Climate change refugia for terrestrial biodiversity

Final Report

April E. Reside, Jeremy VanDerWal, Ben L. Phillips, Luke P. Shoo, Dan F. Rosauer, Barbara J. Anderson, Justin A. Welbergen, Craig Moritz, Simon Ferrier, Thomas D. Harwood, Kristen J. Williams, Brendan Mackey, Sonia Hugh and Stephen E. Williams

CLIMATE CHANGE REFUGIA FOR TERRESTRIAL BIODIVERSITY

Defining areas that promote species persistence and ecosystem resilience in the face of global climate change

James Cook University

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ABSTRACT

We are currently facing the likelihood of severe climate change before the close of the century. In the face of such a global driver of species loss, we urgently need to identify refugia that will shelter species from the worst impacts of climate change. This will be a critical component of successful conservation and management of our biodiversity. Despite this, little is known about how best to identify refugia in the landscape, and the practical strategies needed to identify, protect and expand refugia are just beginning to be developed. Identifying refugia that will protect most species, or large numbers of species, remains a complex and daunting endeavour due to the large variations in climatic and biotic requirements of species.

A first step to identifying refugia for biodiversity across Australia is to locate the areas which show the least change into the future (i.e. the most environmentally stable), particularly along axes of temperature and precipitation. The second and crucial step is to identify the areas that will retain most of their biodiversity and provide opportunities for additional species to relocate to into the future. Using these approaches in this project, we take the first steps to identify refugial areas across the Australian continent under contemporary climate change scenarios. We find that the southern and eastern parts of the continent contain refugia that many species will retreat to over the next 75 years, but that the current reserve system may be inadequate to allow species to shift to and persist in these areas. Disturbingly, we also find that there is a large portion of the Australian vertebrate community for which adequate natural refugia do not appear to exist. Fine-scaled regional analyses will be required to clarify these broad findings, and we examine a number of case studies demonstrating how these regional analyses might best proceed.

Lessons learnt across the multiple techniques employed in this study include:

1. High elevation areas are important refugia.
2. Tasmania and the east coast of mainland Australia contain most of the key areas for refugia into the future.
3. Results are dependent on which objectives, techniques, taxonomic groups and climate scenarios are used.

EXECUTIVE SUMMARY

Climate change is already underway, and we are currently looking down the barrel of a four to five degree Celsius increase in global mean temperatures by the end of the century. This level of climate change will have manifold impacts on human livelihoods and infrastructure, and will also have serious consequences for the world's biodiversity. How can we best conserve biodiversity in the face of this global, ubiquitous driver of biodiversity loss?

The most cost-effective solution for biodiversity conservation under climate change is to identify and protect those places in the landscape that will harbour many species from the worst impacts of climate change. The effect of climate change is not felt equally in all places because local weather systems and landscape features can act to amplify or dampen global patterns. If we can identify parts of the landscape where species can retreat to and persist during the coming century ('refugia'), we are in an informed position to minimise biodiversity loss through management of these key areas.

This report begins the process of identifying and ranking such climate change refugia across the Australian continent. We start broadly, looking at how changes in climate are likely to play out across the Australian continent, and we examine these changes from a biological perspective (led by the Centre for Tropical Biodiversity and Climate Change at James Cook University). This reveals that the Australian continent is likely to experience catastrophic increases in temperature across most of the continent. The dangerous magnitude of these increases in temperature is clearly demonstrated by reference to the normal inter-annual variation in temperature at each location. Against this backdrop, the projected shift in mean temperature at all locations across Australia is alarming. Across most of the continent, mean annual temperatures will shift to be greater than five standard deviations from current temperatures. This is equivalent to *average* temperatures shifting by a magnitude that would only be expected to occur once every 3.5 million years under current levels of variation. That this shift will play out in less than 75 years suggests that most vertebrate species will be unable to adapt, and that retreat to refugia is the only likely viable option for these species to persist.

To retreat to refugia, however, the suitable, more stable conditions need to be in close proximity to the species' current range. Species cannot shift their range instantaneously, and many species are extremely limited in their rates of range-shift. To find the parts of the landscape that are close to refugia, we calculated, for each (c. 1 km) pixel across Australia, the distance that a population would have to shift to stay within two standard deviations of current temperatures. This analysis revealed temperature refugia along the Great Dividing Range, in the MacDonnell Ranges, and in the south of the continent. Species ranges in close proximity to these upland areas will contract uphill. Species that are already endemic to these upland areas, however, will be faced with a situation where their currently favourable environments move beyond the tops of mountains. The closest temperature refugia for many upland species will be inaccessible, being hundreds, to thousands of kilometres to the south; and refugia for some of these species will simply not be present anywhere in continental Australia by 2085. Thus, mountainous regions will act as refugia for nearby lowland species, but will not act as refugia for the species that currently rely on that cool upland habitat.

We also examined projected changes in precipitation, but these were modest relative to current inter-annual variation in precipitation. Our best understanding is that precipitation levels in the future will generally be within the bounds of current inter-annual variation. Thus precipitation alone was not a particularly useful metric for identifying refugia.

Places that have been climatically stable over the last few million years are typically places of high species endemism and lineage-level diversity. We examined paleological stability in temperature and resolved a number of clear paleological temperature refugia at the continental scale. These areas were found in the north and west of the continent; parts of the continent where no clear temperature refuge will exist in 2085. Thus, we can infer that we currently stand to lose much of the species-level and lineage-level diversity that has accumulated in Australia over the last few million years.

Moving on from analysis of raw climatic variables, we modelled the projected range-shift of 1700 vertebrate species across the continent. This exercise confirmed that the same areas identified from the temperature analysis (above) would act as refugia for biodiversity. Again, large areas of the south and east of the continent (associated with the Great Dividing Range), and a small area in central Australia and the south-west are predicted to be refugia under projected climate change. These areas all have a relatively low outright loss of species, and a relatively high influx of immigrant species from surrounding areas.

Overall, then, we conclude that substantial refugial areas exist in the south and east of the continent, as well as smaller areas in central Australia and the far south-west. Many of these refugia are also areas that are heavily modified by human activities, so management action to facilitate species movement and persistence in these areas is recommended. We also conclude that there is a large portion of Australia’s vertebrate fauna that will have no ready access to natural refugia in 2085, and these species are at particular risk of extinction.

To clarify these broad findings at the regional level and determine how we might progress with research efforts, we examined four case studies.

The first of these case studies (led by the CSIRO Climate Adaptation Flagship) is an extensive demonstration of the application of compositional-turnover modelling to identify locations of potential refugia at relatively fine spatial resolutions. It uses new techniques for deriving and projecting topographically adjusted radiation, climate and moisture surfaces. This approach was applied to the entire Australian continent at 250-metre grid resolution, using the best available biological datasets for a wide range of plant, vertebrate and invertebrate taxa. To demonstrate potential applicability at even finer grid resolutions, and using higher quality biological data, the approach was also trialled using comprehensive floristic-survey datasets for all of New South Wales, and for the Tingle Mosaic area in south-west Western Australia.

The second case study (led by the Centre for Biodiversity Analysis at Australian National University) examines how we might rapidly assess the location of current species- and lineage-level diversity for particular ecological communities (in this case, rainforest-endemic lizards). These analyses rest on reconstruction of the paleological distribution of the community and the identification of areas that have been suitable for that community over the long term. These most stable areas are likely to be storehouses of lineage-level diversity, and often also contain unique endemic species. These evolutionary refugia were strongly skewed to higher elevations, which suggests firstly that the places which functioned as refugia from past climate change may be similar to those predicted to be refugia under projected climate change, but secondly, that there are particular concentrations of endemic diversity in these threatened high elevation zones. By adequately assessing the location of this (often cryptic) diversity, we will be in a better position to examine the mismatch between where the biodiversity currently is, and whether or not it can safely survive in the refugia that we identify.

The third case study (led by Griffith University) highlights our emerging capacity to identify areas that might be decoupled from local climate by dint of geological and edaphic peculiarities. This analysis uses high resolution satellite imagery and remote-sensing technology to identify green spots on the continent: places that are wetter than their surrounds and so likely to act as seasonal or drought refugia for many taxa.

Finally, in our fourth case study (led by the Centre for Tropical Biodiversity and Climate Change at James Cook University), we acknowledge that much of the spatial data generated in the process of ‘refugia hunting’, could benefit from the kind of rigorous analysis that can be provided by modern conservation prioritisation tools. We provide a brief example of the use of one of these tools (Zonation) in Australia’s Wet Tropics and show that the tool identifies all known refugia in this nationally significant biodiversity hotspot. Application of this kind of analysis at the regional level will be the obvious way forward in clarifying the location and quality of climate change refugia in a way that can also incorporate socio-economic objectives.

1. OBJECTIVES OF THE RESEARCH

The broad aim of the project was to identify areas that may act as climate change refugia for terrestrial biodiversity. Identification of such areas is key to directing management actions for enhancing the resilience and adaptive capacity of Australia's terrestrial biodiversity in the face of global climate change. We used a variety of approaches to identify refugia, some broadly across the whole continent, and others focussing on key case-study regions. Overall, we examine the results for a consilient signal. The areas that are consistently projected to be high quality refugia across approaches are highly likely to be refugia into the future.

The objectives of the project were:

1.1 Properties of refugia for biodiversity under climate change

A working definition of 'refugia' is required before a meaningful analysis of spatial and temporal dynamics can proceed. As such, we undertook an extensive review of national and international literature on the topic. The review aimed to catalogue the various definitions of 'refugia' in the literature and, working from this, identify the properties of refugia such that we can systematise the identification of refugia under climate change.

1.2 Identifying the spatial location and quality of refugia across the Australian continent

For this objective, we aimed to identify the location of climate change refugia across the Australian continent. We took several analytical approaches to this question, incorporating paleological climate change (inferred over the last 120 000 years), actual climate change since 1950 (observed), as well as projected climate change through to 2085. We examined refugia both from a purely climatic perspective (areas with the smallest shift in climate), as well as from a biotic perspective (areas that minimise species loss while facilitating movements for a broad suite of taxa).

Following this continent-wide exercise, we then explore four case studies that highlight alternative analytical approaches and demonstrate how we might move to regional-level assessments that are of direct use to regional conservation planners.

1.2.1 Case study 1: Assessing refugial potential using compositional-turnover modelling

Here we demonstrate the application of a community-level (as opposed to species-level) approach to identifying locations of potential refugia at relatively fine spatial resolutions. This approach involves a combination of compositional-turnover modelling with new techniques for deriving and projecting topographically adjusted radiation, climate and moisture surfaces.

We applied this approach to the entire Australian continent at 250 m grid resolution, using best-available biological datasets for a wide range of plant, vertebrate and invertebrate taxa. To demonstrate potential applicability at even finer grid resolutions, and using higher quality biological data, the approach was also trialled using comprehensive floristic-survey datasets for all of New South Wales (at 100 m resolution), and for the Tingle Mosaic area in south-west Western Australia (at 30 m resolution).

1.2.2 Case study 2: Pleistocene stability and diversity of herpetofauna

Evolutionary refugia are expected to be hotspots of both species and genetic diversity. Identifying these areas will help target areas needing further biological research or conservation action. Evidence of the location and behaviour of refugia through past climate change is also important for improving our understanding the likely response of species distributions to anticipated climate change and the effectiveness of refugia in mitigating loss of biodiversity over the coming century.

Stability of climate since the last glacial maximum (LGM) has been shown to relate strongly to current endemism of species (Graham et al. 2006, Davies et al. 2009) and genetic variation within a range of species (Carnaval et al. 2009, De Mello Martins 2011) via its effect on the distribution of vegetation types. Here, we assessed the effect of a changing paleo-climate over the past 120 000 years on the distribution of rainforest on Australia’s eastern seaboard. From this we identified the areas which have been most climatically stable for rainforest and therefore may function as evolutionary refugia for rainforest specialist taxa.

Infraspecific diversity provides a sensitive measure of persistence, because even where species are widespread, they may contain locally endemic lineages which imply local persistence of the species in particular areas. We modelled the distribution of independent lineages within rainforest lizard species, and identified their centres of endemism as indicators of places that have functioned as evolutionary refugia, retaining local diversity through late Pleistocene climate cycles.

1.2.3 Case study 3: Drought refugia in monsoonal Australia

Our objective here is to make use of the latest remote-sensing technology and satellite imagery to identify ‘greenspots’ across the Australian continent. These greenspots represent areas of higher photosynthetic activity in each bioregion. Given that photosynthesis is ‘thirsty work’, these greenspots point to places in the landscape that are wetter than their surrounds. Typically, these greenspots will not be the result of broader climatic variables, but reflect instead peculiarities of topography, geology, and soil that allow these areas to accumulate and store water. Thus, these greenspots represent locations where microclimate is decoupled from the regional situation, and therefore likely represent important seasonal refugia, as well as refugia against extreme drought events.

1.2.4 Case study 4: Using conservation planning tools to identify regional refugia

Here we demonstrate the use of conservation planning software (Zonation) as a means of identifying regional refugia. We used current and future modelled species distributions for 191 terrestrial vertebrates from the Australian Wet Tropics Bioregion to prioritise the landscape for current and future conservation. Areas ranked highly for both current and future conservation are likely to function as refugia, more so if these areas are in close proximity.

2. PROPERTIES OF REFUGIA FOR BIODIVERSITY UNDER CLIMATE CHANGE

2.1 Authors

April E. Reside, Justin A. Welbergen, Ben L. Phillips, Luke P. Shoo, Steve E. Williams (James Cook University)

2.2 Summary

In this section we review the recent diversification of the term ‘refugia’ and clarify our working definition. We then discuss the key properties that make ‘refugia’ effective in promoting species persistence and ecosystem resilience, and point to ways in which we might identify refugia under climate change.

2.3 Introduction

Climate change and associated changes to sea level, fire regimes and extreme weather events, are expected to affect terrestrial biodiversity at all system levels, including species-level reductions in range size and abundance, exposing many taxa to increased risk of extinction (e.g., Thomas et al. 2004, Malcolm et al. 2006, Jetz et al. 2007, Sekercioglu et al. 2008, Thuiller et al. 2008). In this report we predominantly take the view that ***refugia are habitats that components of biodiversity retreat to, persist in, and can potentially expand from under changing climatic conditions*** (Keppel et al. 2012). Indeed, because the same area will often act as a refugium for many species, protecting refugia can greatly increase the cost effectiveness of conservation measures. Therefore, the identification of refugia in the landscape has been nominated as a key climate change adaptation priority (Groves et al. 2012, Shoo et al. 2013).

There is ample evidence that refugia have facilitated the survival of species during past climatic changes (Taberlet et al. 1998, Tzedakis et al. 2002, Byrne 2008a, Binney et al. 2009, Carnaval et al. 2009). This has resulted in expanded interest in refugia due to their potential to be safe havens for biota under projected anthropogenic climate change (Noss 2001, Loarie et al. 2008). This increased interest in refugia has led to a confusing diversification in the use of the term; hence our clarification of how we use refugium in this report. The increasing recognition of the importance of refugia from climate change has lead to a surge in conceptual and practical deliberations regarding the defining properties of refugia and how best to find them in the landscape (Ashcroft 2010, Keppel et al. 2012, Keppel and Wardell-Johnson 2012). To help bring this discussion forward, we review the key properties that make climate change refugia effective in promoting species persistence.

2.4 Key properties of refugia

2.4.1 Safeguarding long-term population viability and evolutionary processes

The properties required by refugia to safeguard evolutionary processes are similar to the modern principles of reserve system design: individual refugia need to be of sufficient size to sustain a population without any erosion of genetic diversity (Ovaskainen 2002). Moreover, a set of refugia should capture a large enough range of habitats and areas so that within-species genetic diversity can be maintained. A set of refugia meeting this latter criterion allows longer term evolutionary processes, such as speciation and lineage sorting, to play out.

The size of a refugium is obviously species-specific. Small body size, capacity for asexual reproduction (clonal growth or parthenogenesis) and light genetic loads favour survival in small refugia (Mosblech et al. 2011). Thus, if an area acts as a refuge for larger, sexual species (such as vertebrates), then it will also likely be of sufficient size for the more numerous smaller species that use the same habitat (Simberloff 1998). Therefore, a focus on identifying refugia for vertebrates likely captures areas that will act as refugia for invertebrates and many plants (subject to proximity constraints, see 2.4.2). Minimum refugium size will also depend on site-based factors such as latitude, productivity and environmental heterogeneity. Greater within-site heterogeneity provides more opportunities for species to withstand change and therefore greater refugial potential. Overall, however, larger refugia, and a larger set of refugia, have a higher likelihood of maintaining viable populations of many species (Ovaskainen 2002).

2.4.2 The availability, or proximity, of refugia

A critical attribute of a refugium is its availability. Is it close enough for a given species to use in the future? The most obvious demarcation point in this regard is whether the refugium is in situ (within a species' range) or ex situ (outside the species' range). In-situ refugia provide better prospects for species persistence because fewer (and shorter) range-shifts are required. The ability of species to reach ex-situ refugia, on the other hand, will depend on the distance from the current species range, the range-shifting ability of the species, whether individuals can survive and reproduce in the intervening habitat, and whether there are any physical barriers to dispersal (e.g. rivers, mountain ranges).

Landscape position and structure influence refugial availability. High topographic variability can reduce the distance a species is required to move to track its climatic envelope, and therefore rugged regions often provide effective refugia (Tzedakis et al. 2002, Sandel et al. 2011). However, the reverse may be true for species already confined to mountain tops. In this case, the nearest refugia may be many thousands of kilometres away at higher latitudes, with lowlands creating a dispersal barrier (Laurance et al. 2011). In this light, it is important to remember that there is a latitudinal gradient in dispersal ability for some taxa, with tropical species physiologically and behaviourally less suited to dispersal than their temperate counterparts (Salisbury et al. 2012).

Connectivity of habitats throughout the landscape will facilitate species movement to ex-situ refugia, especially as the spatial locations of refugia themselves may shift. Connectivity will also allow species to track their climatic niche more generally. Connectivity is difficult to quantify; the many different metrics all seem to perform better in some situations than others. Generally, however, patches that are closer together tend to be more highly connected. In the context of climate change, then, we see that areas of future suitable habitat that are close to current habitat will usually be more highly connected.

2.4.3 Protecting species from the impact of climate change

Protecting species from the direct impacts of climate change is arguably the most important attribute of contemporary refugia. Refugia for Australian species need to provide protection from changes in temperatures and precipitation, and from their flow-on effects such as changes in fire regimes and in the frequency and intensity of cyclones, droughts and floods (BoM-CSIRO 2006, IPCC 2007, Beaumont et al. 2011). Climatic change influences fire regimes, but due to the complex interactions between fire, rainfall, temperature, wind, vegetation, carbon dioxide enrichment and land management, predicting future fire has many uncertainties. Species differ in their requirements with regards to fire; therefore, refugia for some species might be an absence of fire, or maintenance of the preferred fire regime (Roques et al. 2001, Andersen et al. 2005).

Climate change will also drive distributional shifts in many species (Taberlet and Cheddadi 2002). These abiotic changes will impact on species interactions, which has already been observed in a range of studies (Visser and Holleman 2001, Winder and Schindler 2004), and this is considered one of the key proximate causes of population declines and extinctions related to climate change (Cahill et al. 2012). Our working definition of refugia as places where species can 'move to and persist in' (sensu Keppel 2012) implies that we look favourably on places where there are many immigrant species. This approach obviously runs the risk that novel, possibly negative, species interactions erode the biodiversity benefits of such high immigrant refugia. Thus effective refugia may also be areas where species turnover is low, such that the cohesiveness of ecosystems is maintained and deleterious interactions from invasive or new competitor species are minimised. We explore both situations in this report.

2.5 The 'ideal' climate change refugium

In general, ideal climate change refugia are areas where the current climate will be best conserved into the future. Additionally, the ideal refugium is environmentally stable, accessible, and large enough to allow population persistence and the maintenance of evolutionary processes. Where such areas are, however, obviously depends on the species in question. One unifying theme, however, is the idea of stability over time. An area with the least environmental change into the future has a greater likelihood of suiting the most species that are currently in situ, when compared to landscapes that are changing at a greater rate. Evidence for this can be found in studies that look at endemism and diversity in relation to past climatic stability (Sandel et al. 2011): climatic stability has been shown to be an important component of long-term refugia (Tzedakis et al. 2002, Jansson 2003, Carnaval et al. 2009, Mosblech et al. 2011), particularly for species with low dispersal abilities (Graham et al. 2006, Carnaval et al. 2009).

2.6 Planning with refugia

Identifying refugia that can protect against multiple threats will be essential for the persistence of biodiversity. It is increasingly recognised that it is usually a suite of processes that causes species extinction. Effective refugia provide buffers against climate change in addition to other threatening processes, particularly land modification. However, conservation decisions do not happen in a vacuum. They are influenced by other objectives, such as the increasing requirement for food crops as human populations grow and the increasing need to preserve ecosystems that are good carbon traps (Thomas et al. 2012). Optimising these various objectives and projecting solutions onto maps, is the domain of conservation planning; a field that now has some very sophisticated tools at its disposal. Chief among these are the planning optimisation tools such as Marxan and Zonation (Moilanen et al. 2012 and references therein), which balance competing priorities to determine locations of maximum conservation worth. Given the right inputs, these tools not only delineate areas that will act as refugia, but can rank them according to numerous metrics of quality (e.g. cost, connectivity, carbon capture capacity).

2.7 Conclusions

Natural systems are under threat from unprecedented planetary engineering by human activities (Brook et al. 2008). This erosion of the ecological baseline results in species that are less resilient to rapid climate change (Millennium Ecosystem Assessment 2005). A concerted effort will be required to moderate all threats if biodiversity conservation is to be achieved into the future. Identifying and protecting refugia in the landscape that shield species from all aspects of climate change are crucial steps to fulfilling this aim. Effective refugia will be those that protect biodiversity from multiple climate change threats through buffering against climatic change and minimising species losses. In addition, refugia will also need to protect against other non-climatic threatening processes and meet other socio-economic goals. Spatial conservation planning tools now exist to identify optimal sets of areas that meet all these criteria.

3. IDENTIFYING REFUGIA THROUGH SPECIES DISTRIBUTION MODELLING

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3.2 Introduction

Buffering from climate change is one of the properties of a good refugium as identified in our review (section 2). We examine this first by looking at the shift in climate across the continent, both in the past and into the future. We then identify areas where a small shift in space can mitigate the climate shift at a specific location (e.g. a small shift uphill can reduce temperatures by several degrees). In this way we identify areas where species have been or will be buffered from climate change.

Following these analyses, we examine the responses of individual species distributions. We aimed to identify areas where large numbers of species could retreat to or persist in over the next 72 years. We acknowledge that minimising species turnover might be an alternative aim (because this buffers against novel, but as yet unknown species interactions), but we address this aim briefly here and more extensively in Case Study 1. To identify areas where large numbers of species could retreat to or persist in over the next 72 years, we analysed shifts in the distribution of individual species as a consequence of both past and future climate change. By mapping these shifts for many species, we can then identify areas where local species are maintained (minimising species requirements to move into the future), but which also act as refugia for nearby immigrant species.

3.3 Research activities and methods

3.3.1 Climate data

Current climate was generated from daily weather surfaces of temperature and rainfall accessed from the Australian Water Availability Project (AWAP: Jones et al. 2007, Grant et al. 2008). Current climate was defined as the 30-year average centred on 1990; therefore, it is the average climate from 1976 to 2005. Future climate projections were sourced from the Tyndall Centre (http://climascope.wwfus.org/). Eighteen global circulation models (GCMs) and four representative concentration pathways (RCPs) were selected to yield projections of future climate at 2085 (APPENDIX 1. Climate scenarios and bioclimatic variables).

Standard bioclimatic variables 1–19 (Table A1-4 in APPENDIX 1. Climate scenarios and bioclimatic variables) were generated using the 'climates' package in R (VanDerWal et al. 2011a) and are equivalent to the bioclim variables derived using Anuclim 5.1 software (Hutchinson et al. 2000). Analyses were based on the RCP scenarios (APPENDIX 1. Climate scenarios and bioclimatic variables), as recent work has shown that the range of emissions and temperature increases predicted by the RCPs is consistent with the Intergovernmental Panel on Climate Change (IPCC) Special Report on Emission Scenarios (SRES) (Nakicenovic et al. 2000). In addition, the temperatures projected for the highest RCP (8.5) is mostly consistent with the highest RCP reported in the SRES (A1FI) which lends support to the realism of both classes of scenarios (Rogelj et al. 2012). We focus our analyses on the worst-case scenario, RCP 8.5. This is justified for a number of reasons: (i) the current trajectory of radiative forcing and emissions are most closely aligned with this RCP; (ii) by using the worst-case scenario we have covered the spectrum of outcomes, as the difference between the RCPs is the severity of change, rather than the direction of change; and (iii) presenting several scenario outputs results in a dizzying proliferation of outputs which are difficult to assimilate. Examination of future climates under the different RCPs are detailed in APPENDIX 2. Climate stability.

Past climates were based on snapshot retrodictions at up to 1-kyr intervals covering the last 120 000 years using the Hadley Centre Coupled Model (HadCM3) (Singarayer and Valdes 2010). These were prepared for the project as per Fuchs et al. (2013). Monthly temperature and precipitation anomalies were downscaled using a bilinear spline to 0.2 degrees Celsius and then bicubic spline to 0.0466667 degrees globally and the anomalies were then applied to current monthly climates given the ‘125 m lower sea levels’ provided by Robert Hijmans (unpublished data; methods as per Hijmans et al. 2005). Mean annual temperature, temperature seasonality, mean temperature of the warmest and coldest quarters, mean annual precipitation, precipitation seasonality and precipitation of the wettest and driest quarters were recreated for each time slice into the past. All climate surfaces were clipped to ‘dry land’ based on sea levels. Past sea levels were estimated as the consensus of three sources: Lea et al. (2002), Robert A. Rohde (unpublished data, Global Warming Art project available at http://en.wikipedia.org/wiki/File:Post-Glacial_Sea_Level.png and derived from (Fleming et al. 1998, Fleming 2000, Milne et al. 2005) & http://www.ncdc.noaa.gov/paleo/ctl/clisci100k.html#sea.

All downscaling and calculation of climate surfaces were done using the climates package (VanDerWal et al*.* 2010) and R2.9.0 (www.r-project.com).

3.3.2 Environmental stability

Maps were created that show the projected change in climate that species will be exposed to (referred to here as ‘exposure surfaces’). Exposures surfaces generated for Australia include the absolute change in annual mean temperature (‘temperature’ hereafter) and annual mean precipitation (‘precipitation’ hereafter) as well as the relative change in temperature and precipitation. The relative measure was made using the standard deviation (SD) of current inter-annual variation in these climate metrics. Why the standard deviation? We know that 67% of current annual mean temperatures are within 1 SD of the total (across-year) mean; 95% of current temperatures are within 2 SDs of the total mean. This means that if an area experiences an increase in annual mean temperature of 2 SDs, then 97.5% of current annual mean temperatures in this area are less than the shifted mean temperature. This is important information because most organisms have evolved within the bounds of the inter-annual variation in their environment. When the mean temperature begins to exceed even the bounds set by inter-annual variation in temperature (>2 SDs), the likelihood of the organism being adapted to the new conditions is very low indeed.

The exposure surfaces were created for both future projected climate, as well as for retrodicted past climate. For the future exposure surfaces, the absolute change is represented as the absolute change in temperature between current and 2085, and the proportional change in precipitation between current and 2085. The next exposure surfaces represent the number of standard deviations away from the current climate the future temperature and precipitation are at 2085. The exposure surfaces were calculated for each RCP and GCM for 2085. The results for RCP8.5 are presented in this report. These outputs were summarised across the 18 GCMs to produce the 10th, 50th and 90th percentiles to represent the medium range and the extreme climates predicted by the GCMs (for detailed output, see APPENDIX 2. Climate stability), and were done in conjunction with another NCCARF project (James et al. 2013). For the retrodicted past climate, the absolute change and relative change away from current climate were summarised for 7000, 24 000 and 120 000 years before present; these times represented the extremes of climate over the last 120 000 years: the Holocene Climatic Optimum, Last Glacial Maximum and Last Interglacial Period.

We use the median across GCMs of the future layers of temperature and precipitation as the basis for all further analyses. We take the median of the future projections and calculate the 10th percentile of the absolute and relative shifts to highlight the areas that are projected to change the least into the future. We will use the tenth percentile (or 90th percentile, where appropriate) extensively in summarising our results. Using the 10th percentile identifies the 10% of the continental area where climates changes the least. The 10th percentile of the retrodicted past layers of temperature and precipitation for each of the three time points was also calculated. The 10th percentile layers were converted to binary, so that everything below the 10th percentile scored one, and everything above the 10th percentile scored zero. To identify parts of the continent with the least paleological change, the binary past 10th percentile models for the three paleological snapshots were averaged. Therefore, together the three past layers had equal weighting as the future layers when we calculated the sum of these with the future 10th percentile binarised layer. This sum across paleological and future layers gives us an indication of which places were stable in the past and remain stable into the future.

Using the same methodology, recent past climate layers were also created to show the rate of change of temperature and precipitation between 1950 and 2010 (VanDerWal et al. 2013). The analyses were conducted in R version 2.15.0 using the ‘SDMTools’ package (VanDerWal et al. 2011b).

3.3.3 Distance surfaces

The climate may change dramatically at a focal location, but if there is large variation in climates in the location’s vicinity, a population may track its suitable climate by moving only a small distance. On the other hand, if climate is largely homogenous for large distances around the focal location, a population will have to move too far and too fast to track its suitable climate across the landscape. Thus, a useful measure of climate change impact is the distance a population would have to move to remain within a suitable climate space.

Distance surfaces were created which represent the shortest distance a population would need to move to remain within 2 SDs of current temperature, and 1 SD of current precipitation, for each time step, and each RCP and GCM. Two SDs was considered a meaningful limit for species (Palmer and Raisanen 2002, Beaumont et al. 2011), but we used the more stringent 1 SD for precipitation because of the extreme inter-annual variation inherent on this measure in Australia. The Euclidean distance between the cell of interest and the nearest cell within the required SD (one for precipitation, two for temperature) was recorded for each cell. These surfaces were summarised across GCMs to produce the 10th, 50th and 90th percentiles. The analyses were created using both the ‘SDMTools’ (VanDerWal et al. 2011b) and ‘parallel’ packages in R (R Development Core Team 2011).

3.3.4 Species data

The study generated species distribution models (SDMs) for Australian vertebrates. We selected species for which adequate samples of presence records (i.e. locations at which the species has definitely been observed) were available. Species data were accessed from the Australian Atlas of Living Australia (ALA: http://www.ala.org.au/), the Centre for Tropical Biodiversity and Climate Change (CTBCC: https://plone.jcu.edu.au/researchatjcu/research/ctbcc) species data base (Williams et al. 2010) and from the Queensland Museum (http://www.qm.qld.gov.au/).

Only occurrence records which had been identified to species level were used, excluding undefined species and reassigning subspecies to species level. Aquatic species, amphibians, birds and mammals with fewer than five records, and reptiles with fewer than four records were excluded from our analyses. We chose to retain species of amphibians, mammals and reptiles with extremely restricted distributions and very small sample sizes (fewer than 10 records) on the basis that these taxa are of high conservation concern and that few records may still be adequate to characterise available environmental conditions within restricted ranges (for details see APPENDIX 3. Species distribution modelling data and model results). For species with adequate data for modelling, there were 239 mammal, 599 bird, 218 amphibian and 625 reptile species (Table 3). Vertebrate data were vetted by excluding points that fell into states or bioregions (Interim Biogeographic Regionalisation for Australia, Version 7; Environment Australia 2000) in which the species was known not to occur. Species' known occurrence range was taken from relevant field guides (Menkhorst and Knight 2001, Churchill 2008, Tyler and Knight 2009, Wilson and Swan 2010), online databases (http://www.arod.com.au/arod/) and from expert opinion.

Table 1: Vertebrate species presence data compiled for the project. 'Total records' is the total number of records for the whole class, 'mean records' is the mean number of records across all species within a class.

Class	Total records	Mean records
amphibians	151 943	394
birds	5 873 874	9806
mammals	355 580	1451
reptiles	249 551	664

3.3.5 Species distribution modelling

Species distribution models incorporating baseline climate data at 0.01 degree (~1x1 km) resolution and species occurrences were created using the Maxent package (Phillips et al. 2006). Maxent uses presence-only data to statistically relate distribution records to environmental variables and uses the principle of maximum entropy to develop the best model fit. Studies have compared techniques across species and biomes to rank their performance (Elith et al. 2006, Guisan et al. 2007), and although different techniques vary in their performance, there is generally more variation in performance across species within technique than across techniques (Guisan et al. 2007). However, detailed comparisons of techniques found that the newer methods, and in particular Maxent, consistently outperformed other techniques (Elith et al. 2006). SDMs are increasingly being used to predict species responses to anthropogenic climate change. There is evidence to show that this approach is likely to reflect realistic changes, such as the documented shifts in species distributions in recent times (Thomas and Lennon 1999, Parmesan and Yohe 2003, La Sorte and Thompson 2007, Maclean et al. 2008). In addition, the few new phenotypes found in the Pleistocene fossil record corresponding with rapid temperature shifts suggests that species are more prone to shift their ranges to track favourable climatic conditions rather than to remain in place and evolve new forms (Parmesan 2006).

The climate variables used in this study were: (i) annual mean temperature; (ii) temperature seasonality; (iii) maximum temperature of the warmest period; (iv) annual precipitation; (v) precipitation of the driest period; vi) precipitation of the wettest period; and (vii) precipitation seasonality. Presence-only modelling methods can be subject to sampling bias (Yackulic et al. 2013); we account for this potential bias by using a target-group background, which consisted of the locations of the occurrence records for the species within that class, as recommended by Phillips et al. (2009). Using the target group as our background points, it is assumed that any sampling bias in our occurrence records for a single species can also be observed in our background points; in effect cancelling out the impact of any spatial sampling bias in the modelling exercise (Phillips and Dudik 2008, Elith and Leathwick 2009, Phillips et al. 2009).

Species distribution models were projected onto future scenarios consisting of the worst-case scenario RCP8.5 and 18 GCMs for 2085. This RCP was used for the same reason it was used for examination of future climate. Namely, the current trajectory of radiative forcing and emissions are most closely aligned with this RCP, and by using the worst-case scenario we have covered the spectrum of outcomes, as the difference between the RCPs is the severity of change, rather than the direction of change. Across the 18 GCMs, the 10th, 50th and 90th percentiles were calculated to give the median projection and a measure of across-model variance (a measure of uncertainty in our projections). Due to the large number of species used in this analysis, we focussed on the shifting climate space of potential distributions by assuming that all species had unlimited dispersal. This assumption is clearly unrealistic, but interpretation of our results (section 3.4) is not dependent on the assumption being true.

The default Maxent distribution output is a continuous prediction of environmental suitability for the species. The output species distribution models for current climate were vetted by comparing the predicted distribution model to the published distributions (generally equivalent to the Extent of Occurrence based on a minimum convex polygon) of the species: again, taken from relevant field guides (Menkhorst and Knight 2001, Churchill 2008, Tyler and Knight 2009, Wilson and Swan 2010, Vanderduys 2012), online databases (http://www.arod.com.au/arod/) and from expert opinion. A binary distribution output was created by applying an appropriate threshold obtained from the Maxent results output file. Two Maxent-generated thresholds were trialled: ‘equate entropy of threshold and original distributions logistic threshold’ and ‘Maximum training sensitivity plus specificity logistic threshold’ for each species. The one best representing the known distribution of the species was used (APPENDIX 3. Species distribution modelling data and model results). The same threshold was used for the species current and future distribution projections. Applying this threshold generates a map of where we realistically expect the species to be under a given climate.

Model performance was evaluated by the area under the receiver operating characteristic curve (AUC). AUC measures each model’s consistency and predictive accuracy (Ling et al. 2003). An AUC score of 1 is a perfect model fit of the data; 0.5 is no better than random (Elith et al. 2006, Phillips et al. 2006). AUC values ≥ 0.7 indicate ‘useful’ models, whereas values ≥ 0.9 indicate models with ‘high’ performance (Swets 1988). Models for each species were screened for low AUC (<0.7) so that underperforming models were not included in further analyses. In cases where the AUC for a widespread species was low (0.683–0.739), but the output model was a good representation of the species range (as determined by the vetting process outlined above), this species model was included in the species richness analyses. The

AUC score is negatively correlated with distribution area, and widespread species often have lower AUC scores (Reside et al. 2011). This happened for eight mammals, half of which were bats (APPENDIX 3. Species distribution modelling data and model results).

Using these species distribution maps, current spatial patterns of species richness were created for all four taxonomic groups (amphibians, birds, reptiles, mammals) by summing the binary species distribution layers. Similarly, for future projections of species richness, the species models for each of the GCMs were summed to provide a species richness model per GCM. Species richness across the 18 GCMs were then summarised for the 10th, 50th and 90th percentiles (to demonstrate uncertainty across climate projections). The future projected species richness was also calculated as the proportion of the baseline species richness by dividing the predicted median species richness in 2085 by the baseline species richness.

Species richness and *changes* in species richness alone are not necessarily useful metrics. If there were originally 10 species in an area, and all those species are replaced by a different 10 species, then richness does not change despite a complete upheaval of the original community. Thus, we also explicitly calculated species turnover for each grid cell. To do this, we calculated the number of species that are projected to move into each grid cell by 2085 (‘immigrants’) and species that occurred in each grid cell but are projected to move out by 2085 (‘emigrants’). The total species turnover is simply the sum of immigrants and emigrants.

The individual immigrants’ and emigrants’ metrics were also expressed as a proportion of the species richness in 1990. Again, this proportion gives us a sense of the degree of compositional change likely to happen to any given community: a value of four for this metric indicates that the number of species moving into and out of a grid cell is four times greater than the current species richness at that cell. To summarise these outputs, we again used the areas representing the highest 10th percentiles of immigrants and lowest 10th percentiles of emigrants for each of the taxonomic groups. We created binary maps of these 10th percentiles. These eight layers (10th percentiles of immigrants and of emigrants for each of the four taxonomic classes) were summed, showing the areas of that maximised the biotic refugial potential. We also examined the areas with the least number of immigrants, as these are important for finding the areas of greatest stability in species composition. The lowest 10th percentile of immigrants were calculated for each taxonomic group.

3.4 Results and outputs

We present here models of the areas of Australia with the overall lowest shifts in climate (across both past and future) as well as areas with the greatest biotic refugial potential (across both past and future) (Figure 1). The figures demonstrate a clear overlap in refugial potential of areas assessed from both a climatic and biotic perspective. Across both climate and species metrics, southern and eastern Australia change the least. The details of each step taken to reach these outputs are detailed in the rest of this section.

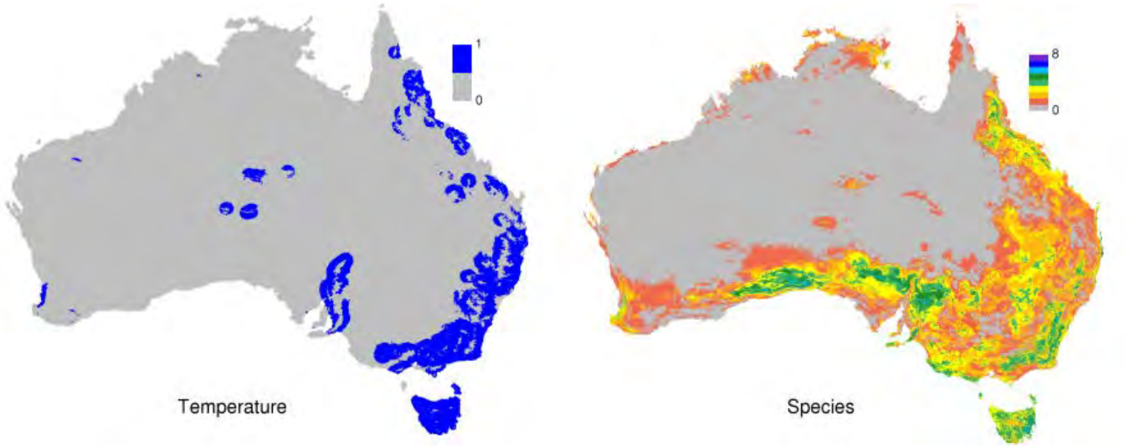


Figure 1: (Left) The areas of Australia that have the greatest stability in temperature (the 10th percentile of the minimum distance an organism would have to travel by 2085 to stay within 2 SDs of current norms are shown in blue); (Right) the areas with the greatest biotic refugia potential between now and 2085. The biotic refugia potential index (as shown in Figure 24) is the aggregation of the highest percentile for modelled incoming and lowest percentile for modelled outgoing species in each of the four taxonomic groups summed together. The darker colours indicate the highest score, which corresponds to the greatest overlap of indices. The two approaches give broadly concordant results. Increasing values on the scale bars indicate increasing climate stability and increasing biotic stability respectively.

3.4.1 Environmental stability

Here we investigated change in climate in the past as well as that of a projected future. We measured shift in climatic variables on both an absolute scale (for annual mean temperature), a proportional scale (proportional difference from current precipitation), and a relative scale (for both temperature and precipitation). The relative measure was the SD of current inter-annual variation in our climate metrics.

When examining future climate projections, there is inevitable uncertainty, much of which is captured by variation across the various GCMs used to develop climate projections. Therefore, for all our inference about the future, we report results across the 18 GCMs under the RCP that we are most closely tracking (RCP 8.5, which is the IPCC’s worst- case scenario).

The future climate projections show that here are very few parts of the Australian continent that will see temperature shifts less than two SDs above current conditions. The full range of outcomes across different RCPs and GCMs can be found in APPENDIX 2. Climate stability. These are shifts of similar magnitude (but opposite in direction) to those seen during the last ice age (changes which occurred over thousands of years, instead of the 72 years of our forecast period).

As well as assessing the projected climate change, we also assessed paleological climate change. The reason paleological climate change is important is because regions with little climate change in the past tend to be rich in endemic species and species that are less resilient to future climate change. By identifying areas with high paleological climate stability, we expect to identify areas where the largest number of endemic, low- resilience species are likely to live. If these areas are not the same as our refugia under climate change, then we are at increased risk of biodiversity loss.

Finally, we assess climate change through time as well as through space. If small range-shifts can ameliorate climate change, then species will persist in these areas (by moving) despite a changed climate in their original range.

3.4.2 Past: interglacial

The paleological record of annual mean temperature between the current day and those of 7000, 24 000 and 120 000 years ago shows that temperature has fluctuated from a little over four degrees cooler, to just over two degrees warmer than current (Figure 2). In particular, many coastal areas had the greatest relative shift in annual mean temperature during the Last Glacial Maximum. During the Holocene Climate Optimum and Last Interglacial, many of the areas that differed least from current climate were found in the east of the continent.

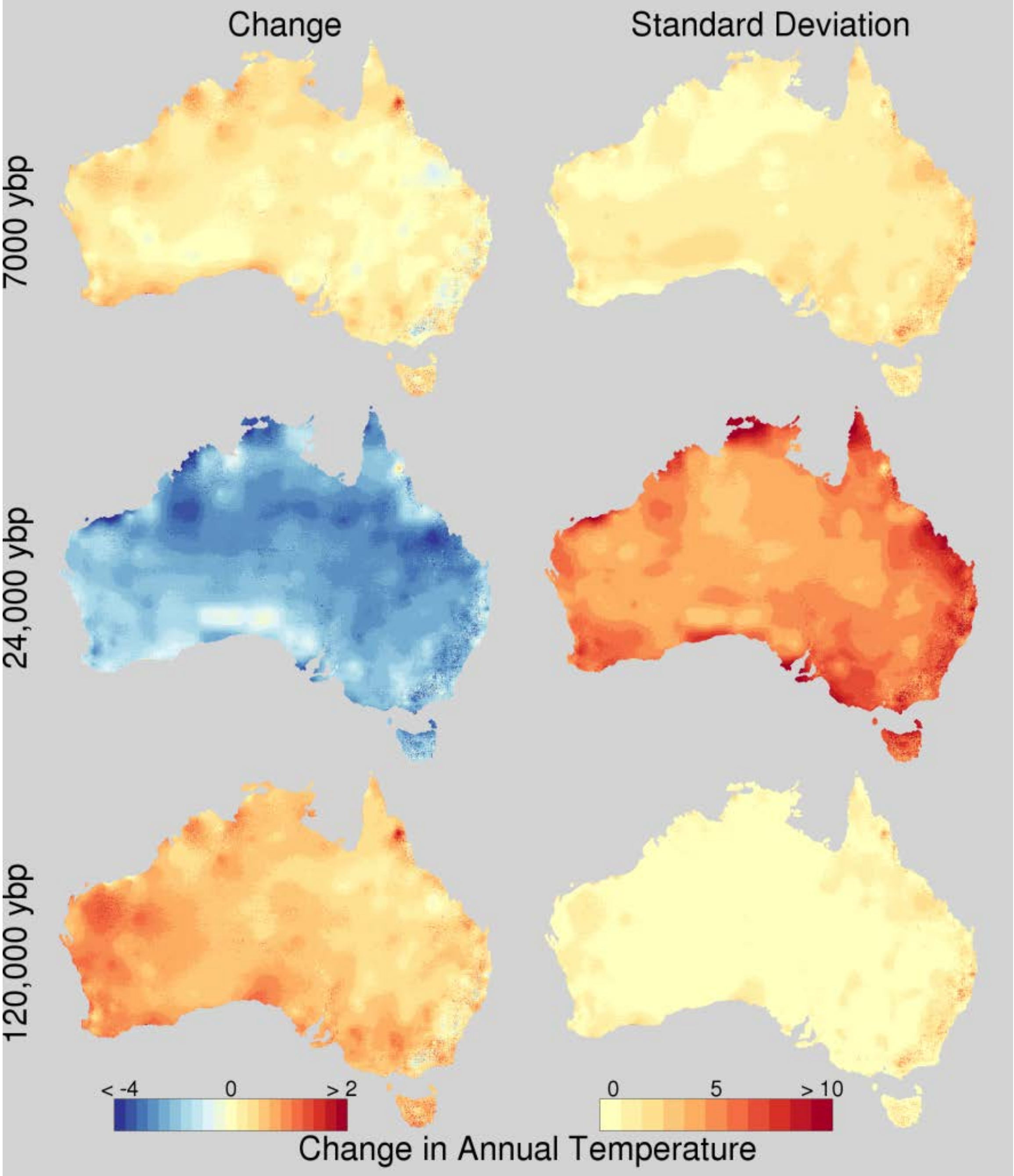


Figure 2: The absolute change (left) and number of standard deviations away (right) from annual temperature in 1990 (°C), shown for the retrodicted temperature of 7000, 24 000 and 120 000 years ago. For the absolute change, blue colours indicate a cooler temperature than current, warm colours indicate a warmer temperature than current.

Precipitation did not shift as uniformly over the three past time points as did temperature (Figure 3). The north of the Northern Territory was consistently wetter for all three time periods, but this was most pronounced during the Last Glacial Maximum when it was over 50% greater than today. The upland regions of the Einasleigh Uplands and Wet Tropics of north-east Queensland consistently received more rainfall than present, although other parts of the Wet Tropics were consistently drier. Central Australia was largely drier than current across the Holocene Climate Optimum and the Last Glacial Maximum, but was wetter in some areas during the Last Interglacial. The areas that differed most from current variation include the northernmost Northern

Territory, the Great Australian Bight and western Tasmania, and this was most pronounced during the Last Glacial Maximum.

Importantly, and this is a theme that recurs with precipitation, the relative measure consistently suggests very low overall shifts in precipitation relative to the inter-annual variation. That is, much of the Australian continent experiences very high inter-annual variation in rainfall, and against this backdrop, paleological climate change has not shifted annual precipitation levels greatly.

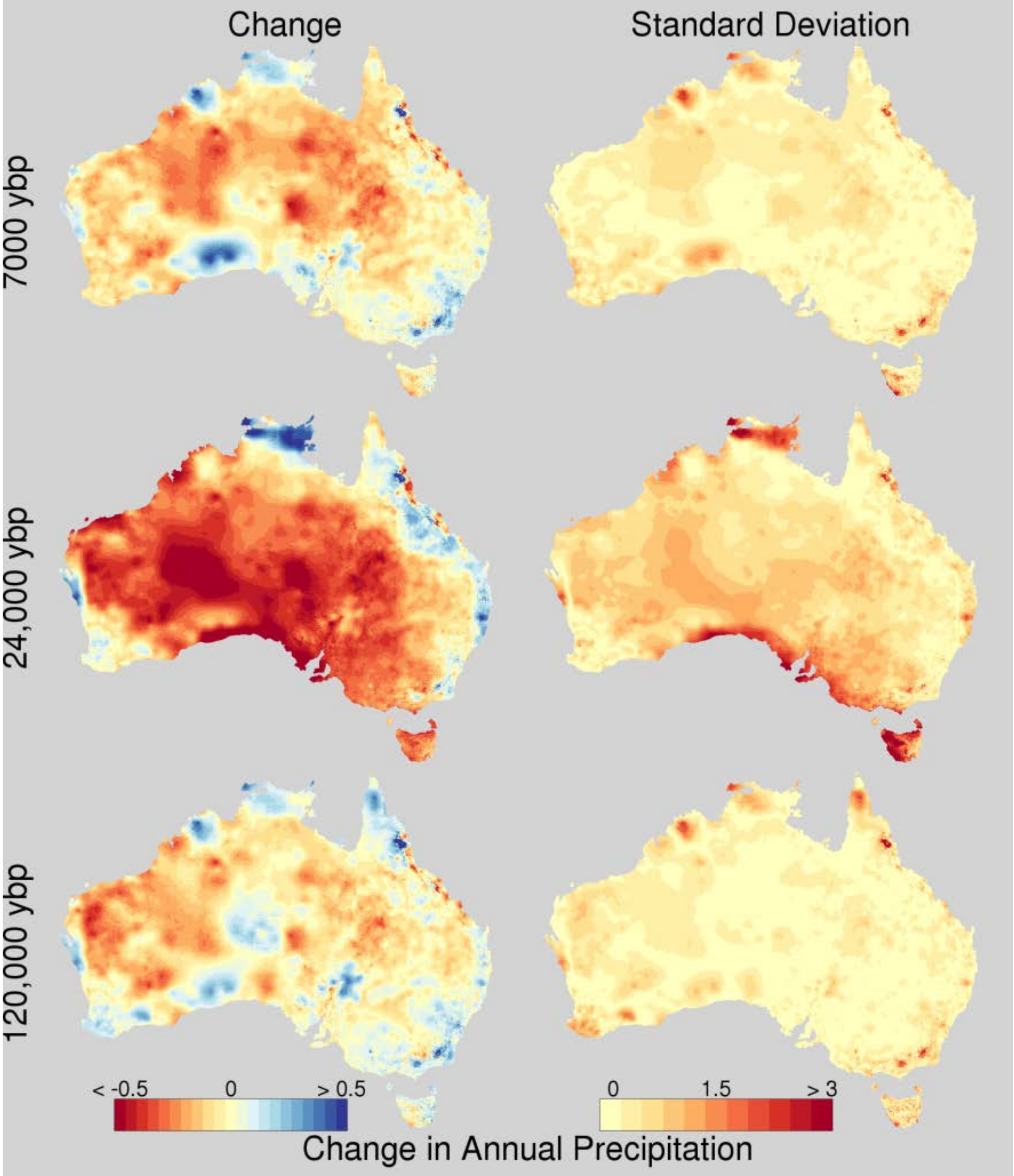


Figure 3: The proportional change in (left) and number of standard deviations away from (right) annual precipitation (mm) in 1990, shown for the retrodicted annual mean precipitation of 7000, 24 000 and 120 000 years ago. For the relative change, blue colours indicate higher precipitation than current, warm colours indicate less precipitation than current.

The binary models showing the 10th percentile of temperature change from current highlight the areas that have changed the least (Figure 4). The southern coast and the south-west of the continent consistently show the least change for both the Holocene Climate Optimum and the Last Glacial Maximum. The area that shifts the least from current variation in temperature was found in the north-west Northern Territory, from the Victoria Bonaparte down to the Tanami Desert.

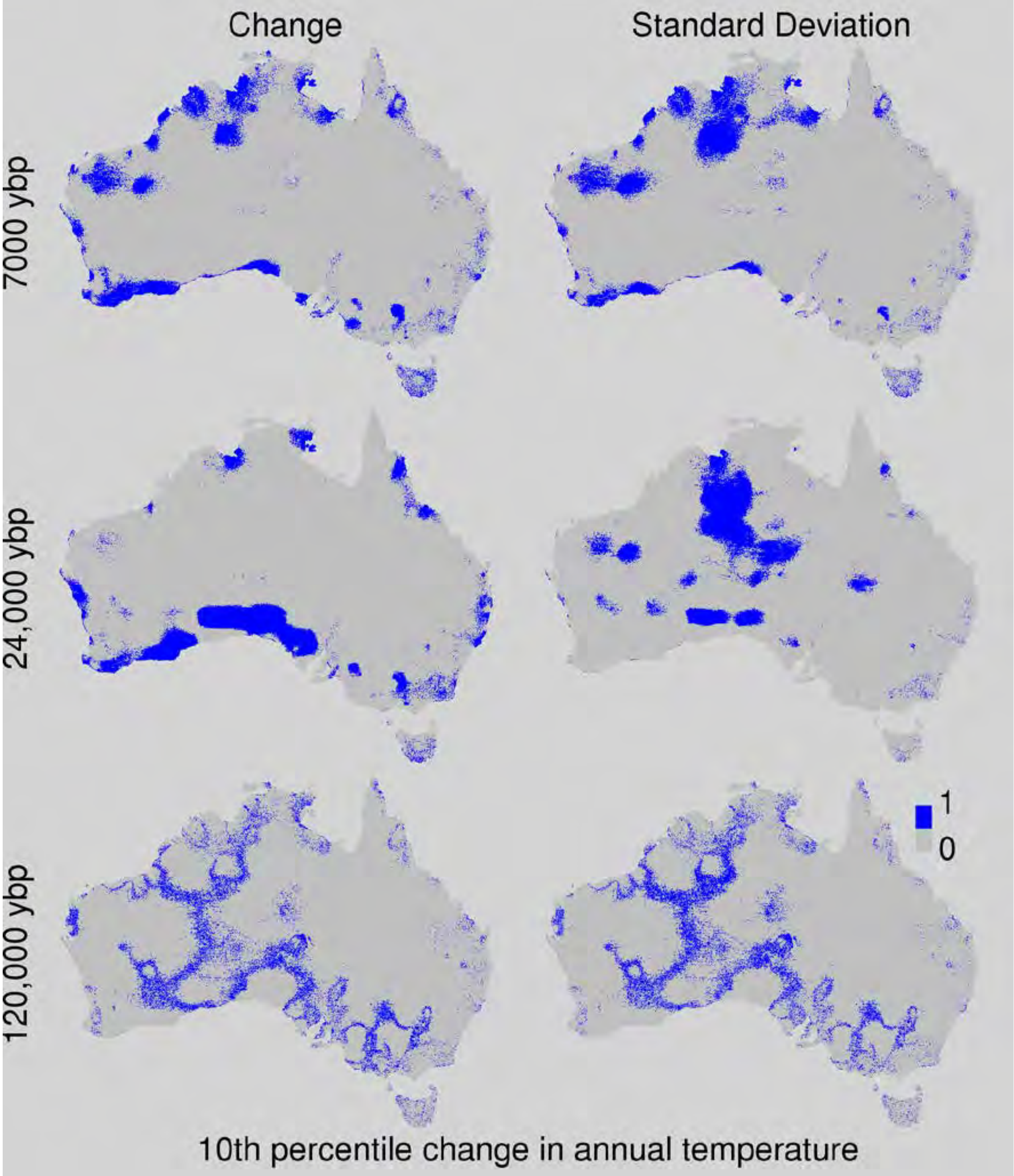


Figure 4: The 10th percentile of least paleological change for annual mean temperature.

The areas of least change in paleological precipitation are largely concentrated around the coast, and this is most pronounced during the Last Glacial Maximum (Figure 5). Eastern Australia contains the areas of least change in precipitation for each of the three time periods, but the exact areas within eastern Australia shift.

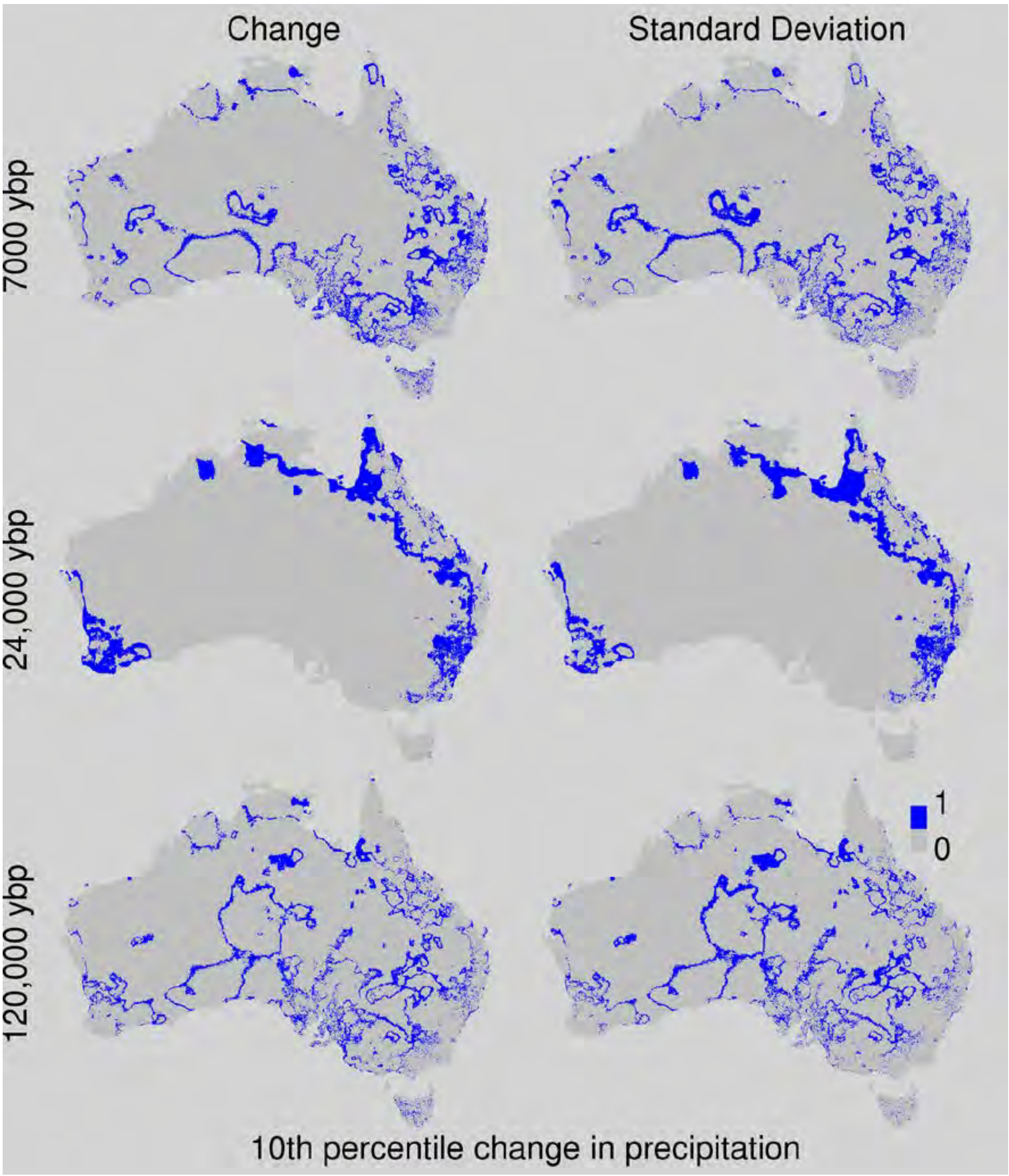


Figure 5: The 10th percentile of least paleological change in annual precipitation.

3.4.3 Recent: previous 60 years

Climate over the recent past indicates our current climate trajectory. Alarmingly, some parts of the country are already experiencing annual mean temperatures two degrees warmer than those of the 1950s. Precipitation has also shown pronounced shifts, with an overall small shift in continental precipitation belying strong spatial patterns — some of the most arid regions of Australia now experience double the annual precipitation they were receiving in the 1950s.

Recent changes of climate per year were examined for the time period with adequate data, which was from 1950–2010 (VanDerWal et al. 2013). Temperature has increased most in inland central Queensland, and northern Tasmania (Figure 6). Other areas with large increases in temperature since 1950 include some areas of the Nullarbor and south-western Western Australia. The areas with the least increase, and even very slight decreases, in temperature are north-west, including the northernmost part of Western Australia and the Northern Territory. Much of Australia has seen an average increase in precipitation per year. The greatest increases in precipitation over the recent past were found in the north-west of Australia, whereas decreases in precipitation were found along the east coast.

We did not express these changes in relative terms (as SDs as per previous sections) because of the uncertainty associated with estimating an instantaneous inter-annual variance in temperature and precipitation. The absolute changes are, nonetheless, strongly informative.

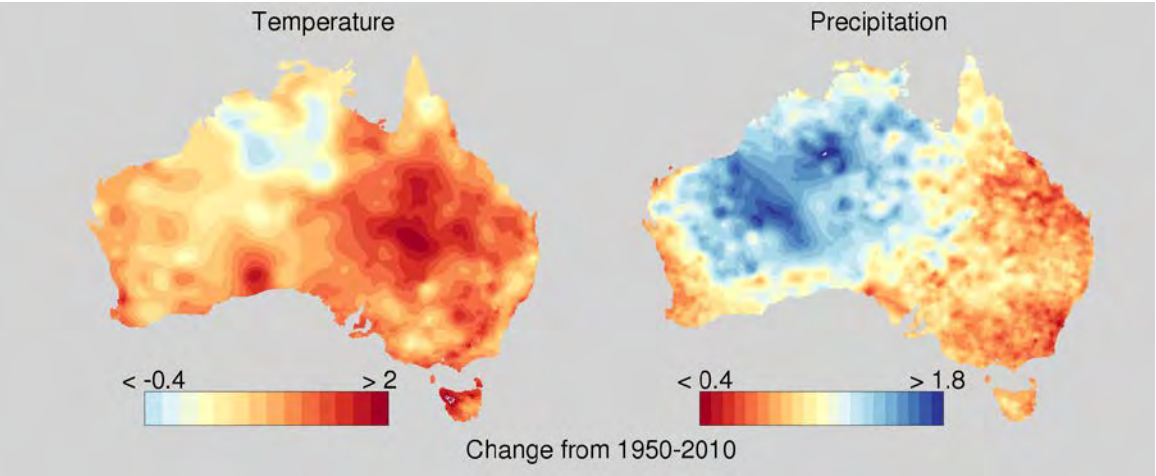


Figure 6: The average absolute change in temperature (°C) and proportional change in precipitation for the period 1950–2010.

The areas with the lowest absolute change (10th percentile) in temperature and precipitation for the period 1950–2010 are highlighted in Figure 7.

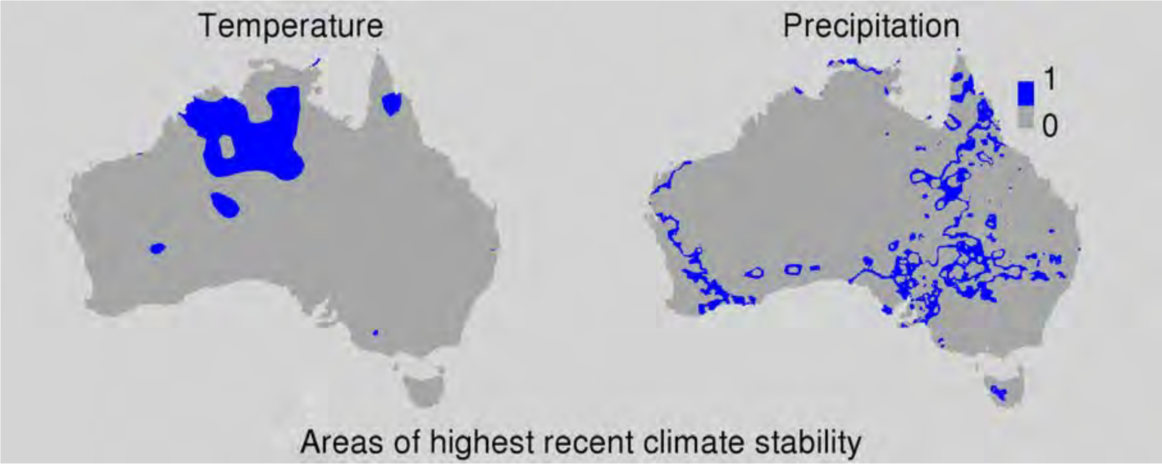


Figure 7: The lowest 10th percentile of absolute change in temperature and proportional change in precipitation over the period of 1950–2010, highlighted in blue.

3.4.4 Future: current–2085

The absolute change in temperature measure, shown for the 10th, 50th and 90th percentiles across 18 GCMs for RCP 8.5 at 2085, shows that north-west Western Australia has the greatest projected absolute change in temperature, particularly the Pilbara and Great Sandy Desert regions (Figure 8). The southern coast of Australia, much of the east coast and Tasmania have the least absolute change in temperature.

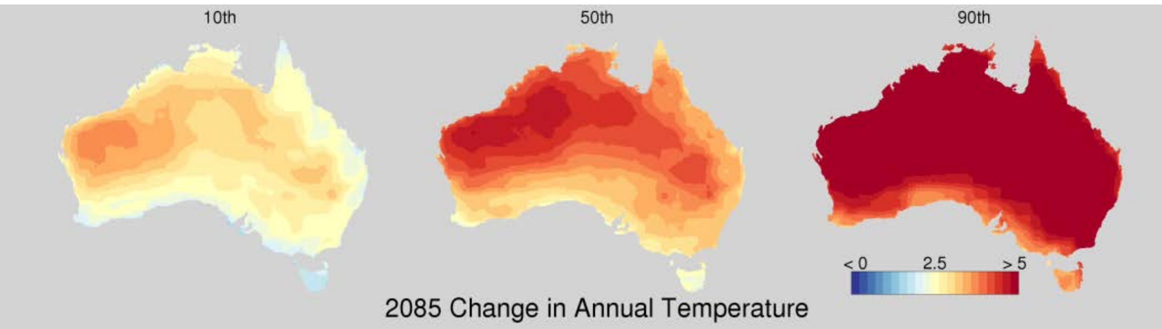


Figure 8: The absolute predicted change in temperature (°C) projected for 2085. The 10th, 50th and 90th percentiles across 18 GCMs are shown for RCP 8.5. All other RCPs are shown in APPENDIX 2. Climate stability.

Expressing this absolute change in relative terms (relative to current inter-annual temperature variation) gives a particularly alarming result (Figure 9). Our best estimate of future temperature change (e.g. most likely) has most of the continent experiencing temperatures that are around 5 to 7 SDs above the current inter-annual variation in temperature. To put this in perspective, **a shift of 5 SDs above normal inter-annual variation moves the *average* annual mean temperature to a temperature that might be experienced once every 3.5 million years under current levels of variation.** To put it bluntly, at this scale, there is likely to be no place on the continent that will not experience catastrophic increases in local temperature in the next 75 years.

If we ignore this stark prediction and focus instead on ranking areas by minimal impact, it is clear that coastal areas will face the greatest relative shift from current temperatures. **The 50th percentile output for 2085 shows that most of the coast of mainland Australia is likely to face temperatures greater than 7 SDs away from the current temperature mean** (average annual temperatures that might be experienced once every 781 billion years or so under current variation, which is a time period about 200 times older than the universe).

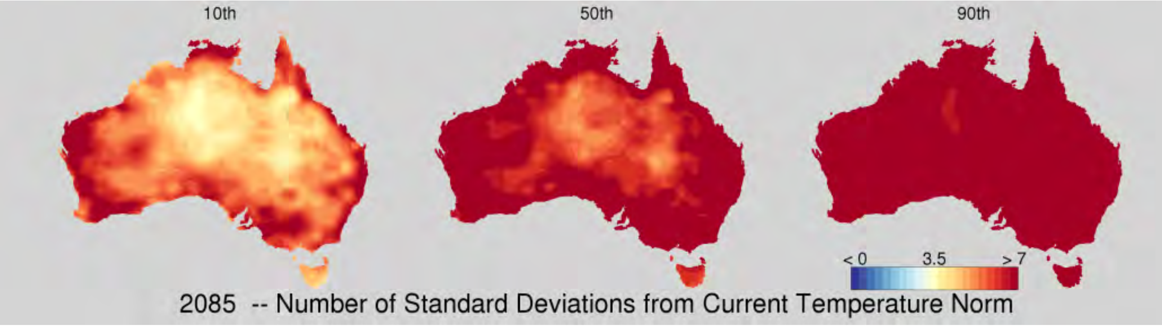


Figure 9. The number of SDs from current temperature (°C) projected for 2085. The 10th, 50th and 90th percentiles across 18 GCMs are shown for RCP8.5. All other RCPs are shown in APPENDIX 2. Climate stability.

By comparison, future projections of precipitation are far less daunting and vary substantially across different GCMs (Figure 10). The 10th percentile of precipitation (across GCMs) shows lots of areas with marked decreases in precipitation proportional to current; whereas the 90th percentile (across GCMs) shows many areas projected to increase in precipitation proportional to current. The main consistency across each of the percentiles is that south-west Western Australia is projected to experience a decrease in precipitation. The Northern Gulf country is projected to either not change or increase in precipitation, and for much of the rest of the country, the projections indicate either an increase or decrease depending on the GCM.

Thus there is considerable uncertainty in our projections of the impact of anthropogenic climate change on precipitation. Nonetheless, examining projected shifts in precipitation on the relative scale shows that, irrespective of the uncertainty, shifts in precipitation are likely to be very modest relative to current inter-annual variation in precipitation. At most, it seems, precipitation will increase or decrease by only around 1 SD of current inter-annual variation. That is, irrespective of the GCM, most parts of Australia will see annual rainfall totals that overlap substantially with those that we currently observe.

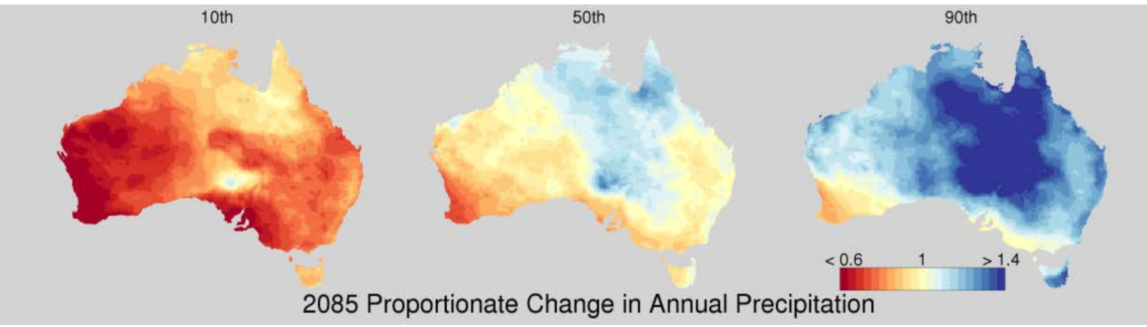


Figure 10: The proportional change in precipitation projected for 2085. The 10th, 50th and 90th percentiles across 18 GCMs are shown for RCP8.5. All other RCPs are shown in APPENDIX 2. Climate Stability.

The relative shift in precipitation shows a similar pattern to the proportional change in precipitation (Figure 11). Again, south-west Western Australia is projected to have the greatest decrease in precipitation compared to the current precipitation variability. The Northern Territory and northern Queensland are likely to experience an increase in precipitation outside the current range, but projections vary substantially across GCMs.

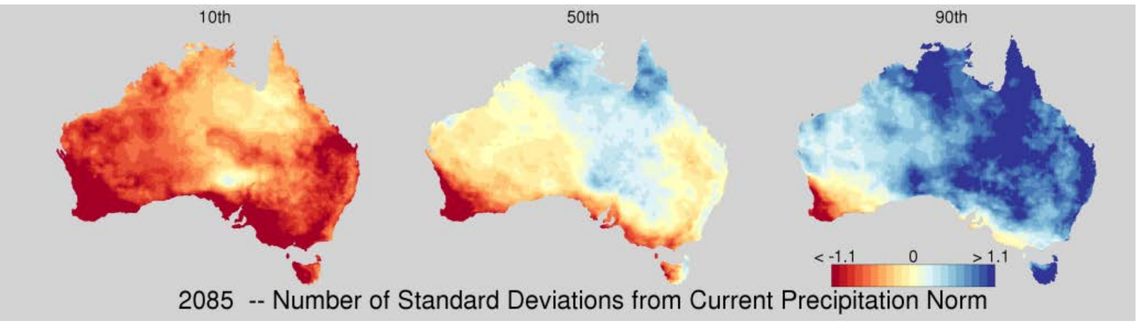


Figure 11: The number of SDs from current precipitation (mm) projected for 2085. The 10th, 50th and 90th percentiles across 18 GCMs are shown for RCP8.5. All other RCPs are shown in APPENDIX 2. Climate stability.

Interestingly, there are some consistencies between the recent past (60 years) climate (Figure 6) and the future projections to 2085. Areas of central Northern Territory were found to have the least average change in recent temperature, and these areas are likely to deviate the least from current variation in the future (Figure 9). In addition, the northern half of the Northern Territory has both experienced some of the greatest increases in average precipitation since 1950 (Figure 6 and Figure 7), and is projected to experience some of the greatest increases in precipitation into the future (Figure 10 and Figure 11).

3.4.5 Distance measures

At a given location, the climate may change dramatically, but if there is large spatial variation in climates in the vicinity of this location, a population can track its suitable climate by moving a short distance. On the other hand, if climate is largely homogenous for large distances around the point of interest, a population needs to move a long way to track its suitable climate. Thus, a useful measure of climate change impact is the distance a population would have to move to remain within a suitable climate space. We estimated this metric for both annual mean temperature and annual mean precipitation. In the former case, we calculated the distance a population would have to move by 2085 to stay within 2 SDs of the annual mean temperature at that location. For annual mean precipitation, given the much smaller relative shifts in this metric, we used a more stringent criteria; having to stay within 1 SD of local annual mean precipitation. These measures were calculated for each of the 18 GCMs for four RCPs (APPENDIX 2. Climate Stability). The 10th, 50th and 90th percentile across the 18 GCMs for RCP 8.5 are detailed in Figure 12.

The results for temperature were compelling, with small required movement distances surrounding areas of topographic relief (because lowland species can retreat upwards to these areas as temperature increases). Upland areas at the centre of this topographic relief, however, typically show very long required movement distances, because equivalent temperatures in these areas move off the top of mountains and, by 2085 can only be found at far removed locations. This is true for parts of the Great Dividing Range such as the high elevation areas of the Australian Wet Tropics, the central Queensland coast uplands, and the New South Wales (NSW) and Victorian alpine areas. Also, the high elevation areas of the MacDonnell Ranges, Northern and Central Kimberley, the Pilbara, the Flinders Lofty Block and the Tasmanian Central Highlands. Interestingly, the low elevation areas of Arnhem Land, the Nullarbor and south-west Western Australia have no nearby analogous temperatures in 2085. For the Nullarbor and south-west Western Australia, this is likely to be a consequence of being situated at the southern edge of the landmass where there are no areas available to the south that would provide suitable temperatures into the future.

Tellingly, some cells had no corresponding cell within 2 SDs of current temperature; **for these locations there is no place on the continent with equivalent temperatures in 2085** (APPENDIX 2. Climate Stability). In fact, over 9000 km^2 across the continent had no corresponding cell within 2 SDs of current predicted by at least one GCM. For 993 km^2, all 18 GCMs predicted that there would be no area with a similar temperature by 2085. The areas projected to have no corresponding temperature within 2 SDs are all high elevations of southern Australia (mostly Victoria and Tasmania). These areas are currently the coldest parts of Australia, and no area is predicted to be as cold by 2085 (APPENDIX 2. Climate Stability). Many other cells required movements of greater than 500 km by 2085; distances that are likely impossible for many low vagility taxa.

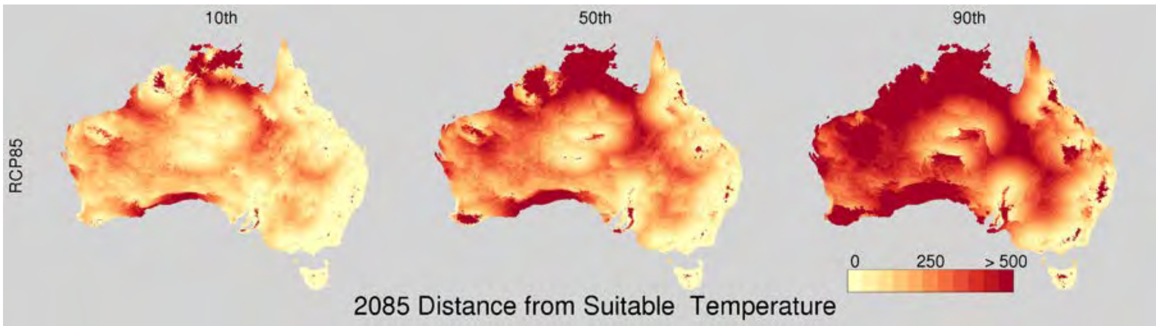


Figure 12: The distance (km) an organism would have to travel by 2085 to stay within 2 SDs of the current annual mean temperature. The distance measure is shown for RCP8.5, and the 10th, 50th and 90th percentiles across 18 GCMs.

The distance measures for precipitation are less confronting (Figure 13). This is likely to be due to the wide SD in current inter-annual precipitation. Therefore, there is a reduced likelihood that future measures of precipitation will be outside the current bounds of variation. Here the distance from the current grid cell to the nearest grid cell at 2085 within 1 SD of current precipitation is shown. It is typically a modest distance: often 0 km and is rarely above 50 km.

The largest impact for precipitation occurs for south-west Western Australia, where a population would be required to move greater than 50 km by 2085 to stay within 1 SD of current precipitation. For the 90th percentile of precipitation projections for 2085, much greater areas of south-west Western Australia are expected to be impacted. Additionally, north-eastern Northern Territory, Cape York Peninsula, much of inland Queensland, south-east South Australia and south-east Tasmania are likely to have greater distance measures.

Overall though, it is clear that projected shifts in precipitation, despite their considerable uncertainty, will have much smaller impacts on species than the expected shifts in temperature. Across most of Australia, species can stay within 1 SD of current precipitation levels by not moving at all, and at most, populations would have to move by a relatively modest 50 km by 2085.

Figure 13: The distance (km) an organism would have to travel by 2085 to stay within 1 SD of the annual mean precipitation at its current location. The distance measure is shown for RCP8.5, and the 10th, 50th and 90th percentiles across 18 GCMs.

If we simplify the above figures to show the 10% of the continent with the lowest required movement distances, it is clear that the Great Dividing Range will be a major temperature refugium for lowland species to its east and west (Figure 14). Similar effects are seen for other major areas of relief on the Australian continent (e.g. around the Flinders and MacDonnell ranges). In this analysis, the 10th percentile of required movement for precipitation (Figure 14, right) is meaningless, because across most of the continent, the required movement distance is 0 km. For temperature, however, the 10th percentile equates to less than approximately 150 km.

Figure 14: The 10th percentiles of the minimum distance (km) an organism would have to travel by 2085 to stay within 2 SDs of the current annual mean temperature, and 1 SD of the current precipitation mean.

3.4.6 Summary of climatic stability analyses

From the preceding, it is clear that shifts in temperature are going to be a major impact on Australia's biodiversity. Shifts in precipitation are inherently uncertain, but despite this the range of the projected shift is relatively modest against the backdrop of natural inter-annual variation in precipitation across the Australian continent.

Shifts in temperature are far more certain and are, even against the backdrop of normal inter-annual variation, going to be very large. Indeed the **shifts in temperature will often be larger in magnitude than (though opposite in direction to) climate shifts associated with the last ice age.** Given the magnitude of shifts in temperature, the only response available to most taxa will be to move. **Movement will likely be a feasible option for lowland populations close to areas of major topographic relief. Populations distant from mountainous areas, or which are located on top of these mountainous areas will have to move very large distances to find equivalent temperatures to those they currently experience**. Low vagility taxa in this situation may well risk extinction without management intervention. The habitat of mountaintop species becomes a refugium for lowland species; and the nearest refugium for mountaintop species may well be impossibly distant.

3.4.7 Species distribution modelling

At this point we move from an analysis of raw climate variables to projections of species distributions and how these might shift as a consequence of climate change. The underlying assumption behind this approach is that the climatic envelope currently utilised by a species is indicative of the climatic envelope that species will occupy in the future or did occupy in the past.

Using the Maxent software, we fitted species distribution models for taxa across four major taxonomic groups (birds, mammals, reptiles and amphibians). We then used the species–climate relationships imputed from this modelling process to predict the location of suitable climates for each of these species in the future.

3.4.7.1 Model performance

Performance of species distribution models was evaluated using the area under the receiver operating characteristic curve (AUC). We used the model test AUC scores resulting from the tenfold cross validation. AUC measures each models' consistency and predictive accuracy (Ling et al. 2003). An overwhelming majority of species models had very high AUC scores, with only very few falling lower than the 0.7 cut-off (Figure 15.). The species that fell below the cut-off were excluded from further analyses.

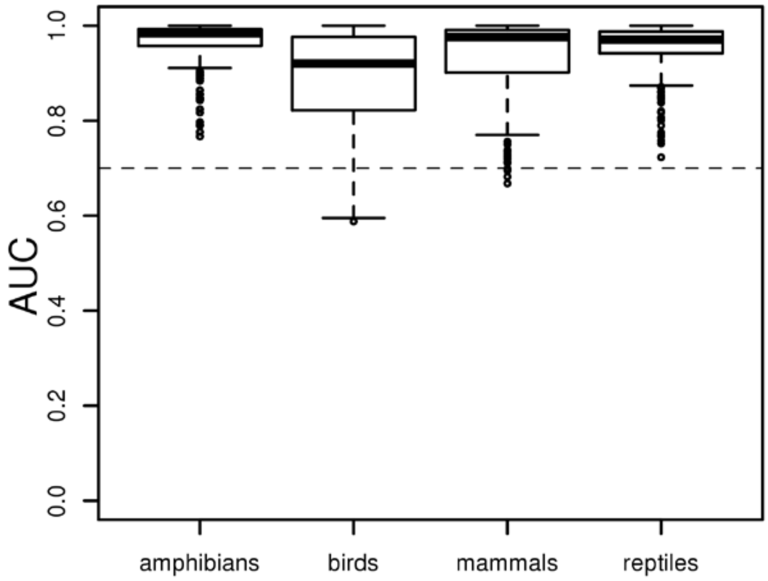


Figure 15: Cross-validation test AUC scores for the each of the species individual Maxent models, shown for each of the four taxonomic groups. For only very few species did AUC scores fall below the 0.7 cut-off.

3.4.7.2 Distribution modelling outputs

A model for each species' current distribution was produced, and then a projected distribution for each of the 18 GCMs and RCP8.5 was generated. The median across the 18 future distribution projections was created. An example of the current and future projected distribution model is shown for three-clawed worm-skink, *Anomalopus verreauxii* (Figure 16). Predicted environmental suitability ranges from 0 (not suitable) to 1 (highly suitable). Parts of the continent where predicted environmental suitability is lower than the occurrence threshold (calculated by Maxent, see 3.3 Research activities and methods for details) have been omitted (shown in grey).

Figure 16: An example of a species distribution model for 1990, and the median across projected distributions for each of the 18 GCMs are shown for RCP8.5 at 2085. The example species is three-clawed worm-skink, *Anomalopus verreauxii*.

3.4.7.3 Species richness

Species richness for 1990 was calculated by summing the binary presence/absence models for each species across all four taxonomic groups. For future projections of species richness, the species model for each of the GCMs was summed to provide a species richness model per GCM. Species richness across the 18 GCMs were then summarised for the 10th, 50th (median) and 90th percentiles. The median of future outputs are shown here, the 10th and 90th percentile outputs are detailed in APPENDIX 4. Projected species richness variability. The proportion change in species richness between 1990 and 2085 (Figure 17) was calculated by dividing the current species richness model by the 2085 median richness model. Shifts are apparent across all species for the species richness model between 1990 and 2085: central, north and west Australia are projected to decrease in species richness, whereas the south-east and parts of the north-east are projected to increase in species richness. A notable exception to the overall declines projected for central Australia can be found in the MacDonnell Ranges and Burt Plains area of the Northern Territory. The largest areas projected to see increases in species richness are the Nullarbor, Gawler and Flinders Lofty Block in South Australia, the uplands Victoria and southern NSW, and much of Tasmania. Importantly, the proportional change in species richness across all taxa identifies broadly the same areas as the climate distance metric (section 3.4.2). That is, the areas the distance metric predicts as major refugia (Figure 12), also appear as places where a large influx of species is predicted to occur.

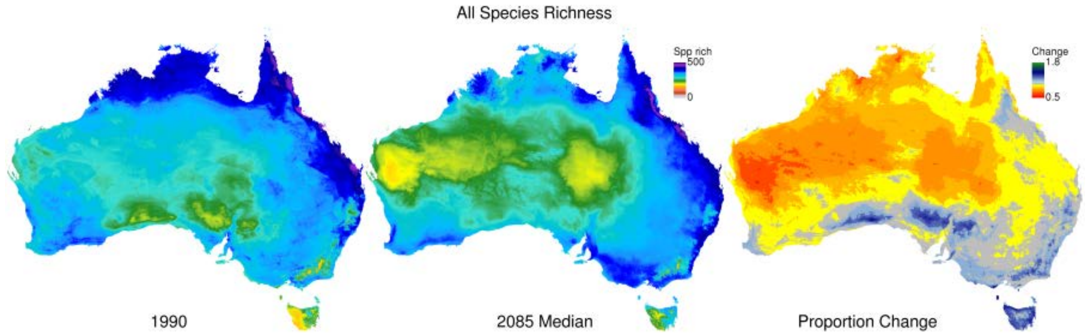


Figure 17: Species richness across all four taxa, shown for 1990, the median (across 18 GCMs for RCP8.5) for 2085, and the proportion change in species richness between 1990 and 2085 median. For the proportion change, the scale indicates where the species richness has increased (>1, blue colours), or decreased (<1, warm colours).

Similar trends in species richness are apparent when looking at the change in species richness for each of the four taxonomic groups separately, although the proportional severity of the change differs, and there are some regional exceptions to the overall trends (Figure 18). Generally, the north and the east of Australia have the highest modelled species richness for 1990. For the amphibians and mammals, northern Australia has the highest species richness in 1990, and is projected to experience some of the greatest proportional loss by 2085. Notable decreases in species richness by 2085 across all species are expected in the north, centre and west of the continent, and increases in species richness are projected to occur in the south and east. For each taxa, the Gascoyne and Murchison areas of Western Australia face the most severe decreases in species richness, whereas Tasmania is projected to increase in species richness. This represents a projected overall shift of species towards the south-east.

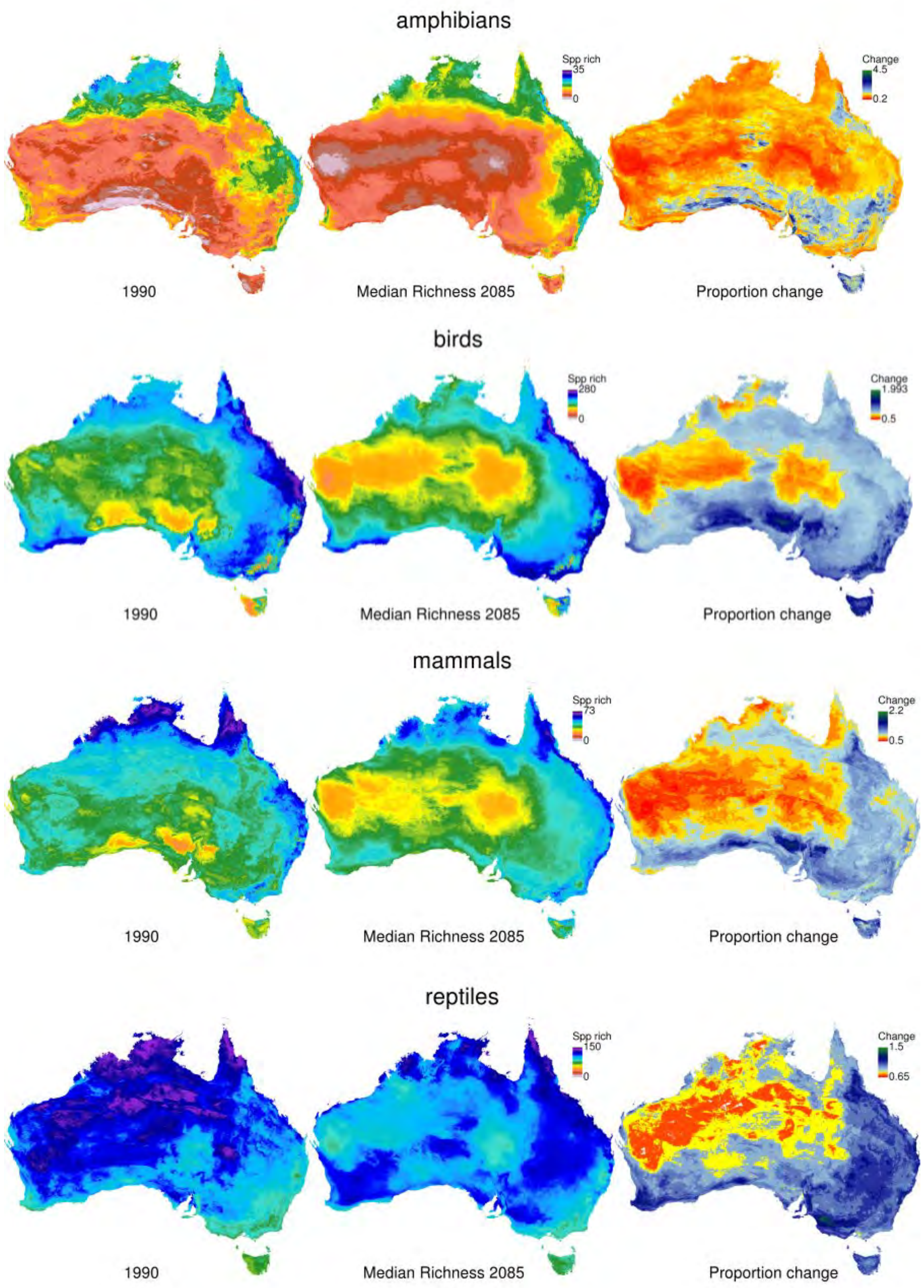


Figure 18: Species richness for each of the four taxa shown for 1990, the median (across 18 GCMs for RCP8.5) for 2085, and the proportion change between 1990 and 2085 median. For the proportion change, the scale indicates where the species richness has increased (>1, blue colours), or decreased (<1, warm colours).

3.4.7.4 Species movement

The projected species turnover was investigated by calculating the number of species projected to move into an area in 2085 that didn't occur there in 1990, otherwise referred to for these purposes as 'immigrants'. In addition, species that were projected to be lost from an area in 2085 where they occurred in 1990 are referred to as 'emigrants'. These models show similar patterns again to those from the distance metrics (3.4.2) and proportional change in species richness (3.4.4.3). Most of the 'immigrating' occurred in the south and the east, along with small areas that species moved into located in the Einasleigh Uplands, Nullarbor and south-west Western Australia (Figure 19). The highest number of species emigrating is predicted to occur in the north and west of the continent; the lowest in the south and east.

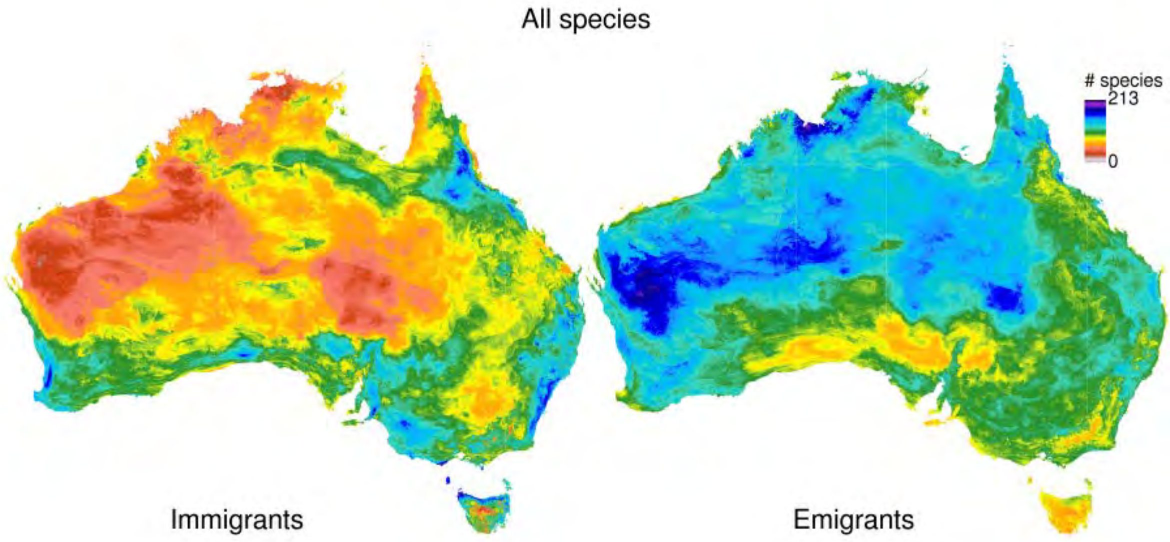


Figure 19: The number of immigrants and emigrants across all species. Left: 'Immigrants' – the number of species that are projected to have suitable climate space in 2085 (median) where they were absent in 1990. Right: 'Emigrants' – the number of species that are projected to lose suitable climate space between 1990 and 2085 (median).

Immigrants and emigrants were then calculated as a proportion of the number of species that originally occurred in the area (the species richness in 1990) (Figure 20). The immigrants and emigrants as a proportion of the original species richness shows a pattern fairly consistent with the absolute numbers of immigrants and emigrants. For the immigrants, South Australia and Tasmania had the highest numbers; whereas most of the east coast and south-east corner of Australia, including Tasmania, had the fewest emigrants. The highest concentration of emigrants for both the absolute numbers and proportional is in central and western Australia, particularly the Murchison and Gascoyne regions. It is the south-east corner of Australia that therefore has the greatest biotic refugial potential by 2085.

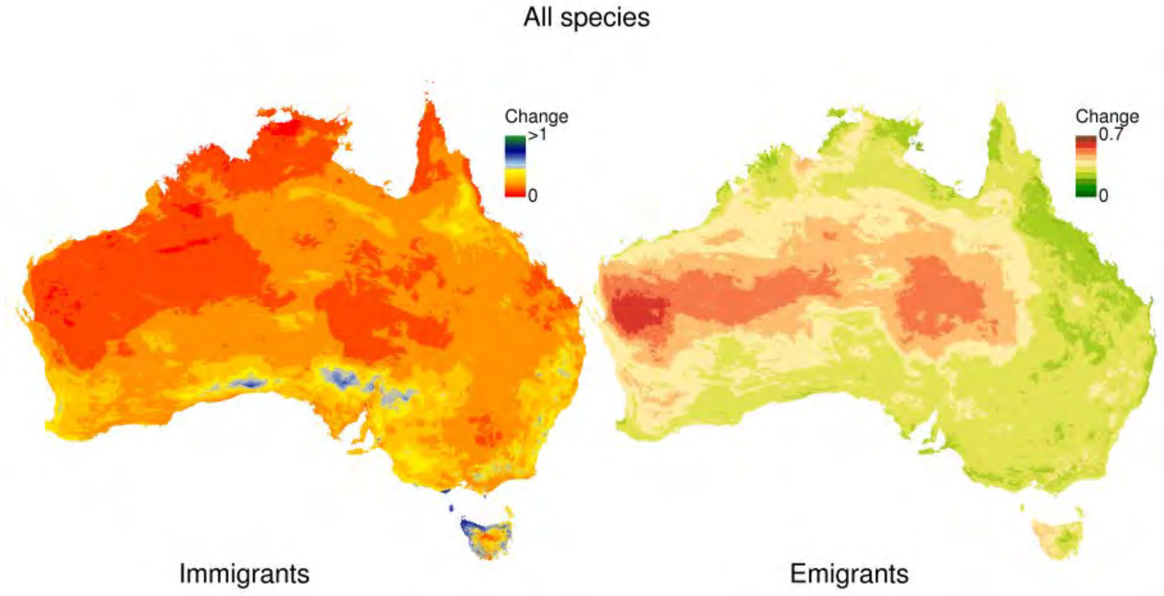


Figure 20: The number of immigrants and emigrants shown as a proportion of the original species richness. Left: 'Immigrants'– the number of species projected to have suitable climate space in 2085 (median) where they were absent in 1990, shown as a proportion of the number of species occurring in 1990. Right: 'Emigrants' – the number of species projected to have lost suitable climate space in 2085 (median) where they were present in 1990, shown as a proportion of the number of species occurring in 1990.

Similar patterns, with varying magnitudes, are shown when we break the analysis down into each of the four taxonomic groups (Figure 21). Immigration was projected to occur mostly in the south and east of the continent, but the far south corner of south-west Western Australia was also projected to have species climate space move into this area, particularly for mammals and reptiles. Emigrating species were projected to be the highest in the north for amphibians, west for birds, and the north and west for mammals and reptiles.

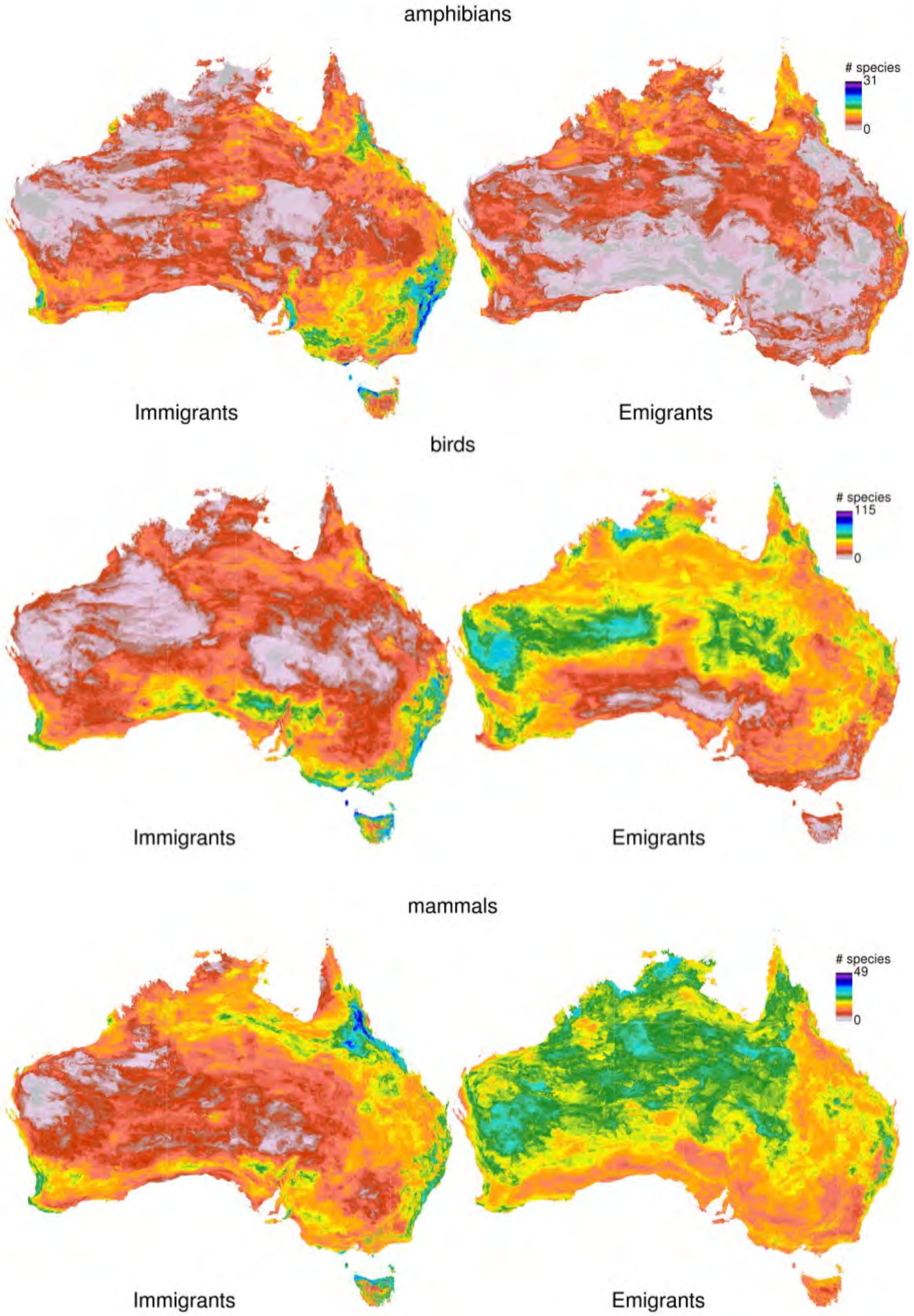


Figure 21: The ‘Immigrants’ and ‘Emigrants’ for each of the taxonomic classes. For each group, the left model shows the number of species that are projected to have suitable climate space in 2085 (median) where they were absent in 1990. On the right are the ‘Emigrants’ – the number of species projected to have lost suitable climate space in 2085 (median), where they were present in 1990.

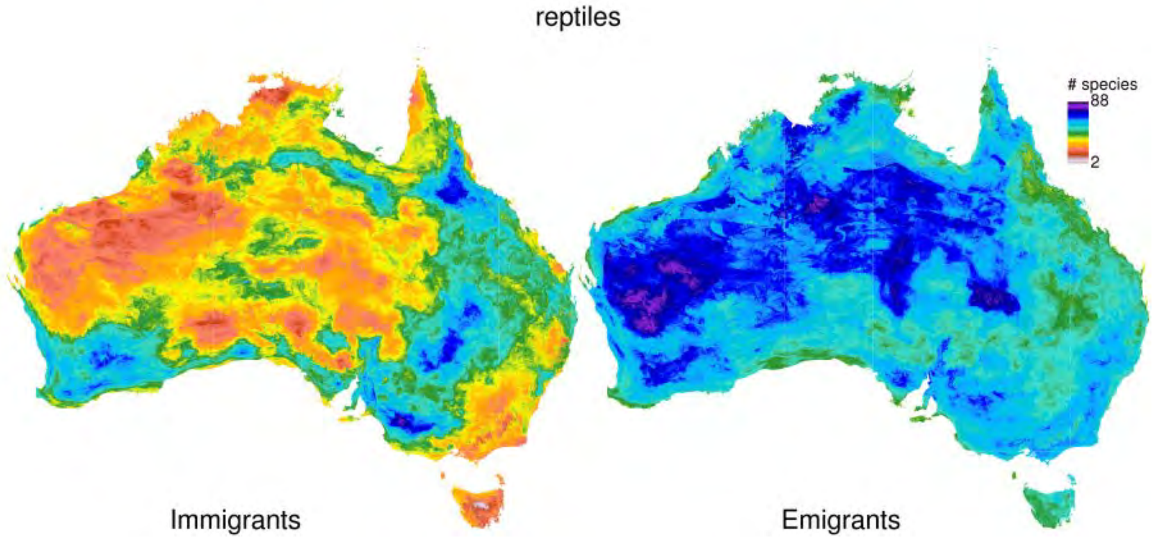


Figure 22 (cont.): The 'Immigrants' and 'Emigrants' for each of the taxonomic classes. For each group, the left model shows the number of species that are projected to have suitable climate space in 2085 (median) where they were absent in 1990. On the right are the 'Emigrants' – the number of species projected to have lost suitable climate space in 2085 (median), where they were present in 1990.

Across most of Australia, the number of species projected to gain climate space into a previously unsuitable area is less than the number of species that already occur there (Figure 22). This is true for almost all areas except for pockets of South Australia, Victoria, NSW and Tasmania, shown in blue. Areas of inland NSW are also projected to have a greater number of immigrants than the number of species already recorded to occur there for amphibians and reptiles. This is the result of relatively low original species diversity coupled with the general southward and eastward trend of projected species movements. The number of emigrants proportional to the number of species originally occurring in the area show consistent patterns: fewer species are being driven out in the south and east, and the number of emigrants is greater in central and western Australia. In central and western Australia, we see almost no immigration and almost total emigration. Thus, **these areas are predicted to face massive vertebrate diversity loss by 2085**. For each taxonomic group, the number of emigrants is also low in northernmost Northern Territory. For birds and mammals, the areas of fewest emigrants proportional to the original species richness is concentrated in the south-east. For amphibians and reptiles the lowest areas are concentrated in central and north Queensland, and the Brigalow Belt, Darling Riverine Plains and Mulga Lands areas.

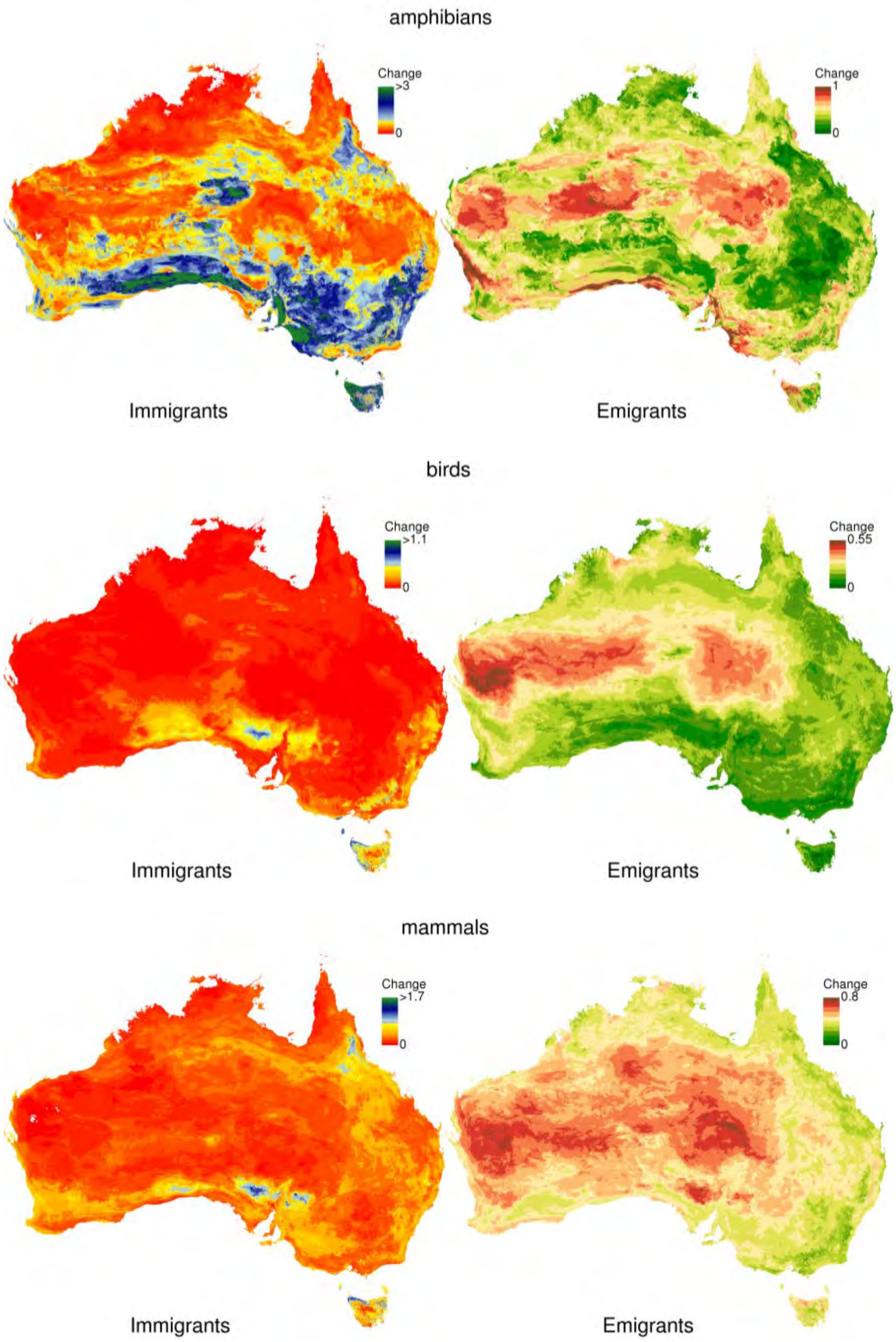


Figure 23: The immigrants and emigrants for each taxonomic group shown as a proportion of the number of species in each pixel as of 1990. Left: 'Immigrants' – the number of species projected to have suitable climate space in 2085 (median) where they were absent in 1990, shown as a proportion of the number of species occurring in 1990. Yellow–red colours indicate that the number of immigrants is less than the number of species that already occurs in that area, cool colours indicate that there are projected to be more immigrants than the number of species already occurring. Right: 'Emigrants' – the number of species that are projected to lose suitable climate space between 1990 and 2085 (median), shown as a proportion of the number of species occurring in 1990.

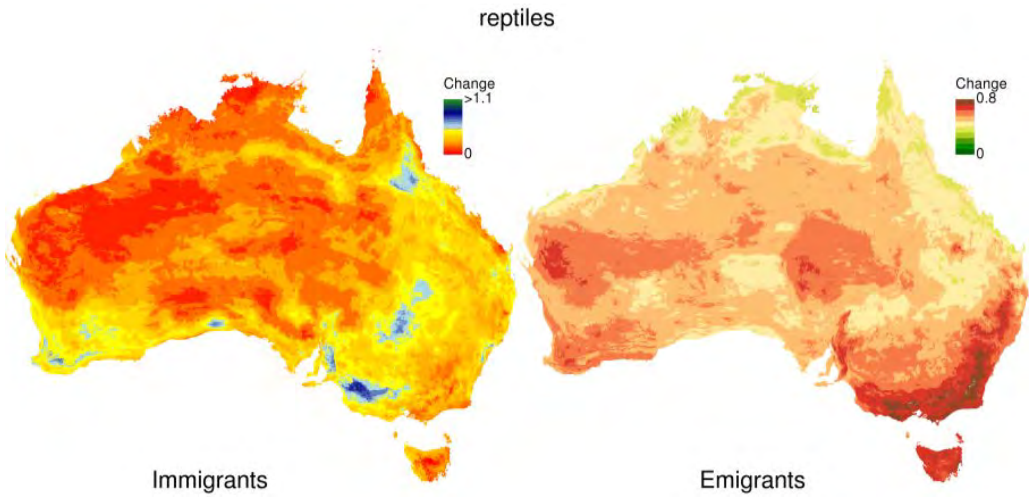
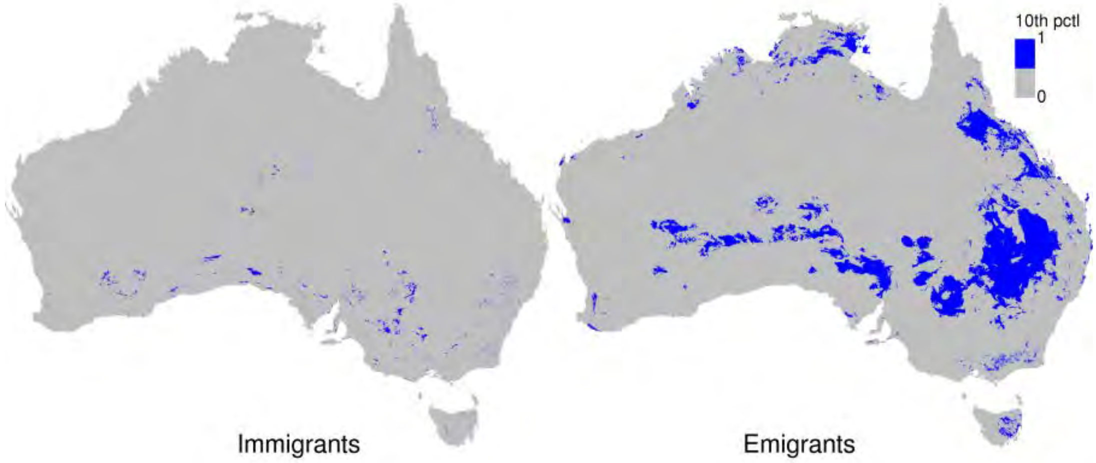


Figure 24 (cont.): The immigrants and emigrants for each taxonomic group shown as a proportion of the number of species in each pixel as of 1990. Left: 'Immigrants' – the number of species projected to have suitable climate space in 2085 (median) where they were absent in 1990, shown as a proportion of the number of species occurring in 1990. Yellow–red colours indicate that the number of immigrants is less than the number of species that already occurs in that area, cool colours indicate that there are projected to be more immigrants than the number of species already occurring. Right: 'Emigrants' – the number of species that are projected to lose suitable climate space between 1990 and 2085 (median), shown as a proportion of the number of species occurring in 1990.

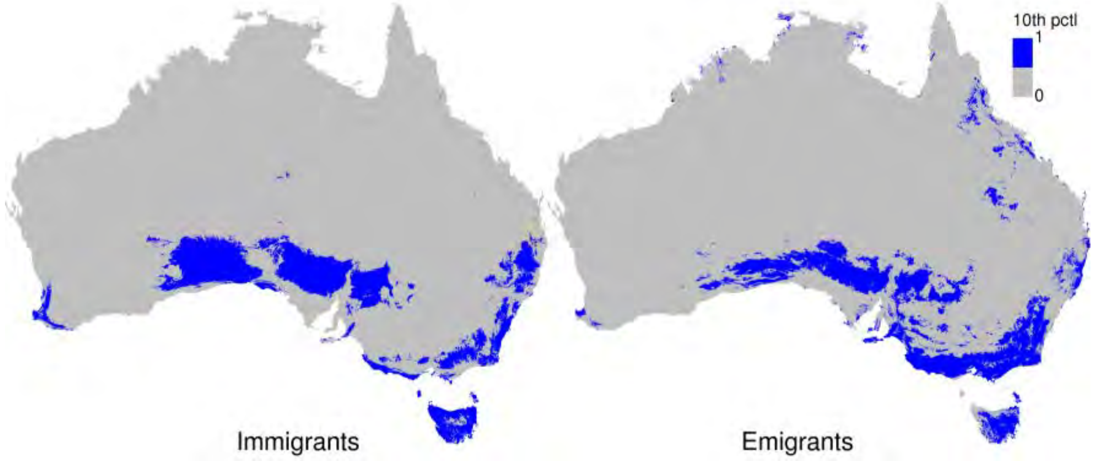
If we consider a refugium as a place that species move to, or persist in, during changing climatic conditions (sensu Keppel et al. 2012), it is clear that refugial areas will be identified by having a high number of immigrants, a low number of emigrants, or both. To visualise these regions, we thus take the 90th percentile of immigrants (the 10% of Australia receiving the most immigrants), and the 10th percentile of emigrants (the 10% of the continent losing the fewest species).

The areas identified as the highest number of immigrants and lowest number of emigrants proportional to the original species richness (above and below the 90th and 10th percentiles respectively), are shown in Figure 23. The highest concentration of immigrants is projected to be in the south and south-east of the continent for most taxonomic classes, as well as in Tasmania and the most south-west corner of Western Australia. The areas with the fewest emigrants show a very similar distribution across the continent, largely being represented in the south and east for birds and mammals, in Central Arnhem Land and Queensland for amphibians, and much of the east coast for mammals and reptiles.

amphibians



birds



mammals

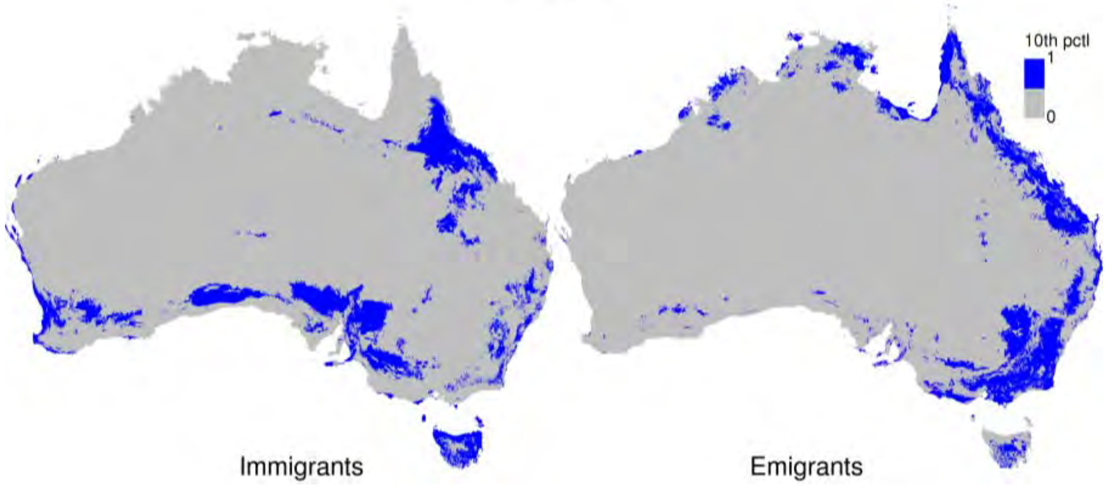


Figure 25: The areas with the highest 10th percentile of immigrants and lowest 10th percentile of emigrants, highlighting the areas with the biotic refugial potential.

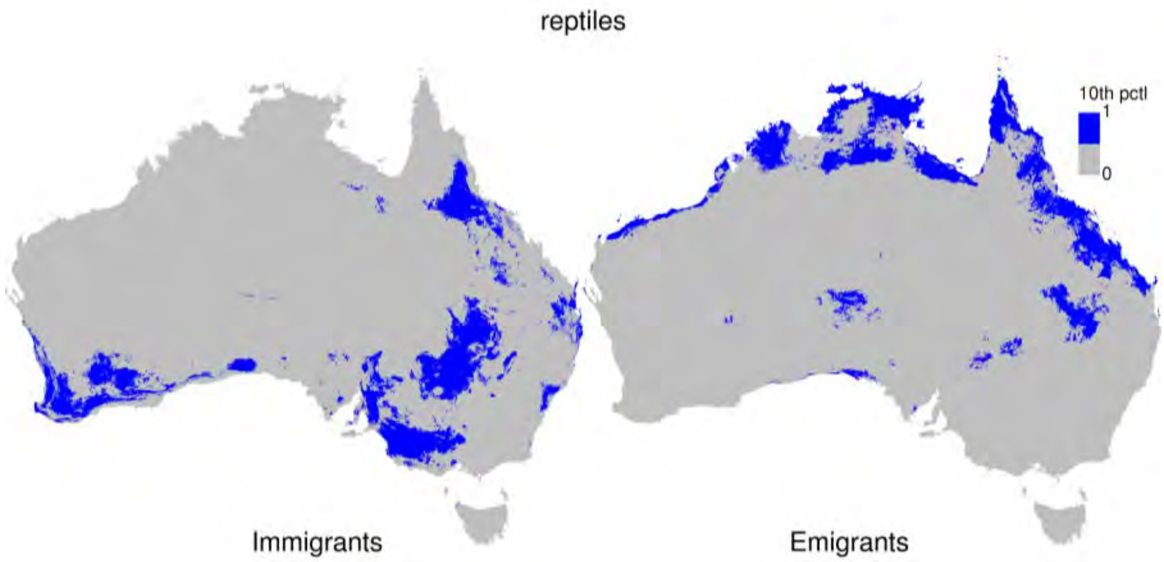


Figure 26 (cont.): The areas with the highest 10th percentile of immigrants and lowest 10th percentile of emigrants, highlighting the areas with the biotic refugial potential.

3.4.7.5 Future biodiversity hotspots

Identifying the areas with the smallest loss, and greatest gain, of species is clearly an important way of identifying future refugia under climate change. To identify these areas in a taxonomically representative fashion, we summed the layers in the previous figure (Figure 23). The resulting models (Figure 24) show the areas with the most immigrants and fewest emigrants summed over taxonomic groups. The final summed layer identifies those places in the Australian continent that look to act as climate change refugia across all taxonomic groups we investigated. Hereafter, we refer to these places as the projected refugia areas for 2085. The areas that rank the highest under this analysis are similar to those identified in the temperature distance analysis (section 3.4.2) as well as the proportional change in richness analysis (section 3.4.4.3), being largely confined to the south and east of Australia. High elevation areas are well represented in the highest rankings. The high elevation areas in the central Northern Territory such as the MacDonnell Ranges and Burt Plain stand out as some of the few high ranking areas of central Australia. In Queensland, the high elevation areas of the Wet Tropics, the Einasleigh Uplands and Central Mackay Coast have the highest rankings in the state. In the south-eastern states; the New England Tablelands, South Eastern Highlands, Victorian Midlands, south-east Tasmania and Ben Lomond contain the greatest biotic refugial potential. A few notable high ranking areas had low elevations: these include Nullarbor, Gawler and Kanmantoo in South Australia; and the Murray Darling Depression, Riverina, Daring Riverine Plains and the south-east corner across Victoria and NSW. In the Northern Territory, the Arnhem Coast was a notable high-ranking, low elevation area.

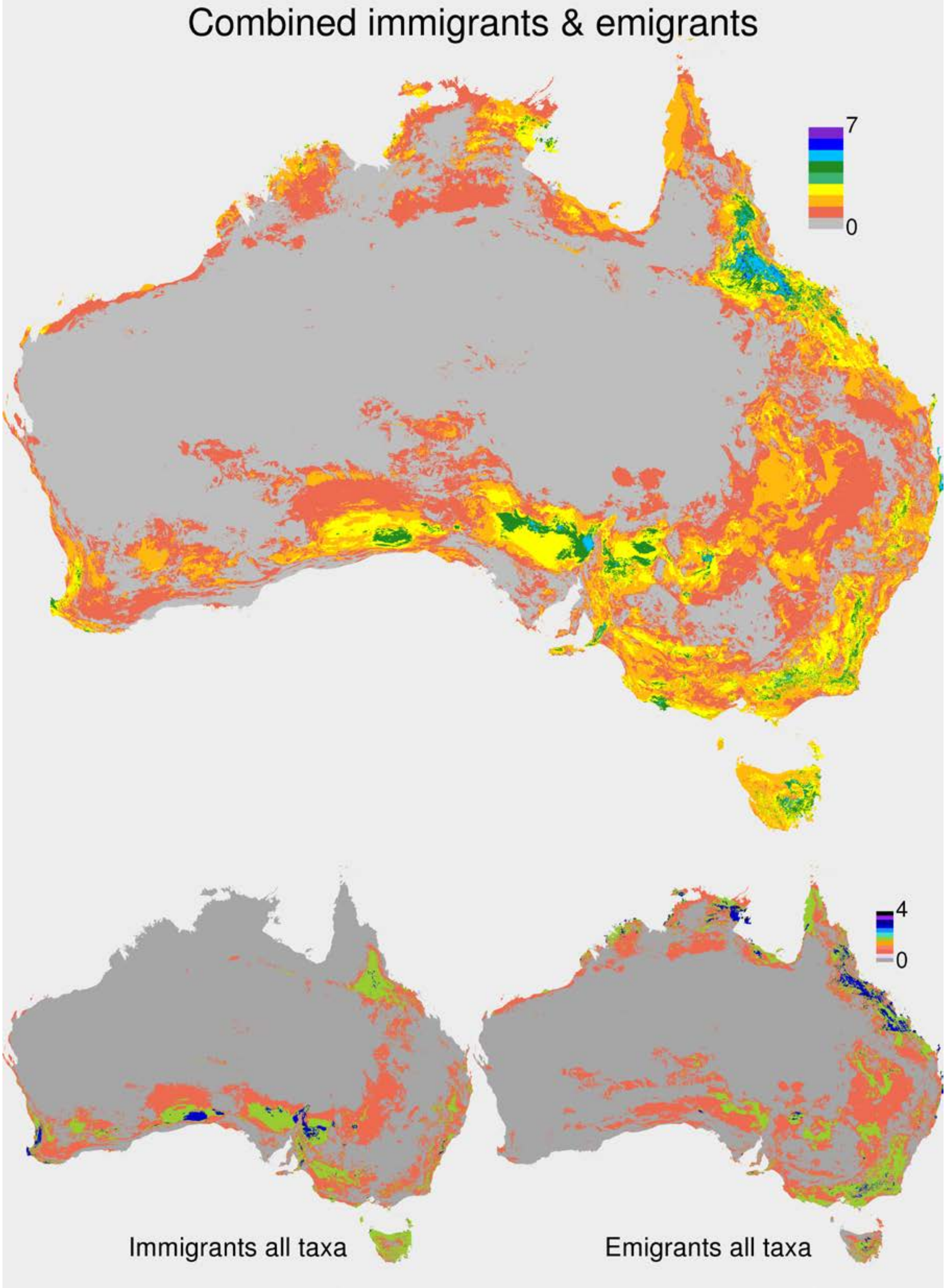


Figure 27: The aggregation of the 90th percentile for immigrants and 10th percentile for emigrants of the four taxonomic groups summed. The darker colours indicate the highest score, which corresponds to the greatest overlap of indices. The scale for the overall refugial potential model is 0–7 instead of 0–8, because no area had the highest score for both immigrants (4) and emigrants (4).

3.4.7.6 Areas of stability

Understanding the areas of lowest species turnover, and in particular, areas with the fewest incoming species are important because of the potential negative impacts of invasive species on the existing species. Additionally, areas of both minimal incoming and departing species will therefore have the highest stability in biological communities. There is a fairly consistent pattern across the four taxonomic groups, which are each projected to have the fewest immigrants in the north and west of Australia (Figure 25). Additionally, areas of central Queensland will have few incoming species of amphibians, birds and reptiles.

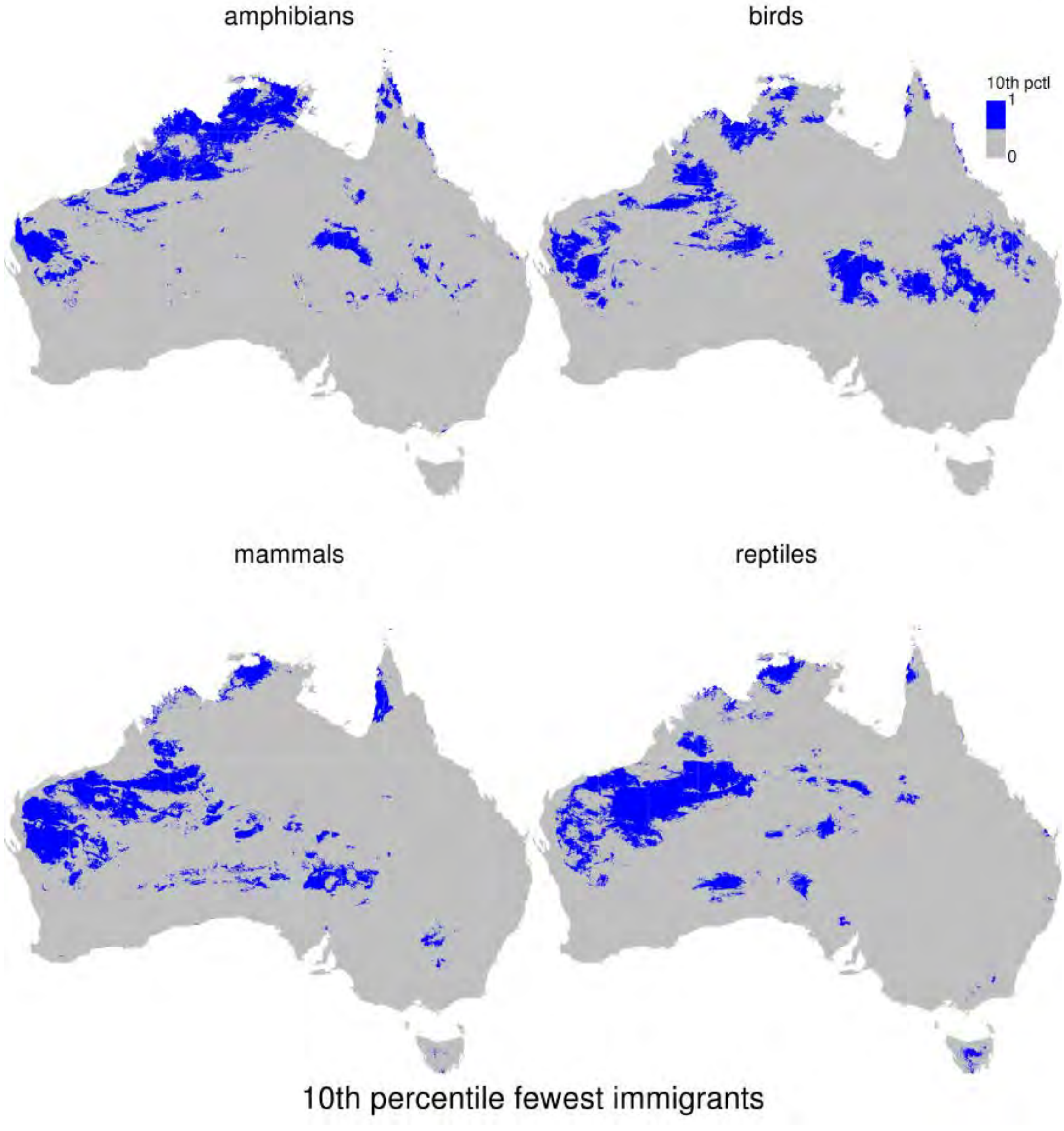


Figure 28: The areas of the 10th percentile of the fewest immigrants for each of the four taxonomic groups.

Combining the four taxonomic groups highlights the areas of fewest incoming species across all vertebrates (Figure 26). The areas of greatest overlap are largely contained within the Northern Territory in the Darwin Coast and Pine Creek bioregions, and in Western Australia in the Dampierland, Ord Victoria Plain, Great Sandy Desert, Gascoyne, Carnarvon and Murchison bioregions. There are small regions of overlap in

Cape York Peninsula, and central Australia across the abutting borders of the Northern Territory, Queensland and South Australia. There are not many areas with few incoming species in south-eastern Australia, and where these occur, they generally only contain one taxonomic group. Overall, the regions with the fewest immigrants are occurring in parts of the continent most likely to lose species. Thus, refugial areas that species persist in and which also have few immigrant species are likely to be rare indeed.

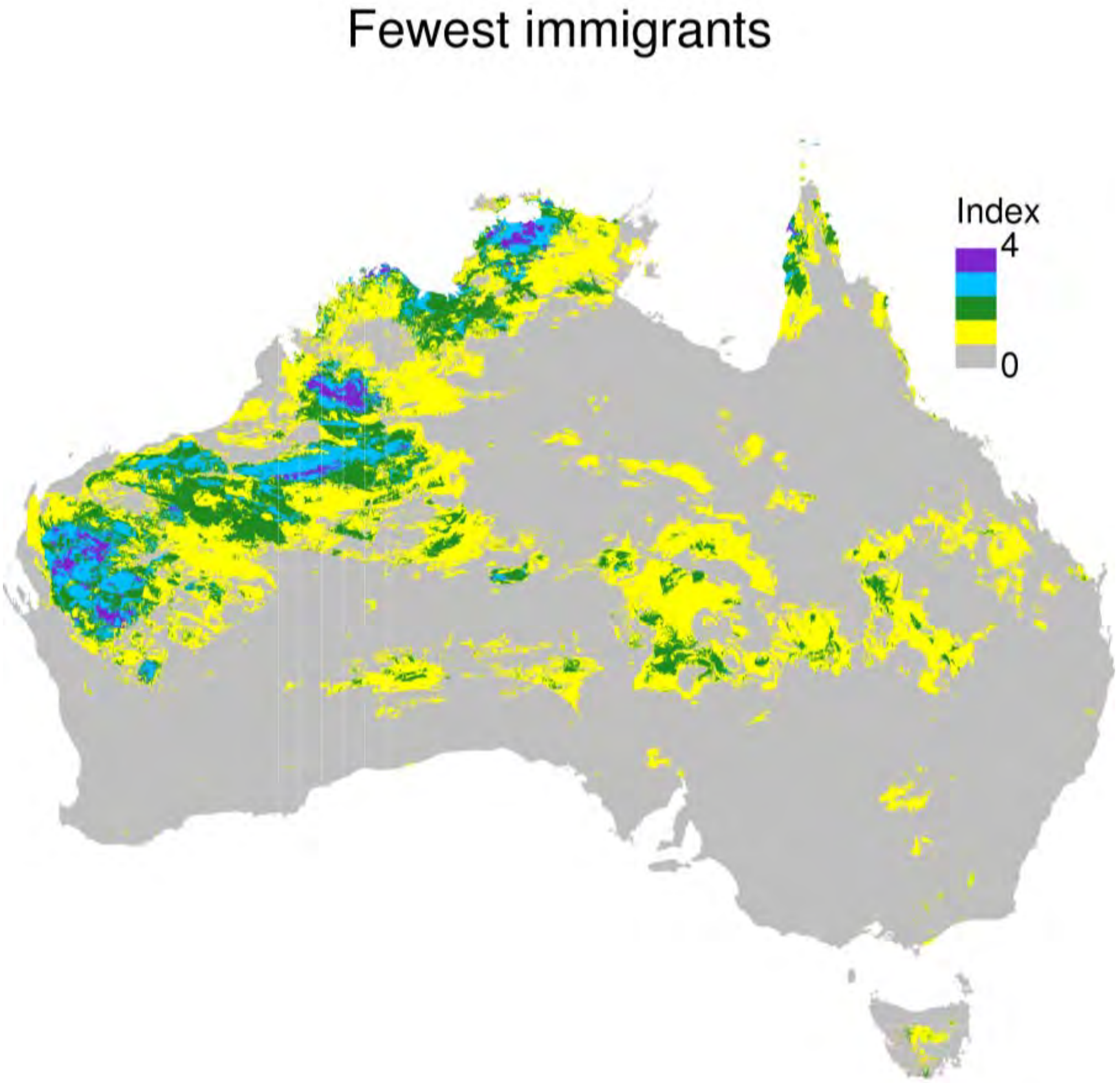


Figure 29: The areas of overlap of the fewest immigrants for all four taxonomic groups.

3.4.8 Refugia and the national reserve system

Our analyses found that southern and eastern Australia come out consistently as the areas that will be of greatest importance to biodiversity into the future. Much of this area — particularly the south-east, the east coast and to a lesser extent the south-west — also corresponds to the greatest human densities. Correspondingly, these areas have the highest concentrations of small and very small protected areas (DSEWPaC 2010), and are the areas most likely to conflict with human population interests (Figure 27).

An exception to this general trend can be found along the southern Australian coast. Areas of high climate and species stability overlap with the large protected areas including the Nullarbor Regional Reserve and National Park, Yellabinna Regional Reserve and Wilderness Protected Area. Additionally, areas of moderate climate stability and high biodiversity stability fall within the extensive reserve system of western Tasmania, including the Southwest National Park and the Franklin-Gordon Wild Rivers National Park. However, the areas of highest climate and species stability in eastern Tasmania correspond with the areas of smallest reserves.

In the south-east of continental Australia where high climate and biodiversity stability are found, the greatest overlap with a protected area is with the Kosciuszko National Park of NSW, and the Alpine National Park of Victoria. Large areas with high importance for future biodiversity and high climate stability such as south-west Victoria, and areas of central NSW such as the borders between the Darling Riverine Plains, Cobar Peneplain and NSW South Western Slopes, have very few and only small protected areas.

Unfortunately, the largest conservation reserves on continental Australia, particularly the Ngaanyatjarra Lands Indigenous Protected Area and other protected areas in central Australia, correspond with the areas of lowest biodiversity stability; and in some cases, only moderate climate stability. Despite this, these areas are likely to still be of importance to the species that are confined to these habitats.

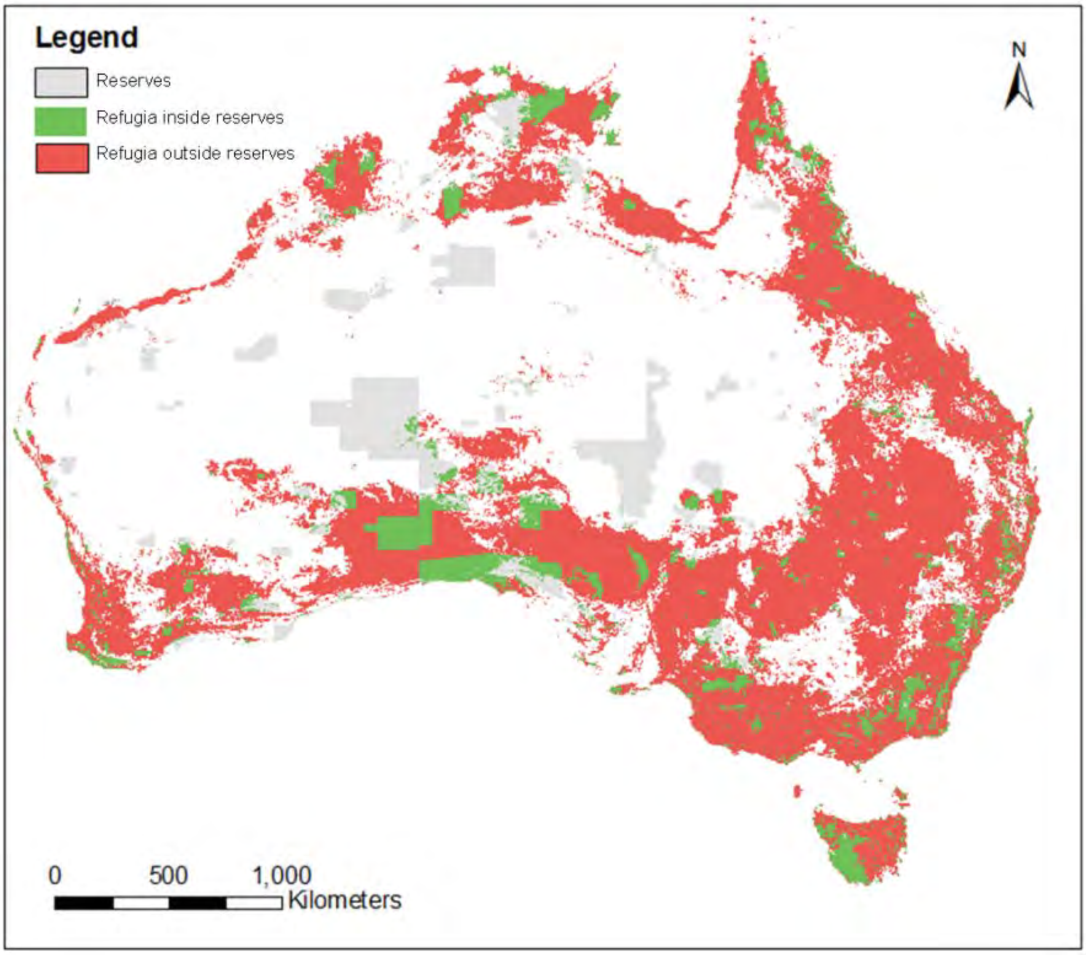


Figure 30: The protected areas in Australia's national reserve system, and how they relate to the projected refugia areas in 2085. For easy visualisation, the refugia are treated equally, despite relative ranking.

Figure 28 shows the same protected areas and refugia areas, but with the refugia ranking shown. Large areas of high ranking refugia within north-eastern, southern and south-eastern Australia fall out of the current reserve system.

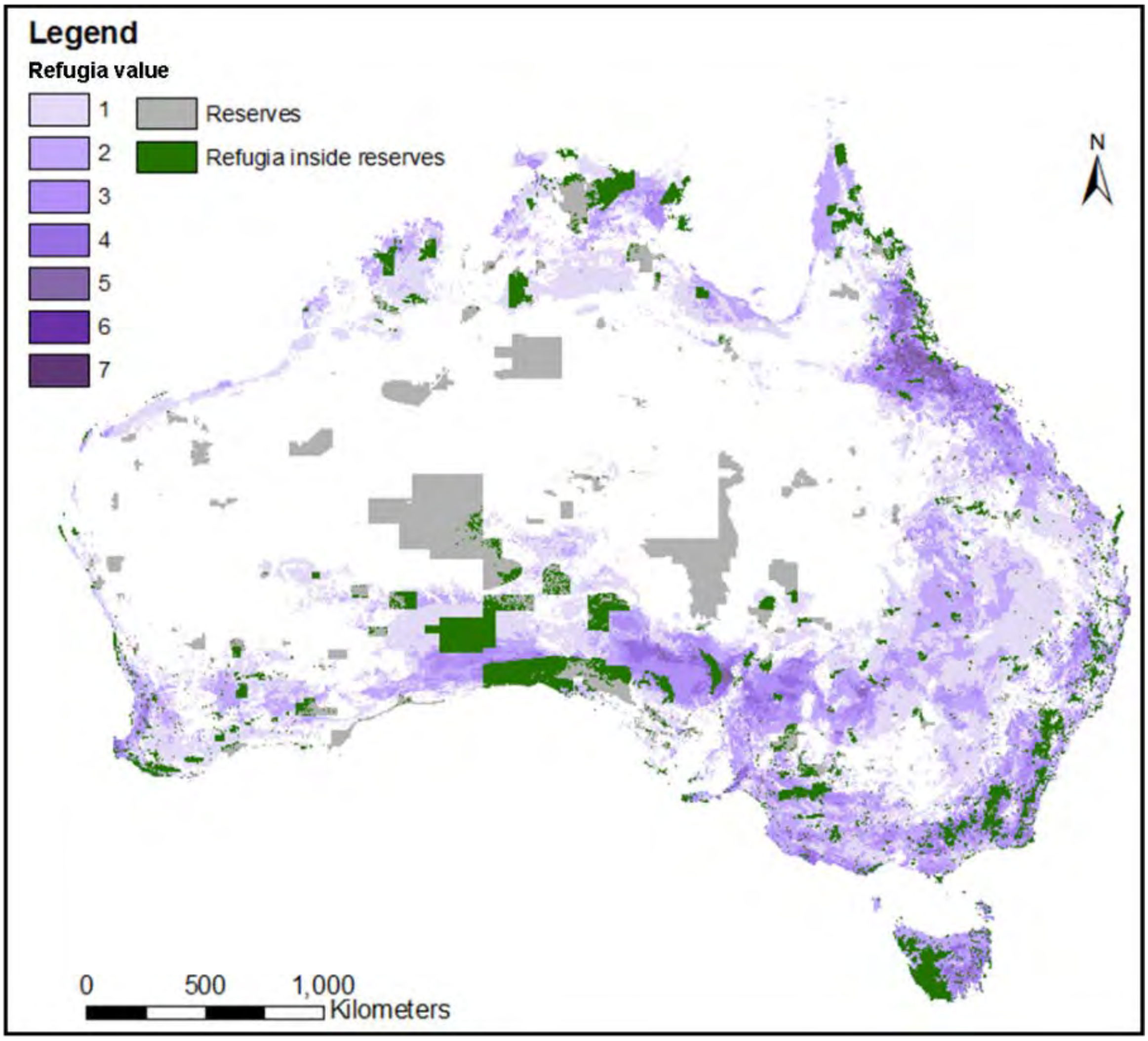


Figure 31: The protected areas in Australia’s national reserve system, and how they relate to the projected refugia areas in 2085. The detailed refugia are displayed using the same scale as the refugia analysis shown in Figure 24, scaled from 1 (lowest priority) to 7 (highest priority), as the highest possible score ‘8’ was not realised for any location.

Overall, only 14% of refugia identified by our analyses fall within the current protected areas (Table 2). For better quality refugia — those ranked four and above — less than 1% exist within protected areas. No area ranked with the highest refugia score fell within a protected area. Interestingly, only 17% of the current protected areas have no refugia value.

Table 2: The different classes of refugia (0–7) and the protected areas (0=unprotected, 1=within protected area) and their summed areas. The 'Percent of refugia' refers to the percentage of each class of refugia (>1) that falls within a protected area.

Refugia	Protected area	area in km^2	Percent of refugia
0	0	4140633	
1	0	1374601	44.73
2	0	775645	25.24
3	0	348916	11.35
4	0	111971	3.64
5	0	28248	0.92
6	0	1706	0.06
7	0	2	0.00
0	1	531449	
1	1	197549	6.43
2	1	134125	4.36
3	1	71225	2.32
4	1	26862	0.87
5	1	1886	0.06
6	1	72	0.00
7	1	0	0.00

There are large differences in the proportion of areas within particular bioregions that are projected to be important refugia with regards to their level of protection under the national reserve system. Figure 29 shows that both the Wet Tropics bioregion and the neighbouring Einasleigh Uplands are projected to contain high proportions of refugia, yet the Einasleigh Uplands has a much smaller proportion of refugia within protected areas.

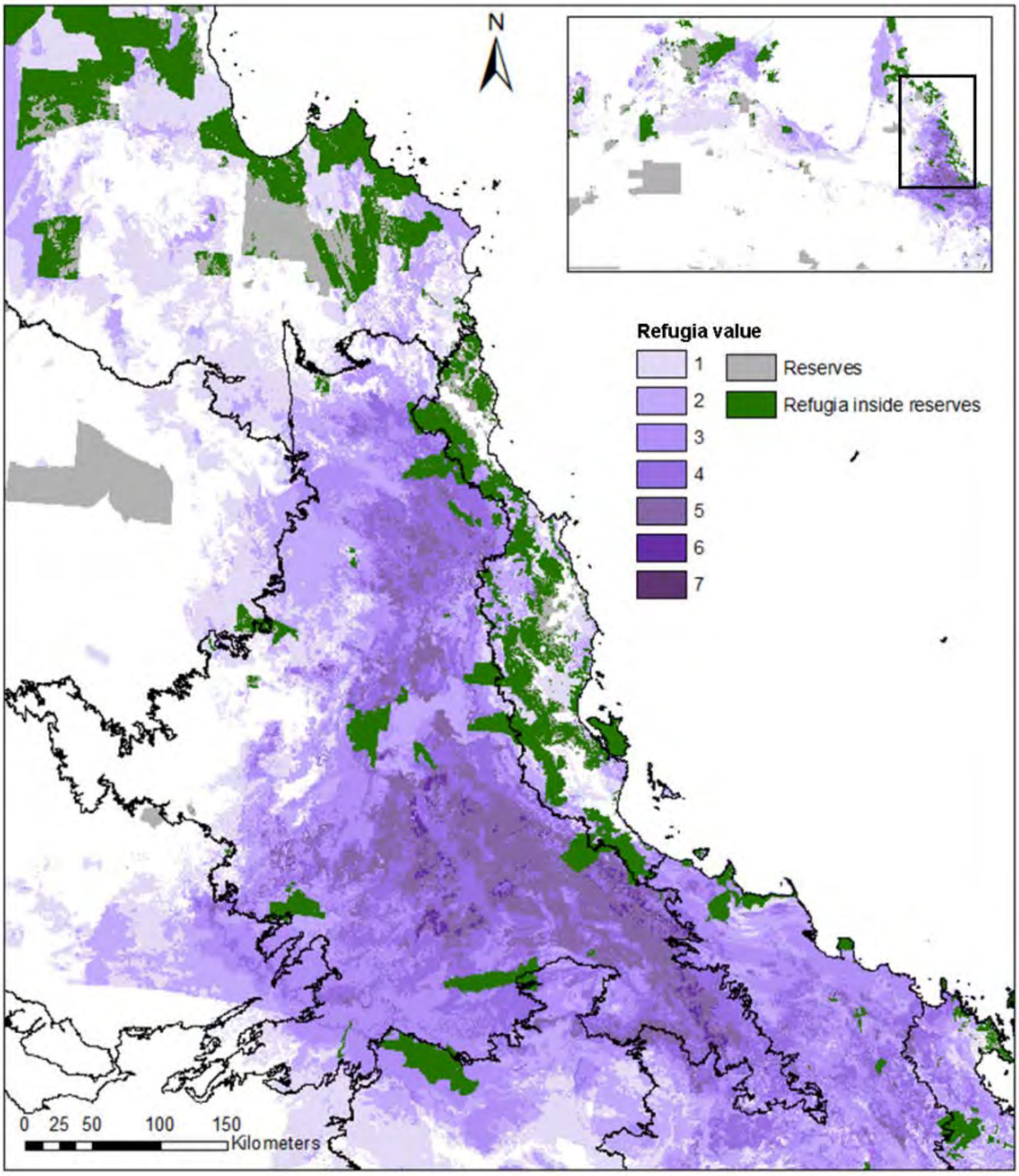


Figure 32: A detailed view of the protected areas in Australia's national reserve system, and how they relate to the projected refugia areas in 2085 for north-eastern Australia within the bioregion boundaries outlined in black. The detailed refugia are displayed, using the same scale as the refugia analysis, scaled from 1 (lowest priority) to 7 (highest priority), as the highest possible score '8' was not realised for any location.

3.5 Discussion

3.5.1 Climate change across the continent

Our mapping of likely climate change across the continent suggests that changes in temperature are going to be severe. Our best estimate from using RCP8.5 is that local annual mean temperatures across the continent will increase by between 5 and 7 SDs above current inter-annual variation. This is equivalent to **mean temperatures across**

most of the continent by 2085 that might under current conditions only be experienced once every 3.5 million years. Importantly, shifts in temperature are already strongly apparent in some parts of the continent. Observed climate data since 1950 suggest increases in annual mean temperature of up to two degrees have already occurred in some areas.

This magnitude of projected increase in temperature over a 75-year period is likely **beyond the adaptive capacity of most vertebrates**. Because of the rate and magnitude of temperature change, range-shift to refugial areas is likely to be the major mechanism by which species will persist.

Projections of rainfall changes across the continent were, by contrast, much more uncertain and notably less severe relative to normal inter-annual variation in precipitation. Thus, the uncertainty in future projections of precipitation is less important than it might otherwise be. Our best prediction is that most of the biotic impacts of climate change are likely to be driven by temperature.

In our search for refugial areas, we examined both past climate changes as well as future projected climate change. The projected future shifts in temperature over the next 75 years are typically of greater magnitude than any temperature shift that has occurred in the last 120 000 years. As well as this, they are opposite in direction, because the last major climate shift was into an ice age.

We examined paleological climate because one of the major predictors of endemism and within-species diversity is paleological climate stability (Graham et al. 2010). Our analysis of the location of climatically stable areas over the last 120 000 years identified numerous regions in northern-western, central and south-western Australia that have experienced relatively stable temperatures during this period. Interestingly, these areas of temperature stability are centres of current species-level diversity, much of which is still in the process of being discovered (Moritz, pers. comm.). Unfortunately, there appears to be very little correspondence between the areas of least change in paleological temperature (section 3.4.1.1) and areas with the least change in projected future temperature (section 3.4.1.3). This suggests that **many areas that have acted as paleological refugia in Australia's north and west will not act effectively as refugia under projected climate change**. The many endemic species in these northern and western paleological refugia are, therefore, at severe risk.

The areas of least change in precipitation are distributed patchily throughout the continent across most metrics of stability for the past, the previous 60 years, and the future. Given the lack of spatial coherence in these results, and the fact that shifts in precipitation seem unlikely to be major drivers of biodiversity loss, we make no further inference on the role of precipitation in past and future refugia at the continental scale.

Given that most species will need to shift their range to avoid the extremes of temperature, and that rates at which species can shift their range is limited, we calculated the distance that populations would have to move to stay within 2 SDs of their current temperature regime. This 'distance' analysis showed that the **areas with the lowest required rates of range-shift are concentrated around areas of topographic relief**: The Great Dividing Range, Tasmania, and the MacDonnell Ranges of central Australia. It is clear from this analysis that **these upland areas will act as major refugia for nearby lowland species**.

In general though, the core of these high elevation areas have extremely high 'distance' measures. Species currently in these upland locations have to move a very long way to find equivalent temperatures by 2085. **Thus, uplands will act as critical**

refugia, but not for the species that are currently there. Suitable refugia for upland species are often thousands of kilometres away from the current locations of those species. The sharp gradient in temperature between the upland areas and the surrounding lowlands results in the closest areas with similar temperature being much further south or, in some cases, simply not present anywhere in continental Australia by 2085.

Tasmania features with moderate consistency across many climatic stability metrics. Tasmania contains areas of least change for the past temperature and precipitation, and least change in precipitation of the previous 60 years. Tasmania is also projected to experience low absolute change in temperature and precipitation between current and 2085, and have a moderate shift in terms of the number of SDs for both temperature and precipitation. **Tasmania will act as an important refugial area for many species, provided they are already present there or can cross Bass Strait**.

3.6 Climate change and biodiversity across the continent

When we modelled current and projected species distributions across the continent, some very clear patterns emerged. First, there are projected to be very large shifts in species richness across most of the continent. The models predict net species loss in the north, west and centre of the continent; and net species gain in much of the south and east of the continent. **Large parts of central and western Australia are predicted to lose approximately half of all vertebrate species currently in these areas (**Figure 22**). By contrast, species richness may almost double in parts of southern and eastern Australia**. It is important to note that species gain to an area (but not species loss) assumes that the species is capable of dispersing to that area. Thus, although the inference regarding species loss is probably a robust estimate, **the inference regarding species gain is almost certainly an overestimate of the realised species gain to these areas**.

The areas predicted to gain and lose species are largely consistent in their proportional increase in species richness across the four vertebrate classes we investigated. These changes in species richness can be broken down into the species predicted to move into an area by 2085 (‘immigrants’) and species predicted to move out of (i.e. be lost from) areas (‘emigrants’). That the highest proportion of incoming and lowest proportion of outgoing species are both found largely in the south and east reflects losses of the north and western edges of species ranges, and contractions towards the south-east. This observation is in agreement with observed shifts in bird species ranges over the last 60 years (VanDerWal et al. 2013).

Our definition of refugia as places where species contract to, and persist in, during unfavourable climates (sensu Keppel et al. 2012) suggests that refugia can be defined as places with the highest number of immigrants and the lowest number of emigrants. When we summed the accumulation of these areas (in a taxonomically representative manner), we **clearly identified numerous parts of southern and eastern Australia as important refugia for terrestrial biodiversity**.

The broad congruence between patterns found by modelling species, as well as patterns found by inferring required rates of range-shift (based on climate) is encouraging. However, caution must be exercised when evaluating this congruence, as the same climate data were used in both the investigations of future climates and projections of species distributions into the future.

3.7 Gaps and future research

The next steps required for the species distribution modelling approach to understand future refugia across Australia should include extensive attention to appropriate dispersal scenarios for species, so that realistic estimates of species ability to reach their future climatic niche can be made (Reside et al. 2012). This process is currently hampered by a lack of dispersal data for many of the lesser-known vertebrates in Australia, uncertainty for lag times between changes in climate and corresponding change to habitats, and for this study, time and resources (Bateman et al. In press). Understanding the likelihood of species' ability to reach suitable climate space in the future, and the availability of habitat when climate space shifts, will be large factors in species' capacity to withstand climate change. In addition, identification of microrefugia within species' ranges will be another major step forward for predicting species' future distributions and their need to shift. Computational limitations restrict the resolution of distribution modelling at a continent scale, so while the resolution used in this study was far greater than for most continent-wide distribution modelling exercises, increased computation capacity will aid further developments in this field.

Further refinements to using species distribution modelling for identifying refugia will require weighting for species endemism, and prioritising areas for representativeness and complementarity. Preliminary attempts to incorporate species endemism (using species range size as a proxy) were conducted (APPENDIX 4. Projected species richness variability); however, the ideal way forward is to use the species distribution model outputs in sophisticated systematic conservation planning software, such as that found in Case study 4 (section 7). This is a rapidly developing field, and the computational capacity to include thousands of species at a continent scale at a 1 km resolution will be within reach in the near future.

4. CASE STUDY 1: ASSESSING REFUGIAL POTENTIAL USING COMPOSITIONAL-TURNOVER MODELLING

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4.2 Introduction

Keppel et al. (2012) describe two main approaches to identifying the location of potentially important refugia. The first approach uses biogeographic patterns emerging from analyses of palaeobiological, ecological, genetic and phylogeographic data to identify areas in which higher levels of biodiversity appear to have persisted despite past changes in climate; for example, temperature oscillations during the late Quaternary (Byrne 2008b, Hampe et al. 2013). The second approach, that adopted here, focusses more on the future than the past. It uses best-available understanding of the processes producing refugial habitats to predict where such habitats are most likely to occur under spatially explicit scenarios of future climate change.

Many of the same analytical techniques already employed in assessing potential impacts of climate change on biodiversity more generally can be used to identify likely refugia under this second approach. Most of these techniques are manifestations of two broad analytical paradigms. The most widely applied paradigm involves modelling, and thereby projecting, change in the distribution of particular biological entities (mostly species, but also ecosystem types, e.g. rainforest) as a spatially explicit function of projected change in climate (Botkin et al. 2007, Dawson et al. 2011). The popularity of this paradigm has resulted in a proliferation of correlative and mechanistic modelling approaches, and of techniques for addressing a growing number of relevant biological and ecological factors within these models (e.g. dispersal capacity, population dynamics, adaptive potential, lag effects, species interactions).

Concerns regarding sparseness and unevenness in the geographic and taxonomic coverage of data needed for such modelling, and the high level of uncertainty associated with many aspects of modelled responses to climate change, have at times motivated interest in an alternative analytical paradigm. This involves focussing purely on patterns of change in climatic attributes over space and time, without any direct use of biological data or any explicit modelling of biological responses (Ackerly et al. 2010). Manifestations of this paradigm include analyses of climate-change velocity (Loarie et al. 2009, Burrows et al. 2011), climate stability (Iwamura et al. 2010), novel and disappearing climates (Williams et al. 2007), and various guidelines and methodologies for configuring conservation areas across abiotic environmental gradients (Game et al. 2011, Schloss et al. 2011).

An arguable strength of these analyses is that, compared with more explicit model-based approaches, they assume very little about how particular biological entities (e.g.

individual species) will respond to climate change. They are, nevertheless, underpinned implicitly by one simple, yet fundamental, assumption. This is that magnitude of change in climate serves as a reasonable indicator of potential magnitude of change in overall biological composition, both across geographic space at any given point in time, and across time at any given geographic location. Many decades of ecological and biogeographical research suggest cause for concern regarding this assumption. Even under present conditions, the level of turnover in biological composition observed between two locations exhibiting a given difference in a climatic attribute (e.g. a 2°C difference in mean annual temperature) can vary dramatically. This will depend on the biological group of interest, the climatic position of the locations (e.g. at the low versus high end of a temperature gradient), and the biogeographic history of the region concerned (Ferrier et al. 2004, Buckley and Jetz 2008, Soininen 2010, Qian and Ricklefs 2012).

We here employ a third emerging alternative to the 'bioclimatic modelling' and 'climate-only analysis' paradigms outlined above, one that purposely seeks to balance the respective strengths and weaknesses of these approaches. This third paradigm uses best-available data on recorded occurrences of all species in a biological group of interest (e.g. all beetles) to fit a statistical model describing turnover (dissimilarity) in species composition between geographical locations as a nonlinear, multivariate function of the relative positions of these locations along relevant environmental gradients. This 'compositional-turnover modelling' provides a means of effectively scaling (transforming) the multidimensional climatic space normally employed in climate-only analyses (e.g. of climate-change velocity, climate stability, novel and disappearing climates) to better reflect spatial patterns of compositional turnover observed under current climatic conditions (Ferrier and Guisan 2006, Fitzpatrick et al. 2011).

The particular approach to compositional-turnover modelling used in this study; that is, generalised dissimilarity modelling (GDM) (Ferrier 2002, Ferrier et al. 2007), has been applied extensively over recent years to 'biotically' (or 'ecologically') scale potential impacts of climate change on terrestrial biodiversity across the Australian continent (Dunlop et al. 2012, Prober et al. 2012, Williams et al. 2012b). Recent evaluations elsewhere in the world of the extent to which GDM-based projections of compositional turnover under climate change hold up against projections from species-level modelling approaches, and against actual changes observed in fossil-pollen data from the 20 000 years, have been encouraging (Fitzpatrick et al. 2011, Blois et al. in press, Blois et al. in revision).

A major challenge in using compositional-turnover modelling (or indeed any of the other modelling and analysis approaches outlined above) to identify potential refugia under climate change is adequately addressing effects of local topography in determining meso- and micro-climate. As demonstrated by several recent studies, consideration of finer-scaled topographic effects on radiation, temperature and moisture can lead to quite different conclusions regarding the likelihood of species being able to persist under climate change in any given location, or region, relative to conclusions based on macro-climatic modelling alone (Randin et al. 2009, Austin and Van Niel 2011, Dobrowski 2011, Scherrer and Korner 2011, Ashcroft et al. 2012, Gillingham et al. 2012). Widely used approaches to estimating and projecting climate surfaces for use in bioclimatic modelling (e.g. ANUCLIM, WorldClim) do a reasonable job of accounting for the effects of elevation on temperature and precipitation. However, these approaches do not typically consider other important topographic effects operating at finer scales, including impacts of aspect and slope on radiation and temperature, and impacts of topographic position on soil moisture. We incorporate these effects by linking several recently developed techniques in terrain analysis, soil water-balance modelling, and remote sensing.

The overall objective of this case study was to explore and demonstrate the applicability of compositional-turnover modelling for identifying locations of potential refugia under explicit scenarios of climate change and, in doing so, make effective use of new techniques for deriving and projecting topographically adjusted radiation, climate and moisture surfaces. Our approach focusses strongly on species turnover as a metric for refugial quality. That is, we identify areas on the landscape likely to see the least change in community composition, rather than places in the landscape which species both persist in and move to under future climates. The approach was applied to the entire Australian continent, using best-available national datasets for a wide range of plant, vertebrate and invertebrate taxa. To demonstrate potential applicability at finer spatial resolutions, and using higher quality biological data, the approach was also trialled using comprehensive floristic-survey datasets for NSW, and for the Tingle Mosaic area in south-west Western Australia.

4.3 Research activities and methods

4.3.1 Study areas

We conducted our study at three spatial scales: continental Australia using environmental data compiled at 9-second resolution (approximately 250 m grids), NSW at 3-second resolution (approximately 100 m grids) and the Tingle Mosaic of southwestern Australia at 1-second resolution (approximately 30 m grids) (Figure 30). These regions represent considerable diversity in landform, soils and climates, and their associated biodiversity.

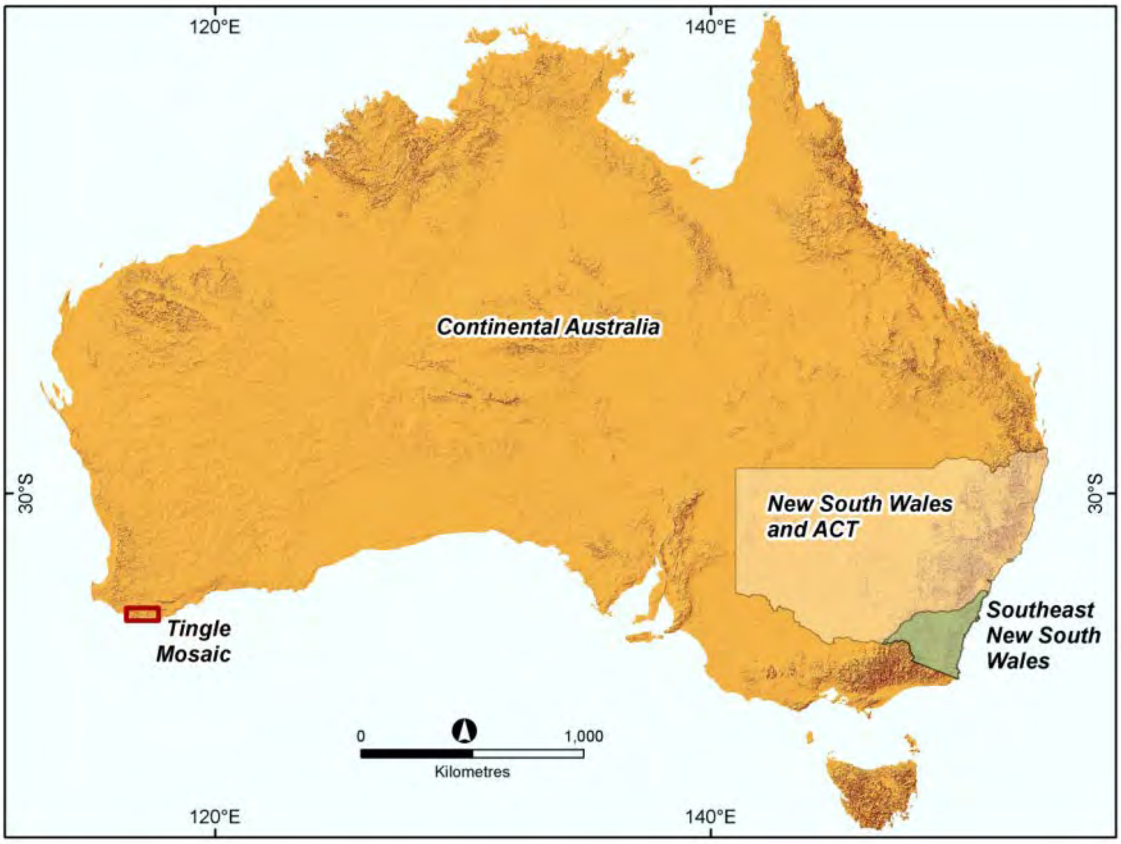

Figure 33: Study areas for assessing refugial potential using compositional turnover modelling.

4.3.2 Topographically adjusted climatic variables

Topography affects local environmental conditions through two main mechanisms: the modification of incoming weather (topo-climate); and the movement of water and nutrients across and below the ground surface. Both these processes may be considered important for the definition of refugia under climate change, whereby topographic modification of local environment can maintain environments more similar to the current state than occurs in surrounding areas. As a simple example, under a warmer and drier future, areas which are locally cooler and wetter than their surroundings (such as shaded gullies) will be more similar to current conditions. These local refugia will act in concord with broader climatic refugia (e.g. large-scale cooler and wetter areas).

Under current climate, these topographically driven distinct environments often have community compositions distinct from their surroundings. In order to capture the full range of future environments, the decision was taken to downscale future climate projections with topographic adjustment. Although some processes, such as wind and orographic effects, are difficult to project adequately, the effects of radiation and to some extent the flow of water may be considered invariant over time. For example, a cool shady spot will remain cooler and shadier, and a wetland will remain wetter, than their surroundings. Two forms of terrain effects were modelled: the effect of radiation balance on maximum temperature and evaporation; and the effect of surface and groundwater flow on the distribution of available water. Whilst our approach to the former was able to draw on longstanding principles and methodologies, a novel approach was developed to address the latter.

4.3.2.1 Topographically adjusted radiation, temperature and evaporation

The MTCLIM (Mountain Microclimate Simulation Model) approach (Hungerford et al. 1989) as used in the SRAD software package (Wilson and Gallant 2000) was adopted as the basis for radiative modification of radiation, maximum temperature, evaporation and derived variables. Essentially the approach uses the ratio of topographically shaded and slope/aspect-corrected incoming shortwave radiation relative to the unshaded radiation on a horizontal surface (S) to adjust both radiation and daily maximum temperature. These variables then feed into evaporation modelling. In the original MTCLIM model, temperature was corrected for elevation lapse rate, but in this study, ANUCLIM was used to carry out this elevational adjustment prior to radiative correction. The radiative correction (*S*) grids were generated incorporating slope, aspect and hill-shade adjustment using the r.sun package in GRASS for each DEM. Critically, the approach adopted needed to be suitable for application to climate change studies, and consequently had to be calculated from readily available GCM outputs. Temperature and precipitation are usually available as GCM outputs; whereas, wind speed and humidity are not normally available, and modelled ground level radiation is based on a uniform daily distribution of precipitation (constant drizzle) so may not reflect the global radiation balance.

The standard FAO 56 approach (Allen et al. 1998) to the estimation of unknown variables from monthly average maximum and minimum temperature (as described in Example 20: Determination of ETo with missing data) was applied to calculate radiation (which was then corrected using S), and potential evaporation as a function of terrain-modified maximum temperature. Minimum temperature was not adjusted for radiation as it typically occurs at night. Cold air down-welling in areas of high elevation range may result in significant topographic variation in minimum temperature. However, this was not modelled, partly because this is a complex process for which a continentally applicable model is not yet available (see Chung et al. 2006) for a simple locally applicable solution) and partly because as Lundquist et al. (2008) point out, weather stations are often situated in areas of cold air down-welling. So although local variation may be modelled, the relationship with splined temperature surfaces is ill-defined.

4.3.2.2 Topographically adjusted soil moisture

Topographically corrected potential evaporation and raw precipitation were used as inputs into a tipping bucket water balance model using the Budyko framework. A layer of topographically adjusted plant-available, water-holding capacity was used to define a bucket size. The model was run monthly to equilibrium, and the annual sum of actual evaporation recorded. Predicted actual evaporation was corrected relative to remotely sensed actual evaporation, by scaling on the Budyko curve, allowing future predictions of actual evaporation (Figure 31). For further details see APPENDIX 5. Projecting ETa under climate change.

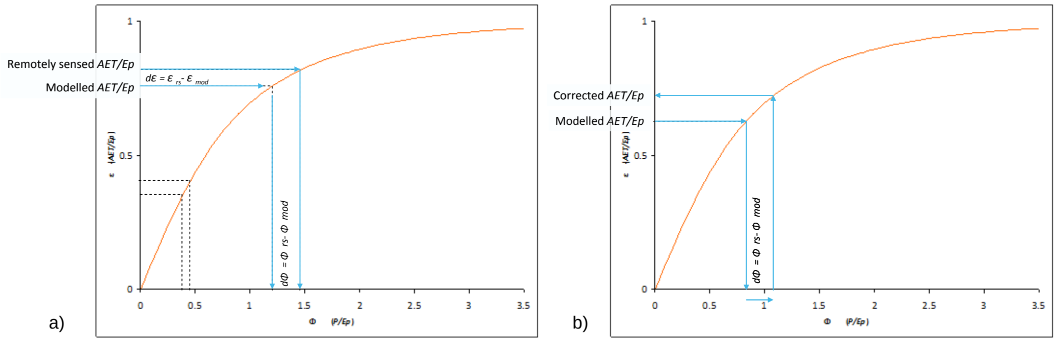

Figure 34: Scaling the difference between modelled and remotely sensed actual evapotranspiration using the Budyko framework. a) derivation of the x-axis offset using current modelled and remotely sensed data; b) adjustment of future model outputs using the derived offset.

This allowed the prediction of future actual evaporation, which is largely water limited in Australia, providing a simple index of the total availability of water in the future. The approach necessarily assumes that the redistribution of ground- and surface water remains broadly constant, and is most reliable where large-scale climatic distributions of precipitation do not change significantly (e.g. where rain ceases to fall in the catchments for the Channel Country).

4.3.3 Workflow

Figure 32 shows the workflow for the calculation of downscaled climate statistics for both current and future climates. Lapse rate correction of input temperature and precipitation surfaces was carried out using ANUCLIM 6.1. S grids were generated using the r.sun package in GRASS. These inputs were provided to the UNIX based TerraFormer software written for this project, running on the CSIRO High Performance Computing clusters, which calculates first the monthly output grids, and second the derived statistics: Annual Mean/Sum as appropriate, Annual Monthly Maximum, Annual Monthly Minimum, and the maximum and minimum rates of month to month change, as described in Williams et al. (2012a).

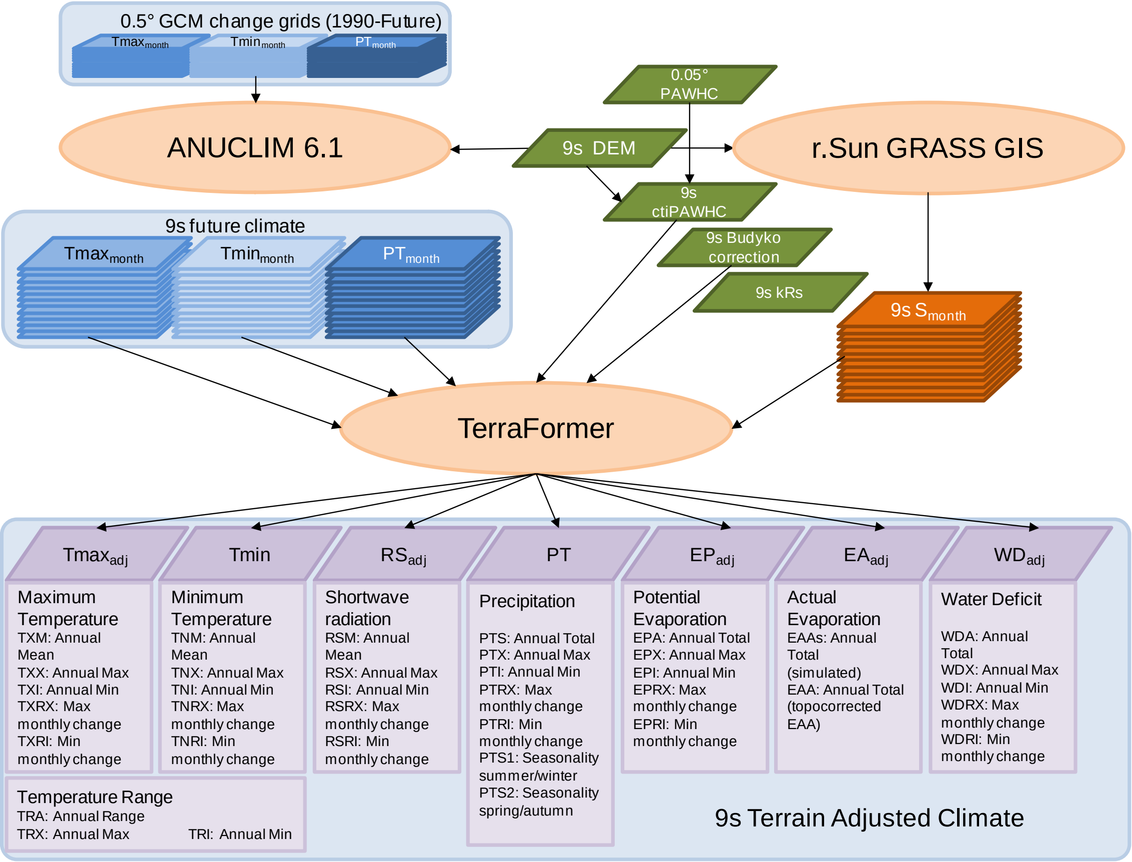

Figure 35: Workflow for the terrain downscaling of climate, with topographic and surface-/ground water corrections.

4.3.4 Other environmental variables

Three groups of environmental variables were compiled as candidate predictor variables – climate, regolith and landform (see APPENDIX 6. Environmental variables used in GDM modelling). Nine-second (Hutchinson et al. 2008), 3- and 1-second resolution (Gallant 2011) digital elevation models (DEM) were used with ANUCLIM version 6.1 (Xu and Hutchinson 2011) to derive monthly climate variables, representing 30-year averages centred on 1990. As described above, relevant climatic variables were adjusted for local topography using a scaling factor. A series of climate predictors describing annual minimum and maximum conditions and facets of seasonality were generated from the monthly variables (described in Williams et al. 2012a).

A series of primary and secondary derivatives of each DEM were compiled as supplementary landform predictors, where relatively independent of the topographically adjusted climate variables. In addition to the types of substrate and landform variables listed in Williams et al. (2012a), soil attributes modelled from soil spectra measurements (Viscarra-Rossel and Chen 2011, Viscarra Rossel 2011) and composites from soil mapping (Jacquier 2011b, Jacquier 2011a) were also compiled. An index of soil water-holding capacity was derived from the topographic wetness index (Gallant et al. 2012), the soil depth variable derived from the Atlas of Australian soils (Bureau of Rural Sciences 2000, McKenzie et al. 2000) and soil water-holding capacity (Jacquier 2011a), applying the method developed by (Claridge et al. 2000).

4.3.5 Biological data

For the continental case study, we accessed presence data for selected invertebrate and vascular plant groups via the biocache portal (http://biocache.ala.org.au/) of the

Atlas of Living Australia (Table 3). Vertebrate data were compiled and vetted by A. Reside and collaborating researchers. Across NSW, three sources of vascular plant data were compiled and applied in separate case studies. Across the entire state, we used the floristic survey data compiled and vetted by the NSW Office of Environment and Heritage (OEH) for GDM analysis (Logan et al. 2009). In south-eastern NSW, we used CSIRO's survey data for tree species capable of reaching the canopy (Austin et al. 1996). In far southern Western Australia we used the Tingle Mosaic survey data (Wardell-Johnson and Williams 1996). More detailed descriptions of these datasets are provided in APPENDIX 7. Compositional turnover modelling.

The biological response variable used for fitting the GDMs was the Sørenson compositional dissimilarity between pairs of sites. The number of possible site-pairs in a dataset is frequently beyond the capacity of conventional computing. A Perl script written as an extension to Biodiverse (Laffan et al. 2010) was used to generate site-pairs and their Sørenson dissimilarity values (described in Rosauer et al. in review). We randomly sampled approximately 300 000 site-pairs, evenly stratified by Australian bioregions (DSEWPAC 2012) for the continental data and subregions for the NSW data. Equal weighting was applied to each bioregion or subregion with a slight emphasis (10%) on sampling more site-pairs from within regions relative to between regions. The sampling of NSW floristic survey data was further weighted by the log of the total number of species within each subregion. For sampling purposes, a site is defined by the resolution of the spatial analysis grid (9-second, 3-second, 1-second). Lists of species were aggregated within each site.

To account for variation in survey adequacy, we used the number of species occurring at a site as a threshold in generating site-pair samples for the continental case study. Presence-only data, such as that aggregated by the Atlas of Living Australia, are dominated by ad hoc observations that under-sample biodiversity at the site level. Under-sampled sites can lead to inflation of estimated levels of compositional dissimilarity between sites, and contribute to model error. The threshold number of species was determined after testing alternative site-pair sample data with the same predictors in GDM models. As the threshold for the number of species is increased, the number of occurrence sites and species represented decreases, the model deviance explained increases and the sum of predictor coefficient values decreases. Where the sums of predictor coefficient values were similar, but the deviance explained increased, the model with a lower threshold number of species was selected. This ensured more sites (and species) were available for site-pair sampling. Any overall inflation of estimated dissimilarities remaining after applying this threshold was accounted for, and adjusted, through the inclusion of an intercept term in the fitted models. This term effectively accounts for the average level of dissimilarity expected to be observed between two sites with identical environmental attributes, given the average level of under-sampling exhibited by the model-fitting dataset. Survey adequacy, and the effects of under-sampling, were much less of an issue for the biological datasets used in the NSW and Tingle Mosaic case studies, despite the smaller grid-cell sizes employed. This was because these data were derived from thorough presence–absence sampling of floristic survey plots rather than from aggregation of presence-only records.

Table 1: Biological groups compiled for species compositional turnover models. The number of species and sites are totals prior to site-pair sampling. A different threshold minimum number of species per site to be included in a model were identified following preliminary testing. Site-pairs were samples taking into account the minimum number of species per site.

Taxonomic group	# species	# sites	# site-pairs	# minimum species per site
Class Mammalia (mammals)	245	239 162	292 845	≥5
Class Aves (birds)	599	432 019	296 308	≥15
Class Reptilia (reptiles)	646	110 221	291 888	≥3
Class Amphibia (amphibians)	235	75 285	289 683	≥2
Order Apocrita (wasps and bees)	3840	11 292	297 907	≥2
Order Coleoptera (beetles)	9288	16 024	297 441	≥3
Order Aranae (spiders)	2207	10 959	298 138	≥1
Order Asparagales (lilies and onions)	2308	121 364	296 845	≥2
Order Asterales (daisies)	2179	208 571	295 982	≥1
Order Fabales (peas)	3317	299 443	297 145	≥5
Division Gymnospermae (fruitless seed plants)	212	24 459	294 418	≥3
Order Myrtales	2564	288 059	294 963	≥2
Order Poales (grasses and sedges)	2918	266 241	296 777	≥4
Order Proteales	1159	108 572	294 652	≥2
Kingdom Fungi	3818	28 156	296 155	≥2
NSW plant survey[1]	4847	40 190	885 376	≥1
Southeast NSW plant surveys[2]	749	13 300	542 361	≥7
Tingle Mosaic plant surveys[1]	773	312	48 205	≥1

1. Vascular plants – ferns and allies, gymnosperms and angiosperms
2. Trees capable of reaching the canopy (includes gymnosperms and some angiosperms)

4.3.6 GDM model fitting

GDM model fitting followed the procedure outlined in Williams et al. (2012a). Each correlated group of variables (climate, regolith, landform) was initially tested to identify redundancy. Remaining candidate predictors were combined (typically around 35–40 variables) and further screened for redundancy using a backward elimination procedure. Variables were retained if they contributed at least 0.05% partial deviance explained. Geographic distance between site-pairs was included as a predictor based on the selection criteria after testing environmental predictors. This procedure resulted in around 20 predictors in the final model. A detailed description of the GDM model fitting process and outputs is given in APPENDIX 7. Compositional turnover modelling.

4.3.7 Climate scenarios

Two distinct workflows were applied to the selection and application of climate scenarios within this study. As an initial test of the refugial analysis, SRES scenarios were applied to the NSW study region for two GCMS extracted from OzClim, with standard topographic adjustment. Following development of the complete climate-change consistent downscaling methodology, two GCMs were selected from the suite used for the species distribution modelling component of the project, and downscaled to 9 second (250 m) resolution for the whole continent and to 30 m resolution for the Tingle Mosaic study area. The future climate predictors were used along with the existing regolith and terrain predictors to develop projections of each fitted GDM model. Where this occurred, the last 10% of the trendline from each end of the fitted functions for each climatic predictor was extrapolated into novel climates. These environmental predictors, scaled by the coefficients of the fitted compositional turnover models, are the inputs to the analysis of refugial potential.

4.3.7.1 NSW (3-sec resolution) scenarios

Eight climate change scenarios were generated at 3-second resolution for the year 2070 using two emission scenarios (A1FI equivalent to an RCP of 8.5; A1B equivalent to an RCP of 4), with two levels of climate sensitivity to emission concentrations (high or medium as defined in OZCLIM, Ricketts and Page 2007), and two GCMs with contrasting estimates of future rainfall: the MIROC-M model (wetter future, Hasumi and Emori 2004) and the CSIRO Mk 3.5 model (drier future, Gordon et al. 2010). These GCMs are among the top-performing models assessed for Australian conditions (Crimp et al. 2012) and represent the best- and worst-case outcomes with respect to plausible temperature and rainfall futures for a given emissions scenario (Clarke et al. 2011). The monthly climate scenario data were obtained from OZCLIM (CSIRO 2007, Ricketts and Page 2007) downscaled using ANUCLIM 6.1 software (Xu and Hutchinson 2011), as described in (Harwood et al. 2010), with the current climate representing a 30-year average centred on 1990.

4.3.7.2 Continental (9-sec resolution) and Tingle Mosaic (1-sec resolution) scenarios

The full downscaling approach outlined in section 4.3.2 was applied for both the continental 9s analyses and the 30 m Tingle Mosaic region. Prior to this, change grids at 0.5° were supplied by J. VanDerWal to maintain compatibility between the change grids that were subsequently downscaled to different grid resolutions for the species-level and community-level analyses. Due to the computational, data storage and i/o requirements of the 9s grid (134 GB per resultant scenario) two representative GCMs were selected, based on the same criteria as for the NSW study region. Given that the Tyndall Centre outputs used for the species distribution modelling study (section 3.3.1) had only the poorly performing CSIRO 3.0 GCM, the GFDL-CM2 model (Delworth et al. 2006, Gnanadesikan et al. 2006, Wittenberg et al. 2006) was selected for the drier future, whilst using the high resolution MIROC model for compatibility with the NSW region. These change grids were converted to the input format required for ANUCLIM 6.1, and downscaled over the v3.1 9s DEM for the continental analysis and the 30m DEM for the Tingle Mosaic region. Downscaled maximum and miniumum temperatures and precipitation were used as inputs to the TerraFormer software, as shown in Figure 32, and resultant summary variables derived.

4.3.8 Analysis of refugial potential

The potential of a given location (grid cell) to serve as a refugium, for a given biological group under a given climate scenario, was estimated using predictions from the fitted GDM model for that group. This model predicts the level of compositional dissimilarity d_{ij} , and conversely similarity $s_{ij} = 1 - d_{ij}$, expected between two locations i and j knowing only the values of relevant environmental variables at these locations. Predicted similarities can range between zero (where two locations are predicted to have no species in common) and one (where the locations are predicted to be identical in terms of species composition).

When predicting compositional similarity between location i and j under present environmental conditions, we can denote this as:

$$s_{i_{present}\, j_{present}}$$

Invoking space-for-time substitution, a fitted GDM model can also be used to predict the compositional similarity between a given location *i* in the present and this same location in the future under a given climate scenario:

$$s_{i_{present}\, i_{future}}$$

This provides an indication of the amount of change in species composition expected at this location, and has been used extensively in previous GDM-based studies mapping potential levels of compositional turnover (*vs.* compositional stability) under climate change across the Australian continent (Dunlop et al. 2012, Prober et al. 2012, Williams et al. 2012b) and across North America (Fitzpatrick et al. 2011, Blois et al. in revision).
Three further types of compositional similarity can be readily estimated using this same approach:

$$s_{i_{present}\, j_{future}}$$

(the compositional similarity expected between location *i* under present environmental conditions, and a different location *j* in the future under a given climate scenario);

$$s_{i_{future}\, j_{present}}$$

(the compositional similarity expected between location *i* in the future under a given climate scenario, and location *j* under present conditions); and

$$s_{i_{future}\, j_{future}}$$

(the compositional similarity expected between locations *i* and *j* in the future under a given climate scenario).

These different types of predicted similarity can be combined in various ways to produce a wide range of biotically scaled measures of climate stability, the velocity of climate change, and novel and disappearing climates. Refer to Dunlop et al. (2012) and Williams et al. (2012b) for GDM-based examples of such applications for the Australian continent and Queensland respectively.

For the current project we developed a new measure, tailored specifically to the challenge of identifying potential refugia under climate change. This calculates the refugial potential *r* of grid-cell *i* under a given climate scenario as:

$$r_i = \frac{\sum_{j=1}^{n} s_{i_{future} j_{present}}}{\left(\sum_{j=1}^{n} s_{i_{future} j_{future}}\right)^2}$$

The set of *n* grid-cells with which cell *i* is compared in these calculations is drawn from within a specified spatial radius around the cell of interest (Figure 33). To assess the effect that variation in dispersal capacity between different organisms is likely to have on refugial potential, each analysis (for a given combination of biological group and climate scenario) was repeated using three different sets of surrounding grid-cells:

- all cells within a 1 km radius of cell *i*

- a sample of 20 000 cells within a radius of 100 km of cell *i* with these cells selected randomly according to a half-Cauchy distribution (Shaw 1995) with a mean dispersal distance of 10 km
- as for the previous sample but with a mean dispersal distance of 50 km.

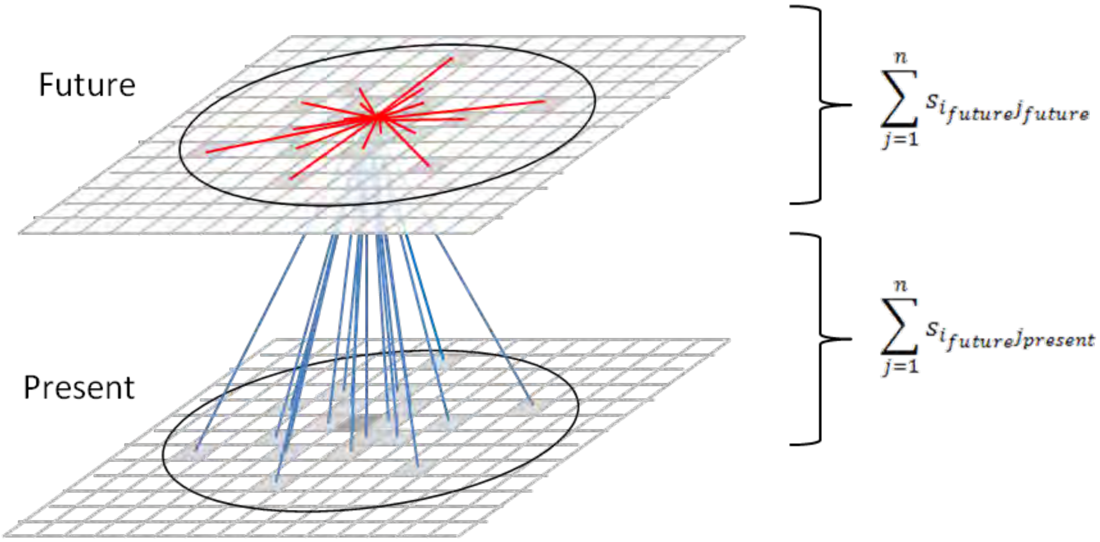

Figure 36: The two types of predicted compositional similarities used to calculate refugial potential for a given grid-cell *i* under a given climate scenario: in red, predicted similarities, in the future, between cell *i* and each of *n* cells within a surrounding radius; and in blue, predicted similarities between cell *i* under future environmental conditions and each of the same *n* cells under present conditions.

This particular measure of refugial potential assesses the extent to which a given location is predicted to exhibit an environment in the future (i.e. under a given climate scenario) that is likely to have undergone a marked proportional reduction in extent, and will be relatively rare throughout the surrounding landscape as a result of climate change (note that the squared denominator in the above formula results from dividing the proportional reduction in extent by the extent remaining in the future). This general concept is illustrated in Figure 34 in which, for ease of explanation, both geographical space and environmental space have been simplified to a single dimension each (the geographical dimension can be thought of as a straight-line transect across a landscape, whereas the environmental dimension can be thought of as a biotically-scaled temperature gradient). The concentric ellipses centred on each of the labelled locations depict decreasing levels of compositional similarity with increasing distance from a location in biotically scaled environmental space, and decreasing likelihood of dispersal with increasing distance in geographical space.

A visual impression of the refugial potential of each of the labelled locations (A to E) can be obtained by comparing the extent to which the concentric ellipses, centred on the future environment of that location, overlap with current environments in the surrounding landscape *versus* the extent of overlap with future environments in the same landscape. For example, the future environment at location B (think of this as situated on a flat plain surrounded by an expanse of similar elevation, and therefore temperature) is expected to be much more extensive in the surrounding landscape under climate change than it is at present, and this location therefore has very low refugial potential. In contrast, the future environment of location E (a mountain peak) is expected to be considerably less extensive in the surrounding landscape than it is a present, indicating good potential for this location to serve as a refugium for biota associated with this particular environment. Applying the same logic to the other labelled locations, location A (a relatively high outcrop, or sheltered topographic position in the middle of a flat plain) and location D (at mid-elevation in highly dissected terrain) exhibit moderate levels of refugial potential (but less than location E), whereas location C has relatively low refugial potential (but more than location B).

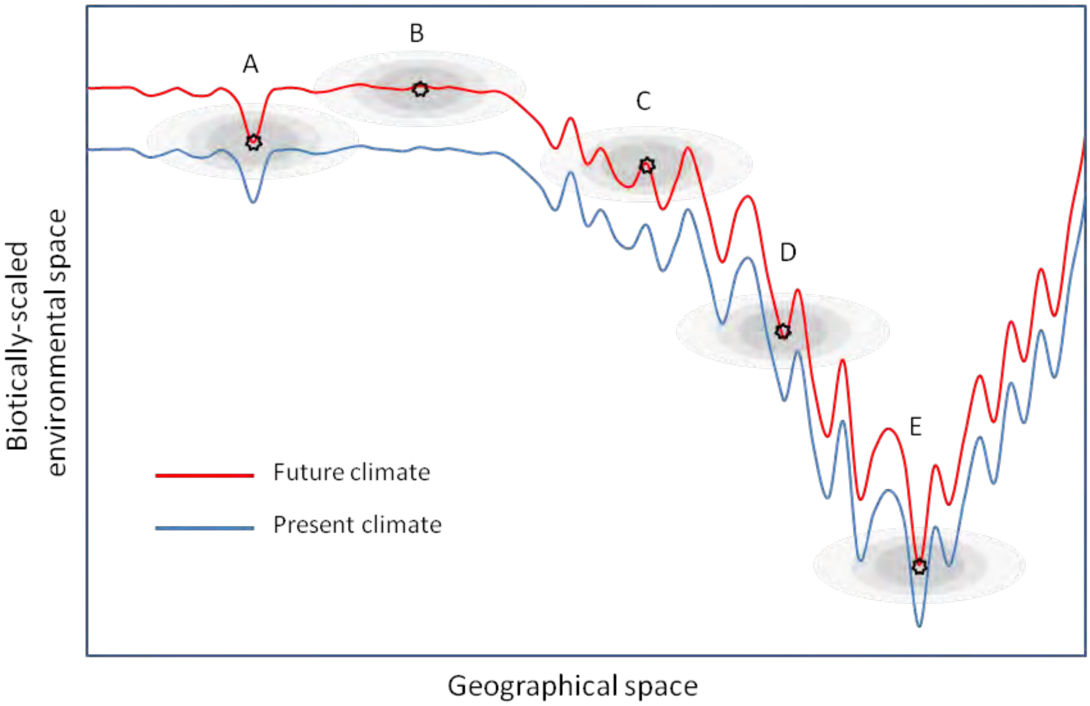

Figure 37: Diagrammatic representation of the shifting relationship between geographical space and biotically scaled environmental space under climate change. For ease of explanation, both geographical space and environmental space have been simplified to a single dimension each. The geographical dimension can be thought of as a straight-line transect across a landscape, and the environmental dimension can be thought of as a biotically scaled temperature gradient. The labelled locations (A to E) are discussed in the text. The concentric ellipses centred on each of these locations depict decreasing levels of compositional similarity with increasing distance from a location in biotically scaled environmental space, and decreasing likelihood of dispersal with increasing distance in geographical space.

The calculation of refugial potential was carried out using the MPI/ OpenMP hybrid implementation of the Muru GDM model, developed by Tom Harwood and Maciej Golebiewski at CSIRO. Utilising 120 to 160 parallel processes, the required CPU time of 344 hours (for each combination of biological group, climate scenario, and dispersal distance, across the entire continent at 250 m resolution) was reduced to a more manageable 3.6 hours, subject to availability of the required number of nodes on the CSIRO High Performance Computing cluster.

4.4 Results and outputs

4.4.1 Fitted compositional-turnover models

Models of compositional turnover were developed for 15 different taxonomic (biological) groups across continental Australia using 9-second gridded predictor data.

Models of compositional turnover in vascular plants were also developed using floristic survey data for three regions: all of NSW (3-second resolution), south-east NSW (3-second resolution), and the Tingle Mosaic in south-west Western Australia (1-second resolution) (Table 4). Environmental predictors overall explained substantially more of compositional-turnover patterns (estimated from the sum of coefficients fitted to each predictor) than did geographic distance in all models except that for amphibians, where geographic distance was marginally more important (see details in APPENDIX 7. Compositional turnover modelling). As expected, climate variables were the strongest predictors of compositional turnover, particularly among the continental models, compared with regolith (soil and related proxies) and landform variables. Regolith was proportionally more important for most plant groups, especially the nitrogen-fixing Fabales and for the local model of the Tingle Mosaic. All models included one or more of the topographically adjusted climate variables. The continental models incorporated the index of topographic-moisture (EAA) derived from the 9-second MODIS actual evapo-transpiration dataset. This variable was amongst the most important climatic predictors along with continental patterns of summer to winter rainfall seasonality (PTS1), maximum precipitation deficit (WDI) and minimum temperature regimes (TXI, TNX) (see APPENDIX 6. Environmental variables used in GDM modelling for definitions of variables).

Table 2: Fitted compositional-turnover (GDM) models. Continental models were applied to the taxonomic subgroups using presence data (first 15 groups listed) and regional models were applied to presence–absence survey data of vascular plants (last three groups listed).

Taxonomic group	% deviance explained	Summed coefficients	# predictors
Class Mammalia (mammals)	32.40	9.96	20
Class Aves (birds)	24.79	4.60	11
Class Reptilia (reptiles)	37.07	13.30	18
Class Amphibia (amphibians)	45.33	19.50	19
Order Apocrita (wasps and bees)	20.14	16.48	16
Order Coleoptera (beetles)	22.57	13.80	19
Order Aranae (spiders)	20.91	18.40	20
Order Asparagales (lilies and onions)	21.67	17.92	17
Order Asterales (daisies)	37.83	26.51	18
Order Fabales (peas)	37.62	20.12	22
Division Gymnospermae (fruitless seed plants)	35.17	24.47	20
Order Myrtales	29.09	19.59	19
Order Poales (grasses and sedges)	48.17	25.94	19
Order Proteales	42.57	35.06	20
Kingdom Fungi	49.64	34.12	20
NSW plant survey[1]	45.78	14.00	20
Southeast NSW plant surveys[2]	33.82	10.59	17
Tingle Mosaic plant surveys[1]	26.27	6.75	14

1. Vascular plants – ferns and allies, gymnosperms and angiosperms
2. Trees capable of reaching the canopy (includes gymnosperms and some angiosperms)

4.4.2 Refugial potential – Continental 9-second analyses

Due to the considerable computation time required to run each of the continental refugial potential analyses (section 4.3.8), the full analytical process was completed for only four of the 15 biological groups: Order Proteales (banksias, grevilleas etc.), Order Fabales (peas, including acacias), reptiles and amphibians. However, all required inputs for the remaining biological groups have been prepared, including all projected environmental variables, biotically scaled at 250 m resolution, using the fitted GDMs for these groups. Potential therefore exists to undertake the final stage of processing; that is, the refugial analysis itself, for each of these groups in the future, if resourcing of required staff time can be secured beyond this project.

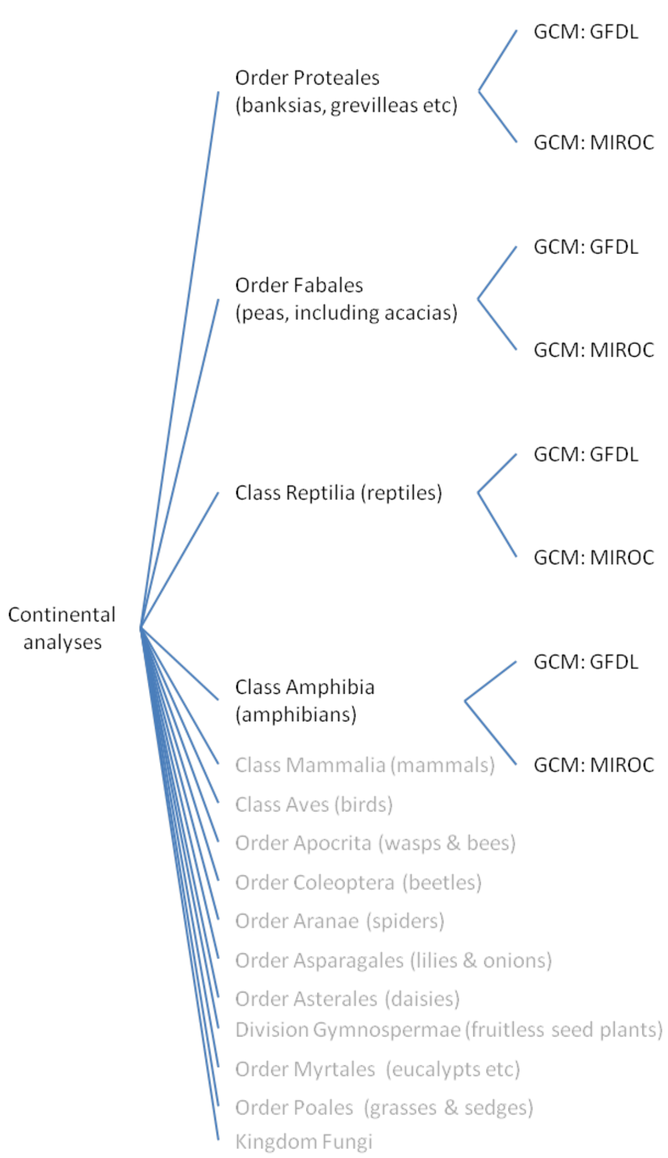

Figure 38: Continental analyses of refugial potential (based on compositional-turnover modelling).

We first assessed the effect that varying assumed dispersal capacity has on the identification of refugial potential for a single combination of biological group, Order Proteales, and climate scenario, RCP8.5 using the GFDL GCM. While the results exhibited some sensitivity to the choice of 1 km, 10 km or 50 km dispersal capacity, overall patterns of refugial potential generated by these three analyses were reasonably consistent, at least at continental scale (Figure 36). The remaining continental analysis runs completed for this report were therefore performed using a single dispersal value, that is, the intermediate distance of 10 km.

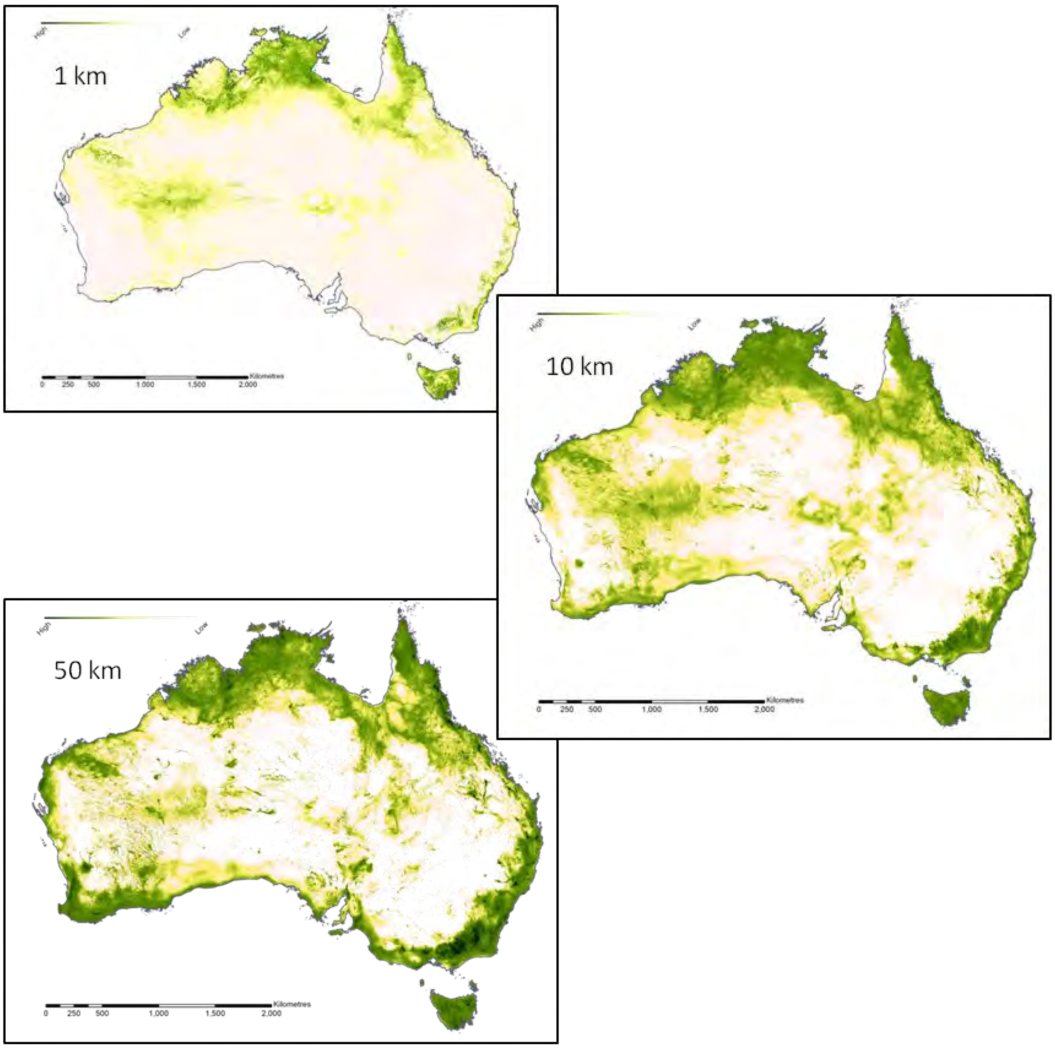

Figure 39: Refugial potential based on compositional-turnover modelling of the Order Proteales (banksias, grevilleas etc.), assuming three different dispersal capacities. GCM: GFDL. RCP: 8.5 (to 2085).

Results obtained from analyses of all possible combinations of the four selected biological groups, two GCMs (GFDL vs MIROC) and two RCPs (6.0 and 8.5) exhibited considerable variation both between climate scenarios within a given biological groups, and between groups within a given scenario. Examples of this variation are presented in Figure 37 (four climate scenarios for a single group, the Proteales) and Figure 38 (four biological groups for a single climate scenario, GCM: GFDL , RCP: 8.5).

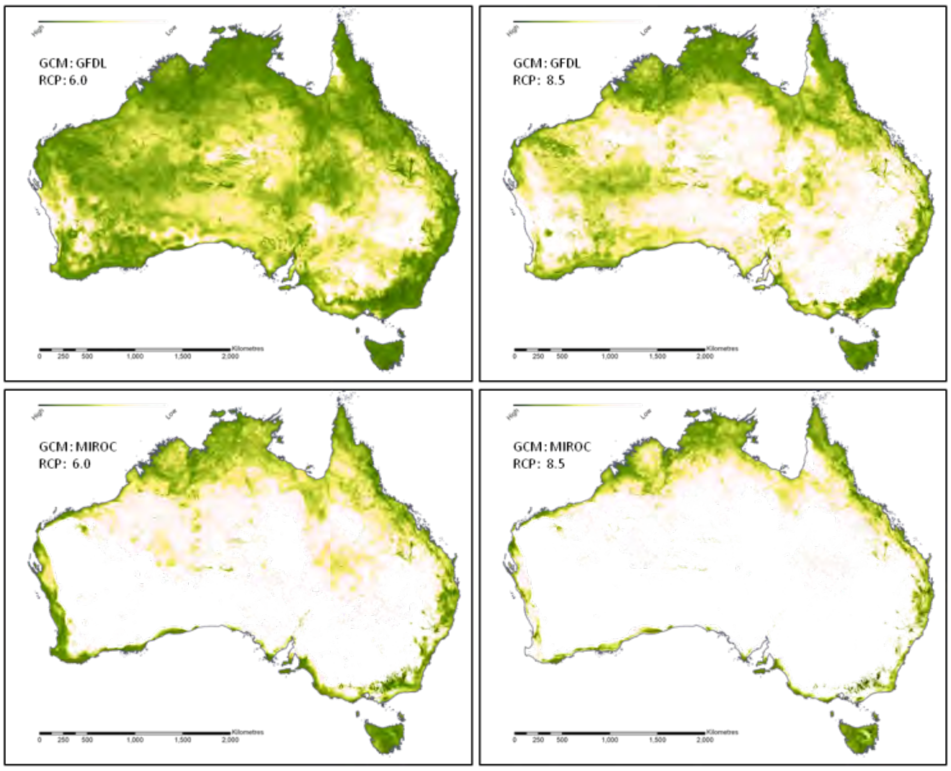

Figure 40: Refugial potential based on compositional-turnover modelling of the Order Proteales (banksias, grevilleas etc.), for four climate scenarios (to 2085).

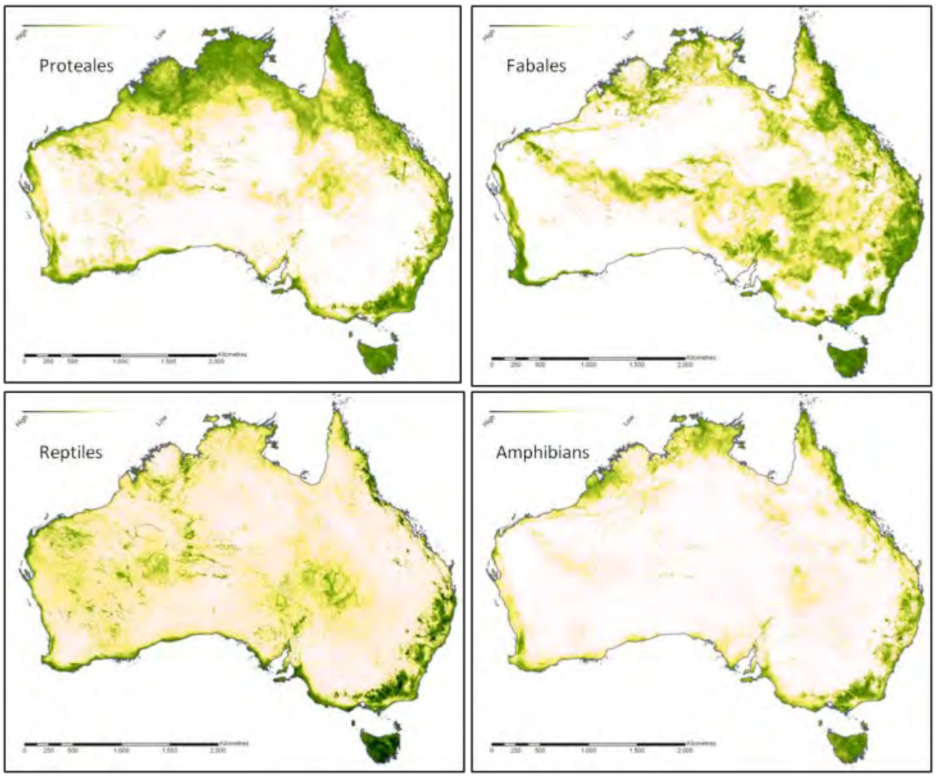

Figure 41: Refugial potential based on compositional-turnover modelling of four different biological groups: Order Proteales (banksias, grevilleas etc.), Order Fabales (peas, including acacias), reptiles, and amphibians. GCM: GFDL. RCP: 8.5 (to 2085).

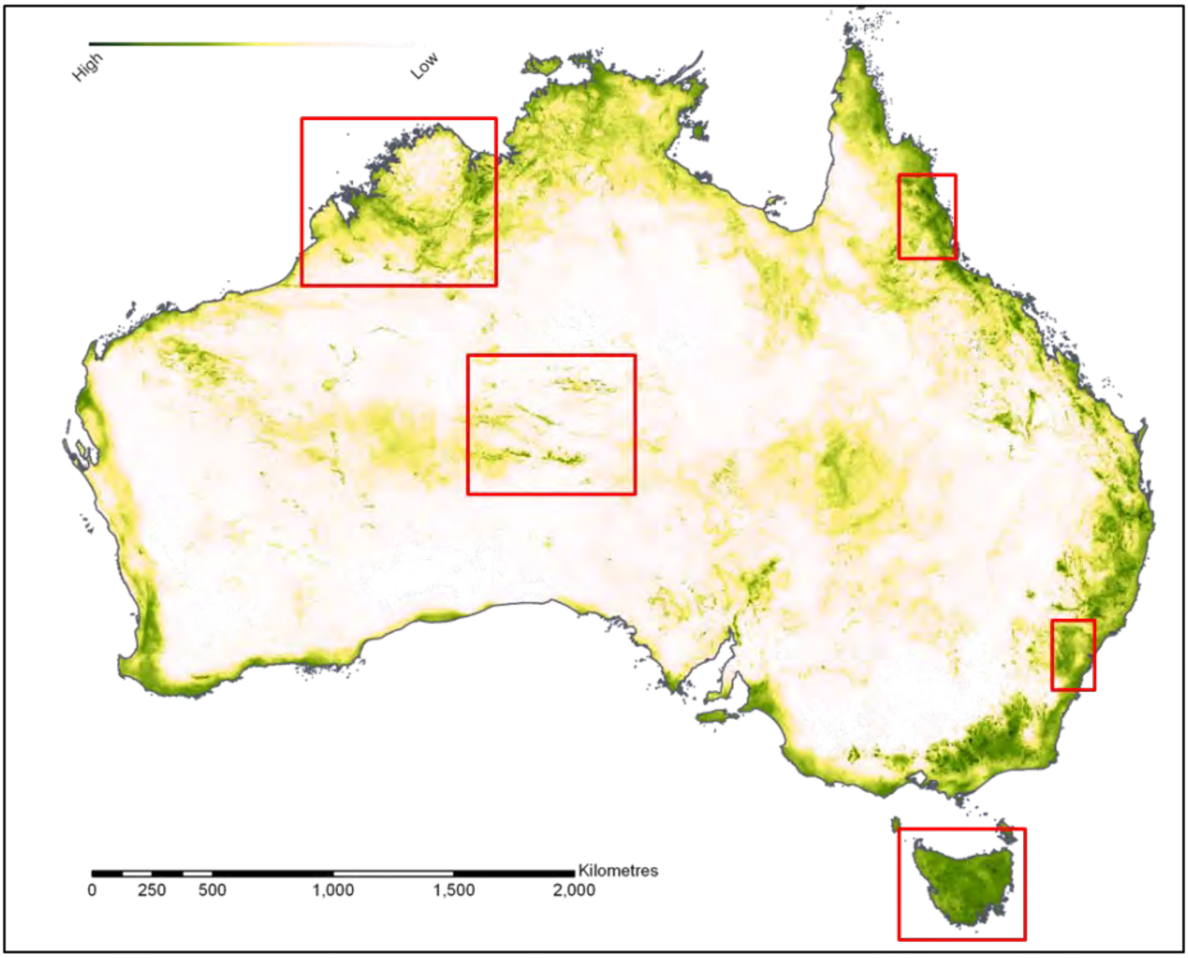

Figure 42: Refugial potential averaged across Proteales, Fabales, reptiles, and amphibians, and four climate scenarios (to 2085). The red rectangles indicate areas depicted in greater detail.

To provide an indication of overall refugial potential across biological groups and across climate scenarios, the results of all 16 combinations of groups and scenarios were averaged, yielding the continental map presented in Figure 39.

Selected portions of this map are enlarged, and presented in greater detail, in Figure 40 to Figure 44, thereby providing a clearer indication of the 250 m spatial resolution of the analysis, and the effects of topography on refugial potential at finer scales. These enlarged maps also depict the location of protected areas within the National Reserve System (NRS), and mask out areas of land from which native vegetation has been ostensibly removed (based on mapping from the National Vegetation Information System, NVIS).

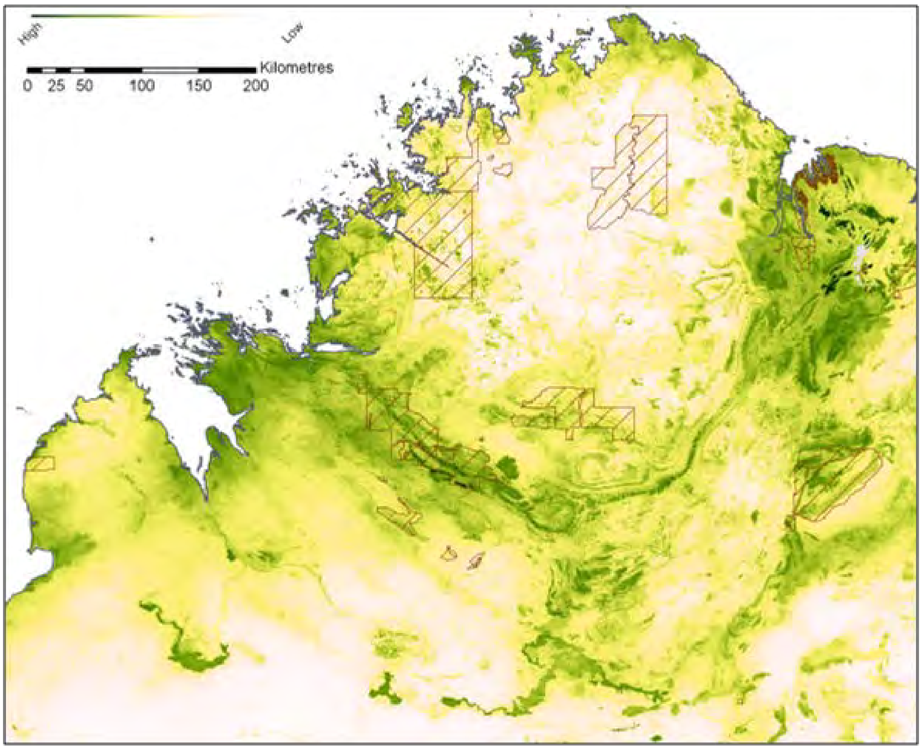

Figure 43: Enlarged portion (Kimberley region) of map presented in Figure 39, depicting refugial potential averaged across Proteales, Fabales, reptiles, and amphibians, and four climate scenarios (to 2085). Protected areas included as hatched overlay.

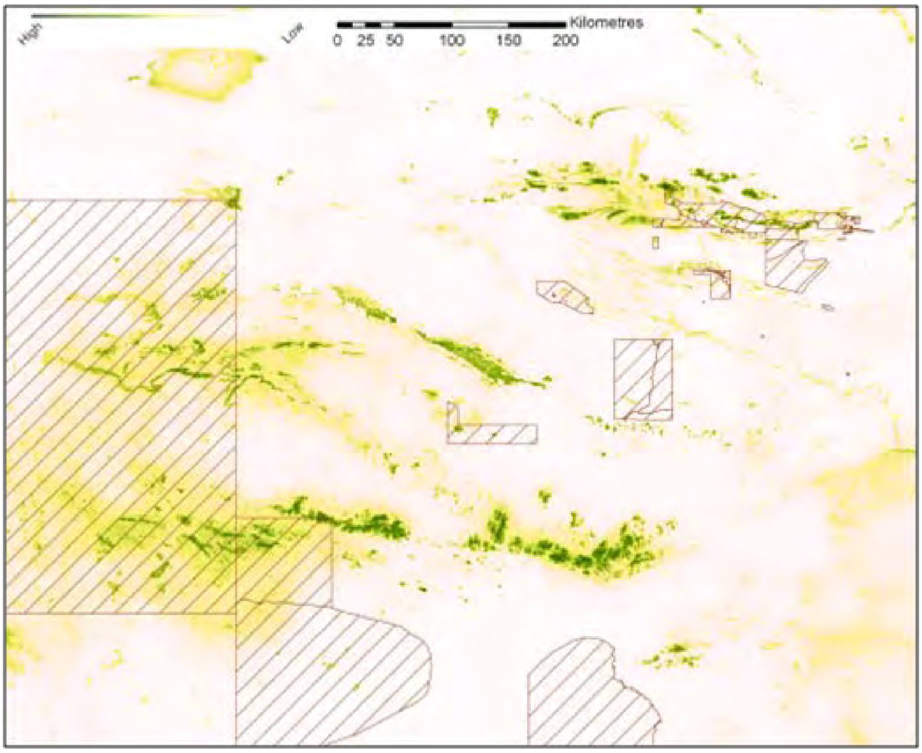

Figure 44: Enlarged portion (Central Ranges) of map presented in Figure 39, depicting refugial potential averaged across Proteales, Fabales, reptiles, and amphibians, and four climate scenarios (to 2085). Protected areas included as hatched overlay.

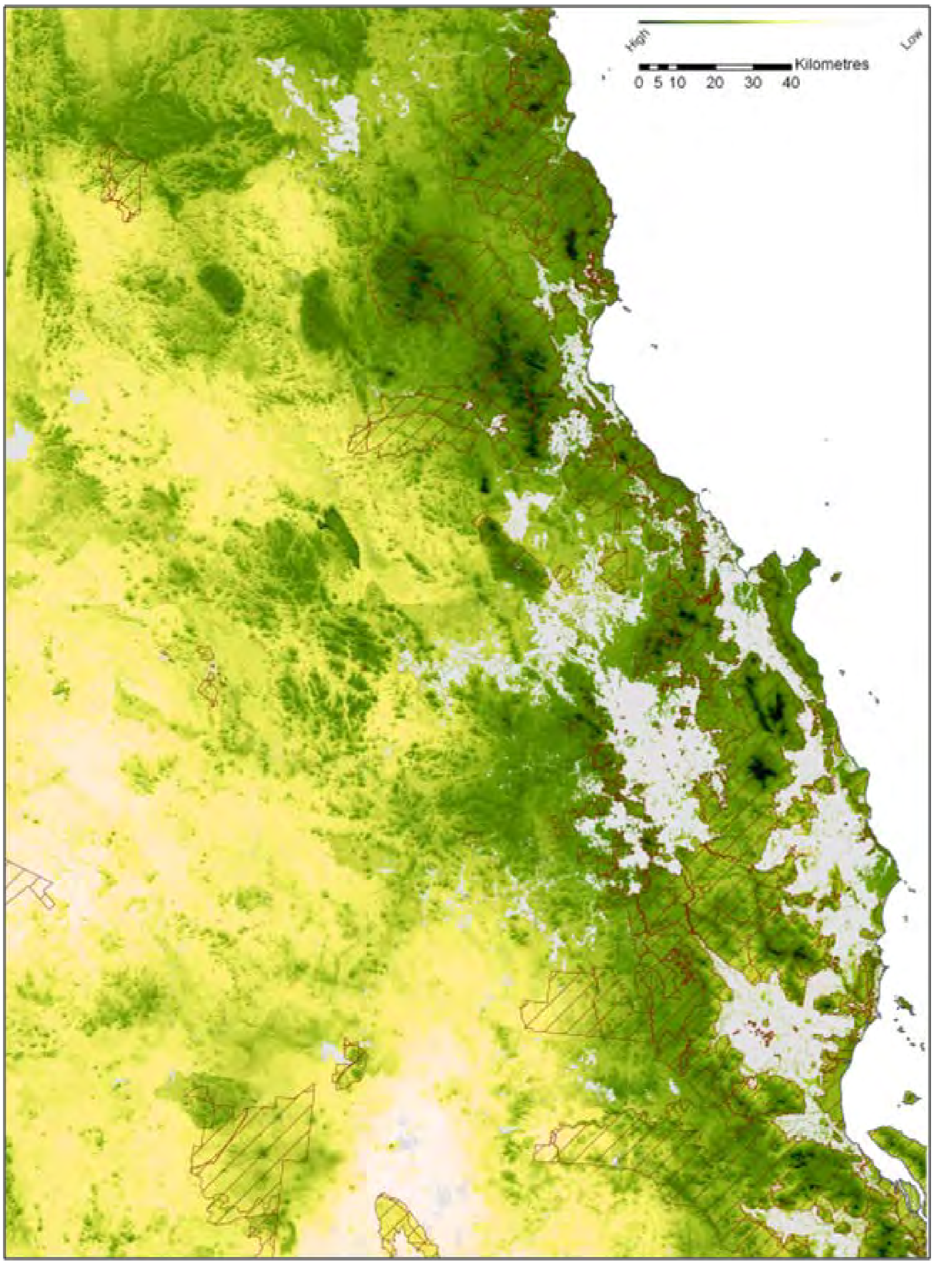

Figure 45: Enlarged portion (Wet Tropics) of map presented in Figure 39, depicting refugial potential averaged across Proteales, Fabales, reptiles, and amphibians, and four climate scenarios (to 2085). Protected areas included as hatched overlay. Cleared land depicted in grey.

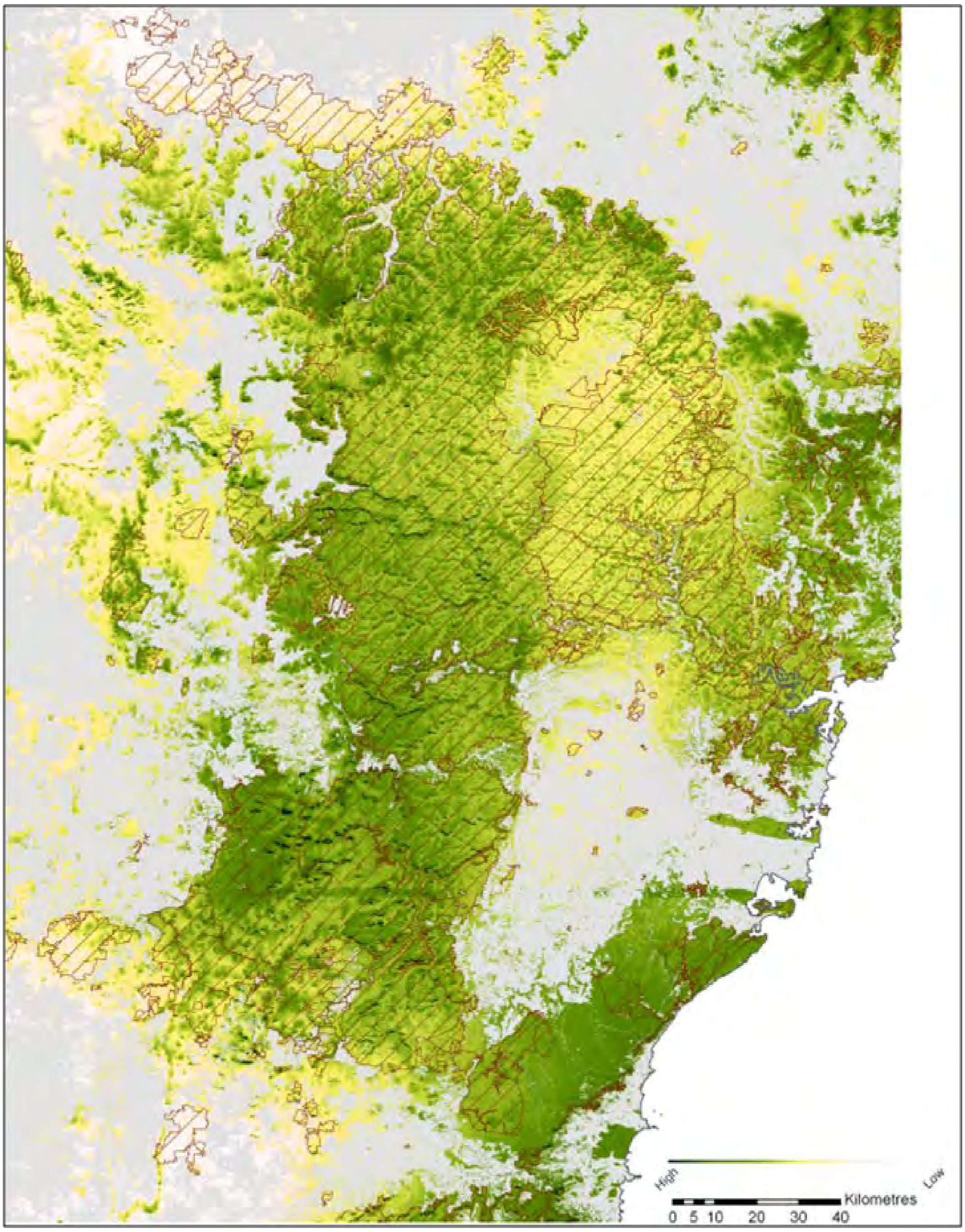

Figure 46: Enlarged portion (Sydney Basin) of map presented in Figure 39, depicting refugial potential averaged across Proteales, Fabales, reptiles, and amphibians, and four climate scenarios (to 2085). Protected areas included as hatched overlay. Cleared land depicted in grey.

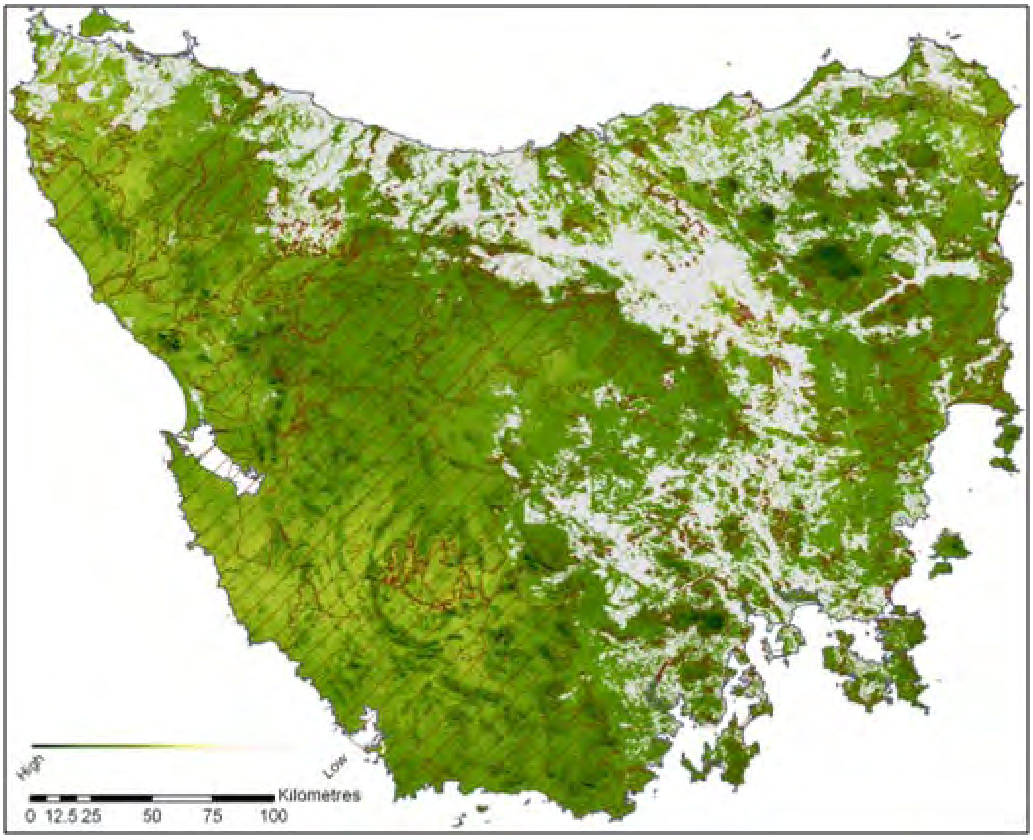

Figure 47: Enlarged portion (Tasmania) of map presented in Figure 39, depicting refugial potential averaged across Proteales, Fabales, reptiles, and amphibians, and four climate scenarios (to 2085). Protected areas included as hatched overlay. Cleared land depicted in grey.

An overall indication of the current level of protection of areas of high refugial potential afforded by the National Reserve System (NRS) is provided in Figure 45 and Figure 46. These maps colour areas of relatively high refugial potential, extracted from Figure 39, according to whether these lie inside or outside current boundaries of NRS.

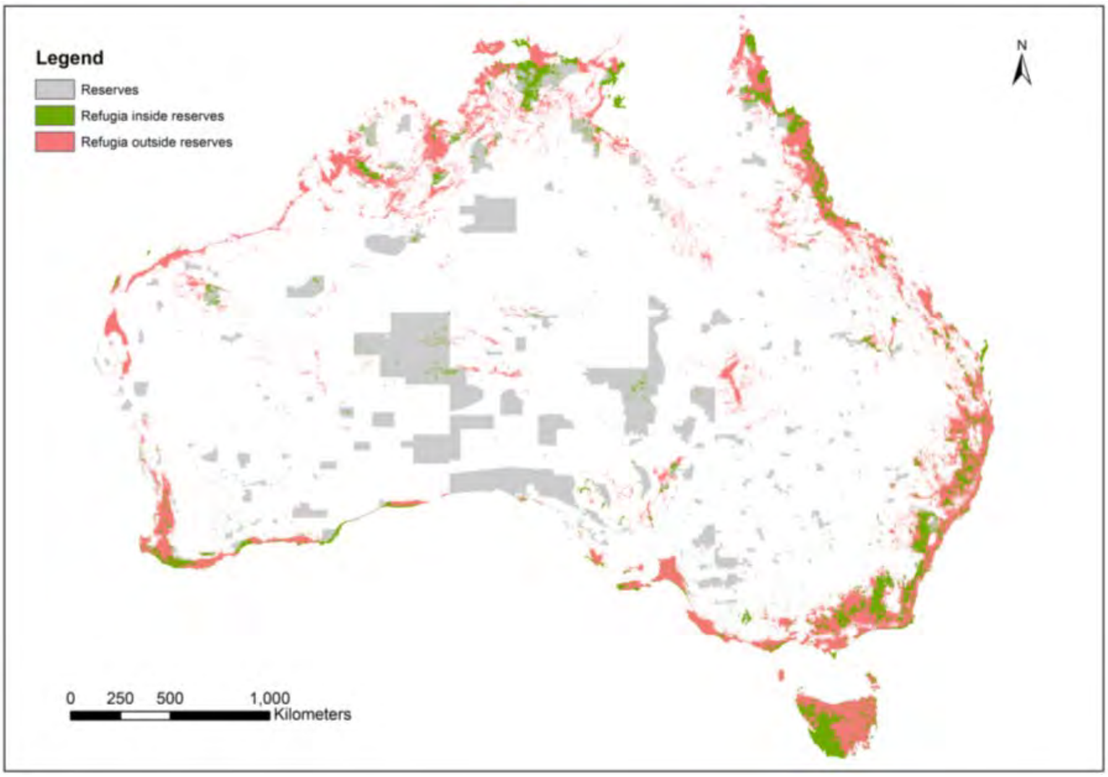

Figure 48: Inclusion of areas of highest refugial potential (based on the averaged results for Proteales, Fabales, reptiles and amphibians) within the National Reserve System.

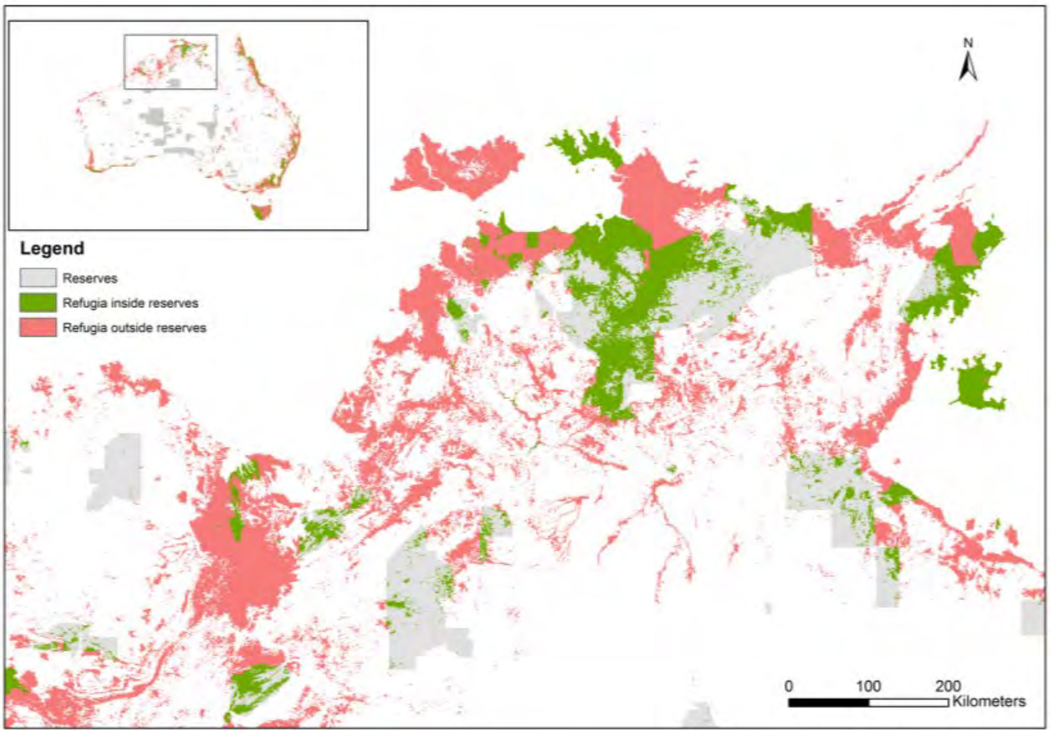

Figure 49: Inclusion of areas of highest refugial potential (based on the averaged results for Proteales, Fabales, reptiles and amphibians) within the National Reserve System, detail for the 'Top End'.

4.4.2.1 Refugial potential – NSW 3-second analyses

Results from the trial application of the refugial-potential analysis to higher quality biological data (floristic survey plot data), and 100 m grid-resolution environmental layers, for NSW are illustrated in Figure 47.

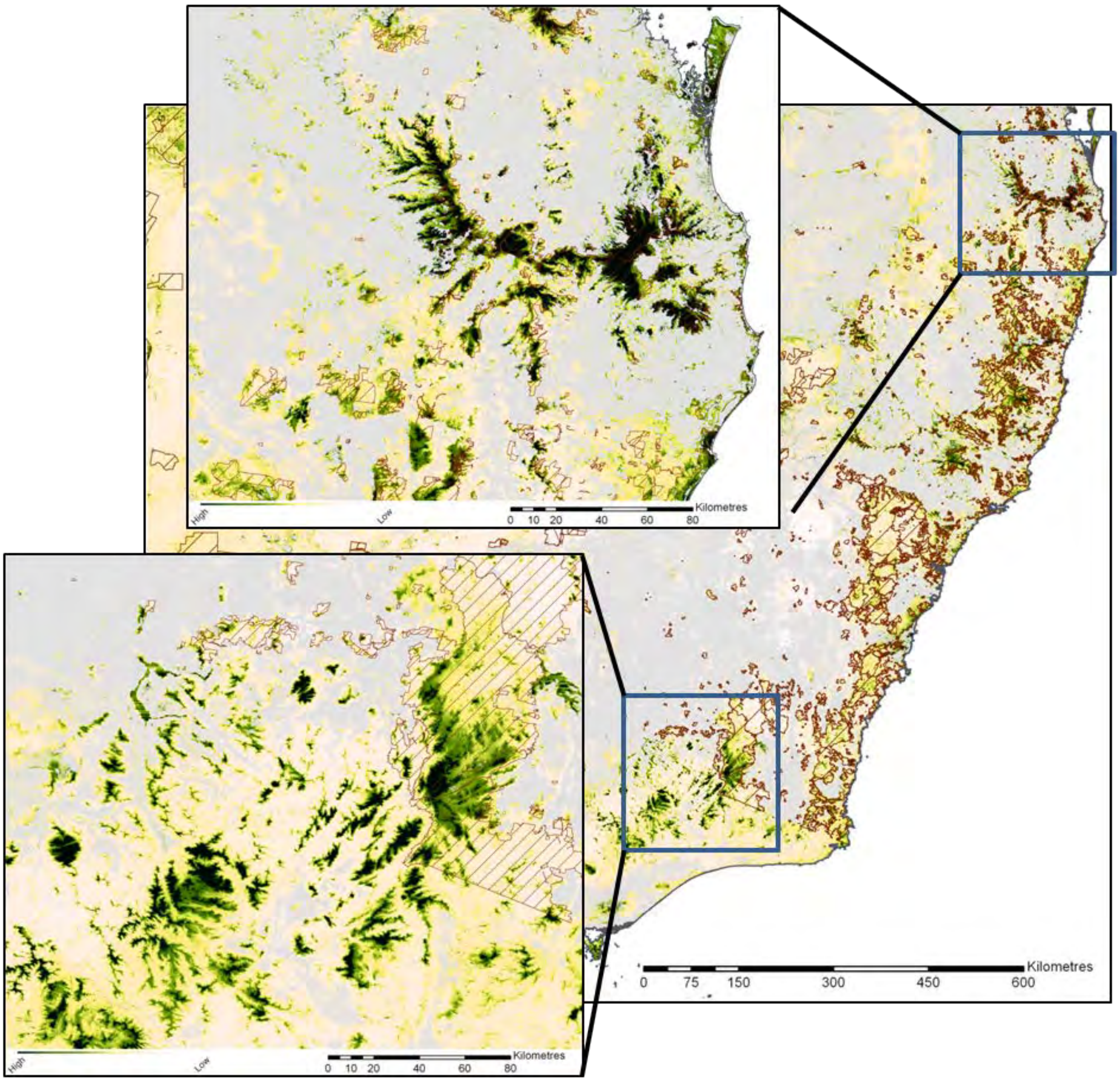

Figure 50: Refugial potential in NSW based on compositional-turnover modelling of vascular plants at 100 m grid resolution. GCM: CSIRO Mk 3.5. Emission scenario: A1B (to 2070). Protected areas depicted as hatched overlay. Cleared land depicted in grey.

4.4.3 Refugial potential – Tingle Mosaic 1-second analyses

Application of the refugial-potential analysis at an even finer spatial resolution is illustrated in Figure 48 for four climate scenarios at 30 m grid resolution within the Tingle Mosaic study area.

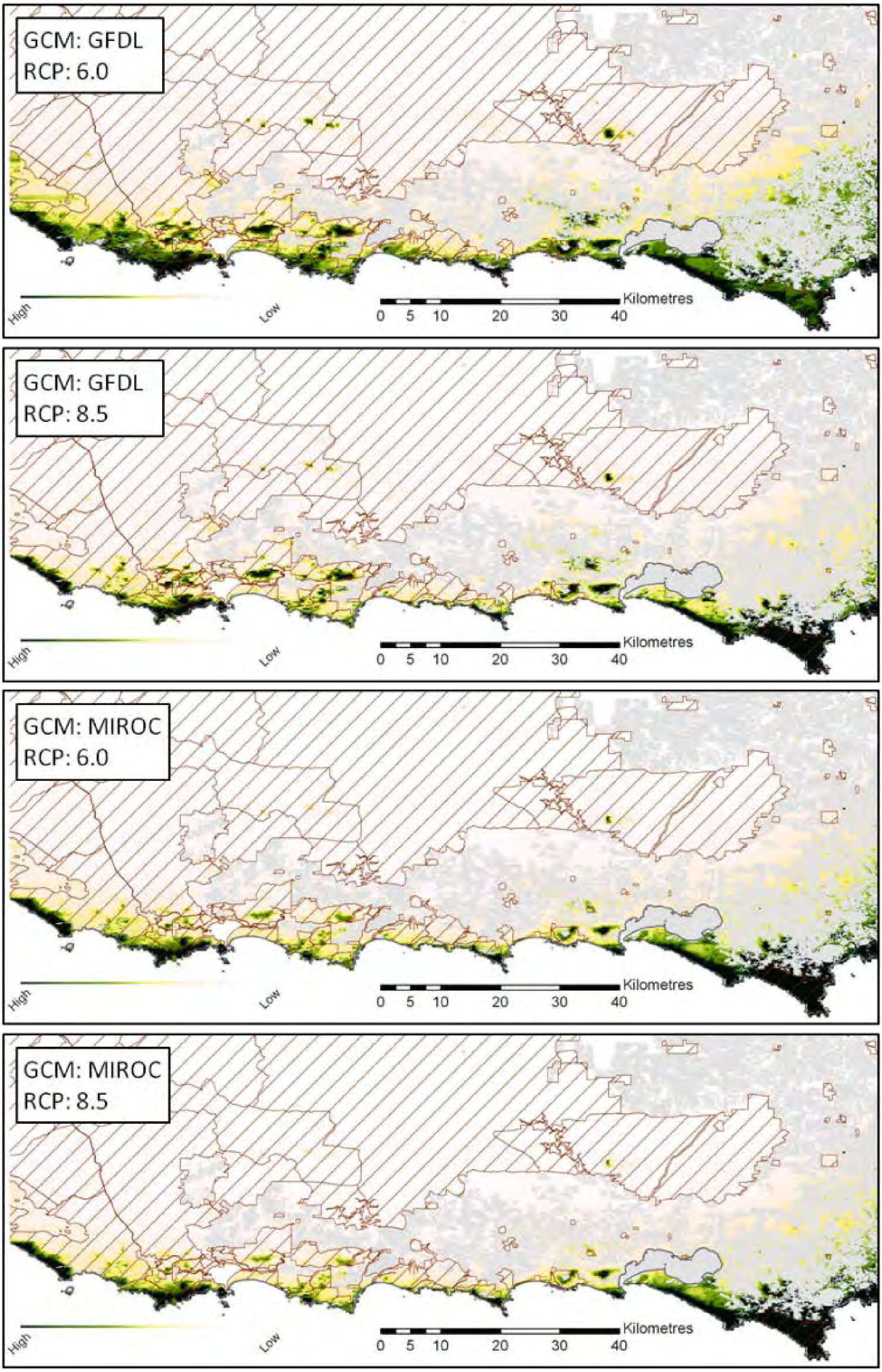

Figure 51: Refugial potential in the Tingle Mosaic (south-west Western Australia) based on compositional-turnover modelling of vascular plants at 30 m grid resolution, for four climate scenarios (to 2085). Protected areas depicted as hatched overlay. Cleared land depicted in grey.

4.5 Discussion

Although computational challenges eventually constrained the number of biological groups that could be fully analysed at continental scale for this report, this case study has clearly demonstrated the important contribution that compositional-turnover modelling can make to assessing refugial potential across a wide range of biological taxa and spatial resolutions. The analysis here also demonstrates the importance of considering finer-scaled effects of topography on local climate when identifying and mapping potential refugia. Failure to consider such effects risks underestimating the potential for biodiversity to persist in topographically heterogeneous landscapes and, in turn, the relative importance of these areas for conservation attention. Such effects are likely to be particularly relevant for biological groups with limited dispersal capacity, and the results of this study therefore complement those of the species modelling work presented elsewhere in this report (which focussed on vertebrate groups with relatively good dispersal capacity, particularly in the case of birds and mammals).

A few trends emerging from the continental analyses of refugial potential are worth noting:
Locations of potential refugia appear to be quite sensitive to the choice of climate scenario (Figure 37), which points to the importance of considering multiple scenarios in developing robust ‘no-regrets’ mapping of refugia for conservation planning.
Locations of potential refugia also appear to exhibit some marked differences between biological groups (Figure 38), pointing to the desirability of extending the refugial analyses completed here to encompass the remaining 11 groups for which GDM models have been fitted in the current study.
Potential refugia can occur in a wide variety of situations (Figure 39 to Figure 44) including for example: areas of higher elevation relative to the surrounding landscape (e.g. mountain tops); topographically sheltered locations; areas close to the ocean; and areas likely to remain moister than surrounding landscapes due to hydrological factors (e.g. in the Channel Country).
Many areas of high refugial potential are already included within reserves, but many others are not (Figure 45 and Figure 46), and these exclusions therefore deserve closer attention in future conservation prioritisation efforts.

The two finer-scaled analyses — NSW at 100 m grid resolution, and the Tingle Mosaic at 30 m resolution — have served the intended purpose of demonstrating potential applicability of the analytical approach to higher quality biological and environmental datasets. However, the results of these analyses (Figure 47 and Figure 48) should be regarded as indicative only. Further work will be required before outputs such as these can be regarded as having a sufficient level of rigour to inform planning and decision-making at these scales.

4.6 Gaps and future research

The GDM-based modelling of compositional turnover performed in this study can now serve as a continent-wide foundation for applying a range of analytical techniques. These can move beyond the relatively static identification of potential refugia addressed here towards more dynamic whole-system assessments of the capacity of landscapes to retain biological diversity under climate change, and the contribution that alternative actions to protect, restore or connect habitat could make to strengthening this capacity.

There is also considerable potential to further refine the GDM models of compositional turnover employed in this work. Past experience suggests that models derived using species presence–absence data from precisely geo-referenced ecological survey plots (as employed here in the NSW and Tingle Mosaic models) are generally of a higher quality than those derived using presence-only data from herbarium/museum collections and opportunistic observations (as employed here in the continental models). Ongoing efforts (e.g. by the Terrestrial Ecosystem Research Network, TERN) to amalgamate ecological survey datasets, particularly floristic plot data, across all Australian states and territories into an integrated national database should be encouraged.

The utility of the GDM modelling for projecting biological responses under climate change could be improved through stronger consideration of inter-annual variability and extremes in the climate attributes used as predictors of turnover in biological composition. The robustness of these projections could also be strengthened through more rigorous consideration of, and improved data on, a range of other factors likely to shape actual, as opposed to potential, responses. This includes for example biotic interactions, dispersal ability (such as effects of habitat degradation and fragmentation), indirect effects of changed ecosystem processes (fire regimes etc.), lag effects, adaptation capacity and plasticity.

5. CASE STUDY 2: PLEISTOCENE STABILITY & DIVERSITY OF HERPETOFAUNA

5.1 Authors and contributors

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5.2 Introduction

The importance of evolutionary refugia in maintaining species and lineages through late Pleistocene climate change is well known. Understanding their location and function is directly relevant to approaches that identify areas that may act as refugia for biodiversity through current and anticipated climate change. Evolutionary refugia are expected to be hotspots of both species and genetic diversity, so the ability to identify likely refugia will help to better target areas needing further biological research or conservation action. Evidence of the location and behaviour of refugia through past climate change is also important for improving our understanding of the likely response of species distributions to anticipated climate change and the effectiveness of refugia in mitigating loss of biodiversity over the coming century.

We modelled the distribution of independent lineages within rainforest lizard species, and identified their centres of endemism as indicators of places that may have functioned as evolutionary refugia, retaining local diversity through late Pleistocene climate cycles. Infraspecific endemism provides a sensitive measure of persistence, because even where species are widespread, they may contain locally endemic lineages which imply local persistence of the species in particular areas. In contrast, areas which a species has occupied more recently when expanding its range from refugia, would be expected to harbour less infraspecific diversity. We compiled a large body of published and unpublished research on the phylogeography of lizards in eastern Australia to model the distribution of evolutionarily distinct lineages within these species, and identify areas of greatest lineage endemism. We also identified centres of diversity and endemism of rainforest specialist reptiles and frogs at species level.

We also assessed the effect of changing paleo-climate over the past 120 000 years on the distribution of rainforest on Australia’s eastern seaboard, to identify areas which have been most continuously suitable for rainforest, and thus for the rainforest lizards. Stability of climate since the last glacial maximum (LGM) has been shown to relate strongly to current endemism of species (Graham et al. 2006, Davies et al. 2009) and genetic variation within a range of species (Carnaval et al. 2009, De Mello Martins 2011) via its effect on the distribution of vegetation types.

The patchwork of rainforest areas that span Australia’s east and south-east from Cape York Peninsula (CYP) to Tasmania provide an excellent case study for this approach. Compared to the surrounding biomes, they represent areas which are environmentally and compositionally distinct which, with changing climate, have varied repeatedly in size and connectivity. We used paleo-climate models to assess climate stability of these areas over the past 120 000 years to identify comparatively stable areas, where climate has been most continuously suitable for rainforest, and which may function as evolutionary refugia for rainforest specialist taxa.

5.3 Research activities and methods

5.3.1 Estimating late Pleistocene climate stability

Climate stability since the LGM has been shown to relate strongly to current species endemism (Davies et al. 2009, Graham et al. 2010). It can also provide an explanation for variation within species (Carnaval et al. 2009, De Mello Martins 2011) via its effect on the distribution of vegetation types.

Until recently (Fuchs et al. 2013), assessments of paleo-climate stability (Carnaval et al. 2009, Davies et al. 2009, VanDerWal et al. 2009b, Graham et al. 2010, De Mello Martins 2011) have typically analysed changes in climate back to the LGM (18–21 kya). Our stability estimates are based on snapshot simulations at up to 1-kyr intervals covering the last 120 000 years using the Hadley Centre Coupled Model (HadCM3; Singarayer and Valdes 2010), prepared for this project as per Fuchs et al. (2013). This dataset (see also section 3.4.1) consists of climate reconstructions for 62 past time slices representing 1000-year intervals from the present up to the LCM (22 000 years ago), continuing with 2000-year intervals until 80 000 years ago, and then every 4000 years up to 120 000 years ago at 2.5 arc-minutes (~4.5km) resolution across Australia. Downscaling and recreation of climate surfaces were performed using the *climates* package (VanDerWal et al. 2011a) in R (www.r-project.com) to generate eight derived climate variables for each of the 62 time slices. These variables represent a subset of the widely used Bioclim (Houlder et al. 2000) variables (APPENDIX 1. Climate scenarios and bioclimatic variables): mean annual temperature (bioclim 1), temperature seasonality (bioclim 4), mean temperature of the warmest and coldest quarters (bioclim 10 & 11), mean annual precipitation (bioclim 12), precipitation seasonality (bioclim 15) and precipitation of the wettest and driest quarters (bioclim 16 & 17).

We extracted rainforest areas for the stability models from the National Vegetation Information System map of estimated vegetation cover prior to European land clearing (NVIS 4.1; Australian Government Department of Sustainability Environment Water Population and Communities 2012). We used pre-clearing rather than current rainforest extent to better reflect the full environmental space suitable for rainforest (VanDerWal et al. 2009b). We extracted three rainforest types from this dataset encompassing tropical, subtropical, warm temperate and cool temperate rainforest and resampled from the 100-m resolution to 4.5 km to match the climate surfaces (Figure 49). Pixels containing any rainforest were classed as rainforest so as to include areas where rainforest occurs in numerous small patches (such as southern NSW and Victoria).

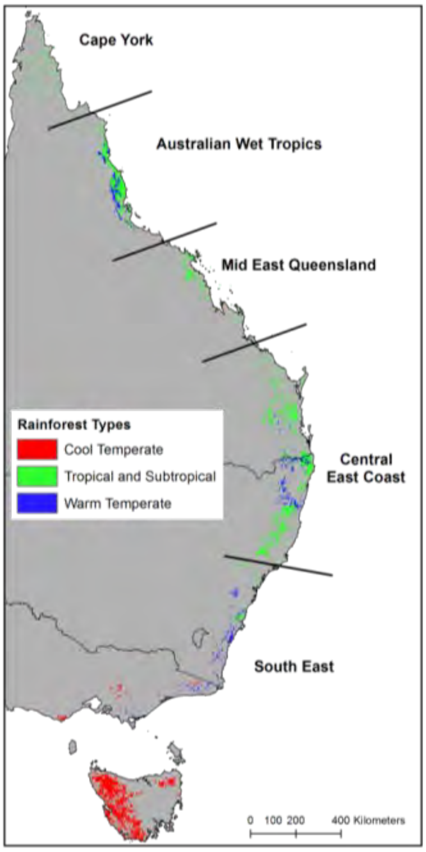

Figure 52: Distribution of rainforest types, and names of regions used in this study.

We assessed stability for all rainforest in Figure 49 and – because the climatic limits for rainforest would not be consistent across this range – separately for each of the 5 rainforest regions shown, based on the method of Graham et al. (2010), as follows. We modelled the environmental niche of the rainforest pixels using maximum entropy modelling (Maxent; Phillips et al. 2006) and the eight bioclim variables for present-day climate. This model was then projected to each of the 62 time slices to estimate the distribution of suitable habitat at each time, using clamping to limit prediction into climate space beyond the range of conditions available to train the present-day model.

For each rainforest model, we calculated stability as the mean of the negative log of suitability through time for each cell of the surface. We took the exponent of this value to give to a habitat stability value (ranging from 0 to 1). This represents the degree to which that cell has continuously provided suitable climate for rainforest (Graham et al. 2010). At the extremes 1 indicates continuous high suitability, and 0 indicates that the area was highly unsuitable for rainforest during some periods. The value cannot be interpreted as an average cell residence time. It is a multiplicative measure, so a period of low suitability (i.e. a temporal gap in suitable habitat) downweights the index strongly, to reflect the degree of continuity. The result of this analysis was a 120 000-year habitat stability surface for all rainforest and for each rainforest region.

An area of suitable habitat that functions as a refuge over geological time need not be a static location. It may instead move to track suitable conditions, for example, by shifting downslope in cooler times. We allowed continuity between suitable locations by specifying a maximum velocity of movement, to represent the ability of rainforest to expand into newly suitable areas nearby. This model, described in detail by Graham et al. (2010), estimates suitability at each time period, but also allows dispersal between time periods to a distance calculated for a particular maximum dispersal speed. The cost of dispersing to a given area is proportional to the linear distance. Here we will report results based on static refugia, and refugia shifting at a rate of up to 10 m per year.

5.4 Species and lineage distributions

5.4.1 Species distributions

We identified those frog and reptile species that are principally restricted to rainforest. For these 55 reptile and 42 frog species, we used the species distribution models described in section 3.3.5.

5.4.2 Lineage distributions

We compiled location data from published and unpublished phylogeographic studies that identified evolutionarily distinct lineages within species of rainforest specialist lizards. These lineages are units with long-term isolation that behave, effectively, as species. Our interest here is in the distribution of lineages, rather than their taxonomic status. So in cases where a species has been found to comprise a single lineage, it was included in this analysis as a lineage. Similarly, where the identified lineages have subsequently been described as distinct species, they are treated as lineages of a closely related monophyletic group, regardless of the taxonomy. Of the 51 rainforest specialist lizard species, we obtained location records for 79 identified lineages within 40 species 5).

Table 5: Lineages of rainforest specialist lizards included in the study.

Family	Genus	Species	Lineages	Data sources
Agamidae	Hypsilurus	1	2	(Moritz et al. 2009)
Carphodactylidae	Carphodactylus	1	4	(Schneider et al. 1998)
Carphodactylidae	Phyllurus	7	7	(Stuart-Fox et al. 2001, Hoskin et al. 2003, Couper et al. 2008a)
Carphodactylidae	Saltuarius	5	6	(Schneider et al. 1998, Couper et al. 2008b)
Gekkonidae	Cyrtodactylus	5	5	(Shea et al. 2011)
Scincidae	Carlia	2	4	(Stuart-Fox et al. 2001, Dolman and Moritz 2006)
Scincidae	Eulamprus	3	6	(Stuart-Fox et al. 2001, Moritz et al. 2009)
Scincidae	Glaphyromophus	1	3	(Moritz et al. 2009; Moritz, unpublished)
Scincidae	Gnypetoscincus	1	2	(Schneider et al. 1998, Moritz et al. 2009)
Scincidae	Lampropholis	3	9	(Bell et al. 2010; Hoskin, unpublished)
Scincidae	Saproscincus	11	31	(Moussalli et al. 2009)
	TOTAL	**40**	**79**	

These data sources provide known locations for each lineage, based on sequenced specimens. The Atlas of Living Australia (ALA; www.ala.org.au) identifies many other locations where the species are known to live, but without genetic data to specify their lineage membership. Further, there are unsampled locations where the species could be expected to occur, based on the suitability of the habitat. Although techniques exist to model spatial patterns of within-species diversity (Vandergast et al. 2008, Thomassen et al. 2010), they are not suitable for quantifying lineage ranges in order to estimate endemism.

To address this limitation, we developed a new approach to model the likely distribution of infraspecific lineages. The goal, similar to species distribution modelling methods, is to estimate how likely it is that a given infraspecific lineage occurs in each grid cell. If a species occurs at a given location but the lineage occurring there has not been determined, it would be more likely to be a member of the lineage with the closest known location, than of other lineages. But suitability of the intervening habitat may facilitate or block movement between locations, and could be as important as geographic distance in determining the ability of a lineage to disperse to a given location. Confidence in whether a specific lineage is present in a cell is thus conditional on (i) the habitat suitability of the cell for the species as a whole; (ii) the relative distance to known locations of each lineage; and (iii) the degree to which the cell is connected by suitable habitat to known lineage locations.

To reflect these conditions in a spatial model, we first generated a distribution model for each species. We used a combination of checked ALA records and locations of our own and collaborators' collections. The models were generated in Maxent at a 0.01 degree resolution using the first 19 bioclim variables as well as slope and topographic wetness index (Beven and Kirkby 1979). So that the models would emphasise those factors relevant locally in distinguishing suitable from unsuitable sites, we restricted background points to a radius of 2.5 degrees (~275 km) around the location records for the species.

We then partitioned the modelled habitat suitability value for the species, dividing the value for each cell among the infraspecific lineages in proportion to the square of the distance to the nearest known location of the lineage. To take account of barriers to dispersal, we measured cost distance rather than linear distance to the nearest known location of each lineage. The cost of traversing each cell, for the cost-distance analysis, was calculated from the Maxent model for the current species range, as -log(habitat suitability).

The resulting model gives an estimated likelihood of each lineage occurring at each cell, with the values across all lineages summing to the species level habitat suitability value for that cell. We thus avoid placing sharp boundaries on the distribution of lineages in the absence of supporting information, instead creating a gradient of likelihood informed by known locations for the lineages and habitat suitability. This method is consistent with the observation that the transition or contact zone between lineages is more likely to occur in areas of lower habitat suitability (Moritz et al. 2009).

5.4.3 Richness and endemism

5.4.3.1 Species richness

We calculated species richness as the sum of the habitat suitability scores across all species models. In this case, rather than applying a threshold to the models to translate suitability into predicted presence and absence, we used the suitability scores directly. In this way, a low suitability score for a grid cell makes a small contribution to richness in that cell. The resulting values should be interpreted as a relative measure of richness, not as an absolute count of species.

5.4.3.2 Species endemism

Range weighted endemism (WE; Crisp et al. 2001) is a relative measure of endemism based on range size. For a set of species found in a given area, WE sums the proportion of the total geographic range of each species which occurs in the area. An area which represents all or most of the range of a number of species has a high WE score. WE is normally calculated as the sum of $^{1}/_{\text{range size}}$ across the species found in an area. This can be thought of as counting species to measure richness, but with the value of the species distributed evenly across all cells where it occurs.

In order to adapt this method to assess endemism directly from modelled ranges, for each model we summed the suitability values across all cells, and then calculated the proportion of this suitability found in each cell. Where *s* is one of *n* species, each with an SDM:

$$WE = \sum_{all\ species} {local\ suitability_s}/{total\ suitability_s}$$

So each species has a total value of 1, which is distributed across cells unequally in proportion to the value of the SDM at that cell. The aim of this calculation, the result of which we call model weighted endemism, is to give a likelihood-based assessment of endemism. However, as environmental suitability has been found to predict maximum abundance (VanDerWal et al. 2009a), it could potentially also be of use in estimating concentrations of abundance across multiple species.

5.4.3.3 Lineage endemism

Endemism of diversity within species can be quantified using phylogenetic endemism (PE; Rosauer et al. 2009) or related measures (Faith et al. 2004, Cadotte and Davies 2010) using branch lengths on a phylogeny, rather than species, as the unit of biodiversity. In this case, with data sourced from many studies, and with sampling from different genes, we could not use a single phylogeny with comparable branch lengths across taxa. Accordingly, we used WE (lineage ranges only), rather than PE (lineage branch length and distribution), to measure lineage endemism (Rissler et al. 2006).

We used the same method as for species endemism (described above) to estimate lineage endemism from the lineage distribution models.

5.5 Results and outputs

5.5.1 Paleo-climate stability

The models of present distribution for all rainforest and the individual rainforest zones fitted strongly, with AUC values in the range 0.94 to 0.99 (median 0.991). The occurrence of rainforest overall was most strongly related to precipitation (annual and dry quarter) and to temperature seasonality. These three variables were the dominant predictors of occurrence for all five rainforest zones.

Projecting these models into the past, we generated a stability surface based on the niche for all rainforest, and for each rainforest zone (Figure 50 and Figure 51). For comparison, see the same maps, with the NVIS areas of pre-clearing rainforest overlaid (Figures 1 & 2 of APPENDIX 8. Pleistocene stability and diversity of herpetofauna). Although the most stable areas correspond to the larger concentrations of current (pre-clearing) rainforest, rainforest is also found in areas of lower paleo-stability, where its occurrence was likely less continuous through time. We can thus distinguish between areas of current rainforest, those where the long-term climate has been most conducive to maintenance of evolutionary refugia for rainforest species.

We also analysed stability separately for each rainforest region (Figure 50 and Figure 51). The region-specific stability results were broadly similar to the composite rainforest model, differing principally in the extent and connectivity of the most stable areas. The notable exception was the Australian Wet Tropics (AWT). Stability in the composite rainforest model is comparable to that found in previous paleo-climate studies of the AWT (VanDerWal et al. 2009b, Graham et al. 2010), although more restricted in its prediction of stability for the northern end of the AWT. The independent AWT model, however, shows exceedingly low stability (Figure 3 in APPENDIX 8. Pleistocene stability and diversity of herpetofauna) compared to both previous, paleo-ecologically informed climate models of stability (e.g. Graham et al. 2006; VanDerWal et al. 2009b) and the spatial patterns of long-term persistence of rainforest species, as inferred from comparative phylogeography of the AWT (Moritz et al. 2009). Stability in the AWT is predicted for the niche of mid-east Queensland (MEQ) rainforest (Figure 50b, Figure 51b) and areas further south (Figure 50a).

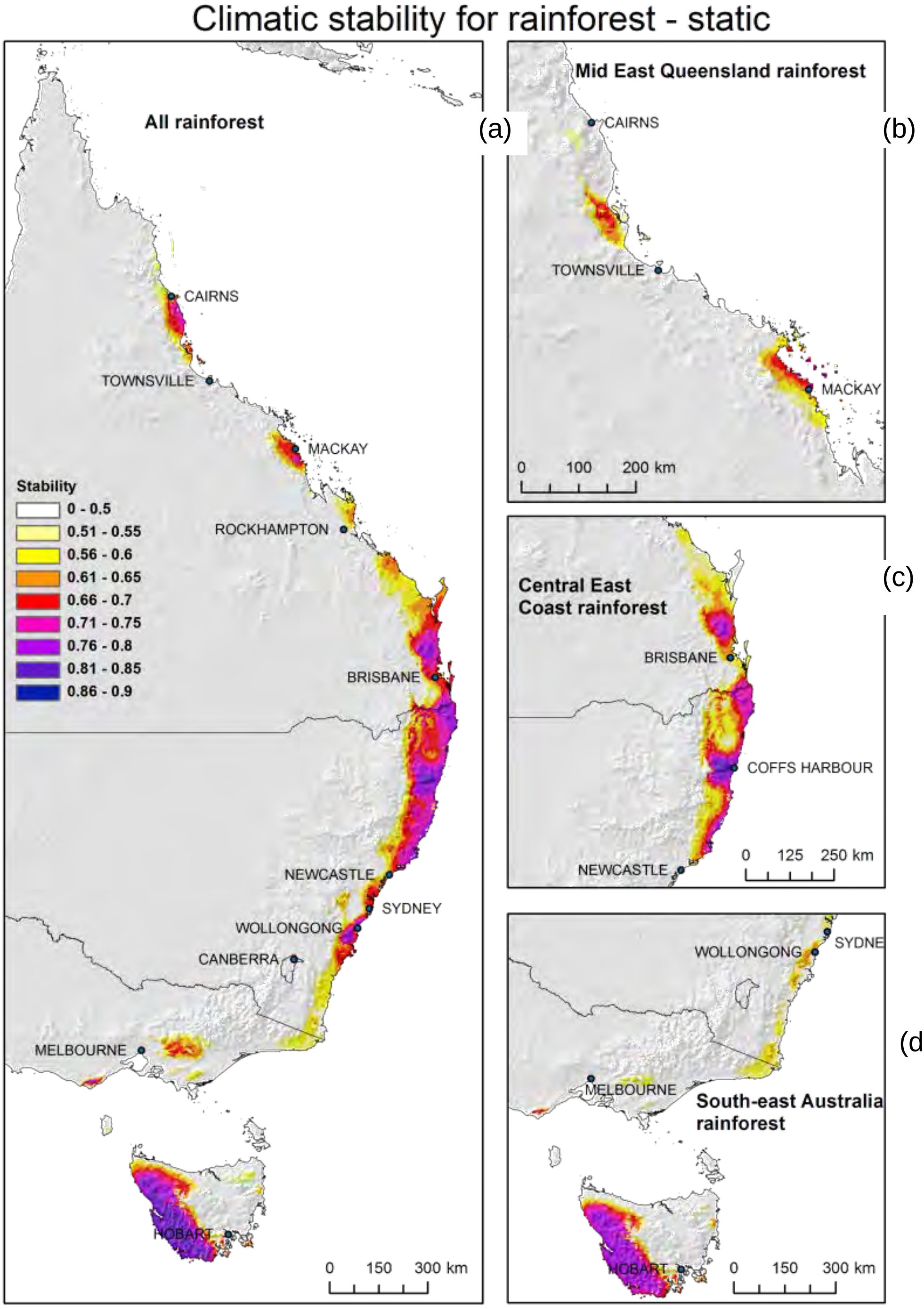

Figure 53: Stability of climatic niche of rainforest since 120 kya. Blue areas were the most continuously suitable for rainforest. Stability of the niche of (a) all rainforest; (b–d) specific rainforest zones treating each rainforest zone as independent. The zonal results differ from the all-rainforest model in details, particularly in the location, connectivity and extent of the most stable areas. Note: mid-east Queensland result (b) models the niche of the rainforest near Mackay, although stable conditions for this niche were projected into parts of the AWT.

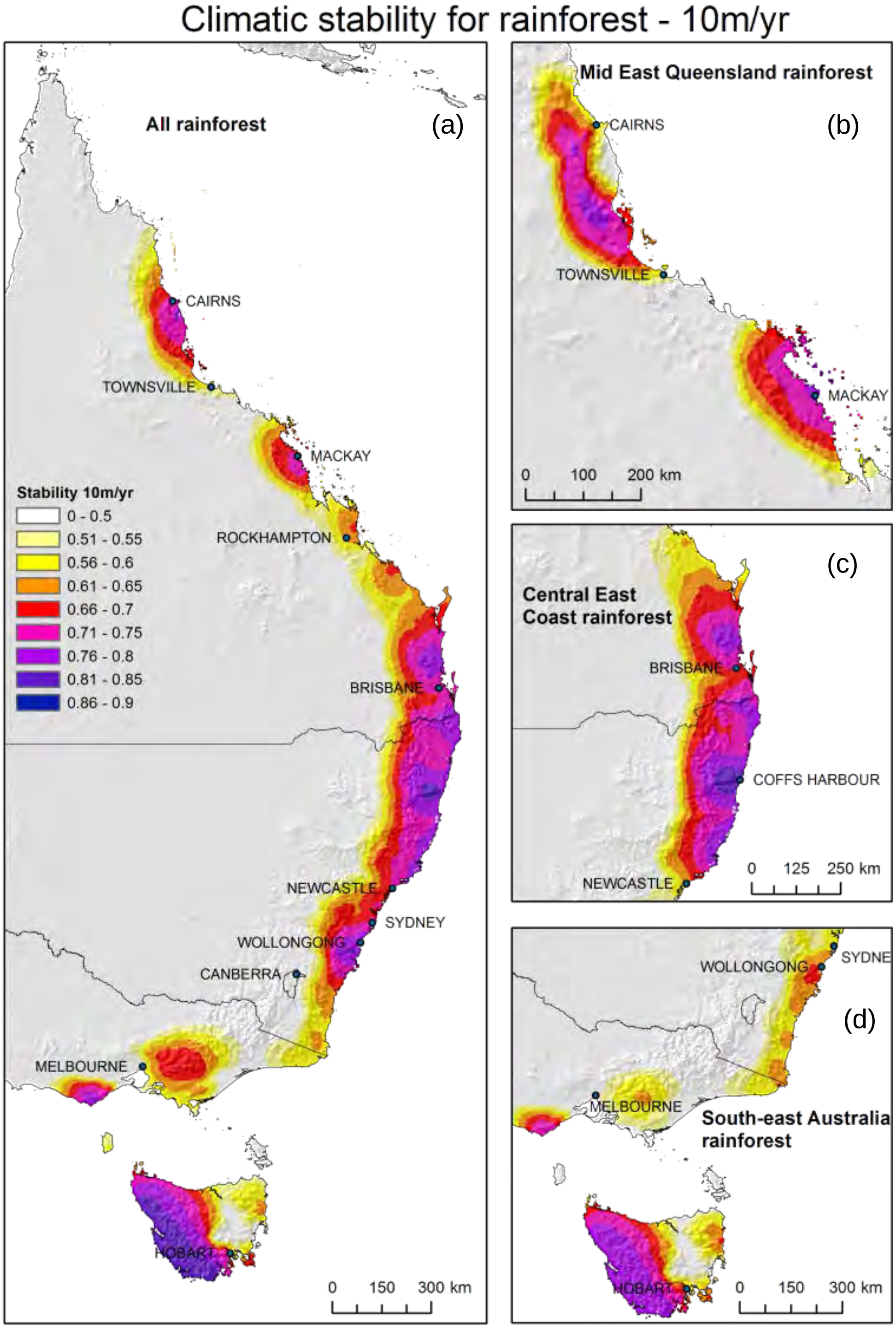

Figure 54: Stability of the climatic niche of rainforest over the past 120kya allowing refugia to shift up to 10 myr^{-1}. Larger zones of stability are generated, but the distinct islands of stability are evident. (Details as for Figure 50.)

The trajectory of changing climate and vegetation reflected in these models can be understood by considering how these values change over time at a single point, and how they compare between more and less stable locations (Figure 51). Two rainforest sites located only 30 km apart near Dorrigo in north-east NSW, differ moderately in current habitat suitability (A=0.56, B=0.71), but have very different histories and levels of stability. That is, site B (elevation ~500 m) has maintained high suitability for rainforest through climate cycles; site A (elevation ~1300 m) has only recently become suitable under late Holocene conditions.

A clear result from viewing the data in this way for various locations is that although the LGM (18–21 kya) was a recent and severe cold (and generally dry) period for Australia, it was by no means the key limiting point for rainforest distributions in these analyses. The time of lowest suitability for rainforest varied widely between areas. For example, at site A in Figure 52, the lowest suitability was at 30 kya; whereas at site B, the minimum suitability was at 108 kya, with the most recent low point at 32 kya.

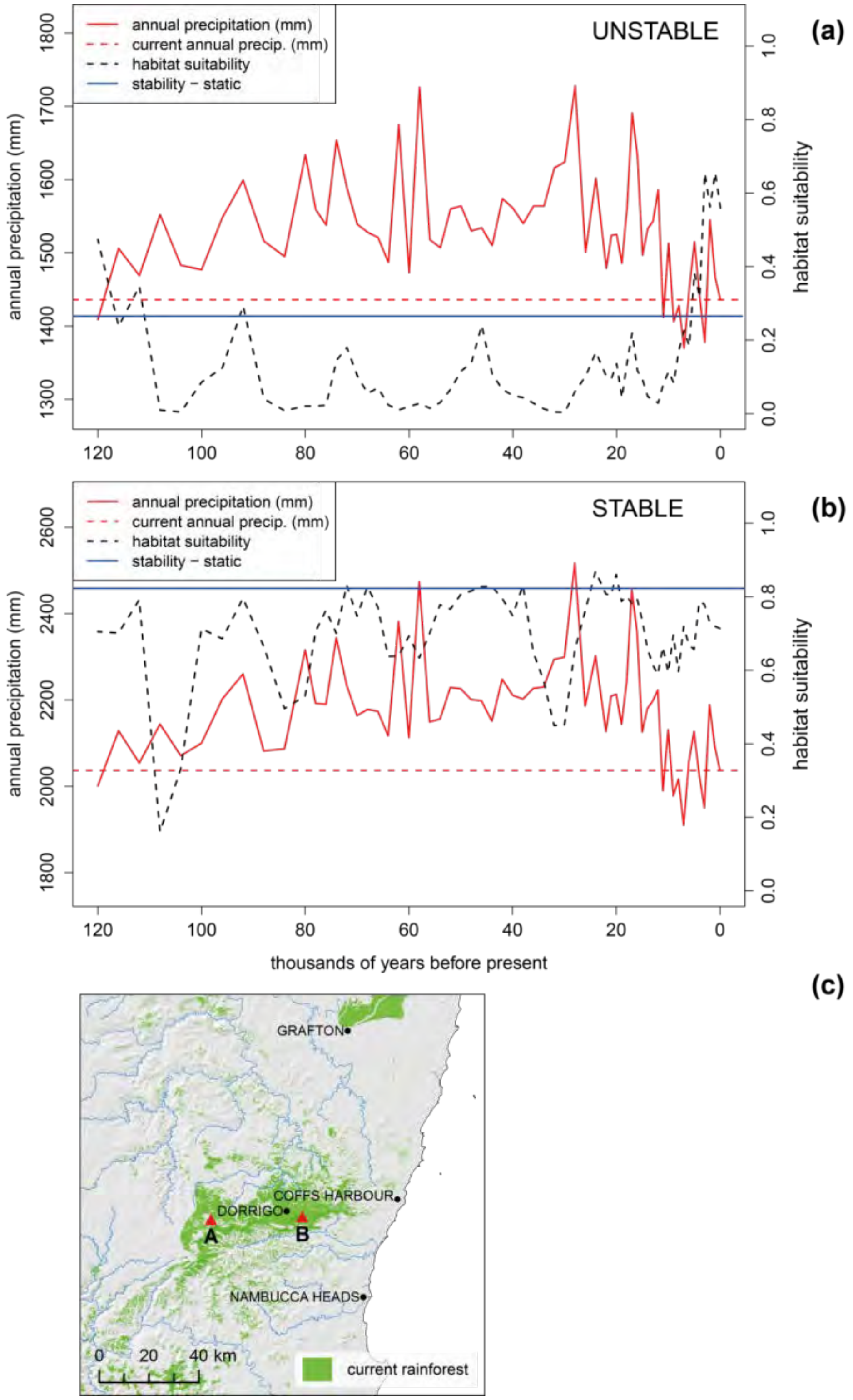

Figure 55: Climate and habitat suitability over 120 kyr at two locations. These rainforest sites near Dorrigo in north-east NSW have similar current suitability for central east coast rainforest (black dotted line). However, site B, at lower elevation, has maintained higher suitability over time, and thus has higher stability (blue) for rainforest than site A. Site A was largely unsuitable for rainforest until the mid-Holocene. Annual precipitation (solid red, left axis), is the strongest predictor in distribution model, with the red dashed line highlighting the current value.

5.5.2 *Richness and endemism*

5.5.2.1 Lineage modelling

Using the lineage modelling method described in section 5.4, we generated a separate occurrence surface for each of the 79 lineages. Figure 53 shows an example for the skink species *Saproscincus rosei*, using data from a phylogeographic study of the genus (Moussalli et al. 2005), with the likelihood of occurrence for each lineage resulting from the interaction of habitat suitability for the species, proximity to known locations of each lineage, and the suitability of the intervening areas as habitat.

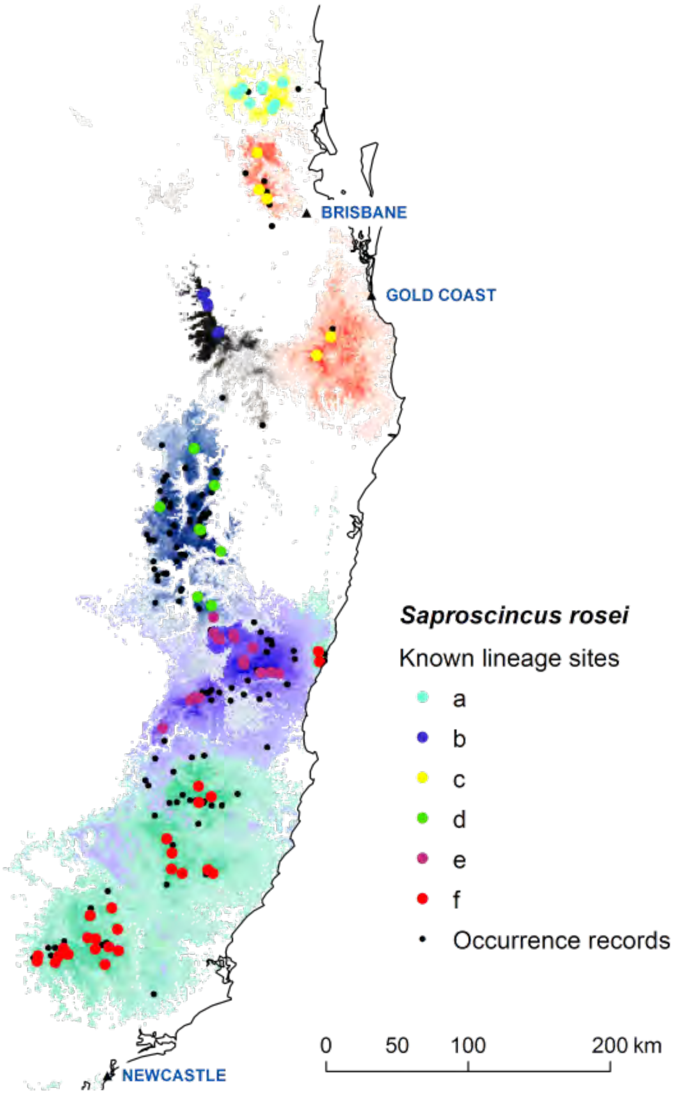

Figure 56: Lineage distribution models for the six lineages of *Saproscincus rosei*. Suitability for each lineage is show as a gradient in a colour contrasting to the known lineage sites.

5.5.2.2 Endemism

The concentrations of lineage and species endemism (Figure 54) are within the major rainforest areas, as expected given the selection of rainforest taxa for this case study. Within each rainforest region however, particular locations are centres of endemism at a finer scale, such as the Border Ranges, the Conondale Range and Glass House

Mountains in Queensland, the Eungella-Mackay region and Conway National Park in MEQ, and several well-known regions of endemism in the AWT. Relative to species endemism, mapping of lineage-scale endemism in reptiles provides more discrimination and resolution of hotspots within each major area; for example, within AWT, MEQ and the central east coast (CEC).

From these models, we have identified five specific areas of greatest endemism where a large component of diversity is concentrated in the rainforest specialist taxa we studied. These areas, shown in greater detail in Figure 55, Figure 56 and Figure 57 and listed in Table 5, represent concentrations of endemic diversity, and potentially evolutionary refugia.

The identified areas of endemism tend to be skewed towards higher elevations; moderately for our taxa in the Wet Tropics, very strongly in the Border Ranges and Conondale areas. Mid-east Queensland presented contrasting patterns for different taxa, with frog endemism strongly associated with higher elevations, whereas lizard lineage endemism was biased towards lower elevations (refer to graphs in Figure 56).

Infraspecific lizard endemism was notably low for the Northern Tablelands, which principally indicates a lack of phylogeographic data. Further, we were not able to obtain meaningful endemism results for areas south of Wollongong due to the low number of rainforest specialist frog and reptile species, and particularly the lack of phylogeographic data on which to base the lineage endemism analysis.

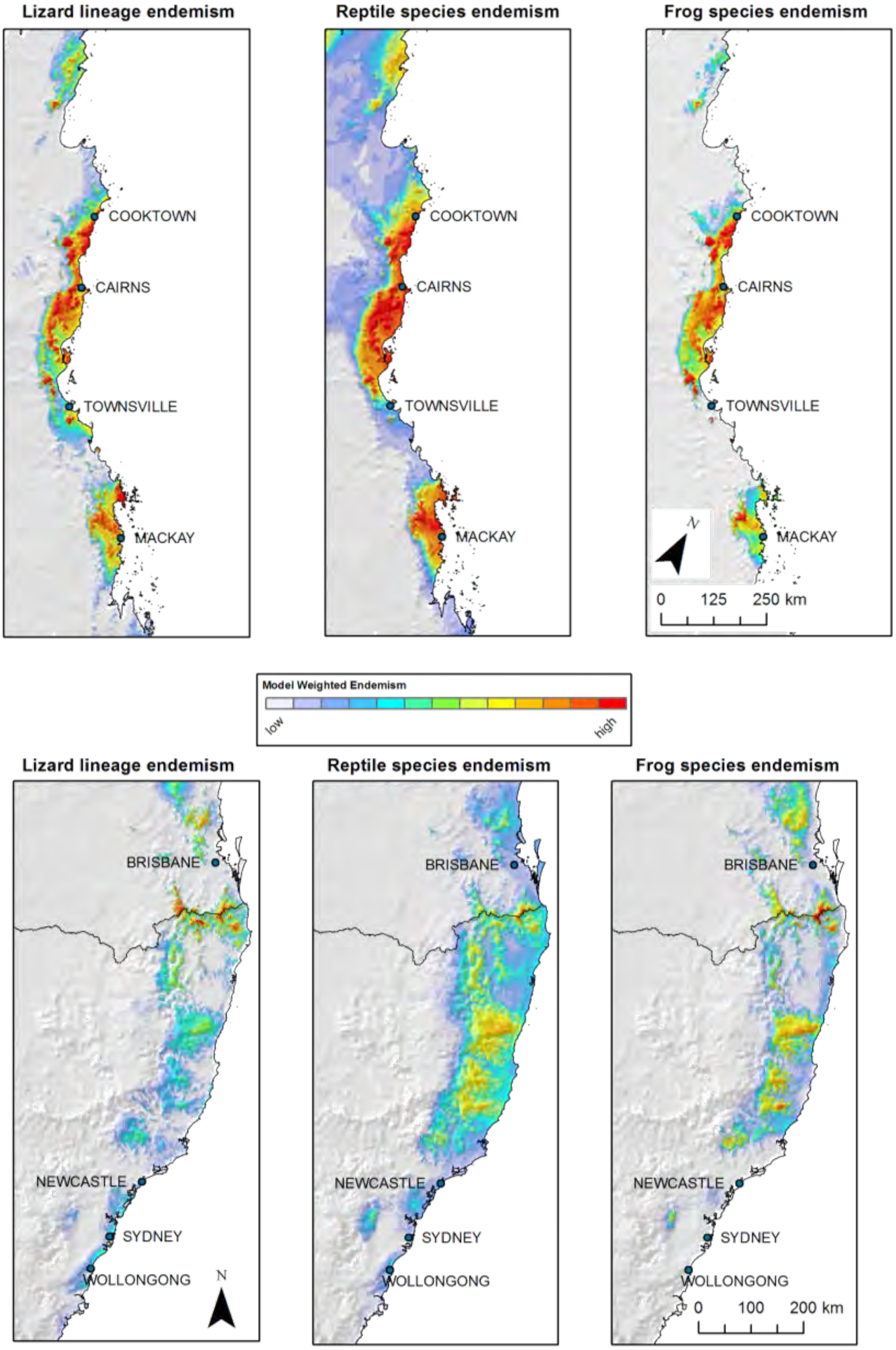

Figure 57: Rainforest specialist species and lineage endemism. Model-weighted endemism of rainforest specialist lizard lineages and species of reptiles and frogs. Colours by quantile classes within each of the three endemism analyses. Scores in the lowest 8 percentile are not shown.

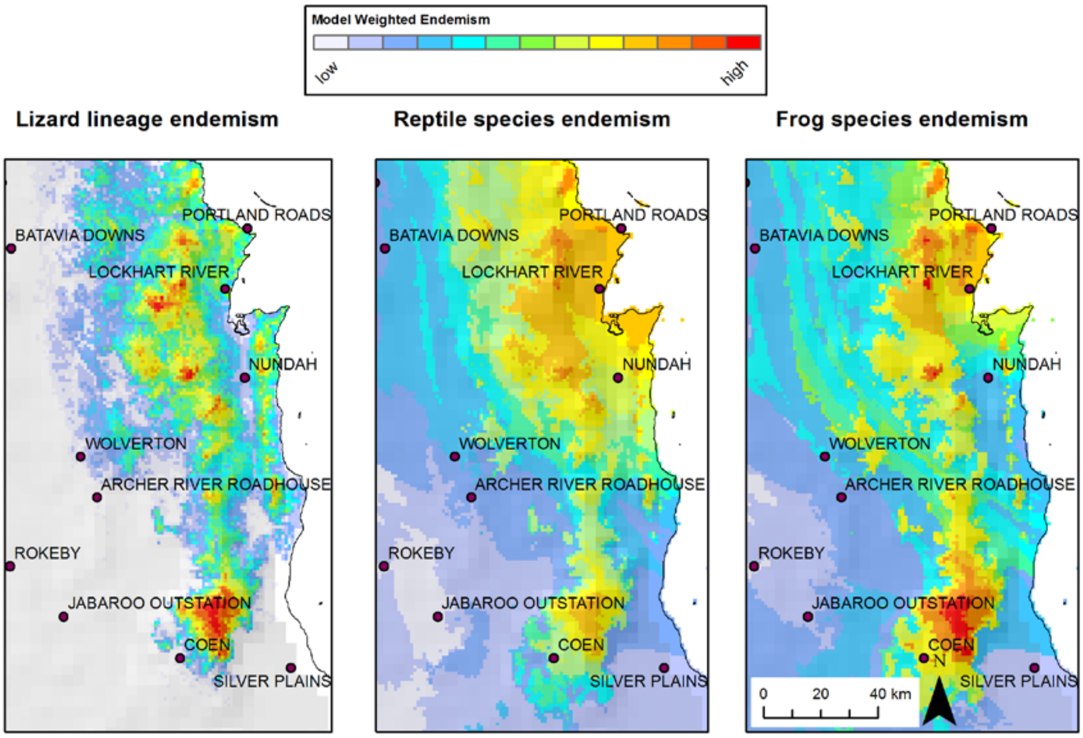

Figure 58: Areas of endemism in the Iron Range and Coen areas of Cape York Peninsula.

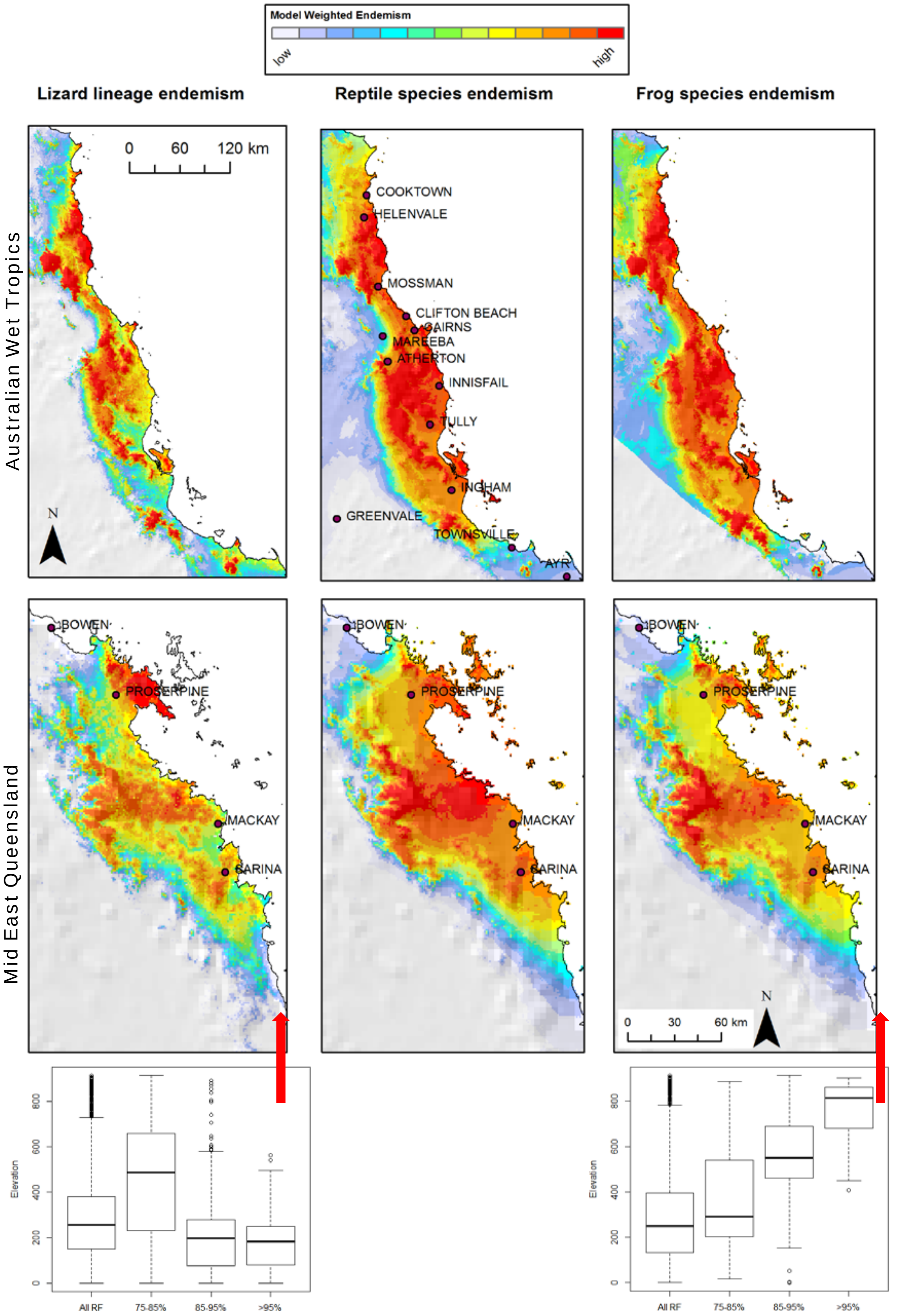

Figure 59: Areas of endemism in the Wet Tropics and mid-east Queensland. Boxplots compare the elevation range for all rainforest in the region to the areas of high endemism grouped by percentile rank. Endemism in the Wet Tropics has a wide elevational spread with both montane and lowland components. In mid-east Queensland, frog endemism is predominantly montane, whereas lizard lineage endemism peaks in low-lying coastal areas.

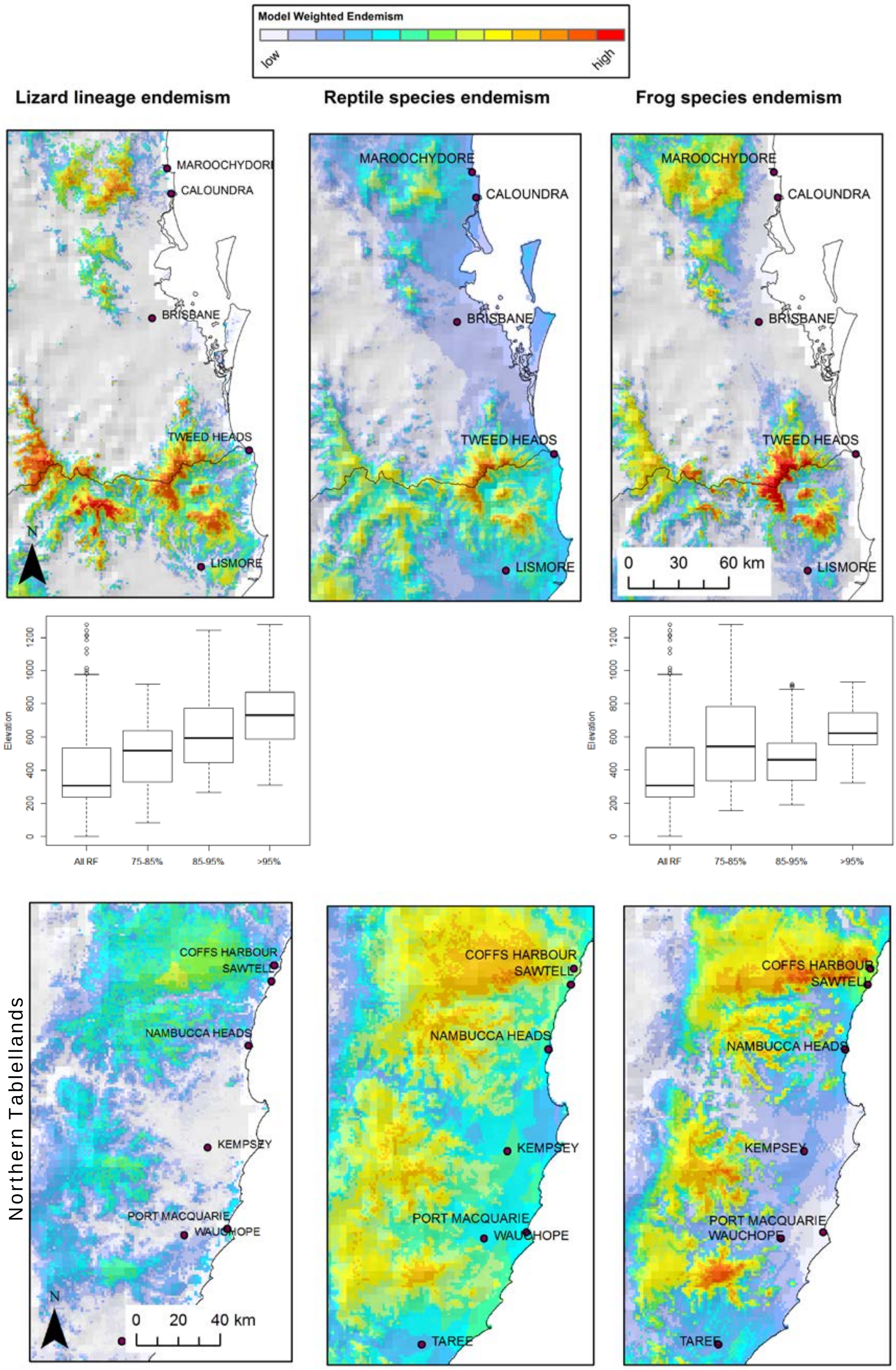

Figure 60: Glass House/Conondale, Border Ranges and Northern Tableland areas of endemism. Boxplots show elevation in the Border Ranges south of Brisbane grouped by percentile rank for endemism. Note the high congruence of lizard lineage and frog species endemism in the Border Ranges and Glass House/Conondale areas.

Table 6: Principle areas of endemism identified for rainforest reptiles and frogs.

Area	Groups	Reservation status
Iron Range – Coen	lizard lineages, frog species	Generally good. Some significant gaps.
Wet Tropics	all	Excellent
Mid-east Queensland	all	Poor for lowland rainforest e.g. between Mackay and Eungella, ranges north of Eungella.
Conondale – Glass House	lizard lineages, frog species	Good for Conondale. Poor for more easterly areas.
Border Ranges	all	Well reserved except most westerly area near Killarney and Warwick.
Northern Tablelands	frog and lizard species	Generally good. Some significant gaps e.g. Comboyne Tableland between Wauchope and Taree.

5.5.2.3 Stability and endemism

We tested the relationship between the measures of paleo-climate stability diversity measures — endemism and richness — for rainforest areas and found a positive relationship between them in almost all cases, but of highly variable strength and significance.

For all rainforest areas as a single entity, stability was unrelated to endemism or richness. Model fit was weakest in the north (CYP, AWT), improving towards the south, with strong relationships to all biological measures in MEQ, and to the frog and reptile species measures in the CEC and south-east Australia (SEA) regions. High values indicate that variation in richness or endemism within the rainforests of region is associated with variation in stability within the region. The shifting refugia model outperformed the static model in most cases, particularly for MEQ. The strongest relationship to stability overall was for reptiles in CEC and frogs in SEA. With the exception of MEQ, the models performed poorly for lizard lineages, but in contrast to the species level analyses, did best in the areas for which our coverage of species with lineage level data was most complete (AWT, MEQ).

Table 7: Correlations of stability to richness and endemism using a linear regression at 2.5 minute (~4.5 km) resolution. R2 values over 0.15 are in bold. The acronyms are as follows: CYP = Cape York Peninsula, AWT = Australian Wet Tropics, MEQ = Mid East Queensland, CEC = Central East Coast and SEA = South East Australia.

Region	Lizard lineages		Reptile species				Frog species			
	Endemism		Endemism		Richness		Endemism		Richness	
	Static	Shifting	Static	Shifting	Static	Shifting	Static	Shifting	Static	Shifting
ALL	0.00	0.00	0.01	0.00	0.00	0.00	0.01	0.01	0.00	0.00
CYP	0.07	-0.01	0.03	0.00	0.02	0.01	-0.01	0.01	-0.01	**0.15**
AWT	0.15	0.14	0.03	0.03	0.00	0.01	**0.23**	0.12	0.05	0.03
MEQ	**0.18**	**0.31**	0.06	**0.28**	0.13	**0.38**	-0.01	**0.16**	0.08	**0.33**
CEC	0.09	0.05	**0.21**	**0.33**	**0.52**	**0.46**	**0.15**	**0.15**	**0.22**	**0.21**
SEA	-	-	0.13	**0.32**	0.11	0.11	**0.19**	**0.32**	**0.39**	**0.51**

5.6 Discussion

5.6.1 Endemism in refugia

Within the broad sweep of rainforest areas in eastern Australia, the centres of endemism for rainforest specialist lizards and frogs are far more localised, which may indicate the locations of evolutionary refugia. Centres of reptile (Powney et al. 2010) and frog (Slatyer et al. 2007) species endemism in Australia are known at a coarse resolution (50–100 km cells). In this study, by working at a finer resolution, both spatially and taxonomically, we can be far more specific about the particular areas that have retained a disproportionate amount of locally restricted evolutionary diversity.

This study represents the most detailed and spatially fine-grained comparison of endemism patterns between reptile and frog species, as well as between phylogeographic lineages and species of reptiles (see also Rissler et al. 2006). The lineage endemism analysis presented here includes phylogeographic data for more than half of Australia's known rainforest-specialist lizard species. However, the selection of species is biased towards the more widespread taxa and does not guarantee a representative sample for assessment of overall patterns of lizard endemism.

In partitioning currently recognised species of lizards into their component genetic lineages, we have focussed on the most deeply divergent clades in mtDNA phylogeographies. For many of these, especially in the AWT, we have evidence from nuclear genes (Moritz et al. 2009, Bell et al. 2010, Hoskin et al. 2011) and from genetic analyses of hybrid zones (Phillips et al. 2004, Singhal and Moritz 2012 and submitted) that such deep phylogeographic clades do indeed correspond with long-isolated and independently evolving evolutionary lineages, which themselves warrant recognition as phenotypically 'cryptic species'. An intriguing result is that the fine-scale patterns of species-level endemism of frogs more closely resemble lineage-endemism, than species-endemism in lizards. This highlights the value of incorporating lineage-endemism for discovery of diversity hotspots and putative evolutionary refugia.

The highest levels of endemism were found in several areas of the Wet Tropics, strongly linked to topography. These areas are comparatively well known from previous studies, which have confirmed the existence of a number of distinct paleo-climatic refugia in the Wet Tropics (Schneider et al. 1998, Stuart-Fox et al. 2001, Moritz et al. 2005, Graham et al. 2006, Moritz et al. 2009, VanDerWal et al. 2009b, Graham et al. 2010). The distinct areas of endemism identified around Mackay in mid-east Queensland, the Border Ranges and montane areas of northeast NSW and Cape York warrant further investigation as key evolutionary refugia in rainforest specialists across various taxonomic groups.

Though also recognised for their biodiversity value (e.g. as declared national parks, the rainforests of mid-east Queensland have often been regarded as the 'poor' relation of the more diverse systems in the AWT and the central coast. However, for the herpetofauna, this is not the case; mid-east Queensland forests harbour moderate species richness, but proportionally high local endemism for frogs and reptiles (Moritz et al. 2005). Our new endemism analyses, and especially results for lineages of reptiles and species of frogs, reinforce the high conservation value of these forests and also identify two separate foci of endemism — the Clarke Range and outliers around Mackay, and the Conway Ranges east of Proserpine (see also Stuart-Fox et al. 2001). The notable difference in the elevation profile of endemism between lizards and frogs, and between the lineage and species levels, offers an interesting line of inquiry into differences in the distributions of these faunas through recent climate cycles. For Cape

York, where richness is much lower than for other rainforest regions, our endemism analyses, especially for frog species and reptile lineages also highlight the high conservation value of the McIlwraith Ranges and, to a lesser extent the lower-elevation Iron Ranges to the north as well. It will be useful to extend this result to other groups of species to determine how general the patterns of endemism (and thus conservation importance) are to taxa that are less dispersal limited than the rainforest lizards and frogs included in this study. For less dispersal-limited species, for example some bird taxa and butterfly taxa, one could expect that current habitat suitability would be far more important than local habitat history in defining areas of endemism.

The preponderance of montane areas in the centres of endemism is consistent with two explanations derived from our understanding of the effects of late Pleistocene climate cycling, one specific to our current position in the climate cycle, the other more general. Firstly, given that current mean annual temperatures are at a historic high point relative to recent climate cycles, we would expect that the species and lineages that have their ranges most reduced would be those dependent on cooler temperatures, which are currently restricted to higher elevations. This effect would, of course, be increased by the current trajectory of climate change. Secondly, the greater elevational range and topographic complexity in most montane areas may support the persistence of species and lineages through climate cycles by providing a range of locally available climatic variation related to elevation, aspect and topographic shading, through which species may track their climatic niche (Sandel et al. 2011).

The new lineage modelling technique developed for this study represents an incidental benefit of the research. It supports a more informed approach to spatial analysis of infra-specific diversity that makes optimal use of available data and may help to better target new data collection. Our approach integrates two distinct types of information into the models: species occurrence locations, and lineage membership within the species. Although the current study estimates isolation between lineages as a function of current habitat suitability, it may also be possible to estimate dispersal cost varying over time with changing climate, using a method analogous to the habitat stability model, and thus to model lineage ranges based on longer term isolation. One assumption of our approach is that while the overall species distribution is limited by its environmental niche, the intraspecific lineages all share the niche requirements of their species, with their distribution within that niche defined by isolation. This may understate the degree to which lineages have evolved divergent physiological traits or habitat requirements within the species (Hoskin et al. 2011, Moritz et al. 2012), but it is surely better than the alternative of using a traditional SDM to model each lineage independently. The latter approach would treat all lineage boundaries as environmental limits and model accordingly, ignoring the role of isolation in defining the distribution of lineages.

5.6.2 Paleo-climate stability

Our analysis identified distinct areas of stability which are broadly consistent with the analysis of endemism in identifying major evolutionary refugia. This confirms that each of these regions contained areas resilient to late Pleistocene climate change, with correspondingly high regional endemism. The broad-scale model also identified mid-stability areas just north and south of Rockhampton, which today harbour small patches of low elevation rainforest and warrant further sampling and analysis.

Although our models for most regions gave very plausible results, the discrepancy between the low stability predicted for the Wet Tropics in our model for that zone, and the distinct areas of high stability in previous studies (VanDerWal et al. 2009b, Graham et al. 2010) requires further investigation. Low stability was similarly found for rainforest areas on Cape York. This result was not due to our model going further back in time (back to 120 kya compared to LGM in previous studies), because the main discrepancy (i.e. total lack of suitability) was evident from our projected distribution of Wet Tropics rainforest at the LGM (Figure 3 in APPENDIX 8. Pleistocene stability and diversity of herpetofauna).

There is a significant difference between the climate model used for our approach and previous models of paleo-climate stability. Firstly, previous studies, such as those for the Wet Tropics (Hugall et al. 2002, Graham et al. 2006, VanDerWal et al. 2009b, Graham et al. 2010) used a local climate model which applied adjustments to current climate surfaces based on paleo-ecological evidence of past climate (Kershaw and Nix 1988, Hilbert et al. 2007), or for broader regions using a combination of paleo-ecological evidence and a latitude-based heuristic (Moritz et al. 2005). In contrast, this study used the downscaled output of GCMs (HadCM3; Singarayer and Valdes 2010) for each time period (Fuchs et al. 2013). Such an approach enables the extension of paleo-distribution and stability analysis to far larger areas. Whether this specific paleo-GCM fully captures the dynamics of the Asian-Australian paleo-monsoon, which has a large effect on precipitation values for the AWT in particular, is unknown, and warrants further investigation.

The correlation analysis of the relationship between stability, endemism and species richness was similarly structured, with low values in the most northerly areas, potentially due to issues with the stability models. Furthering this line of inquiry may also involve investigating finer scale climatic influences on species habitat such as local effects of topography and drainage which may moderate the impact of broader scale climate changes.

5.7 Gaps and future research

Our research to date has developed improved methods for combining species and genetic data with spatial modelling and has provided an initial assessment of the location of major evolutionary refugia across east Australian rainforests. Nonetheless, it also highlighted opportunities for further comparative studies and areas for improvement in modelling of paleo-stability. These are:

to more fully evaluate the reliability of paleo-climate surfaces by (i) evaluation against paleo-ecological climate proxies (e.g. late Quaternary pollen records) across eastern Australia, and (ii) comparison of the surfaces used here with those emerging from the PMIP3 project (pmip3.lsce.ipsl.fr/) and ensemble modelling, as is now commonly used for forecasting of future impacts.

Given results from the above, to extend modelling of paleo-stability to other major biomes and to compare periods with contrasting climates to identify what combinations of change in temperature and precipitation are predicted to be the most restrictive across different regions and biomes.

to extend the analyses of lineage endemism from rainforest reptiles alone to rainforest frogs and birds to contrast patterns across taxa with different habitat constraints and dispersal potential.

Given more reliable estimates of paleo-climate and the lineage endemism data, to test the importance of fine-scale topography and habitat features (e.g. boulder habitats for mesic taxa (Hoskin et al. 2011) by combining appropriate layers for topographic buffering of climate and primary productivity (Mackey et al. 2012) into analyses of paleo-climatic stability.

6. CASE STUDY 3: DROUGHT REFUGIA IN MONSOONAL AUSTRALIA

6.1 Authors

Brendan Mackey and Sonia Hugh (Griffith University)

6.2 Introduction

Microrefugia might exist in a landscape that cannot be identified using broad-scale climate data. Such refugia might buffer populations from climate variation because of peculiarities of topography, geology, and ecological feedback, rather than peculiarities in the surrounding climate. For many species, hydrological cycles are crucial to persistence. Therefore, identifying and protecting ‘drought micro-habitat refuges’ is an important consideration for conservation. The term micro-habitat refuge is used here to refer to contractions in the range of suitable habitat for wildlife species over relatively shorter timescales (days, years, decades, centuries). They comprise networks of locations that maintain the habitat resources needed to enable populations of particular species to persist through a climatic drought event that renders most of their usual home range uninhabitable (Mackey et al. 2012).

There is a very tight relationship between water availability and plant growth as photosynthesis is a very ‘thirsty business’. During drought conditions certain locations stay wetter than the surrounding landscapes, providing a more reliable supply of water for plant growth. More continuous plant growth leads to higher and more sustained supplies of those vegetation-based wildlife habitat resources needed for food, shelter and reproduction (Berry et al. 2007). There are various factors that can lead to a location staying wetter than the surrounding landscape. The location may experience higher precipitation, occupy a topographic location that receives run-on from the upslope contributing areas, be topographically shaded leading to lower potential evaporation rates, receive groundwater discharge, or any combination of these factors.

Monsoonal tropical Australia by definition experiences extreme seasonal variation in precipitation. Thus, drought-like conditions are an annual event. Furthermore, like the Australian continent writ large, northern Australia experiences high year-to-year variability in total rainfall, the timing of the wet season, and spatial variation in both these parameters. At these annual and decadal timescales, micro-habitat refuges can be thought of as ‘source habitat’ locations sensu Pullium (1988) where population births tend to exceed mortality (sink habitats, in contrast, suffer population declines and extirpations, requiring replenishment via dispersal of individuals from source habitats).

6.3 Research activities and methods

We used the ‘greenspot’ modelling approach as documented in Mackey et al. (2012). In summary, our analyses are based on a continental time series of remotely sensed vegetation greenness (fraction of photosynthetically active radiation intercepted by the sunlit canopy; fPAR). The primary data for this analysis were NASA MODIS 16-day L3 Global 250 m (MOD13Q1) satellite imagery.

The greenspot analysis was undertaken on a geographically stratified basis using the sub-regions delineated by the interim biogeographic regionalisation for Australia (Environment Australia 2000); these are shown in Figure 58. We selected bioregions in northern Australia that experience a monsoonal climate. However, for the sake of geographic coherence, we included bioregions on the east coast of Cape York Peninsula that are more mesic and support rainforest.

Within each sub-region, potential ecosystem greenspots were identified, at a range of thresholds, based on an index derived from: the mean and coefficient of variance (COV) of fPAR over the 10-year time series; the minimum mean annual fPAR; and the COV of the 12 values of mean monthly fPAR. We calculated and mapped the greenspot index using the following percentiles: 10th, 25th, 50th, 75th, 90th and 95th. The 10th greenspot percentile class represent those 250 m cells which over the time series had the highest and most constant fpar values. The 95th greenspot percentile class corresponds with those grid cells with the lowest and most variable fpar values.

We then intersected the greenspot index map with the boundaries of protected areas that comprise the Australian National Reserve System (DSEWPaC 2010) and calculated the area and percentage of each greenspot percentile class that falls within a protected area. These statistics were calculated for each IBRA sub-region and then aggregated for all of monsoonal Australia.

6.4 Results and outputs

Figure 58 shows the Interim Biogeographic Regionalisation for Australia (IBRA) regions that were used to define the boundary of monsoonal Australia for this study. As noted above, the greenspot index was calculated for each of the IBRA sub-bioregions. Figure 59 shows a map of greenspot index percentile classes for monsoonal Australia and and Table 6 provides a statistical summary of the results. These values are based on the aggregation of the sub-regional analyses. Table 6 also provides estimates of the area and percentage of each greenspot percentile class found within the protected areas of the National Reserve System. Table 8 shows these statistics for one sub-region, Gulf Fall & Uplands. Table 7 provides a statistical summary of the results.

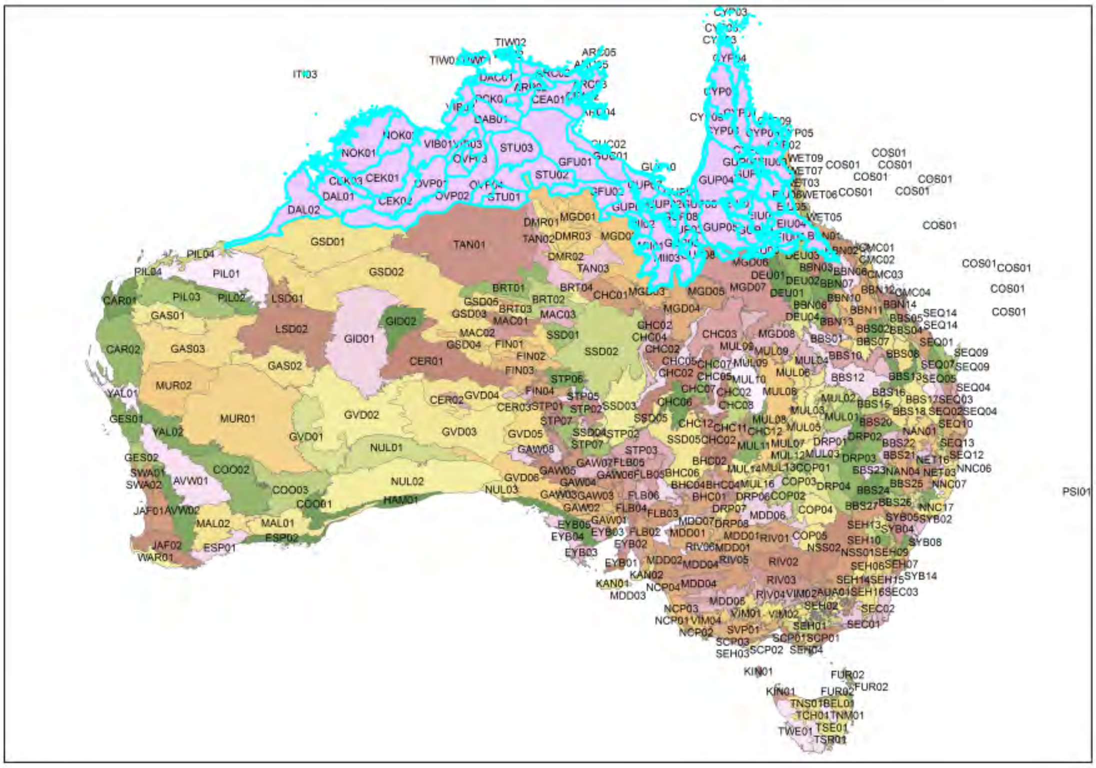

Figure 61: The Australian bioregions (IBRA) selected for the greenspot analysis of monsoonal Australia.

These values are based on the aggregation of the sub-regional analyses. Table 7 also provides estimates of the area and percentage of each greenspot percentile class found within the protected areas of the National Reserve System. Table 8 shows these statistics for one sub-region, Gulf Fall and Uplands.

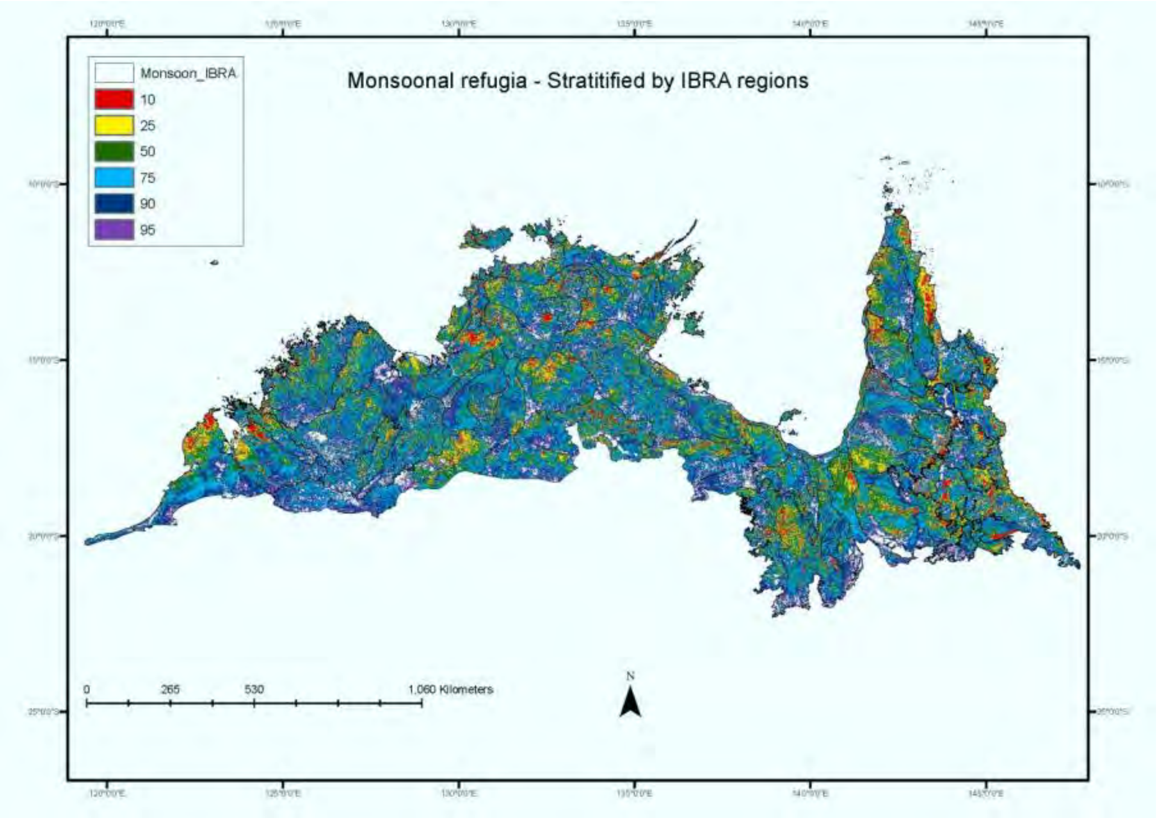

Figure 62: This map shows the results of the greenspot analysis for monsoonal Australia. The greenspot index is mapped in percentiles —10% corresponds with those 250 m resolution grid cells that have the relatively highest and most stable values of fPAR for each of the IBRA bioregions in Figure 58.

Table 8: Greenspot spatial statistics for monsoonal Australia as defined in Figure 58 and Figure 59. The total area of monsoonal Australia as defined in Figure 58 is 139 332 046 ha. The total area of monsoonal Australia in protected areas is 15 155 499 ha. This is 10.9% of monsoonal Australia.

A	B	C	D	E
10	6 177 600	990 976	4.4	0.7
25	12 345 089	1 599 564	8.9	1.1
50	29 057 644	3 507 979	20.9	2.5
75	39 720 164	4 488 210	28.5	3.2
90	30 203 223	2 796 058	21.7	2.0
95	10 577 584	861 372	7.6	0.6

Key:
A – Greenspot percentile class
B – Total area of greenspot percentile class in monsoonal Australia (ha)
C – Area of greenspot percentile class located within protected areas (ha)
D – Percentage of greenspot percentile class in monsoonal Australia
E – Percentage of greenspot percentile class located in protected areas in monsoonal Australia

Table 9: Greenspot statistics for one IBRA sub-region Gulf Fall and Uplands (GFU, IBRA Region GFU01). Total area of subregion is 9 330 938 ha.

Greenspot % class	Area in IBRA sub-region	Percentage in IBRA sub-region	Area within protected area in IBRA sub-region	Percentage within protected area in IBRA sub-region
10	253 169	2.7	15 109	0.2
25	563 447	6.0	70 312	0.8
50	1 621 906	17.4	251 403	2.7
75	2 707 706	29.0	393 510	4.2
90	2 497 097	26.8	243 987	2.6
95	841 954	9.0	68 019	0.7

6.5 Discussion

Grassy savanna woodlands dominate the landscapes of monsoonal Australia. However, the landscape’s ecological matrix includes finer-grained variation in vegetation types including grasslands, woodlands and open forests along with gallery rainforests and wetlands (Woinarski et al. 2007). These characteristic vegetation ecosystems of Northern Australia are the consequence of its monsoonal climate. Total annual rainfall is relatively wet, but there is a severe winter drought period. Figure 60 shows long-term average monthly rainfall for a typical monsoonal Australian location (Katherine Council). The average annual rainfall is 979, but only around 15 mm of rain falls during the ‘five winter’ months, with 652 mm falling in the three ‘wet summer’ months (BoM 2013).

Networks of drought micro-refuges probably play a critical role in enabling many species to persist through the prolonged dry season experienced across monsoonal Australia and then to repopulate the broader landscapes with the return of the wet season. In this context, drought micro-habitat refuges correspond with locations that have persistent surface water or near-surface water resources. Groundwater is critical for maintaining dry season base-flows in many rivers, and for maintaining hyporheic (i.e. sub-surface river channel) flows which in turn maintains riparian zones, billabongs and oxbow lakes during the long dry season. Groundwater outflow areas (perennial springs) are important sources of base-flows for certain rivers, and spring-fed water holes may be important as refuges for biota and probably also constitute special dry season habitats (Mackey et al. 2001). It is very likely that the greenspot percentile classes 10 and 25 correspond with grid cells that encompass these drought micro-habitat refuges (Figure 59). However, further analysis and fieldwork is needed in order to better understand their land cover and condition, their land-use settings, and the underlying causal hydrological processes.

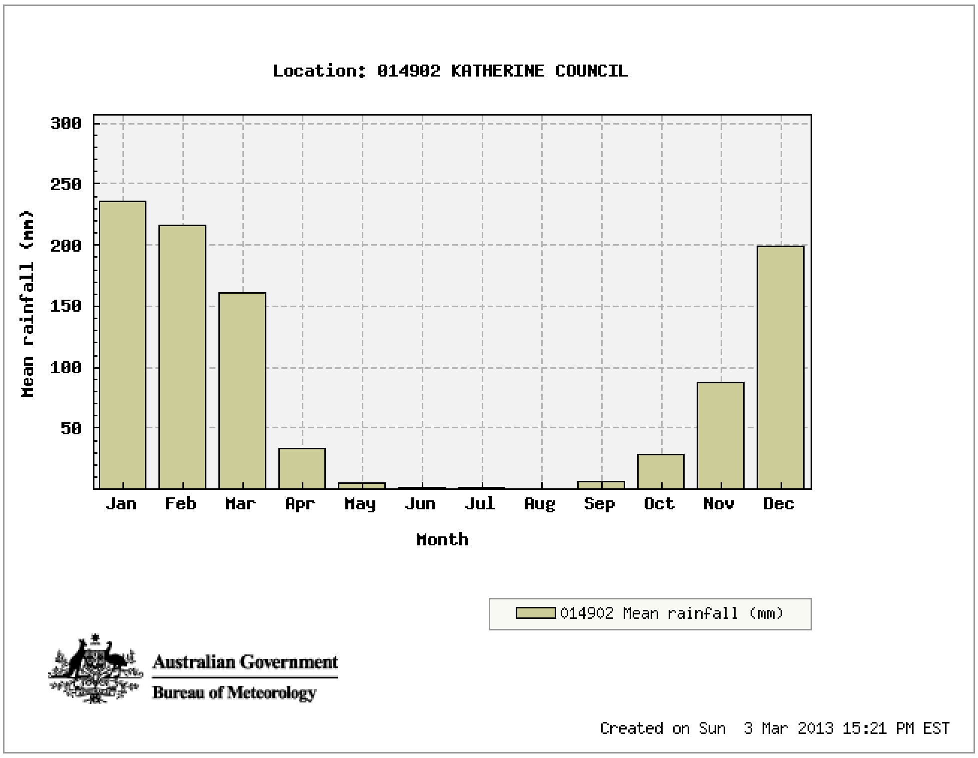

Figure 63: Long-term average monthly rainfall for a typical location in monsoonal Australia (Katherine Station). The long-term average annual rainfall is 979 mm. Graph generated 3 March 2013 by Bureau of Meteorology services available at http://www.bom.gov.au.

Projections of future climate for northern Australia remain ambiguous largely due to the difficulty in modelling the long-term potential response of the Intertropical Convergence Zone which controls the timing and severity of the monsoon season. Therefore, there remains a relatively high degree of uncertainty about changes in the region's precipitation regimes (see Figure 10 and Figure 11). Should global climate change result in the region experiencing a strengthening, lengthening or shift in the timing of the monsoonal dry season, then the networks of drought micro-habitat refuges will be of increased importance to the persistence of many native species in the region. Although many climate-change models are predicting little shift in northern Australia's rainfall regime (Figure 13), rising temperatures will increase the heat stress and energy burden on plants and animals. This again highlights the significance of the networks of drought micro-refuges to the long-term resilience of the region's ecological communities.

The ability of the drought micro-refuges to continue to function will depend on their ecological condition. Protected areas that comprise the Natural Reserve System constitute the primary means by which we can ensure landscapes are conserved for their ecological and natural heritage values. As detailed in Table 6, greenspot percentile classes 10 and 25 cover around 13% of monsoonal Australia but only 1.8% is found within a protected area. The land tenure in monsoonal Australia is dominated by pastoral leases (~75%) and Aboriginal Land (~15%). Protected areas in Northern Australia have been shown to be effective in conserving wildlife species, and particularly threatened species, relative to other land tenures (Woinarski et al. 2013). However, this positive result was considered to be the consequence of appropriate conservation management. If the remaining ~12% of greenspot percentile classes 10 and 20 that lie outside protected areas are to continue remain healthy and function as drought micro-refuges, then targeted conservation management agreements may be needed with the landowners and managers to help ensure they are not degraded.

In the context of a rapidly changing climate, micro-habitat refuge networks contribute to the persistence of species in a landscape and help maintain beta diversity at the bioregional scale. The maintenance of source habitats and beta diversity contribute to the resilience and adaptive capacity of monsoonal Australia’s species and ecosystems.

7. CASE STUDY 4. USING CONSERVATION PLANNING TOOLS TO IDENTIFY REGIONAL REFUGIA

7.1 Authors

Barbara J. Anderson, Jeremy VanDerWal, Ben L. Phillips, Yvette M. Williams, April E. Reside (James Cook University)

7.2 Introduction

Identifying areas with high species richness, species turnover or species endemism is an important first step in determining likely refugia both now and in the future. By using conservation prioritisation software, we can ensure that the areas of highest priority incorporate complementarity across both species and sites.

In meeting our main objective under this report, we created many layers of relevant variables (species turnover, climate stability, etc.; see section 3), and then visualised the parts of the continent with the lowest/highest values at these layers by applying a threshold (at the 10th or 90th percentile as appropriate). This thresholding is a very coarse approach and loses much information. In designing refugia based on such thresholds, we have no guarantee that we have maximised overall species diversity for our dollar. The very clear way forward with this problem is to apply the tools of conservation planning to identify refugial areas that maximise species probability of survival given climate change using much more of the available information.

We used freely available and widely used software Zonation to produce a conservation prioritisation for a small but internationally important bioregion of Australia – the Australian Wet Tropics (AWT). This area was specifically chosen as it has an exceedingly well understood biogeography and paleo-history, such that it represents a learning landscape for the rest of the world. We know where the historical refugia were in the AWT; and we know this because complementary phylogeographic, palynological, and contemporary biogeographic data all paint the same picture. Rainforest in the AWT has consistently expanded out of and retracted back to major refugial areas within the region (Graham et al. 2010).

This analysis should be seen specifically as the first, preliminary analysis designed as a pilot study to demonstrate the utility of applying these types of analyses. Zonation can provide cohesive and applied answers to the questions this report addresses using as inputs the data that this report has generated (specifically from section 3). The future development section examines and outlines some of the more important features which could and should be dealt with, time allowing, before applying these methods at a continental scale.

7.3 Research activities and methods

Zonation is a widely used *landscape* conservation prioritisation software (Moilanen et al. 2012 and references therein) designed to identify the areas of highest conservation priority for many species (or other biodiversity features) over a large landscape.
The Zonation analysis proceeds by iteratively calculating the biological value of each planning unit in the landscape, and then removing the unit which has the lowest biological value until all units have been removed (Moilanen et al. 2012). The order of removal then gives a hierarchical conservation prioritisation across the landscape. Which planning unit has the lowest biological value depends on the removal rule being used, and the relative weightings placed on different preferred outcomes by the user.

The iterative recalculation of all values ensures that Zonation achieves maximum complementarity in its ranking process. The basic output of Zonation is a hierarchical ranking of the landscape based on the series of biodiversity feature layers. This allows the user to immediately assess and visualise the importance of grid cells for any given fraction of the landscape. We report this basic output below as maps.

‘Value’ in Zonation, as with other conservation planning tools, is determined by the input layers and the weightings placed on different preferred outcomes by the user. Here we used the current and future projected distributions for the 191 terrestrial vertebrates of the study area weighting each species by its affinity to rainforest; the main habitat type for the region (APPENDIX 9. Conservation planning species information). The summed total value of each layer is transformed within Zonation to sum to ‘1’. So that each species is given an equal weighting in the analysis, these values are then multiplied by the user identified species weightings, in this case the affinity to rainforest.

7.3.1 Current and future refugia

As a first pass to assess the usefulness of Zonation in locating key refugia in the AWT, we ran two separate analyses using Zonation’s Added Benefit Function (ABF). Both analyses sought to find areas that maximised the representation of species-level biodiversity in the region. The first analysis was conducted on current patterns of biodiversity, and the second on projected patterns of biodiversity in 2085. Current and future distributions were modelled based on observation records and distribution models associated with Williams et al. (2010). The future scenarios were the same used throughout the report (18 GCMs for RCP8.5 at 2085) only downscaled to 9 arc-seconds (~250 m x 250 m resolution) for the study region. We use 191 biodiversity feature layers, where each layer is the modelled (current or future) species distribution for the species based on the standard Maxent outputs as described in (section 3.1.5, although here run at a much higher spatial resolution, with 499 085 (~250 m x 250 m resolution) grid cells.

We present the future analysis as the median, that is, for each species we calculated the median across all 18 GCM projections for that species. In effect this gives the median as our best estimate of the likely future distribution of the species and represents the best comparison to previous analyses presented in this report. Individual solutions for the set of projected species distributions generated from each of the 18 GCMs can be found in APPENDIX 10. Conservation planning variability across GCMs. In addition, variability across these different GCMs is taken into account in the uncertainty analysis that follows.

We then present a combined current plus future analysis, where each species is represented by both a current- and a future-projected distribution.

7.3.2 Connectivity analysis

The current conservation prioritisation map represents the best set of locations to protect as current refugia. The future conservation prioritisation map represents potential future refugia, that is, the best set of locations to represent climate space that is suitable for this set of species. However, in order for these future refugia to truly function as refugia, the species in question must be able to reach them. Incorporating a set of species-specific connectivity layers between the current and potential future species distributions and vice versa allows the analysis to emphasise regions where the current and future climatically suitable areas for a species are close. This is intended to provide species with the best opportunity to shift their ranges from current climatically suitable regions to a future climatically suitable region.

7.3.3 Uncertainty analysis

If each set of potential future distributions is treated as an equally likely but certain outcome, two important questions remain. Firstly, how should management decisions weight the results of one GCM against another? Secondly, how do we account for considerable variation in the degree to which the 18 different projected future distributions agree across the region? The current case study answers the first by presenting a simple analysis based on the median projected future species distributions across the 18 GCMs. As known uncertainty, the second question can be resolved through the use of an uncertainty layer. Here we use the difference between the median and the 10th percentile as a measure of the variability in suitability of each location for each species. Integrating known uncertainty in the analysis places greater weight on locations where there is both high suitability and a higher degree of agreement across the various future projected species distributions.

7.4 Results and outputs

The Zonation analysis under current conditions perfectly selected the core of the major biogeographic regions of the Wet Tropics (Figure 61). These areas are not only centres of species-level biodiversity, but have also been major refugial areas under the climatic fluctuations of the last two million years (Moritz et al. 1997, Schneider et al. 1998, Schneider and Moritz 1999). Importantly, the analysis highlights the largest tract of intact upland rainforest of the Atherton Uplands as highest priority refugia. This area has already been the focus of restoration, being recognised as crucial for endemic rainforest species persistence into the future (Shoo et al. 2011). Other key areas for refugia, indicated for both current and future from the Zonation analysis, are the Windsor Uplands, Carbine Uplands, Lamb Uplands, Bellenden Ker and Bartle Frere mountains. The Black Mountain Corridor is identified as important (top 25%) for current conditions, but drops in importance in the future; this area has previously been a dispersal barrier for genes and species in the past (Moritz et al. 2009) and appears also to be a barrier into the future. Areas that are projected to increase in importance into the future include the Thornton Uplands and Lowlands, and Cairns/Cardwell Lowlands between the Malbon Thompson Uplands and Bellenden Ker. These areas may be of consideration for restoration and conservation in the future.

Under projected future distributions of biodiversity, Zonation identifies that many of the same areas will remain as important refugia under contemporary climate change. Although it is also clear that the Herberton Range in the central highlands and parts of the southern highlands will become relatively more important under a median 2085 future climate.

Importantly, prioritisation is hierarchical such that the top 2% of cells (red) are within the top 5% (burgundy) which are in turn within the top 10% (pink), 25% (yellow), 50% (blue), 80% (dark blue); the lowest priority 20% are black. Maps for all 18 GCMs are in APPENDIX 10. Conservation planning variability across GCMs.

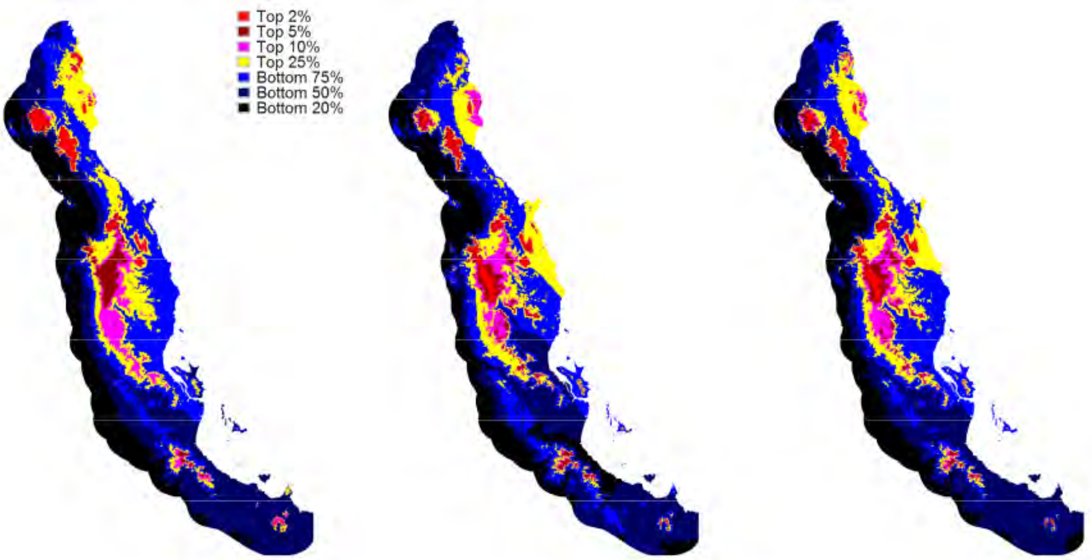

Figure 64: Zonation conservation prioritisation analysis of the AWT bioregion. The analysis presented is based on 191 terrestrial vertebrates' projected species distribution models for a) 1990; b) the median of 18 GCMs for 2085; and c) current plus future projections incorporating connectivity between current and future, that is, four layers for each species current projection, future projection, connectivity between current and future projections, and connectivity between future and current projections. Zonation correctly identifies known centres of species and within-species diversity in this region under current climate conditions, and predicts that many of these areas will remain important refugia into the future under climate change.

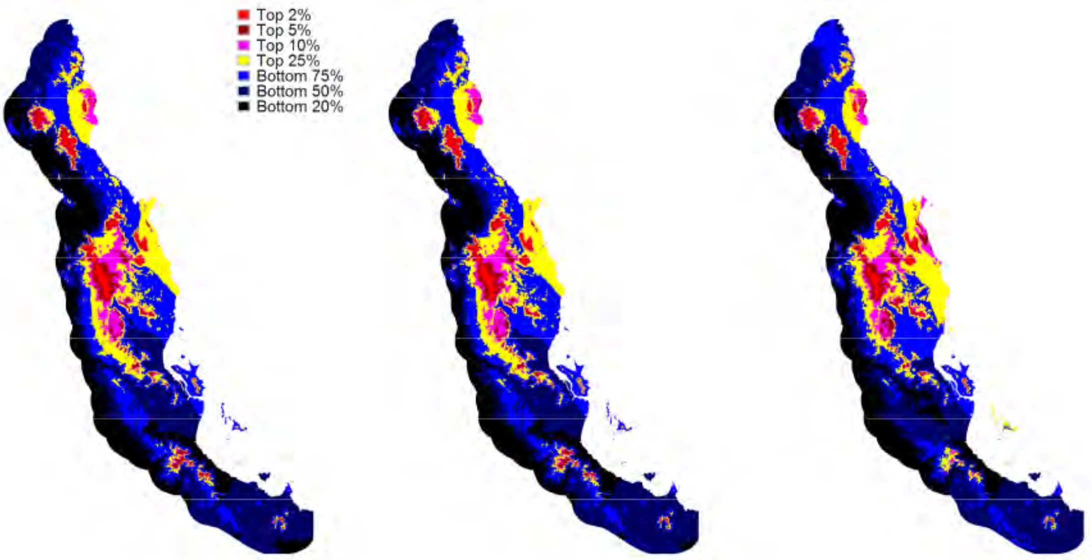

Figure 65: Accounting for uncertainty in the future projected species distributions (RCP8.5, 2085, based on the median model across all 18 GCMs). Conservation prioritisation of the AWT bioregion based on projected species distribution models for 191 terrestrial vertebrates. Panels represent the median with increasing amounts of uncertainty a) α = 0.0; b) α = 0.5; c) α = 1.0. Prioritisation is hierarchical so that the top 2% of cells (red) are within the top 5% (burgundy) which are in turn within the top 10% (pink), 25% (yellow), 50% (blue), 80% (dark blue); the lowest priority 20% are black.

7.4.1 Connectivity analysis

When the current and future species distributions, and the connectivity between these, are simultaneously used as biodiversity feature layers within the Zonation analysis, the results highlight areas which should be high priority refugia. Given that the current (Figure 61 left) and future (Figure 61 centre) conservation priority areas are overall very similar, adding connectivity (Figure 61 right) changes the overall pattern little. However, small differences in specific areas are noticeable. For example, when connectivity is taken into account, the highest priority areas (top 5%) extend east from the Atherton Uplands down towards Bellenden Ker/Bartle Frere. Based on the current analysis only (Figure 61 left), the Carbine and Windsor Uplands are relatively more important than the Atherton Uplands. In contrast, in both the future only analysis (Figure 61 centre) and the connectivity analysis (Figure 61 right), the Atherton Uplands are as important as the Carbine and Windsor Uplands.

7.4.2 Uncertainty analysis

When uncertainties in the projected future distributions of species are taken into account subtle differences emerge (Figure 63). This analysis places increased weighting on areas where the distribution models based on the 18 GCMs agree. This means that areas with more stable/certain projections will be favoured above less stable areas with similar median values. For example, Malbon Thompson Range is categorised as a higher prioritisation when uncertainty is included as is the South Eastern edge of the Atherton Uplands indicating that these areas show relative consistency across the 18 GCMs in terms of projected future species distributions. On the other hand, the Spec Uplands ranges decreased in priority indicating a high level of uncertainty in the projected future species distributions across the 18 GCMs. Incorporating uncertainty into the conservation prioritisation represents a low risk strategy placing greater weight on those areas of relative certainty across the GCMs.

7.5 Discussion

Running Zonation for the endemic rainforest vertebrates of the AWT bioregion demonstrates the efficacy of this approach. We demonstrated that the conservation prioritisation tool (Zonation) applied to the well-studied AWT could identify the already-known paleological refugia areas in this region. The preliminary analysis of vertebrate data from the AWT in Zonation accurately identified all the biogeographic regions in the area including both major refugia (such as the Carbine, Windsor, and Atherton tablelands), as well as smaller refugia, such as Mt Elliot, and the Malbon Thompson Range. Given our results, we can recommend expanding this analysis to a continent-wide conservation prioritisation as far as computational limitations would allow.

This analysis builds on the species distribution modelling approach by allowing for ranking, representation and complementarity in the spatial prioritisation of refugia. The results enable a prioritisation of adaptation options in this region. For areas of high refugial potential already in reserves, focus can be on management options that enhance resilience, such as controlling pest species. Areas of high refugial potential outside the current reserve system can be prioritised for restoration and conservation. It was a simple matter to run the same analysis based on projected 2085 species distributions for the area to find the places of highest conservation value into the future. This was a very basic analysis relative to what Zonation is capable of, and we suspect that regional refugial mapping projects will be greatly facilitated by judicious use of this approach.

7.6 Gaps and future research

The conservation prioritisation performed in this study for the AWT bioregion serves as a small in extent, fine resolution example of the most basic of Zonation analyses. The size of the analysis possible is a trade-off between the number of cells in the landscape (extent and resolution of the study area), the number of taxa in the analysis and the computing power available. Future analyses would aim to produce a continent-wide analysis at a resolution that is relevant to identifying continental-scale refugia (25 km^2 or 1 km^2). Increasing the extent of the analysis implicitly increases the number of taxa included in the analysis, further increasing the computational requirements. However, the Zonation software is under constant development and recent developments should allow us to take advantage of the high performance computing network at JCU.

There is considerable potential to expand the analysis to include a greater proportion of the biodiversity. Here we used the terrestrial rainforest vertebrates (birds, mammals, reptiles and amphibians) building on the considerable body of data and species distribution modelling available through the Centre for Tropical Biodiversity and Climate Change at JCU. It is hoped that a system of refugia which caters to these iconic, easily sampled and identifiable taxa will also to some extent act as a surrogate for other non-sampled taxa. However, previous studies suggest the best strategy is to include more species in the analysis, particularly small range species and taxa with different ecological requirements. Most noticeable in the current study is that there is insufficient data available to include plants or invertebrates in the analysis. Future work should be directed towards collecting and collating the distribution data required to adequately model these species' current and likely future ranges.

There is also considerable scope to improve the relative weightings of the taxa in the analysis. These weightings allow the user to increase or reduce the emphasis the analysis places on each taxon depending on the importance that society, policy or management place on them. Some taxa may be given higher weightings where they are of particular conservation concern due to past declines or interactions between different threats. In contrast, those species adapted to heavily human-modified environments may be given lower weightings as they are likely to derive little added benefit from such protection. Alternatively, weightings might be used to represent the degree of taxonomic, phylogenetic or genetic distinctness of the taxa. The current case study is on the AWT where rainforest is the main habitat of concern. Here we applied a simple scale of weightings based on how dependent each species is on rainforest. However, degree of endemism, IUCN ranking or some compound index of perceived risk, vulnerability or relative importance could also be applied. Ongoing consultation with relevant stakeholders will allow these relative weightings to be re-evaluated.

The current case study presents one conservation prioritisation based on the current species distributions and one based on future projected species distributions for a range of GCMs. Further comparison between these two outputs would allow us to identify which landscape units are most important as refugia for their current species composition and which are likely to be most important as future refugia. Including additional layers in the analysis representing cost of acquiring land, current and past condition of the land, potential biodiversity gain and potential biodiversity loss under a range of management scenarios; alternative, commensal or conflicting land-use requirements would greatly improve the utility of this analysis for both policy and management. These analyses depend on the production of a suitable input layer and future work should be directed towards collecting and collating these data.

8. DISCUSSION AND CONCLUSIONS

8.1 Comparison of techniques

8.1.1 Australia-wide SDM and GDM comparison

There was broad spatial congruence across the final refugia models generated using the species distribution (SDM) and generalised dissimilarity (GDM) modelling approaches (Figure 63). In particular, both approaches found the coastal areas around the continent, and particularly the east coast, to be the most crucial refugial areas. Tasmania in particular rates highly, with most of Tasmania projected to contain refugia with both analyses. Given that Tasmania is so consistently projected to contain future refugia, and that a large proportion is already in the national reserve system and recognised for its current biodiversity values, Tasmania should be a high priority for future refugia considerations. South-west Western Australia and the coastal Northern Territory also overlap as high priority refugia. Upland areas of the Wet Tropics, Australian Alps, Flinders Lofty Block and New England Tablelands are also recognised as high priority refugia using both techniques.

We would expect the refugial areas identified under the GDM approach to differ in some respects from those identified under the SDM approach for two reasons. First, the GDM approach prioritises locations that are expected to support an environment in the future that will have become increasingly rare in the surrounding landscape, and that biota dependent on this environment can reach by moving relatively short distances. On the other hand, the SDM approach has focussed on minimising the loss of local species, but also on maximising the immigration of non-local species that are capable of moving longer distances to reach these locations. Much of the discrepancy between GDM and SDM approaches stems from this definitional difference in what constitutes a good quality refuge. The second reason we would expect the GDM areas to differ from SDM areas is simply that the GDM analysis was undertaken at a much finer spatial resolution, and gave more consideration to the effects of local topography on radiation, temperature and moisture.

There are, therefore, some areas that were found to have high potential refugial values for the GDM analyses, but not for the SDM. These include the inland regions such as the Channel Country, Mount Isa Inlier, the Gibson Desert and the Pilbara. Conversely, the SDM analyses found regions such as the Nullarbor, and much of central and inland Queensland and NSW to have high refugial potential in comparison to findings of the GDM analyses.

Overall, the GDM analysis identifies places expected to act as refugia **within** landscapes. These are clearly important refugial areas because they are areas where species will need to move only short distances to persist through unfavourable future climates. The SDM analysis also points to another kind of refuge; those where species will need to move longer distances, including **between** landscapes, as a means of persistence through unfavourable future climates. Given that there are many species for which suitable climate space will not exist in 2085 within their current range, we will need to consider both refugial options if we are to maximise biodiversity outcomes.

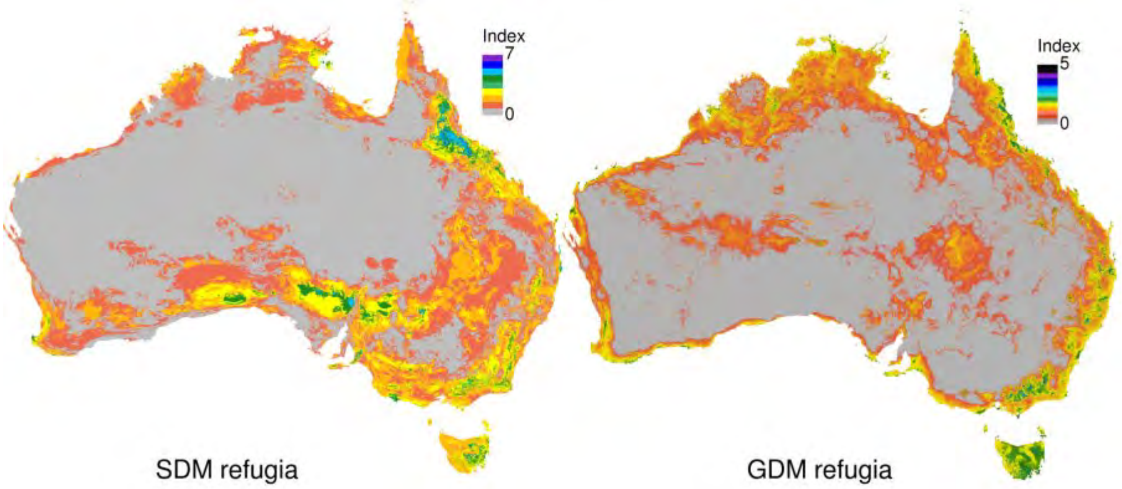

Figure 66: The refugia areas resulting from the species distribution modelling analyses (left: SDM refugia) from section 3.4.4 and the generalised dissimilarity modelling (right: GDM refugia) from section 4 for comparison.

Differences in the spatial predictions for refugia using the different techniques are also expected given the differences in the input data used: different taxa will use different refuges. Additionally, different input climate data were used for projecting future outcomes: the SDM were projected to each GCM and then a median output was generated for examination, while the GDM was projected using specific GCMs. The GDM approach had the advantage of using finer resolution data. The SDM approach also had the advantage of projecting the outcomes for individual species, which can be valuable for informing conservation prioritisation analysis such as that used in Case study 4.

8.1.2 Comparison of the different methods for a case study area

Most of the primary analytical techniques (except for 'greenspot' modelling of drought refugia) are represented in the AWT bioregion (species distribution modelling, generalised dissimilarity modelling, evolutionary refugia modelling and Zonation). This allows for direct comparison of techniques within a common geographically defined region. A detailed map of the subregions for the AWT region can be found in Figure 2 of Williams (2006). The comparison shows that while there are some differences, there is good spatial congruence for the important refugia areas. In particular, the upland areas in the north (Carbine, Windsor, Thornton), central (Bellenden-Ker/Bartle-Frere, Lamb and Herberton ranges) and south (Spec and Elliot) are all represented by each of the four techniques (Figure 64). These upland areas are recognised as conservation hotspots, being centres of evolution and containing endemic species (Williams 1996).

Differences across the techniques in this comparison can be found either side of the uplands. The SDM results favour the inland (western) area which is the transition zone from rainforest to sclerophyll forest. The SDM refugia would probably have mirrored the Zonation results if the detailed, fine resolution SDMs were used for the AWT region, with a stronger focus on the subset of rainforest-dependent species (Williams et al. 2003, Williams et al. 2010). The differences in the SDM approach in comparison to the others are almost certainly because this approach focusses on areas that will act as refuges for immigrating species: in this case species moving uphill from the lowland areas of the western slopes. Additionally, the SDM results do not account for endemism, or for specific habitats (e.g. rainforest endemics). The GDM results particularly highlight the upland areas, and the evolutionary refugia and Zonation results emphasise some coastal regions including the Daintree, which is not as well represented by the other techniques. The current protected areas largely encompass the refugial areas predicted by the GDM, evolutionary refugia and Zonation; however, large areas of refugia predicted by the SDM approach fall outside the current protected areas.

The southern Atherton Tablelands contains the largest tract of upland rainforest and has some of the highest diversity and abundance of rainforest species, as well as high productivity. This region was well-represented by the Zonation analysis, and by the evolutionary refugia, but under-represented by the two Australia-wide analyses (GDM and SDM). In contrast, the northern uplands of Windsor and Carbine Uplands gain particularly high refugia status across all techniques (Moritz et al. 2005). In the case of Windsor, it is currently moderately depauperate in comparison to other upland areas, with a fauna that is likely to have been recolonised after rainforest contractions in the past. It is also likely to be particularly vulnerable to changes in future rainfall, which is difficult to predict given the uncertainty around future rainfall projections.

The southern upland rainforest of the AWT, particularly Hinchinbrook Island, Paluma Range and Mt Elliot, come out as important refugia across all techniques. Mt Elliot is the southernmost upland area of the AWT, has three endemic vertebrates, and is the southern outlier for many rainforest species distributions. Despite the importance of Mt Elliot for its endemics, these southern upland regions are all relatively depauperate and lack the current diversity found in the extensive tracts of rainforest of the Atherton Tablelands. The analyses containing future projections (SDM, GDM and Zonation) are likely to all emphasise the importance of upland areas, even if current diversity is low, because the upland areas hold high potential for species currently at lower elevations to move into. The evolutionary refugia are also concentrated at high elevations in most regions, indicating their importance as refugia from past climate change. Despite the differences, the congruence across techniques gives us confidence that the techniques used in this study are able to point to high value refugia.

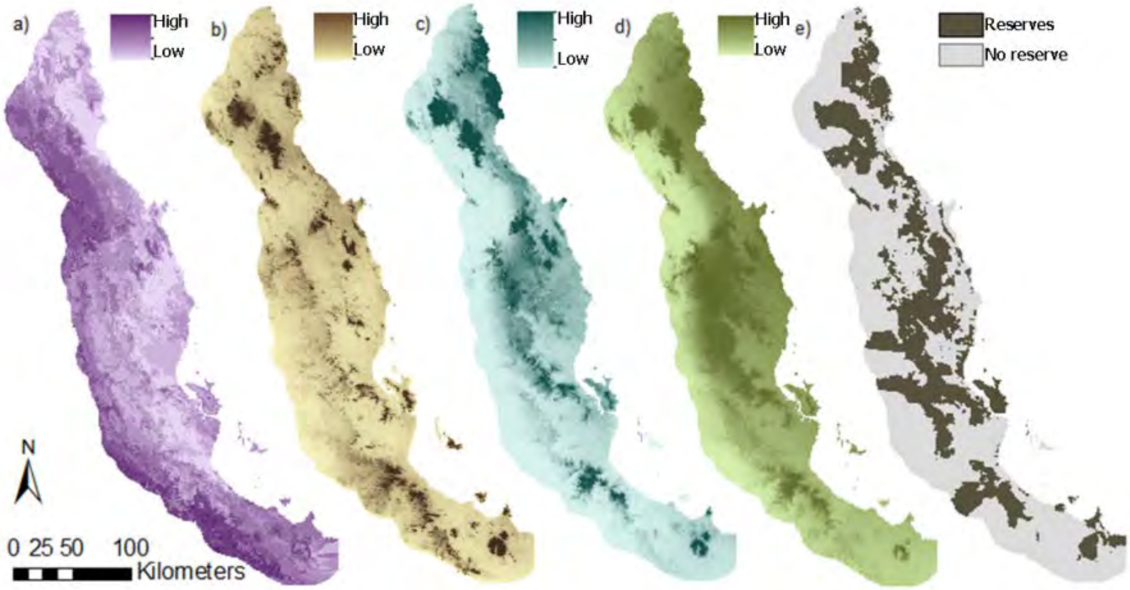

Figure 67: Comparison of techniques for a common region, the AWT bioregion of north-east Queensland. a) the SDM refugia analyses from section 3.4.4; b) the GDM refugia analyses from section 4.4.2; c) the evolutionary refugia from section 5.5; all compared to d) the Zonation analysis from section 7.4; and e) the current protected areas within this region.

8.1.3 Overall lessons from the different techniques

Overall, the different techniques used throughout this study have each highlighted the areas projected to be refugia depending on the particular parameters used. Given the diverse set of techniques, areas that are identified as refugia by more than one of these techniques should be high priorities for further investigation into their potential refugial properties and conservation status. In addition to spatial congruence, a few overarching lessons apply across the different techniques. These include:

8.1.3.1 High elevation areas are important refugia

Areas of high elevation relative to the surrounding landscape came out consistently as being important future refugia areas. Upland areas such as the Australian Alps and other parts of the Great Dividing Range, and the MacDonnell Ranges had few emigrants and were predicted to have high numbers of incoming species. The fine-scale (100 m grid resolution) GDM analyses focussed on NSW showed high elevation areas including the Border Ranges and the Australian Alps. The comparison of techniques for the Australian Wet Tropics region showed that the high elevation areas were consistently important across all techniques examined. However, despite concordance across techniques that high elevation areas will be important refugia, our distance analyses (section 3.4.2) suggest that they will be most important for species in the surrounding lower elevations, but not for the species that are currently there which remain of high conservation concern.

8.1.3.2 Tasmania is important

Three of our analyses — SDM, GDM and evolutionary refugia — identified that large areas of Tasmania are important refugia for terrestrial biodiversity. Indeed, each of these techniques showed that the vast majority of the land area of Tasmania had refugial value. This was the case for each of the taxonomic groups studied. Both the GDM and the evolutionary refugia techniques showed that western Tasmania was of the highest refugial value. Extensive protected areas already established in this region mean that it is well positioned to realise this potential.

8.1.3.3 East coast Australia is important

Both the SDM and GDM analyses that covered the whole continent showed that the east coast of Australia had a high proportion of refugia when compared to the rest of Australia. This is likely to be a result of the east coast providing an opportunity for species to track their climatic niche south, where temperatures are lower, at the same time finding hydric refugia. While in combination Tasmania and the east coast of mainland Australia will be crucial for species persistence into the future; the refugia found away from the east coast will be crucial for maintaining the unique fauna in habitats other than what is found on the east coast.

8.1.3.4 Results are dependent on the exact objective being investigated, the technique, the taxonomic group, and the climate scenario

The exact areas projected to be refugia were in some cases dependent on the objective being considered. For instance, the SDM study showed that different areas would be selected as refugia depending on whether refugia were designated to be the highest number of immigrating species compared with the lowest number of immigrating species. Also, different taxonomic groups were predicted to have different refugial areas due to their different climatic associations and also their different dispersal abilities. Additionally, the scale at which the analyses are conducted will dictate whether the refugial areas recommended are broad regional or local fine-scale refugia. Therefore, translating refugia analyses to a prioritised management plan requires careful consideration of the scale, taxonomic group, time horizon and explicit overall objectives incorporated into a systematic conservation planning framework.

8.2 Further considerations

Even though we can identify numerous climate change refugia in southern and eastern Australia, the relative dearth of refugia in other parts of the country, the lack of congruence between paleological and future refugia, and the clear inference that upland species will not be able to reach suitable refugia, are causes for concern. **There is clearly a large portion of Australia's fauna for which there are no natural macro refugia from impending climate change.**

Identifying which species will be safe in our identified refugia, and which species will not requires further work. It is clear, however, that many species will be required to shift their range to accommodate climate change. Species have strongly different abilities to range-shift (Devictor et al. 2008, Tingley et al. 2009), and the species with the highest rates of range-shift are those with high dispersal potential and high rates of population growth. Thus, impending climate change will act to filter out specialist, low dispersal, and low fecundity species; species traits that are often associated with endemism. Thus, the clear prediction from our analysis is that **Australia is set to lose a large number of regionally endemic species, particularly those in the north and west of the continent** in places that have paleologically stable climates.

An additional potential issue that will act to diminish biodiversity are species interactions. Another very clear inference from our continent-wide analyses is that species will be shifting to places they have never been before. This reshuffling of species through space will result in utterly novel assemblages, with protagonists that may have very little co-evolutionary history. The outcomes of such novel species interactions are difficult to guess (Jones and Gomulkiewicz 2012), but are considered one of the key proximate causes of population declines and extinctions related to climate change (Cahill et al. 2012). So again, even if species are capable of moving to refugial areas, their arrival may result in no net increase (or even a decrease) in richness if strong negative interactions between species play out.

Across all metrics of stability in climate (both past, current and future), species distributions (future) and GDM, southern and eastern Australia consistently emerge as the areas that will be of greatest importance to biodiversity into the future. Much of this region corresponds to areas of greatest human population density. Correspondingly, these areas have the highest concentrations of small and very small protected areas (DSEWPaC 2010), and are the most fragmented and disturbed areas in the continent, except along the south-Australian coast. Additionally, areas of moderate climate stability, and high biodiversity stability fall within the extensive reserve system of western Tasmania. However, the areas of highest climate and species stability in eastern Tasmania correspond to the areas with the smallest reserves. **Large areas with high importance for future biodiversity and high climate stability are very fragmented and have very few, small protected areas**. Unfortunately, **the largest conservation reserves on continental Australia are not predicted to be refugia for biodiversity under climate change**.

Because connectivity has been highlighted as an important characteristic of refugia (Mosblech et al. 2011), and that refugia must be of adequate size to facilitate evolutionary processes (Ovaskainen 2002); the small and fragmented nature of the reserve system that largely overlaps the areas of highest importance is of concern.

9. GAPS AND FUTURE RESEARCH DIRECTIONS

The strongest future direction is that the refugial analyses need to be carried out at a finer scale and in a conservation planning framework. Although this project has identified broad regions of interest for terrestrial biodiversity at a national scale, it is possible that small refugial areas that will be important for species persistence under climate change have been missed. It is critical, therefore, that detailed analyses of regional refugia are conducted. Our case studies touch on some ways forward in this regard.

Australian protected areas fall within state government responsibilities, so it is recommended that downscaled analysis at a state and then regional scale be carried out to clearly highlight region-specific conservation priorities and to identify regional refugia. The sub-continental-scale case studies provided in this project showcase the possibilities available. It is clear that downscaling to even finer local scale analyses, and locating micro-refugia (such as relatively wet areas), both inside and outside areas likely to be important for macro-scale biodiversity will be critical if we are to manage the local persistence of populations under climate change.

Broadening the smaller case study analyses — the greenspot modelling, evolutionary refugia modelling and Zonation — would be of great use for refugia analyses across Australia. The greenspot analyses, in particular, can add an additional layer of information; pointing to places that might be decoupled from regional climate patterns by virtue of geological or edaphic peculiarities. Likewise, a broadened evolutionary refugia analysis would highlight areas of important historic refugia across Australia; areas that should be upweighted in a conservation analysis by dint of their evolutionary uniqueness. This latter analysis would depend critically on phylogenetic and phylogeographic data that is currently being collected (by Moritz and many collaborators). Finally, careful consideration of how to best weight and combine the various approaches is required, and conservation prioritisation tools such as Zonation from Case study 4 will likely play a strong role in achieving that synthesis.

Indeed, conservation planning tools have an immense capacity to synthesise data and develop priorities taking into account highly complex planning objectives. As an example, approaches that take into account alternative ecosystems (such as marine and freshwater ecosystems as well as terrestrial ecosystems) in sensible ways is a strong current focus of conservation planning theorists. There is, for example, obvious connectivity between terrestrial and freshwater ecosystems: the freshwater ecosystem in most cases would benefit from a more ‘intact’ terrestrial ecosystem surrounding a catchment, and vice versa. Combining the conservation prioritisation for the Australian Terrestrial and Australian Freshwater ecosystems would allow a more holistic approach, with considerable advantages to both. Emerging tools for making this synthesis across traditionally disparate biological ecosystems may enable this kind of broad synthesis within the next few years.

The quantitative examination of the spatial pattern of refugia with respect to the existing protected area network and the condition of refugia to inform restoration priorities will be core to the uptake of this project by stakeholders. Ideally, this analysis would look at the protected areas that already fall within the refugia identified in this project and will then make recommendations on key areas to be included in the protected area network to maximise diversity retention and resilience into the future.

The broader application of systematic conservation prioritisation tools to optimise protection and restoration priorities of identified refugia for all of Australia is the next logical step to complete this project. However to undertake this analysis, substantial time and resources would be required, primarily due to the substantial benefits to be gained from downscaling the SDM analyses from national to regional and local scales.

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APPENDIX 1. CLIMATE SCENARIOS AND BIOCLIMATIC VARIABLES

Table A1-3: Representative Concentration Pathways used in analysis.

RCP	Short Description	Detailed Description
RCP3PD	Low RCP with Peak & Decline (2005-2500)	The RCP 3-PD is developed by the IMAGE modeling team of the Netherlands Environmental Assessment Agency. The emission pathway is representative for scenarios in the literature leading to very low greenhouse gas concentration levels. It is a so-called peak scenario its radiative forcing level first reaches a value around 3.1 W/m2 mid-century returning to 2.6 W/m2 by 2100. In order to reach such radiative forcing levels greenhouse gas emissions (and indirectly emissions of air pollutants) Are reduced substantially over time. The final RCP is based on the publication by Van Vuuren et al. (2007).
RCP45	Medium-Low RCP with stabilisation from 2150 onwards (2005-2500)	The RCP 4.5 is developed by the MiniCAM modeling team at the Pacific Northwest National Laboratorys Joint Global Change Research Institute (JGCRI). It is a stabilization scenario where total radiative forcing is stabilized before 2100 by employment of a range of technologies and strategies for reducing greenhouse gas emissions. The scenario drivers and technology options are detailed in Clarke et al. (2007). Additional detail on the simulation of land use and terrestrial carbon emissions is given by Wise et al (2009).
RCP6	Medium-High RCP with stabilisation from 2150 onwards (2005-2500)	The RCP 6.0 is developed by the AIM modeling team at the National Institute for Environmental Studies (NIES) Japan. It is a stabilization scenario where total radiative forcing is stabilized after 2100 without overshoot by employment of a range of technologies and strategies for reducing greenhouse gas emissions. The details of the scenario are described in Fujino et al. (2006) And Hijioka et al. (2008).
RCP85	High RCP	The RCP 8.5 is developed by the MESSAGE modeling team and the IIASA Integrated Assessment Framework at the International Institute for Applies Systems Analysis (IIASA) Austria. The RCP 8.5 is characterized by increasing greenhouse gas emissions over time representative for scenarios in the literature leading to high greenhouse gas concentration levels. The underlying scenario drivers and resulting development path are based on the A2r scenario detailed in Riahi et al. (2007).

*source: https://tntcat.iiasa.ac.at:8743/RcpDb/dsd?Action=htmlpage&page=welcome#descript

Table A1-4: Eighteen Global Climate Models used in analysis.

Abb.	Global Climate Model	Group	URL for further info
cccma-cgcm31	Coupled Global Climate Model (CGCM3)	Canadian Centre for Climate Modelling and Analysis (CCCma)	http://www.ipcc-data.org/ar4/model-CCCMA-CGCM3_1-T47-change.html
ccsr-miroc32hi	MIROC3.2 (hires)	CCSR/NIES/FRCGC - Japan CCSR = Center for Climate System Research - University of Tokyo NIES = National Institute for Environmental Studies FRCGC = Frontier Research Center for Global Chance - Japan Agency for Marine-Earth Science and Technology (JAMSTEC) (The University ofTokyo is a National University Corporation and NIES and JAMSTEC are Independent Administrative Institutions)	http://www-pcmdi.llnl.gov/ipcc/model_documentation/MIROC3.2_hires.pdf
ccsr-miroc32med	MIROC3.2 (medres)	CCSR/NIES/FRCGC - Japan CCSR = Center for Climate System Research - University of Tokyo NIES = National Institute for Environmental Studies FRCGC = Frontier Research Center for Global Chance - Japan Agency for Marine-Earth Science and Technology (JAMSTEC) (The University ofTokyo is a National University Corporation and NIES and JAMSTEC are Independent Administrative Institutions)	http://www-pcmdi.llnl.gov/ipcc/model_documentation/MIROC3.2_hires.pdf
cnrm-cm3	CNRM-CM3	Centre National de Recherches Meteorologiques - Meteo France - France	http://www.ipcc-data.org/ar4/model-CNRM-CM3-change.html
csiro-mk30	CSIRO Mark 3.0	The CSIRO Mk3.5 Climate Model The Centre for Australian Weather and Climate Research	http://www.ipcc-data.org/ar4/model-CSIRO-MK3-change.html
gfdl-cm20	CM2.0 - AOGCM	Geophysical Fluid Dynamics Laboratory - NOAA	http://www.ipcc-data.org/ar4/model-GFDL-CM2-change.html
gfdl-cm21	CM2.1 - AOGCM	Geophysical Fluid Dynamics Laboratory - NOAA	http://www.ipcc-data.org/ar4/model-GFDL-CM2_1-change.html
giss-modeleh	GISS ModelE-H and GISS ModelE-R (which differ only in ocean	Goddard Institute for Space Studies (GISS) - NASA - USA	http://www.ipcc-data.org/ar4/model-NASA-GISS-EH-change.html

	component)		
giss-modeler	GISS ModelE-H and GISS ModelE-R (which differ only in ocean component)	Goddard Institute for Space Studies (GISS) - NASA - USA	http://www.ipcc-data.org/ar4/model-NASA-GISS-ER-change.html
iap-fgoals10g	FGOALS1.0_g	LASG - Institute of Atmospheric Physics - Chinese Academy of Sciemces - P.O. Box 9804 - Beijing 100029 - P.R. China	http://www.ipcc-data.org/ar4/model-LASG-FGOALS-G1_0-change.html
inm-cm30	INMCM3.0	Institute of Numerical Mathematics - Russian Academy of Science - Russia.	http://www.ipcc-data.org/ar4/model-INM-CM3-change.html
ipsl-cm4	IPSL-CM4	Institut Pierre Simon Laplace (IPSL) - France	http://www.ipcc-data.org/ar4/model-IPSL-CM4-change.html
mpi-echam5	ECHAM5/MPI-OM	Max Planck Institute for Meteorology - Germany	http://www.ipcc-data.org/ar4/model-MPIM-ECHAM5-change.html
mri-cgcm232a	MRI-CGCM2.3.2	Meteorological Research Institute - Japan Meteorological Agency - Japan	http://www.ipcc-data.org/ar4/model-MRI-CGCM2_3_2-change.html
ncar-ccsm30	Community Climate System Model - version 3.0 (CCSM3)	National Center for Atmospheric Research (NCAR) -	http://www.ipcc-data.org/ar4/model-NCAR-CCSM3-change.html
ncar-pcm1	Parallel Climate Model (PCM)	National Center for Atmospheric Research (NCAR) - NSF (a primary sponsor) - DOE (a primary sponsor) - NASA - and NOAA	http://www.ipcc-data.org/ar4/model-NCAR-PCM-change.html
ukmo-hadcm3	HadCM3	Hadley Centre for Climate Prediction and Research - Met Office - United Kingdom	http://www.ipcc-data.org/ar4/model-UKMO-HADCM3-change.html
ukmo-hadgem1	Hadley Centre Global Environmental Model - version 1 (HadGEM1)	Hadley Centre for Climate Prediction and Research - Met Office United Kingdom	http://www.ipcc-data.org/ar4/model-UKMO-HADGEM1-change.html

Table A1-5: Thirty-year climate coverage

Year Represented	30-year climate coverage: Start	End
Current		
1975*	1961	1990
1990	1976	2005
Future		
2015	2001	2030
2025	2011	2040
2035	2021	2050
2045	2031	2060
2055	2041	2070
2065	2051	2080
2075	2061	2090
2085	2071	2100

*used only in perenniality analysis

Table A1-6: Bioclimatic variables

BIO1	Annual Mean Temperature
BIO2	Mean Diurnal Range (Mean of monthly (max temp - min temp))
BIO3	Isothermality (BIO2/BIO7) (* 100)
BIO4	Temperature Seasonality (standard deviation *100)
BIO5	Max Temperature of Warmest Month
BIO6	Min Temperature of Coldest Month
BIO7	Temperature Annual Range (BIO5-BIO6)
BIO8	Mean Temperature of Wettest Quarter
BIO9	Mean Temperature of Driest Quarter
BIO10	Mean Temperature of Warmest Quarter
BIO11	Mean Temperature of Coldest Quarter
BIO12	Annual Precipitation
BIO13	Precipitation of Wettest Month
BIO14	Precipitation of Driest Month
BIO15	Precipitation Seasonality (Coefficient of Variation)
BIO16	Precipitation of Wettest Quarter
BIO17	Precipitation of Driest Quarter
BIO18	Precipitation of Warmest Quarter
BIO19	Precipitation of Coldest Quarter

APPENDIX 2. CLIMATE STABILITY

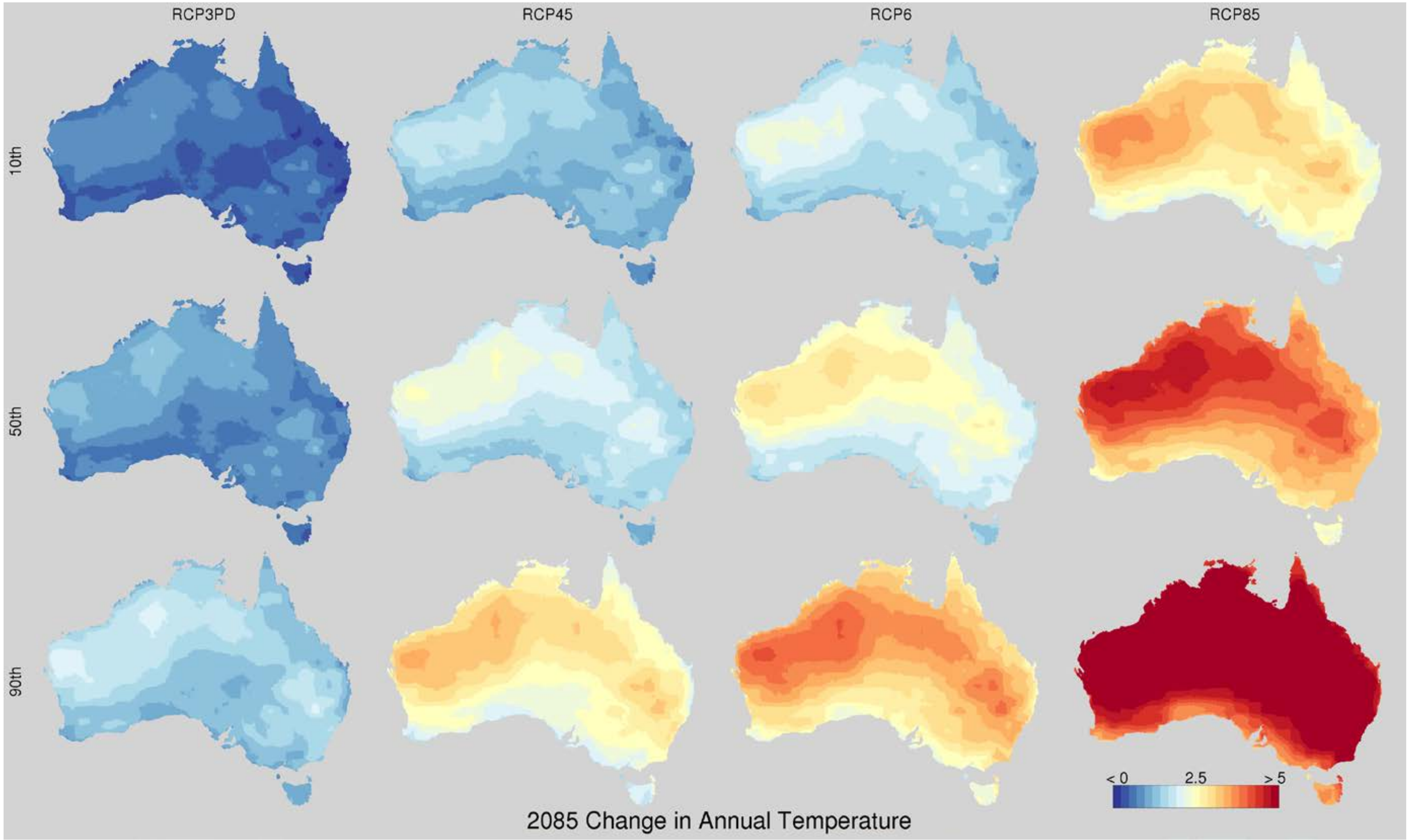


Figure A2-68. Change in temperature (°C) for a 30-year average centred on 2085 relative to a 1990 baseline. Rows represent the 10th, 50th and 90th percentiles across 18 GCMs; columns represent four emission scenarios (RCPs – representative concentration pathways) increasing in greenhouse gas emissions from left to right.

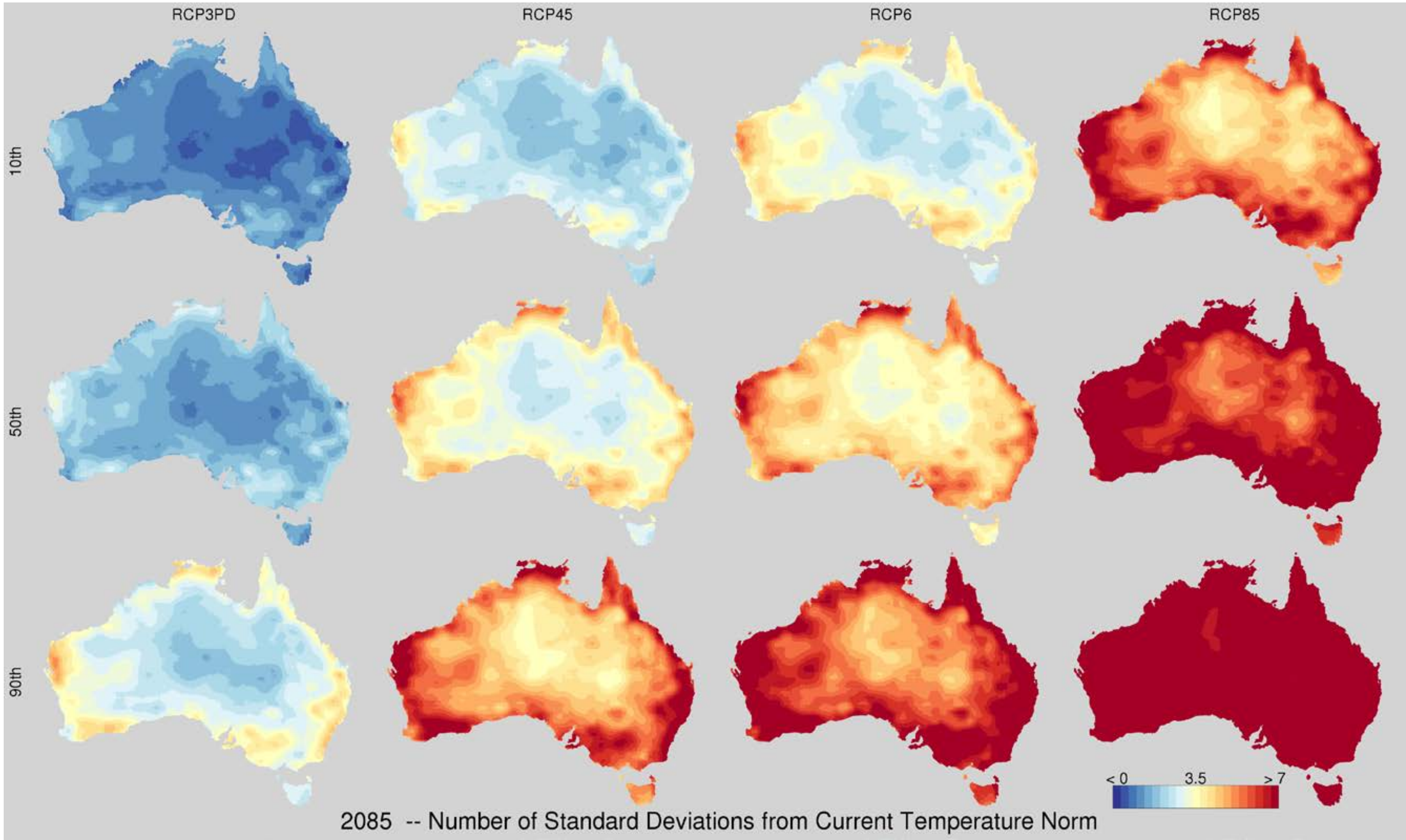


Figure A2-69. The novelty of future climate for 2085 as estimated by the number of standard deviations from the mean (and variance) associated with a 30-year baseline centred on 1990. Rows represent the 10th, 50th and 90th percentiles across 18 GCMs; columns represent four emission scenarios (RCPs – representative concentration pathways) increasing in greenhouse gas emissions from left to right.

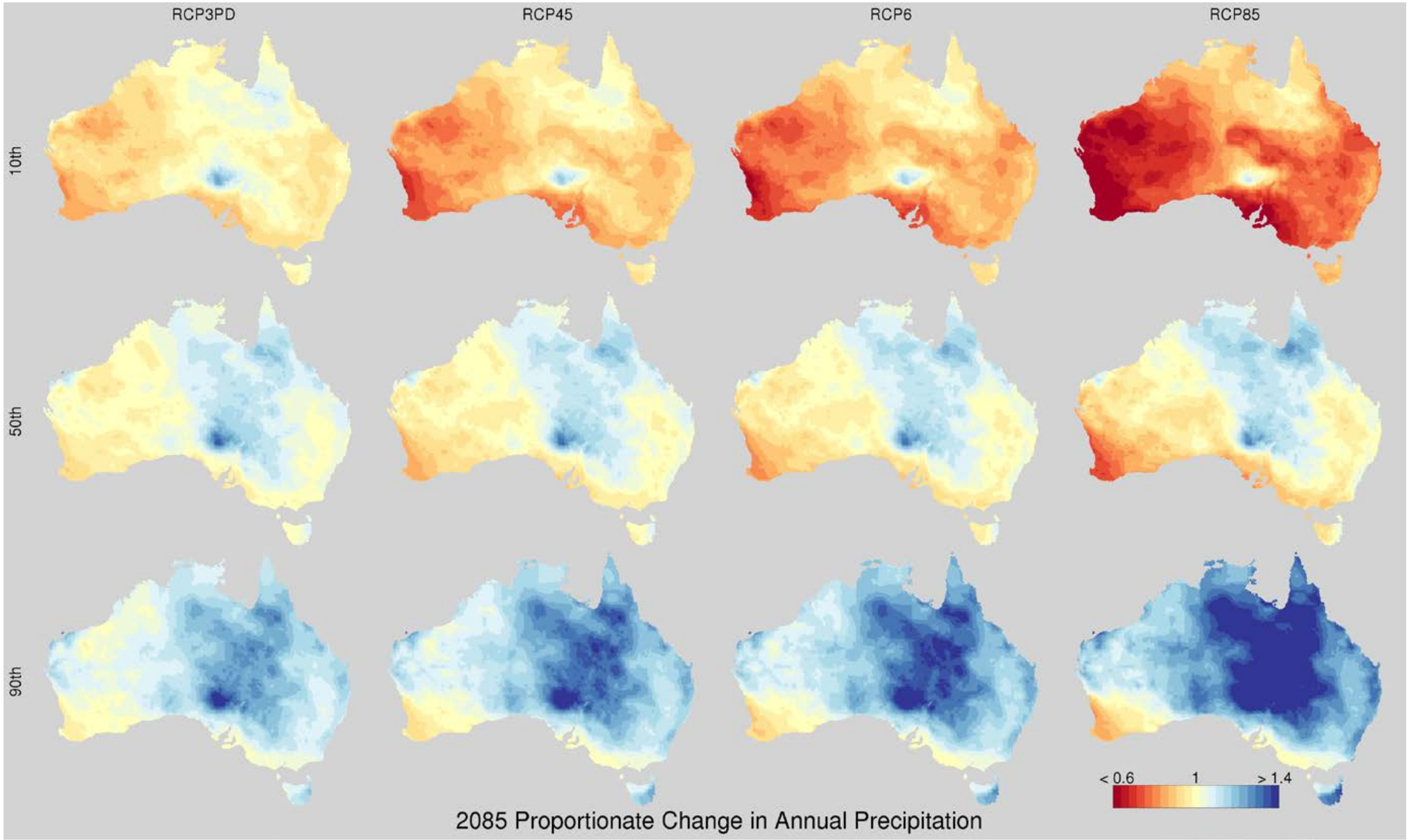


Figure A2-70. Proportionate change in rainfall for a 30-year average centred on 2085 relative to a 1990 baseline. Rows represent the 10th, 50th and 90th percentiles across 18 GCMs; columns represent four emission scenarios (RCPs – representative concentration pathways) increasing in greenhouse gas emissions from left to right.

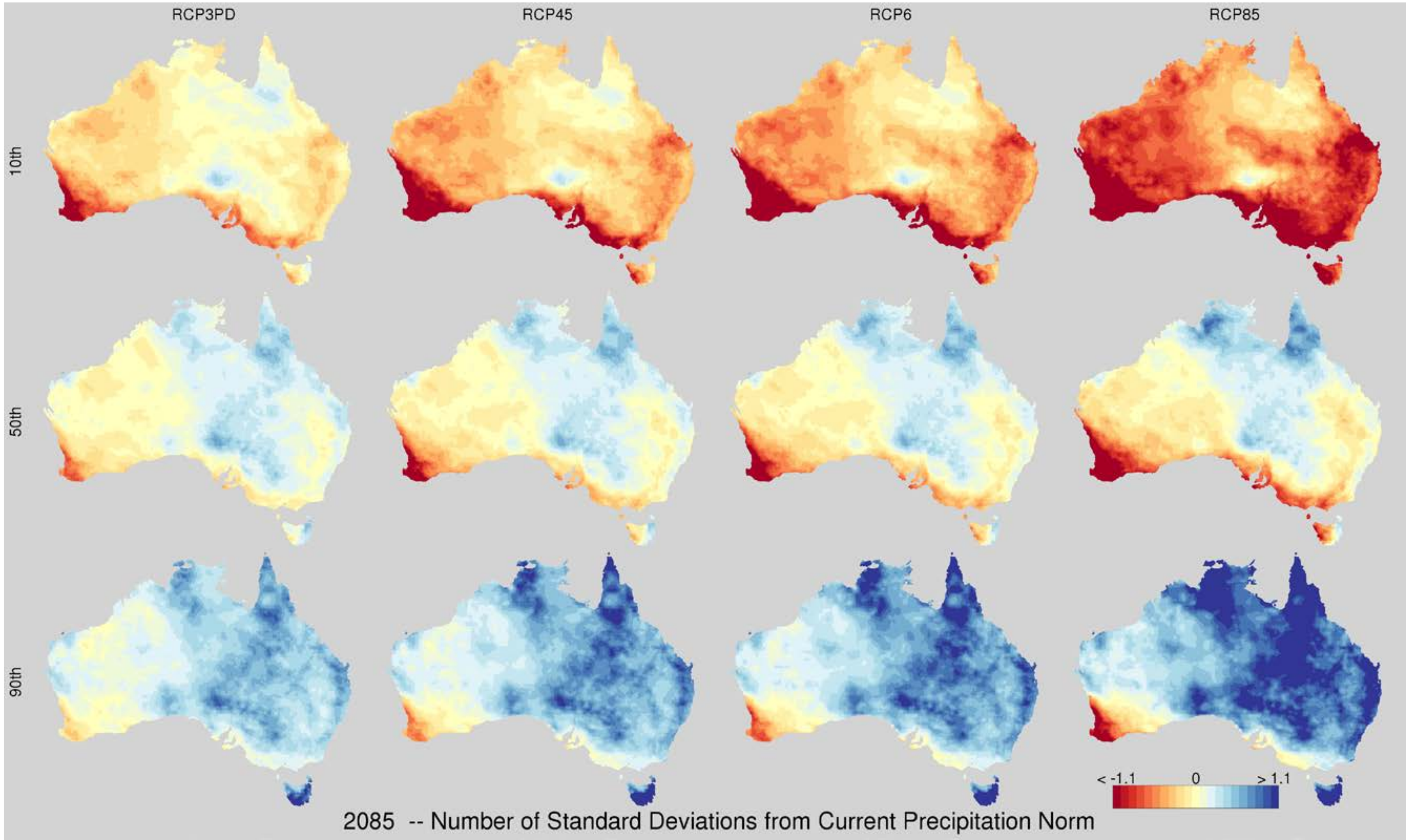


Figure A2-71. The novelty of future climate for 2085 as estimated by the number of standard deviations from the mean (and variance) associated with a 30-year baseline centred on 1990. Rows represent the 10th, 50th and 90th percentiles across 18 GCMs; columns represent four emission scenarios (RCPs – representative concentration pathways) increasing in greenhouse gas emissions from left to right.

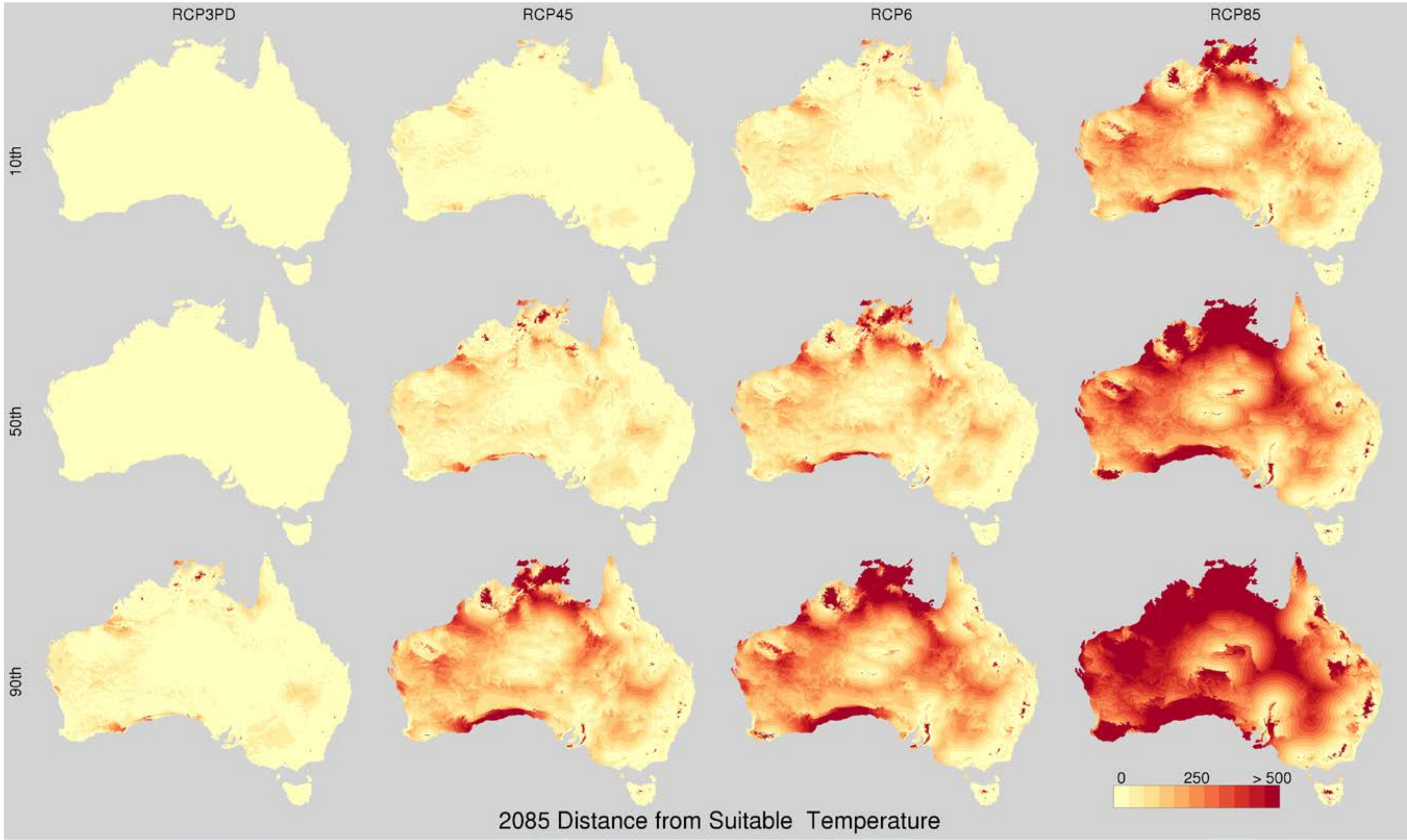


Figure A2-72. The distance an organism would have to travel by 2085 to stay within two standard deviations of the current temperature mean. The distance measure is shown for the 10th, 50th and 90th percentiles across 18 GCMs for each of the four RCPs.

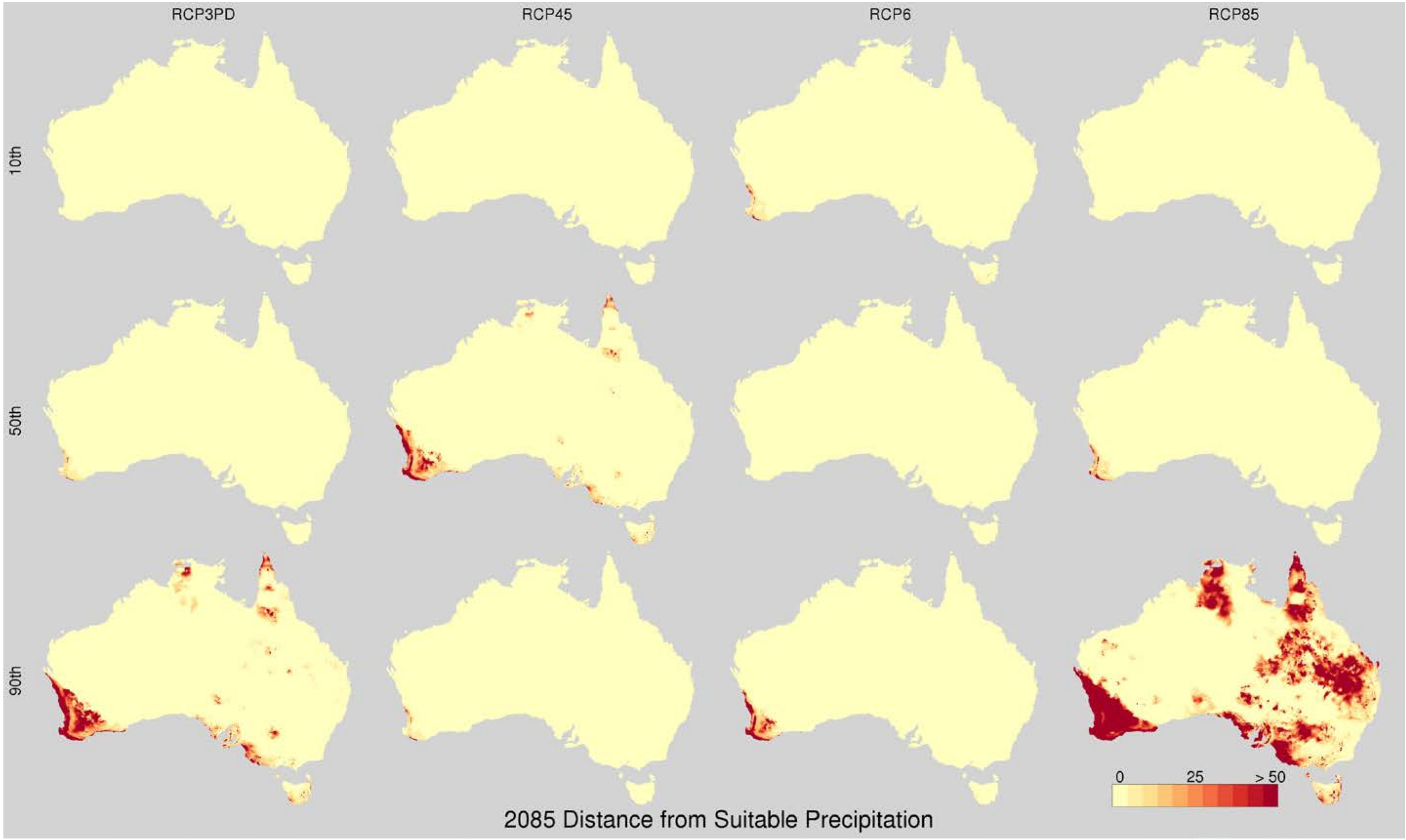


Figure A2-73. The distance an organism would have to travel by 2085 to stay within one standard deviation of the current precipitation mean. The distance measure is shown for the 10th, 50th and 90th percentiles across 18 GCMs for each of the GCMs.

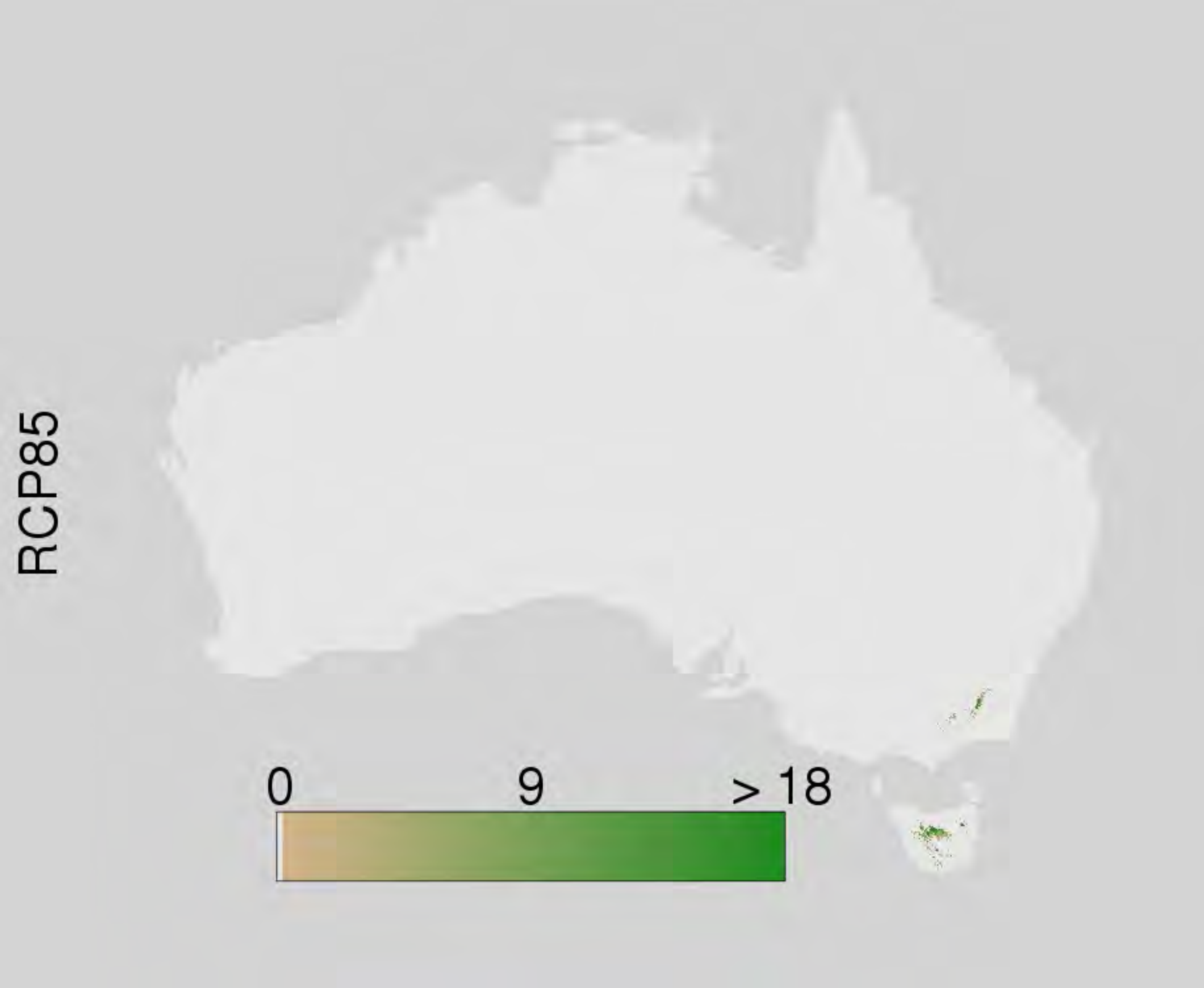


Figure A2-74. The areas for which there is no analogous temperature predicted for 2085, for RCP8.5. Analogous climate was defined as being within two standard deviations of the current temperature mean. The scale bar indicates the number of GCMs that predict a no analogous climate; the green indicates all GCMs show no analogous climate for 2085.

Table A2-7. The area for which there is no analogous temperature predicted for 2085, for RCP8.5. Analogous climate was defined as being within two standard deviations of the current temperature mean. The “No. GCMs” in the left column relates to the number of GCMs for which no analogous climate is identified. Therefore, there is 993 km^2 where each of the 18 GCMs all predict no analogous climate.

No. GCMs	Area km^2
0	7930192
1	711
2	2885
3	658
4	929
5	351
6	470
7	348
8	401
9	451
10	46
11	48
12	92
13	328
14	138
15	542
16	138
17	140
18	993

APPENDIX 3. SPECIES DISTRIBUTION MODELLING DATA AND MODEL RESULTS

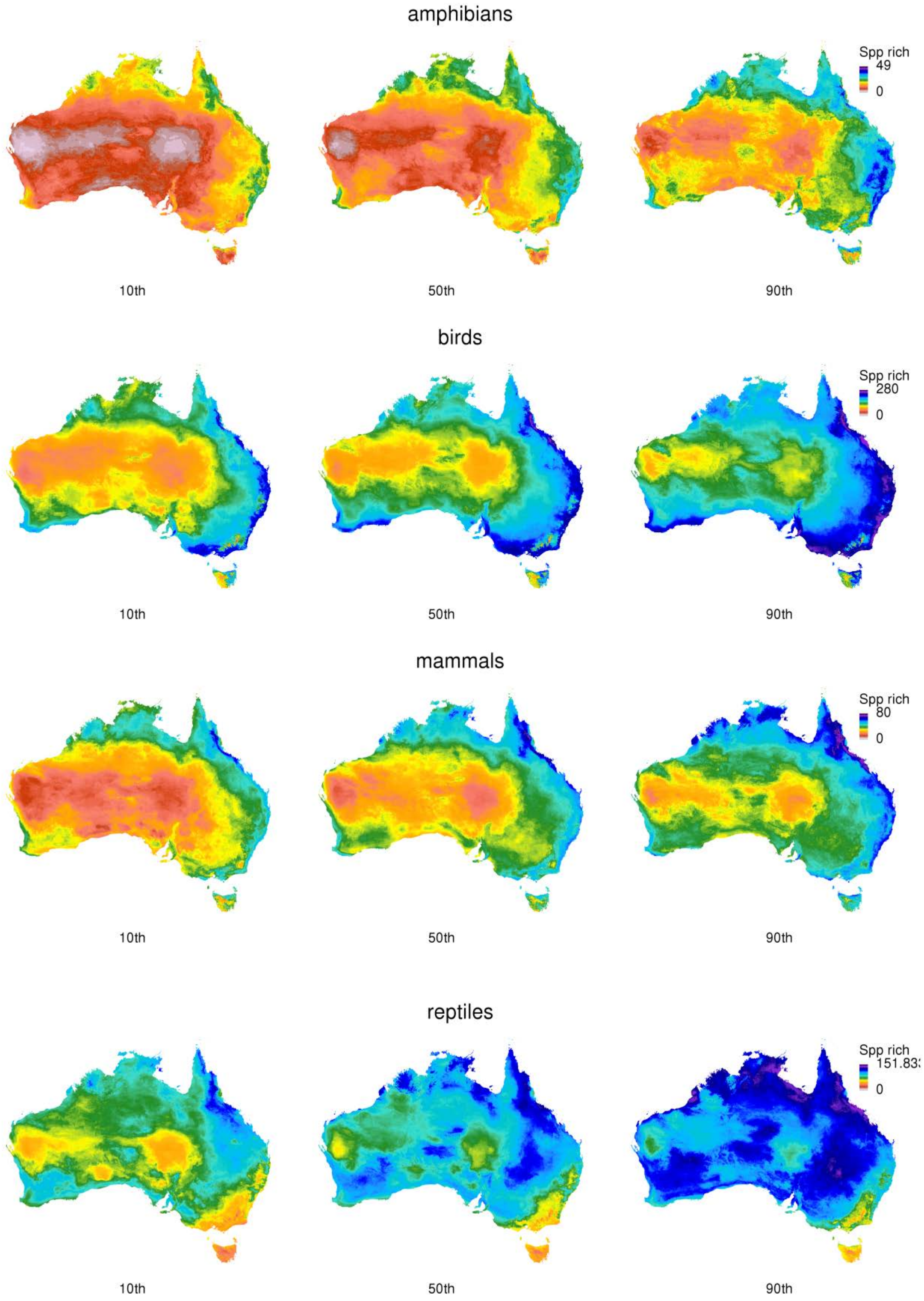


Fig. A3-1. The 10th, 50th (median) and 90th percentiles of species richness of the projected species richness for 2085 across 18 GCMs for each of the taxa.

The lowest change in species richness for each of the four taxa groups added together shows overlaps in areas that change the least (Fig.A3-2). The median shows the areas of low species change being concentrated in the south and east. This is shown more strongly for the 10th percentile across the 18 GCMs.

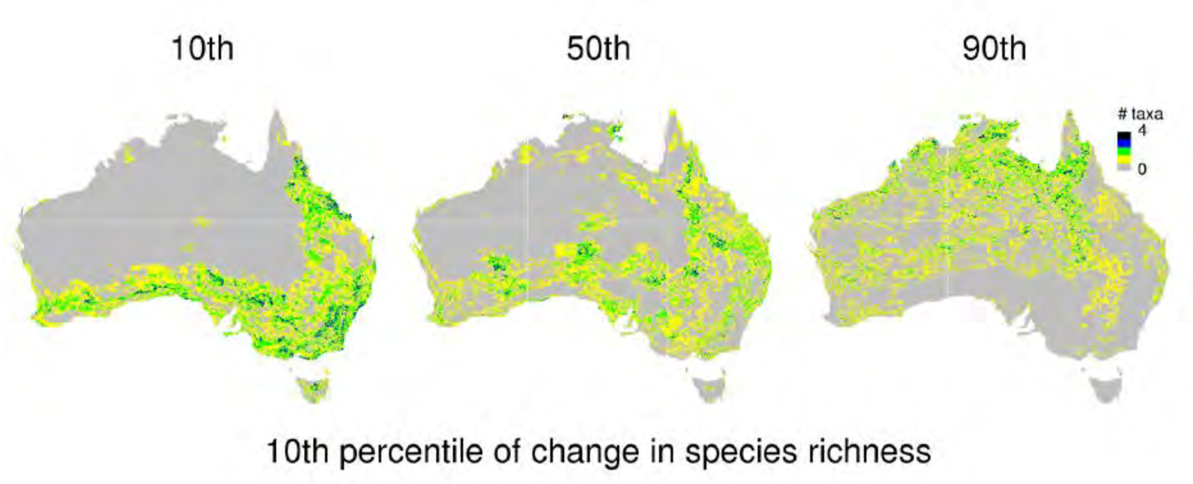
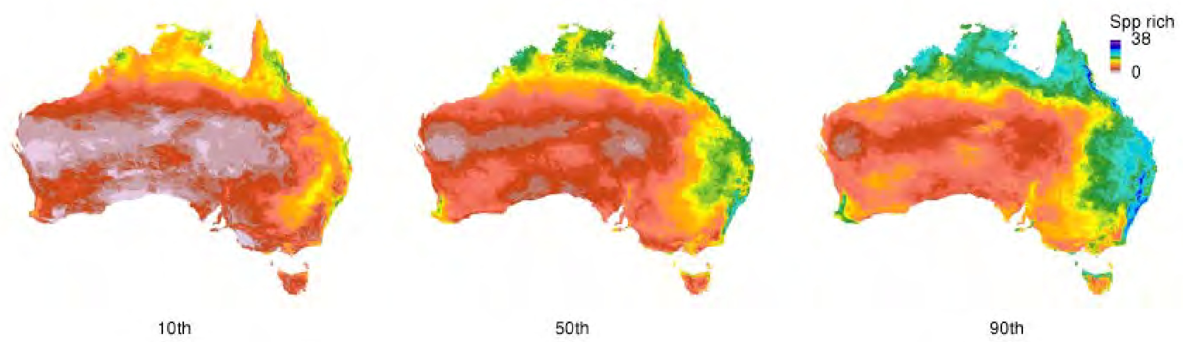


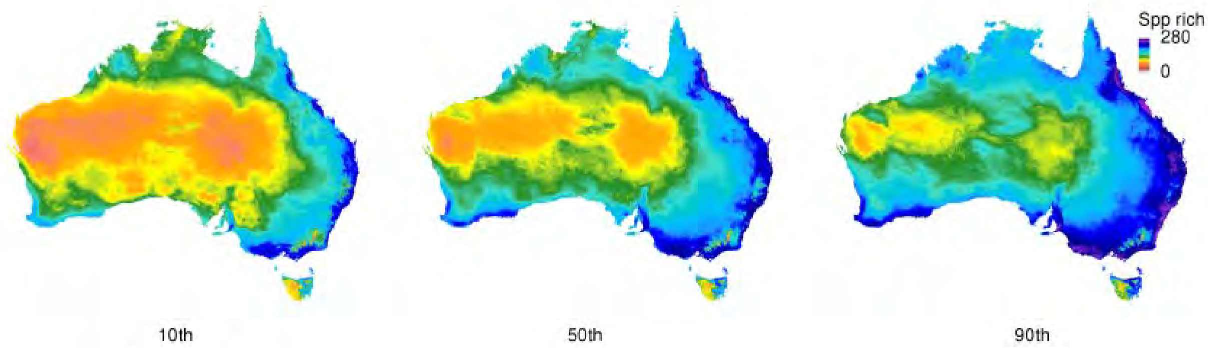
Fig. A3-2. The areas with the lowest change in species richness (10th percentile and below) for each taxa, summed together to show the overlap in areas with low change in species across multiple taxa, for the 10th, 50th and 90th percentiles of species richness across the 18 GCMs. Yellow areas indicate only low change in species richness for one taxa; black indicates areas with low change in species richness for all four taxa.

APPENDIX 4. PROJECTED SPECIES RICHNESS VARIABILITY

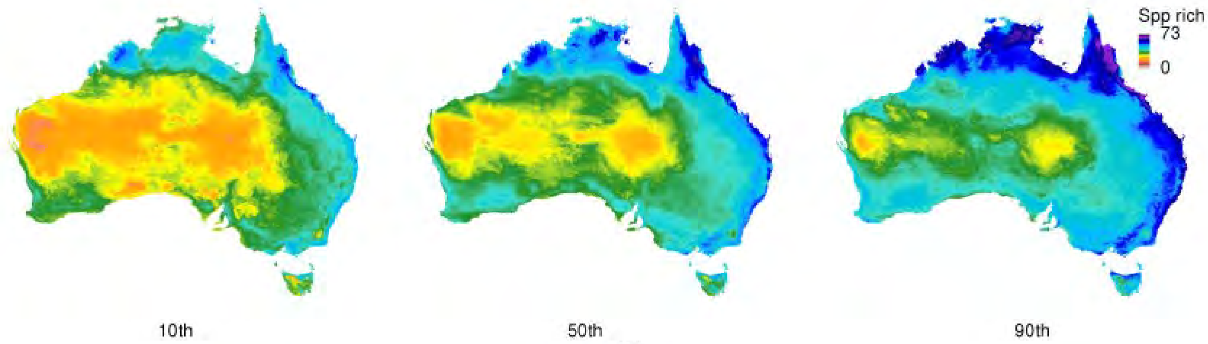
amphibians



birds



mammals



reptiles

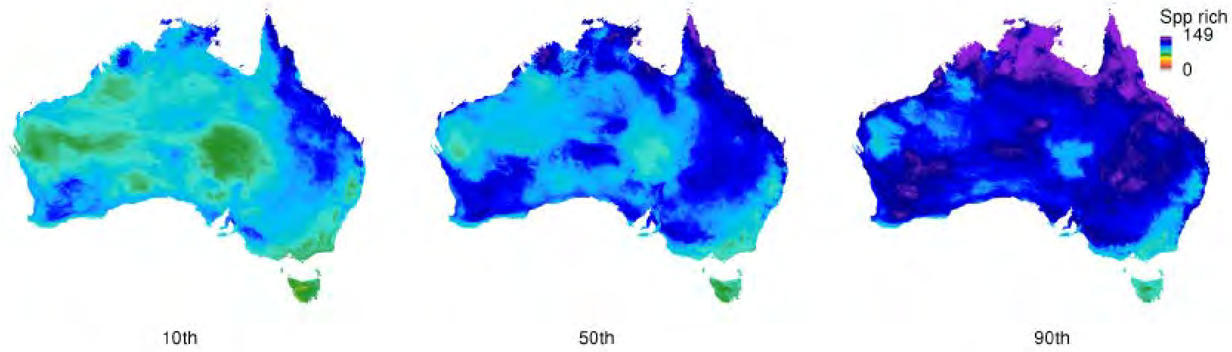
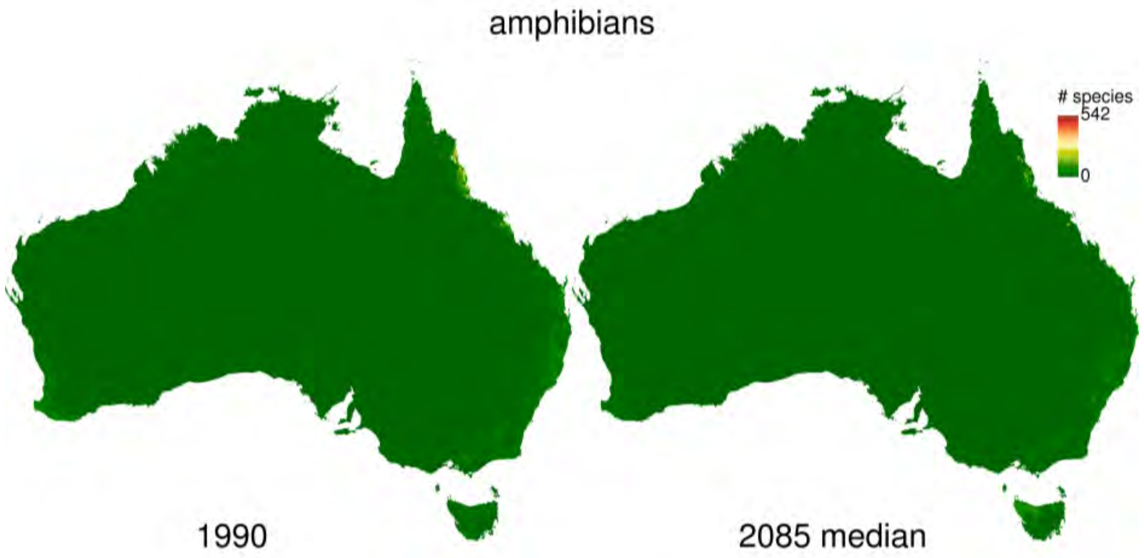


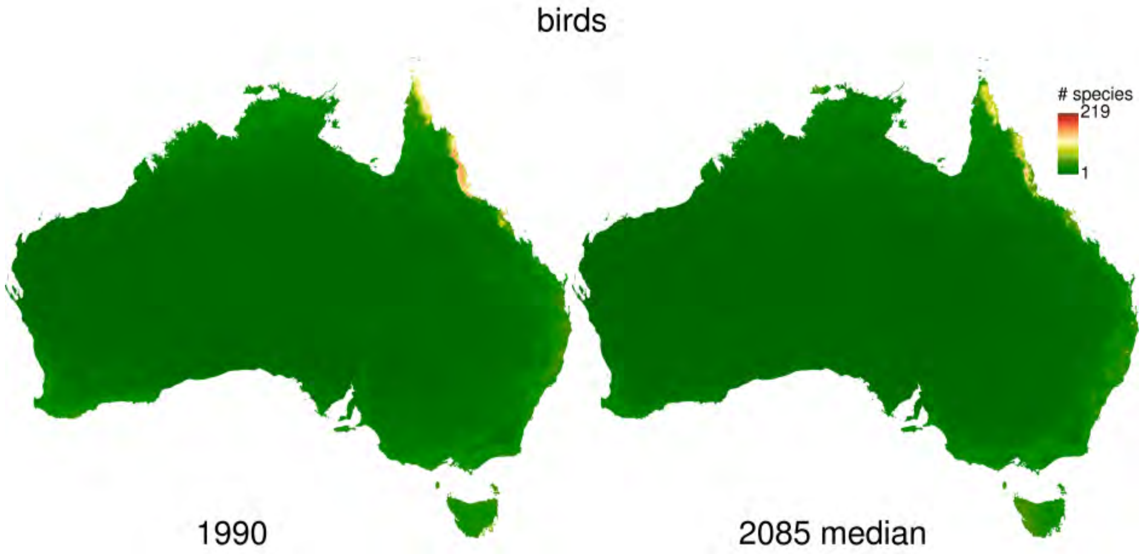
Figure A4-1. The 10th, 50th (median) and 90th percentiles of projected species richness by 2085 for RCP8.5 across 18 GCMs for each of the four vertebrate taxa.

Species Richness scaled by range size

In order to account for the both the number of species in an area but also the relative “endemism” of the species that occur there, a richness measure that was scaled according to species’ range size was calculated. This measure gave greater weighting to small-ranged species (Figure 2). These models show that the largest concentrations of small-ranged species occur within a small margin of the coast, with the highest concentrations occurring in the Wet Tropics, followed by the high elevation areas of the Great Dividing range, Arnhem Land, Cape York Peninsula, Tasmania and south-west Western Australia.

Comparing the 1990 “rangesize richness” to the 2085 version for each taxa shows some shift. The areas of highest concentration of small ranged species, such as the Wet Tropics, are projected to experience a reduction in small-ranged species. However, the tropical savannas may increase in the number of small ranged species, particularly mammals and reptiles.





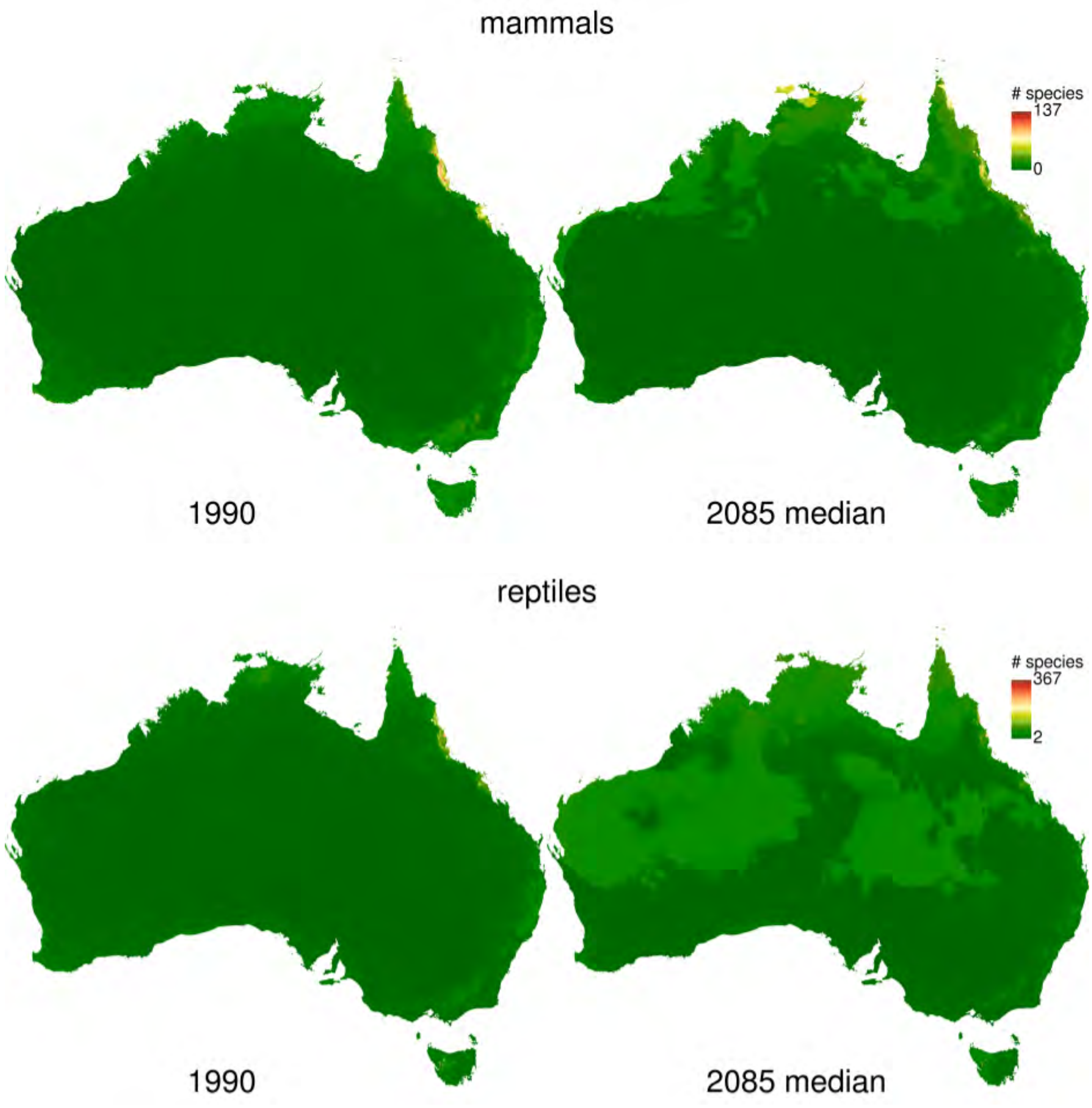


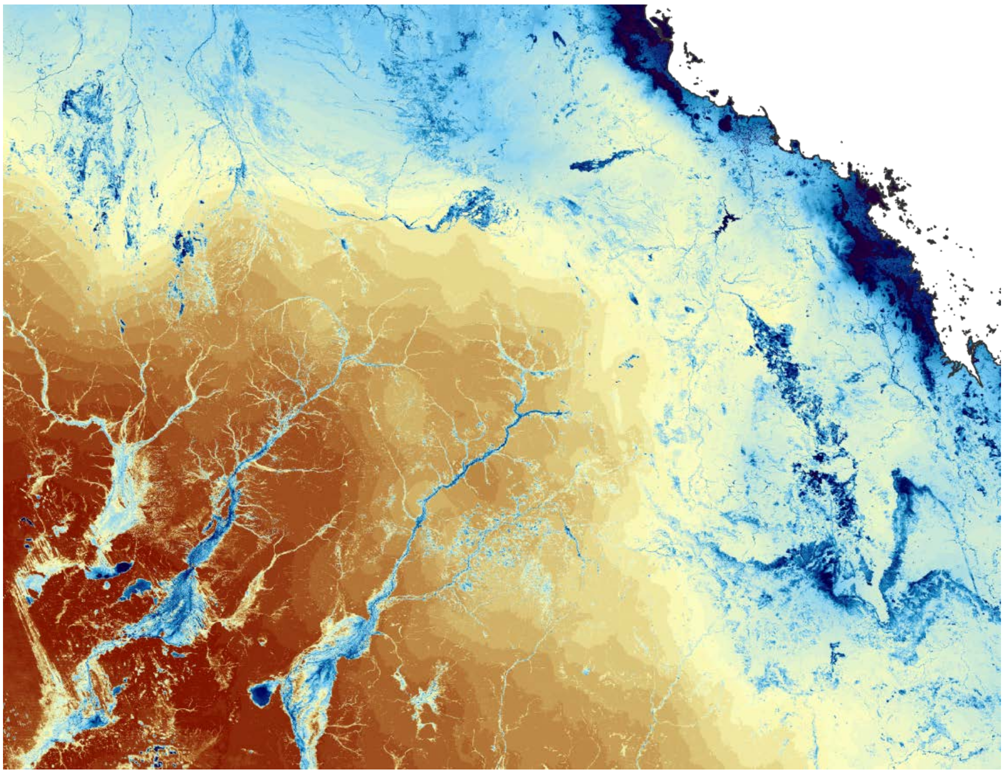
Figure A4-2. The species richness scaled by the range size of each species, so that species with larger ranges get a low score and species with restricted ranges get high scores, shown for the four taxonomic groups, for the 1990 and the median 2085 distributions.

APPENDIX 5. PROJECTING ETA UNDER CLIMATE CHANGE

Projecting remotely derived estimates of actual evapotranspiration (ET_a) under climate change in Australia

CSIRO Climate Adaptation Flagship

Thomas Harwood, Randall Donohue, Tim McVicar, Kristen J Williams, Justin Perry, Jeremy Vanderwal, Cassandra James, Simon Ferrier



Cover image: T. Harwood

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ABSTRACT

Climate change presents a challenge for the management of water resources and for the management of systems dependent on those water resources. In particular, the effect of water flow across and below the ground surface is rarely adequately represented. Our motive was to capture this effect for water limited Australia, to assist with the identification of climate change refugia. We present a new algorithm for the rescaling of actual evapotranspiration (ET_a) under future climate. The algorithm uses standard topographic adjustment of radiation and temperature to spatially rescale remotely sensed ET_a, estimated for current conditions in accordance with the Budyko framework. Calculations were limited by those inputs which could reasonably be derived from Global Circulation Model (GCM) outputs with minimal assumptions. Priestley-Taylor potential evapotranspiration was calculated based on topographically adjusted temperature and radiation, and annual total ET_a was subsequently calculated as the sum of monthly ET_a using the Budkyo framework, incorporating a best estimate of plant available water holding capacity as a tipping bucket. The discrepancy between modelled and remotely derived ET_a under present conditions was used to generate a cell by cell correction along the Budyko curve which was then applied to GCM driven future ET_a. The approach assumes a consistent large scale spatial pattern of surface and ground water movement.

EXECUTIVE SUMMARY

A new method is presented which allows the fine scale (250m) resolution projection of actual evaporation under climate change, by rescaling terrain sensitive modelled outputs based on Global Circulation Model outputs according to the current remotely sensed distribution. The mapped outputs capture the local accumulation of water from surface and sub-surface flow, which is ignored in all downscaled climate projections to date. Since for much of the year, evaporation is water limited for most of Australia, the new projected variable indicates where the wetter parts of the landscape can be found. Under a warmer, drier future climate, this information is likely to be critical to the identification of potential future refugia.

INTRODUCTION

Terrain modifies local conditions above ground, through radiation interception, the channelling of wind and more complex orographic processes. However, there is a further effect of the movement of water across and immediately below the land surface, and through deeper groundwater systems. This may result in large areas such as the Channel Country in SW Queensland in Australia which are apparently decoupled from their local climate. Under climate change, the redistribution of water through altered rainfall and evaporation is likely to have a marked impact on many terrestrial systems. For those systems which are dominated by surface and groundwater flow, the impact of a changing climate cannot be adequately projected in the absence of a treatment of these critical processes. Here we develop an algorithm for the projection of actual evapotranspiration under climate change, taking into account the effects of terrain driven radiative and surface/groundwater modification and apply this algorithm to the Australian continent.

Modelling the effects of terrain on the physical environment can be carried out at a number of scales, with varying degrees of success. Here we rely largely on those aspects of the system which can be reliably estimated from a digital elevation model and the outputs of Global Circulation Models. This rules out a number of relevant processes. Whilst topographic effects on wind can be modelled at the landscape scale this is a computationally expensive process dependent on reliable future wind projections at the broader scale. McVicar *et al* (2008) successfully generated 0.01° wind surfaces for the recent past for Australia, but these do not take into account topographic channelling effects which are likely to be important at finer scales. Whilst a consistent stilling trend was successfully modelled over the past few decades, this cannot reasonably be extrapolated (the logical endpoint being complete stilling), and GCMs provide little, if any, information on wind speed. Wind has a direct effect on evaporation through mass transfer, but if one were to include wind in a full Penman-Monteith evaporation calculation, future input values would be spurious. Whilst the full Penman-Monteith equation is recommended by Donohue *et al* (2010), the authors point to a requirement for future GCM outputs of windspeed and albedo to allow this to be practically realised. Furthermore, the Penman-Monteith equation requires adequate projection of relative humidity. Again this is not a standard GCM output, and calculation of humidity as a function of temperature alone would be misleading. As such the energy driven Priestley-Taylor equation was chosen. This has the added advantage of consistency with the Guershman et al (2009) algorithm used to derive the remotely sensed ET_a surfaces later used for the modification of modelled ET_a.

Most projections of future climate change show a reduction in rainfall across Australia, which combined with elevated temperatures (and therefore potential evaporation) will result in a reduction in available water. Areas which have greater local water availability will remain more similar to the present, and may thus be expected to act as local refugia for the present biota. Identification of these areas, and the extent to which their local water availability interacts with other environmental variables is a critical step in the identification of climate change refugia in an already water limited country. Ecological processes drive turnover in species at very fine scales, with striking differences in composition, for example, on either side of a valley or hill. Under climate change, we expect the development of conditions with no current geographic analogue, and a non-linear response for many physical variables. As such it would be misleading to apply a coarse resolution approach, particularly for sessile organisms which are closely coupled to the climate near the ground.

In a recent advance in remote sensing (Guerschman et al 2009) MODIS satellite data was used to scale potential evaporation, and to map actual evapotranspiration (ET_a) at a 9 second (250m) resolution across the whole continent. The annual total ET_a shows how much water a given location loses to the atmosphere over the course of the year, which is a function of potential evaporation (how much water would evaporate if water was not limiting) and the water available to evaporate, which is a function of both precipitation and the flow of water across, and below the surface, in the subsoil and deeper in the ground and subsequent storage. Importantly, this may also be a function of local vegetation, with, for example, large trees drawing water from deep in the ground and transpiring. However, this is a complex interaction, since the presence of those trees is only possible where sufficient water is present. Under current conditions this approach effectively highlights the local and continental variation in water availability.

RESEARCH ACTIVITIES AND METHODS

Data

Remotely-sensed ETa 1992-2011

The original MODIS derived ET_a estimates Guerschman et al (2009) cover the period from February 2000 to January 2011. These estimates scale Priestley-Taylor ET_p (derived from climate surfaces) using monthly values of the Enhanced Vegetation Index (EVI) and the Global Vegetation Moisture Index (GVMI – both indices are derived from MODIS) to estimate Eta. To produce results at 9s (250m), at the finest MODIS resolution, the other algorithm inputs were oversampled from their original resolutions: 500 m for the MODIS shortwave infrared data and 0.05° (~ 5 km) Priestley-Taylor ETp grids. However, the period of MODIS data is, for Australia, dominated by the long drought at the beginning of the 21st century. Whilst the relative spatial distribution of water may be correct, the absolute values are likely to be low. We therefore extended the time series back to April 1992 using AVHRR derived estimates of Normalised Difference Temperature Index (NDTI, Kalma et al., 2008; McVicar and Jupp, 1999; McVicar and Jupp, 2002) at 0.01° (~ 1 km), for which data were available from April 1992 to December 2005.). The NDTI approach is similar to SEBAL (Bastiaanssen et al., 1998a; Bastiaanssen et al., 1998b), with several key differences: (i) the 'wet' and 'dry' values are objectively modelled as opposed to be subjectively selected by an image analyst; and (ii) changes in meteorological fields as a function of geographic position, as occurs in large extent imagery (e.g., MODIS and AVHRR McVicar and Jupp, 2002, Figure 5), and elevation (e.g., McVicar et al., 2007, Figure 3), are accounted for. There were 71 months of temporal overlap (i.e., February 2000 to December 2005) between the Guerschman et al ET_a and NDTI ET_a series. To minimise the step-change in ET_a per-pixel, regression equations were developed for these 71 months that have been applied to the NDTI ET_a series acquired before February 2000; these resultant images were oversampled to a 250 m spatial resolution in accordance with the MODIS-based ET_a estimates. Monthly and annual (Figure 1) ET_a estimates were then generated for the whole 1992-2011 time period, and used as the yardstick for all subsequent analysis.

Plant available water holding capacity

A 9s grid of plant available water holding capacity was generated by scaling the soil depth variable from the Atlas of Australian Soils (McKenzie et al. 2000, Bureau of Rural Sciences 2000) and soil water holding capacity (Jacquier 2011), by a compound topographic wetness index, using the method developed by (Claridge et al. 2000), which assumes that local variation in soil depth is captured by the topographic wetness index. For the purposes of this analysis, the FD8 multiflow specific catchment area algorithm (Freeman, 1991) was implemented for the 9s DEM (ANU Fenner School, 2008)),and a topographic wetness index derived in Whitebox GAT (Lindsay, 2011). The resultant layer (Figure 2) shows clear state and regional boundary issues as expected from the AAS expert data, but represents a current best estimate.

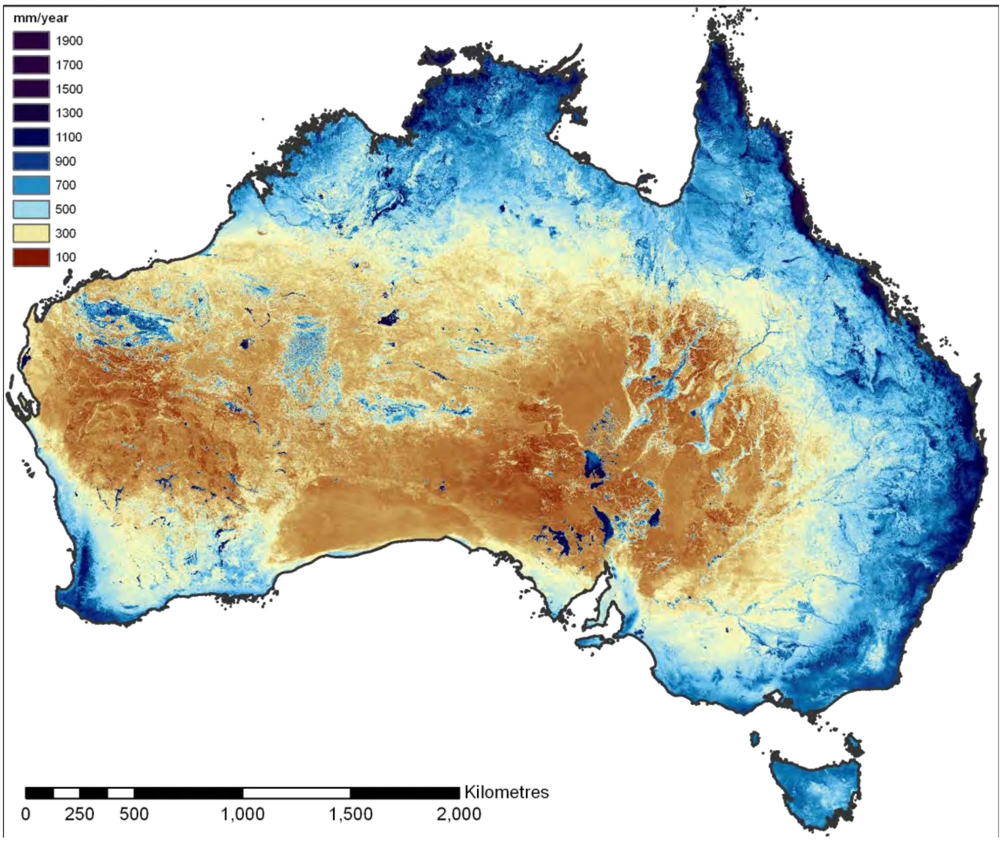

Figure A5-1: Remotely sensed annual *ETa* for Australia 1992-2011.

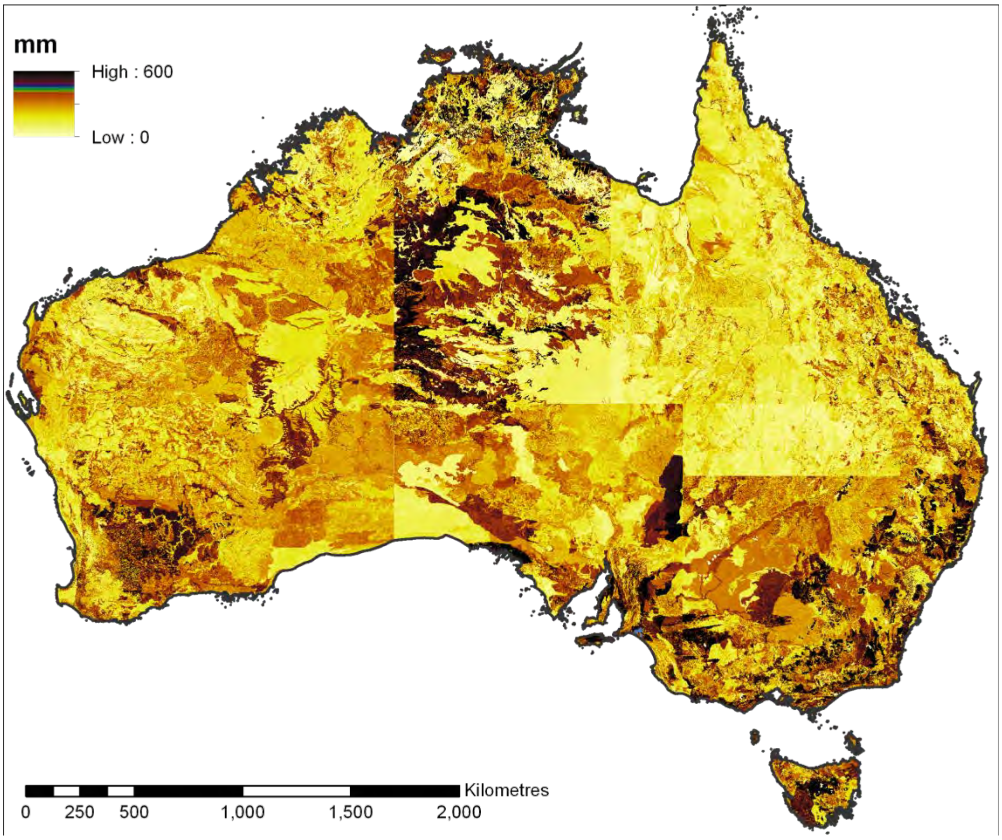

Figure A5-2: 9 second compound topographic index adjusted plant available water holding capacity used as input to the Budyko water balance model

Land Cover

The Geosciences Australia Dynamic Land Cover (DLC) data set was used as the basis for the application of remotely sensed correction of modelled ET_a, where correction was not applied for highly anthropogenically modified areas. This dataset is MODIS time series derived, and consequently compatible with the Guerschman data set. The DLC data is notable for the lack of urban areas, so these were superimposed based on 1: 1000000 scale mapping to avoid misrepresentation. All irrigated crops and urban areas were excluded from the correction. The DLC data was further used to assess the broad variation in modelled and remotely sensed ET_a.

Topographically adjusted climate

Lapse rate adjusted monthly average precipitation and maximum/ minimum temperature grids for the period 1982-2010 were extracted from ANUCLIM 6.1 (Xu & Hutchinson 2011) for current climates based on the 9s DEM (ANU Fenner School, 2008). Future climate surfaces were generated from delta values as described in the main report. The r.sun package in GRASS GIS was used to calculate monthly radiation correction grids which were used as the input to a MTCLIM (Hungerford et al 1989) corrected implementation of the FAO 56 (Allen *et al* 1996) estimation of Priestley-Taylor ET_p (Figure 3). The resultant monthly precipitation and potential evaporation grids were used as the inputs to the Budyko framework model described below.

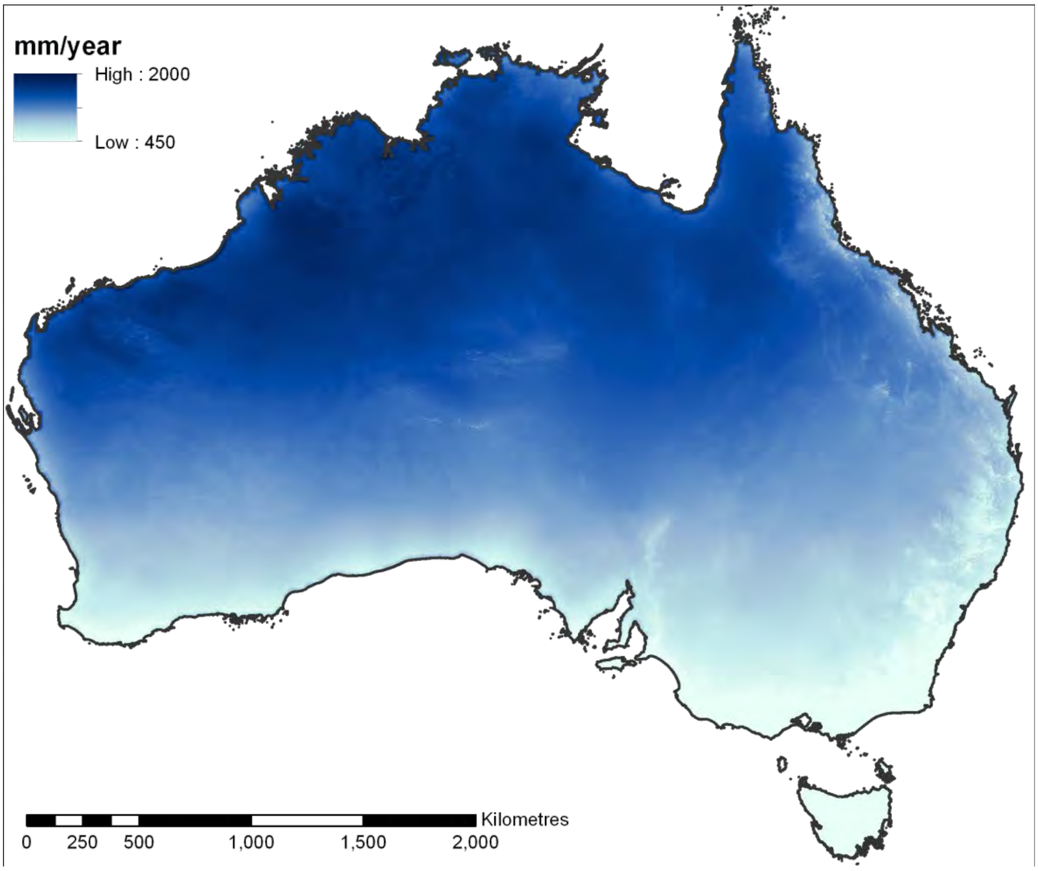

Figure A5-3 Terrain adjusted modelled annual *ETp* for Australia 1982-2010.

Projection of actual evaporation

Actual Evapotranspiration

Actual evapotranspiration was calculated by running a standard Budyko framework (Budyko, 1958, 1974) bucket model according to Pike (1964) and Choudhury (1999), as shown in Equation 1.

$$ET_a = \frac{(V+P).ET_p}{\left[(V+P)^n+ET_p^n\right]^{1/n}} \qquad [1]$$

where actual evapotranspiration ET_a is a function of the total water available to evaporate, (given by monthly precipitation, P and the stored volume V, up to a maximum store size equivalent to the plant available water holding capacity) and the monthly potential evaporation ET_p derived from topographically adjusted climate. A power (n) of 1.9 was selected in line with Donohue *et al* (2011) as appropriate for Australlia, although Choudhury (1999) suggested that higher values (e.g. 2.6) could be appropriate at spatial scales finer than our 9s grid. (The effect of this value was investigated relative to land cover ..Fig.5). The model was initialised with half the total store size, and was run to equilibrium (4 years) for each month, and the monthly totals summed to provide an estimate of annual ET_a. Analysis of seasonal variation between months indicated that failure to capture storage and between cell flow exaggerated seasonality in the northern half of Australia, but the annual distribution was appropriate. Whilst monthly ET_a would be desirable, it was deemed outside the capacity of this simple approach, and subsequent calculations were carried out at the annual scale.

Figure 4 shows the spatial distribution of terrain adjusted modelled annual ET_a for the period 1982-2010. If compared with Figure 1, there are notable discrepancies, largely with regards wetter areas in the remotely sensed ET_a, which this work aims to capture.

Correction of modelled ETa using the Budyko curve

The difference between remotely sensed ETa (Fig.1) and modelled ETa (Fig. 4) was assumed to represent the effects of surface and groundwater flow. The mean values of the two layers (&& and && respectively) are comparable (although this is not surprising since positive and negative deviations tend to cancel each other out). The DLC data set was used to provide a simple assessment of the distribution of the discrepancy between these two layers. Figure 5 shows this discrepancy for two 9s models (n=1.9 and n=2.6) and a coarser resolution 0.05° grid for all DLC land classes with added urban categories. Modelled ET_a falls within 50mm of remotely sensed (observed) values for most land cover categories. As expected, irrigated and highly modified environments and waterbodies cluster to the right hand side (underestimated), although we also observe the presence of closed canopy trees. The overestimated categories are mainly the rarer habitats, with the notable inclusion of wetlands. No pattern was observed which indicated strong bias. Nevertheless, when applying a correction factor, urban and irrigated areas were assumed to be best represented by their modelled or ideal state, and no correction was applied. There was further no clear pattern resulting from the two spatial scales of modelling or different values of n, indicating that the selection of a 9s resolution and n value of 1.9 was reasonable.

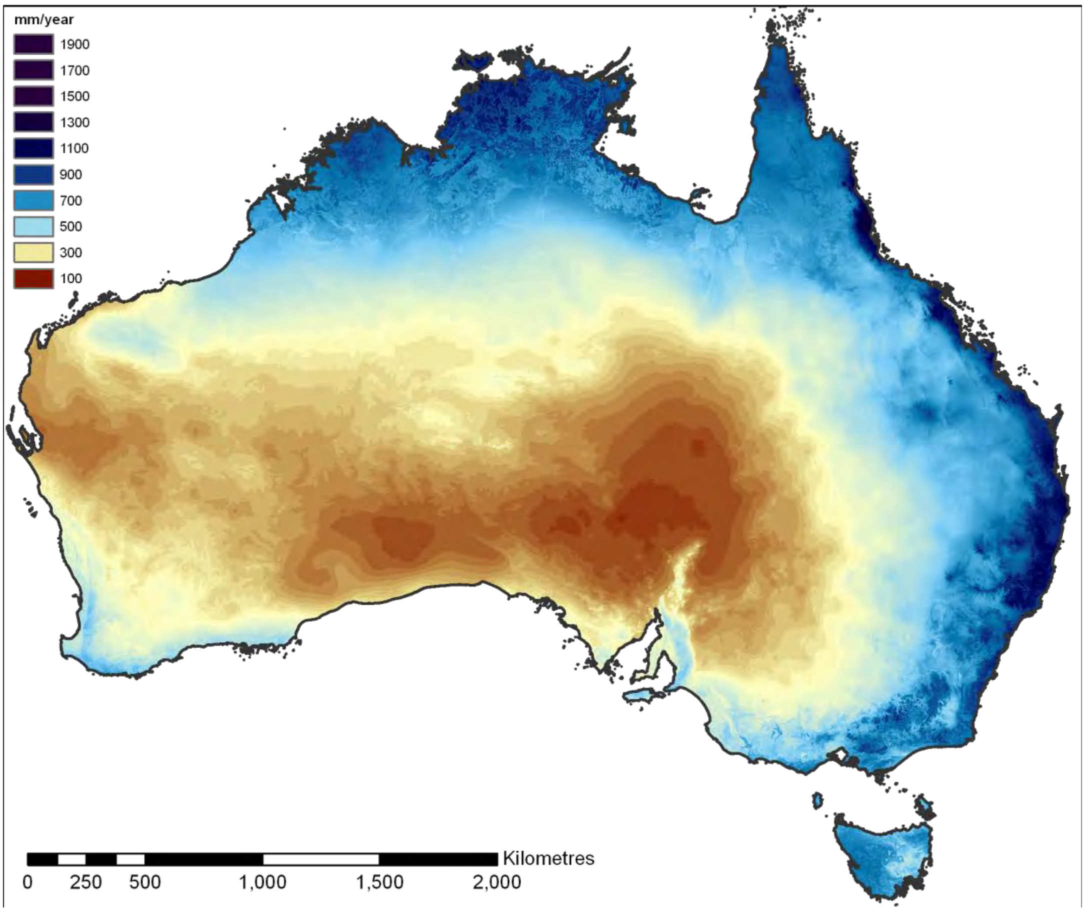

Figure A5-4: Terrain adjusted modelled annual *ETa* for Australia 1982-2010. The map uses the same scale as Figure 1.

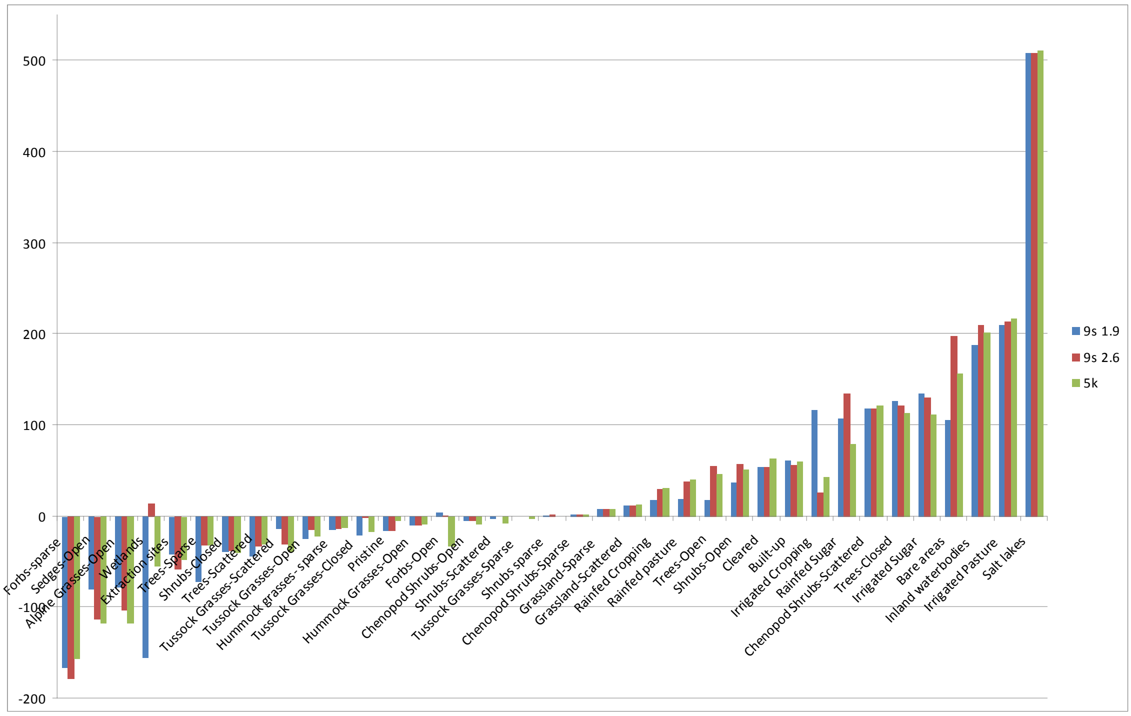

Figure A5-5: Remotely sensed – modelled ET_a (mm/year) by DLC land cover class, for two values of n (1.0 and 2.6) at 9s and n=1.9 at 0.05° resolution.

Rather than directly apply the scaling as an invariant delta value, it was decided that the difference between modelled and remotely sensed ET_a should be applied as an offset on the Φ (P/ET_p) axis on the Budyko curve as shown in Figure 6.

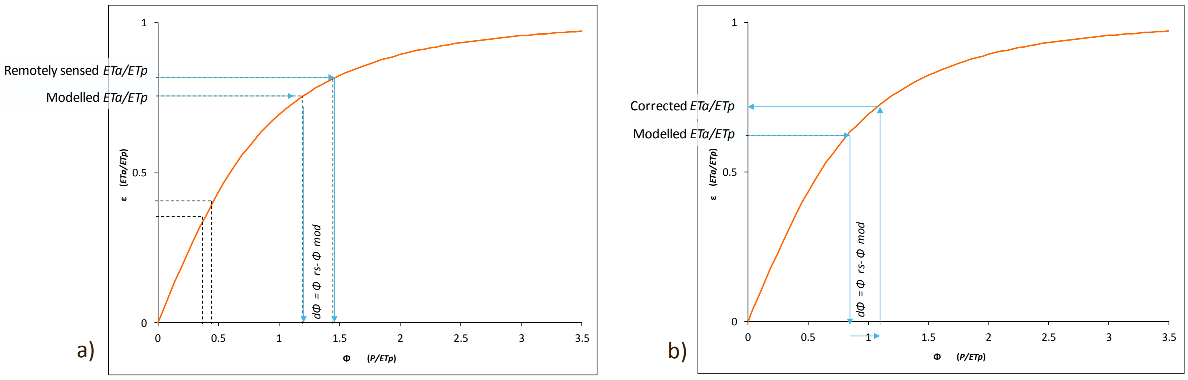

Figure A5-6: Scaling the difference between modelled and remotely sensed actual evapotranspiration using the Budyko framework, a) derivation of the Φ axis offset, using current modelled and remotely sensed data. b) adjustment of future model outputs using the derived offset.

This offset was mapped for all cells, and applied as in Fig.6b to all future cells. Figure 7 shows the spatial distribution of the offset. This map provided a critical input (alongside the Budyko curve to transform the offset back to the ε axis) to the bespoke TerraFormer software used to perform the full terrain downscaling process for future GCM outputs.

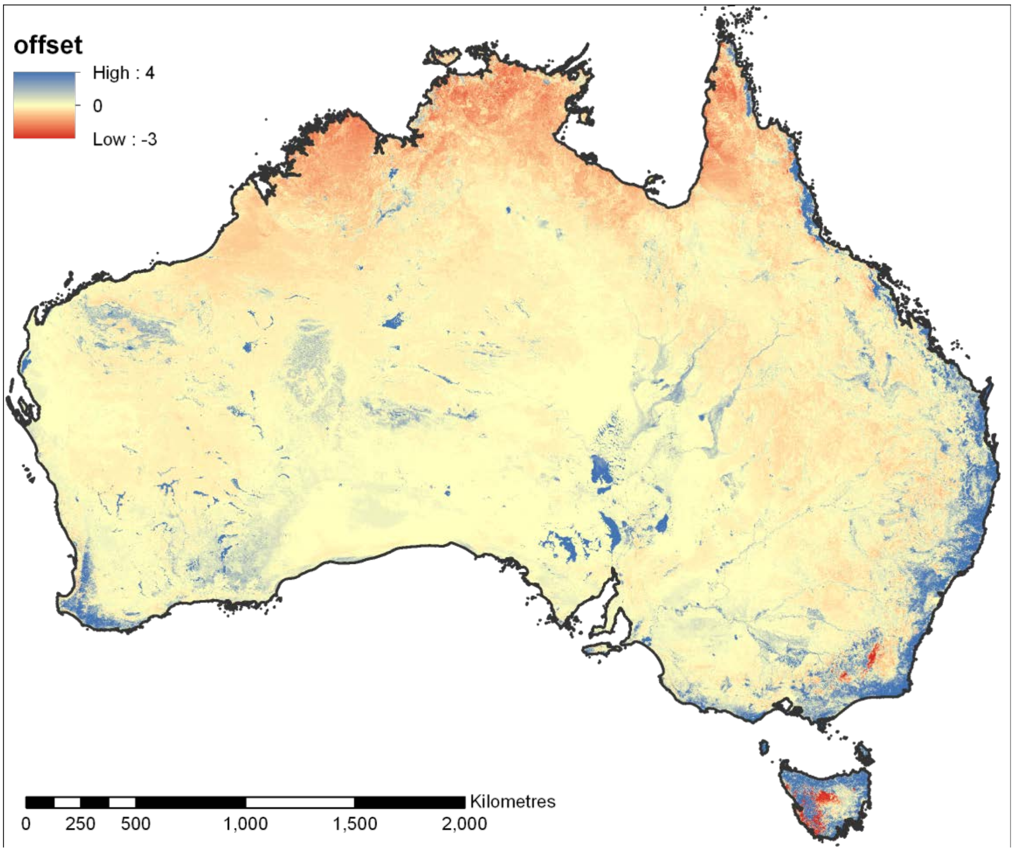

Figure A5-7: Spatial distribution of the Φ (*P/ETp*) axis offset applied to correct future modelled estimates of ET_a.

RESULTS AND OUTPUTS

Figures 8 and 9 show the mapped distribution of ETa in 2085 for the high impact RCP 8.5, for two GCMs, Miroc-H (Hasumi and Emori 2004), representing a wet future, and GFDL-ESM2, (Delworth et al 2006; Gnanadesikan et al, 2006, Wittenberg et al 2006) representing a dryer future. Notably the algorithm predicts little absolute change in total annual ET_a, although spatial distribution varies. It is apparent that many of the topographic features of Figure 1 are preserved, although there is variation in their expression between climate futures.

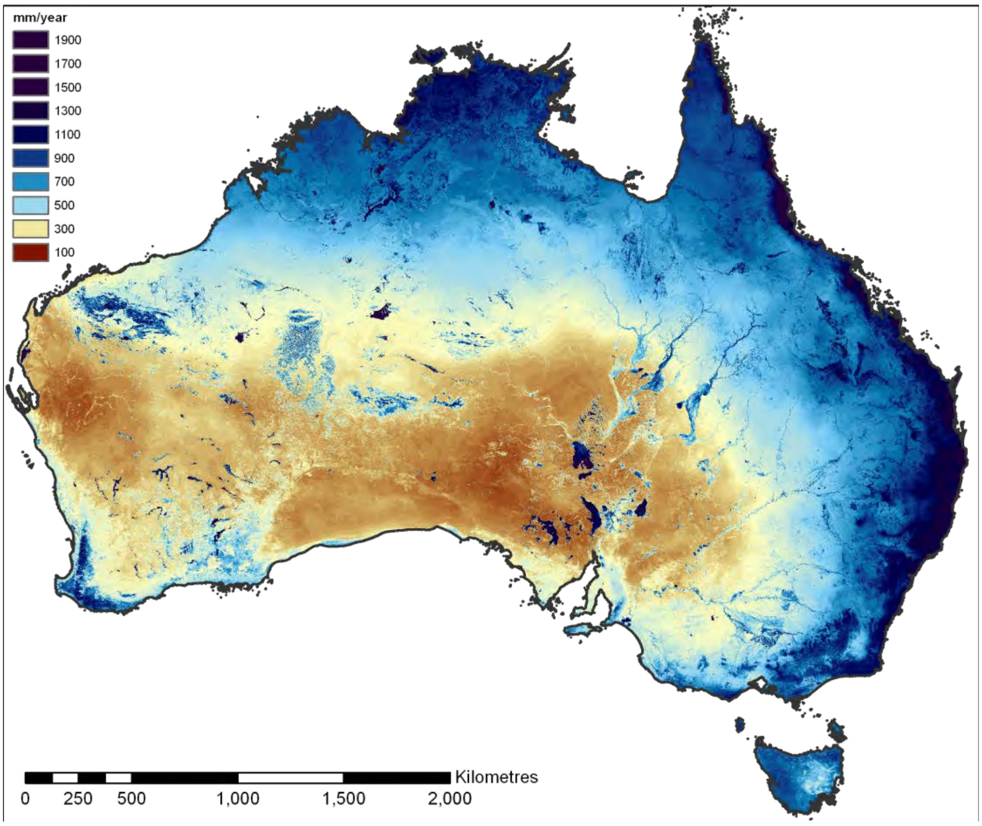

Figure A5-8: Projected ET_a for the "wet" GCM Miroc-h, for 2085, RCP8.5. The map uses the same scale as Figure 1.

Figures 10 and 11 show magnified areas , for the Channel Country and Western Tasmania for the GFDL-ESM2 RCP8.5 climate future, highlighting the topographic resolution of the projected data.

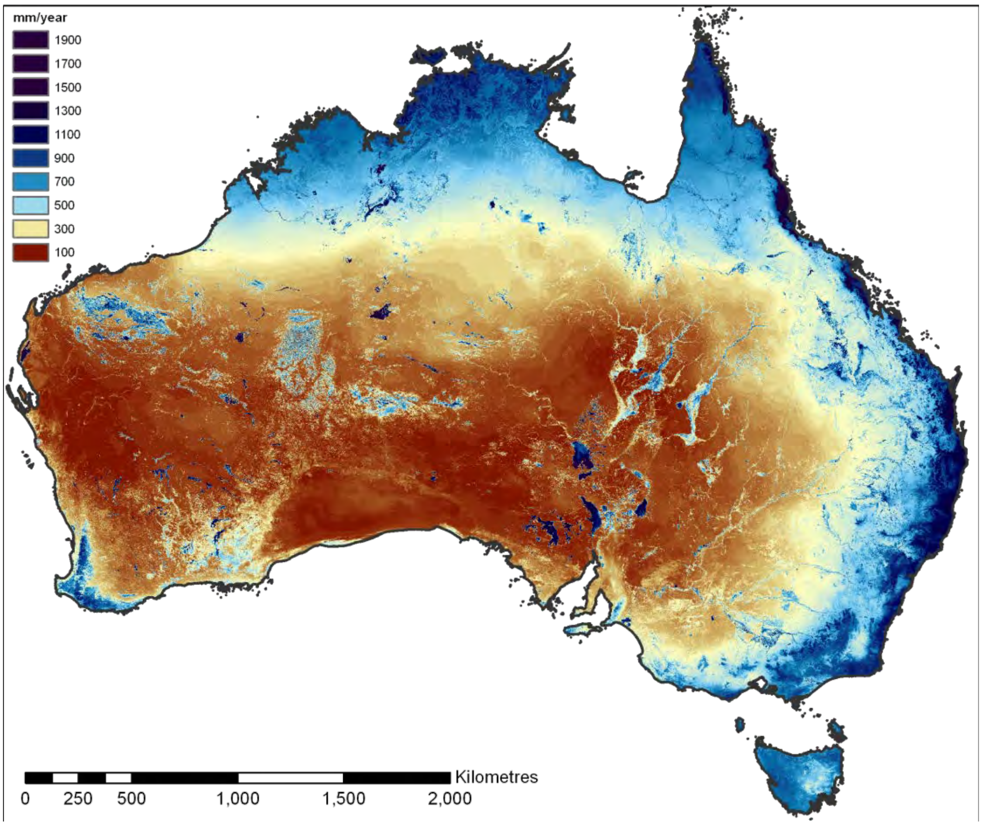

Figure A5-9: Projected ET_a for the “dry” GCM GFDL-ESM2, for 2085, RCP8.5. The map uses the same scale as Figure 1.

DISCUSSION

The novel algorithm delivers an apparently reasonable suite of outputs which address a long ignored feature of the Australian landscape. The topographic variation both in greater ET_a in valley bottoms and on north facing slopes as illustrated in Figure 11 is consistent with theory. Dependency on conveniently available climate and bioclimate variables has led to a history of ecological models which implicitly ignore the flow of water above and below the ground surface. Consequently, most models fail to distinguish ecosystems with inflowing water from those in the surrounding drylands. Whilst this is most obvious for areas such as the Channel Country and the Lake Eyre basin, where the landscape one views from an aeroplane or satellite image is conspicuously absent from ecological models, similar processes occur at all scales across the landscape. Our algorithm and outputs represent a first step to addressing this shortfall, and a critical step on the path to the identification of refugia under climate change.

Nevertheless, these outputs should be critically addressed. Firstly, the use of the Priestley-Taylor algorithm, whilst widespread, is likely to result in evaporation being dominated by temperature effects, and it would be appropriate to move to a parallel full Penman-Monteith approach as the required data becomes available. Secondly, the effects of ground cover require further consideration. Whilst it is an obvious step to exclude wholly anthropogenically modified habitats from the analysis, in many areas there are multiple feedbacks between the abiotic environment and its ecology and land use. Many of the features which appear to be a result of land clearance in Fig.1 also occur on close inspection in Fig.4, indicating that land use may have been driven by

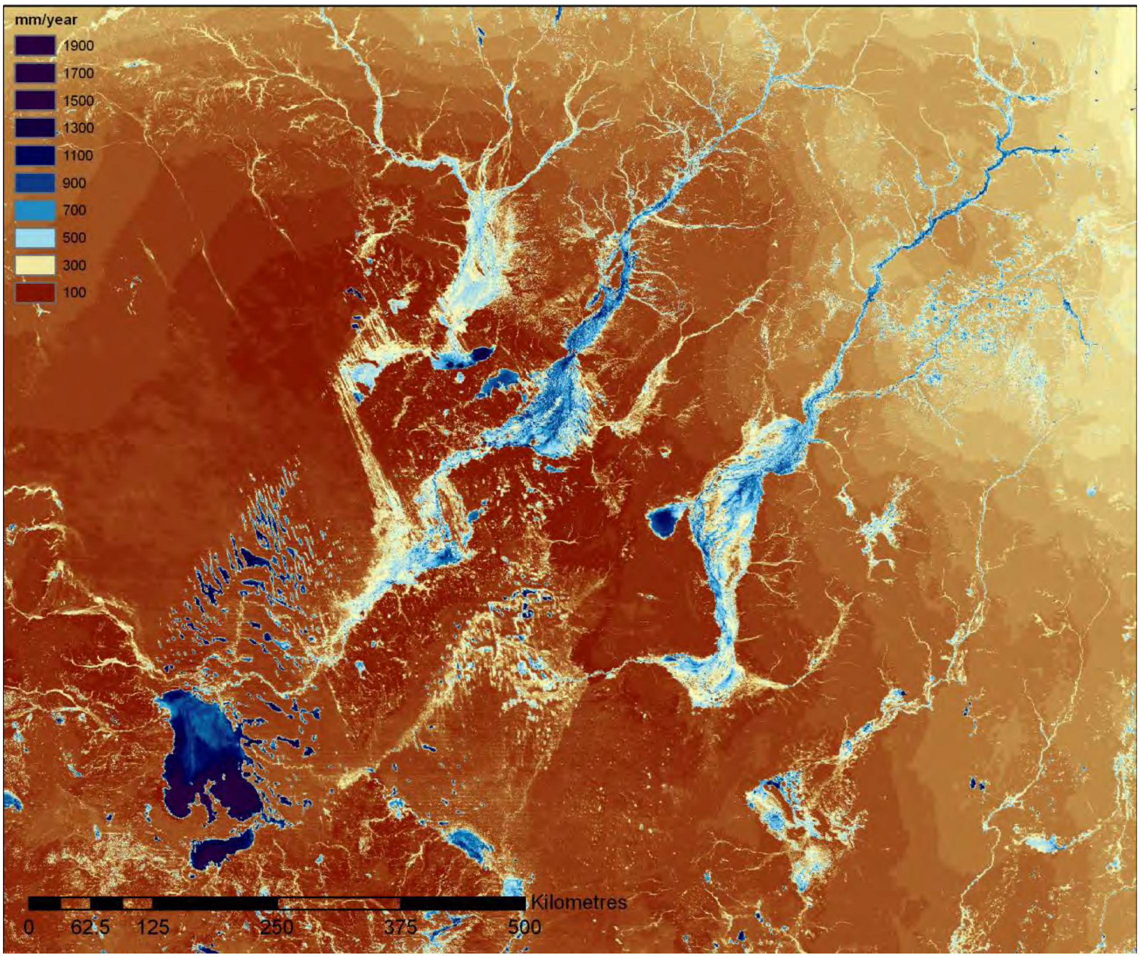

Figure A5-10 Channel Country (SW Queensland). Projected ET_a for the "dry" GCM GFDL-ESM2, for 2085, RCP8.5. The map uses the same scale as Figure 1.

availability of water. Similarly, wetter areas may support a denser canopy, increasing transpiration from the canopy, but decreasing soil surface evaporation. Considering extrapolation of this approach back to pre-human landscapes, it is difficult to see a clear path. Vegetation cover might have changed, but is this a response to or a driver of evaporative change? Figure 5 indicates that this issue may not be of great consequence, but it cannot reasonably be dismissed.

A final issue is the assumption that the broad continental patterns of relative precipitation and flow will remain constant. Whilst this is reasonable over shorter timescales, a shift to a climate with a wetter south and dryer north could bring about significant changes to both surface and artesian water flow.

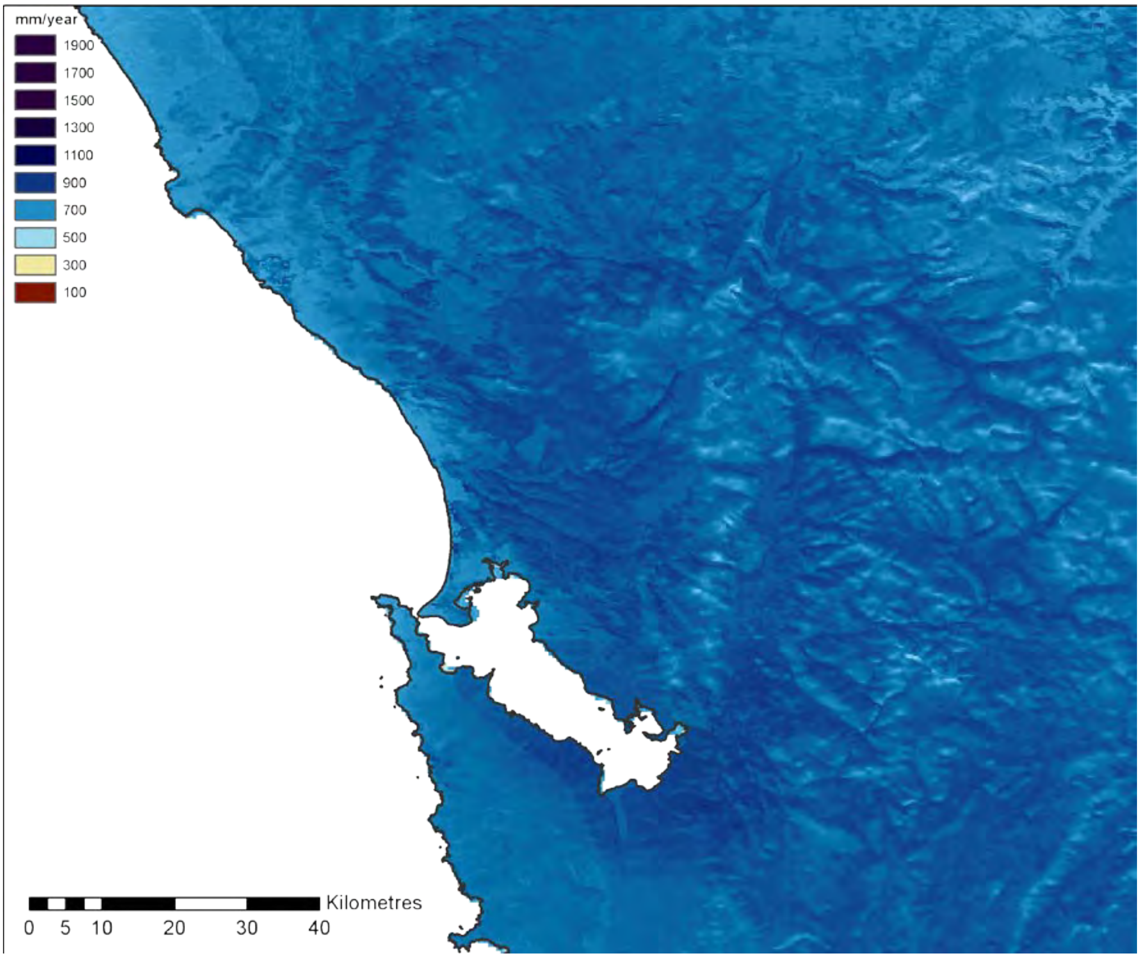

Figure A5-11: Western Tasmania. Projected ET_a for the "dry" GCM GFDL-ESM2, for 2085, RCP8.5. The map uses the same scale as Figure 1.

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APPENDIX 6. ENVIRONMENTAL VARIABLES USED IN GDM MODELLING

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Table A6-1. Candidate environmental variables compiled for use in developing fitted GDM models of species compositional turnover (details given in Appendix 7). Some variables differ in their 9-second and 3-second application.

Group	Short name	Name	Units	Source citation	Grids
Topo-climate	WDI	Atmospheric water deficit (precipitation minus potential evaporation) - monthly minimum	mm	Xu and Hutchinson (2011), Williams *et al.* (2012)	9sec 3sec 1sec
Topo-climate	WDX	Atmospheric water deficit (precipitation minus potential evaporation) - monthly maximum	mm	Xu and Hutchinson (2011), Williams *et al.* (2012)	9sec 3sec 1sec
Topo-climate	WDRX	Atmospheric water deficit seasonality – maximum of differences between successive months	mm/day	Xu and Hutchinson (2011), Williams *et al.* (2012)	9sec 3sec 1sec
Topo-climate	WDRI	Atmospheric water deficit seasonality – minimum of differences between successive months	mm/day	Xu and Hutchinson (2011), Williams *et al.* (2012)	9sec 3sec 1sec
Climate	TNI	Minimum temperature - monthly minimum	°C	Xu and Hutchinson (2011)	9sec 3sec 1sec
Climate	TNX	Minimum temperature - monthly maximum	°C	Xu and Hutchinson (2011), Williams *et al.* (2012)	9sec 3sec 1sec
Climate	TNRX	Temperature - max difference in min between successive months	°C/day	Xu and Hutchinson (2011), Williams *et al.* (2012)	9sec 3sec 1sec
Climate	TNRI	Temperature - min difference in min between successive months	°C/day	Xu and Hutchinson (2011), Williams *et al.* (2012)	9sec 3sec 1sec
Topo-climate	TXI	Maximum temperature - monthly minimum	°C	Xu and Hutchinson (2011), Wilson and Gallant (2000)	9sec 3sec 1sec
Topo-climate	TXX	Maximum temperature - monthly maximum	°C	Xu and Hutchinson (2011), Wilson and Gallant	9sec 3sec 1sec

Group	Short name	Name	Units	Source citation	Grids
				(2000)	
Topo-climate	TXRX	Temperature - max difference in max between successive months	°C/day	Xu and Hutchinson (2011), Wilson and Gallant (2000)	9sec 3sec 1sec
Topo-climate	TXRI	Temperature - min difference in max between successive months	°C/day	Xu and Hutchinson (2011), Wilson and Gallant (2000)	9sec 3sec 1sec
Topo-climate	TRI	Diurnal temperature range - monthly minimum	°C	Xu and Hutchinson (2011), Wilson and Gallant (2000)	9sec 3sec 1sec
Topo-climate	TRX	Diurnal temperature range - monthly maximum	°C	Xu and Hutchinson (2011), Wilson and Gallant (2000)	9sec 3sec 1sec
Climate	TRA	Annual temperature range – TXX – TNI	°C	Xu and Hutchinson (2011), Wilson and Gallant (2000)	9sec 3sec 1sec
Climate	PTI	Precipitation - monthly minimum	mm	Xu and Hutchinson (2011)	9sec 3sec 1sec
Climate	PTX	Precipitation - monthly maximum	mm	Xu and Hutchinson (2011)	9sec 3sec 1sec
Climate	PTRX	Precipitation seasonality – maximum of differences between successive months	mm/day	Xu and Hutchinson (2011), Williams *et al.* (2012)	9sec 3sec 1sec
Climate	PTRI	Precipitation seasonality – minimum of differences between successive months	mm/day	Xu and Hutchinson (2011), Williams *et al.* (2012)	9sec 3sec 1sec
Climate	PTS1MP	Precipitation - solstice seasonality ratio	Ratio	Xu and Hutchinson (2011), Williams *et al.* (2012)	3sec 1sec
Climate	PTS2MP	Precipitation - equinox seasonality ratio	Ratio	Xu and Hutchinson (2011), Williams *et al.* (2012)	3sec 1sec
Climate	PTS1	Precipitation - solstice seasonality composite factor ratio	Ratio	Xu and Hutchinson (2011), Williams	9sec

Group	Short name	Name	Units	Source citation	Grids
				et al. (2012)	
Climate	PTS2	Precipitation - equinox seasonality composite factor ratio	Ratio	Xu and Hutchinson (2011), Williams *et al.* (2012)	9sec
Topo-climate	EPI	Potential (pan) Evaporation - monthly minimum	mm	Xu and Hutchinson (2011), Wilson and Gallant (2000)	3sec
Topo-climate	EPX	Potential (pan) Evaporation - monthly maximum	mm	Xu and Hutchinson (2011), Wilson and Gallant (2000)	3sec
Topo-climate	EAA	Annual total actual evapotranspiration terrain scaled using MODIS	Mm	Guerschman *et al.* (2009)	9sec
Topo-climate	EAAS	Annual total actual evapotranspiration modelled using terrain-scaled water holding capacity	Mm	Appendix 5	9sec
Topo-climate	EAAnn	Annual total actual evapotranspiration modelled using terrain-scaled water holding capacity adjusted for negative values	mm	Appendix 5	9sec
Topo-climate	RAI	Solar radiation (rainfall-cloudiness modified) - monthly minimum	MJ/m^2/day	Xu and Hutchinson (2011), Wilson and Gallant (2000)	3sec
Topo-climate	RAX	Solar radiation (rainfall-cloudiness modified) - monthly maximum	MJ/m^2/day	Xu and Hutchinson (2011), Wilson and Gallant (2000)	3sec
Topo-climate	RSI	Short-wave solar radiation - monthly minimum (cloud influenced)	MJ/m^2/day	Wilson and Gallant (2000)	9sec 1sec
Topo-climate	RSX	Short-wave solar radiation - monthly maximum (cloud influenced)	MJ/m^2/day	Wilson and Gallant (2000)	9sec 1sec
Topo-climate	RHI	Relative Humidity - monthly minimum	%	Xu and Hutchinson (2011), Wilson and Gallant (2000)	3sec
Topo-climate	RHX	Relative Humidity - monthly maximum	%	Xu and Hutchinson (2011), Wilson	3sec

Group	Short name	Name	Units	Source citation	Grids
				and Gallant (2000)	
Regolith	MAG	Magnetic anomalies	nanoTesla, nT	Milligan (2010)	9sec 3sec 1sec
Regolith	GRAV	Bouger gravity anomalies	Gal	Geoscience Australia (2009)	9sec 3sec 1sec
Regolith	DOSE PCTK PPMTH PPMU RATIO_TK RATIO_U2T RATIO_UK RATIO_UT TOTALDOSE	Various radiometric indices	ppm radiation	(Geoscience Australia, 2010, Minty *et al.*, 2009)	1sec
Regolith	WII	Weathering intensity index	Index	Wilford (2012)	9sec 3sec 1sec
Regolith	BD30	soils - bulk density in top 30cm from ASRIS best composite mapping	Mg/m^3	Jacquier (2011b)	9sec 3sec 1sec
Regolith	CLAY30	soils - clay fraction in top 30cm from ASRIS best composite mapping	%	Jacquier (2011c)	9sec 3sec 1sec
Regolith	PAWC1M	soils - plant available water holding capacity 0-1m from ASRIS best composite mapping	mm	Jacquier (2011a)	9sec 3sec 1sec
Regolith	HSTRUCT	Hydrological scoring of pedality	Index	(Bureau of Rural Sciences, 2000, McKenzie *et al.*, 2000, Onweremadu *et al.*, 2007, Williams *et al.*, 2012)	9sec
Regolith	COARSE	Soils dominated by coarse fragments	%	(Bureau of Rural Sciences, 2000, McKenzie *et al.*, 2000)	9sec
Regolith	KSAT	Solum average median horizon saturated hydraulic Conductivity	mm/h	(Bureau of Rural Sciences, 2000, McKenzie *et al.*, 2000)	9sec
Regolith	CALCRETE	Calcrete in or below soil profile	Presence	(Bureau of Rural Sciences, 2000, McKenzie *et al.*, 2000)	9sec
Regolith	GEOLMGE	Mean geological age	Millions of years BP	(Laurie *et al.*, 2008, Raymond, 2009, Williams *et*	9sec

Group	Short name	Name	Units	Source citation	Grids
				al., 2012)	
Regolith	GEOLRGE	Range in geological age	Millions of years BP	(Laurie *et al.*, 2008, Raymond, 2009, Williams *et al.*, 2012)	9sec
Regolith	FERT	Inherent rock fertility	Index	(De Vries, 2009, Raymond, 2009)	9sec
Regolith	PC1_20	Spectra of surficial topsoils 0-20cm – Principal component 1	Index	Viscarra-Rossel and Chen (2011)	9sec 3sec 1sec
Regolith	PC2_20	Spectra of surficial topsoils 0-20cm – Principal component 2	Index	Viscarra-Rossel and Chen (2011)	9sec 3sec 1sec
Regolith	PC3_20	Spectra of surficial topsoils 0-20cm – Principal component 3	Index	Viscarra-Rossel and Chen (2011)	9sec 3sec 1sec
Regolith	PC1_80	Spectra of surficial subsoils 60-80cm – Principal component 1	Index	Viscarra-Rossel and Chen (2011)	9sec 3sec 1sec
Regolith	PC2_80	Spectra of surficial subsoils 60-80cm – Principal component 2	Index	(Viscarra-Rossel & Chen, 2011)	9sec 3sec 1sec
Regolith	PC3_80	Spectra of surficial subsoils 60-80cm – Principal component 3	index	(Viscarra-Rossel & Chen, 2011)	9sec 3sec 1sec
Regolith	ILL20	relative abundance of illite clay minerals in surficial topsoil (0-20cm)	Proportion	Viscarra Rossel (2011)	9sec 3sec 1sec
Regolith	KAO20	relative abundance of kaolinite clay minerals in surficial topsoil (0-20cm)	Proportion	Viscarra Rossel (2011)	9sec 3sec 1sec
Regolith	SME20	relative abundance of smectite clay minerals in surficial topsoil (0-20cm)	proportion	Viscarra Rossel (2011)	9sec 3sec 1sec
Regolith	ILL80	relative abundance of illite clay minerals in surficial subsoil (60-80cm)	proportion	Viscarra Rossel (2011)	9sec 3sec 1sec
Regolith	KAO80	relative abundance of kaolinite clay minerals in surficial subsoil (60-80cm)	proportion	Viscarra Rossel (2011)	9sec 3sec 1sec
Regolith	SME80	relative abundance of smectite clay minerals in surficial subsoil (60-80cm)	proportion	Viscarra Rossel (2011)	9sec 3sec 1sec
Regolith	CTIDEPTH	Soil depth in metres derived from a topographic wetness index scaled by map unit soil depth range	Metres	KJW unpublished, Claridge *et al.* (2000), (Bureau of Rural Sciences, 2000, McKenzie *et al.*, 2000, Western &	9sec 3sec 1sec

Group	Short name	Name	Units	Source citation	Grids
				McKenzie, 2004)	
Regolith	CTIPAWC	Soil water holding capacity in mm derived from a topographic wetness index scaled by map unit soil depth range and water holding capacity	mm	KJW unpublished, Claridge *et al.* (2000), Jacquier (2011a), (Bureau of Rural Sciences, 2000, Western & McKenzie, 2004)	9sec 3sec 1sec
Landform	MRVBF	Multiresolution valley bottom flatness index class	Index	Gallant and Austin (2012a), Gallant and Dowling (2003)	9sec 3sec 1sec
Landform	MRRTF	Multiresolution ridgetop flatness index class	Index	Gallant and Austin (2012a), Gallant and Dowling (2003)	9sec 1sec
Landform	CONAREA	catchment contributing area	m^2	Gallant *et al.* (2012d)	3sec 1sec
Landform	TWI	Topographic wetness index	Index	(Gallant *et al.*, 2012i)	3sec 1sec
Landform	ELVFR1000	elevation focal range within 1000m	M	Gallant *et al.* (2012c)	9sec 3sec 1sec
Landform	ELEVFR300	elevation focal range within 300m	M	Gallant *et al.* (2012a)	3sec
Landform	SLPRELIEF	slope relief class	Index	Gallant *et al.* (2012h)	9sec 1sec 3sec
Landform	PLANCURV	Plan curvature	Index	(Gallant *et al.*, 2012f)	9sec 1sec
Landform	PROFCURV	Profile curvature	Index	(Gallant *et al.*, 2012g)	9sec 1sec
Landform	TPICLASS	Topographic position index	Index	Gallant and Austin (2012b)	9sec 3sec 1sec
Landform	TPIMASK	Topographic position mask	Index	Gallant and Austin (2012b)	9sec 3sec 1sec
Landform	SLOPEDEG	slope in degrees	Degrees	Gallant *et al.* (2012e)	3sec 1sec
Landform	SLPFM300	300m focal median of percent slope	Percent	Gallant *et al.* (2012b)	3sec 1sec

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APPENDIX 7. COMPOSITIONAL TURNOVER MODELLING

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Introduction

Species compositional turnover among vertebrate, invertebrate and vascular plant groups was modelled across continental Australia using 9-second gridded environmental predictors, and modelled for vascular plants across eastern Australia using 3-second gridded predictors and the Tingle Mosiac of southwest Western Australia at 1-second resolution. The scaled environmental predictors resulting from the compositional turnover modelling using generalised dissimilarity modelling (Ferrier *et al.*, 2007) are the primary inputs to the refugia analysis. Generalised dissimilarity modelling (GDM) is a statistical technique for modelling the compositional dissimilarity for a given biological group between pairs of locations in space or time, as a non-linear multivariate function of environmental differences between these locations.

This supporting document details the methods and results from the application of GDM to develop fitted models of species compositional turnover.

Methods

Study areas

The study comprises continental, regional and local scales with considerable diversity in landform, soils and climates, and associated biodiversity (Figure 1). Across continental Australia, environmental data were compiled at 9-second resolution (approximately 250m). Across the regional landscapes in Southeast Australia, data were compiled at 3-second resolution (approximately 100m), and in the Tingle Mosaic of southern Western Australia, 1-second resolution (approximately 30m).

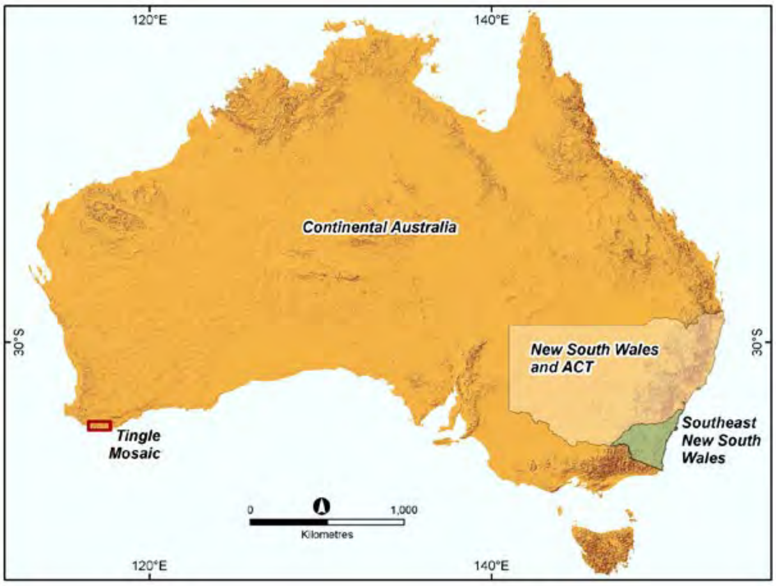


Figure A7-75. Case study areas for modelling species compositional turnover.

Biological data

The continental analysis of species compositional turnover was applied to vertebrate, invertebrate and vascular plant groups of taxa (Table 1). Biological data for invertebrate and vascular plants groups were derived from aggregations by the Atlas of Living Australia (www.ala.org.au) accessed via biocache (http://biocache.ala.org.au/). R-scripts automated the process of downloading and vetting the data as fit-for-purpose. Vertebrate data were compiled and vetted by JCU and collaborating researchers.

Table A7-8. Biological groups applied in continental modelling of species compositional turnover.

Biological Group	Taxonomic group	Number of species	Number of sites
Vertebrates	Class Mammalia (mammals)	245	239,162
Vertebrates	Class Aves (birds)	599	432,019
Vertebrates	Class Reptilia (reptiles)	646	110,221
Vertebrates	Class Amphibia (amphibians)	235	75,285
Invertebrate	Order Apocrita (wasps and bees)	3840	11,292
Invertebrate	Order Coleoptera (beetles)	9288	16,024
Invertebrate	Order Aranae (spiders)	2207	10,959
Vascular plants	Order Asparagales (lilies and onions)	2308	121,364
Vascular plants	Order Asterales (daisies)	2179	208,571
Vascular plants	Order Fabales (peas)	3317	299,443
Vascular plants	Division Gymnospermae (fruitless seed plants)	212	24,459
Vascular plants	Order Myrtales	2564	288,059
Vascular plants	Order Poales (grasses and sedges)	2918	266,241
Vascular plants	Order Proteales	1159	108,572
Fungi	Kingdom Fungi	3818	28,156

Across New South Wales, three sources of vascular plant data were compiled and applied in separate case studies. Across the entire state, we used the floristic survey data compiled and vetted by the NSW Office of Environment and Heritage (OEH) for GDM analysis (Logan *et al.*, 2009). These data have previously been used to model compositional turnover at 9-second resolution (Logan et al. in prep). We apply these data for the first time at 3-second resolution. In south eastern NSW, we used CSIRO's survey data for tree species capable of reaching the canopy (Austin *et al.*, 1996). In far southern Western Australia we used the Tingle Mosaic survey data (Wardell-Johnson & Williams, 1996). These latter three datasets were of sufficiently small size to enable their direct use in the GDM software. The NSW floristic data and the continental datasets required pre-processing to sample site-pairs of sufficient size for analysis.

Table A7-9. Vascular plant data applied to species compositional turnover models in south eastern and far south Western Australia.

Vascular plant data – location	# species	# sites	Attributes	Source
New South Wales	4847	40,190	Comprehensive flora survey data	NSW OEH Flora Information System, vetted by Vicki Logan
Southeast NSW	749	13,300	Surveys of trees capable of reaching the canopy	CSIRO BioGrad database (Austin *et al.*, 1996)
Tingle Mosaic WA	773	312	Comprehensive flora survey data	Curtin University of Western Australia (Wardell-Johnson & Williams, 1996)

Site-pair sampling

The Sørenson compositional dissimilarity between pairs of sites is the response variable for GDM. The number of possible site-pairs in a dataset is $\frac{n \times (n-1)}{2}$ and beyond the capacity of conventional computing. A perl script written as an extension to the spatial analysis program Biodiverse (Laffan *et al.*, 2010) was used to generate site-pairs and their Sørenson dissimilarity values, as described in Rosauer *et al.* (in review). The .NET GD modeller software provides for response data in various formats, including a table of site pairs and dissimilarity (Manion, 2012). We sampled site-pairs in 100,000 increments up to a maximum of one million, representing the memory limit in 32-bit Windows computing systems. Australian bioregions (DSEWPAC, 2012) were used as the stratification unit for the continental datasets and subregions were used with the NSW floristic survey data. Equal weighting was applied to each bioregion or subregion with a slight emphasis (10%) on sampling site pairs from within subregions relative to between subregions. The sampling of NSW floristic survey data was weighted by the log of the total number of species within each subregion (log-richness).

The preferred data type for compositional modelling is presence-absence, also known as occurrence data. However, aggregated ecological data, such as that available from the Atlas of Living Australia commonly include *ad hoc* observations as well comprehensively surveyed sites. Data that consists of a mixture of occurrence and under-sampled sites typically generates noise in a statistical model. As a proxy data quality filter for incomplete sampling of species occurrence, different thresholds for the number of species occurring at a single site were used to generate different site-pair samples. The threshold number of species to use in the final model was determined from a series of test models using the same set of variables. The selected threshold represented a trade-off between improving the sampling of species occurrence and reducing the number of sites available to the analysis. The percent deviance explained and the summed coefficient values for the predictor variables from test model runs guided the choice of threshold. As the threshold is increased, the number of occurrence sites decreases and the deviance explained increases. Where the summed coefficient values were relatively consistent, but the deviance explained increased, the model with the lower threshold number of species (and generally with lower deviance explained) at a site was selected. This ensured more sites were available for site-pair sampling.

Environmental variables

A common set of environmental variables were developed and tested as candidate predictors in GDM models. The spatial environmental data were compiled from best available sources and resampled to a common resolution (9-second, 3-second). As described in Supporting Information 3 (Harwood et al., terrain scaling) relevant climatic variables were adjusted for local topography using a scaling factor derived from using the r.sun routine in GRASS GIS (GRASS Development Team, 2011) with the respective DEM. Representative monthly estimates of radiation relative to an unshaded horizontal surface were obtained for the 15th day. This ratio was used to adjust monthly incoming shortwave radiation, net radiation, maximum temperature and potential evaporation following the procedures in Wilson and Gallant (2000) and Allen et al. (1998). The topographic adjustments were then propagated throughout relevant climate predictors.

For the 3-second gridded predictors, a 3-second digital elevation model, available as a derivative of the 1-second corrected and smoothed SRTM DEM (Gallant, 2011), was used with ANUCLIM version 6.1 software (Xu & Hutchinson, 2011) to derive monthly climate variables, representing 30 year averages centred on 1990, that were then used to generate a series of climate predictors (described in Williams *et al.*, 2012). The climatic predictors describe minimum and maximum monthly conditions and different facets of seasonality associated with temperature and water availability (Supporting Table 1).

A series of primary and secondary derivatives of the 3-second smoothed and hydrologically-enforced DEM, developed by J. Gallant and co-workers (Supporting Table 1) were compiled as supplementary landform predictors, where these are independent of the climate predictors. In addition to the substrate and landform variables listed in Williams et al. (2012), soil attributes modelled from soil spectra measurements (Viscarra-Rossel & Chen, 2011, Viscarra Rossel, 2011) and recent 250m gridded (9 second) composite national soil attributes (Jacquier, 2011a, Jacquier, 2011b, Jacquier, 2011c) were also compiled. Furthermore, a composite index of soil water holding capacity was derived from the topographic wetness index (Gallant *et al.*, 2012), the soil depth variable derived from the Atlas of Australian soils (Bureau of Rural Sciences, 2000, McKenzie *et al.*, 2000) and soil water holding capacity (Jacquier, 2011a) using the method described in Claridge *et al.* (2000).

This compilation of best available, high-resolution climate, landform and substrate variables resulted in 54 candidate predictors being tested for inclusion in the 3-second GDM models and 61 in the 9-second models (Supporting Table 1).

GDM model fitting

We used the .NET GD Modeller software (Manion, 2012) to develop fitted models of species compositional turnover. The .NET software has been developed by NSW OEH to support in house applications and research collaborations. Additional functionality was incorporated into this model to facilitate its use with multiple models.

The GDM model fitting process follows the procedure outlined in Williams *et al.* (2012). Each variable group (climate, topo-climate, substrate, landform) was initially tested to identify redundancy. The remaining variables were combined into a single model and again tested for redundancy. This filtering of candidate variables was implemented using a sample of 300,000 site-pairs that are feasibly applied within the computation limits of a large set of response and predictor variables. In a previous study with amphibians, a sample of around 300,000 site pairs was found to be reasonably robust (Rosauer *et al.*, in review). The final set of candidate variables (around 35-40 variables) were further screened for redundancy due to correlation using a backward stepwise variable elimination procedure. Variables were retained in the model if they contributed at least 0.05% partial deviance explained when each was tested for removal. This procedure often halved the number of predictors retained in the model to around 20. Each variable was then tested for additional complexity by increasing the number of splines from a minimum of 3 to 4. Spline additions that contributed at least 0.05% of the partial deviance explained were retained. Geographic distance between site pairs was then tested for inclusion and retained if at least 0.05% of the partial deviance explained was added to the final model.

Four standard outputs were generated from the final fitted models describing the pattern of the dissimilarity response variables, the relative contribution of the predictor (explanatory) variables, the shape of the overall logit fitted function, and the shape of the individual variable functions as a composite of the fitted functions. Model fitting information such as the percentage deviance explained, intercept, and the summed coefficients representing the level of compositional turnover predicted by the model are summarised in tables. The relative contribution of the environmental variable groups and the inclusion of geographic distance are also summarised, to enable comparison of these model components across biological groups and case studies.

Climate Scenarios

The 9-second and 1-second gridded models were projected using climate change scenario data as described in Supporting Information 3 (Harwood et al., terrain scaling).

The 3-second gridded models were projected for the year 2070 using eight climate change scenarios defined by two emission scenarios (A1FI equivalent to an RCP of 8.5; A1B equivalent to an RCP of 6.0), with two levels of climate sensitivity to emission concentrations (high or medium as defined in OZCLIM, Ricketts & Page, 2007), and two global climate models (GCMs) with contrasting estimates of future rainfall: the MIROC-M model (wetter future, Hasumi & Emori, 2004) and the CSIRO Mk 3.5 model (drier future, Gordon *et al.*, 2010). These GCMs are among the top performing models assessed for Australian conditions (Crimp *et al.*, 2012) and represent the best and worst case outcomes with respect to plausible temperature and rainfall futures for a given emissions scenario (Clarke *et al.*, 2011). The monthly climate scenario data were obtained from OZCLIM (CSIRO, 2007, Ricketts & Page, 2007) downscaled using

ANUCLIM 6.1 software (Xu & Hutchinson, 2011), as described in (Harwood *et al.*, 2010), with the current climate representing a 30-year average centred on 1990.

The same calculations and topographic conditioning as described above were applied to generate an equivalent set of scenario climatic predictors. The future climate predictors were used along with the existing substrate and terrain predictors to develop projections of each fitted model. The future environmental variables scaled by the coefficients of the fitted model are inputs to the refugia modelling. The last 10% of the trend line from each end of the fitted functions for each climatic predictor was extrapolated into novel climates, where this occurred.

Results

Continental 9-second gridded models

Fifteen models of species compositional turnover were developed for continental Australia using 9-second gridded predictor data (Table 3). The modelled percent deviance explained varied from 20% to 55%. The biological data for most of these models were filtered by a richness threshold to improve the adequacy of the occurrence samples. Models developed with a higher richness threshold or with few surveyed sites tend to have higher deviance explained (e.g. Gymnosperms, Amphibians).

The different groups of predictors all contributed in the models and geographic distance was always a significant component (Table 4). The environmental predictors, overall, contributed substantially more to compositional turnover (estimated from the sum of their coefficient values) than did geographic distance in each model, except amphibians, where geographic distance is proportionally more important. Of the environmental variables, the climate and topo-climate variables contribute substantially to compositional turnover compared with the substrate and landform variables, but substrate was proportionally more important for most plant groups, especially the nitrogen-fixing Fabales.

Among the 61 candidate environmental predictors, ten were never included in a final model. Of the remaining 51 variables, the terrain adjusted estimate of actual evapotranspiration (EAA) was always included (Table 4). Two other predictors were present in all but one of the models – the minimum water deficit (WDI) and solstice rainfall seasonality (SRAIN1). These variables and composite surficial soil bulk density (BD30) contributed the most, summed across all models, to compositional turnover (Table 4). The general structure of the fitted model for each biological group is presented in Figure 2 to Figure 16.

Table A7-10. Summary of GDM model fitting for continental 9-sec gridded predictors

Biological Group	# site-pairs	%Deviance Explained	Intercept	Summed Coefficients	# predictors	Richness filter
Mammals	292,845	32.40	0.64	9.96	20	5 or more
Birds	296,308	24.79	1.01	4.60	11	15 or more
Reptiles	291,888	37.07	1.07	13.30	18	3 or more
Amphibians	289,683	45.33	0.55	19.50	19	2 or more
Apocrita	297,907	20.14	1.88	16.48	16	2 or more
Araneae	297,441	22.57	1.44	13.80	19	3 or more
Coleoptera	298,138	20.91	2.36	18.40	20	1 or more
Fungi	296,845	21.67	2.06	17.92	17	2 or more
Gymnosperms	295,982	37.83	0.07	26.51	18	1 or more
Asparagales	297,145	37.62	1.06	20.12	22	5 or more
Poales	294,418	35.17	1.34	24.47	20	3 or more
Asterales	294,963	29.09	1.68	19.59	19	2 or more
Fabales	296,777	48.17	0.91	25.94	19	4 or more
Myrtales	294,652	42.57	0.79	35.06	20	2 or more
Proteales	296,155	49.64	0.37	34.12	20	2 or more

Table A7-11. Relative contribution of predictor variable groups (sum of coefficient values).

Biological Group	Climate (including topo-climate)	Substrate	Landform	Climate, substrate and landform	Geographic Distance
Mammals	6.68	2.64	0.26	9.58	0.38
Birds	3.82	0.42	0.13	4.37	0.23
Reptiles	8.29	2.63	0.30	11.22	2.08
Amphibians	8.49	3.17	0.93	12.59	6.91
Apocrita	12.68	3.30	0.00	15.98	0.50
Araneae	9.34	3.07	0.00	12.41	1.40
Coleoptera	14.40	2.34	0.38	17.12	1.29
Fungi	13.89	3.32	0.44	17.65	0.27
Gymnosperms	19.32	4.51	0.00	24.13	2.37
Asparagales	11.31	5.74	0.00	17.05	3.06
Poales	13.86	9.22	0.50	23.58	0.90
Asterales	11.41	4.89	0.63	16.93	2.67
Fabales	12.58	10.00	0.23	22.81	3.12
Myrtales	18.98	11.14	0.25	30.37	4.70
Proteales	20.91	7.43	0.00	28.34	5.79

Table A7-12. Overall relative importance (sum of spline coefficient values) of predictor variables used in the final fitted models. Variable definitions are given in Supporting Table 1

Variable Group	Predictor variable	Vertebrates (4 models)	Invertebrates and fungi (4 models)	Plants (7 models)	All models	# models represented
Distance	GEODIST	9.61	3.45	22.60	35.66	15
climate	PTS1	2.25	2.50	25.09	29.83	13
t-climate	EAA	3.79	5.21	10.44	19.44	15
t-climate	EPI	5.88	4.03	7.61	17.51	13
t-climate	TXI	0.00	2.02	13.85	15.87	8
t-climate	WDI	2.40	4.35	8.96	15.71	14
climate	TNX	1.32	3.11	9.30	13.73	12
t-climate	TXX	4.52	1.32	4.22	10.05	7
t-climate	WDRX	2.14	3.31	3.33	8.77	9
climate	PTX	0.40	4.05	3.96	8.42	6
t-climate	TRA	0.00	2.73	5.67	8.40	7
climate	TNRI	0.34	2.00	5.42	7.76	10
climate	PTI	0.28	4.63	1.07	5.99	5
climate	WDRI	0.36	1.20	1.72	3.28	4
t-climate	RAX	0.44	1.53	1.26	3.24	4
t-climate	PTS2	0.25	2.70	0.20	3.15	4
t-climate	RAI	0.00	2.92	0.00	2.92	2
t-climate	WDX	0.24	0.00	2.33	2.57	3
climate	RTNX	0.00	0.00	2.53	2.53	3
t-climate	TRI	1.14	0.92	0.00	2.05	4
climate	TXRI	0.45	0.69	0.58	1.72	6
t-climate	TNI	0.45	1.10	0.00	1.55	2
t-climate	TXRX	0.00	0.00	1.12	1.12	1
t-climate	TRX	0.44	0.00	0.00	0.44	1
substrate	BD30	2.90	2.64	25.70	31.23	14
substrate	KAO80	0.00	0.75	3.71	4.46	5
substrate	PC1_80	1.36	0.90	1.62	3.88	8
substrate	CLAY30	0.00	0.41	2.70	3.12	5
substrate	PC3_80	0.53	0.00	2.25	2.77	4
substrate	GEOLMNG	0.36	0.30	2.09	2.75	8
substrate	SME80	1.19	0.79	0.60	2.58	3
substrate	PC1_20	0.36	0.73	1.36	2.45	4
substrate	NUTRIENTS	0.61	1.03	0.78	2.42	3
substrate	GRAVITY	0.88	0.80	0.74	2.41	5
substrate	PC3_20	0.35	0.00	2.03	2.38	3
substrate	PC2_80	0.29	0.00	1.76	2.05	3
substrate	WII	0.00	0.62	1.32	1.94	6
substrate	GEOLRNG	0.00	1.36	0.57	1.93	5
substrate	ILL20	0.00	0.57	1.17	1.74	2
substrate	CTIDEPTH	0.00	0.76	0.78	1.54	2
substrate	KSAT	0.22	0.21	0.73	1.16	6
substrate	COARSE	0.42	0.00	0.64	1.07	6
substrate	SME20	0.00	0.00	0.84	0.84	1
substrate	PC2_20	0.00	0.00	0.77	0.77	1
substrate	HSTRUCT	0.20	0.00	0.57	0.76	4
substrate	CALCRETE	0.15	0.17	0.20	0.52	4
landform	ELVFR1000	1.23	0.82	1.24	3.29	7
landform	SLPRELIEF	0.38	0.00	0.00	0.38	2
landform	MRVBF	0.00	0.00	0.25	0.25	1
landform	TPIMASK	0.00	0.00	0.12	0.12	1

Variable Group	Predictor variable	Vertebrates (4 models)	Invertebrates and fungi (4 models)	Plants (7 models)	All models	# models represented

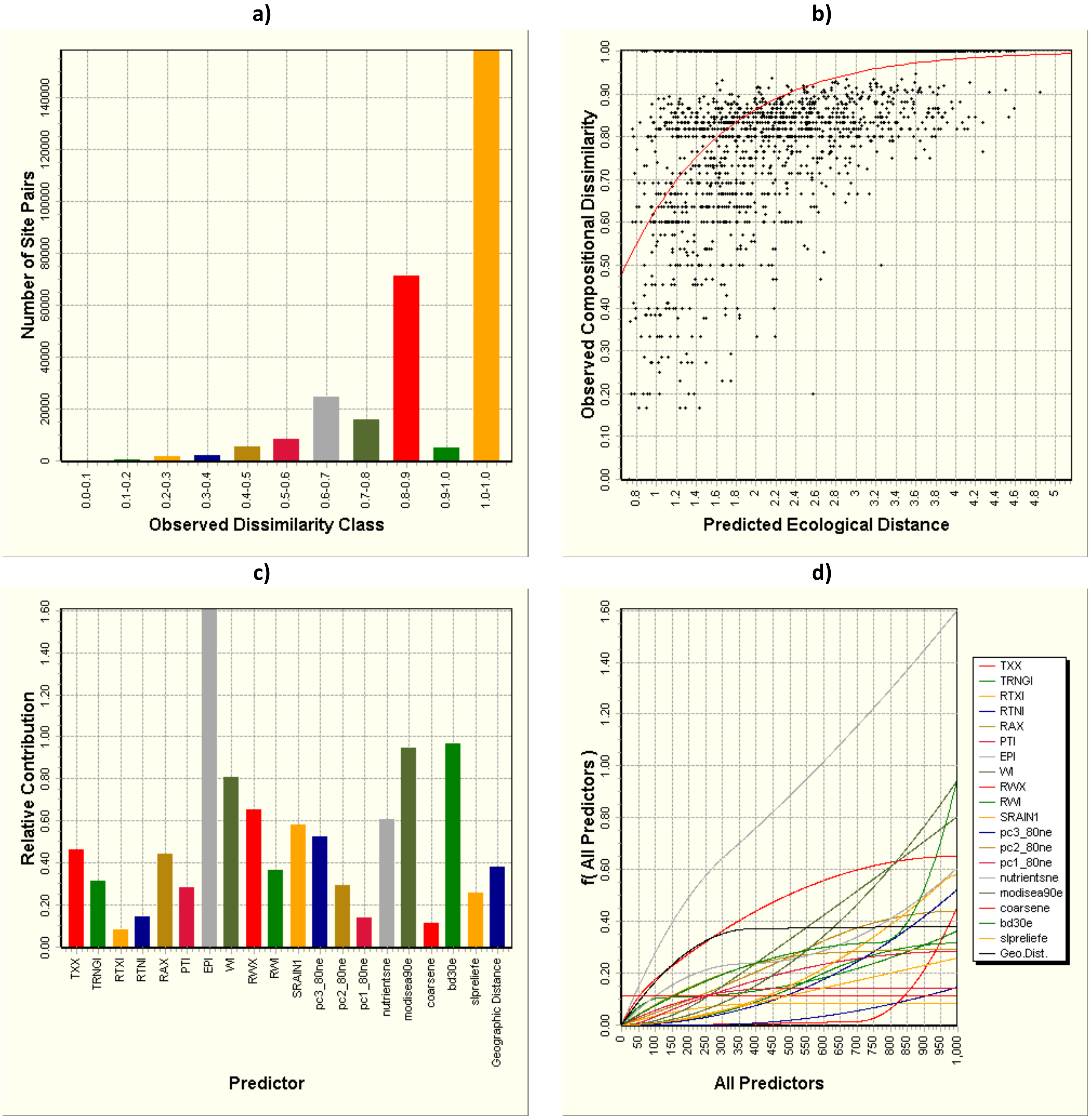


Figure A7-76. Continental Australia fitted model for mammals: a) dissimilarity response variable; b) overall fit of the logit model – observed versus predicted; c) relative contribution of the predictors (sum of spline coefficient values), d) composite of the variable fitted functions.

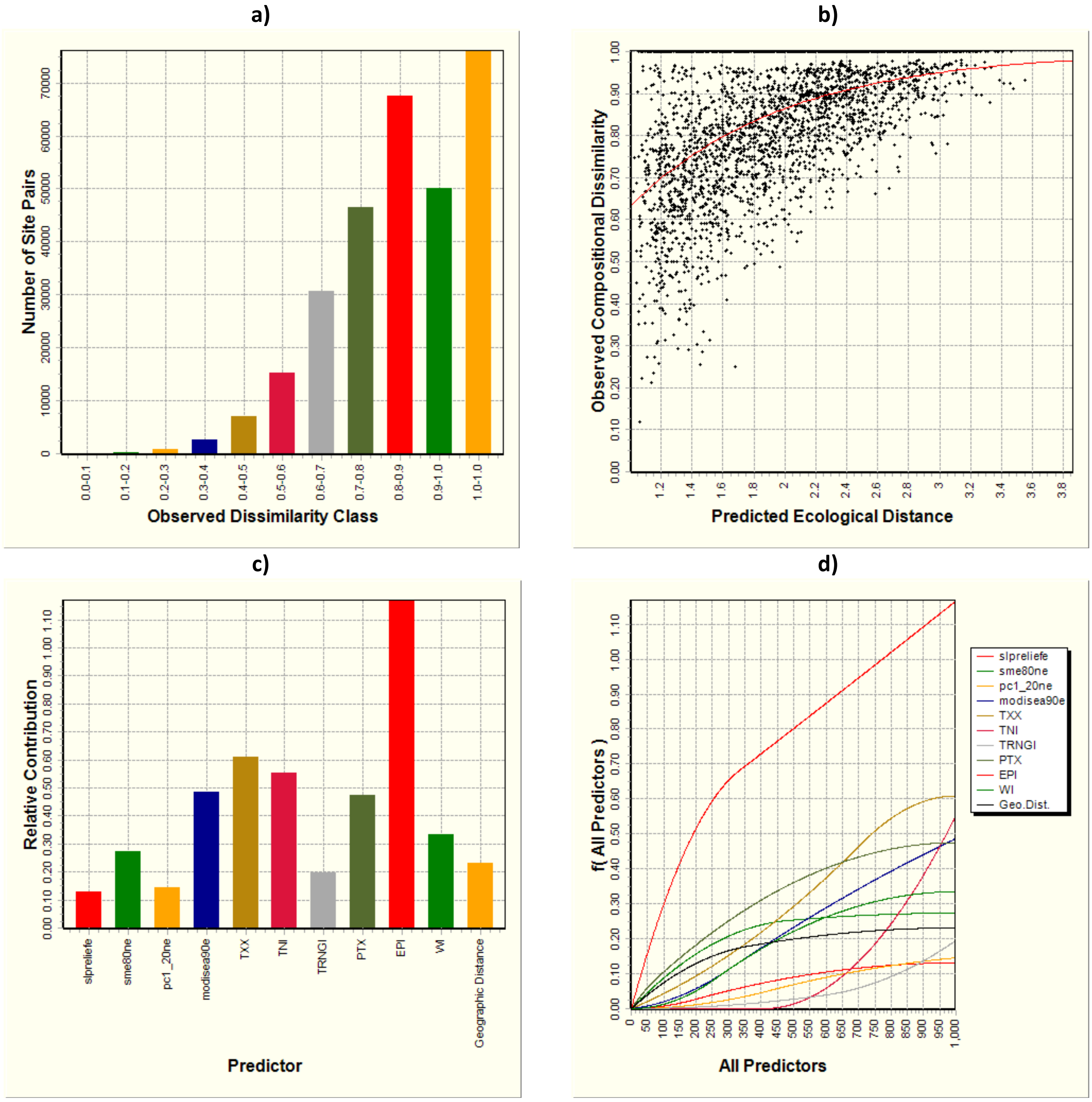


Figure A7-77. Continental Australia fitted model for birds: a) dissimilarity response variable; b) overall fit of the logit model – observed versus predicted; c) relative contribution of the predictors (sum of spline coefficient values), d) composite of the variable fitted functions.

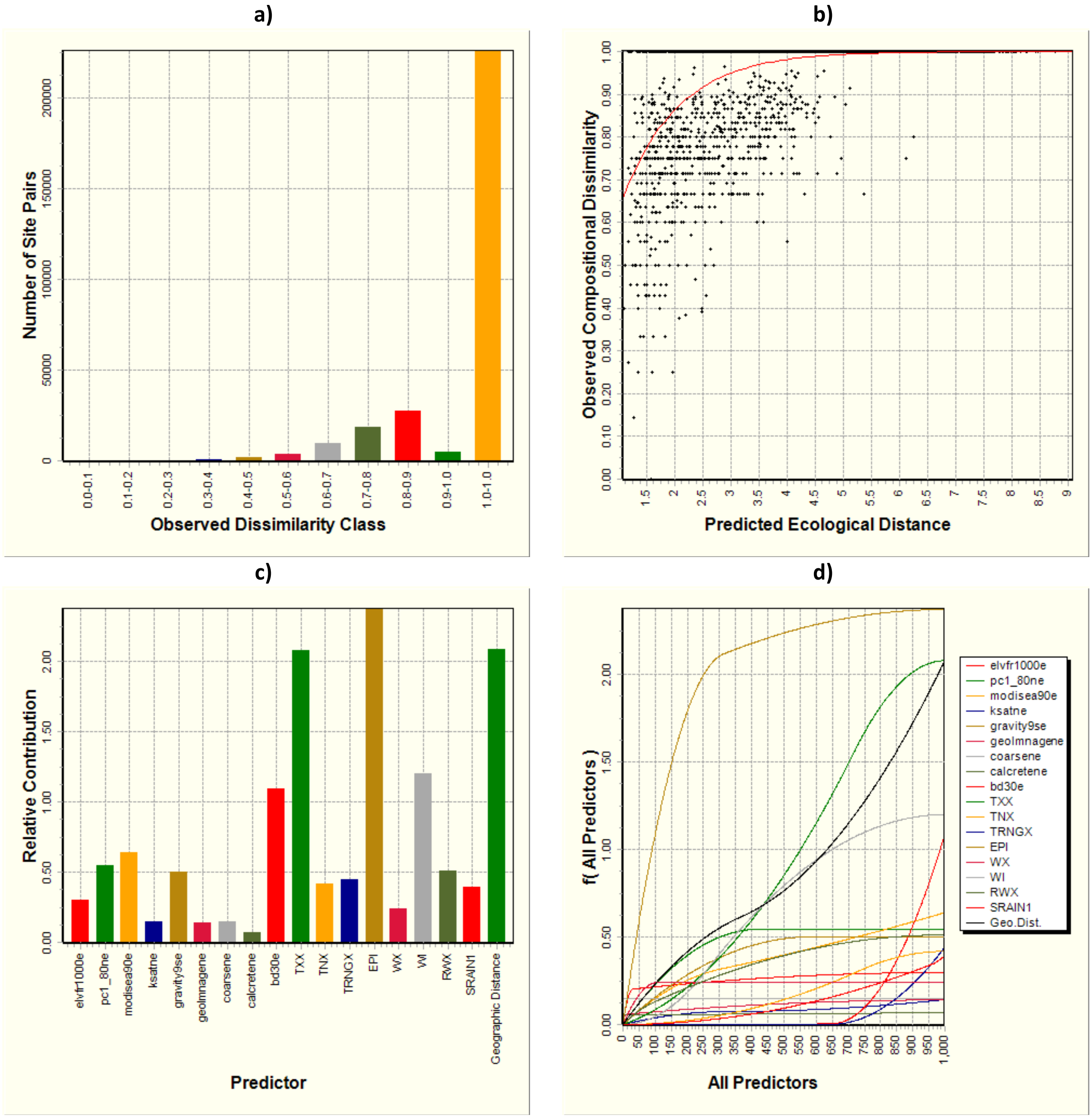


Figure A7-78. Continental Australia fitted model for reptiles: a) dissimilarity response variable; b) overall fit of the logit model – observed versus predicted; c) relative contribution of the predictors (sum of spline coefficient values), d) composite of the variable fitted functions.

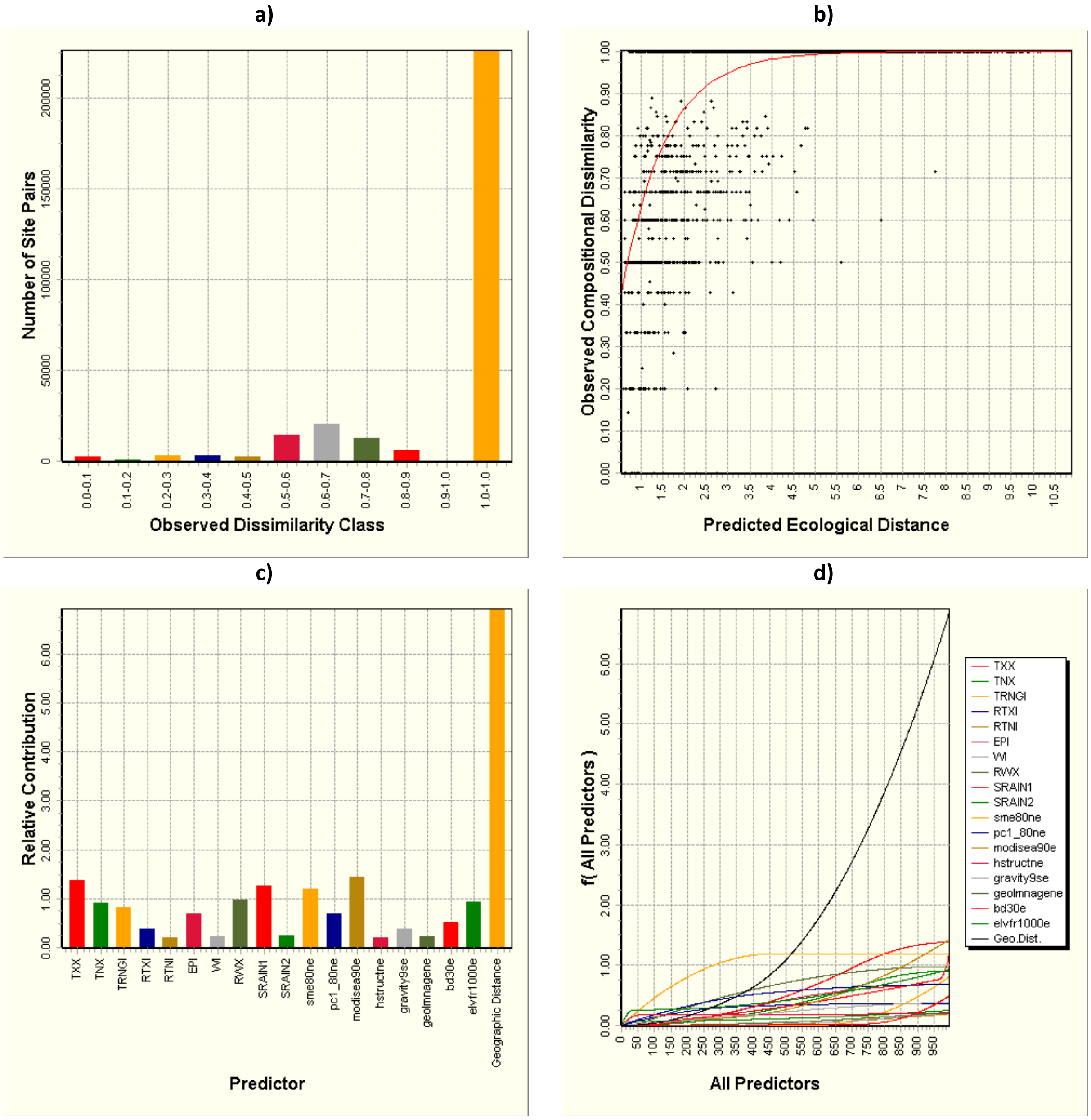


Figure A7-79. Continental Australia fitted model for amphibians: a) dissimilarity response variable; b) overall fit of the logit model – observed versus predicted; c) relative contribution of the predictors (sum of spline coefficient values), d) composite of the variable fitted functions.

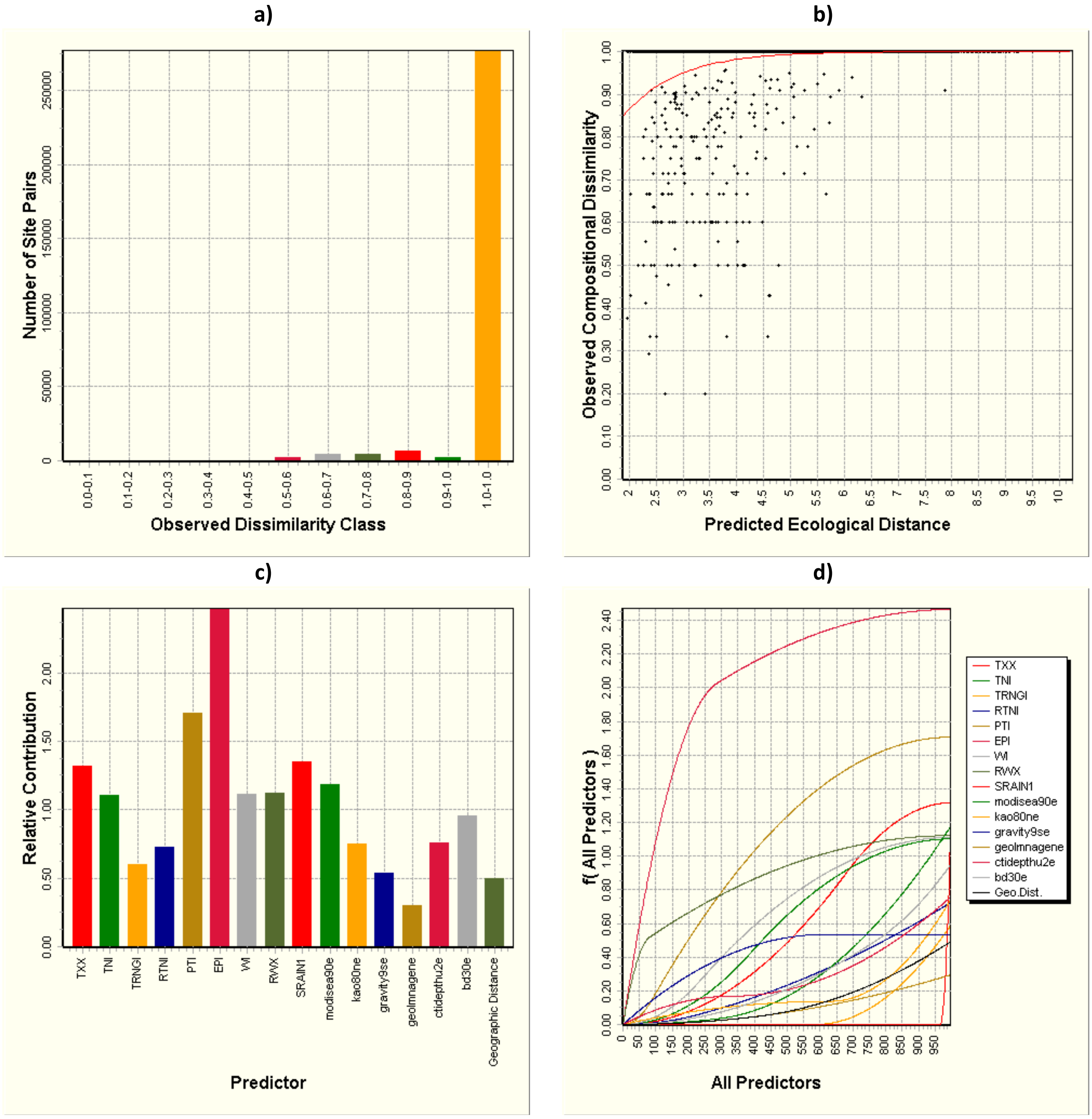


Figure A7-80. Continental Australia fitted model for Apocrita (bees and wasps): a) dissimilarity response variable; b) overall fit of the logit model – observed versus predicted; c) relative contribution of the predictors (sum of spline coefficient values), d) composite of the variable fitted functions.

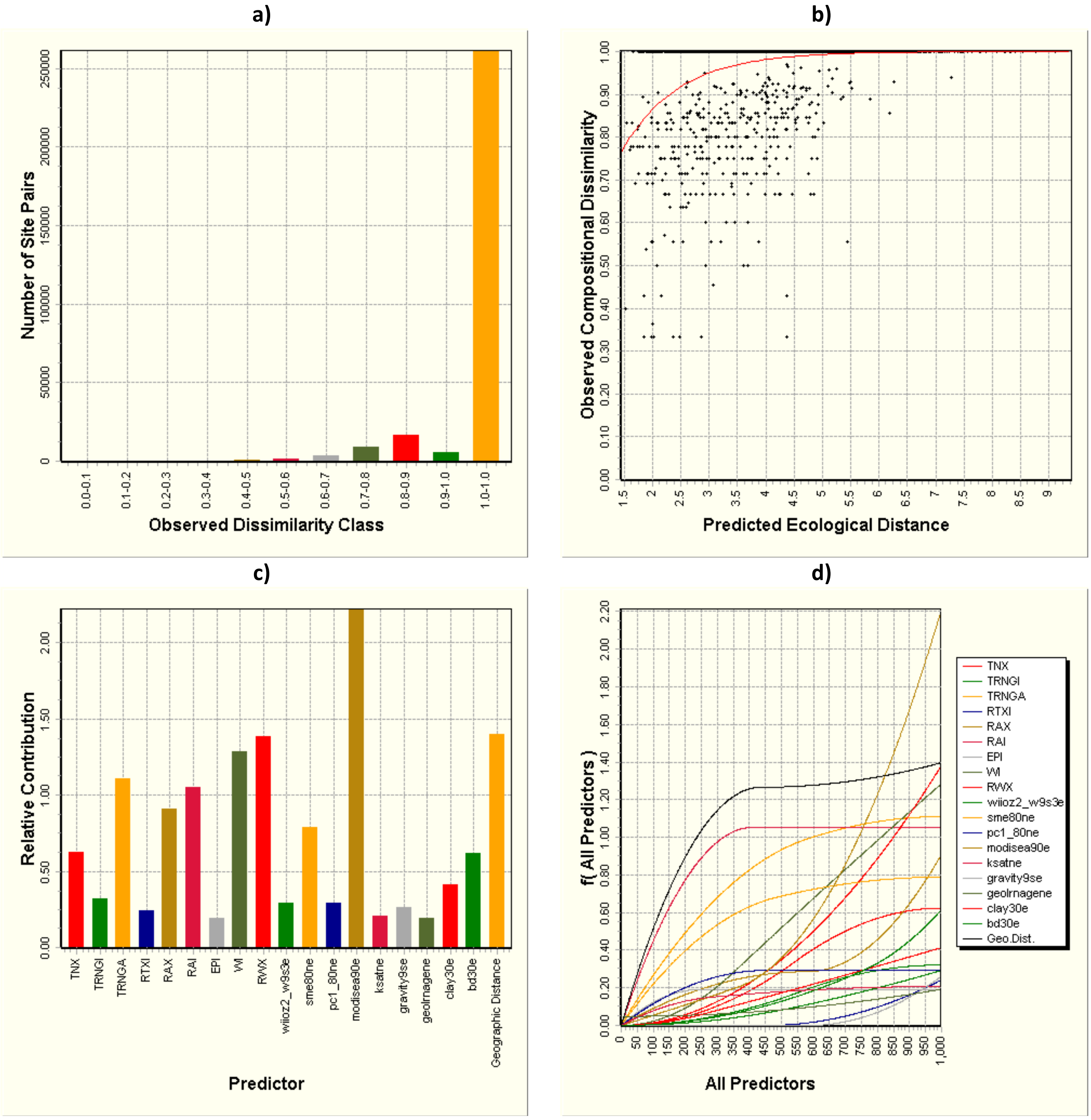


Figure A7-81. Continental Australia fitted model for Araneae (spiders): a) dissimilarity response variable; b) overall fit of the logit model – observed versus predicted; c) relative contribution of the predictors (sum of spline coefficient values), d) composite of the variable fitted functions.

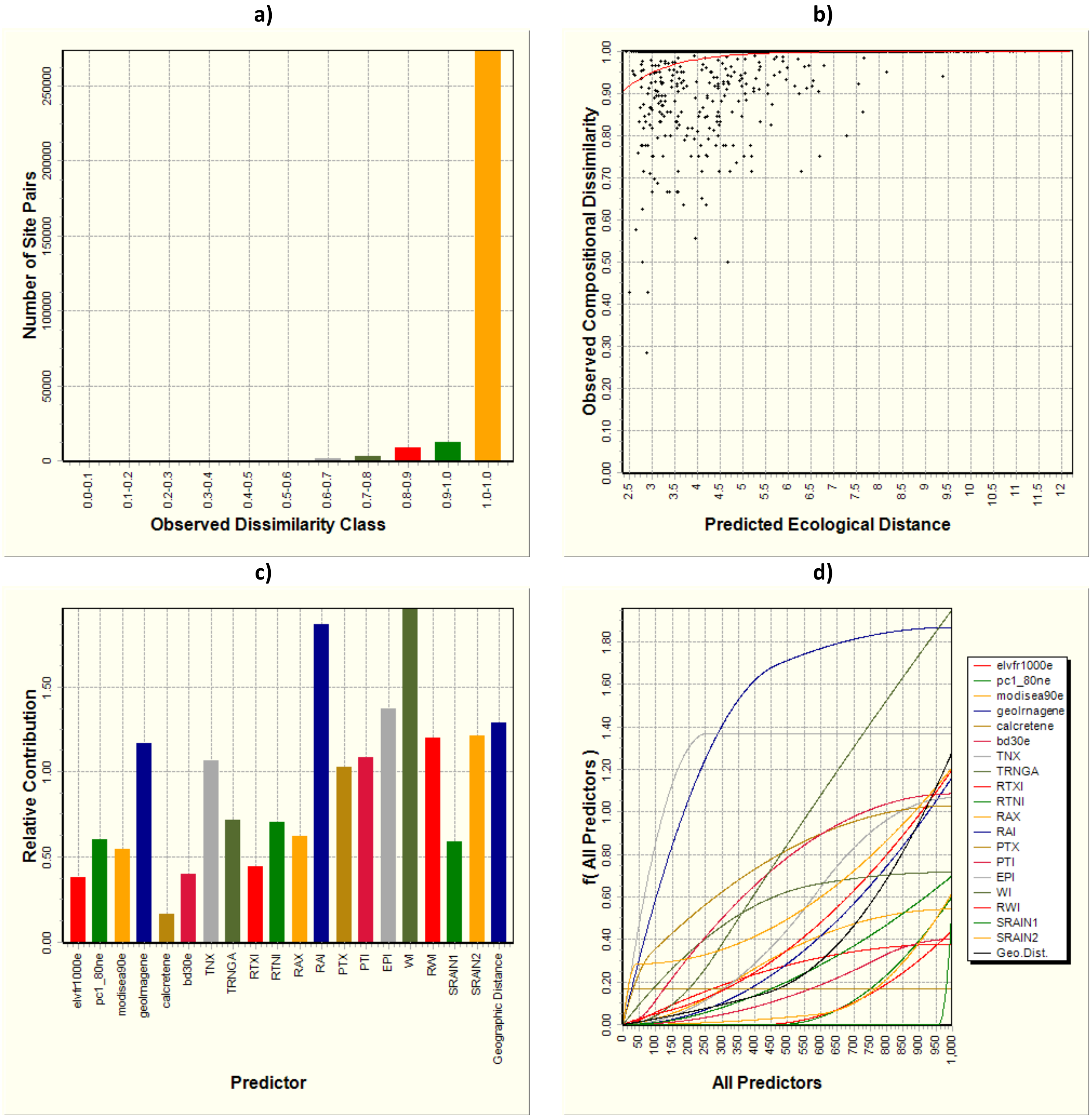


Figure A7-82. Continental Australia fitted model for Coleaoptera (beetles): a) dissimilarity response variable; b) overall fit of the logit model – observed versus predicted; c) relative contribution of the predictors (sum of spline coefficient values), d) composite of the variable fitted functions.

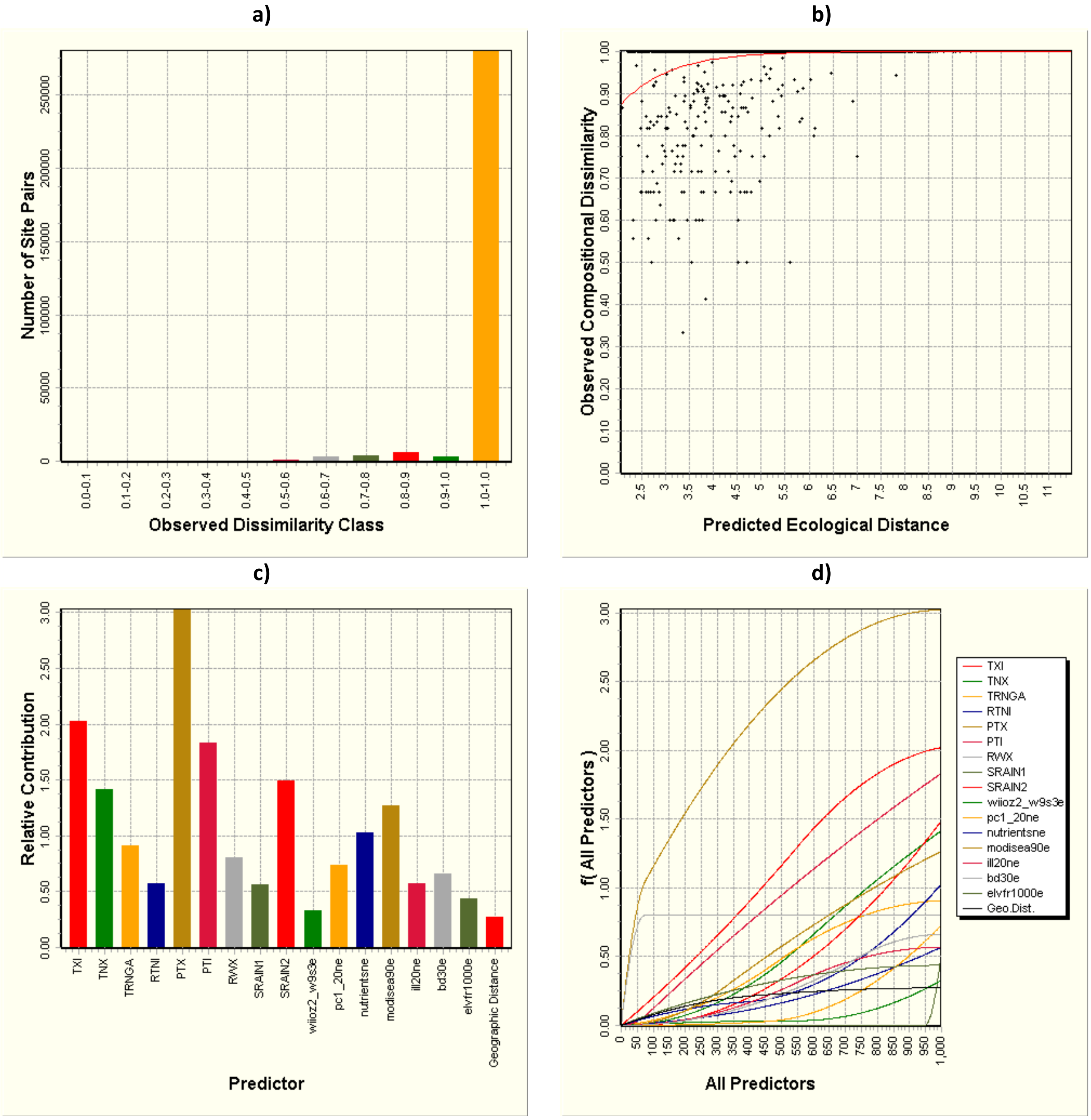


Figure A7-83. Continental Australia fitted model for Fungi: a) dissimilarity response variable; b) overall fit of the logit model – observed versus predicted; c) relative contribution of the predictors (sum of spline coefficient values), d) composite of the variable fitted functions.

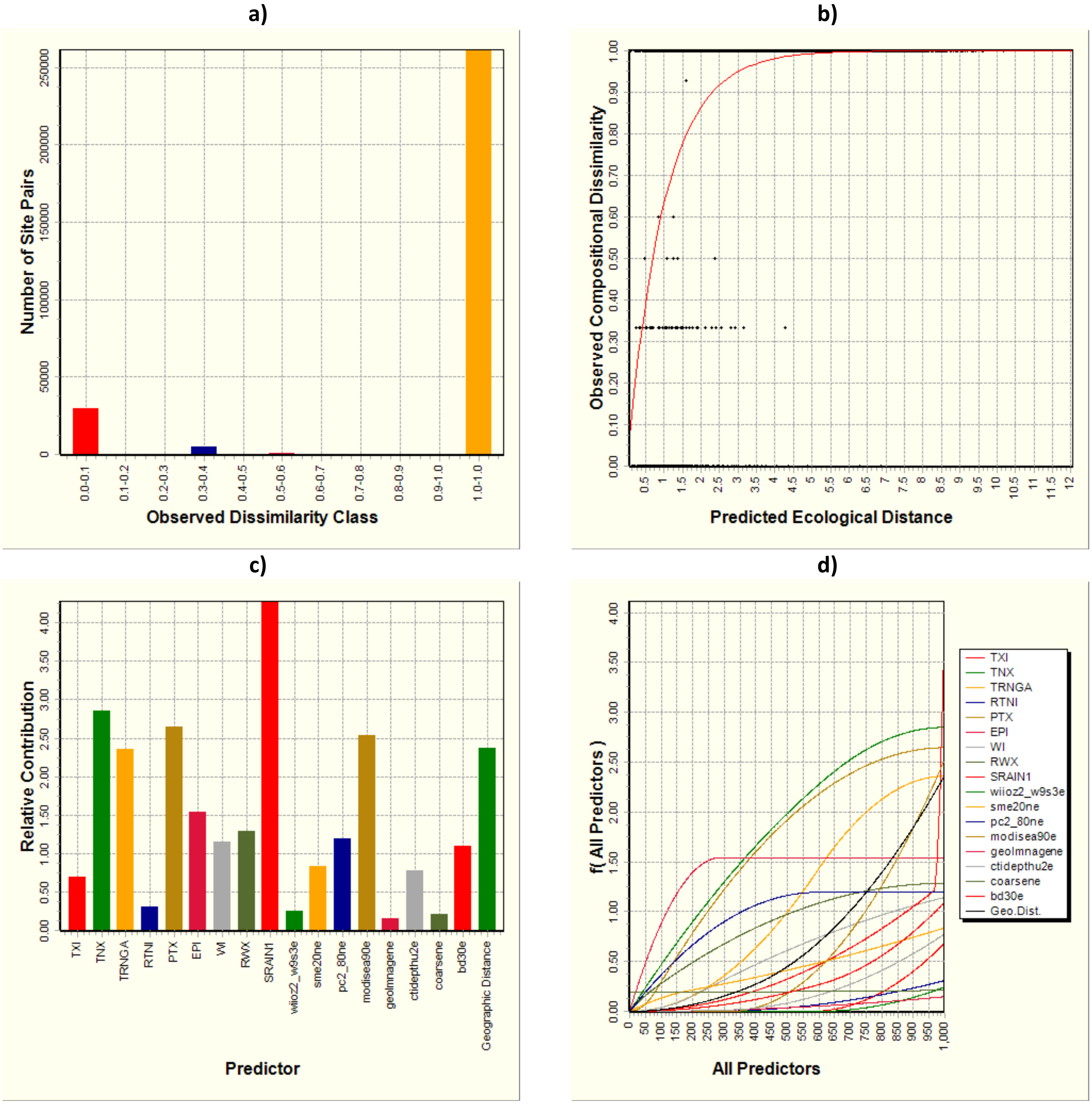


Figure A7-84. Continental Australia fitted model for Gymnosperms (cycads and pines): a) dissimilarity response variable; b) overall fit of the logit model – observed versus predicted; c) relative contribution of the predictors (sum of spline coefficient values), d) composite of the variable fitted functions.

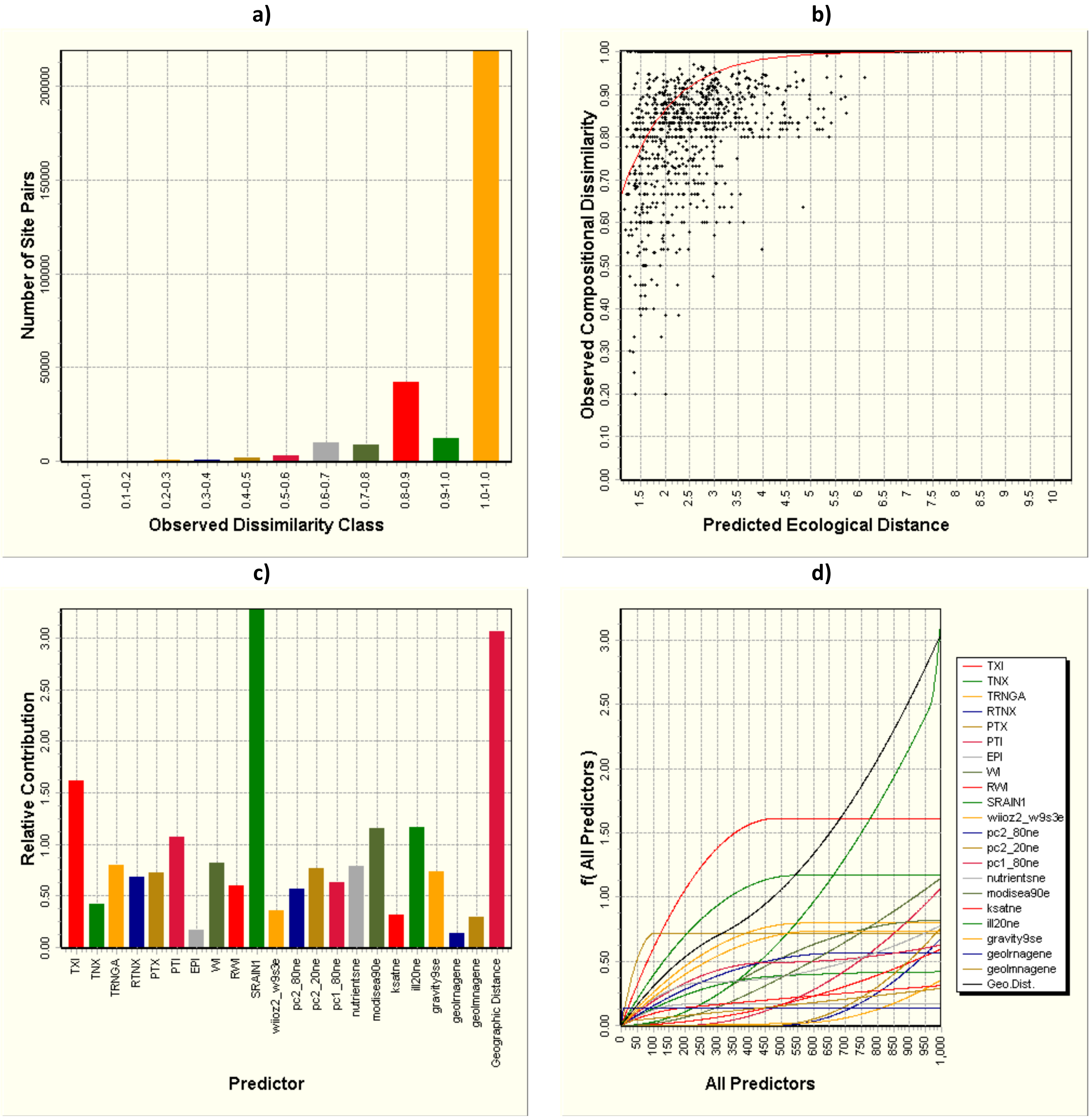


Figure A7-85. Continental Australia fitted model for Asparagales (lilies and related plants): a) dissimilarity response variable; b) overall fit of the logit model – observed versus predicted; c) relative contribution of the predictors (sum of spline coefficient values), d) composite of the variable fitted functions.

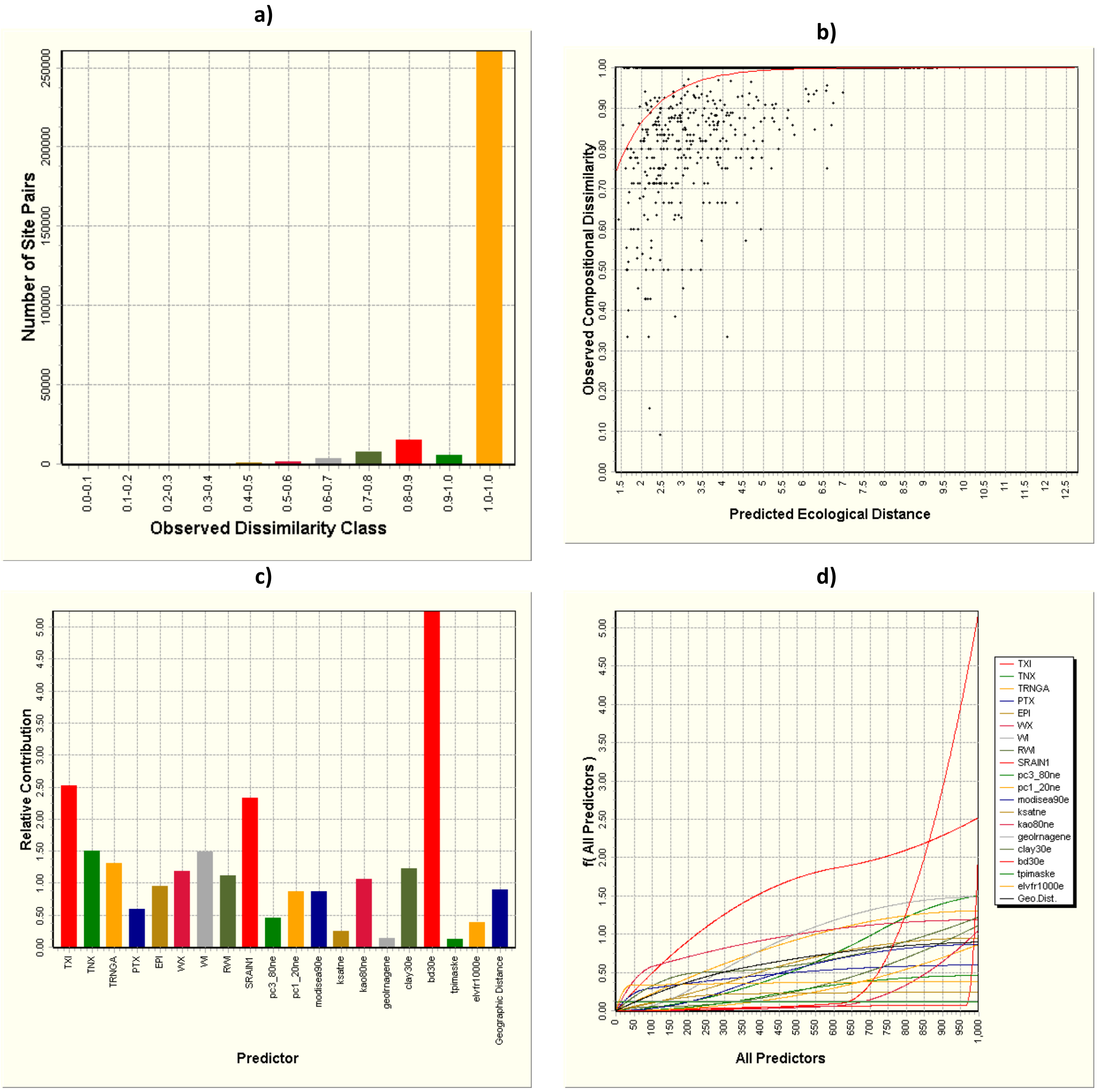
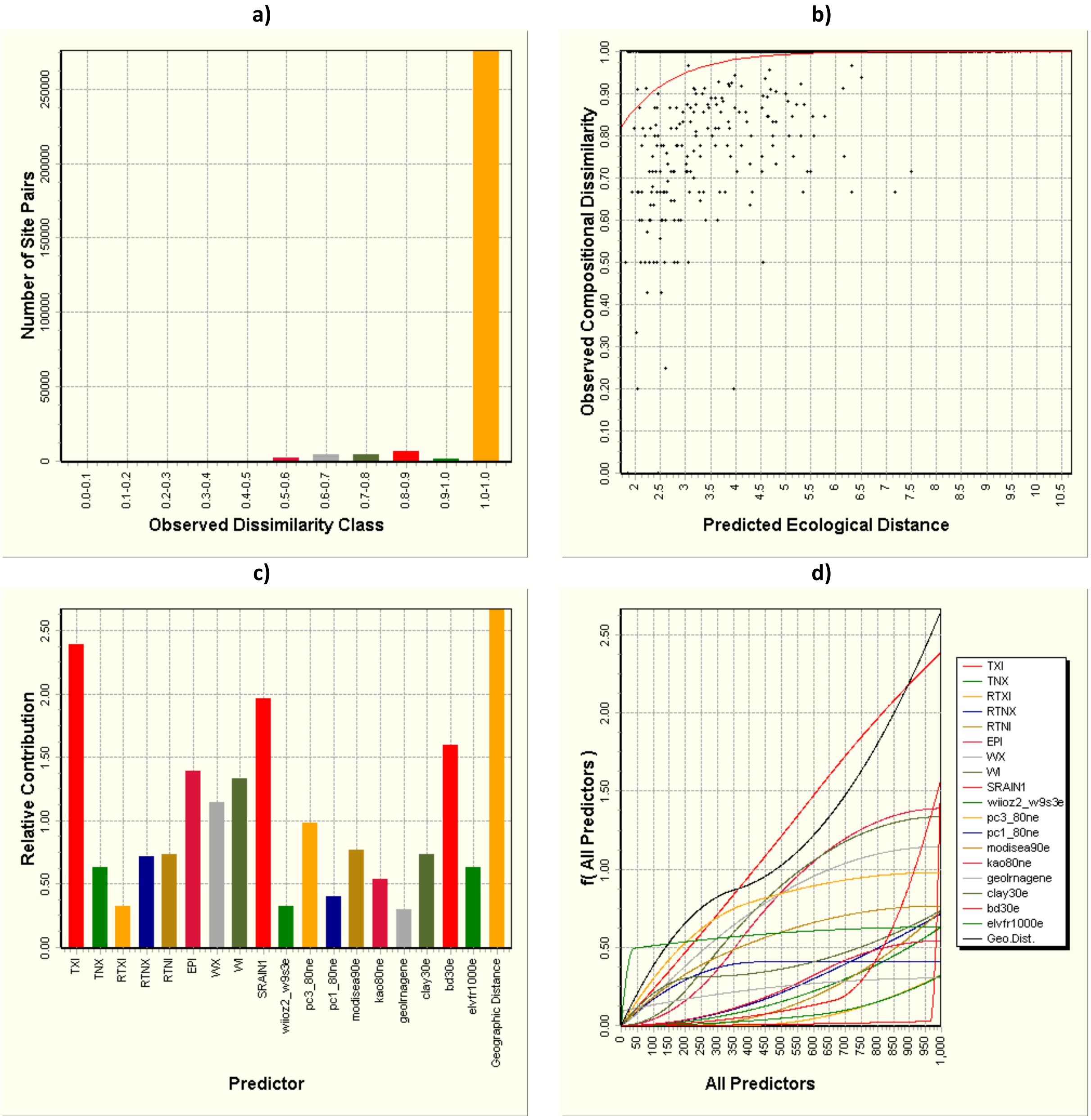


Figure A7-86. Continental Australia fitted model for Poales (grasses and sedges): a) dissimilarity response variable; b) overall fit of the logit model – observed versus predicted; c) relative contribution of the predictors (sum of spline coefficient values), d) composite of the variable fitted functions.


a)

b)

c)

d)

Figure A7-87. Continental Australia fitted model for Asterales daisies): a) dissimilarity response variable; b) overall fit of the logit model – observed versus predicted; c) relative contribution of the predictors (sum of spline coefficient values), d) composite of the variable fitted functions.

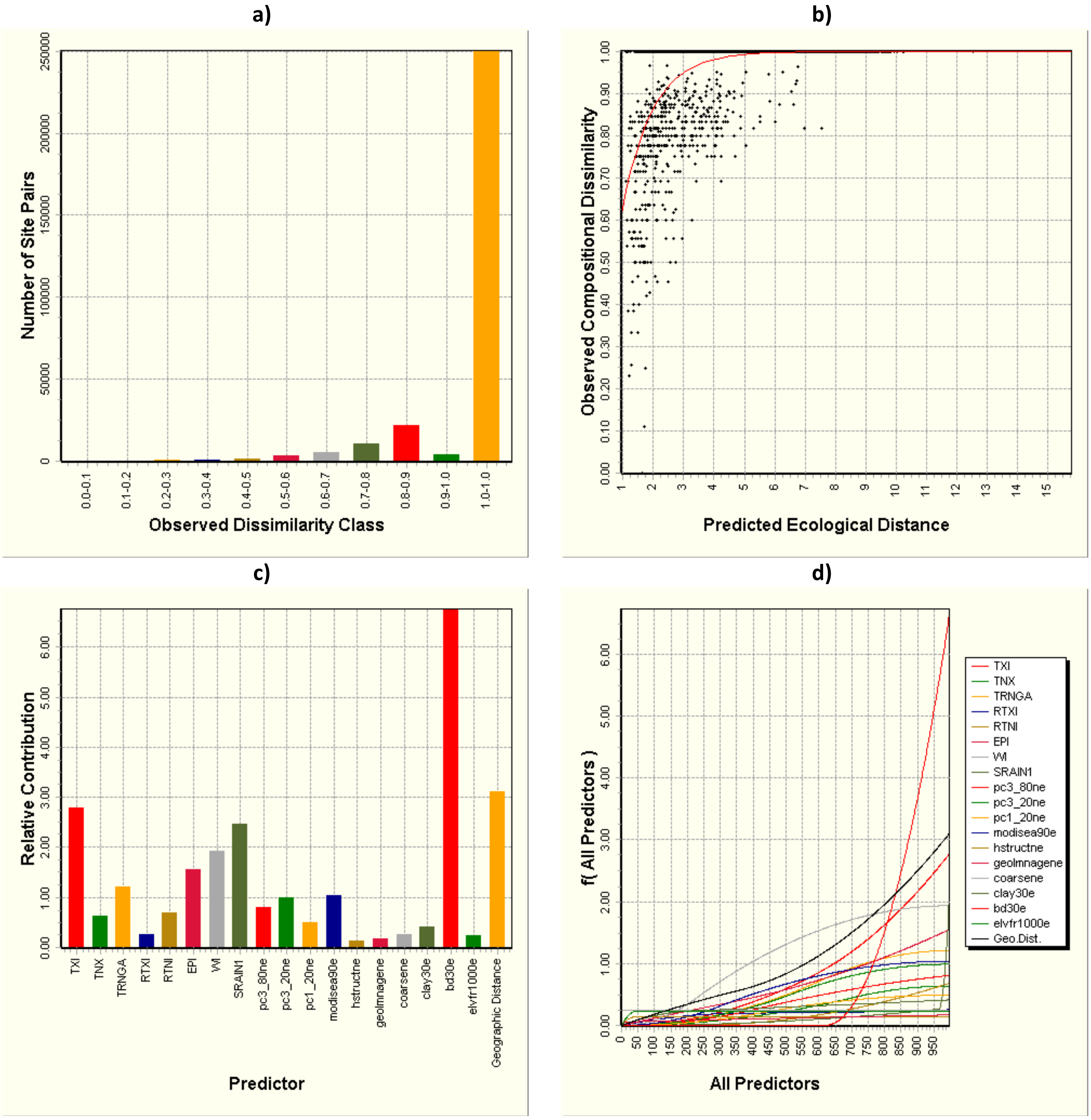


Figure A7-88. Continental Australia fitted model for Fabales (legumes and related nitrogen fixing plants): a) dissimilarity response variable; b) overall fit of the logit model – observed versus predicted; c) relative contribution of the predictors (sum of spline coefficient values), d) composite of the variable fitted functions.

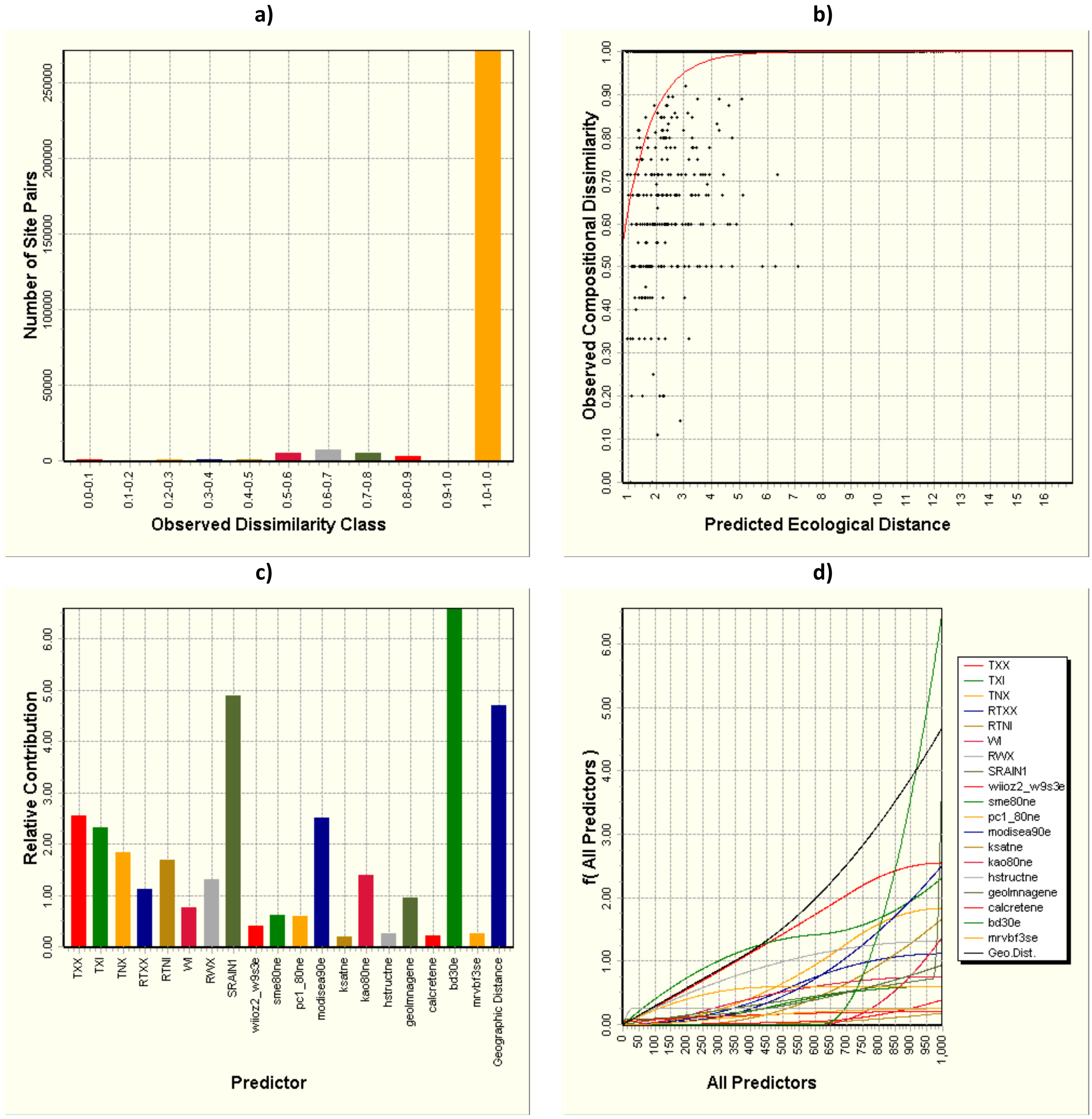


Figure A7-89. Continental Australia fitted model for Myrtales: a) dissimilarity response variable; b) overall fit of the logit model – observed versus predicted; c) relative contribution of the predictors (sum of spline coefficient values), d) composite of the variable fitted functions.

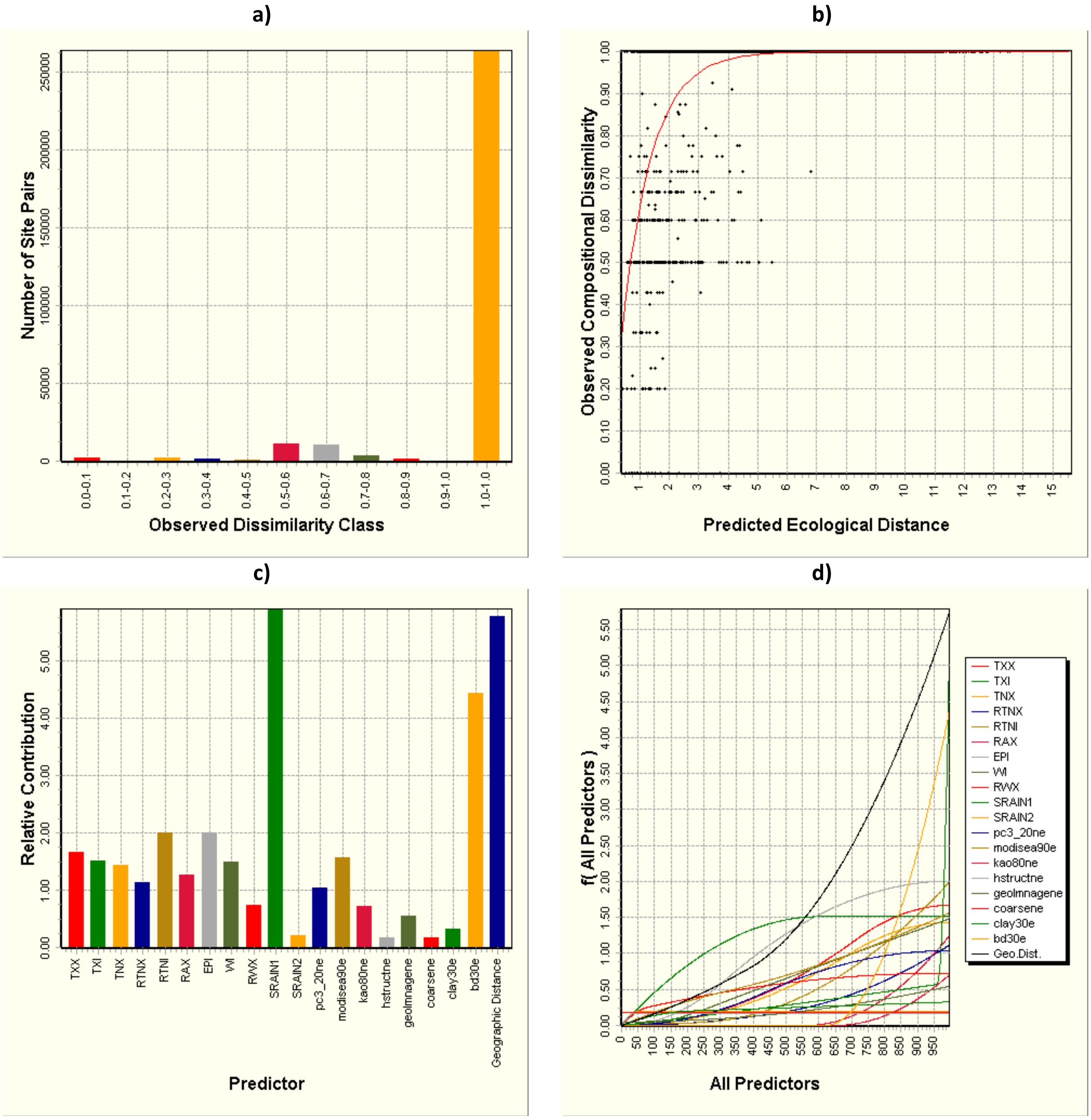


Figure A7-90. Continental Australia fitted model for Proteales (proteas): a) dissimilarity response variable; b) overall fit of the logit model – observed versus predicted; c) relative contribution of the predictors (sum of spline coefficient values), d) composite of the variable fitted functions.

Regional 3-second gridded models

Four models of vascular plant species compositional turnover were developed for case study areas in eastern Australia (Figure 1) using 3-second gridded predictor data (Table 6). The larger number of sites associated with the floristic survey data compiled by NSW OEH required sampling of site-pairs for GDM analysis. Approximately 900,000 site-pairs were applied in the final model. Data from the local case studies derived from CSIRO surveys were used with all site-pairs, after filtering by richness consistent with the restricted survey methodology.

Geographic distance was a significant variable in all four models and proportionally more important in the model applied to NSW (Table 7). Forty-one of the candidate predictors were included in at least one model (Table 8). Monthly minimum temperature (TNI) was particularly important as a predictor in southeast NSW and maximum evaporation (EPX) for the model developed for the entire state. Among the substrate variables kaolinite clay minerals in the lower soil horizon (KAO80) was a significant predictor for the NSW model. The general structure of the fitted model for each dataset is presented in Figure 17 and Figure 18.

Table A7-13. Summary of GDM model fitting for eastern Australian case study areas using 3-sec gridded predictors.

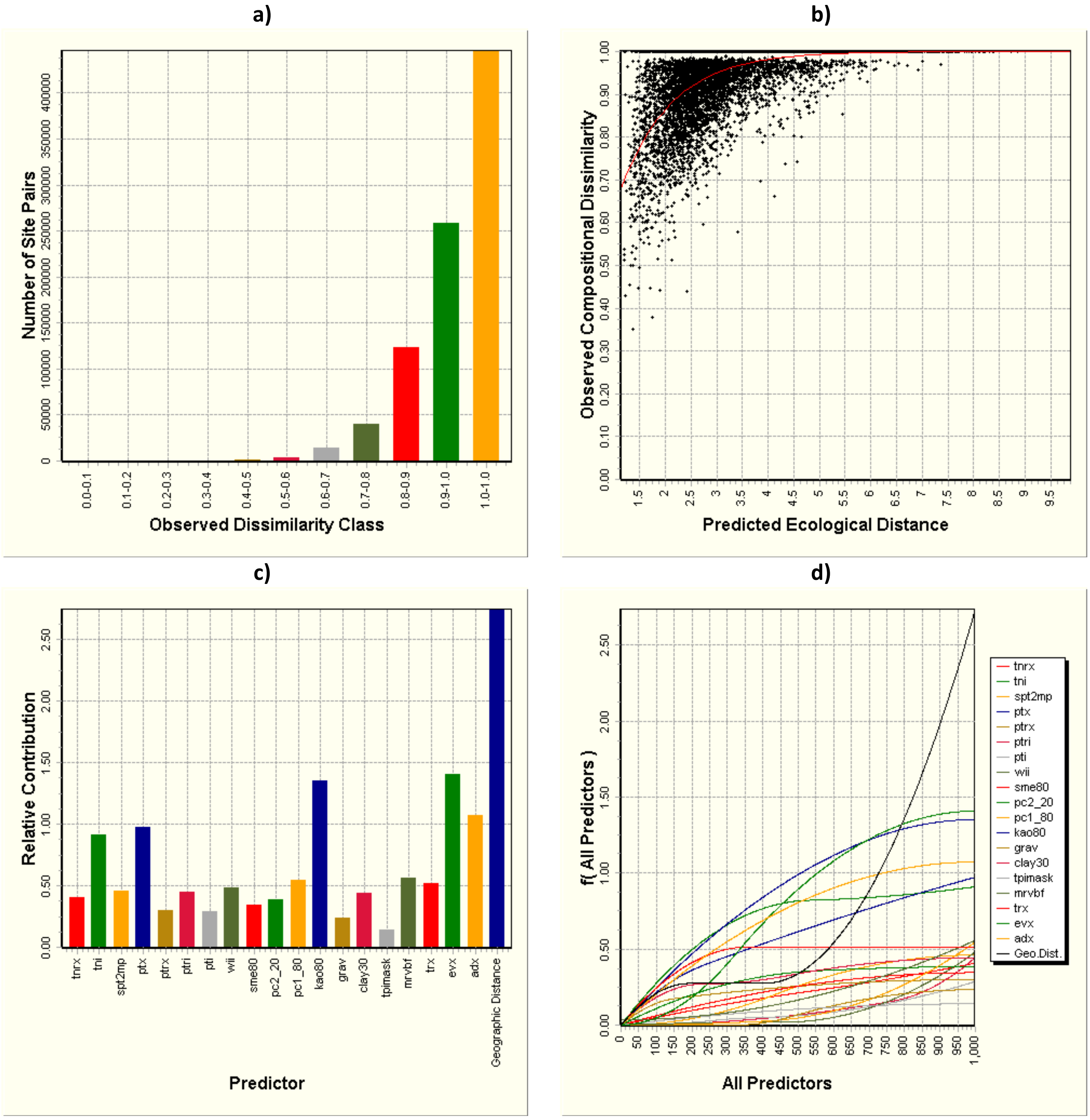
Study dataset	# site-pairs	%Deviance Explained	Intercept	Summed Coefficients	# predictors	Richness filter
NSW OEH	885,376	45.78	1.12	14.00	20	None
CSIRO SE NSW	542,361	33.82	0.57	10.59	17	7 or more

Table A7-14. Relative contribution of predictor variable groups (sum of coefficient values).

Study dataset	Climate (including topo-climate)	Substrate	Landform	Climate, substrate and landform	Geographic Distance
NSW OEH	6.78	3.79	0.70	11.27	2.74
CSIRO SE NSW	5.70	1.65	1.67	9.02	1.57

Table A7-15. Overall relative importance (sum of spline coefficient values) of predictor variables used in the final fitted models.

Variable Group	Predictor variable	NSW (flora)	SE NSW (flora)
Distance	GEODIST	2.74	1.57
Climate	SPT2MP	2.28	-
Climate	TNI	1.16	0.58
Climate	TNRI	-	1.42
Climate	PTX	-	0.67
T-climate	TRX	-	0.69
Climate	PTRI	0.68	-
T-climate	ADI	1.03	-
Climate	PTI	0.24	-
T-climate	ADRI	0.19	-
T-climate	TXRX	-	0.42
T-climate	ADRX	0.13	0.25
T-climate	RHX	-	0.33
Regolith	KAO80	-	0.59
Regolith	CLAY30	-	0.09
Regolith	PC1_20	0.31	1.01
Regolith	SME80	0.34	0.67
Regolith	GRAV	0.56	-
Regolith	CTIPAWC	0.23	-
Regolith	MAG	0.20	-
Landform	ELVFR1000	0.80	-
Landform	SLPFM300	0.53	0.34
Landform	TPIMASK	-	0.18
Landform	TPICLASS	0.20	-
Landform	TWI	-	0.25
Landform	CONAREA	0.13	-



a)

b)

c)

d)

Figure A7-91. Eastern Australia 3-second fitted model for vascular plants across NSW: a) dissimilarity response variable; b) overall fit of the logit model – observed versus predicted; c) relative contribution of the predictors (sum of spline coefficient values), d) composite of the variable fitted functions.

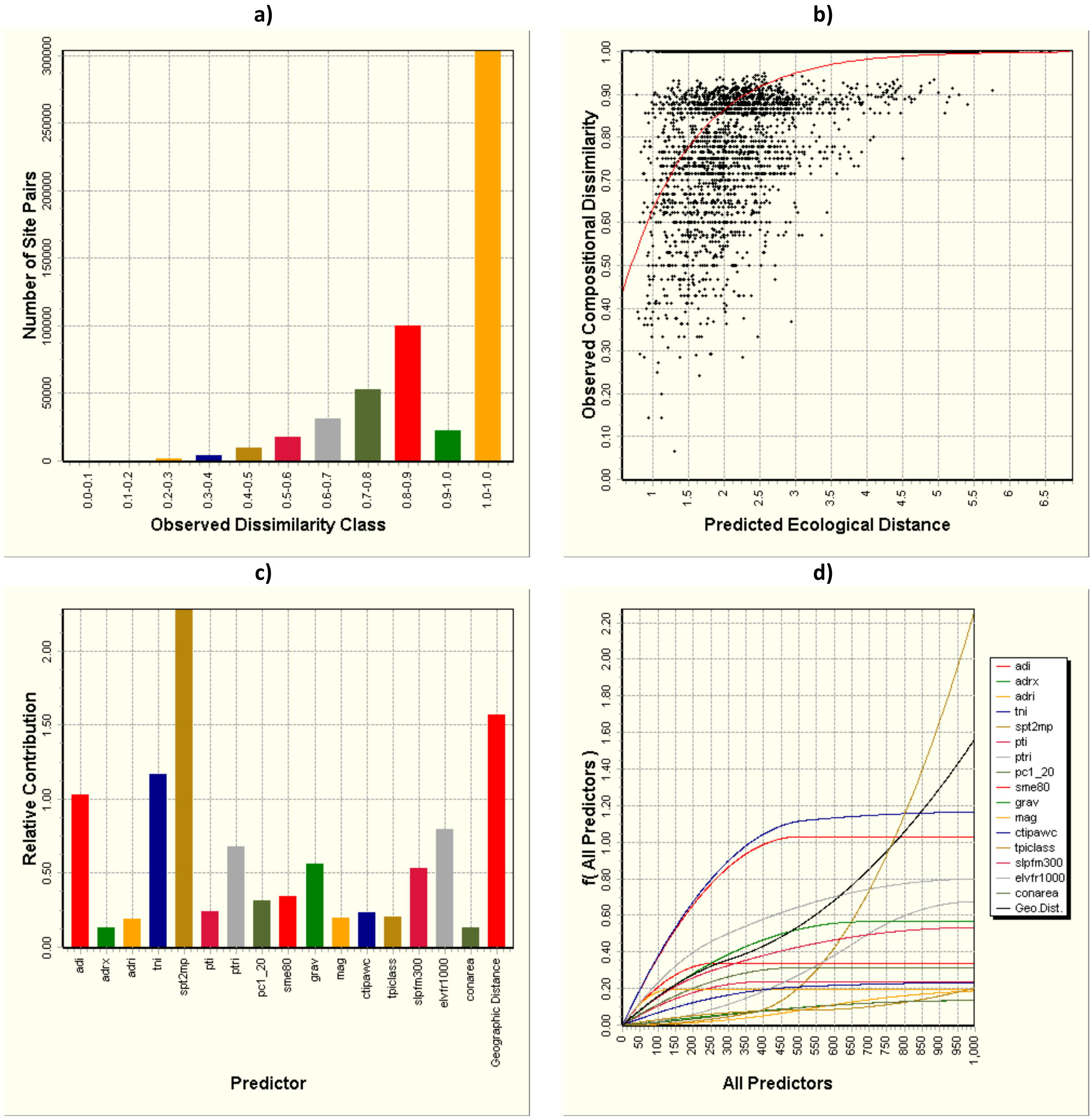


Figure A7-92. Eastern Australia 3-second fitted model for vascular plants for southeast NSW: a) dissimilarity response variable; b) overall fit of the logit model – observed versus predicted; c) relative contribution of the predictors (sum of spline coefficient values), d) composite of the variable fitted functions.

Local 1-second gridded models

The model of vascular plant species turnover developed for the Tingle Mosaic region of southwest Western Australia using 1-second gridded predictor data explained 28% of the variation (Table 9). The floristic data derives from surveys conducted by G Wardell-Johnson and colleagues (Wardell-Johnson & Williams, 1996). The surveys were accompanied by soil sampling for nutrient status. The inclusion of local soil attributes in the GDM model derived using the spatial predictors resulted in a large increase in deviance explained to 39%. This result is consistent with the relatively coarse resolution of the spatial soil predictors (varying scales to around 100m). Climate is consistently represented by four predictors that have been adjusted by topographic effects, dominated by minimum precipitation deficit (WDX), monthly maximum temperature (TXX). Soil and substrate variables related to moisture availability and nutrient status, however, are the main drivers of compositional turnover. These include soil water holding capacity (PAWC1M), smectite clay minerals (SME20, SME80), pH (PH_m) and potassium (K_HCL_m, K_OLS_m). Smectite minerals occur predominantly in drier climates and lower relief landscapes from the weathering of basalt or alluvial and typically have higher water holding capacities than soils with abundant kaolinite minerals (Viscarra Rossel, 2011).

Table A7-16. Summary of GDM model fitting for the Tingle Mosaic case study using 1-sec gridded predictors.

Study model	# site-pairs	%Deviance Explained	Intercept	Summed Coefficients	# predictors	Richness filter
Spatial predictors only	48,205	28.04	0.67	6.62	14	none
Local soil predictors	48,205	39.02	0.31	8.96	20	none

Table A7-17. Relative contribution of predictor variable groups (sum of coefficient values).

Study model	Climate (including topo-climate)	Substrate	Landform	Climate, substrate and landform	Geographic Distance
Spatial predictors only	2.76	3.31	0.55	6.62	0.00
Local soil predictors	2.22	6.19	0.55	8.96	0.00

Table A7-18. Overall relative importance (sum of spline coefficient values) of predictor variables used in the final fitted models.

Variable Group*	Predictor variable	Spatial Predictors	Local Soil Predictors
t-climate	WDX	0.93	0.75
t-climate	TXX	0.70	0.67
t-climate	RSX	0.56	0.32
t-climate	EAA	0.57	0.49
substrate	SME80AM	0.50	0.52
substrate	SME20AM	0.42	0.51
substrate	RATIO_UKAM	0.33	0.19
substrate	PPMTHAM	0.20	0.12
substrate	PAWC1MAM	0.97	1.02
substrate	MAGAM	0.47	0.38
substrate	KAO80AM	0.21	0.00
substrate	CLAY30AM	0.20	0.11
local soil	P_HCL_M	-	0.24
local soil	K_HCL_M	-	0.70
local soil	C_M	-	0.26
local soil	K_OLS_M	-	0.44
local soil	PH_M	-	1.28
local soil	SALTS_M	-	0.41
landform	SLP300AM	0.27	0.16
landform	RELIEFAM	0.00	0.27
Landform	MRRTFAM	0.28	0.12

* Local soil variables: P_HCL_M – Phosphorus; K_HCL_M – Potassium; C_M – Carbon; K_OLS_M – Potassium; PH_M – acidity; SALTS_M – salts.

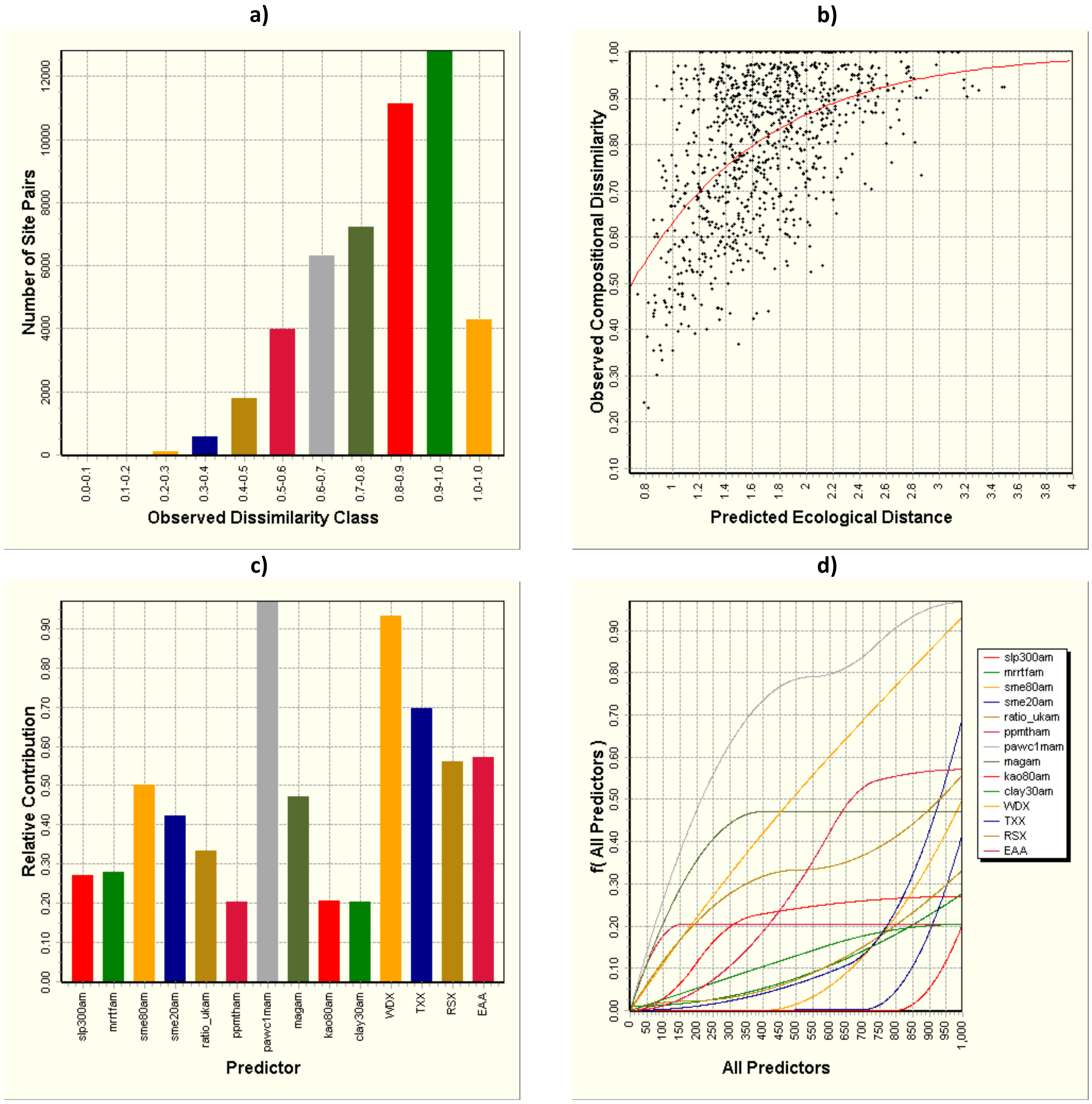

a) b) c) d)

Figure A7-93. Tingle Mosaic survey 1-second fitted model for vascular plants: a) dissimilarity response variable; b) overall fit of the logit model – observed versus predicted; c) relative contribution of the predictors (sum of spline coefficient values), d) composite of the variable fitted functions.

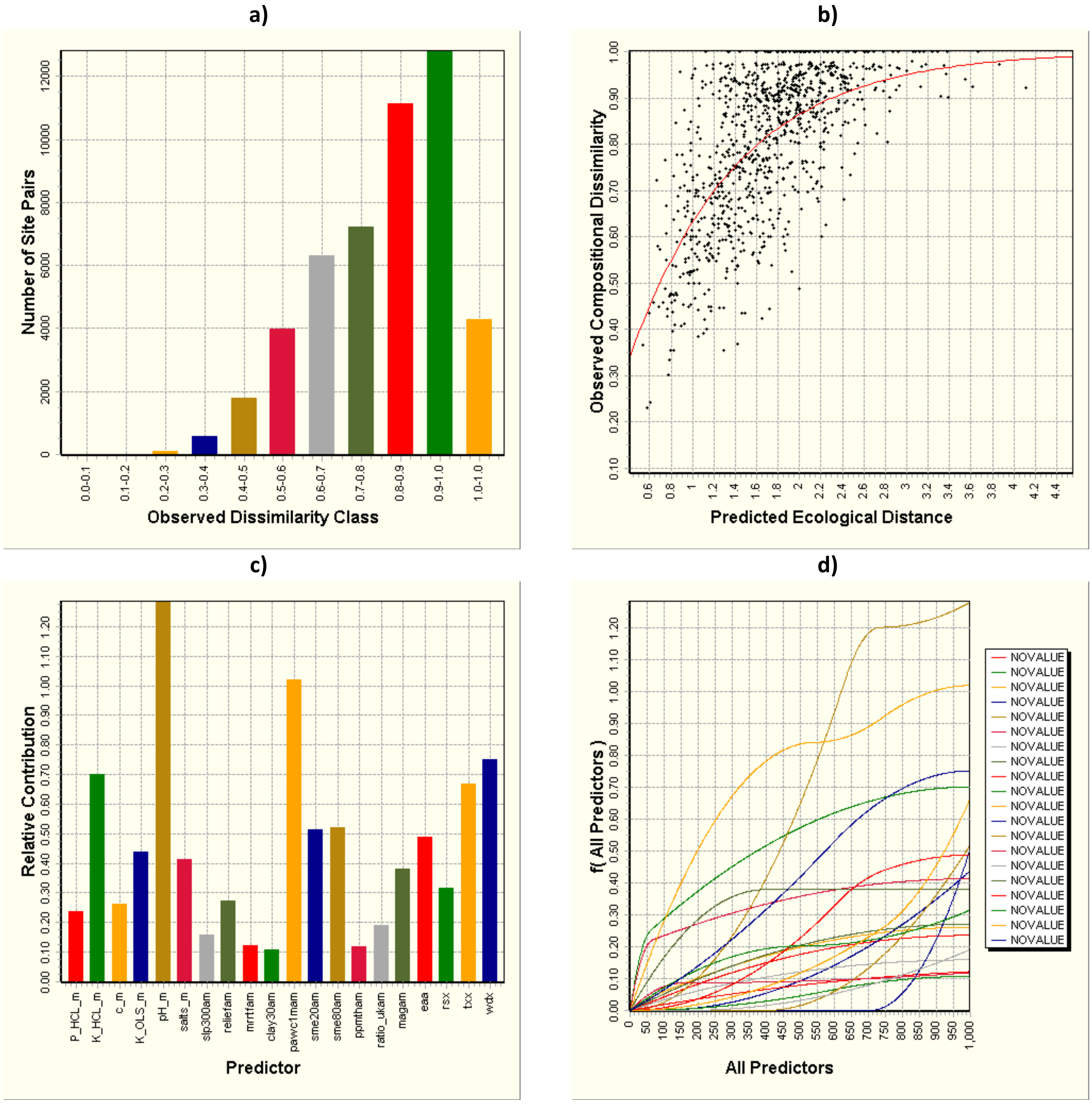


Figure A7-94. Tingle Mosaic survey 1-second fitted model for vascular plants with local soil variable: a) dissimilarity response variable; b) overall fit of the logit model – observed versus predicted; c) relative contribution of the predictors (sum of spline coefficient values), d) composite of the variable fitted functions.

Discussion

We developed 15 continental and 3 regional models of species compositional turnover. The outputs of these models, a set of scaled environmental predictors for each biological group, are the inputs to an analysis of refugia (Ferrier et al. in prep). Individual models for vascular plant taxonomic groups, such as the Proteales, were presented here for the first time. While different predictors were typically selected in each model, the topographically adjusted climatic predictors featured strongly. Climate variables were more important in the continental and regional models with substrate increasingly dominating models at the local scale.

There is potential to improve the explanatory power of these models by using weights and covariates to account for under-sampling across the more remote regions of Australia. Here we used a minimum richness per site to account for under-sampling. An under-sampling covariate based on the number of species per site and the number of independent samples was previously developed and applied to 1km gridded continental modelling of compositional turnover (Williams *et al.*, 2010a, Williams *et al.*, 2010b). Ferrier *et al.* (2007) also reported using weighting by numbers of species applied to the response variable to account for differences in collection effort between locations. This weight functionality and an option to use sampling covariates will be available in future releases of the GDM software.

The bioclimatic indices used in these models derive from long-term average monthly conditions. Climate variability and extremes are also known to be significant drivers of biodiversity distribution patterns and compositional turnover (Jackson *et al.*, 2009). There is potential to explain additional model variance by accounting for inter-annual climatic variability and indices of climatically-driven ecological disturbance regimes and thresholds. This is a topic of ongoing interest and research, requiring also the derivation of similar indices from the outputs of global climate models to enable their use in projections of biodiversity retention and loss.

Acknowledgements

Shawn Laffan provided access to the latest production versions of Biodiverse software and supported trouble shooting to enable representative site-pair sampling for the GDM analysis.

Tom Jovanovic and Debbie Crawford assisted with downscaling of climate scenario data for the 3-second gridded applications.

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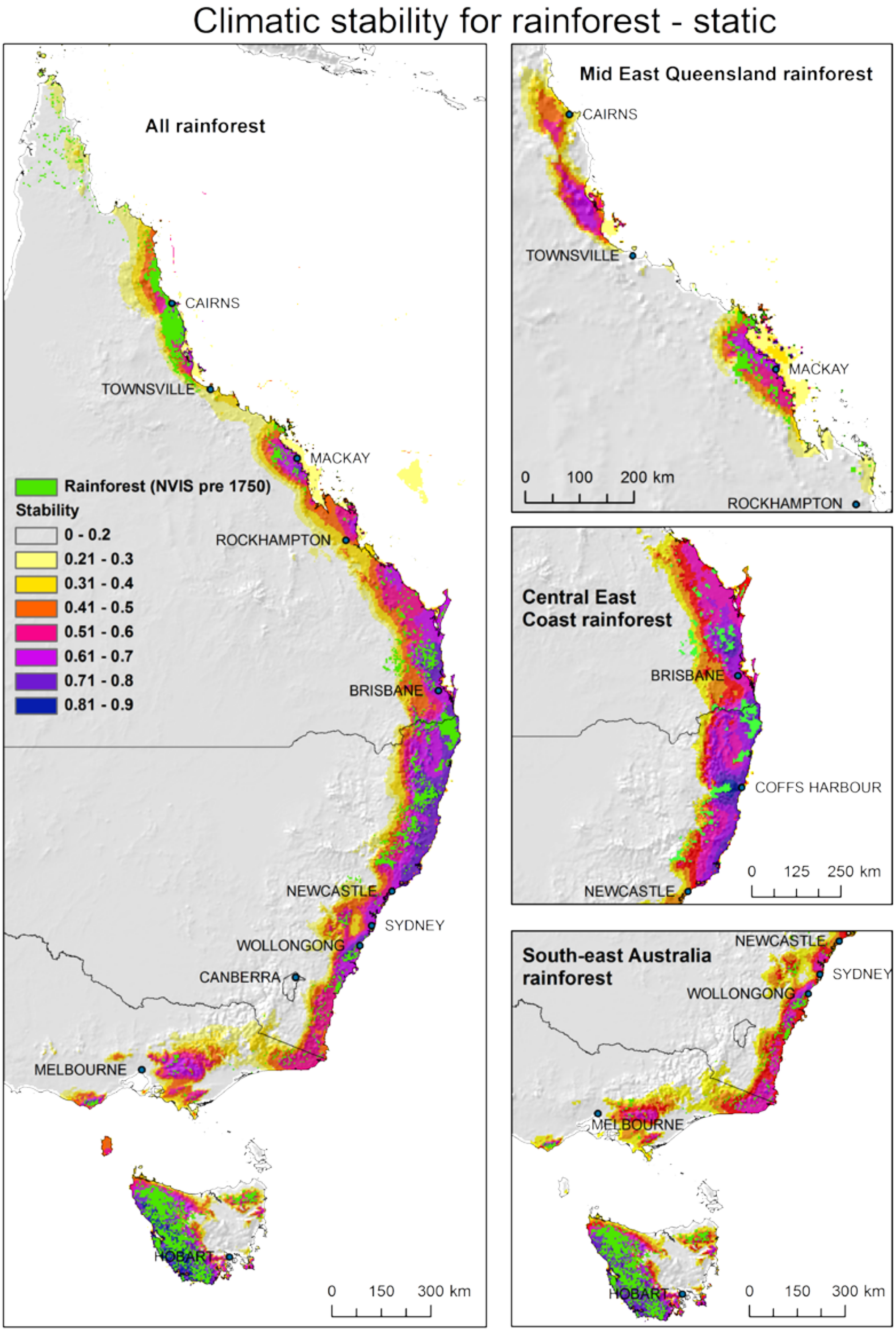
APPENDIX 8. PLEISTOCENE STABILITY AND DIVERSITY OF HERPETOFAUNA



Climatic stability for rainforest - static

Figure A8-1. Stability of the climatic niche of rainforest over the past 120k years - static. Blue areas were the most continuously suitable for rainforest. Rainforest areas from the national vegetation information system (nvis) are shown in bright green. To see the stability values without rainforest, and further explanation, refer to figure 50 in the main report.

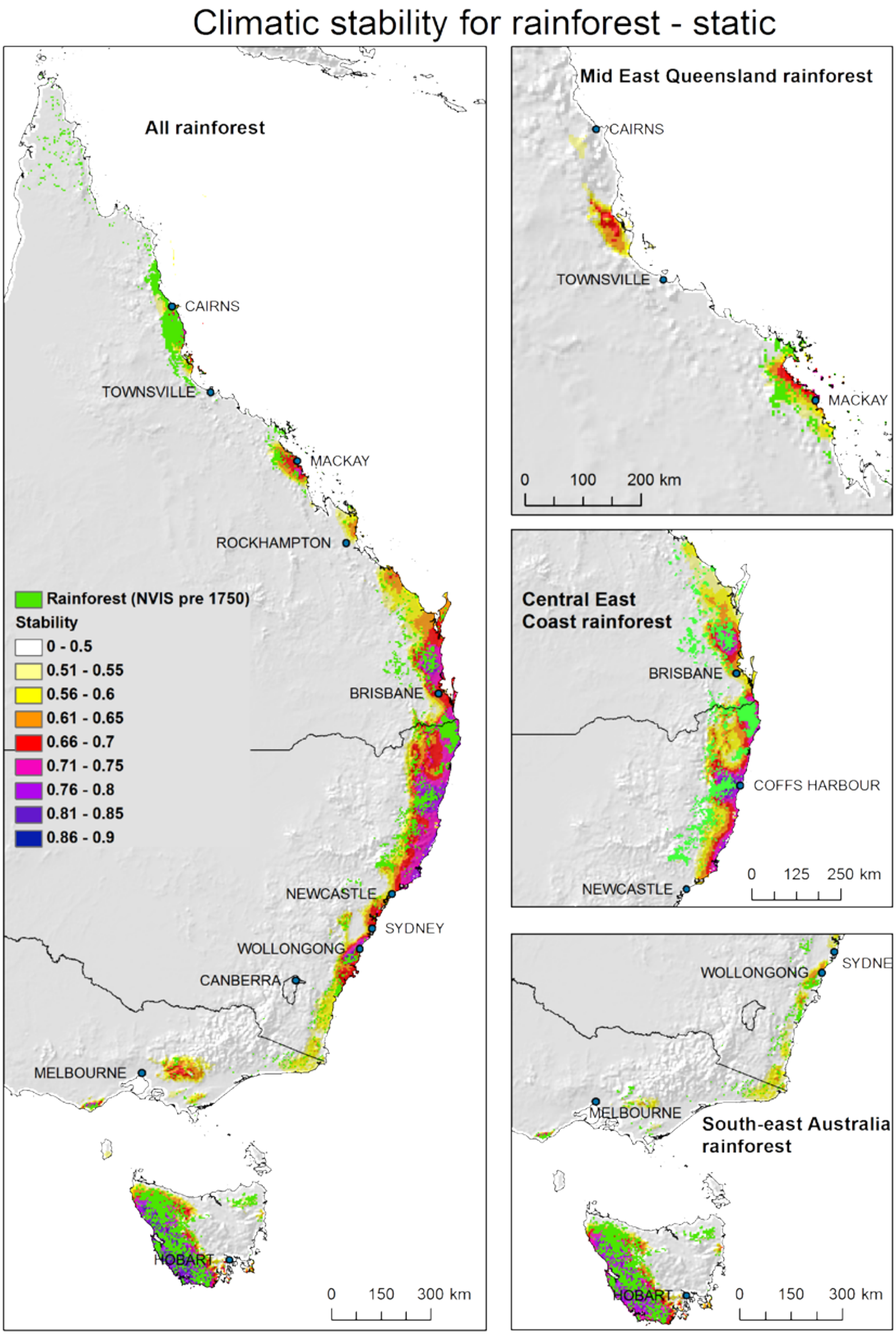


Figure A8-2. Stability of the climatic niche of rainforest over the past 120k years – shifting refugia 10myr^{-1}. Blue areas were the most continuously suitable for rainforest. Rainforest areas from the National Vegetation Information System (NVIS) are shown in bright green. To see the stability values without rainforest, and further explanation, refer to Figure 51 in the main report.

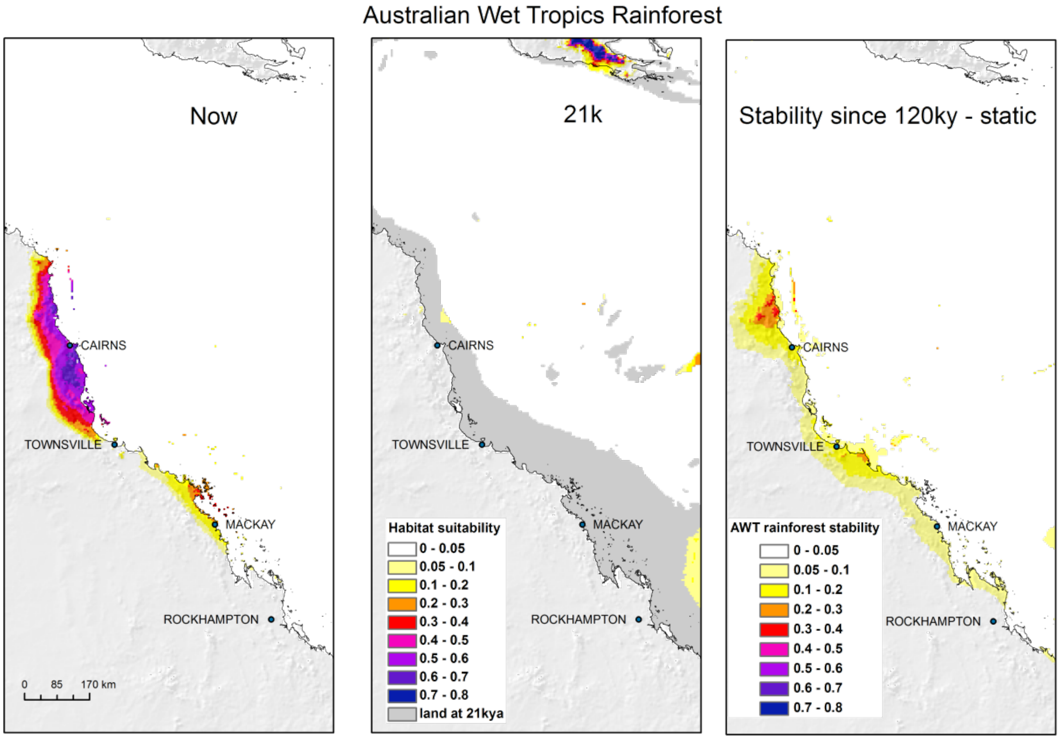


Figure A8-3. Rainforest in the Australian Wet Tropics (AWT). Modelled now, at the last glacial maximum (~21kya) and stability since 120kya. This model is problematic, as it indicates absence of rainforest from the AWT at the LGM, and very low stability for the area.

APPENDIX 9. CONSERVATION PLANNING SPECIES INFORMATION

Table A9-19. Rainforest codes used as species weighting in the conservation prioritization analysis for the Australian Wet Tropics bioregion.

Code	Description
3	Commonly recorded in rainforest however rainforest is not the species core habitat
4	rainforest is the species main habitat however it is common in other forest environments
5	rainforst is the species core habitat but it also occurs in adjacent wet sclerophyll forest
6	rainforest obligate

Table A9-20. Species (n=191) used in the conservation prioritization analysis for the Australian Wet Tropics Bioregion. The species were weighted based on the Rainforest code.

Species	Id code	Taxa	Family	Rainforest code
Alectura lathami	ABT	BIRD	Megapodiidae	4
Antechinus adustus	ANTADUS	MAMM	Dasyuridae	6
Antechinus flavipes	ANTFLAV	MAMM	Dasyuridae	4
Antechinus godmani	ANTGODM	MAMM	Dasyuridae	6
Sericornis keri	ASW	BIRD	Acanthizidae	6
Austrochaperina fryi	AUSFRYI	FROG	Microhylidae	5
Austrochaperina pluvialis	AUSPLUV	FROG	Microhylidae	5
Austrochaperina robusta	AUSROBU	FROG	Microhylidae	5
Ceyx azureus	AZK	BIRD	Alcedinidae	4
Zoothera lunulata	BASTH	BIRD	Turdidae	5
Tanysiptera sylvia	BBPK	BIRD	Halcyonidae	5
Cracticus quoyi	BBUT	BIRD	Artamidae	4
Coracina lineata	BCS	BIRD	Campephagidae	4
Cacomantis variolosus	BCUC	BIRD	Cuculidae	3
Monarcha melanopsis	BFMON	BIRD	Monarchidae	5
Erythrura trichroa	BFPF	BIRD	Estrildidae	4
Gerygone mouki	BGER	BIRD	Acanthizidae	6
Lichenostomus frenatus	BHE	BIRD	Meliphagidae	5
Boiga irregularis	BOIIRRE	REPT	Colubridae	3
Ninox novaeseelandiae	BOO	BIRD	Strigidae	3
Macropygia amboinensis	BPIG	BIRD	Columbidae	5
Colluricincla boweri	BST	BIRD	Pachycephalidae	6
Cacophis churchilli	CACCHUR	REPT	Elapidae	4

Canis lupus dingo	CANLUPU	MAMM	Canidae	3
Carphodactylus laevis	CARLAEV	REPT	Gekkonidae	6
Carlia rhomboidalis	CARRHOM	REPT	Scincidae	4
Carlia rubrigularis	CARRUBR	REPT	Scincidae	5
Casuarius casuarius	CASS	BIRD	Casuariidae	6
Ailuroedus melanotis	CAT	BIRD	Ptilonorhynchidae	5
Cacomantis castaneiventris	CBCUC	BIRD	Cuculidae	4
Scythrops novaehollandiae	CBILCUC	BIRD	Cuculidae	3
Orthonyx spaldingii	CC	BIRD	Orthonychidae	5
Cercartetus caudatus	CERCAUD	MAMM	Burryamyidae	6
Coeranoscincus frontalis	COEFRON	REPT	Scincidae	6
Cophixalus bombiens	COPBOMB	FROG	Microhylidae	5
Cophixalus concinnus	COPCONC	FROG	Microhylidae	6
Cophixalus exiguus	COPEXIG	FROG	Microhylidae	5
Cophixalus hosmeri	COPHOSM	FROG	Microhylidae	6
Cophixalus infacetus	COPINFA	FROG	Microhylidae	6
Cophixalus mcdonaldi	COPMCDO	FROG	Microhylidae	5
Cophixalus monticola	COPMONT	FROG	Microhylidae	6
Cophixalus neglectus	COPNEGL	FROG	Microhylidae	6
Cophixalus ornatus	COPORNA	FROG	Microhylidae	5
Platycercus elegans	CROS	BIRD	Psittacidae	4
Strepera graculina	CURR	BIRD	Artamidae	4
Cyclodomorphus gerrardii	CYCGERR	REPT	Scincidae	3
Dactylopsila trivirgata	DACTRIV	MAMM	Petauridae	5
Dasyurus maculatus	DASMACU	MAMM	Dasyuridae	5
Cyclopsitta diophthalma	DEFP	BIRD	Psittacidae	5
Demansia psammophis	DEMPSAM	REPT	Elapidae	3
Dendrolagus bennettianus	DENBENN	MAMM	Macropodidae	6
Dendrelaphis calligastra	DENCALL	REPT	Colubridae	4
Dendrolagus lumholtzi	DENLUMH	MAMM	Macropodidae	6
Dendrelaphis punctulata	DENPUNC	REPT	Colubridae	3
Myzomela obscura	DUHE	BIRD	Meliphagidae	3
Chalcophaps indica	ED	BIRD	Columbidae	5

Egernia frerei	EGEFRER	REPT	Scincidae	4
Acanthorhynchus tenuirostris	ESB	BIRD	Meliphagidae	4
Eulamprus brachysoma	EULBRAC	REPT	Scincidae	4
Eulamprus frerei	EULFRER	REPT	Scincidae	6
Eulamprus quoyii	EULQUOY	REPT	Scincidae	4
Eulamprus tigrinus	EULTIGR	REPT	Scincidae	6
Psophodes olivaceus	EWB	BIRD	Psophodidae	5
Gerygone palpebrosa	FGER	BIRD	Acanthizidae	3
Sphecotheres vieilloti	FIG	BIRD	Oriolidae	4
Cacomantis flabelliformis	FTCUC	BIRD	Cuculidae	4
Furina ornata	FURORNA	REPT	Elapidae	3
Furina tristis	FURTRIS	REPT	Elapidae	3
Oreoscopus gutturalis	FW	BIRD	Acanthizidae	6
Chalcites minutillus	GBCUC	BIRD	Cuculidae	4
Rhipidura albiscapa	GFAN	BIRD	Rhipiduridae	3
Accipiter novaehollandiae	GGH	BIRD	Accipitridae	5
Meliphaga gracilis	GHE	BIRD	Meliphagidae	5
Heteromyias cinereifrons	GHR	BIRD	Petroicidae	5
Glaphyromorphus fuscicaudis	GLAFUSC	REPT	Scincidae	5
Glaphyromorphus mjobergi	GLAMJOB	REPT	Scincidae	6
Gnypetoscincus queenslandiae	GNYQUEE	REPT	Scincidae	6
Amblyornis newtonianus	GOLDBB	BIRD	Ptilonorhynchidae	6
Pachycephala pectoralis	GOLDW	BIRD	Pachycephalidae	4
Pachycephala simplex	GREYW	BIRD	Pachycephalidae	3
Hemibelideus lemuroides	HEMLEMU	MAMM	Pseudocheiridae	6
Hemiaspis signata	HEMSIGN	REPT	Elapidae	4
Philemon buceroides	HFB	BIRD	Meliphagidae	3
Hypsilurus boydii	HYPBOYD	REPT	Agamidae	6
Hypsiprymnodon moschatus	HYPMOSC	MAMM	Potoroidae	6
Eudynamys orientalis	KOEL	BIRD	Cuculidae	3
Alisterus scapularis	KP	BIRD	Psittacidae	4
Lampropholis coggeri	LAMCOGG	REPT	Scincidae	5

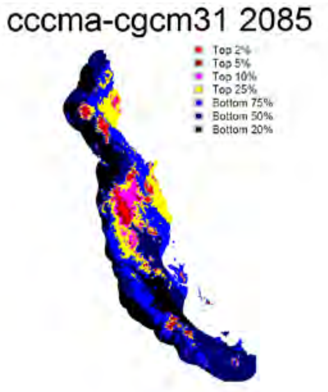
Lampropholis mirabilis	LAMMIRA	REPT	Scincidae	3
Lampropholis robertsi	LAMROBE	REPT	Scincidae	6
Chalcites minutillus	LBCUC	BIRD	Cuculidae	4
Gerygone magnirostris	LBGER	BIRD	Acanthizidae	3
Sericornis magnirostra	LBSW	BIRD	Acanthizidae	5
Meliphaga lewinii	LEWHE	BIRD	Meliphagidae	5
Limnodynastes peronii	LIMPERO	FROG	Myobatrachidae	3
Litoria fallax	LITFALL	FROG	Hylidae	3
Litoria genimaculata	LITGENI	FROG	Hylidae	5
Litoria infrafrenata	LITINFR	FROG	Hylidae	4
Litoria lorica	LITLORI	FROG	Hylidae	5
Litoria nannotis	LITNANN	FROG	Hylidae	5
Litoria nyakalensis	LITNYAK	FROG	Hylidae	6
Litoria revelata	LITREVE	FROG	Hylidae	5
Litoria rheocola	LITRHEO	FROG	Hylidae	6
Litoria xanthomera	LITXANT	FROG	Hylidae	4
Ceyx pusilla	LK	BIRD	Alcedinidae	4
Tyto tenebricosa	LSOWL	BIRD	Tytonidae	5
Colluricincla megarhyncha	LST	BIRD	Pachycephalidae	4
Xanthotis macleayanus	MACHE	BIRD	Meliphagidae	5
Melomys cervinipes	MELCERV	MAMM	Muridae	4
Mixophyes schevilli	MIXSCHE	FROG	Myobatrachidae	5
Morelia kinghorni	MORKING	REPT	Boidae	5
Morelia spilota	MORSPIL	REPT	Boidae	3
Aplornis metallica	MSTAR	BIRD	Sturnidae	4
Dicaeum hirundinaceum	MTB	BIRD	Dicaeidae	3
Acanthiza katherina	MTHORN	BIRD	Acanthizidae	5
Nactus cheverti	NACCHEV	REPT	Gekkonidae	4
Pitta versicolor	NPIT	BIRD	Pittidae	5
Nyctimystes dayi	NYCDAYI	FROG	Hylidae	5
Oriolus sagittatus	OBO	BIRD	Oriolidae	3
Cuculus optatus	OCUC	BIRD	Cuculidae	3
Megapodius reinwardt	OFSF	BIRD	Megapodiidae	5
Ornithorhynchus anatinus	ORNANAT	MONO	Ornithorhyncidae	4
Perameles nasuta	PERNASU	MAMM	Peramelidae	5
Podargus papuensis	PFROG	BIRD	Podargidae	4
Phyllurus amnicola	PHYAMNI	REPT	Gekkonidae	4
Phyllurus gulbaru	PHYGULB	REPT	Gekkonidae	4
Physignathus lesueurii	PHYLESU	REPT	Agamidae	4

Ducula bicolor	PIPIG	BIRD	Columbidae	5
Arses kaupi	PMON	BIRD	Monarchidae	5
Pogonomys mollipilosus	POGMOLL	MAMM	Muridae	6
Pseudochirops archeri	PSEARCH	MAMM	Pseudocheiridae	6
Pseudochirulus cinereus	PSECINE	MAMM	Pseudocheiridae	6
Pseudochirulus herbertensis	PSEHERB	MAMM	Pseudocheiridae	6
Pseudechis porphyriacus	PSEPORP	REPT	Elapidae	4
Tregellasia capito	PYR	BIRD	Petroicidae	5
Ramphotyphlops polygrammicus	RAMPOLY	REPT	Typhlopidae	3
Rana daemeli	RANDAEM	FROG	Ranidae	4
Rattus fuscipes	RATFUSC	MAMM	Muridae	4
Rattus leucopus	RATLEUC	MAMM	Muridae	5
Merops ornatus	RBBE	BIRD	Meropidae	3
Ptilinopus regina	RCFD	BIRD	Columbidae	5
Rhipidura rufifrons	RFAN	BIRD	Rhipiduridae	4
Cryptophis nigrescens	RHINIGR	REPT	Elapidae	5
Trichoglossus haematodus	RL	BIRD	Psittacidae	4
Rallina tricolor	RNCR	BIRD	Rallidae	5
Ninox rufa	ROWL	BIRD	Strigidae	3
Saltuarius cornutus	SALCORN	REPT	Gekkonidae	5
Saproscincus basiliscus	SAPBASI	REPT	Scincidae	5
Saproscincus czechurai	SAPCZEC	REPT	Scincidae	6
Saproscincus lewisi	SAPLEWI	REPT	Scincidae	5
Saproscincus tetradactylus	SAPTETR	REPT	Scincidae	6
Ptilonorhynchus violaceus	SATBB	BIRD	Ptilonorhynchidae	5
Chalcites lucidus	SBCUC	BIRD	Cuculidae	4
Trichoglossus chlorolepidotus	SBL	BIRD	Psittacidae	3
Myzomela sanguinolenta	SCARHE	BIRD	Meliphagidae	3
Cacatua galerita	SCC	BIRD	Cacatuidae	3
Dicrurus bracteatus	SD	BIRD	Dicruridae	3
Zosterops lateralis	SE	BIRD	Timaliidae	4
Ptilinopus superbus	SFD	BIRD	Columbidae	5
Sminthopsis leucopus	SMILEUC	MAMM	Dasyuridae	6
Symposiarchus trivirgatus	SMON	BIRD	Monarchidae	5

Stegonotus cucullatus	STECUCU	REPT	Colubridae	4
Taudactylus acutirostris	TAUACUT	FROG	Myobatrachidae	6
Taudactylus rheophilus	TAURHEO	FROG	Myobatrachidae	6
Scenopoeetes dentirostris	TBBB	BIRD	Ptilonorhynchidae	6
Techmarscincus jigurru	TECJIGU	REPT	Scincidae	6
Thylogale stigmatica	THYSTIG	MAMM	Macropodidae	5
Lopholaimus antarcticus	TPIG	BIRD	Columbidae	5
Trichosurus vulpecula j.	TRIJOHN	MAMM	Phalangeridae	5
Tropidechis carinatus	TROCARI	REPT	Elapidae	5
Tropidonophis mairii	TROMAIR	REPT	Colubridae	3
Uromys caudimaculatus	UROCAUD	MAMM	Muridae	5
Uromys hadrourus	UROHADR	MAMM	Muridae	6
Varanus scalaris	VARSCAL	REPT	Varanidae	4
Varanus varius	VARVARI	REPT	Varanidae	4
Vermicella annulata	VERANNU	REPT	Elapidae	3
Ptiloris victoriae	VRIF	BIRD	Paradisaeidae	5
Lalage leucomela	VT	BIRD	Campephagidae	3
Poecilodryas superciliosa	WBR	BIRD	Petroicidae	4
Sericornis frontalis	WBSW	BIRD	Acanthizidae	4
Artamus leucorynchus	WBWS	BIRD	Artamidae	3
Carternornis leucotis	WEMON	BIRD	Monarchidae	5
Columba leucomela	WHPIG	BIRD	Columbidae	5
Ptilinopus magnificus	WOMP	BIRD	Columbidae	5
Aerodramus terraereginae	WRSW	BIRD	Apodidae	5
Hirundapus caudacutus	WTNT	BIRD	Apodidae	3
Cormobates leucophaea	WTTC	BIRD	Climacteridae	5
Machaerirhynchus flaviventer	YBBB	BIRD	Monarchidae	5
Oriolus flavocinctus	YO	BIRD	Oriolidae	4
Meliphaga notata	YSHE	BIRD	Meliphagidae	5
Sericornis citreogularis	YTSW	BIRD	Acanthizidae	5

APPENDIX 10. CONSERVATION PLANNING VARIABILITY ACROSS GCMS

Zonation conservation prioritization analysis of Australia’s Wet Tropics bioregion based on 191 terrestrial vertebrates projected species distribution models for 2085 using 18 GCMs.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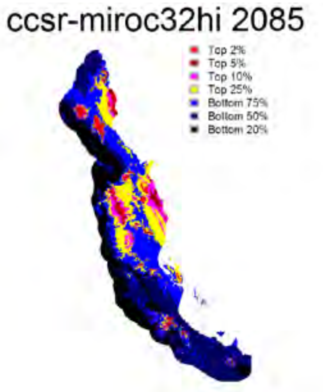
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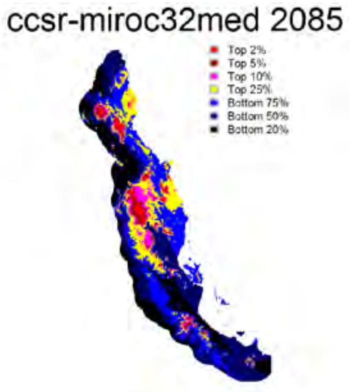
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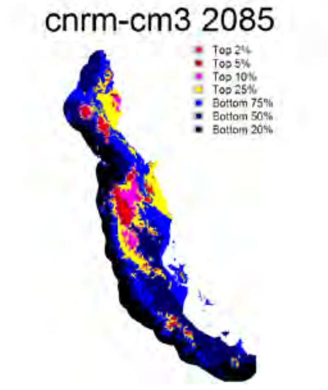
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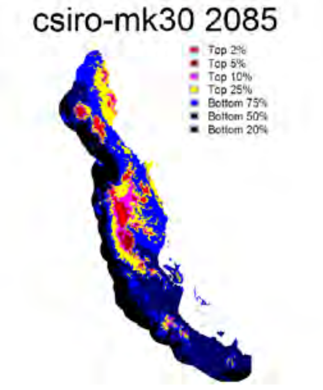
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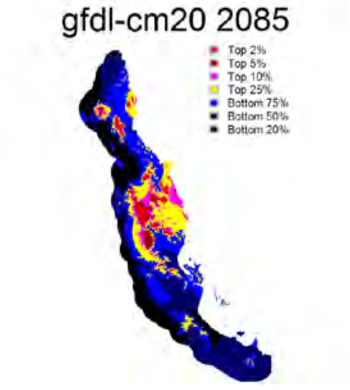
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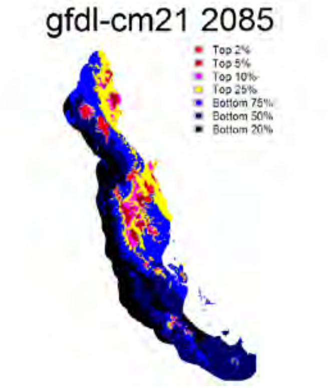
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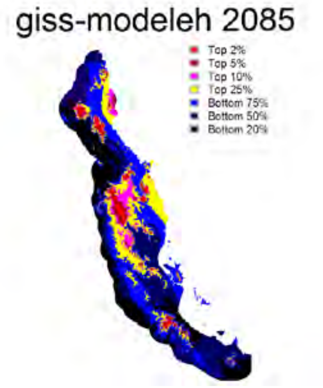
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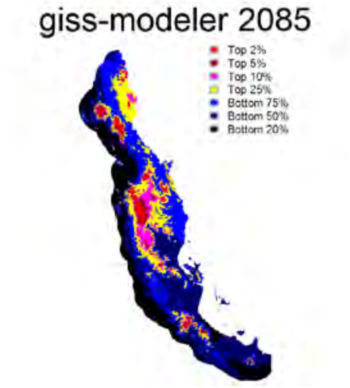
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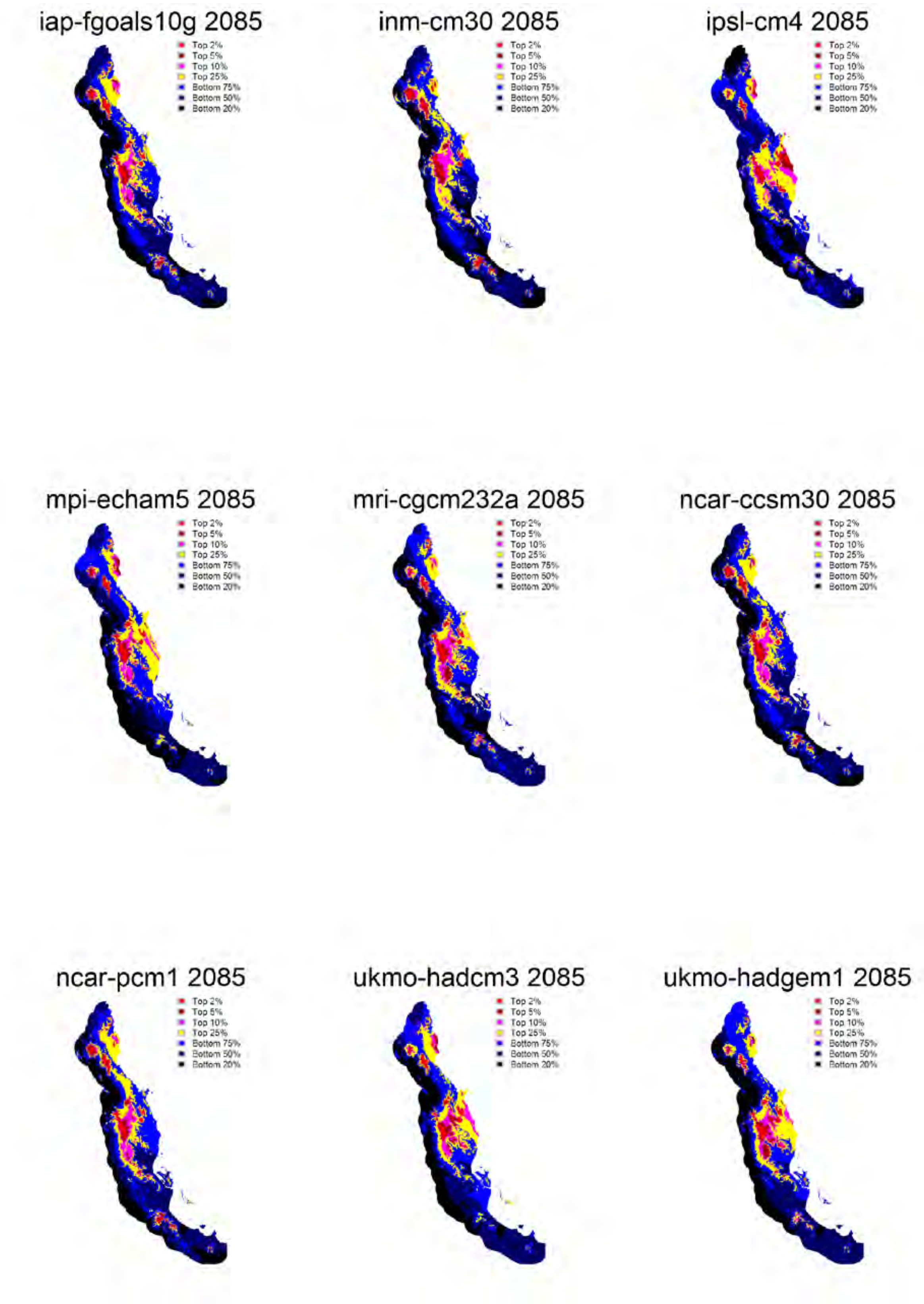

Figure A10-1. Spatial patterns of variation in conservation prioritization zonation for 191 vertebrates within the Wet Tropics for each of 18 GCMs for the year 2085.

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