type	*Habitat variability*	* (+)	-		* (0.23)
Elevational range	*Habitat variability*	-	* (+)	* (+)	* (2.24)
Aridity	*Limiting conditions*	* (-)	-	(-)	-
Soil permeability	*Limiting conditions*	* (-)	-	* (-)	-
Minimum temperature	*Limiting conditions*	-	* (+)	* (-)	-
Maximum temperature	*Limiting conditions*	-	-	-	* (3.6)
Precipitation variability	*Past conditions*	* (+)	-	-	-
Past minimum temperature	*Past conditions*	-	-	-	* (3.23)
Past maximum temperature	*Past conditions*	(-)	-	* (-)	-

Richness was best explained by geologic diversity (positive relationship), precipitation variability (positive), maximum temperature over time (negative), aridity (negative, so increasing in more arid regions) and soil permeability (negative), with all except maximum temperature over time being significant. This means that regions that are more arid, with moisture holding soils, greater variability in past precipitation and greater variation in geology type tend to contain more species (see Figures 6 and 8).

Minimum temperature and elevational range were significant for both beta diversity measures, although the direction of the relationship with minimum temperature was opposite. CWE was also explained by land use (positive) and region area (positive), while PE was also explained by maximum temperature over time (negative relationship) and soil permeability (negative). This means that higher PE is found in areas with complex topography, moisture holding soils and cooler temperatures. Higher endemism is found in larger areas with more human disturbance, greater topographic variability and warmer minimum temperatures.

Overall, elevational range was significant in three of our four models, with geology, soil permeability and minimum temperature significant in half the models (Figure 8).

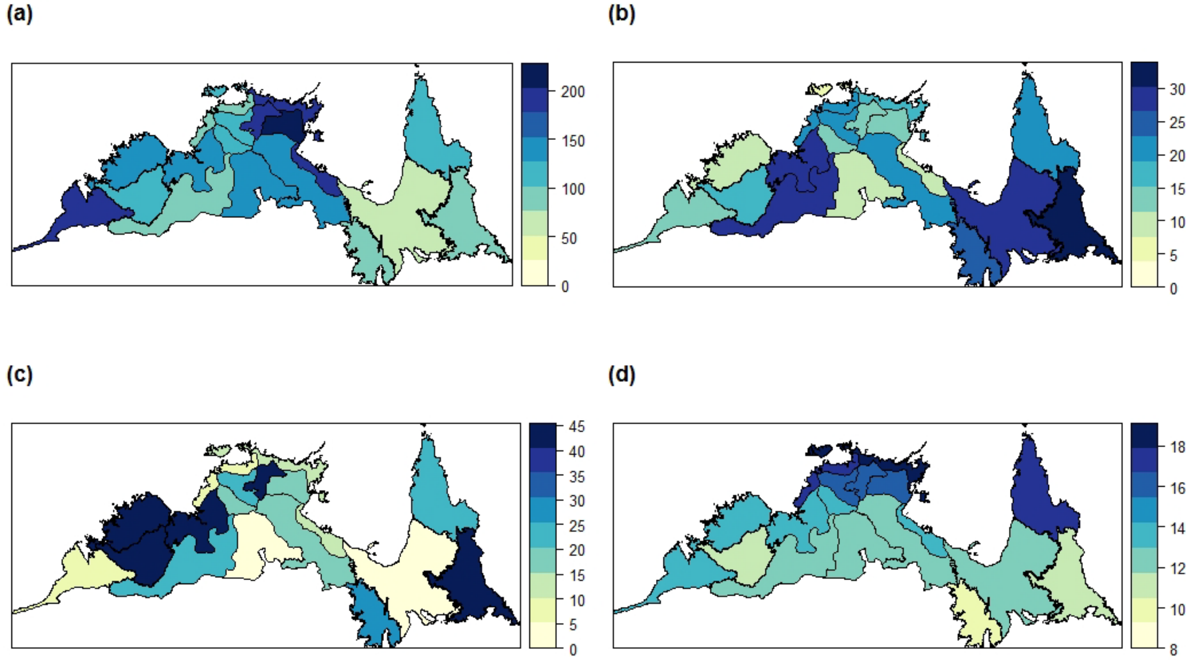

Figure 8. Visual representation of the variables most important in predicting lizard diversity in the AMT: (a) soil permeability (low values indicate less permeable), (b) the number of geological types in each region (low values indicate less geologically complex regions), (c) elevational range (low values indicate less topographically complex regions), and (d) minimum temperature (low values indicate cooler environments).

Conservation

When using our proposed bioregionalisation, the percentage of each province or subprovince conserved ranged from 3% to 93% (Table 5), with one province (the Gulf) below the National Reserve System's 10% target (Natural Resource Management Ministerial Council 2009). This was true whether we included the IBRA region MII, or excluded it to match the WWF bioregions. When using the widely-used WWF bioregionalisation, 11% to 81% of each province is managed for conservation, with all provinces above the target. Using our provinces, the Kimberley (CEK, NOK and DAL) and Gulf (GUP) regions have less of their area managed for conservation than when using the WWF bioregions.

Table 5. Percentage of each province or subprovince managed for conservation, shown using both our proposed provinces and the system used by WWF.

Province	% Conserved	IBRA regions included
PROPOSED		
Eastern	19.86%	CYP, EIU
Gulf	2.68%	GUP (& *MII)*
Western Gulf	40.28%	GFU, GUC
Arnhem Land	92.95%	ARC, CEA
West Top End	60.76%	DAC, TIW, PCK, ARP, DAB
Victoria River	25.38%	OVP, STU, VIB
Kimberley	20.40%	CEK, NOK, DAL
WWF		
Cape York Tropical Savanna	35.10%	CYP
Einasleigh Uplands	10.59%	EIU
Carpentaria Tropical Savanna	17.53%	GUC, GFU, GUP
Arnhem Land Tropical Savanna	80.97%	ARP, PCK, TIW, DAC, CEA, ARC
Victoria Plains Tropical Savanna	19.07%	STU, OVP
Kimberley Tropical Savanna	23.13%	DAL, NOK, CEK, VIB, DAB

DISCUSSION

Proposed bioregionalisation of the AMT for reptiles

We identified four broad biogeographic provinces within the Australian Monsoonal Tropics: the Kimberley, Central, Gulf and Eastern. These align with the widely accepted regions of the Kimberley Plateau, Arnhem Land and Cape York Peninsula (Ebach et al. 2013), although differ from those used in policy such as the WWF bioregionalisation (Olson et al. 2001).

The deepest split in our bioregionalisation was between the Eastern province and the westerly areas. This split is widely supported in biogeographic studies of the area across multiple groups (e.g. González-Orozco et al. 2014, Gambold and Woinarski 1993, Cracraft 1991, Braby

2008). The area we define as the Gulf Province is well recognised as a barrier between the eastern Cape York region and the Top End and Kimberley regions (Kearns et al. 2011, Edwards et al. 2017, Catullo, Lanfear, et al. 2014, Lee and Edwards 2008). This province aligns with the Carpentarian Basin and is an arid intrusion, possibly due to rain shadows from both the Great Dividing Range to the east and the Arnhem Plateau to the west (Edwards et al. 2017). It is also geologically distinct from other regions in the AMT, being largely flat with treeless clay-based soils. The strength of the barrier has varied across glacial cycles (Kearns et al. 2011), with the area existing as a major lake as recently as 10,000 years ago (Chivas et al. 2001). As many bioregionalisations of the AMT recognise only the three major provinces, the Gulf barrier has been variously placed within the Central province (Shelley et al. 2019) and the Eastern province (e.g. González-Orozco et al. 2014), but our analysis suggests it is distinct enough to be classified as its own province. Alternatively, the Gulf could be acting as a 'leaky barrier' (Eldridge et al. 2014), providing a transition zone between the Eastern and Central/Kimberley regions. The transition zone hypothesis is supported by the low endemism of the region and the mixing of communities as indicated by the GDM.

The other major barrier recognised in our biogeographic classification is that between the Kimberley and Central provinces. This boundary is generally placed either on the edge of the Kimberley Plateau, placing the Victoria River and Ord Arid Intrusion within the Central province, or on the edge of the Ord Arid Intrusion, placing it and the Victoria River region within the Kimberley Province. The latter pattern has been found across many groups, including plants (Gonzalez-Orozco 2014), some genera of reptiles (Woinarski 1992, Oliver 2019), fish (Shelley 2019), and mammals (Potter 2012). However our results for reptiles support the boundary occurring at the Durack Range, at the edge of the Kimberley Plateau, as also found in frogs (Catullo 2014). This suggests that the factors impacting turnover differ greatly between groups, with the lizard communities found on the sandstone plateau being highly distinct to those found in the lowlands. The varying placements of the Victoria River district within bioregionalisations is most likely due to this region acting as a transition zone, including Kimberley, Central and arid species. This hypothesis is supported by the high species richness of the area and the GDM results. It is also important to note that the province boundaries identified in our analysis are constrained by our use of IBRA regions, so the true point of turnover may lie within the borders of an IBRA region.

The subprovinces identified in the Central province are also supported by findings in other groups, with the split between the West Top End and East Top End aligning with the edge of the

Arnhem Land Plateau. This has been identified as a barrier in numerous other groups (e.g. Edwards et al. 2017, Oliver et al. 2019), with the Arnhem escarpment containing a unique assemblage of species (e.g. Catullo, Keogh, et al. 2014, Bowman et al. 2010, Slatyer et al. 2007), perhaps acting as a refugium (Ford 1978). The split between the southern and northern areas of the Central province has also been previously identified (Olson et al. 2001, Whitehead et al. 1992), although not as strongly as the east/west split, and is likely due to the aridity gradient.

Linking biodiversity patterns to the environment

Our bioregionalisation was calculated using similarities in lizard communities, meaning understanding what is driving diversity patterns can help us understand the bioregions identified.

As has been found in many studies, we found the drivers of diversity patterns to vary considerably depending on the type of diversity being measured. Overall, habitat variability and limiting conditions were more important than data bias measures or past conditions. The four variables important across most of our measures of diversity (richness, corrected weighted endemism, phylogenetic endemism, and community turnover) were elevational range, geology type, soil permeability and minimum temperature, with the predictions from Table 1 largely supported.

Habitat complexity generally has been linked to species richness in groups within the AMT (e.g. Woinarski et al. 2006, also Hortal et al. 2009). Beta diversity is often linked to topographic variability. These more complex regions generally contain more niches for species to occupy, isolate populations promoting diversification, and are more likely to act as microrefugia (e.g. Crisp et al. 2001, Irl et al. 2015, Smyčka et al. 2017). Many topographically complex areas in the AMT have been identified as potential refugia (e.g. Pepper and Keogh 2014, Byrne et al. 2008, Fujita et al. 2010, Potter et al. 2014, Potter et al. 2012, Catullo, Lanfear, et al. 2014, Noble et al. 2017, Woinarski et al. 2006). Variation in geology also creates more niches for taxa, with some lizard species specialising to particular geology types (Oliver et al. 2017).

Limiting conditions relate to the physiological constraints of taxa, and hence are more dependent on the group being studied than habitat complexity variables. Lizard activity times and reproductive success are constrained by ambient temperature (Schall and Pianka 1978, Adolph and Porter 1993), and previous studies have shown lizards are more diverse in hot environments (Powney et al. 2010, Saladin et al. 2019). This supports our finding that the higher rates of endemism are found in regions with milder minimum temperatures. In contrast, higher rates of PE are found in areas with colder minimum temperatures. Short-range endemic species tend to be constrained by cooler past temperatures, while widespread species are more constrained by current cold conditions (Araújo et al. 2008, Jansson 2003). This suggests that regions with cooler minimum temperatures tend to harbour species with restricted ranges, and thus higher endemism, while more widespread species are able to track climate changes and move to regions with milder temperatures. Another possible explanation is that the regions with cooler minimum temperatures border the Australian Arid Zone. This means they may contain species that, although widespread in the arid zone, are phylogenetically distinct within the AMT context. Calculating PE at a larger spatial extent may remove this correlation.

Although not as important across diversity patterns, the relationships between diversity and both land use and precipitation variability are interesting to examine. CWE is highest in areas with increased levels of human disturbance. This could be caused by human disturbance reducing the current ranges of species that occur in these areas, thus inflating the endemism values, or alternatively by an unmeasured third variable (that is, that humans prefer environments that also support higher lizard endemism).

The link between species richness and greater variability in past rainfall is also interesting, as previous work has linked species richness with greater stability (and thus less variability), within both reptiles (Araújo et al. 2008, Graham et al. 2006, Werneck et al. 2012, Rosauer et al. 2015) and other groups (e.g. Boyer et al. 2016, Fordham et al. 2012). However, new research suggests that while temperature stability over the Quaternary is important for species richness, precipitation instability may also be important (Araújo et al. 2008, Brown et al. 2020), through promoting niche partitioning and habitat expansion and contraction (Brown et al. 2020). Additionally, the patterns we observed could be due to biome interactions, with species from the arid zone mixing with mesic species.

Applications

Bioregionalisations are widely used to help focus conservation efforts, including identifying regions of high endemism or threat, discussions with industry, and reserve design and prioritisation (reviewed in Olson et al. 2001). Our analysis highlights the importance of accurate bioregionalisations when making conservation and policy decisions. When using previous bioregionalisations, such as the WWF bioregions (Olson et al. 2001), all provinces meet the National

Reserve System target of at least 10% managed for conservation. In contrast, when using our proposed provinces the Gulf province does not meet this target, meaning it should be a high priority for conservation efforts.

Our bioregionalisation was conducted using lizard occurrence data. It is not yet clear how well one taxa can be used to represent others, with conflicting results (e.g. Myers et al. 2000, Burgess et al. 2000, Powney et al. 2010, van Jaarsveld 1998). Our provinces agree broadly with recent work in other taxonomic groups, but other research on Australian lizards suggest the patterns and drivers of diversity are very different to those in other groups (Powney et al. 2010). This suggests the need for further research into other groups to enable comparisons, and perhaps unification, between different bioregionalisations.

Additionally, while our analysis contains current taxonomic and distribution data, it is important to note that work in the AMT is still being undertaken. Taxonomic changes may cause changes in the biogeographic provinces we identified. In particular, ongoing genetic work is uncovering cryptic speciation across many genera, including *Diporiphora* (Melville et al. 2019), *Gehyra* (Oliver et al. 2020) and *Oedura* (Laver et al. 2018). The areas of high beta diversity identified in our analysis should be used to guide future survey and taxonomic work, as they are likely to harbour new small-range species.

CONCLUSION

In this paper we conducted the first major revision of the biogeography of AMT lizards in 25 years, taking advantage of the large increase in taxonomic, survey and environmental data available. We found the AMT comprises four major provinces, the Kimberley, Central, Gulf and Eastern, with these differences driven largely by current climate and habitat variability. While our findings largely align with biogeographic analyses of other groups in the region, it differs substantially from bioregionalisations used in policy. Our analysis highlights the importance of accurate bioregionalisations when making conservation decisions, and points to a need for increased work in the region to enable unification between the bioregions of different taxa.

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CJM led conceptualisation, data analysis and writing. DFR and CCM contributed substantial conceptual and editorial advice. All authors contributed to writing and approved the final manuscript.

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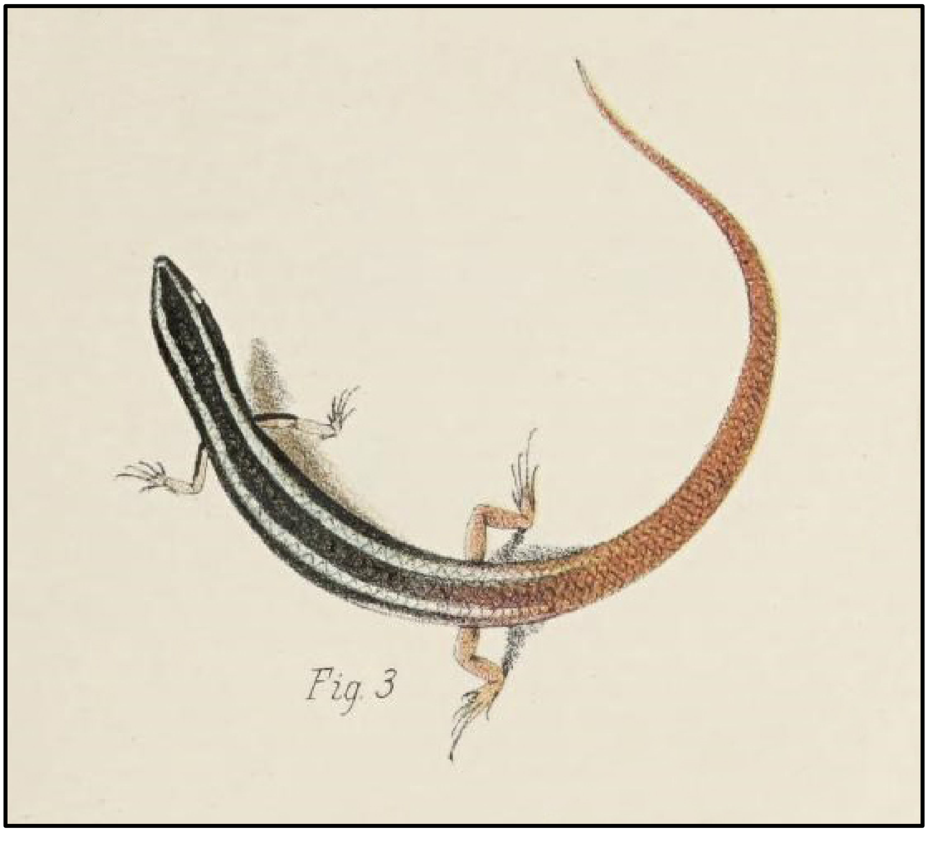
CHAPTER 4

Refugia in the Kimberley across spatial and temporal scales



Ablepharus lineo-ocellatus var. ruficaudus, now *Morethia ruficausa,* from *Report on the work of the Horn Scientific Expedition to Central Australia*, 1896

Refugia in the Kimberley across spatial and temporal scales

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ABSTRACT

Stability and refugia are widely used as predictors of diversity, however there is little research into impacts of the scale at which stability is measured. Here we examine stability across different metrics and spatial and temporal scales to see which best predicts phylogenetic endemism in the Kimberley, in north western Australia. We found that spatial scale has a larger impact on results than temporal scale, and that phylogenetic endemism increases with past variability. We also identified novel refugia in the region, including the central and south west Kimberley and the Durack Range.

INTRODUCTION

Understanding what has driven the development of the patterns of biodiversity we see today is a central question of biogeography and macroecology. One possible driver of diversity hotspots is refugia: areas of stability that allow groups to persist when the surrounding landscape becomes unsuitable. Refugia have been linked to hotspots of richness, endemism and genetic diversity (e.g. Araújo et al. 2008, Rosauer et al. 2015, Fordham et al. 2016, Carnaval et al. 2009, Gavin et al. 2014), and have also been proposed for conservation planning to protect taxa from future climate change (Keppel et al. 2015, Reside et al. 2013, Keppel and Wardell-Johnson 2012). Refugia exist on a continuum from landscape level macrorefugia—large areas where the general climate is favourable over time—to small microrefugia, which provide microclimates in which taxa persist (e.g. Rull 2014, Ashcroft 2010). Many studies on refugia have occurred at global scales, or in biomes with clear climatic boundaries such as rainforests. Modelling refugia at finer geographic scales within landscapes with more subdued topography and climatic gradients is more challenging.

The Kimberley, in north western Australia, is a hotspot of diversity, with large numbers of endemic species and radiations across groups including plants, fish, mammals, and invertebrates, particularly snails (Gibson and McKenzie 2012, Criscione et al. 2012, Köhler and Criscione 2013, Rosauer et al. 2016, Shelley et al. 2019). Reptiles are particularly diverse, with high levels of cryptic diversity (Pepper et al. 2011, Oliver et al. 2012, Fujita et al. 2010, Moritz et al. 2016, Maddock et al. 2015, Kealley et al. 2018, McKenzie et al. 1991, Gibson et al. 2013). The Kimberley is part of the Australian Monsoonal Tropics biome, and is a seasonally dry landscape with summer monsoon rainfall. Temperatures are high, with monthly averages between 25°C and 35°C (Waples 2007). The region's landscapes are highly heterogenous, with steep escarpments, alluvial plains, mound springs, gorges and rivers (Pepper and Keogh 2014). The topography is most complex in the west and south, with the west Kimberley containing some of the most rugged topography in Australia (Woinarski et al. 2007), although it has moderate elevation overall, with a maximum of 906m.

Many have proposed that the Kimberley region as a whole acted as a refugium from Pleistocene aridification (Byrne et al. 2008, Pepper et al. 2011), with others proposing smaller refugia within the region. For example, increasing biodiversity work across northern Australia has shown endemism hotspots in the Mitchell Plateau and other topographically complex areas of the Kimberley (e.g. Crisp et al. 2001, McKenzie et al. 1991, Slatyer et al. 2007, Doughty et al. 2011, González-Orozco et al. 2011, Maslin et al. 2013, Cameron 1992), with hotspots of phylogenetic endemism in the Kimberley islands and the southern karst limestones (e.g. Catullo et al. 2014, Moritz et al. 2016, Oliver et al. 2017, Potter et al. 2012, Afonso Silva, Santos, et al. 2017, Gibson et al. 2013). Many have suggested that these areas have acted as refugia, and have been important in driving the accumulation of biodiversity (Potter et al. 2014, Catullo et al. 2014, Pepper and Keogh 2014, Byrne et al. 2008, Pepper et al. 2011, McKenzie et al. 1991, Oliver et al. 2017). The importance of microrefugia, such as small boulder outcrops or gorges, has also been raised (Köhler and Criscione 2013), as these protect populations and allow metapopulations to persist in otherwise unsuitable landscapes.

Increasing aridification in the Kimberley began in the late Pleistocene, and has been followed by several changes in monsoon intensity, particularly in the last 30ky (Pepper and Keogh 2014, Reeves et al. 2013, Williams et al. 2009). The last glacial maximum (LGM, 18-22kya) was characterised by further aridification and cooler temperatures (Fitzsimmons 2013), particularly in the lowland regions (Reeves et al. 2013). The monsoon reactivated approximately 15kya (Fitzsimmons et al. 2013), followed by long periods of cool dry climate in the early Holocene, with increasing local aridity and variability in the monsoon in the late Holocene (Reeves et al. 2013). Sea levels rose in the Holocene, reaching their present level approximately 6kya (Lees 1992). Population genetic analyses of lizards indicate species in northern Australia experienced large range fluctuations during this late Pleistocene to Holocene period (Potter et al. 2018, Afonso Silva, Bragg, et al. 2017). This large amount of climatic change suggests refugia were important in allowing species to persist and could have shaped current diversity patterns as seen in other systems.

Refugia can be identified using a variety of methods, including analyses of fossils and genetics, but the most commonly used method is to identify areas of stability. There are many methods of measuring stability, and McDonald-Spicer et al. (2019; Chapter 1) hypothesised that the method chosen will impact on the results and biological interpretation of any analyses. Previous work has tested the impact of the chosen method of summarising stability (see Chapter 2), however no studies on stability have systematically varied the temporal and spatial scale on which stability is measured. This is despite many studies indicating the scale of macroecological studies is important to consider (Wiens 1989, Hortal et al. 2010, Ashcroft et al. 2012, Chave 2013).

Here, we use two methods of measuring stability (standard deviation and geometric mean of suitability in species distribution models) at two different spatial and temporal scales, to see which best predicts phylogenetic endemism (PE) in Kimberley lizards. PE is a measure of endemism incorporating phylogenetic relationships, weighting taxon occurrences by both unique branch length and geographic restriction (Rosauer et al. 2009). We attempt to identify microrefugia using fine spatial scale data, and larger, mesoscale refugia using data at a coarse spatial scale. We also look at refugia from Holocene aridification by measuring stability at 1ky intervals over the last 12ky, and across a full glacial cycle by measuring at 2ky intervals over the last 80ky. We predict that analyses using the fine spatial scale will identify more pockets of stability in the arid sections of the Kimberley than those using the coarse spatial scale. Additionally, we predict that stability across the Holocene will better predict current diversity than across the Pleistocene due to its finer temporal resolution (e.g. Fordham et al. 2018).

MATERIALS AND METHODS

Spatial and taxonomic extent

The Kimberley lies in north western Australia and is here defined as the union of the Interim Biogeographic Regionalisation for Australia (IBRA) regions Northern Kimberley, Central Kimberley and Dampierland (as defined by reptile distributions in Chapter 3).

The region is bordered by the Tanami and Great Sandy deserts to the south, the Ord Arid Intrusion and Top End to the east, the Timor Sea to the north, and the Indian Ocean to the west. Major geographic features of the region include the Mitchell Plateau, Devonian Reef System, King Leopold Range, and the Durack Range, and the towns of Fitzroy Crossing and Broome (Figure 1). Approximately 20% of the region is managed for conservation, including national parks, private land and Indigenous Protected Areas.

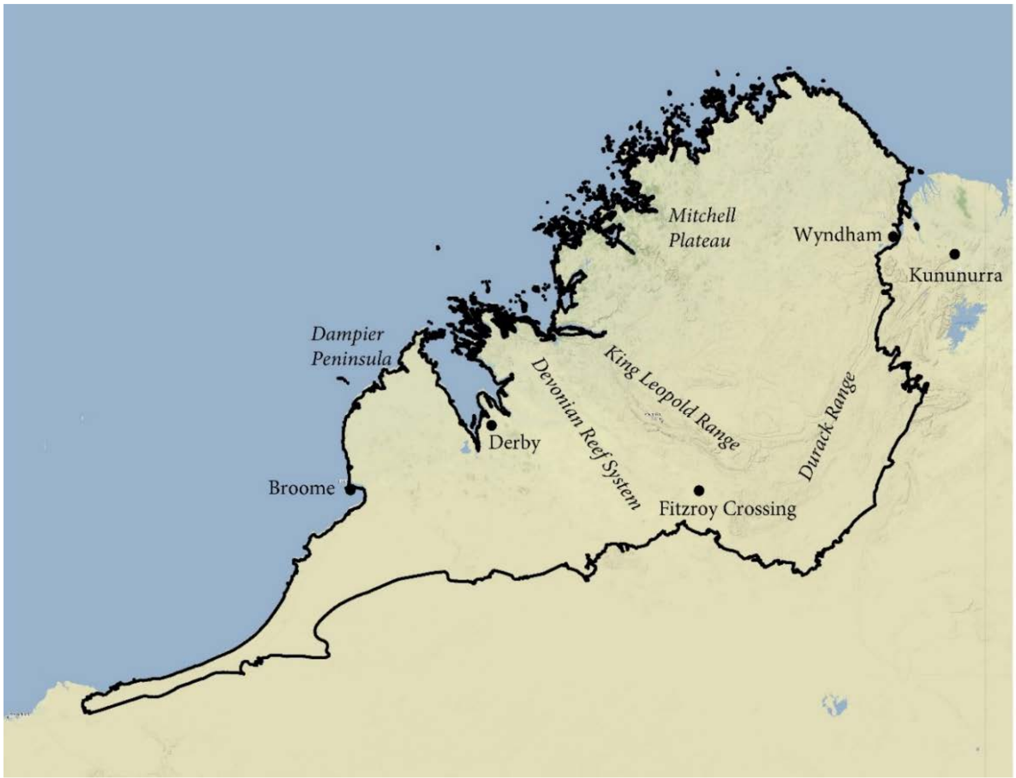


Figure 1. Major geographic features of the Kimberley, with the study area outlined in black.

We focus on lizards for two key reasons. Firstly, increasing field and genetic work in the Kimberley has identified patterns of cryptic speciation and high levels of endemism in lizards. Secondly, tropical lizards are highly sensitive to climate and have low dispersal abilities, meaning their current distributions are strongly shaped by past climates (Araújo et al. 2008, Deutsch et al. 2008, Sinervo et al. 2010). Our analysis includes 47,941 records for 150 species, based on data from the Atlas of Living Australia, recent publications and our own fieldwork (see Chapter 3 for details). We included only species identified as occurring within the Kimberley biogeographic province, but for the SDMs used distribution records for these species from a broader region (Figure 2). We were not able to explore spatial variation in species richness or endemism due to the sampling bias in the region, with many records collected along roads or to the south and many grid cells having few or no samples (see Chapter 3). This necessitates the use of modelled distributions to estimate richness, and so using these estimates in our models would introduce circularity into our analyses.

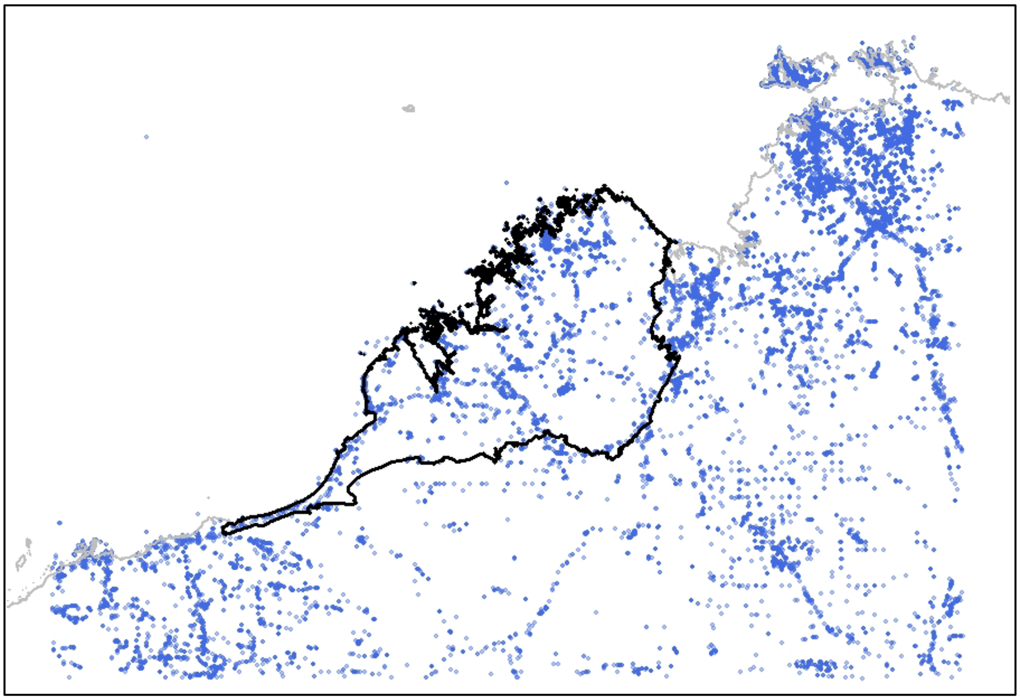


Figure 2. Spatial records used in our analyses. Blue points indicate species records, the Kimberley is outlined in black.

Phylogenetic endemism

Phylogenetic endemism measures to what extent phylogenetic lineages are geographically restricted. Here, we use PE calculated by Rosauer et al. (2016) (Figure 3). This was calculated for the Kimberley and Top End at 0.01 degree resolution, with major intraspecific mtDNA lineages from the genera *Carlia, Ctenotus, Cryptoblepharus, Eremiascinus, Glaphyromorphus, Morethia, Gehyra, Heteronotia, Oedura,* and *Pseaudothecadactylus*. Not all species included in the stability analyses were also included in the PE analysis, due to limited genetic data. The uncertainty in the lineage range models was carried throughout the PE calculation.

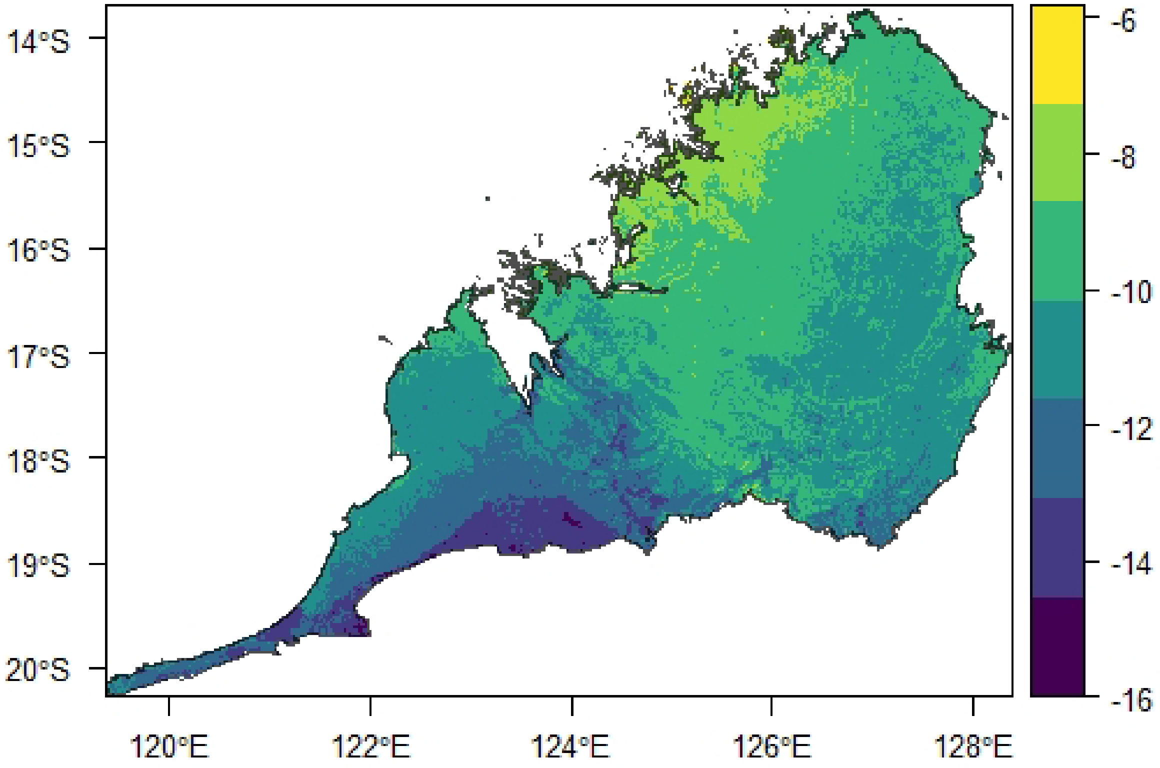


Figure 3. Phylogenetic endemism in the Kimberley, plotted on a log-scale. Yellow areas, such as the islands in the north, have high PE while blue areas have low PE.

Scales of the analysis

To identify refugia, we measured stability at two different spatial and temporal scales.

Our fine spatial data was 0.01 degree, or 1km resolution, with values derived from 90m resolution data. The 90m data was aggregated to 0.01 degree due to computational constraints. This scale enabled us to identify microclimates caused by topography. The coarse spatial data was at 0.04 degrees, or 4.5km resolution, enabling us to identify landscape-level patterns.

Stability measures at a small temporal scale captured refugia from Holocene variability. We calculated these using data from 12kya to the present day at 1ky intervals, the finest temporal resolution available in the dataset. This time period was chosen to reflect the strong fluctuations in climate and sea level that occurred in the Holocene, supported by evidence of range shifts in northern Australian *Carlia* skinks (Potter et al. 2018). Those at the large temporal scale used data from 80kya to the present day, at 2ky intervals, measuring refugia through glacial cycles. These temporal scales differ in both extent (Holocene vs Pleistocene) and resolution (1ky vs 2ky).

This gave a total of four scales that stability was measured at:

- Fine spatial resolution, small temporal scale (fineHolocene)
- Fine spatial resolution, large temporal scale (finePleistocene)
- Coarse spatial resolution, small temporal scale (coarseHolocene)
- Coarse spatial resolution, large temporal scale (coarsePleistocene)

For each of these combinations of scale we fitted species distribution models for each species, and calculated stability by both taking the standard deviation and geometric mean of suitability across time.

Environment and Paleoclimate data

When fitting the stability measures, we used a combination of eight geology variables and three climate variables. The former were held constant whereas the climate variables varied over time.

Inherent rock fertility, mean geological age, the presence of calcrete in the soil, the hydraulic connectivity of the soil, soils dominated by coarse fragments, gravity anomalies and magnetic anomalies (ASRIS 2011, Geoscience Australia 2012, Geoscience Australia 2008, Milligan and Petkovic 2002) were chosen based on previous literature which found them important at predicting compositional turnover (Williams et al. 2012; Chapter 3). For the coarse spatial scale analysis, these were resampled from the original 0.01 degree resolution to 0.04 degrees using bilinear interpolation (for continuous variables) or nearest neighbour interpolation (for categorical variables). Elevational variation was calculated from DEMs at both 90m (0.00083 degrees) resolution (for the fine scale analyses) and 0.01 degrees (for the coarse scale analyses) resolution (Geoscience Australia 2015, Hutchinson et al. 2008). These were aggregated to match the analysis resolutions by taking the range of values occurring within the larger cell in order to measure topographic complexity. All geologic variables used were assumed to have stayed constant over the timeframe of the analysis, as the region is highly geologically stable (Pepper and Keogh 2014). Our models also included latitude and longitude, following Brown et al. (2020).

For the coarse spatial resolution (0.04 degree) we used annual precipitation (Bioclim 12), mean temperature (Bioclim 1) and precipitation seasonality (Bioclim 15) as our climatic variables. These are downscaled from the HadCM3 global circulation model (as in Rosauer et al. 2015), which was found to be the most appropriate paleoclimate model for the Asian-Australian monsoon (DiNezio and Tierney 2013).

For the fine spatial resolution (0.01 degree) we used present-day climatic variables at 90m resolution, to enable us to identify microclimates caused by topography (Ashcroft et al. 2012). These were created using topographic downscaling, as described in Reside et al. (2013). The climatic data was projected back in time by taking the difference between each grid cell in the current-day coarse scale climate data and the same grid cell in each time period. We then applied this difference to the fine spatial scale climate data (Figure 4).

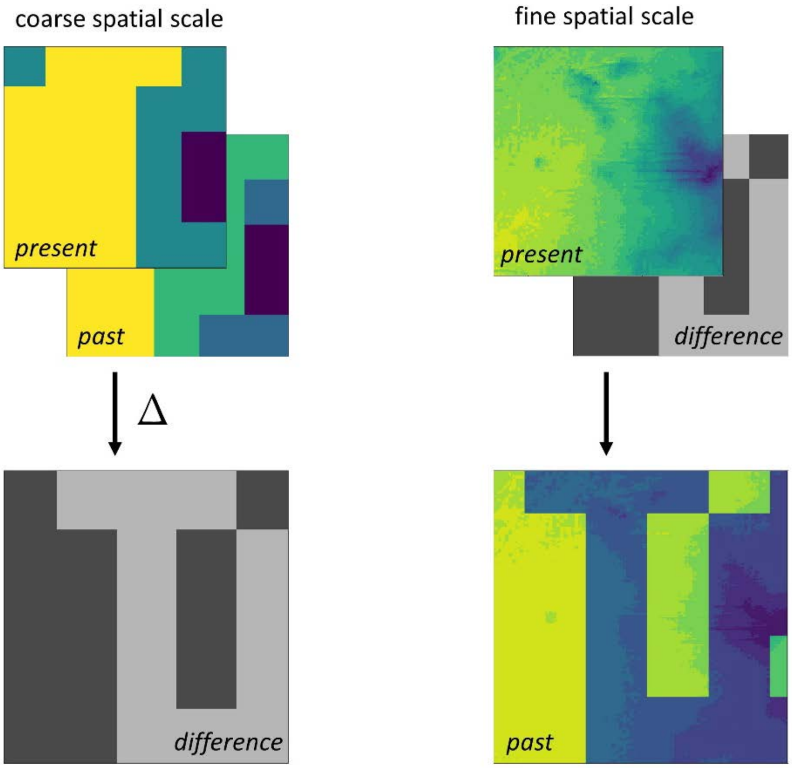


Figure 4. Method of projecting the fine spatial scale climate data. We took the difference between the coarse scale data in the present and each time step. This difference was then applied to the fine spatial scale climate data.

For computational reasons, the fine scale data was then aggregated to 0.01 degrees. Mean temperature and annual precipitation were aggregated by taking the minimum value present within the larger cell, while precipitation seasonality was aggregated using bilinear interpolation.

Species distribution models

We fitted species distribution models (SDMs) to all species at both spatial scales. All SDMs were fitted at a broader spatial extent (between 116 and 134°E, 23 and 10°S; including parts of the Top End and arid zone, Figure 2) to minimize edge effects and include more distribution points and environmental space in the models. We fitted SDMs using Maxent in the R package 'dismo' (Hijmans et al. 2017), reserving 20% of our data for testing. Species with less than five records were excluded from subsequent steps (see Supplementary Material for more details).

For every species, the models were then projected back to each time point, and the standard deviation of suitability through time calculated for each temporal scale. To summarise across species, we took the arithmetic mean of the standard deviations, excluding species not predicted to occur in a grid cell at any point in time (i.e. removing NA values for each grid cell). This method of measuring stability measures the amount of change in species' habitat suitability that has occurred across time. Areas of high stability are areas where the suitability has not changed much through time.

We also took the geometric mean of suitability through time for each species, and summarised across species using the arithmetic mean. The geometric mean was chosen as this is more sensitive to periods of low suitability than the arithmetic mean. This method identifies areas that have remained mostly suitable through time across species. It is similar to measures used previously to model continuity of suitable conditions for biomes such as rainforest (Graham et al. 2010, Carnaval et al. 2014, Rosauer et al. 2015).

Generalised additive models

To measure which type of stability best predicts PE across the Kimberley we fitted generalised additive models (GAM) using the 'mgcv' package in R (Wood 2019), including geographic distance and each of our stability measures (after Brown et al. 2020) (see Supplementary Material). Using bilinear interpolation, we downscaled those stability measures using coarse spatial resolution predictor data to 0.01 degrees to match the PE data.

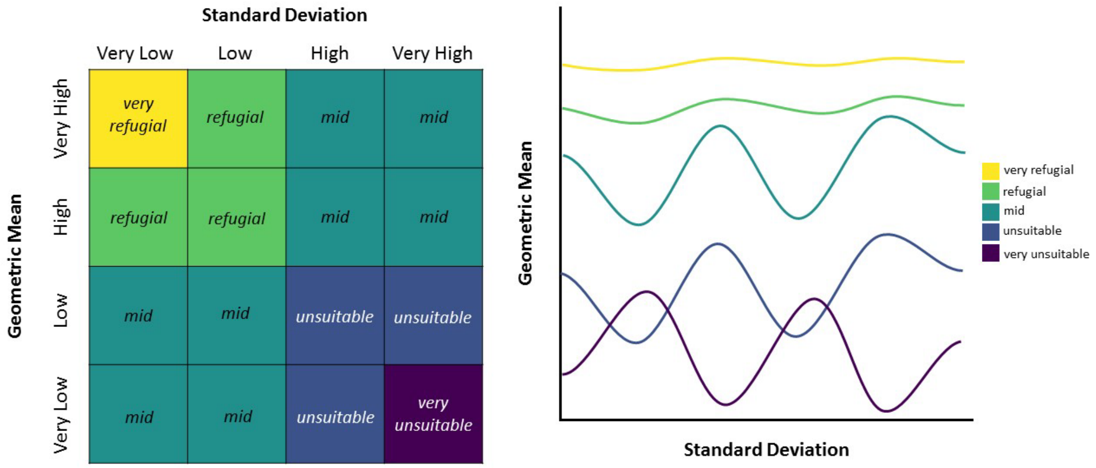
Refugia

To identify refugia we categorised each cell in our continuous stability layers into one of four groups – highly stable (cells falling within the lower quartile of values), stable (second quartile), unstable (third quartile) and highly unstable (upper quartile).

We then combined the standard deviation and geometric mean layers for each scale to categorise how refugial areas are (Figure 5). We had five categories:

- very refugial (very low SD and very high geometric mean through time)
- refugial (low SD and high geometric mean through time)
- mid (low or very low SD and geometric mean; high or very high SD and geometric mean)
- unsuitable (high SD and low geometric mean through time)
- very unsuitable (very high SD and very low geometric mean through time).

That is, we defined refugia as regions that had experienced high suitability and little variation in that suitability through time.



Geometric Mean \ Standard Deviation	Very Low	Low	High	Very High
Very High	*very refugial*	*refugial*	*mid*	*mid*
High	*refugial*	*refugial*	*mid*	*mid*
Low	*mid*	*mid*	*unsuitable*	*unsuitable*
Very Low	*mid*	*mid*	*unsuitable*	*very unsuitable*

Figure 5. Definitions of refugia used, and possible suitability through time for each category.

RESULTS

Species distribution models

SDMs were fitted to the current environment for all 150 species, with 10 species removed due to insufficient data. All models had an AUC above 0.7, with most having an AUC above 0.95 (Figure 6).

Annual precipitation was the most important variable for the majority of SDMs, at both spatial scales (Figure 6). Precipitation seasonality was also highly important for SDMs fitted at the fine spatial scale, while the age of the geological substrate and latitude was more important for those fitted at the coarse spatial scale.

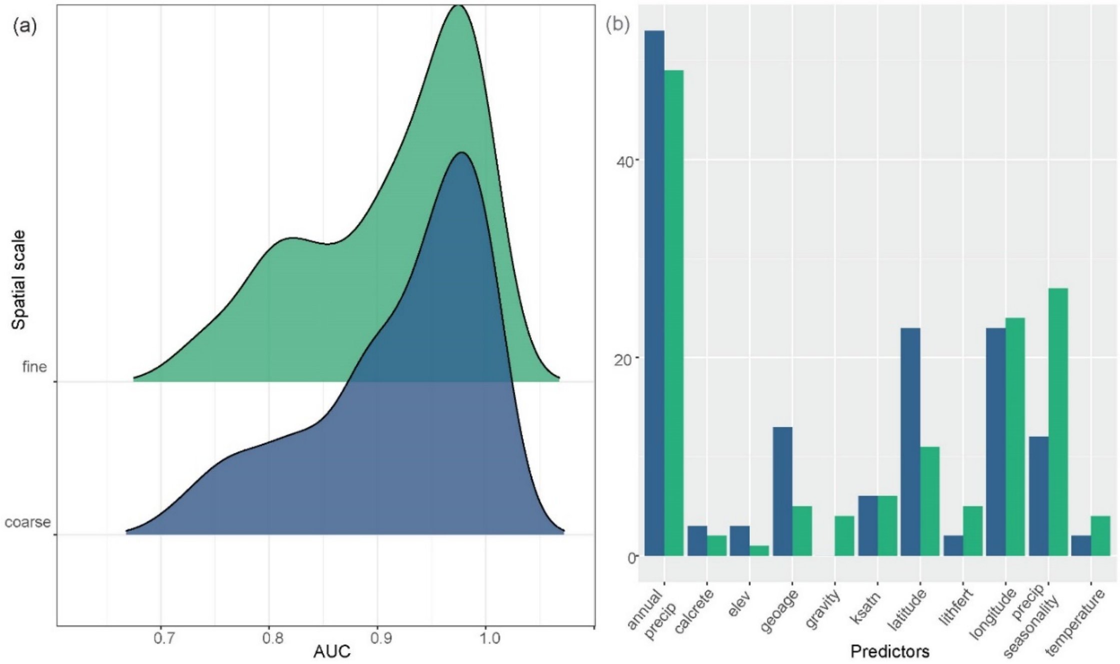


Figure 6. Results of the SDM fitting, with results for the coarse spatial scale in blue and the fine spatial scale in green. a) shows a density plot of the AUC scores for the SDMs at each scale; b) shows the most important variable for each species, at each spatial scale. The y-axis shows the number of species for which each predictor was found to be the most important.

Stability

For both method of measuring stability, the patterns varied across our four scales, with the biggest difference between the two spatial scales. The areas of highest and lowest stability were similar between the Holocene (with data every 1ky) and Pleistocene (with data every 2ky) at each spatial scale (Figure 7; Figure 8), although the coarseHolocene measure showed overall less variability than the other measures (Figure 9). The geometric mean measures showed more agreement between the scales than the standard deviation measures.

For the geometric mean stability measure, the mesic coastal regions and King Leopold Range were generally more continuously suitable through time, with the southern regions more unsuitable (Figure 7). The fine spatial scale measures identified more pockets of suitability in the arid region and dissected landscapes than the coarse spatial scale, particularly in the central and southeast Kimberley.

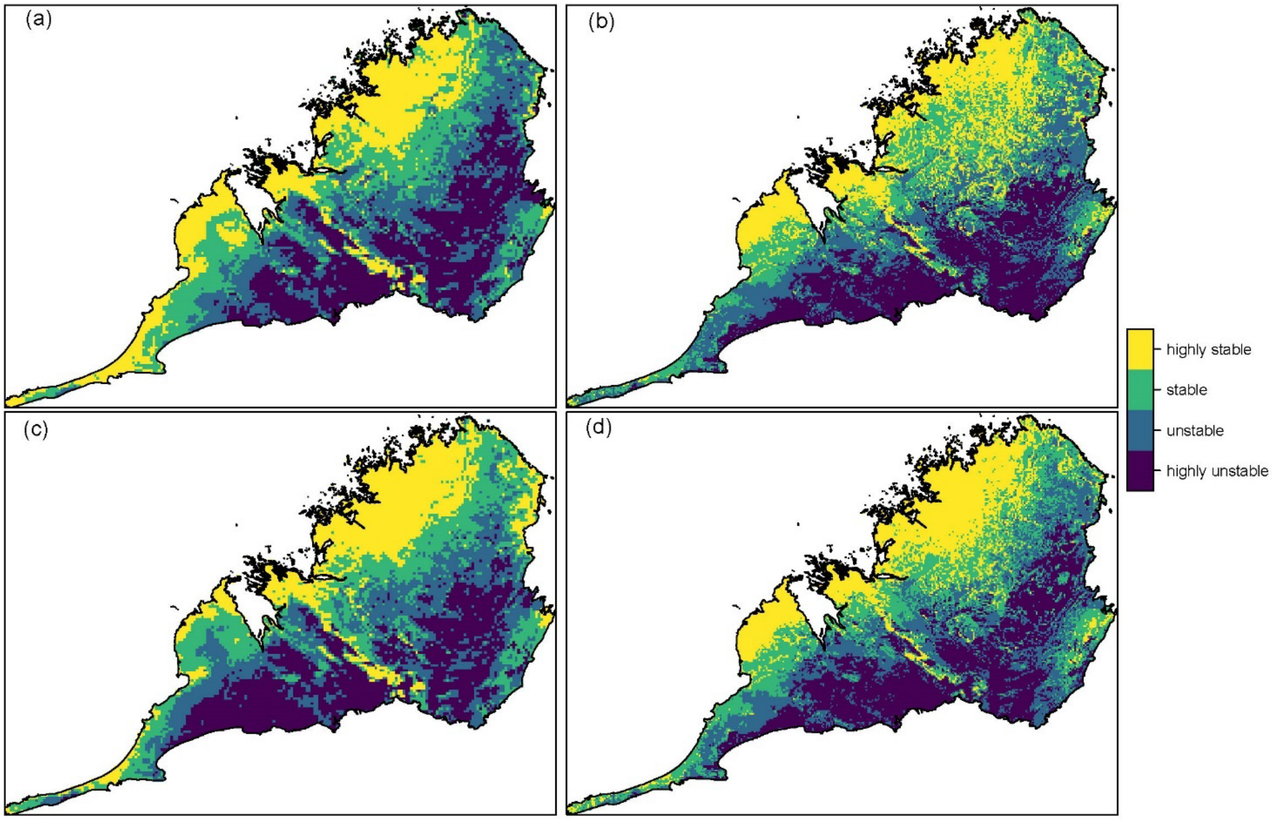


Figure 7. Stability in the Kimberley, measured using the geometric mean. (a) shows the stability measure for coarsePleistocene, (b) finePleistocene, (c) coarseHolocene, (d) fineHolocene.

For the standard deviation measure, the Kimberley shows high variability in the north west and around the King Leopold Range, with the southeast of the Kimberley identified as stable (Figure 8). The measures at a coarse spatial scale identified more variability across the northern coast, and an extra area of stability in the south west near Fitzroy Crossing. The fine spatial scale measures identified a north-south band of variability across the central Kimberley, with stability in the eastern Kimberley and on the Dampier Peninsula in the far west. Overall, the fine spatial scale measures identified more variability in suitability across the Kimberley (Figure 9), with less agreement between the two spatial scales than in the geometric mean measures.

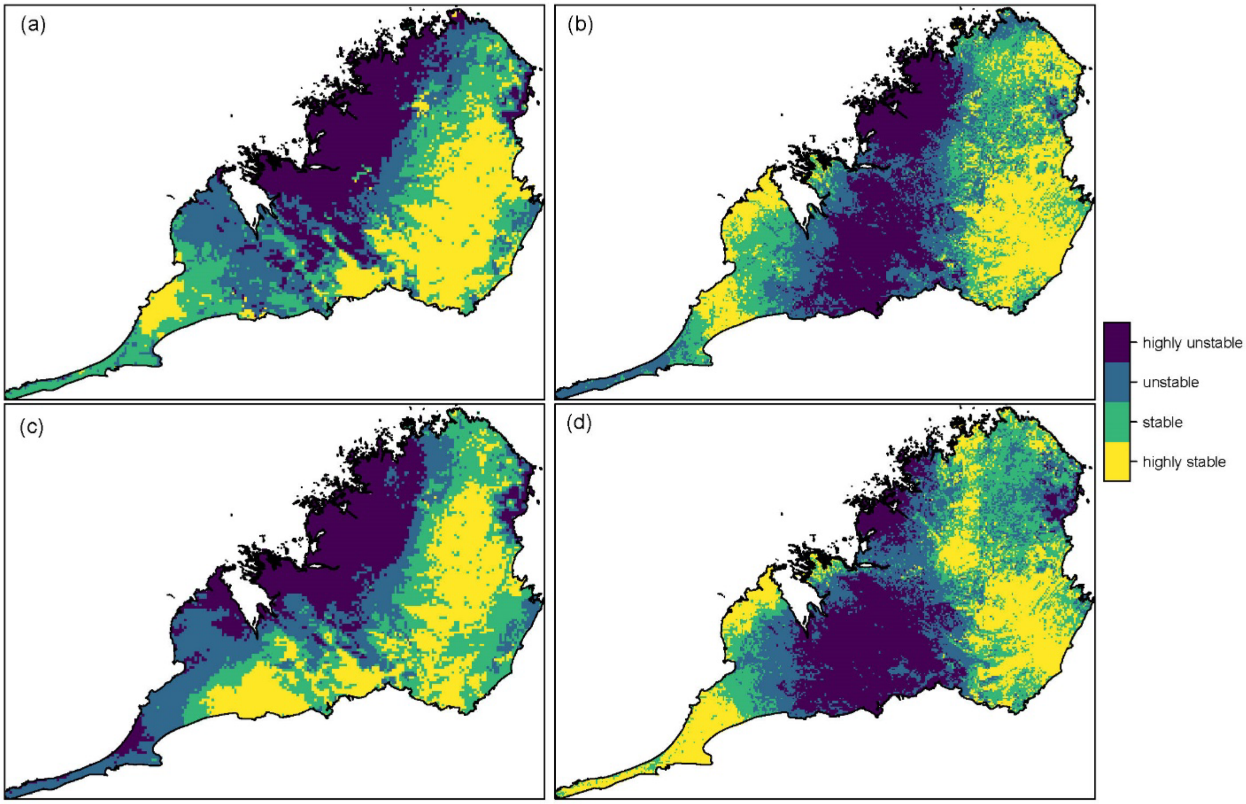


Figure 8. Stability in the Kimberley, measured using the standard deviation. (a) shows the stability measure for coarsePleistocene, (b) finePleistocene, (c) coarseHolocene, (d) fineHolocene.

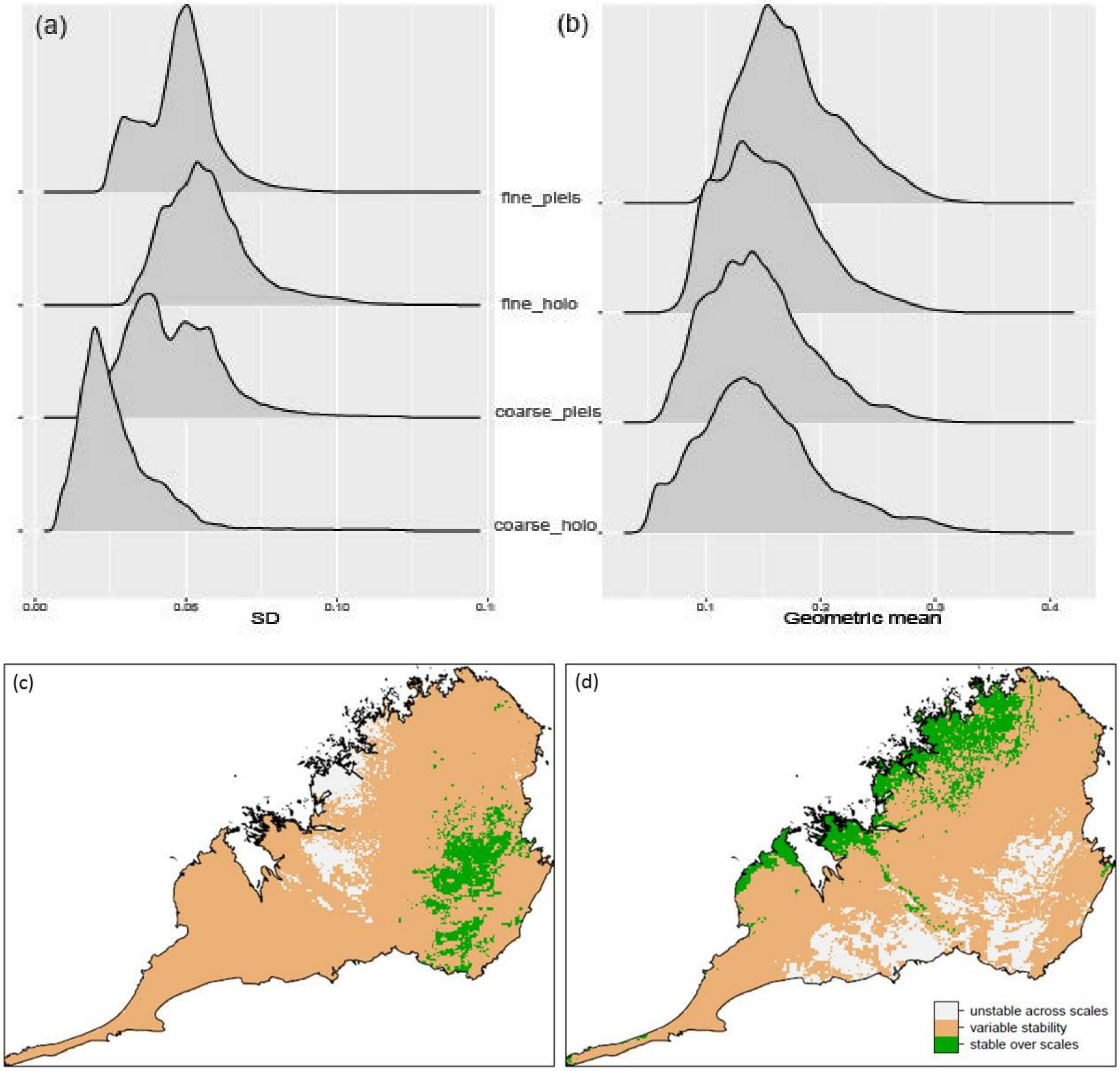


Figure 9. Patterns of stability across scales. (a) and (b) shows density plots of the standard deviation and geometric mean stability measures respectively; (c) and (d) show areas that were stable across the four scales for the standard deviation and geometric mean stability measures respectively.

Predicting PE

PE was best explained by the coarsePleistocene standard deviation stability measure, followed by the coarseHolocene standard deviation measure (Table 1). The stability models measured using fine spatial scale performed worse, as did those summarised using the geometric mean. Overall, the spatial scale of the stability measure was more important than the temporal scale. All measures of stability increased prediction of PE compared to the model fitted using only geographic distance. PE increases in areas of low stability (Figure 10), meaning areas with high variability in habitat suitability tend to have greater diversity.

Table 1. Results from the GAM model, showing the models, amount of deviance explained, and AIC values. Change in AIC is measured against the best model. The best performing model is highlighted in bold.

Model	% deviance	AIC	Δ AIC
pe ~ s(x) + s(y) + s(coarsepleis_sd)	**69.3%**	**-3594086**	**0**
pe ~ s(x) + s(y) + s(coarseholo_sd)	68.3%	-3587745	6341
pe ~ s(x) + s(y) + s(fineholo_mean)	66.1%	-3573817	20269
pe ~ s(x) + s(y) + s(coarseholo_mean)	63.6%	-3559034	35052
pe ~ s(x) + s(y) + s(coarsepleis_mean)	60.4%	-3541190	52896
pe ~ s(x) + s(y) + s(finepleis_sd)	60.3%	-3541128	52958
pe ~ s(x) + s(y) + s(finepleis_mean)	60%	-3539521	54565
pe ~ s(x) + s(y) + s(fineholo_sd)	58.3%	-3530703	63383
pe ~ s(x) + s(y)	55.3%	-3516565	77521

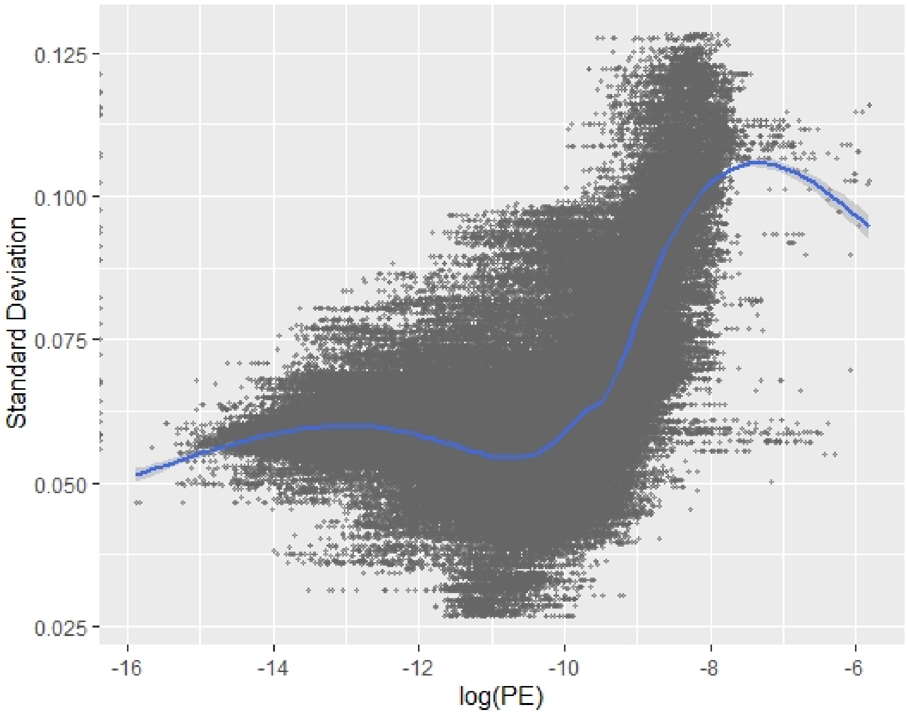


Figure 10. Phylogenetic endemism and the coarsePleistocene standard deviation stability measure, showing higher PE as variability increases. The line represents a GAM smoothing model.

Refugia

The locations of inferred refugia (as classified in Figure 5) were highly dependent on both spatial and temporal scale (Figure 11). The central to eastern Kimberley and the Durack Ranges were consistently identified as refugia. Other areas included the west, particularly the Dampier Penisula, (finePleistocene) and southwest (coarsePleistocene) regions.

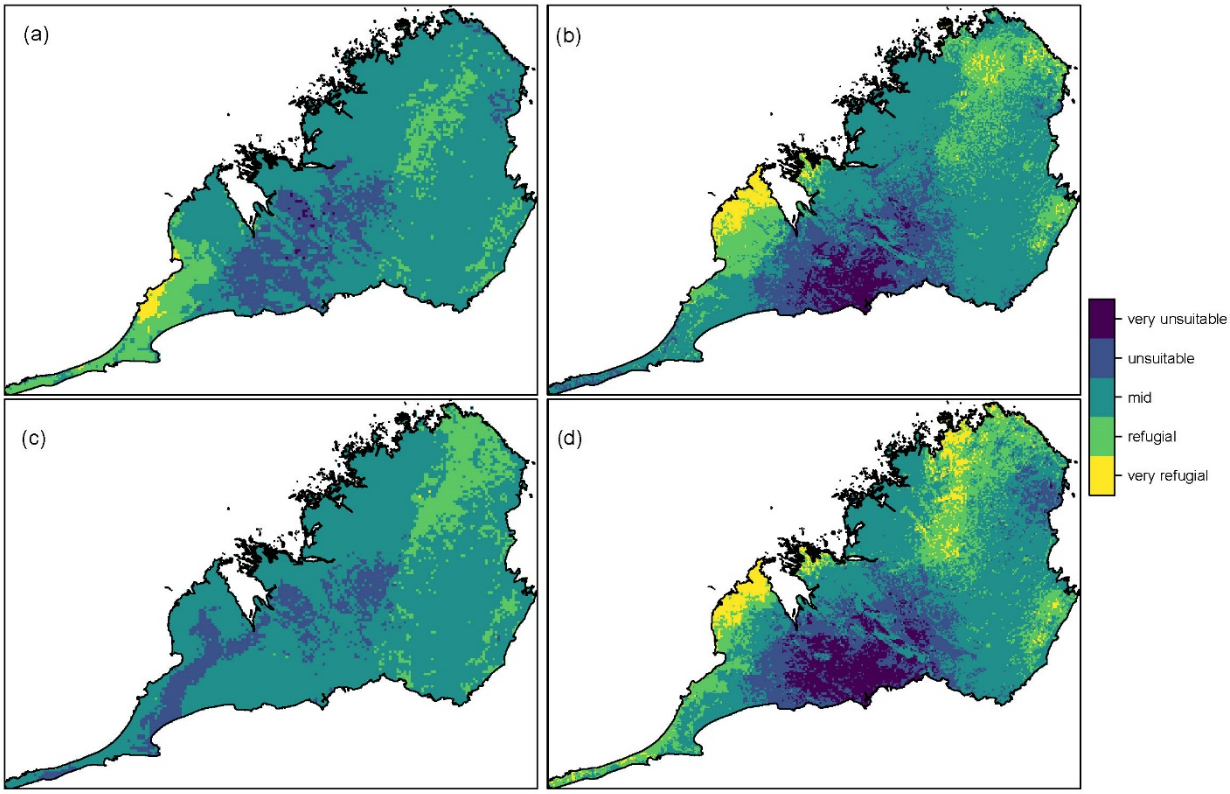


Figure 11. Refugia in the Kimberley for (a) coarsePleistocene, (b) finePleistocene, (c) coarseHolocene and (d) fineHolocene.

DISCUSSION

Refugia in the Kimberley

Our models suggest that detection of refugia in the Kimberley is highly dependent on the scale of the climatic data used. Across scales, the central to east Kimberley has acted as a refugium, as has the Durack Range. As our GAM showed that the coarsePleistocene measure of stability best explained PE in the Kimberley, the remainder of our discussion focuses on refugia as defined by these scales.

Key Pleistocene refugia previously identified, usually from the concentration of short-range endemic species, include the Devonian Reef System to the south (Cameron 1992, Oliver et al. 2017), the East Kimberley near Wyndham (Potter et al. 2014), the north west Kimberley (Catullo et al. 2014) and the islands off the coast of the Kimberley (Gibson et al. 2013) (Figure 12). These areas coincide with the areas identified as high priorities for conservation of evolutionary diversity in the Kimberley (Rosauer et al. 2018).

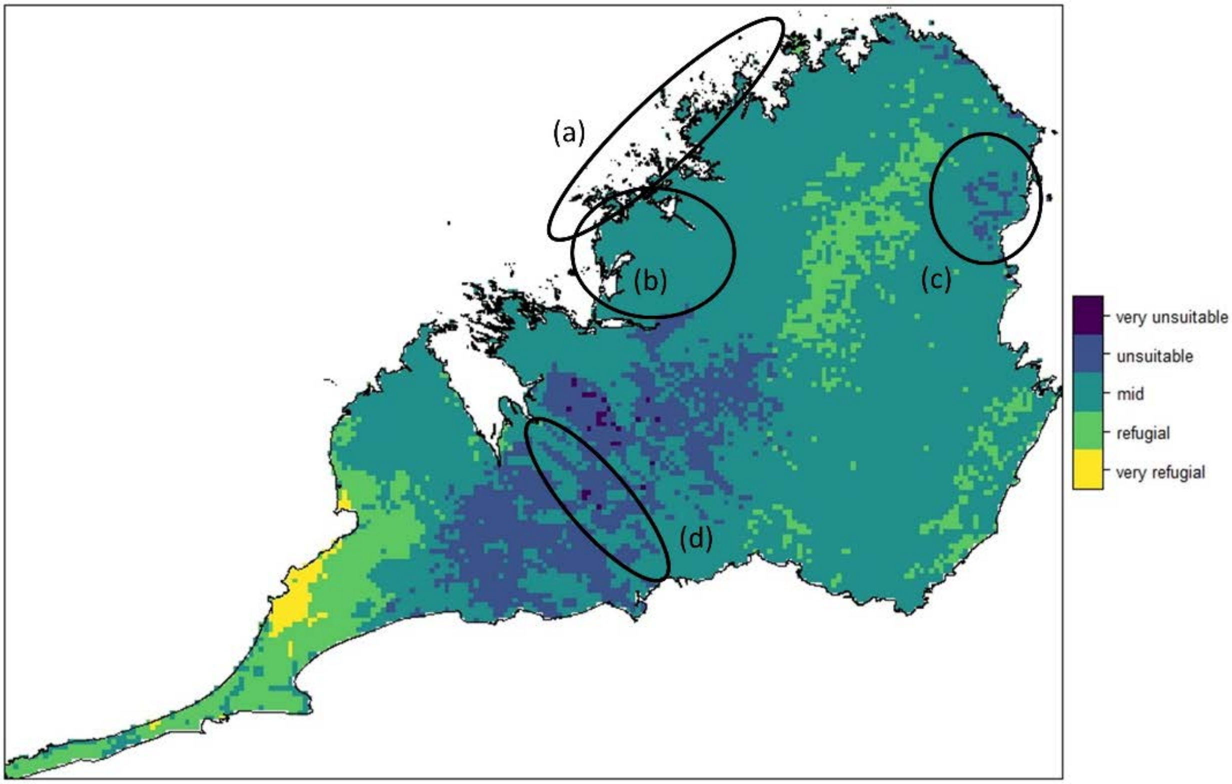


Figure 12. Map showing our refugia with key refugia from other papers marked: (a) the Kimberley islands, (b) the north western Kimberley, (c) eastern Kimberley and (d) the Devonian Reef System.

In contrast, our model supports a refugium in the east to central Kimberley region, with this refugium consistently identified across scales. We also propose refugia along the Durack Range and in the south west Kimberley adjacent to the Pilbara region (see yellow and light green regions Figure 12). The topographically complex north west Kimberley is thermally buffered, with previous work suggesting this could allow it to act as a refugium (see e.g. Pepper and Keogh 2014). This contrasts with our results, perhaps because precipitation was more important than temperature across our SDMs. Additionally, our results may be influenced by our inclusion of latitude and longitude in the SDMs. This may overly restrict spatial shifts in species distributions as climates fluctuate, in turn impacting our estimates of stability.

Stability across scales

Examining stability using both the standard deviation (to capture variability) and the geometric mean (to capture overall trends) (as done elsewhere, e.g. Brown et al. 2020) allowed us to look more closely at the biological drivers of patterns of PE in the Kimberley.

Overall, our models showed the greatest difference in stability between spatial scales rather than between temporal scale. For example, the Dampier Peninsula showed as highly stable in both the fine spatial scale models but not in the coarse spatial scale models. This is most likely due to the difference in which variables drove the underlying SDMs between the two spatial scales. Although there is some overlap in areas identified as highly stable or highly variable between the spatial scales, outcomes for the majority of the region are highly dependent on the spatial, and to a lesser extent temporal, scale chosen. This supports previous theoretical work (McDonald-Spicer et al. 2019; Chapter 1) suggesting that the spatiotemporal scale at which stability is measured has a large impact on the results and biological interpretation of results.

We also found that areas with higher present-day rainfall, such as the northwest Kimberley, tended to have more variability in the past. This may be due to the variable monsoon in the past, with currently wetter areas also experiencing strong aridity in the past, as opposed to areas that are now arid and were perhaps more so in the past such as the surrounding lowlands (Reeves et al. 2013). Additionally, these coastal areas were impacted by sea-level changes, and the associated changes in weather patterns and climate.

PE and stability

We found that PE in the Kimberley increases with past variability, and that it was best predicted by the coarse spatial scale measures. That is, landscape level macrorefugia at coarse spatial scales are more important in describing PE than microrefugia. Extending this study to examine the drivers of species richness and weighted endemism in the region would be valuable, however this requires more consistent and extensive surveys across the Kimberley.

Very few studies have looked at the relationship between PE and past climate, with those that have examined it finding a strong relationship between Quaternary climate stability and high PE (Feng et al. 2019, Rosauer and Jetz 2015, Sosa et al. 2020). These studies have all focused on temperature as a measure of climate, while our models incorporate more climatic variables, and are heavily influenced by past precipitation. Several previous papers (Araújo et al. 2008, Brown et al. 2020) have found that both temperature stability and precipitation variability promote diversity, and this could explain our counter-intuitive results.

Areas with high PE include lineages with long phylogenetic branches and small ranges (Rosauer et al. 2009). Hence, the relationship we observed between variability and PE may be driven by spatial patterns of extinction as well as persistence. High variability in climate may cause extinction of lineages and range contractions in related, surviving lineages. This would cause areas of high PE not in refugia, where many lineages can survive, but in areas of high variability where only a few relictual lineages persist.

Conservation of the Kimberley is of increasing importance, with pressure from development, feral animals including cane toads, and climate change. Previous studies have suggested that explicitly protecting refugia can protect the process of evolution (Ashcroft et al. 2012) and mitigate the effects of climate change (e.g. Game et al. 2011, Groves et al. 2012). However, our results suggest that, at least for reptiles in the Kimberley, this paradigm may not be as useful as it is in other areas, and that conservation priorities should be set based on other factors. More research into different taxa is needed to better understand this relationship.

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SUPPLEMENTARY MATERIAL

Detailed methods - Species Distribution Models

We fitted species distribution models (SDMs) to all species at both spatial scales. All SDMs were fitted at a broader spatial extent (between 116 and 134°E, 23 and 10°S; including parts of the Top End and arid zone, Figure 2) to minimize edge effects and include more distribution points and environmental space in the models.

We fitted SDMs using Maxent version 3.4.0 in the R package 'dismo' version v1.1-4 (Hijmans et al. 2017). For each model, we used k-fold data partitioning to reserve 20% of our data for testing. Latitude and longitude were included to restrict dispersal. Models were smooth, and novel climates were clamped. The output gives an estimate of the probability of the species occurrence in each grid cell, between 0 and 1. For testing, background pseudoabsence points were selected randomly from within the Kimberley region. The AUC for each model was calculated in Maxent.

Although our final models did not explicitly include changing sea levels, due to the geological data being restricted to the current land surface, these sea levels are reflected in our paleoclimate data. This means that the impact of sea levels on paleoclimates (for example a region far inland becoming coastal) is accounted for in our models.

Detailed methods – Generalised Additive Models

To measure which type of stability best predicts PE across the Kimberley we fitted generalised additive models (GAM) using the 'mgcv' package in R (v 1.8-31) (Wood 2019). This assumed Gaussian distribution and the smoothing parameter was estimated using restricted maximum likelihood estimation. Our GAMs included geographic distance (in the form of latitude and longitude) and each of our stability measures (after Brown et al. 2020).

Synthesis

Varanus eremius from *Report on the work of the Horn Scientific Expedition to Central Australia*, 1896

Synthesis

Explaining the patterns of diversity we see in the world is a major question for macroecology, and looking at past environments can help with this. Refugia, and stability more broadly, have been linked to areas of high diversity. My thesis explored two main themes – how to measure stability and refugia, and how refugia have impacted the biogeography of the Australian Monsoonal Tropics (AMT).

The first half of my thesis focused on methodology. In Chapter 1, I presented a conceptual framework for defining measures of stability, allowing for clearer hypotheses, more accurate interpretation of results and easier comparisons across studies. In my second chapter, I examined the impact that choosing different measures of stability has on analyses. I found large differences in the explanatory power and biological meaning of my four stability measures, with different diversity measures best explained by different stability measures.

The last half of my thesis focused on how stability and refugia have influenced the patterns of diversity found in the AMT. In Chapter 3, I conducted a biogeographic regionalisation of lizards in the AMT, and examined the drivers of these patterns. I identified four broad biogeographic provinces, driven largely by habitat variability and physiological constraints, and examined the implications of using older bioregionalisations in conservation planning. In my final chapter, I looked at stability in the Kimberley across multiple temporal and spatial scales to understand which best explains phylogenetic endemism (PE). I found that PE in the Kimberley is best explained by landscape-level stability since the late Pleistocene, with high PE in regions of high variability.

DOES HOW WE MEASURE STABILITY MATTER?

In Chapter 1, I presented a number of aspects of stability measures that may impact on results and their interpretation. In later chapters I built on this theoretical work by empirically comparing stability measures calculated using different summary metrics (Chapter 2), and spatiotemporal scales (Chapter 4). While some other studies have compared static and dynamic stability (e.g. Graham et al. 2006), this is the first time these other factors of stability have been systematically varied and compared. This thesis has shown the large impact that varying the method and scale of a stability measure has, and the large difference this makes in the refugial areas identified, the relationship of stability with diversity, and the biological processes being examined. This provides both a theoretical and empirical framework for future studies of stability to consider.

STABILITY, REFUGIA AND DIVERSITY

Previous work has overwhelmingly linked refugia and areas of stability with diversity hotspots, including high richness, genetic diversity and endemism (see Table 1). In contrast, my results indicate that the role of variability in driving diversity has been overlooked in the literature. In Chapter 2 I found that richness is correlated with regions of stability, while endemism is correlated with community turnover, suggesting instability is more important for the latter. In Chapter 3 I examined the relationship between diversity and variation in past precipitation. I found that richness increases with instability of rainfall, although relationships with beta diversity measures were non-significant. Finally, in Chapter 4 I looked at phylogenetic endemism in the Kimberley, and found it is explained by instability in habitat suitability, driven largely by precipitation.

The different relationships I found across my studies, particularly comparing Chapter 2 and the later chapters, could be due to the different stability measures I used. Overall, those relying heavily on rainfall (Chapters 3 and 4) found that instability promotes diversity. This is supported by emerging research suggesting that while temperature stability is correlated with diversity, precipitation variability is also important (Araújo et al. 2008, Brown et al. 2020). This points to a need for a more nuanced understanding of drivers of endemism and richness across different biomes.

While the relationship between variability and diversity (specifically richness) is supported at ecological timeframes by the intermediate disturbance hypothesis (Connell 1978), where stability leads to competitive exclusion, it is interesting that very few macroecological studies have previously observed this. This may be due to the scale of previous studies, with most focusing on either large-scale global patterns or distinct, easily-modelled biomes such as rainforest. The Australian Monsoonal Tropics and Kimberley regions are much more complex than these broader scale studies, meaning they are likely to show patterns hidden in simpler regions. Additionally, the AMT is an inherently unstable region (Potter et al. 2018, Reeves et al. 2013), meaning the relationships between biota and stability may be different to those in more inherently stable regions, such as rainforests.

Table 1. Summary of key papers exploring the relationship between diversity and stability.

Reference	**Biome/region**	**Diversity metric**	**Stability measure**	**Relationship between diversity and stability**
(Boyer et al. 2016)	Rainforest	Richness & phylogenetic diversity	SDMs across time (18ka to present)	Positive for both metrics
(Araújo et al. 2008)	Europe	Species richness	Difference in climate (LGM to present)	Positive for temperature, negative for precipitation
(Graham et al. 2006)	Rainforest	Richness	SDMs across time (18ka to present)	Positive
(Rosauer et al. 2015)	Rainforest	Endemism	Biome niche models across time (120ka to present)	Positive
(Carnaval et al. 2009)	Rainforest	Genetic diversity	SDMs across time (21ka to present)	Positive
(De Lafontaine et al. 2013)	Temperate forests	Genetic diversity	SDMs across time (LGM to present)	Positive
(Brown et al. 2020)	Global	Richness	Difference in climate (LGM to present)	Positive for temperature, negative for precipitation
(Cabanne et al. 2016)	Rainforest	Genetic diversity	SDMs across time (21ka to present)	Positive
(Sandel et al. 2017)	Global	Endemism	Climate velocity (21ka to present)	Positive

IMPACT OF KNOWLEDGE SHORTFALLS

Biodiversity work in the Australian Monsoonal Tropics is ongoing. As further collection, genetic work and taxonomic work is undertaken, and the Wallacean and Linnean shortfalls are corrected, our understanding of the patterns of diversity may shift.

The Wallacean shortfall, named after Alfred Russel Wallace, is the lack of knowledge around the geographic distribution of species (Bini et al. 2006). Despite ongoing collections work, there remain large under-sampled areas in the AMT, including in the eastern Kimberley and the Gulf region (Chapter 3). The areas that are better sampled are geographically biased towards those with easier access, including around townships and along roads. Similar patterns have been identified globally in other groups (e.g. Schmidt-Lebuhn et al. 2012, Hortal et al. 2007, Reddy and Dávalos 2003). This biased sampling means that endemism may be overestimated in well-sampled areas, due to underestimation of species ranges, and that richness in less sampled areas may be underestimated. Hence, increasing collections across the region may shift our understanding of these hotspots, and thus the relationship they have with refugia. Additionally increased sampling will allow for finer-scale analyses, such as moving from the IBRA regions that I used in Chapter 3 to grid based analyses.

Not only is our knowledge of species ranges changing, but also our knowledge of the species themselves. The Linnean shortfall, named after Karl Linneaus, refers to the lack of knowledge around how many species there are (Bini et al. 2006), and includes new species descriptions, taxonomic revisions, and taxa not yet sampled (Hortal et al. 2015). Across Australia, an average of 11 new reptile species are described every year (Tingley et al. 2019). In the AMT, there is ongoing taxonomic work, including *de novo* species discovery, describing cryptic species and elevating genetic lineages to species-level, and large-scale taxonomic revisions (see Introduction). Even including species known but not yet formally described, the full extent of biodiversity in the AMT is likely to be higher than we know (see e.g. Moritz et al. 2013, Moritz et al. 2016, Rosauer et al. 2016, Moritz et al. 2018). Shifting taxonomies will also impact on the patterns of diversity we observed. Identifying new species will change patterns of species richness, while splitting currently-described species into multiple taxa will decrease range sizes, increasing endemism. Phylogenetic endemism will be less impacted, as it is probabilistically calculated on lineages rather than taxa, although increasing genetic work within and across groups may cause this to change. In particular, PE cannot incorporate currently unknown lineages that increasing sampling and genetic work may uncover.

CONSERVATION

My work has helped understand the current-day patterns of diversity in the AMT. In Chapter 3 I found that bioregionalisations currently used in Australian conservation planning do not accurately reflect turnover patterns in AMT reptiles, and that this changes conservation priorities. It is therefore important that conservation planning is undertaken using current taxonomic and geographic data, and that biogeographic patterns are looked at across different groups before decisions are made.

More generally, identifying and protecting refugia is important to mitigate the impacts of climate change, through both protecting current taxa and allowing for future adaptation (Fordham et al. 2016). Explicitly protecting refugia and the large amount of genetic diversity they often contain (Fordham et al. 2016), can allow for the protection of evolution in progress, recognising the "dynamic nature of biodiversity" (Ashcroft et al. 2012), and allow for future adaptation. Refugia have been previously used to design more effective reserve systems. For example, in California USA, microrefugia were used to create a prioritised reserve system design to protect biodiversity and buffer it from future climate change (Olson et al. 2012). Other analyses have shown that considering refugia in conservation assessments and reserve system design can reduce the amount of change expected to occur in protected areas without increasing the cost of the reserve system (e.g. Game et al. 2011, Groves et al. 2012).

With changing climates and increased development pressure in northern Australia, conservation of the region's unique biodiversity is of growing importance. While it is unclear whether areas that have acted as refugia in the past will continue to do so under future climates (see e.g. Noss 2001, Fordham et al. 2016), identifying past refugia is an important first step. Additionally, understanding the relationship between stability and diversity can help predict how biodiversity patterns will shift under future climates, allowing for more informed conservation planning. For example, this thesis has presented evidence that, at least for lizards in the AMT, variability over time is highly correlated with diversity (e.g. Chapter 4). Further research is required to fully understand this relationship. It may, for example, be driven by range contractions of arid-adapted species in the relatively wet current climate, or it may reach a threshold where the environment is too variable to support high diversity. This future research will help in predicting future patterns of diversity, and thus areas of high conservation priority to mitigate against the adverse effects of climate change.

CONCLUDING REMARKS

In conclusion, in this thesis I have explored methods of measuring stability and refugia, and examined the role that stability has played in the biogeography of northern Australian lizards.

The methods used to define stability measures have a large impact on the results of these measures, and how they should be interpreted. In the AMT, past climates have played a large role in shaping the patterns of diversity present, with variability in past climates driving diversity. Overall, this thesis has revealed the intricacies of modelling stability, particularly in a complex region such as northern Australia.

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