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Locating adaptive diversity in the face of climate change



Thesis submitted by
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Front cover: Rainforest Sunskink (*Lampropholis coggeri*). These magnificent skinks are endemic to the rainforests of the Australian Wet Tropics, an area highly vulnerable to the effects of climate change. Photo by Stephen Michael Zozaya IV.

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This project started out due to my love of adventure and my desire to explore the Kimberley before the arrival of the dreaded cane toad. Unfortunately, Ben ruined all that by moving to Townsville. However, this turned out to be a blessing in disguise, as I ended up working with one of the most charismatic and beautiful creatures in Australia: ~~Stephen Zozaya~~ *Lampropholis coggeri*.

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Publications associated with this thesis

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Chapter 2

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Chapter 3

Macdonald, S.L. & B.L. Phillips (submitted) Are less-connected rainforest patches more climatically extreme? *Diversity & Distributions*

In preparation

Chapter 4

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Chapter 5

Macdonald, S.L., J. Vanderwal, & B.L. Phillips (in prep) Identifying source and recipient populations for assisted gene flow: matching locally adapted populations across current and future climates. *Nature Climate Change*

Animal ethics statement

This research presented and reported in this thesis was conducted in compliance with the National Health and Medical Research Council (NHMRC) Australian Code of Practice for the Care and Use of Animals for Scientific Purposes, 7th Edition, 2004 and the Qld Animal Care and Protection Act, 2001. The proposed research study received animal ethics approval from the JCU Animal Ethics Committee (approval numbers A1976 and A1726).

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Co-authorship of published manuscripts

Co-authors of published manuscripts within this thesis participated in one or more of the following ways: discussions of concept and study design, advice on methods and editing of manuscripts, collation and/or generation of data. Details of contributions are included at the start of each chapter.

Every reasonable effort has been made to gain permission and acknowledge the owners of copyright material. I would be pleased to hear from any copyright owner who has been omitted or incorrectly acknowledged.

Abstract

Climate change will have profound and negative effects on the planet's biodiversity. Conservationists and land managers are turning to a variety of strategies with the hope of mitigating some of these effects. One such strategy is assisted gene flow (AGF): the translocation of individuals between populations with the aim of increasing genetic diversity and introducing specific 'preadapted' genes that will boost the climate change resilience of the recipient population. Assisted gene flow is already in use, and is likely to see increasing use in the coming decades, but the methods needed to deploy it effectively are still being developed. To mitigate climate change impacts, assisted gene flow will be most effective when the source populations are: 1) adapted to their local climate, and 2) close to the recipient population in future climate space.

This thesis details techniques that can be used to identify the environmental drivers of local adaptation (focusing specifically on climatic drivers), and weight them according to the degree to which they drive local adaptation. These weighted climatic axes can then be used to create a climate space that accounts for the degree to which each climatic axis is driving local adaptation; a space in which AGF source and recipient populations can be sensibly matched. These concepts and techniques are demonstrated in the following chapters using a case study of the Rainforest Sunskink (*Lampropholis coggeri*) from the rainforests of north-eastern Australia.

Chapter 1 reviews the threats caused by climate change and outlines some potential mitigation strategies, with particular emphasis on assisted gene flow and novel strategies to make AGF more effective. It then outlines the structure of the thesis and sets the scene for the development of these novel strategies.

Chapter 2 outlines the ecological factors that should be considered when searching for potential source populations: population size, connectivity, and climate. Knowing that isolation (i.e., low connectivity) is conducive to local adaptation, a connectivity index is developed that is used in the analyses that appear in subsequent chapters.

Given that we are looking for local adaptation to extreme climates, and knowing that isolation is conducive to local adaptation, **Chapter 3** then explores the relationship between climatic extremity and habitat connectivity, and finds that more isolated rainforest habitat does indeed experience more extreme climate, and that these shifts towards extremity are in the direction of climate change. As such, isolated habitats, free from gene swamping and subject to extreme climates, are likely to contain populations adapted to the sorts of climates we expect to be more widespread in the future. It is these populations that will make ideal source populations for assisted gene flow strategies.

Chapter 4 develops a method for determining which aspects of the environment most strongly drive local adaptation. It does this by recognizing that high connectivity leads to high levels of gene flow, which erodes local adaptation. This method is demonstrated by determining which aspects of climate are the strongest drivers of local adaptation in the case study system. The relationships between various climatic variables and physiological and morphological traits in the focal skink species are examined, and the degree to which gene flow erodes these relationships is assessed using the connectivity index developed in Chapter 2. In my study system, this highlighted two precipitation variables (annual mean precipitation and precipitation of

the driest quarter) as those aspects of climate that appear to be the strongest drivers of local adaptation.

Chapter 5 combines the connectivity index from Chapter 2 and the climatic drivers of local adaptation from Chapter 4, and develops a technique to match potential source and recipient populations, weighting climatic axes to account for the degree to which they drive local adaptation. It uses a case study involving *L. coggeri* to demonstrate this technique, and then discusses the results of the case study and the generality of the technique.

Finally, **Chapter 6** summarises the main findings and suggests some avenues for future research.

This thesis brings together considerations from both ecology and evolution to argue that isolated patches of habitat on the edge of a species' range are likely to contain populations that will be of great importance if we are to conserve species in the face of climate change. The same characteristics that make these isolated populations so valuable (small size and extreme climates), however, also put them at the highest risk of extinction from climate change. Given the rapid rate at which climate change is progressing, the identification and conservation of adaptive diversity present in isolates is of utmost importance.

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Chapter 1

Introduction

Climate change as a threat to biodiversity

Anthropogenic climate change is one of the biggest threats facing the world's biodiversity (Thomas *et al.* 2004). The coming century will see an increase in global mean temperatures, increases in the frequency and intensity of extreme events, and alterations to precipitation regimes (Meehl *et al.* 2000; Parmesan *et al.* 2000; IPCC 2014; Sherwood & Fu 2014). If we see a 4°C increase in global mean temperature over the next century — a not unreasonable expectation (IPCC 2014) — the planet will be the warmest it has been in the last 40 million years, and this warming will take place up to 40 times faster than past episodes of climate change (Peters 1994). The magnitude and rate of this warming will have severe impacts on global biodiversity. Predicted or observed impacts on species include: shifts in geographical distributions, including complete turnover of some ecosystems (e.g., Parmesan & Yohe 2003; Hilbert *et al.* 2004; Williams *et al.* 2007; Freeman & Freeman 2014); population extinctions (Parmesan 2006); changes to the timing of migration (Chambers & Keatley 2010); changes to nesting regimes or habitats (Pike *et al.* 2006; Telemeco *et al.* 2009); and alterations, including extinctions, of entire montane communities (Pounds *et al.* 1999).

Broad strategies to account for climate change in conservation planning have been developed (Hannah *et al.* 2002; Heller & Zavaleta 2009), and conservation biologists are investigating a variety of specific implementations to mitigate impacts. Many techniques have been suggested or are already in use, such as habitat restoration and

modification (e.g., Naro-Maciel *et al.* 1999; Shoo *et al.* 2011a; Shoo *et al.* 2011b), and relocation of nests for species whose sex ratios may be skewed by increasing temperatures (e.g., Fuentes *et al.* 2012). Many strategies that have been used to test or mitigate other impacts may also be useful in the face of climate change, such as artificial manipulation of hydrological regimes in key habitat (e.g., Mitchell 2001; Channing *et al.* 2006).

One established technique is assisted colonisation (AC) — the conservation translocation and establishment of a new population outside of a species' current distribution (Peters 1994; IUCN 2013; Seddon *et al.* 2015). While most translocations have been in response to threats such as habitat destruction and introduced predators, the number of translocations performed in response to climate change is increasing (e.g., Marris 2009; Willis *et al.* 2009). Although many AC attempts have been successful, and have arguably saved a number of species from extinction (Seddon *et al.* 2015), the strategy is not without critics (Ricciardi & Simberloff 2009). One of the primary concerns with AC is that the translocated species will disrupt the ecosystem into which it is introduced. Given the dismal history of deliberate and accidental translocations across the planet (e.g., toads: Shine & Phillips 2014), this is a valid concern.

Another, less risky, technique that is expected to see increasing use is assisted gene flow (AGF). Instead of attempting to establish entirely new populations in climatically suitable areas, individuals are translocated from a carefully selected source population to an existing population to boost the health and resilience of the recipient population (Weeks *et al.* 2011; Aitken & Whitlock 2013; Frankham 2015;

Kelly & Phillips 2015). Perhaps the most famous example of AGF involves the successful reversal of inbreeding depression in the declining Florida Panther, *Puma concolor coryi* (Johnson *et al.* 2010). A recent Australian AGF example involves the genetic rescue of the Mountain Pygmy Possum, *Burramys parvus* (Weeks *et al.* 2015). This wild-to-wild translocation program was undertaken to increase the genetic diversity of a small, declining population that exhibited very low levels of genetic diversity. While these two examples were not done to mitigate against climate change, they highlight the effectiveness of the technique, and its acceptance by academic and governmental communities. In the face of climate change, the key to effective assisted gene flow efforts will be to find source populations currently experiencing climates that the recipient population will experience in the future. Importantly, however, we also require that these source populations be adapted to their current climate.

Optimal phenotypes vary through both time and space, leading to populations that have higher fitness in their home environment than an immigrant would (Reznick & Travis 1996; Kawecki & Ebert 2004). This is the basis of local adaptation, a widespread, but not ubiquitous, phenomenon (Kawecki & Ebert 2004; Hereford 2009). Local adaptation is eroded in the face of strong gene flow, so isolation can be an important pre-condition for local adaptation (Haldane 1956; Kirkpatrick & Barton 1997). Isolation by itself, however, does not lead to local adaptation. The driving force behind local adaptation is selection from the environment, and selection pressures can change over relatively short timeframes and spatial scales (Reznick & Travis 1996; Losos *et al.* 1997; Kawecki & Ebert 2004; Richardson *et al.* 2014). Past episodes of climate change have required species to shift their range or adjust *in situ*.

Two aspects of current climate change make these past responses inadequate: 1) severely fragmented landscapes reduce connectivity and therefore reduce the ability of a species to disperse to new areas while tracking optimal climatic conditions; and 2) the magnitude and rapid rate at which climate change is proceeding far exceeds anything species have had to contend with historically. Species and populations are vulnerable if the climate they experience changes too much or too quickly.

Across a heterogeneous landscape, different populations of the same species will experience, and therefore will likely be adapted to, different climates. Assisted gene flow exploits this variability by predicting the future climate of recipient populations and looking for source populations whose current climate matches this future.

Climate, however, is multidimensional, and different aspects of climate may drive local adaptation to varying degrees. If, for example, temperature has a bigger influence on fitness than does precipitation, it is more important to match along the temperature axis than the precipitation axis. This is because, in this example, one unit of change away from the species' optimal temperature represents a larger fitness reduction than the same unit of change on the precipitation axis. When matching source and recipient populations in a multidimensional climate space, we should aim to weight the various axes according to how strongly they drive local adaptation. This, in effect, stretches the axes that are more important and compresses those climatic axes that appear to be exerting weaker selective forces. By weighting the various climate axes, we can make better matches between source and recipient populations when planning AGF implementations.

Study region

The rainforests of the Australian Wet Tropics (AWT) make an ideal system in which to demonstrate these concepts and techniques. This bioregion is a mosaic of naturally occurring rainforest fragments surrounded by a matrix of drier forest (Fig. 1.1).

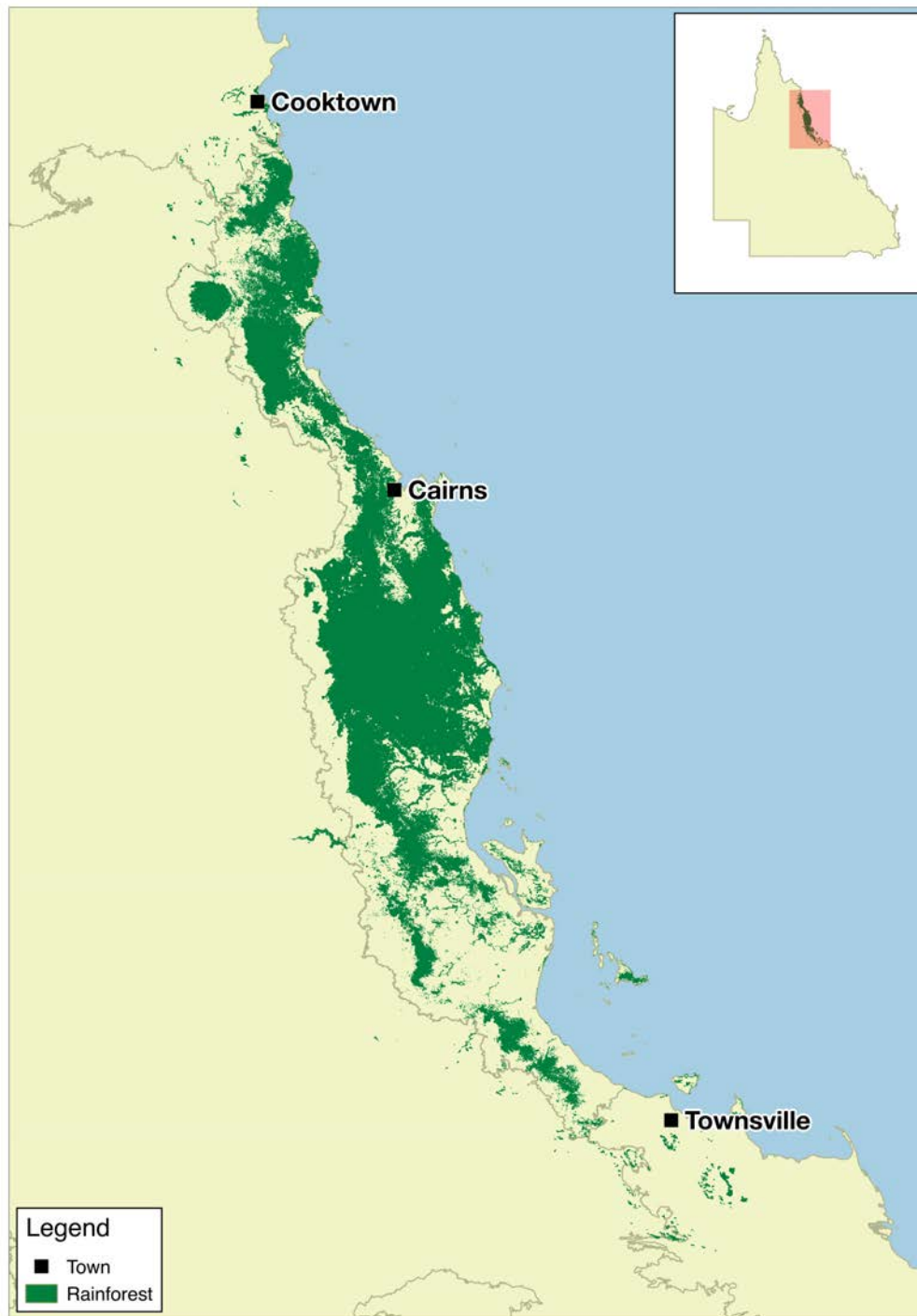


Figure 1.1

Pre-clearing (pre-1750) distribution of rainforest in the Australian Wet Tropics.

These rainforests are home to an extraordinary diversity of species, many of which have been highlighted as being particularly vulnerable to climate change (Williams *et al.* 2003). The region's vegetation has been extensively mapped (Accad & Neil 2006; DERM 2011), and this mapping was used to identify the rainforest patches that were used in my study. The AWT is mapped as having contained 7,095 discrete rainforest patches prior to European settlement (Fig. 1.1). I used the pre-clearing (pre-1750) vegetation layer, as I was interested in the isolation over thousands of years rather than more recent anthropogenic clearing-driven isolation. While patches have generally decreased in extent since European settlement because of land clearing, many patches have expanded their borders due to the decreased incidence of fire (decreased fire favours rainforest over wet sclerophyll forest, even though both habitat types share very similar climatic needs). This region spans significant elevation (0–1600 m ASL), precipitation (annual mean precipitation of 1432–8934 mm, excluding input from cloud stripping), and temperature (annual mean temperature of 16.3–25.8°C) gradients.

The AWT rainforest contains a myriad of species distributed as numerous isolated populations that are all experiencing unique climates and are therefore potentially adapted to those climates. I focused on one species in particular, the Rainforest Sunskink (*Lampropholis coggeri*). This species was chosen because it is rainforest-specific, abundant, highly detectable, and because there is detailed phylogeographic information available for it (Bell *et al.* 2010). I collected survey data for approximately 100 rainforest patches to determine the presence or absence of this species. When present, I collected up to 20 individuals for detailed morphological and physiological analyses. I also collated temperature, precipitation, and vegetation data

layers for the entire region to characterize the climate of each rainforest patch. This dataset allowed me to assess the relationships between the environment (focusing on current and future climates); the presence, morphology, and physiology of my focal skink species; and habitat connectivity. Using these data, I addressed the fundamental aims of this study.

Aims of this study

The aim of this study was to develop techniques for identifying source and recipient populations for AGF to mitigate climate change impacts. Building on evolutionary and ecological theories, this thesis makes the case that, in many systems, peripheral isolates (small, isolated patches of habitat on the periphery of a species' range) will contain populations that are ideal for use as source populations in AGF strategies. I start by detailing the broad reasoning behind this focus on peripheral isolates, then present supporting evidence, and conclude by developing and demonstrating techniques for use in AGF strategies. I answer the following four specific research questions:

1 - Why is isolation important and how do we define connectivity?

Chapter 2 introduces the ecological and evolutionary reasons why peripheral isolates are likely to house important adaptive diversity. One of the most important reasons is that isolation leads to divergence (which may or may not be adaptive). Because isolation is a central theme of this thesis, it is important that I have a robust measure of connectivity. Chapter 2 develops a connectivity index that is then used in all subsequent analyses.

2 - Do isolated areas experience more extreme climates?

Chapter 3 tests one of the major assumptions of Chapter 2; that peripheral populations experience more extreme climates. By using the connectivity index developed in Chapter 2, along with broadscale but high-resolution climate layers, I show that areas of low connectivity experience higher than average temperature extremes, and lower and more seasonal precipitation regimes. These are the types of extreme climates that are predicted to be more common in the future, and so populations currently surviving under these extreme conditions can provide important information on the capacity for a species to adapt to climate change. More practically, these extreme populations may provide the source genetic material needed for AGF strategies hoping to boost climate change resilience in the species' wider range.

3 - How do we detect the environmental drivers of local adaptation?

Chapter 4 develops a technique for identifying local adaptation, and most importantly, the environmental drivers behind that adaptation. This novel technique relies on the way in which increasing gene flow erodes local adaptation. By looking for correlations between the environment (e.g., climate) and species traits (e.g., morphological or physiological traits), and then assessing the way in which connectivity (as a proxy for gene flow) alters those correlations, we can separate environment–trait relationships that are due to local adaptation from those that arise through other processes (such as phenotypic plasticity). This technique can also be used to provide a relative measure of the strength of local adaptation, and so identifies the aspects of the environment that appear to be the strongest drivers of adaptation. In my study system, two aspects of precipitation (annual mean precipitation and

precipitation of the driest quarter) appear to be the main drivers of local adaptation in the climate-relevant physiological traits I examined.

4 - Where will we find adaptive diversity in the landscape?

Chapter 5 builds on the idea that isolation and climatic extremity lead to the development of local adaptation that will be valuable in the face of climate change, and identifies source patches that are isolated and climatically extreme, but still likely to be occupied by the focal skink species. It then takes the drivers of local adaptation from Chapter 3 and uses them to weight the axes of a climate space in which recipient populations can be matched to their ideal source populations. This enables me to identify a source patch that is likely to contain a population that is adapted to extreme climates, and then highlight the areas in the landscape that will match that climate in the future. It is to these areas that AGF efforts should translocate individuals from the source patch. This process can be repeated for numerous source patches, or reversed so that recipient populations are identified first and then matched with the best source patches.

Conservation in the face of climate change

This thesis unites ecological and evolutionary theories to argue that isolated patches of habitat on the edge of a species' range are likely to contain populations that represent the absolute limits of what a species can achieve. These populations will be of great importance if we are to conserve species in the face of climate change. The same characteristics that make these isolated populations so valuable as sources for AGF (i.e., their small size, isolation, and the climatic extremity they experience), however, also put them at the greatest risk of extinction from climate change. The fact

that they are already on the precipice of climate space means that it may only take a small change to tip them over the edge. Given the rapid rate at which climate change is advancing, identifying and capturing the adaptive diversity present in isolates should be considered a high priority.

Thesis structure

This thesis is made up of this introduction, four data chapters, and a general discussion. Each data chapter has been written as a standalone entity to facilitate publication in a peer-reviewed journal. Each chapter also builds on ideas and data presented in the preceding chapters. While I have attempted to minimize repetition throughout the thesis, the standalone nature of the chapters necessitates some content overlap. The general theme of climate change and AGF is repeated throughout the thesis. It is detailed in Chapter 2, and then touched on as necessary in subsequent chapters, expanding on the particular concepts that are the focus of each chapter.

Chapter 2 was written with a particular focus on peripheral isolates — geographically, and often ecologically, marginal populations. This is a convenient categorization, and one that is used in much of the literature. Subsequent chapters discard this dichotomy, however, and instead focus on connectivity being a continuum, represented here by the connectivity index developed in Chapter 2. Thus, while the terms 'core' and 'peripheral' are not used extensively in the later chapters, the reader is reminded that these terms are still applicable and merely represent the two extremes of the connectivity continuum.

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CHAPTER 2

A FRAMEWORK FOR LOCATING ADAPTIVE DIVERSITY IN THE FACE OF CLIMATE CHANGE

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Abstract

As climate change progresses, there is increasing focus on the possibility of using assisted gene flow (the movement of pre-adapted individuals into declining populations) as a management tool. Assisted gene flow is a relatively cheap, low-risk management option and will almost certainly come into increased use over the coming decades. Before such action can be taken, however, we need to know where to find pre-adapted individuals. We present a framework for locating adaptive diversity in a landscape, and argue that, for many species, the obvious place to look for this diversity is in peripheral isolates: isolated populations at the current edges of a species' range. Both evolutionary and ecological considerations suggest that the bulk of a species' adaptive variation may be contained in the total set of these peripheral isolates. Moreover, by exploring both evolutionary and ecological perspectives it becomes clear that we should be able to assess the potential value of each isolate using remotely sensed data and three easily estimated axes of variation: population size, connectivity, and climatic environment. Using these axes as a springboard, and Australia's Wet Tropics rainforests as a model system, we have developed a simple framework to guide future research aimed at locating valuable climate-related adaptive variation.

INTRODUCTION

The reality of anthropogenic climate change is no longer in doubt. Climatic changes have already occurred (Jones *et al.* 1999; Meehl *et al.* 2007), and in biological systems there is mounting evidence that these relatively minor changes have already resulted in altered phenology, range shifts, and population declines (e.g., Parmesan 2006; Freeman & Freeman 2014). Much greater climate change lies in our immediate future (Meehl *et al.* 2007), and the impacts of this impending change are likely to be manifold and complex (e.g., Atkins & Travis 2010; Norberg *et al.* 2012). Despite inherent uncertainties in how, exactly, climate change will play out, and how this will impact biodiversity (Moritz & Agudo 2013), there are certainly grounds for deep concern regarding the future of many species (Thomas *et al.* 2004).

In the last decade or so, ecologists have moved from mounting arguments as to why climate change should be minimised/avoided (e.g., Flannery 2006), to accepting the inevitability of a substantial change in climate, and pondering how the biodiversity impacts of that change might be mitigated. There now exist, for example, frameworks for assessing species' vulnerability to climate change (e.g., Williams *et al.* 2008), and various decision tools for determining appropriate management options (e.g., Shoo *et al.* 2011; Miller *et al.* 2012). For species that are clearly at high risk of extinction (e.g., many range-restricted species, especially mountain-top endemics; La Sorte & Jetz 2010) it has been argued, albeit controversially, that extinction might be averted by assisted colonisation; the movement of populations to areas outside the species' normal range (McLachlan *et al.* 2007; Hoegh-Guldberg *et al.* 2008). Although there may be a good case for assisted colonisation in some circumstances, it is not without risks (Ricciardi & Simberloff 2009). Assisted colonisation also requires the identification of suitable habitat for the focal species – potentially difficult for rare and range-restricted taxa (i.e. the species at highest risk of extinction; McLachlan *et al.* 2007).

Another strategy for minimising biodiversity loss, a strategy known as genetic translocation or assisted gene flow (AGF), is to move individuals within their existing range to bolster general within-population genetic variation or introduce specific adaptive traits in the recipient population (Hoffmann & Sgrò 2011; Weeks *et al.* 2011; Aitken & Whitlock 2013). If we think of climate change as a velocity — the rate and direction that local climate moves across the earth’s surface (Loarie *et al.* 2009; Sandel *et al.* 2011; VanDerWal *et al.* 2013) — then locally adapted genes need to keep pace with this velocity. It is clear that such local adaptation is already occurring (e.g., Umina *et al.* 2005; Lavergne *et al.* 2010), but for taxa that have long generation times, low reproductive rates, and/or low levels of gene flow, it might not be happening fast enough (Quintero & Wiens 2013). Although complex to implement, AGF carries far fewer ecological risks than assisted colonisation because species are not being introduced to new areas and ecological communities; however, the genetic risks (e.g., outbreeding depression) of AGF still need to be considered.

The next several decades will likely see an increasing use of both assisted colonisation and AGF. Indeed, community groups and government agencies are already performing both actions (e.g., Marris 2009; Weeks *et al.* 2015), so the challenge might not be having these actions performed, but having them performed in a planned, strategic manner (e.g., Hoegh-Guldberg *et al.* 2008; Willis *et al.* 2009). Whether the intent is AGF or assisted colonisation, it is clear that the presence of appropriate adaptive variation in the source population is important. Assisted colonisation efforts risk failure if the introduced individuals are maladapted to the release locality; AGF requires the identification of adaptive variation suited to the future climate of the intended release localities. Locating adaptive variation is particularly important for AGF because this conservation strategy is based on the redistribution of adaptive variation and the subsequent evolutionary response. Here we draw on both ecological and evolutionary theory to develop a framework that identifies hotspots of climate-relevant adaptive diversity across a landscape. While the framework can be used without

any prior assumptions regarding the location of these hotspots, we argue here that in many systems the obvious place to look for adaptive variation is in peripheral isolates: genetically isolated (through natural means, as opposed to recent anthropogenic habitat fragmentation), yet persistent, populations on the margin of the species' existing range. In our discussion we follow Lesica and Allendorf (1995) in that these peripheral populations are always geographically marginal, and may also be ecologically marginal.

The ranges of many species are made up of large, central populations surrounded by many, smaller peripheral populations. These small, isolated populations have long been recognised as an important source of adaptive diversity (e.g., Bush 1975). Indeed, it has been twenty years since Lesica and Allendorf (1995) first highlighted the conservation value of the adaptive diversity held in such populations. Although the value of marginal populations under climate change is recognised (e.g., Hampe & Petit 2005), there has been little work done to develop a framework for assessing the value of peripheral isolates. In addition, our goalposts have shifted: from looking at peripheral isolates as places where evolutionary novelty might occur, to looking at them as potential sources for AGF or assisted colonisation. Both ecological and evolutionary theory show remarkable agreement regarding the habitat and population characteristics that determine a population's likely degree of adaptive divergence for climate-relevant traits. Both perspectives identify population size, connectivity, and climatic environment as key factors. Evolutionary considerations also point to the importance of long-term persistence in isolation. Although ecological and evolutionary perspectives agree on these fundamental axes of importance, there is less agreement about optimal positioning along each axis, and new empirical data will be critical in addressing this uncertainty.

To demonstrate our framework, we use the rainforests of Australia's Wet Tropics as a model system. The Australian Wet Tropics bioregion is in the north-east of the continent (Fig. 2.1 inset), and consists of a complex network of rainforest patches (naturally occurring fragments of rainforest

habitat shaped by past climate change, and continuing to be shaped by anthropogenic disturbance) in a matrix of monsoonal woodlands. The highly endemic rainforest biota has been highlighted as being sensitive to both past (Graham *et al.* 2006) and future (Williams *et al.* 2003) climate change. For rainforest-restricted species, rainforest patches represent potential habitat that can be scored according to their size, connectivity, and climate.

Following page:

Figure 2.1

The Australian Wet Tropics (AWT) Bioregion is located in the north-east of the continent (inset). Here we show A) the distribution of naturally occurring rainforest patches within the AWT prior to European settlement; B) connectivity of extant rainforest (See Supp. Info. for methods), and; C) potential maladaptation (relative migrant load) at the patch level as a function of connectivity and spatial heterogeneity in annual mean temperature (see Supp. Info. for methods). Note that the connectivity in B remains high right up to the western edge of several patches. This is probably because the areas to the west are climatically suitable for rainforest, but rainforest is unable to grow there due to incompatible fire regimes. See text for further details.

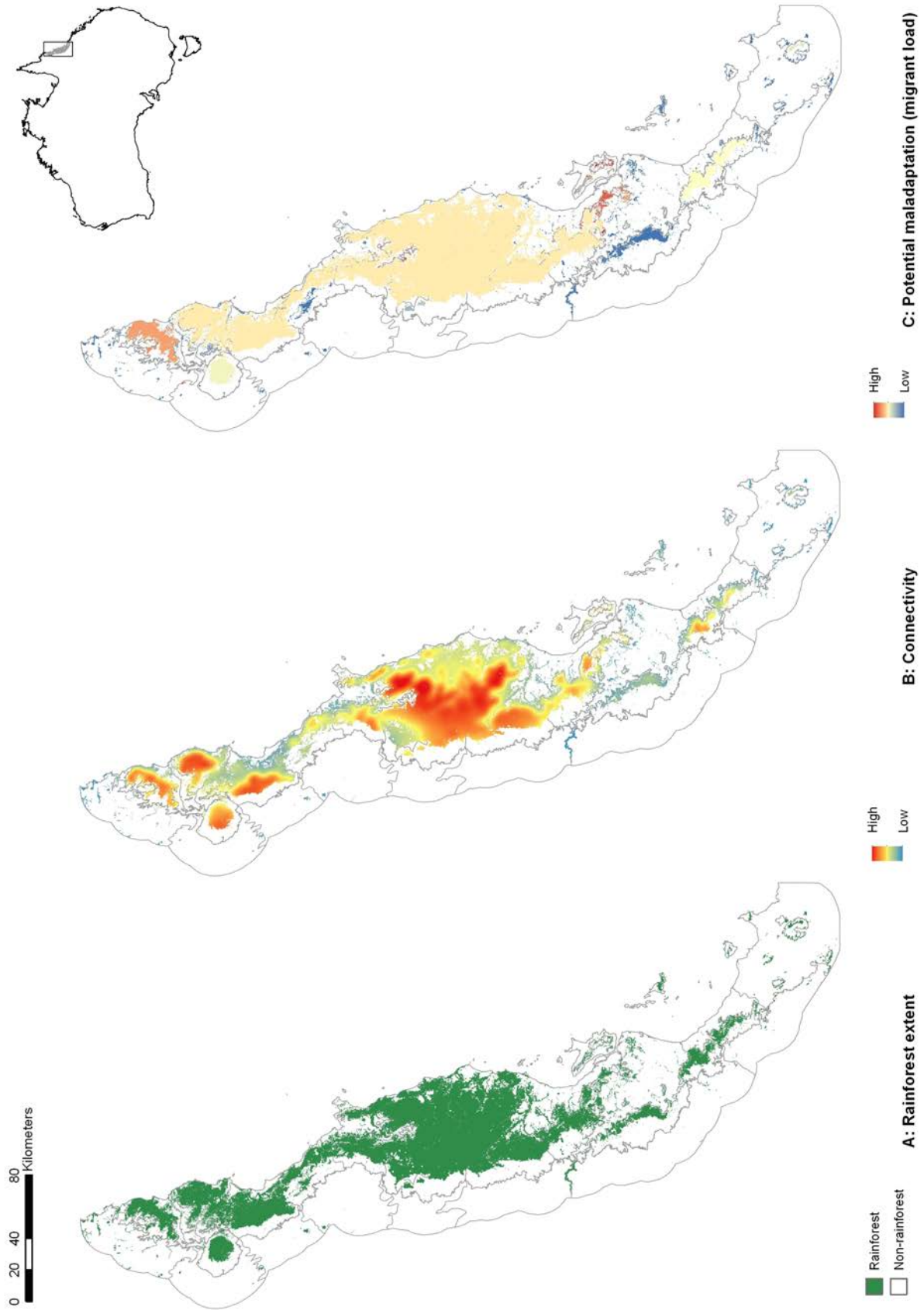


Figure 2.1

THE EVOLUTIONARY ECOLOGY OF ISOLATION

The geometry of isolation

Our argument for the likely importance of peripheral isolation flows from the geometric and definitional fact that peripheral isolates occupy habitat patches at the periphery of the species' range. As such they are likely a) numerous, and b) spread across a broad range of climatic conditions. In Australia's Wet Tropics rainforests, for example, we see a central spine of core habitat, surrounded by numerous (> 7000) naturally isolated patches of rainforest (the pre-clearing distribution of rainforest: Fig. 2.1A). Here we have defined 'core' patches as the largest patch of rainforest in each of 21 major faunal subregions within the Wet Tropics bioregion (Williams & Pearson 1997), with all other patches being classed as 'peripheral'. Note that some large, contiguous blocks of rainforest pass through several faunal subregions, so there are fewer core patches than subregions. Although the peripheral patches represent approximately 10% of the area of rainforest habitat in the region, they encompass almost all of the regional climatic variation (Fig. 2.2). The only climate spaces not sampled in peripheral patches are the most extreme wet and cool areas, found at the top of the mountain ranges around which the core areas are located. Conversely, the peripheral patches contain climate spaces (particularly the warmer, drier climates) that are not represented in the core patches (Fig. 2.2). While it is convenient to think of habitat patches as being either core or peripheral, connectivity is in reality a continuous variable, with patch connectivity ranging from low (peripheral) to high (core). Patches located in the geographic 'core' of a species' range may in fact have low connectivity if the landscape is heavily fragmented. For convenience, we continue to refer to our patches as either core or peripheral; however, all our analyses have been performed with a continuous connectivity index. Given that these peripheral patches sample most of the climate space of the region, especially at the warmer/drier end of the spectrum, the next question is whether populations inside these patches (our "peripheral isolates") show adaptations

matching their particular part of climate space; is this sampling of climate space matched by sampling in trait space?

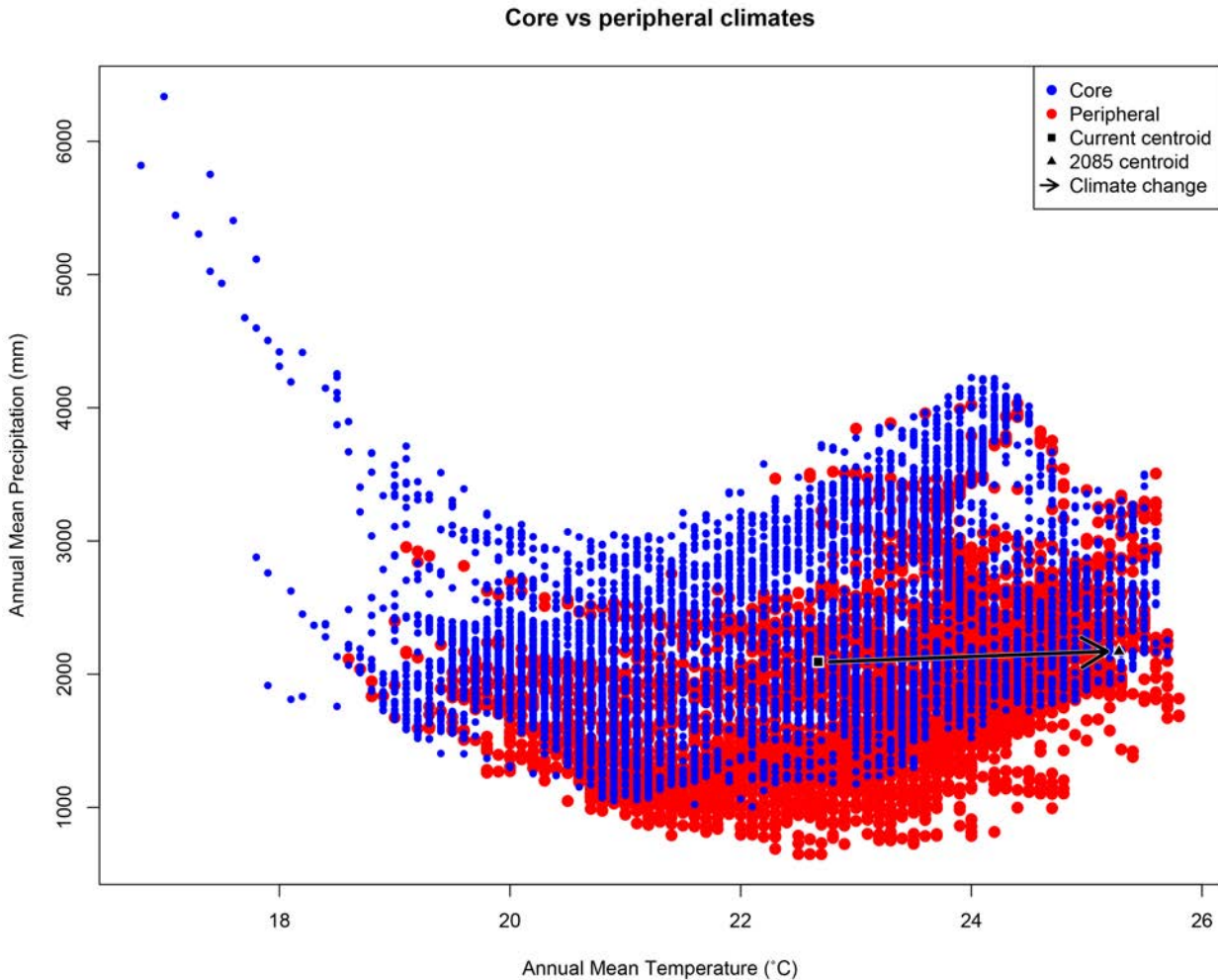


Figure 2.2

Scatterplot showing spatial variation in two important axes of climate (annual mean temperature and annual mean precipitation) in Australia's Wet Tropics (AWT). Variation is shown for random points in each of 7095 peripheral AWT rainforest patches (red); and, 7095 random points in core AWT rainforest patches (blue). In the AWT, the only climate space not represented by peripheral patches is in the extreme wet-and-cool corner surrounding core patches (i.e. mountain tops in the AWT). Conversely, peripheral patches contain some climate spaces (particularly the warmer, drier climates) that are not represented in core patches. Current climate data represent the AMT and AMP BioClim layers for the 30-year period centred on 1990. The 2085 centroid has been calculated using the 2085 climate predictions for the same BioClim layers under the RCP8.5 CSIRO Mk 3.0 model.

Consideration of evolutionary theory would suggest that, by dint of their isolation, populations in peripheral isolates should adapt more closely to their environment than core populations. The degree to which a population can adapt to its environment depends not only upon the rate of environmental change, but also on how much maladaptive gene flow a population receives (Polechová *et al.* 2009). This “migrant load”, M , scales directly with the interaction of the number of migrants, m , and the environmental variation, b (Kirkpatrick & Barton 1997; Polechová *et al.* 2009). Populations receiving many immigrants from climatically divergent areas are less likely to be closely adapted to local conditions than are populations that do not receive these migrants, or that only receive migrants from climatically similar environments.

We can map a very rough estimate of potential relative migrant load in our system by multiplying a measure of habitat connectivity ($\approx m$) with a measure of environmental heterogeneity ($\approx b$; see Appendix S1 for methods). Doing this reveals clear variation in relative migrant load through space (Fig. 2.S1 in Supp. Materials). When we average this relative migrant load back to the patch level it is clear that peripheral patches in our example tend to have far lower migrant loads than core patches (Fig. 2.1C). Thus, peripheral patches sample the climate space well, and likely suffer less from the influence of maladaptive gene flow. Together, these results suggest that peripheral patches may provide a useful source of climate-associated adaptive variation from which we can draw for management purposes. There are additional reasons that populations surviving in peripheral patches might be particularly good candidates as sources of adaptive variation under climate change, and we expand on these below. And of course, not every patch will be suitable as a source for AGF: not every patch will be occupied by the species of interest, and even those patches that are occupied might still make poor sources for reasons which we also discuss below. While there are numerous potential factors that affect a population’s suitability, ecological and evolutionary perspectives suggests that three axes of variation are critical for determining the eco-evolutionary trajectory of the population with respect to climate: population size, population connectivity, and climatic

environment. We now briefly discuss how each of these attributes affects a population's suitability as a source of adaptive variation.

Population size

Peripheral patches and the populations they contain are, by definition, smaller than their core counterparts. In our Wet Tropics example, peripheral patches are, on average, a mere 0.47% of the size of core patches. Their small area is one of the characteristics that make them interesting; it allows many of them to be scattered across a broad sample of environmental space. The size of isolates also has other consequences — evolutionary and ecological — that will determine the likelihood of both population persistence and local adaptation.

From an ecological perspective, patch size (and, by extrapolation, population size) is seen as a critical determinant of population persistence, because small populations are more prone to extinction through demographic and environmental stochasticity (Lande 1993). From an evolutionary perspective, population size also determines the balance between genetic drift and selection. While local adaptation is common, it is by no means universal (Hereford 2009). We might, for example, expect smaller populations to be less locally adapted, due to the stronger effects of genetic drift. Because of genetic drift, small populations might be expected to have lower diversity and less standing variation on which novel selection pressures can act, than do larger contiguous populations (Weiss & Goodman 1972; Petren *et al.* 2005; Lopez *et al.* 2009). In a review of local adaptation in plants, Leimu and Fischer (2008) found that populations with fewer than 1000 flowering individuals were less likely than larger populations to show signs of local adaptation. Indeed, in sufficiently small populations, genetic drift can overwhelm selection and even deleterious mutations can drift to fixation (Kimura 1979). Thus, as populations become small they may diverge substantially from the parental population, but for reasons having nothing to do with adaptation. Finally, as populations become exceedingly small, ecological and evolutionary

effects interact strongly; high levels of inbreeding and demographic stochasticity combine to create an ‘extinction vortex’ (Gilpin & Soulé 1986). Thus, both evolutionary and ecological theory agree that, to persist as a viable locally adapted population, patches need to be large enough to support populations that are buffered from the worst excesses of genetic drift and demographic stochasticity.

A corollary to the extinction vortex, however, is that the small isolated populations that do persist, despite the inherent challenges, will more than likely carry traits that adapt them to living in that small patch. We are not talking here about sink populations that persist only because they are constantly bolstered by immigration (see next section); rather, we are talking about populations that persist largely on their own merit. Such persistent isolates will be locally adapted either because of selection in situ or because, through selective extinction of less resilient populations through time, the only populations still present are those resilient to living in isolates (Balmford 1996); a kind of group selection. One way, therefore, to measure the likelihood of local adaptation in a patch is to consider the population dynamics in that patch; populations that show genetic signatures of long-term isolation and demographic stability (e.g., Leblois *et al.* 2014) likely are composed of individuals well adapted to local conditions. Although there is scant work on this issue at the individual-trait level, there is clear evidence at the species-trait level. For example, the most obvious solution to living in small patches is to live at high density (to pack many individuals into a small space), and small species that occur at high density are often particularly well represented in isolates (see Reif *et al.* 2006).

Resilience to environmental variation is also likely to be important for the persistence of small isolates. This resilience is important because populations restricted to small patches cannot migrate to track preferred conditions when the environment changes. If they are to survive, they must contend with the changed conditions in their isolate. Consequently, populations that have persisted

in small isolates are likely to be resilient to environmental variation. This resilience might be achieved through high rates of population increase (allowing rapid recovery), but also through resilient life histories: high degrees of phenotypic plasticity, overlapping generations, and/or long-lived adults. For example, and at the species-trait level again, asexual species have high rates of population increase by avoiding the production of males, and this form of reproduction is particularly prevalent in isolates (Kawecki 2008). Similarly, long-lived species of plants tend to be resilient to change, and these species are also more prevalent in isolates (Hampe & Jump 2011).

Small isolates, therefore, select at both individual and group levels for resilience to demographic and environmental stochasticity. If we were to look for populations pre-adapted to the increasing regime of extreme events resulting from anthropogenic climate change, peripheral isolates offer a promising target. Thus, perhaps the most interesting populations from an AGF perspective are those that are small, but not too small. Or to put it another way, populations that are small but which, nonetheless, show evidence of persistence despite long-term isolation.

Population connectivity

As well as its size, an isolate's physical proximity to other isolates will greatly influence its immigration rate. This, in turn, has implications for population size and stability, with well-connected patches typically having more persistent, stable populations (Levin *et al.* 1984). Thus, ecological theory generally sees high connectivity as beneficial because of its stabilising influence on demographics. Evolutionary theory, however, takes a more dichotomous view. On one hand connectivity increases gene flow, which, even at low levels, increases genetic variance and evolutionary potential (Polechová *et al.* 2009). On the other hand, high connectivity increases migrant load, and when maladaptive gene flow is high enough it can overwhelm (or swamp) local adaptation (Haldane 1956; Kirkpatrick & Barton 1997). Not only is the level of gene flow critical, but so too is its source. Sexton *et al.* (2011), for example, found that cross-pollination of a plant

between warm-edge peripheral populations increased fitness, whereas cross-pollination between a peripheral and a core population decreased fitness. This highlights the need to choose source populations carefully to ensure they come from the climate space the recipient population is likely to experience in the future.

This concept of migrant load swamping the effect of natural selection is the reason that isolation is considered so important for adaptation (García-Ramos & Kirkpatrick 1997). If an isolated population has sufficient genetic variation, it will adapt to its local conditions, and this adaptation can occur rapidly. For example, the work of Losos *et al.* (1997) on experimentally isolated Caribbean *Anolis* lizards showed that morphological divergence driven by differences in habitat appeared within 10–14 years. In the face of strong gene flow from environmentally distinct populations, however, theory suggests that adaptation to local conditions will likely take substantially longer, if it occurs at all (Holt & Gomulkiewicz 1997; Bridle *et al.* 2009; Polechová *et al.* 2009; Phillips 2012).

Therefore, because they receive some influx of genetic diversity but not enough to swamp local adaptation, weakly connected populations should be very well adapted to local conditions. Choosing populations that do not experience strong gene flow also ensures that we avoid ecological-sink populations; those maintained purely by immigration.

An additional consideration here is that evidence of some gene flow suggests that a population has not developed coadapted gene complexes that work against successful admixture by reducing fitness of admixed individuals: “outbreeding depression”. For AGF to be successful, the genes from translocated individuals need to introgress into the recipient population, and this may be less successful when a population has been reproductively isolated for very long periods of time (Coyne & Orr 1998; Singhal & Moritz 2013). These genetic barriers to introgression have likely been

greatly overstated (Weeks *et al.* 2011) and are only likely to be relevant where there are very long divergence times in which incompatibilities have developed across large sections of the genome. Despite no morphological differences, genetic data for our focal species (a small lizard: *Lampropholis coggeri*, see Appendix S1) show two deeply divergent lineages: a northern and a southern lineage that likely represent different species (Bell *et al.* 2010), and whose hybrids exhibit substantial reductions in fitness (Singhal & Moritz 2013). In this example, AGF should be restricted to within each lineage. Without this extensive distribution of incompatibilities, we would expect advantageous (but not disadvantageous) alleles to introgress into the recipient population relatively unimpeded (Barton 1979; Aitken & Whitlock 2013). In summary, evolutionary theory, in contrast to ecological theory, suggests that low connectivity is optimal for isolates that may act as a source for AGF.

Although connectivity is not necessarily easy to measure – it can vary over time, as well as space – there are numerous simple proxy measures of connectivity, using geospatial data that perform adequately against genetic metrics (e.g., Palmer *et al.* 2011). Using modelled habitat suitability in the Wet Tropics, and integrating these suitabilities over space (using species-specific dispersal expectations, see Appendix S1), we generated both point- and patch-level indices of connectivity for the Wet Tropics. When we score connectivity in this way we get the unsurprising result that connectivity declines towards the edges of large habitat blocks, and is generally much lower in isolated patches than in larger habitat blocks (Fig 2.1B). The exception to these generalities in the Wet Tropics is the western extent of the larger blocks, in which connectivity (premised on climatic suitability) remains high even to the edge of the larger blocks. This result reflects the effect of fire in this system: the western rainforest edge of the Wet Tropics is highly dynamic, expanding and contracting around fire events (Harrington & Sanderson 1994). This dynamism probably does lead to connectivity through time above what might be expected from a simple map of the habitat. Thus, many of the peripheral patches in our region – particularly along the western edge – have likely

experienced much stronger connectivity than their current static configuration would suggest. Of course, genetic data on immigration rates between patches would be useful to ground-truth such landscape connectivity measures, and available evidence for our focal species does suggest long-term isolation in peripheral patches in the Wet Tropics (Bell *et al.* 2010). In the absence of these data, useful measures of relative predicted/potential connectivity can be derived from readily available GIS data.

While partial isolation facilitates evolution, it is not a driver of adaptation; it simply provides ideal conditions under which populations can respond to selection pressures without undue migrant load (Dawson & Hamner 2005). Those selection pressures come from the environment, which brings us to our third important axis: the climatic environment.

Climatic environment

Geographic variation in climate is ubiquitous. Factors such as latitude, vegetation cover, elevation, and distance from the coastline can all create substantial spatial variation in climate (e.g., Shoo *et al.* 2010; Shoo *et al.* 2011). Indeed, microclimate may differ over even very small landscape scales (e.g., Pinto *et al.* 2010). For all of these reasons, isolates at the geographic edge of a species' range will likely experience a different climate (both in mean and extreme values) from the climate at the centre of the species' range (Lesica & Allendorf 1995) that is, geographic marginality may often correlate with ecological marginality, particularly for climate. In the Wet Tropics, for example, it is clear that isolated patches have more extreme climates (Fig. 2.3).

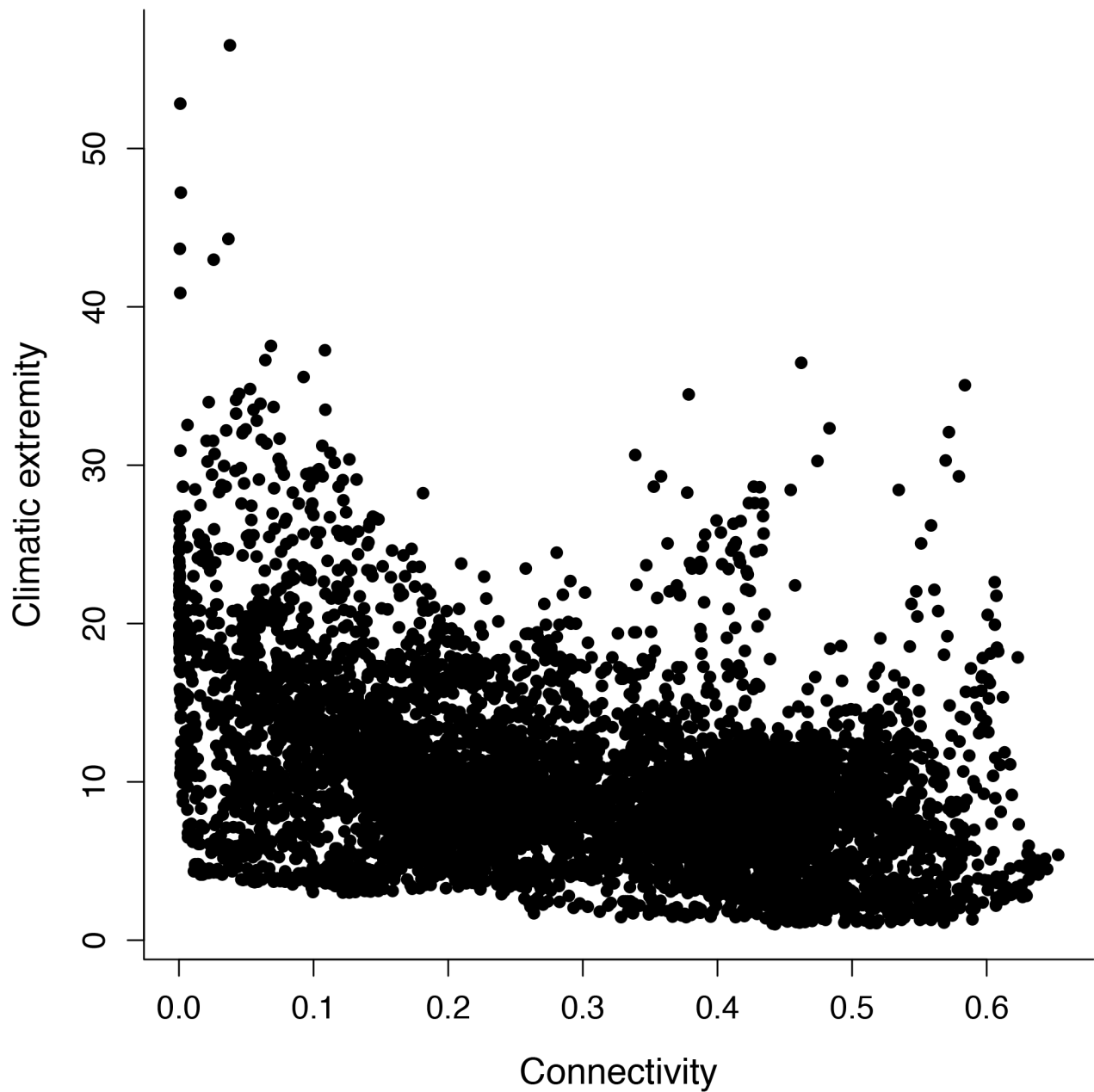


Figure 2.3

In our study system there is a negative correlation ($r^2 = -0.38$; $p < 0.001$) between rainforest patch connectivity and climatic extremity (see Appendix S1 for details of how climatic extremity was calculated): isolated patches have more extreme, less suitable climates for our focal lizard species.

One of our rationales for focussing on peripheral isolates as a source of adaptive diversity is precisely because they likely sample these extreme climates and, subject to persistence, are more than likely adapted to the climatic conditions in their habitat patch. Given the current trajectory of climate change (we are tracking towards a $> 4^{\circ}\text{C}$ increase in mean global temperature by 2100; Meehl *et al.* 2007), it is inevitable that source populations of interest to managers will tend to be at the extremes of the sampled climate space. Insofar as species distributional limits are associated with climate (and they often are: Kearney & Porter 2004; Gaston 2009), these extremes of climate space will tend to be found in isolates, at the extremes of geographic space. If we examine patches that are too far into extreme climate spaces, however, it is unlikely that the species will be present. If we do not go far enough, it is likely that we will ineffectively sample the adaptive diversity contained within the species' range. Thus, we are searching for populations that exist on the borderline (in climate space) between extinction and persistence through adaptation.

If we examine this edge (in climate space) between population persistence and extinction, we not only survey the locations containing important adaptive diversity, but we also learn about the limits of adaptation to climate. Because these peripheral isolates are naturally occurring and have often been in existence for at least several thousand years (many could be early Holocene relicts, *sensu* Hampe and Jump (2011)), they provide a good snapshot of the adaptive capacity of a species. If, based on size and connectivity, a species should be present in a patch but is not, then there might be a case that the environment in that location is too extreme, and beyond the limits of that species' capacity to adapt.

Given the breadth of environmental sampling by peripheral patches, it is likely that a subset of isolates are currently in climate space beyond that occupied by core populations. This appears true in the Wet Tropics, where warmer, drier climates are better represented in peripheral patches than in the core patches (Fig. 2.2). Some of these isolates are already in a climate space that will manifest

in core populations under climate change; such isolates could provide the adaptive variation needed by core populations to evolutionarily respond to the changing conditions. If, however, the additional climate space captured by peripheral isolates falls counter to the direction of climate change (as it might in another system), the utility of AGF may be badly undermined and more intensive actions (e.g., assisted colonisation) may be required.

Importantly, peripheral patches will not only tend to differ in mean climate variables (e.g., annual mean temperature and precipitation), but will also likely differ in the variation around those climatic means. As alluded to above (section: *Size*), isolates, by virtue of their small size and geographic marginality, likely experience more extreme events than populations in the core of a species' range. Thus, plasticity in individual behaviour and physiology that increases survival during these extreme events should be favoured by recurrent selection in isolates. One manifestation of this idea is that increased exposure to extreme events may prevent useful genes from becoming dysfunctional. This is because extreme events create stressful conditions that expose genes to selection that would otherwise remain hidden (Hoffmann & Parsons 1991). In a population that never experiences extreme stressful events, these genes are never expressed and the genes that encode them are not subject to selection. Given sufficient time these unexpressed genes accumulate mutations that render their proteins dysfunctional. This process of “DNA Decay” (Hoffmann & Sgrò 2011) is expected to occur in the environmentally stable or buffered core of a species range, but to be prevented in environments that regularly experience extreme conditions. Should this be true, isolates that have experienced regular extreme events in the past could be better adapted to deal with extreme events in the future.

The climatic environment is a key third axis that requires consideration when searching for populations suitable for AGF. The reality is that this axis is not simple: for example, here we have discussed climatic extremity (a distance in climate space), as well as the direction of climate shift (a

direction in climate space), as two aspects of obvious relevance. We acknowledge, however, that climate space is multi-dimensional and that additional metrics might be relevant for specific situations. Nonetheless, it is clear that, for the purposes of AGF, we are looking for habitat patches at the climatic extremes of the species range, and that represent the climatic future of the core populations we wish to manage. These patches will often be at the periphery of a species' geographic range (Hampe & Petit 2005).

THE CONSERVATION SIGNIFICANCE OF PERIPHERAL ISOLATES IN A CHANGING WORLD

While fragmented and peripheral populations are likely to be important for evolutionary reasons, their small size and isolation also put them at a higher risk of extinction. Despite the fact that peripheral habitats may contain populations that are pre-adapted to the future climate of core areas, they may still be some of the first populations to go extinct as climate change progresses. This counter-intuitive outcome occurs because, as conditions in the core areas of the species' range approach the extreme conditions found in an isolate, the conditions in the isolate become yet more extreme. This, coupled with their small size and isolation from other populations, means that peripheral isolates (and particularly the ones we are interested in: hot-adapted and rear-edge isolates) may well be some of the first local populations to be extirpated by climate change. Thus, if we are to understand and harness the adaptive diversity expected in peripheral isolates, we must do so as a matter of urgency (Hampe & Petit 2005).

For any given threatening process, appropriate adaptive variation may be more likely to exist in peripheral isolates than anywhere else (though this is certainly not always the case — the level of standing genetic variation across the entire range should be considered, but we suggest starting with peripheral isolates). Eckert *et al.* (2008) reviewed 134 studies of neutral genetic diversity in

peripheral-*vs*-core populations and found that most studies (70.2%) reported increased between-population divergence amongst peripheral isolates. Whether this broad survey of neutral diversity reflects patterns in phenotypic diversity, however, still remains to be seen (Eckert *et al.* 2008). Further evidence for this proposition comes from recent observations of ‘extinct’ species being rediscovered on the very margins of their former ranges. Fisher (2011), for example, found that mammals presumed to be extinct were more likely to be rediscovered at the periphery of their former range, rather than the centre, and a similar pattern may be emerging from recent frog ‘extinctions’ (e.g., Puschendorf *et al.* 2011). As well as representing perhaps the bulk of adaptive diversity in a species, peripheral isolates may provide evidence of what species are capable of adapting to and may also provide the raw genetic material that will enable species to adapt and/or shift in response to uncertain climatic change in the future (Budd & Pandolfi 2010). Of course, we are not advocating the preservation of all peripheral isolates at the expense of core populations; rather, our point is that it is important to assess the diversity within them and potentially harness this diversity for conservation and management purposes, before it is lost to climate change. The methods we have outlined above are useful for generating hypotheses about the best places to look for that important adaptive diversity. While this framework may well highlight areas of the core as being most likely to contain adaptive diversity in some systems, peripheral isolates will often be the best places to look.

So far we have identified three axes of variation that can be used to characterise patches: size, connectivity and climatic environment. These three patch characteristics are likely to have a profound influence on the diversity — both species diversity (i.e., species richness) and intra-species diversity (e.g., quantitative trait and genetic diversity) — contained within a fragment of habitat. These axes, then, can be used to examine the historical conditions through which species have persisted, and to predict the current locations at which climate-relevant diversity occurs. Unfortunately, our recommendations with regard to where along each of these axes we would

expect to see the highest diversity are vague, and will continue to be so until empirical data have been collected. Candidate isolates should be small, but not so small that drift overwhelms selection. Candidate isolates should experience low levels of gene flow: less than in a contiguous population (to avoid swamping effects, and to ensure that the population is not a sink and not reproductively isolated), but enough gene flow to prevent excessive erosion of genetic diversity through drift, inbreeding, and selection. Also, isolates should come from extreme climatic environments: at the climatic edges of what the species is capable of. Although vague, many of these constraints can be satisfied by the very fact of a population's persistence. If a small isolate is persisting in a peripheral climate, and there is evidence that it has done so for a considerable period of time, then it has likely adapted to its local conditions. If it had failed to adapt, it simply would not be there.

To inform conservation actions for a given species and system, these recommendations should be backed up with relevant data. Importantly, readily available spatial and climate data allow us to identify patches and examine their distribution along each of these three axes. This allows us to position each patch in a three-dimensional state-space representing the three critical axes, and to design a sampling regime around this. We have demonstrated the development of this state-space with reference to Australia's Wet Tropics. Determining where those peripheral isolates with the most value as sources of adaptive diversity are — populations that have persisted and adapted through time — requires further data. A useful sampling regime would examine presence/absence and phenotypic and molecular diversity in a representative sample of patches as a means of identifying the region inside this state-space in which we can expect to see the most adaptive divergence. It would allow us to identify the boundary between extinction and adaptation. The isolates in this region of state-space are the subset of isolates in which we should see represented the bulk of a species' adaptive diversity, and it is from among these isolates that we could expect to find populations of maximum utility to AGF strategies. Collecting these data is not a small task, but

it is a necessary one if we are to locate populations containing important adaptive variation and harness this variation for management.

Once we have identified the likely location of adaptive variation, and located appropriate source populations for AGF, the remaining issue for management is then one of genetic compatibility with a recipient population. There has traditionally been much concern in the conservation genetics literature about outbreeding depression, and/or the mixing of geographically distinct populations (Broadhurst *et al.* 2008). Much of this concern centres on questions of provenance (source populations are thought to be less locally adapted as distance from the source increases) and outbreeding depression. For AGF, however, we are looking to introduce into the recipient population a relatively small number of climatically pre-adapted individuals. The premise is that the pre-adapted alleles from these individuals will be captured by selection and introgress into the recipient population. Theoretical work suggests that this can be achieved with surprisingly small numbers of translocated individuals (Lopez *et al.* 2009). Further, deleterious alleles introduced at low frequency should also be removed rapidly by selection. While outbreeding depression and maladaptation may be an issue, its demographic impact can be minimised if the numbers of translocated individuals are a small proportion of the recipient population (Aitken & Whitlock 2013). Meanwhile, the advantageous alleles carried by translocated individuals will likely introgress despite outbreeding issues, because they are selectively advantageous (Barton 1979). Ideally, AGF individuals should be sourced from multiple suitable populations, to limit the effects of outbreeding depression (however small these effects may be) and to maximise the amount of adaptive variation introduced into the recipient population.

CONCLUSION

Because isolated populations as a set may represent the bulk of within-species phenotypic diversity, these isolated populations are where we should look for the genetic variation necessary to bolster populations threatened by climate change. The very characteristics that make these isolates important (i.e., their small size, isolation, and marginal climate), however, also mean they may be some of the first populations to go extinct under anthropogenic climate change. Given the rapid rate of climate change, a focus on the adaptive diversity present in isolates, particularly those at the rear edge of climate-shifting populations, should be a matter of urgency. Above, we have outlined a framework that uses easily measured patch-level characteristics (i.e., size, connectivity and climatic extremity) to provide a first-pass assessment of the potential conservation value of these isolates. This framework is built on a number of theories and assumptions that still need to be tested with empirical data before assisted gene flow is implemented. In a thorough examination, a user of this framework would need to (1) collect presence/absence data and perform patch occupancy modelling; (2) use genetic tools to assess gene flow across the landscape, and to assess population demographic history; (3) assess how trait variation (e.g., in climate-relevant physiological traits) is spread across the landscape; and (4) test the strength of local adaptation as a function of connectivity/gene flow. Together with these empirical data on the presence/absence of species, geographic variation in climate-relevant traits, and molecular data on connectivity and demographic stability, this three-axis framework can be used to guide management actions and future research.

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S1 – Supplementary Information

The Australian Wet Tropics — a case study

The identification of important peripheral isolates is crucial to their effective management and conservation. We have classified every naturally occurring fragment of Australian Wet Tropics (AWT) rainforest (7095 individual patches) along each of the axes mentioned in the main text — patch size, connectivity and climatic extremity — using existing large-scale datasets. Patch size (m²) was calculated from a state-wide vegetation mapping dataset (DERM 2011). A connectivity index for each patch was calculated by integrating habitat suitability and proximity through space (see below for full methods). As mentioned in the text, connectivity may vary between and within species. Our connectivity index was calculated for a focal species of lizard (*Lampropholis coggeri*), using an estimate of the lizard's dispersal capabilities (from Singhal & Moritz 2012). A lizard-specific climatic extremity measure for each habitat patch was also generated, by calculating the species' observed climatic envelope (using the values for various climatic variables at each of a large set of point locations for the species) and calculating the Mahalanobis distance from each patch's climatic envelope (using the same climatic variables).

Methods

The vector-based vegetation mapping for the Australian Wet Tropics (AWT) bioregion was converted to a binary ASCII grid format (cell size of 80 x 80 m), with rainforest patches represented by 1 and matrix represented by 0. Patches were uniquely identified using the SDMTools package in the R statistical programming environment (R Core Team 2014).

Size

The PatchStats function in the SDMTools package was used to calculate patch size in m².

Climatic extremity

Climatic extremity was calculated as the Mahalanobis distance between the patch's average climate and the centroid of the lizard species' climatic envelope. Six bioclimatic variables were used: annual mean temperature, temperature seasonality (coefficient of variation), maximum temperature of warmest period, annual mean precipitation, precipitation of driest quarter, and precipitation seasonality (coefficient of variation). A total of 821 point locations of the focal species were obtained from various data sources (Macdonald unpublished data; Queensland Museum collections database; Queensland National Parks & Wildlife Service WildNet database) and used to calculate the species' climatic envelope.

Connectivity index

A connectivity index was developed based on a modelled suitability surface — a grid covering the entire AWT bioregion with the value in each cell representing the suitability, from 0–1, of that cell for growth of rainforest vegetation at that time (Graham *et al.* 2010). While Graham *et al.* (2010) generated suitability surfaces at 500-year intervals going back 18,000 years, we used only the present day suitability surface as inclusion of all historic suitability surfaces drastically increased processing time and produced very similar results (unpublished).

The connectivity at each location, I , was calculated as the weighted mean of rainforest suitability in the area around I . The weighting through space was achieved with a Gaussian function assuming dispersal values estimated for a lizard species endemic to the region (which has a root mean squared displacement of 80 m per generation; Singhal and Moritz (2012)) convoluted over 500 generations.

This process yielded, for each location, y , a value of connectivity, I :

$$I_y = \frac{\int S(x)N(D(x, y), \sigma)dx}{\int N(D(x), \sigma)dx}$$

Where $S(x)$ is the suitability of location x for rainforest, $N()$, is the Gaussian function (zero-centred), $D(x, y)$ is the distance between location x and y , and σ is the scale of gene flow. Here we imagined gene flow over 500 generations with a root-mean dispersal of 80 m per generation, which was given by the 500-fold convolution of the Gaussian function, or $\sigma = 80\sqrt{500}$.

We then calculated an estimate of environmental heterogeneity over the same spatial domain around each cell. In our case we calculated environmental heterogeneity in one climatic variable, annual mean temperature. For each cell we then calculated the weighted mean squared deviation of this variable from its value in the focal cell. The weighting was achieved in the same manner as for the connectivity measure, except that cells falling outside rainforest habitat were given weightings of zero. This process yielded, for each cell, a value of spatial heterogeneity in mean annual temperature, S .

To generate a measure of relative migrant load at each cell, we simply multiply I and S at each cell (Fig. 2.S1). This cell-level migrant load value was then used to calculate patch-level average migrant load values shown in the main paper.

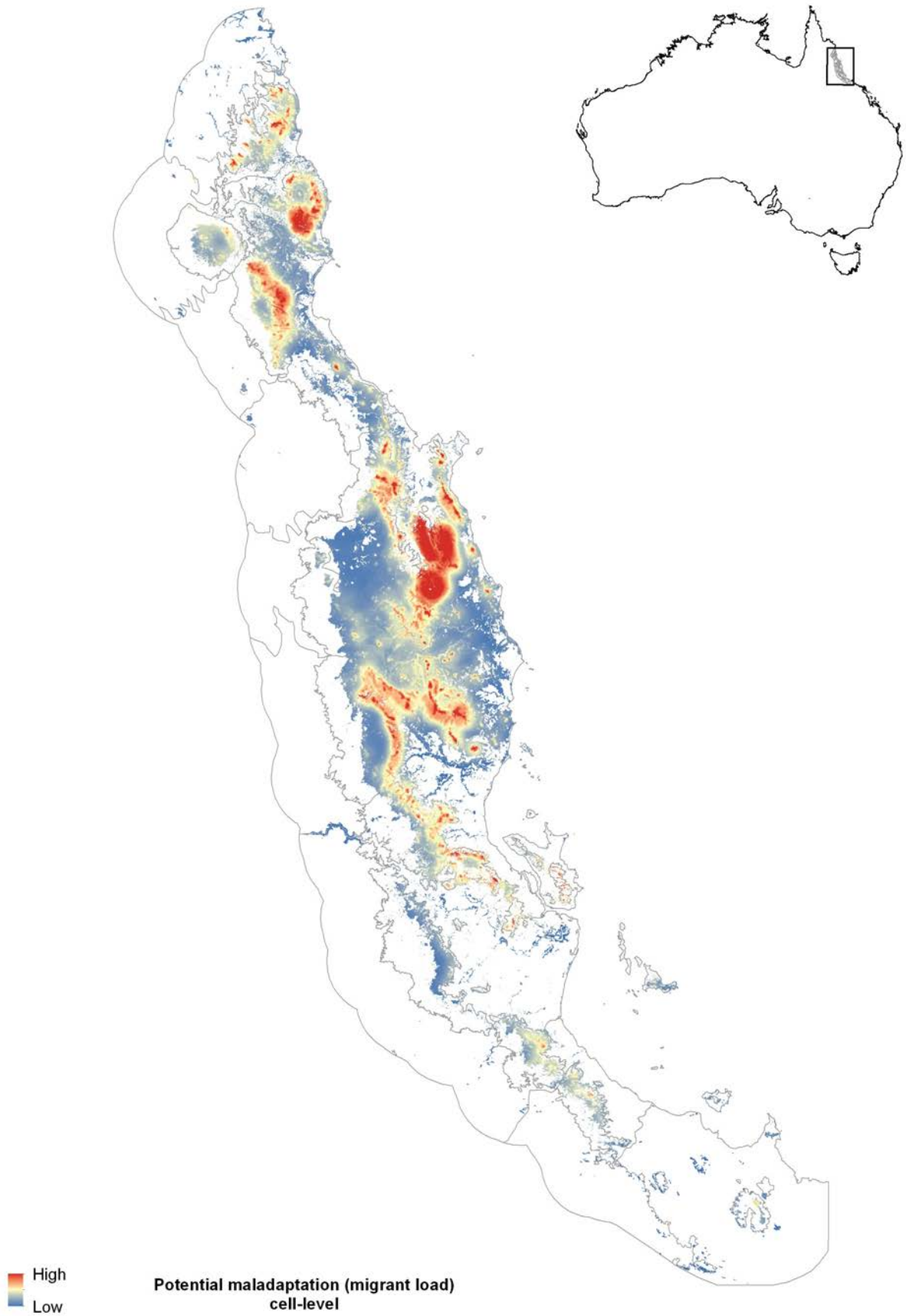


Figure 2.S1

Map of relative cell-level migrant load in the Wet Tropics.

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Chapter 3

Are less-connected rainforest patches more climatically extreme?

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Abstract

In the face of climate change, land managers and conservationists must look to a variety of strategies to protect biodiversity. One strategy receiving increased attention is assisted gene flow (AGF): the translocation of pre-adapted individuals into a recipient population to increase its climate change resilience. Isolated populations, free from maladaptive gene swamping, are more likely to be locally adapted. If these isolated populations are also experiencing extreme climates they may make ideal AGF source populations. We investigated the relationship between habitat connectivity and climatic extremity in the rainforests of the Australian Wet Tropics. We found that isolated rainforest habitat experiences higher temperatures and lower, more seasonal rainfall than more highly connected habitat. Isolated habitat, although composed of numerous small patches, did not, however, sample a greater range of climatic variation. These results suggest that ideal AGF source populations may be contained in isolated habitats, but their existence in an already-extreme climate also makes them among the most vulnerable to climate change.

Introduction

Understanding how species will respond, or are responding, to changing climate is important if we are to develop strategies to mitigate the impacts of climate change (e.g., Umina *et al.* 2005; Parmesan 2006; Williams *et al.* 2008; Lavergne *et al.* 2010). Given the rapid rate of climate change, we cannot afford to passively observe how species respond over time. We can, however, swap time for space and look at how species have responded to climatic heterogeneity across contemporary landscapes. By doing so, we will gain an understanding of species' limits to adaptation and which mitigation strategies may be most effective.

Assisted gene flow (AGF) – the human-assisted movement of individual organisms between populations to boost genetic diversity – is increasingly proposed as a technique to mitigate the impacts of climate change (Weeks *et al.* 2011; Aitken & Whitlock 2013) with such actions already having taken place (Weeks *et al.* 2015). The question of whether we should use AGF is giving way to the question of how best to use AGF. Assisted gene flow is used to achieve either, or both of, two related goals: 1) increase general genetic diversity within a vulnerable population; 2) introduce specific genes that impart an adaptive advantage to the recipient population (Hoffmann & Sgrò 2011; Weeks *et al.* 2011; Aitken & Whitlock 2013). For many species where AGF is a consideration, there are sufficient suitably sized populations to enable managers to be selective when choosing source populations. When options are available, the populations selected as source populations should not only boost genetic diversity, but also introduce genes that confer an adaptive advantage under climate change (Aitken & Whitlock 2013). How do we identify these optimal source populations?

Finding populations with specific advantageous genes is not a simple task. When using AGF to mitigate the impacts of climate change, ideal source populations will be from those areas of the species' range that are currently in a climate space that we expect to see more of in the future. We assume that by matching the climate of the source population with the future climate of the recipient population, we are introducing appropriate genetic diversity to future-proof the recipient population. Is this assumption valid? Unfortunately, it may not be: for reasons of high gene flow and/or drift, populations may not always be adapted to their local climate (Willi *et al.* 2006; Leimu & Fischer 2008; Hereford 2009; Yeaman & Otto 2011). A simple climate match may therefore often identify inappropriate source populations.

Because populations may not always be adapted to their local environment, there is an argument that peripheral isolates — moderate-sized, isolated populations on the periphery of a species' range — are likely to be the best sources for AGF (see Chapter 1 for further details). The reasons for this are: 1) they experience low levels of gene flow, which encourages divergence and local adaptation (Haldane 1956; Kirkpatrick & Barton 1997); 2) their small size allows there to be many of them, so we potentially have many independent responses to a wide array of climatic conditions; and 3) geographic marginality is often correlated with ecological marginality (i.e., peripheral populations have already adapted to climates that are more extreme than the core population experiences; Lesica & Allendorf, 1995).

Climate change will cause local climates to become more extreme relative to current values, and these shifts will typically be to higher maximum and minimum temperatures, with greater variation and less predictability in both temperature and

precipitation (Hughes 2003; CSIRO 2015). The expected shifts in climate are profound, and for many populations, the new conditions will be at (or beyond) the species' capacity to adapt. When looking for source AGF populations, we will be looking for those populations existing at the current extremes of a species' occupied climate space. If arguments 2 and 3 (above) hold, these populations will be represented in peripheral isolates.

Do peripheral isolates sample climatic extremities? Do isolates, as a set, sample more climatic space than the core of a species range? If we assume that climate determines a species' range (and it often does; e.g., Parmesan 1996; Kearney & Porter 2004; Gaston 2009; Calosi *et al.* 2010), then it follows that areas on the edge of the range will be more climatically extreme. These areas represent the location where climate changes from being suitable to unsuitable for that species. There is, however, ample evidence that climate is not the sole determinant of many species' ranges. Competitive interactions provide one well documented reason for range edges, and while such competitive interactions may be moderated by underlying climatic gradients (e.g., Davis *et al.* 1998), they may also act independent of climate (e.g., Rand & Harrison 1989). Additionally, alternative stable ecosystem states often partially decouple climate from range edges (Favier *et al.* 2012). The transition between forest and savanna systems, for example, is weakly related to rainfall. In a broad intermediate rainfall zone, however, the transition is strongly contingent on history: places that are currently savanna are maintained as savanna (by fire) even as rainfall increases (Bowman 2000; Hirota *et al.* 2011; Bowman *et al.* 2015). Finally, dispersal limitations may also drive species' boundaries, independent of climate (Normand *et al.* 2009).

Knowing that climate is not the only force acting to shape species' ranges, it is not certain that range edges are more climatically extreme. Are our assumptions about the climate sampling of peripheral isolates true? Although we cannot be sure they are true on first principles, we can test whether they hold in particular systems. Here, we focus on the Wet Tropics rainforests of Australia and assess the relationships between habitat connectivity (a proxy for the degree of isolation) and climate, using a landscape-scale connectivity index and publically available broad-scale climate data. Our landscape is composed of a central spine of core, well-connected habitat, surrounded by many (> 7000) isolated patches (Fig. 1.1 in Chapter 1). Thus, connectivity is a good surrogate for peripherality in our system. Herein, we use this connectivity index to assess whether geographic marginality is correlated with climatic marginality in our study system.

Methods

Study site and species

Our study region was the Australian Wet Tropics (AWT) bioregion of north-eastern Australia (see Fig. 1.1 in Chapter 1). The AWT consist of a complex mosaic of more than 7000 rainforest patches (naturally occurring fragments of rainforest habitat shaped by past climate change, and continuing to be shaped by anthropogenic disturbance) in a matrix of monsoonal woodlands. These rainforests and the highly endemic biota they contain have been highlighted as being sensitive to both past and future climate change (Hilbert *et al.* 2001; Williams *et al.* 2003; Graham *et al.* 2006). Our larger project focuses on potential climate change adaptations in a common, Wet Tropics-endemic scincid lizard, the Rainforest Sunskink (*Lampropholis coggeri*).

This is a small, diurnal, heliothermic skink that spends most of its time in the rainforest leaf litter. Our connectivity index (see below) is species-specific and reflects the particular dispersal capabilities of this species. Although particular to this species, the dispersal capabilities of *L. coggeri* are likely representative of the dispersal capacity of many low-vagility rainforest taxa; a contention that is reinforced by the common phylogeographic patterning found across a broad suite of low-vagility rainforest taxa in our system (e.g., Schneider *et al.* 1998; Hugall *et al.* 2002).

Climatic variables

We used seven temperature and precipitation variables, some of which appear to be important drivers of local adaptation in our study system (see Chapter 4). The climatic variables we use represent temperature extremes and variance, along with precipitation. These climate variables are detailed below and in Table 3.1.

Australia-wide temperature and precipitation data layers at 5 km resolution were obtained from the Australian Water Availability Project (AWAP; Jones *et al.* 2009). The temperature layers were then downscaled to a resolution of 250 m for the Wet Tropics region (Storlie *et al.* 2013). Data layers were available for Tmax (maximum daily temperature in °C) and Tmin (minimum daily temperature in °C), representing the daily maximum and minimum air temperatures experienced under the canopy 1 m above ground level. We used the 20-year (1991–2010) average of the daily minimum and maximum temperatures in our analysis, as well as the 20-year average daily variance for Tmin and Tmax. These variance values are largely driven by seasonal changes in temperature (see Phillips *et al.* in press).

Table 3.1: Climatic variables used in analysisAWAP = Australian Water Availability Project (Jones *et al.* 2009).

Variable	Description	Source
Tmin (°C)	20-year average (1991–2010) of daily minimum temperatures.	Downscaled from AWAP* base data to 250m resolution. Downscaled data from Storlie <i>et al.</i> (2013).
TminVar	20-year average (1991–2010) of variance of daily minimum temperatures.	Downscaled from AWAP base data to 250m resolution. Downscaled data from Storlie <i>et al.</i> (2013).
Tmax (°C)	20-year average (1991–2010) of daily maximum temperatures.	Downscaled from AWAP base data to 250m resolution. Downscaled data from Storlie <i>et al.</i> (2013).
TmaxVar	20-year average (1991–2010) of variance of daily maximum temperatures.	Downscaled from AWAP base data to 250m resolution. Downscaled data from Storlie <i>et al.</i> (2013).
Annual mean precipitation (mm)	30-year average (1976–2005) of annual monthly rainfall.	Downscaled from AWAP base data (Jones <i>et al.</i> 2009) to 250m resolution.
Pseasonality	30-year average (1976–2005) of standard deviation of the weekly precipitation estimates expressed as a percentage of the mean of those estimates (i.e., the annual mean).	Downscaled from AWAP base data (Jones <i>et al.</i> 2009) to 250m resolution.
Pdry (mm)	30-year average (1976–2005) of total rainfall in mm for the 13 consecutive weeks that had the minimum total rainfall in a year.	Downscaled from AWAP base data (Jones <i>et al.</i> 2009) to 250m resolution.

The 5 km precipitation data layers were downscaled to 250 m resolution using linear interpolation. Mean annual precipitation was calculated as a 30-year average (1976–2005). Precipitation of the driest quarter (13 consecutive weeks) was calculated for each year (1976–2005) and then averaged to give a 30-year average. Average precipitation seasonality was calculated over the same time period in the form of the coefficient of variation for precipitation (a value of 0 indicates that weekly rainfall is equal across the year, with values > 0 representing increasing seasonality in the form of increasingly uneven weekly rainfall).

Climatic variables were calculated for the entire Wet Tropics region, then clipped to the extent of pre-European rainforest distribution to match the spatial extent of our habitat connectivity index (see below). This resulted in 1,471,887 data points, corresponding to the same number of 80 m² grid cells in our landscape that contain rainforest.

To understand how the Wet Tropics' climate may change in the future, we used BioClim layers for 2085 created using the RCP8.5 CSIRO Mk 3.0 model at a 250 m resolution. This RCP (representative concentration pathway) scenario represents a high-emissions scenario, one that is unfortunately very realistic. Values from each of these layers were extracted for each rainforest cell in our landscape. The means of these values were then compared to the mean values for the same variables from the 1990 BioClim data layers. Future TmaxVar and TminVar values were generated from monthly averages, rather than daily data, and therefore likely underestimate the variances of maximum and minimum future temperatures.

Habitat connectivity

As mentioned previously, our connectivity index was developed for a low-vagility rainforest-restricted species (a skink, *Lampropholis coggeri*) and the details of this process are provided in the Supplementary Materials of Chapter 2. Briefly, however, our landscape was divided into a grid, and a habitat suitability value assigned to each pixel (an 80×80 m grid cell) based on bioclimatic modeling of rainforest distribution (Graham *et al.* 2010). These suitability values were averaged over space with a spatial weighting derived from a species-specific dispersal kernel (Singhal & Moritz 2012). This resulted in high connectivity values for areas of the landscape that are rainforest and are surrounded by rainforest, and low values for areas of rainforest surrounded by non-rainforest matrix. Connectivity values were only calculated for the pixels that were mapped as being rainforest. The raw indices were mean-centered and scaled (divided by their standard deviation) for analysis.

Analyses

Simple linear models were used to assess the relationships between the connectivity index of each grid cell in our study system and the corresponding value of each climatic variable, according to the following equation:

$$C_v = A + B_v \times \text{conn} + \text{error}$$

where:

C_v = climatic variable of interest

A = intercept

B_v = coefficient of connectivity effect

conn = connectivity index

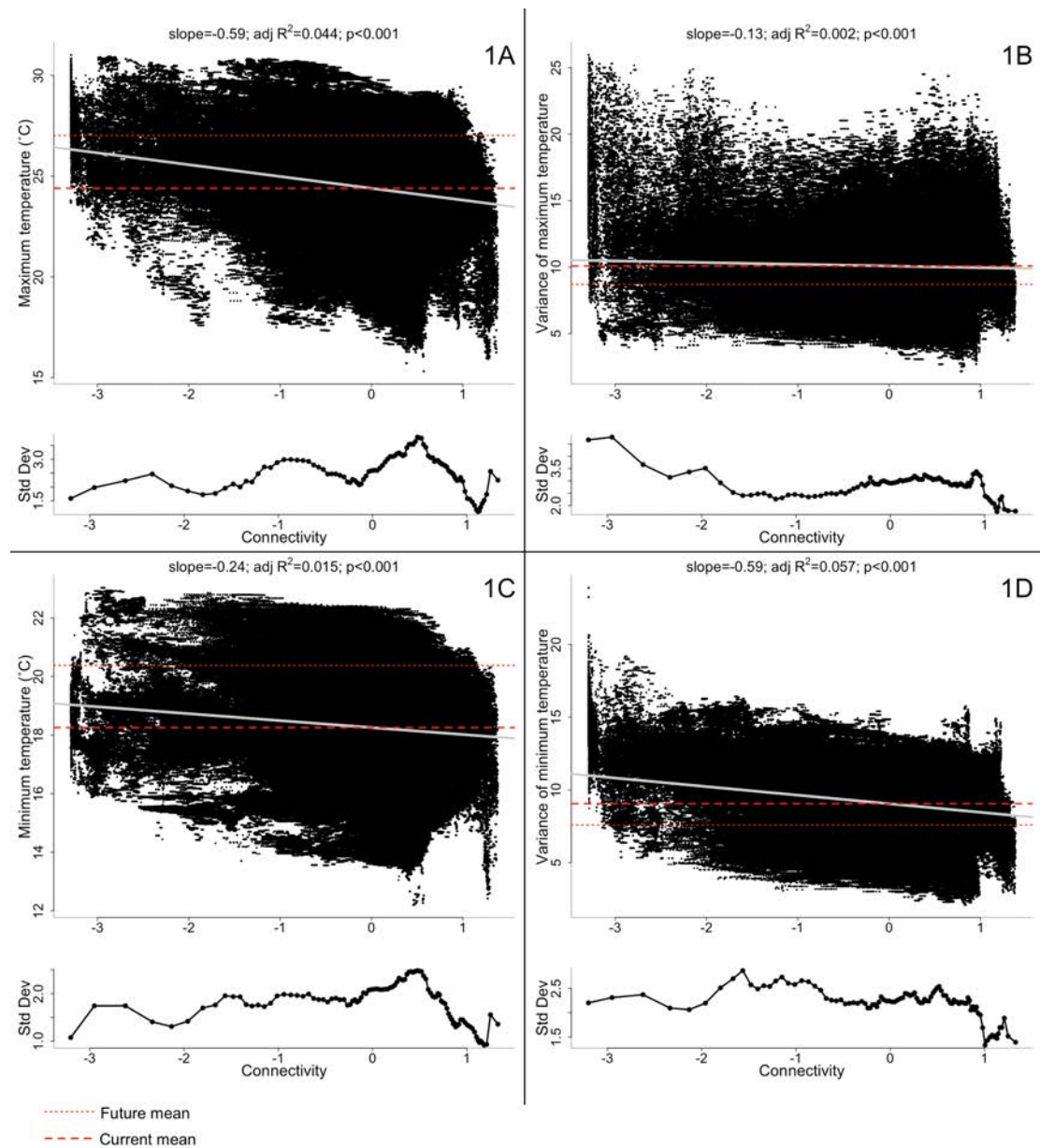
error = residual error

All data manipulation and analysis was conducted in R v3.2 (R Core Team 2015).

To assess how well variation in each climatic variable was sampled across different values of connectivity, the data ($n = 1,471,887$) were divided into 100 connectivity bins of approximately equal sample size ($n = 14,718.5 \pm 0.5$). The standard deviation of each bin was calculated and plotted against connectivity. To maintain equal sample sizes in each bin, the range of connectivity values spanned by each bin differs.

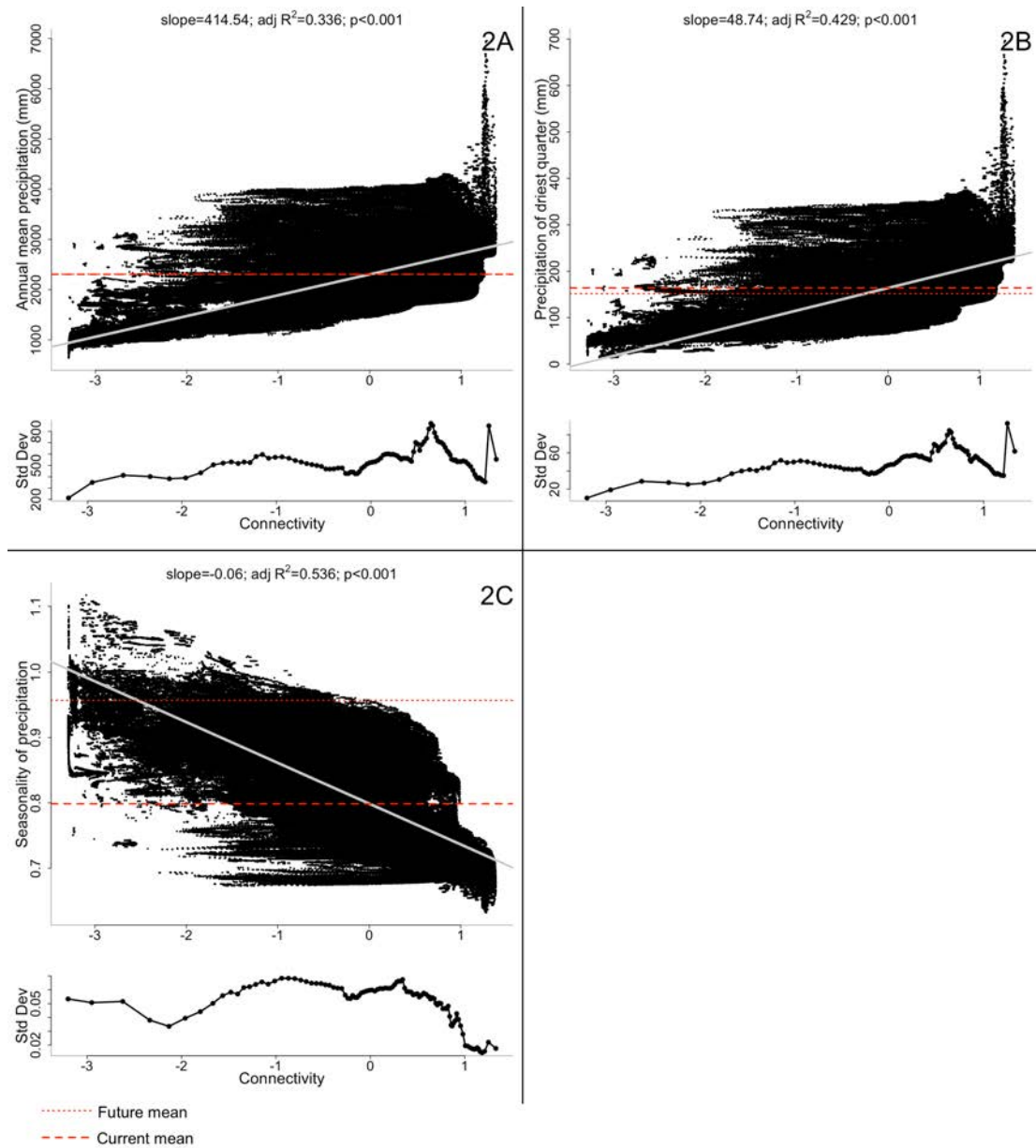
Results

In our system, less-connected habitat pixels experience more extreme climates. This is true for both temperature and rainfall. Plots of temperature variables against connectivity appear in Fig. 3.1, along with a plot of the standard deviation of that variable against connectivity. Plots of precipitation variables appear in Fig. 3.2.



Figures 3.1A–D

The relationship between connectivity and A) average maximum daily temperature (Tmax); B) variance of Tmax; C) average minimum daily temperature (Tmin); and D) variance of Tmin. Dashed lines represent current means, and dotted lines represent future means. Also shown is the relationship between connectivity and the standard deviation of each of the above climatic variables.



Figures 3.2A–C

The relationship between connectivity and A) annual mean precipitation (AMP); B) precipitation of the driest quarter (Pdry); and C) seasonality of precipitation (Pseasonality). Dashed lines represent current means, and dotted lines represent future means. Also shown is the relationship between connectivity and the standard deviation of each of the above climatic variables.

Current temperature

Compared to those with high connectivity, low connectivity habitat pixels (associated with isolates): 1) have higher average maximum temperatures (slope = -0.59; adj r^2 = 0.044; $p < 0.001$; Fig. 3.1A), and also collectively sample a smaller range of maximum temperature values; 2) have slightly higher variance of average maximum temperatures (slope = -0.13; adj r^2 = 0.002; $p < 0.001$), and sample a higher range of that variance (Fig. 3.1B); 3) have higher average minimum temperatures (slope = -0.24; adj r^2 = 0.015; $p < 0.001$), but sample a smaller range of minimum temperatures (Fig. 3.1C); and 4) have higher variance of average minimum temperatures (slope = -0.59; adj r^2 = 0.057; $p < 0.001$; Fig. 3.1D) than more connected localities, but sample an approximately equal range of those variances.

Current precipitation

Low connectivity habitat pixels have lower average annual rainfall (slope = 414.54; adj r^2 = 0.336; $p < 0.001$; Fig. 3.2A) and sample a smaller range of rainfall than more connected habitat pixels. They also experience lower rainfall in the driest quarter (slope = 48.74; adj r^2 = 0.429; $p < 0.001$; Fig. 3.2B) and sample a smaller range of that rainfall. Finally, they also experience a precipitation regime that is more seasonal (slope = -0.06; adj R^2 = 0.536; $p < 0.001$; Fig. 3.2C) but sample a range of seasonality values that is comparable to more connected pixels.

Future climates

In line with global predictions, the average daily Tmax of Wet Tropics rainforest is expected to increase under the RCP8.5 CSIRO Mk 3.0 model, from 24.4°C to 27.1°C in 2085 (an increase of 2.7°C). Tmin is also predicted to increase, from 18.3°C to

20.3°C. The average variance of both Tmax and Tmin is predicted to decrease slightly, but our future estimates of these variables are based on monthly rather than daily averages, and so future variance is likely to be higher than predicted here. Mean annual rainfall is predicted to increase slightly, from 2305 mm to 2308 mm in 2085. Precipitation of the driest quarter is expected to decrease from 164 mm to 152 mm. Precipitation is also expected to become more seasonal, with the coefficient of variation for precipitation increasing from 0.8 to 0.96. Current and future means are represented in Figs. 3.1 & 3.2 by dashed and dotted lines, respectively.

Discussion

Under climate change mean climate values will change as well as the frequency and/or intensity of extreme weather events (Parmesan *et al.* 2000; Rosenzweig *et al.* 2001; IPCC 2014). In Australia, landscapes are likely to experience: an increase in the number of days with high and very high Fire Danger Indices (Williams *et al.* 2001), likely leading to an increase in the frequency and severity of bushfires; an increase in the mean and maximum intensity of tropical cyclones (Walsh & Ryan 2000); increased mean and maximum temperatures (CSIRO 2015); and more intense 'extreme rainfall events', although there is much greater uncertainty in future precipitation projections (CSIRO 2015). If we are to employ assisted gene flow in the face of climate change, we should aim to find source populations that currently experience similarly extreme climates. Ideally, to ensure that they are locally adapted, these source populations should also come from isolates: parts of the landscape with low connectivity. The current study was conducted to assess the hypotheses that, compared with more-connected habitat, climate in less-connected habitat: 1) is more extreme (i.e., has shifted mean climate compared with core, highly connected

localities); and 2) represents a larger sample of climate space than core, highly connected localities. Our results show that, in our system, poorly connected habitat does experience more extreme climate, but does not necessarily sample more climatic variation.

Extreme climates

For each of the four temperature variables we examined, low-connectivity cells in our gridded landscape had mean temperatures that were different from those experienced in highly connected parts of the landscape. Importantly, in our system, this shift associated with low connectivity was also in the direction of climate change (i.e., less-connected areas were hotter than more-connected areas). Low-connectivity areas also experienced more extreme precipitation regimes — lower, more seasonal rainfall. It is difficult to be certain whether these shifts in rainfall are in the direction of climate change or not, as there is more uncertainty regarding predictions of future precipitation regimes. Some models, including the RCP8.5 CSIRO Mk 3.0 model we used, suggest many regions will receive more rainfall. Most models agree, however, that this rainfall is likely to be more seasonal, meaning that the region may be drier (than present) at certain times of the year, and wetter at other times (CSIRO 2015). On the precipitation seasonality axis, in particular, our less-connected areas again appear to be shifted towards future climatic conditions

Climate sampling

Our other prediction was that less-connected areas would, collectively, sample a greater range of each climatic variable (expressed as a higher standard deviation) than their more-connected counterparts. With the exception of TmaxVar, this was not true

in our system. On reflection, this is likely a result of the multidimensionality of the rainforest community's climate niche. Given that climate space is multidimensional, it is unlikely that any one aspect of climate is constraining a community's distribution at all locations. Rather, different aspects of climate will be acting to constrain distribution at different locations. It takes only one required factor to drop below a certain threshold for a point in space to become unsuitable, even if other factors remain within tolerance limits. Thus, the extremes of temperature, for example, may not be sampled because at the cool end of the community's range, it may be rainfall that is the limiting factor, not temperature.

This multidimensionality issue explains why low-connectivity areas in our rainforest system span only a small range of values for absolute measures of rainfall (i.e., annual mean precipitation, precipitation of the driest quarter). This is because rainfall, along with its interaction with fire, has a large effect on rainforest extent (Bowman 2000). Low rainfall is a general limit on the distribution of rainforest and so rainfall gradients will see decreased rainforest connectivity at the lower end of the gradient. By contrast, high rainfall is less likely to be limiting for rainforest distribution. These arguments are likely true for all rainforest systems, and so our results concerning connectivity and rainfall will likely hold beyond our system, to rainforest more generally.

The decreased sampling of variation in temperature variables in less-connected patches in our system warrants further explanation. Many of the most isolated areas in our system occur on the far western edge of the region. These are also the furthest from the coastline, and so should experience larger temperature variations (i.e., lower

and higher values of temperature) than are experienced on the coast. Results for our system show that this is not true: most of the areas with low Tmax values ($T_{\max} \leq 20^{\circ}\text{C}$) are closer to the coast; an observation that is explained by the fact that these near-coastal locations are also more than 750 m above sea level. Mountain ranges form the core of the rainforest blocks in the Wet Tropics, and accordingly have high connectivity values. These highly connected, high altitude regions account for the bulk of the rainforest areas below the mean line in Fig. 3.1A, and represent a large portion of the climate space that is not sampled by poorly connected regions.

While low-connectivity areas in our system have only slightly higher Tmax values and variance of Tmax, they nonetheless cover the upper ranges of those two variables at least as well as do areas with higher connectivity. Thus, in our system, areas of habitat that experience all aspects of likely future climates (i.e., high seasonality of rainfall, high maximum temperatures) can be found at the low end of the connectivity spectrum.

Global implications

In Australia, rainforest distribution is largely constrained by fire, and to a lesser extent by rainfall (Bowman 2000). Fire is a major constraint on the distribution of many other habitat types globally (Bond *et al.* 2005). The distribution, likelihood, and intensity of fire is driven by a number of factors, including topography and climate. With the frequency and intensity of fire expected to increase in the future (Williams *et al.* 2001), the higher temperatures and lower, more seasonal rainfall experienced by isolated habitat may make these areas particularly vulnerable. This may lead to the counterintuitive situation of isolated, peripheral populations, despite harbouring

variation critical for assisting the broader population to adapt, also being some of the first populations to be extirpated under a changing climate. As such, it is of utmost importance that these areas are investigated and their adaptive diversity captured, before it is lost.

It is interesting to note that all the climate variables assessed here (with the possible exception of annual mean precipitation and the variances of maximum and minimum temperatures) currently have, in low-connectivity areas, their means shifted in the direction of climate change. Many of the climate variables assessed here have been identified as axes of climate to which populations exhibit local adaptation (see Chapter 4). Thus, low-connectivity areas in Australia's Wet Tropics rainforest likely harbour adaptive genetic diversity that can assist species in adapting to impending climate change. While these results will not apply to all habitat types globally, it is possible that they will apply to other rainforest systems. If our results do indeed apply more broadly, isolated fragments of the world's rainforests maybe be harbouring important adaptive diversity. Given that rainforests are among the most species-rich terrestrial ecosystems (Turner & Corlett 1996), yet account for only a small fraction of the Earth's land area, capturing adaptive diversity in isolated rainforest fragments should be considered a high priority.

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Chapter 4

Using connectivity to identify environmental drivers of local adaptation

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Abstract

Local adaptation has been studied ever since Darwin and his finches. Despite this long and famous history, and despite being able to demonstrate local adaptation, we are still often unable to objectively determine the exact environmental drivers of local adaptation. Given the rapid rate of global change, understanding the specific drivers of local adaptation is vital. Conservation strategies designed to mitigate the impact of climate change on vulnerable species are urgently needed, and assisted gene flow (the translocation of pre-adapted individuals into more vulnerable populations) is one such strategy. Assisted gene flow, however, requires knowledge of where in the landscape we can find populations with pre-adapted climate-relevant traits; we cannot find these populations if we do not know the dominant climatic drivers of local adaptation.

While simple assessments of geographic trait variation are a useful first step towards identifying drivers of adaptation, geographic variation — and its associations with environment — may represent plastic, rather than evolved differences. Additionally, the vast number of environment–trait combinations makes it difficult to determine which aspects of the environment populations adapt to. Here we argue that by incorporating a measure of landscape connectivity as a proxy for gene flow, we can differentiate between environment–trait relationships that are under selection versus those that reflect phenotypic plasticity. By doing so, we can rapidly shorten the list of environment–trait combinations that may be of adaptive significance. We demonstrate this method using data on geographic trait variation in a lizard species from Australia’s Wet Tropics rainforest.

Introduction

It is only relatively recently that we have begun to appreciate the extent to which evolution can happen not only over relatively short timespans (e.g., Losos *et al.* 1997; Reznick *et al.* 1997; Reznick & Ghalambor 2001; Stuart *et al.* 2014), but also at small spatial scales (Richardson *et al.* 2014). Some of the best known examples of rapid or highly localized evolution are increases in melanism in moths after the industrial revolution (Kettlewell 1961) and heavy metal tolerance in plants growing on contaminated soils (Hedrick *et al.* 1976; Macnair 1987). Climate is another major driver of local adaptation (e.g., Olsson & Uller 2003; Kelly *et al.* 2012), and understanding the way in which species respond to climate is of increasing importance. Despite a demonstrated capacity for species to adapt to dynamic environments, anthropogenic climate change is proceeding at such a rate that there are concerns that many species will be unable to evolve rapidly enough to avoid extinction (Sinervo *et al.* 2010; Hoffmann & Sgrò 2011).

Evolution leads to optimal phenotypes that vary through both time and space (Reznick & Travis 1996; Kawecki & Ebert 2004), in turn leading to populations ('demes') that have, on average, higher fitness in their home environment than an immigrant would: local adaptation. While adaptive optima for traits almost always vary geographically, it does not follow that all geographic trait variation is due to local adaptation. Geographic trait variation can arise due to other factors, such as phenotypic plasticity (including developmental plasticity and maternal effects) and environmental factors (such as geographic variation in fitness-reducing parasites). These factors, and particularly phenotypic plasticity, can give the appearance of local adaptation, despite having no underlying heritable basis (Kawecki & Ebert 2004;

Hoffmann & Sgrò 2011), complicating our identification of climate-relevant adaptive variation.

To circumvent these issues, evolutionary biologists use experimental approaches to demonstrate local adaptation (Reznick & Travis 1996). Experiments designed to detect local adaptation typically utilise one of two techniques: 1) reciprocal transplants, which are done *in situ*, and are considered the gold standard for demonstrating local adaptation; or 2) common garden experiments, which are usually done in the lab where it is easier to control each environmental variable (Reznick & Travis 1996). Both of these techniques can be difficult, for reasons of time, expense, logistics, or ethics. This difficulty increases as the number of separate demes and environmental variables to be tested increases. For both techniques, to remove any maternal effects, the F2 progeny should be tested (Reznick & Travis 1996). This requires lengthy experimental times for species with long generation times.

Additionally, although reciprocal transplants will detect signs of local adaptation, they are not necessarily suited to identifying the environmental drivers of that local adaptation (Wright *et al.* 2006). This is because *in situ* reciprocal transplants necessarily encompass all the environmental variables that may give rise to local adaptation. Lab-based common garden approaches may, in principle, be more suited to identifying environmental drivers (because the environment may be under a degree of control), but in practice it remains difficult to identify the environmental drivers of trait variation seen in the wild. Thus, the best experimental tools we have for studying local adaptation are demanding in terms of time and cost, and are unsuitable for assigning environmental drivers (such as climate variables) to adaptive variation. If we are looking for climate-driven local adaptation, this is a problem: we want to know

which climate variable or variables are the main drivers of adaptation, and we urgently need this information for many species.

By definition, local adaptation has a genetic basis and is consequently weakened by gene flow (Wright 1931; García-Ramos & Kirkpatrick 1997; Kawecki & Ebert 2004). Demes with high levels of inward gene flow are therefore likely to be less optimally adapted, causing an observable mismatch between optimal and actual phenotypes. Some examples of this are birds dispersing and producing clutch sizes that are not optimised for the habitat quality in which they are now nesting (Dhondt *et al.* 1990), larval salamander colouration not matching streambed colouration due to high levels of gene flow from nearby but predator-free streams (Storfer *et al.* 1999), and stick insects ('walking sticks') in smaller habitat patches having non-cryptic colouration when the surrounding patches are larger and environmentally dissimilar (Sandoval 1994). These observations of "migrant load" suggest an alternative technique for identifying and assessing local adaptation. First, we look across populations for correlations between the environment (e.g., mean annual temperature) and traits (e.g., morphology, physiology). By themselves, these correlations are not sufficient evidence of local adaptation — they could also be caused by phenotypic plasticity. Second, knowing that local adaptation is hindered by gene flow, we can look at whether gene flow diminishes the environmental effect. In cases where data on gene flow are absent (which is often the case), habitat connectivity can be used as a substitute for gene flow. Environment–trait correlations that are strong, but which are also weakened by connectivity, are indicative of environment–trait correlations that have arisen through local adaptation.

If we now collect data on a large number of environment–trait correlations, and their interaction with connectivity, we can imagine several possible patterns emerging. These possibilities are depicted in Figure 1. Each panel represents a possible relationship between environment–trait correlations (environmental coefficients on the x-axis) and the interaction between environment and connectivity (y-axis). Panel A shows a set of environment–trait relationships that are strong, but that are not influenced by connectivity (i.e., no environment–connectivity interaction). This pattern is indicative of a system in which environment–trait correlations are predominantly driven by plastic responses of traits to their environment (i.e., traits always match the local environment, regardless of the level of inward gene flow). Plastic responses are still of interest, and many species are likely to show such plasticity as the climate changes (Seebacher *et al.* 2015). Panel B shows a system in which environment–trait relationships are eroded by connectivity: increased connectivity diminishes the correlation between the environment and the trait. In this situation, the interaction between the environmental variable and connectivity is negative when the environmental coefficient is positive (i.e., greater connectivity causes the environmental coefficient to decrease towards zero; bottom-right quadrant), and positive when the environmental coefficient is negative (i.e., greater connectivity causes the environmental coefficient to increase towards zero; top-left quadrant). This is the pattern we would expect if there is a genetic basis to the environment–trait correlation, i.e., local adaptation. Panel C shows the situation where the effect of the environment tends to be enhanced by connectivity. This pattern might arise in organisms that are highly mobile and can actively move to their ideal environment, thus avoiding the selective pressures that would lead to local adaptation.

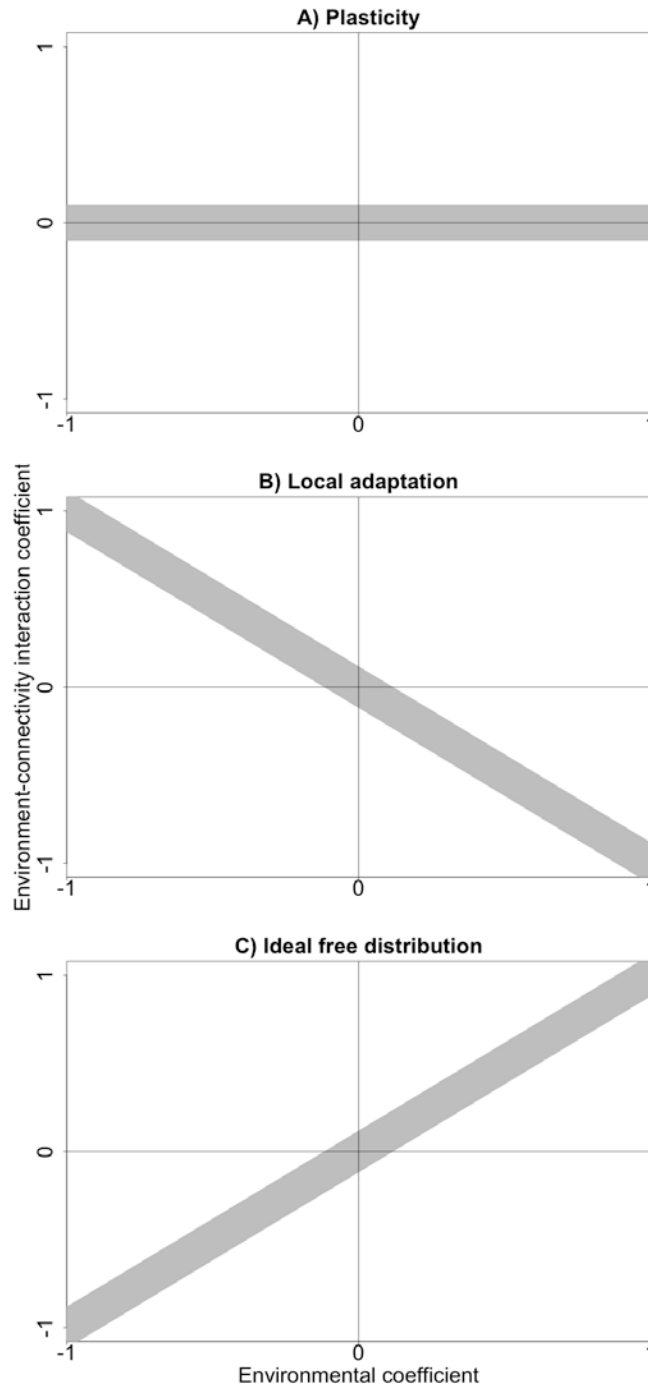


Figure 4.1

Graphs showing the concepts illustrated by plotting a set of environment–trait coefficients (x-axis) and the corresponding environment–connectivity interaction coefficients (y-axis). A) Phenotypic plasticity is suggested when environment–trait relationships are strong, but are not influenced by connectivity. B) Local adaptation is suggested when increasing connectivity diminishes the correlation between the environment and the trait. C) The effect of the environment is enhanced by connectivity. This latter pattern might arise in organisms that are highly mobile and can actively move to their ideal environment, thus avoiding the selective pressures that would lead to local adaptation.

Understanding how species respond to specific aspects of their environment is vital if we are to have any hope of halting the current rapid loss of biodiversity. Climate change is undoubtedly one of the biggest threats to global biodiversity (Meehl *et al.* 2007; IPCC 2014), and conservation biologists are looking to a variety of techniques to assess and help mitigate the impacts of climate change on vulnerable species (Williams *et al.* 2008; Weeks *et al.* 2011; Aitken & Whitlock 2013). One technique that is likely to see increasing use is assisted gene flow [AGF; for review, see Aitken and Whitlock (2013)]. This technique involves the spatial redistribution of long-standing adaptations, and acts to increase genetic diversity in recipient populations, thereby bolstering capacity for evolutionary adaptation (Hoffmann & Sgrò 2011; Weeks *et al.* 2011; Aitken & Whitlock 2013). When applying AGF to help species adapt to climate change, the simplest approach would be to predict the future climate, find an existing location that currently mimics the future climate, and then translocate animals from that source location. Such an approach is, however, pointless if the individuals at that source location are no better adapted to handle the future climate than individuals from the recipient population. Correct use of AGF requires knowledge of where to find populations that have already evolved the necessary climate-relevant traits.

Our present study uses a lizard model system to examine correlations between individual traits (both morphological and physiological) and climatic variables. We assess how habitat connectivity affects these correlations and use the interaction between environmental variables and connectivity to rank environment–trait combinations. In doing so, we reveal a set of environment–trait relationships dominated by local adaptation.

Methods

Study species and site selection

The Rainforest Sunskink (*Lampropholis coggeri*) is a small (snout–vent length up to 45 mm), diurnal scincid lizard restricted to the rainforests of the Wet Tropics region of northeastern Australia (Wilson & Swan 2010). The rainforests of this region cover a wide range of environmental conditions, spanning significant elevation (0–1600 m ASL), precipitation (annual mean precipitation of 1432–8934 mm, not including input from cloud stripping), and temperature (annual mean temperature of 16.3–25.8°C) gradients. This heliothermic skink is active year-round, often seen basking in patches of sunlight on the rainforest floor. Lizards were captured by hand from sites that were selected to maximize the environmental heterogeneity sampled (Fig. 4.2).

Morphological measurements were obtained from 532 skinks from 32 sites.

Physiological measurements were obtained from 563 skinks from 12 sites. While there was substantial overlap between the two groups, not all skinks used for morphology were also used for physiology, and vice versa. From 8–20 skinks were caught at each site on each collecting trip. While most sites were sampled only once, two sites were sampled on multiple occasions over a one-year period to assess seasonal differences in physiology (Llewelyn *et al.* submitted). Following capture, skinks were transported to James Cook University (JCU) in Townsville for trait measurement. All procedures involving lizards were approved by the JCU animal ethics committee (projects A1976 and A1726).

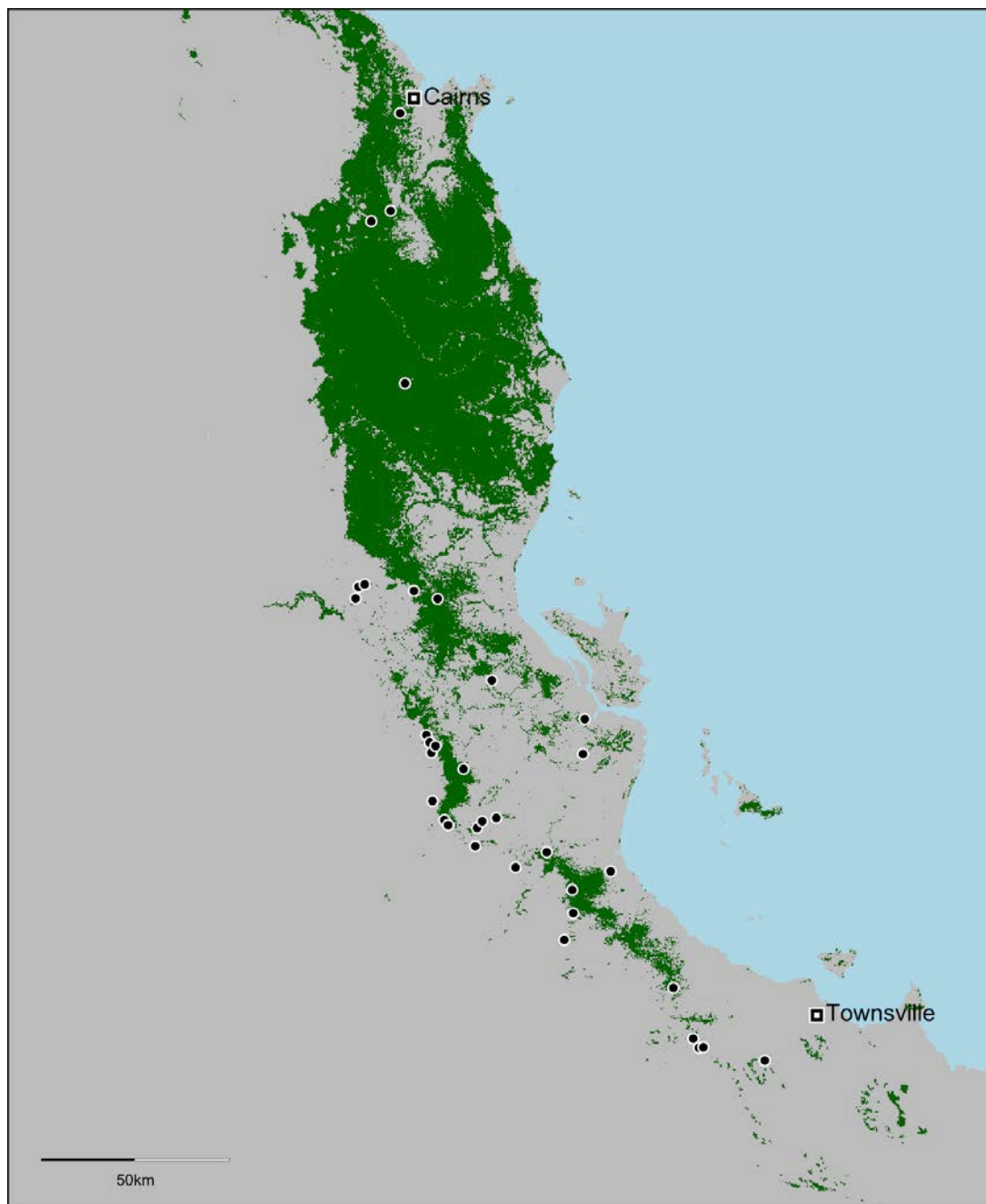


Figure 4.2

Map of the southern Australian Wet Tropics bioregion, showing sampling locations.

Lizard husbandry

Skinks being held for physiological trials commenced trials within seven days of collection from the field; skinks being used only for morphology were measured and released back at their point of capture within seven days. During physiological trials, skinks were housed individually in long plastic tubs (340 x 120 x 160 mm). Each tub had several small pieces of paper (mimicking leaf litter) and a container (84 ml) of moist vermiculite to provide the skinks with two types of shelter. Tubs were sprayed with clean water regularly to maintain appropriate levels of humidity and to enable the skinks to drink from the water droplets. Skink tubs were placed on heat racks, producing a thermal gradient (21 to 40°C) inside the tubs and allowing the skinks to behaviourally thermoregulate. Lighting in the animal room was set to follow the natural day/night cycle (i.e., lights on between 08:00 and 18:00), and this lighting was supplemented with ultraviolet-enriched light for 2 hours each morning. Skinks were fed crickets every second day, but no animals were fed in the morning prior to physiological trials (i.e., all tests were done while skinks were post-absorptive).

Physiological trials

The following measures were taken from each skink ($n = 563$) during laboratory trials: critical thermal minimum (CT_{min}), critical thermal maximum (CT_{max}), thermal-performance breadth for sprinting (breadth₈₀), maximum sprint speed (R_{max}), temperature at which sprint speed is optimized (T_{opt}), active body temperature as measured in a thermal gradient (T_{active}), and desiccation rate (des) (Table 4.1). All trials were conducted by one person (AH, not an author) to minimize observer bias. For additional details of physiological trials, see Llewelyn *et al.* (submitted) and Phillips *et al.* (2014).

Table 4.1: Description of lizard traits used in analysis

Measurement	Description
MORPHOLOGY	
HWidth	Head width at the widest point of the skull in mm.
HeadL	Head length in mm from tip of snout to anterior edge of ear opening. Left and right sides were measured and averaged to generate one value.
ILimbL	Interlimb length in mm from axilla to groin when fore- and hindlimbs are perpendicular to body. Left and right sides were measured and averaged to generate one value.
HindLL	Hindlimb length in mm from sole of foot to above knee, measured when femur is perpendicular to long axis of body and tibia is perpendicular to femur. Left and right sides were measured and averaged to generate one value.
SVL	Snout–vent length measured from tip of snout to anterior edge of cloaca, in mm.
Total length	From tip of snout to tail tip in mm.
Mass	In grams to three decimal places.
PHYSIOLOGY	
CTmin	Critical thermal minimum; the lower temperature at which the skink’s righting response is lost, in °C.
CTmax	Critical thermal maximum; the upper temperature at which righting response is lost, in °C.
Rmax	Rate of maximum sprint performance, in cm/sec.
Topt	The temperature at which maximum sprint performance is achieved, in °C.
Breadth80	Thermal-performance breadth; the temperature range that encompasses the middle 80% of the performance curve, in °C.
des	Water loss rate. The rate at which mass is lost when challenged by desiccating conditions, in g/min.

Morphological measurements

The following measurements were taken from each skink ($n = 532$) by hand using digital calipers: head width (HeadW); head length (HeadL); interlimb length (ILimbL); hindlimb length (HindLL). We also recorded snout–vent length (SVL), total length, and mass (see Table 4.1 for further details). Left and right measurements were averaged to obtain one measurement for that trait. All measurements were taken by one person (SLM) to minimize observer bias. All morphological variables were log-transformed prior to regression analyses.

Climatic variables, and connectivity

As our study aimed to assess adaptation to local climate, various temperature and precipitation variables were extracted from a variety of sources representing both means and extremes (Table 4.2). It is important to consider climatic extremes, because temperature extremes may be increasing faster than mean temperatures (Easterling *et al.* 2000), and many species are likely to be particularly vulnerable to these extremes (Parmesan *et al.* 2000). Many environmental variables are highly correlated (Braunisch *et al.* 2013), so only the less-derived variables were used in analyses, viz.: annual mean precipitation (AMP); seasonality of precipitation (Pcov); precipitation of the driest quarter (Pdry); annual mean temperature (AMT); coefficient of variation of temperature (Tcov); average minimum daily temperature (Tmin); average maximum daily temperature (Tmax); average variance of daily maximum temperature (TmaxVar); and average variance of daily Tmin (TminVar).

Table 4.2: Description of the environmental variables used in analysis

Variable	Description
Annual mean precipitation (AMP)	Average annual rainfall in mm, calculated from 1976–2005 using AWAP data (Jones <i>et al.</i> 2009).
Seasonality of precipitation (Pcov)	The coefficient of variation of precipitation is the 30-year average (1976–2005) of standard deviation of the weekly precipitation estimates expressed as a percentage of the mean of those estimates (i.e., the annual mean).
Precipitation of the driest quarter (Pdry)	Total rainfall in mm for the quarter (90 consecutive days) that had the minimum total rainfall in a year, calculated over 1976–2005 from AWAP data (Jones <i>et al.</i> 2009).
Annual mean temperature (AMT)	From ANUCLIM (McMahon <i>et al.</i> 1995).
Seasonality of temperature (Tcov)	From ANUCLIM (McMahon <i>et al.</i> 1995).
Average minimum daily temperature (Tmin)	20-year average (1991–2010) for daily minimum temperature. From data in Storlie <i>et al.</i> (2013).
Average maximum daily temperature (Tmax)	20-year average (1991–2010) for daily maximum temperature. From data in Storlie <i>et al.</i> (2013).
Variance of Tmax (Tvar)	20-year average (1991–2010) of variance of Tmax. From data in Storlie <i>et al.</i> (2013).
Connectivity	A connectivity index for each grid cell of rainforest was calculated by integrating habitat suitability and proximity through space. For full details see Supplementary Material S1 in Chapter 2.

Our connectivity index is detailed in Chapter 2. Briefly, it is a measure of habitat suitability for our focal skink species, averaged over space using species-specific dispersal expectations. As our species is an obligate rainforest-dweller, grid cells in the landscape that are rainforest and that are surrounded by rainforest have high connectivity indices, while grid cells of rainforest surrounded by non-rainforest matrix have low indices. See Table 4.2 for further details on all variables, and Figure 4.3 for correlations between all variables.

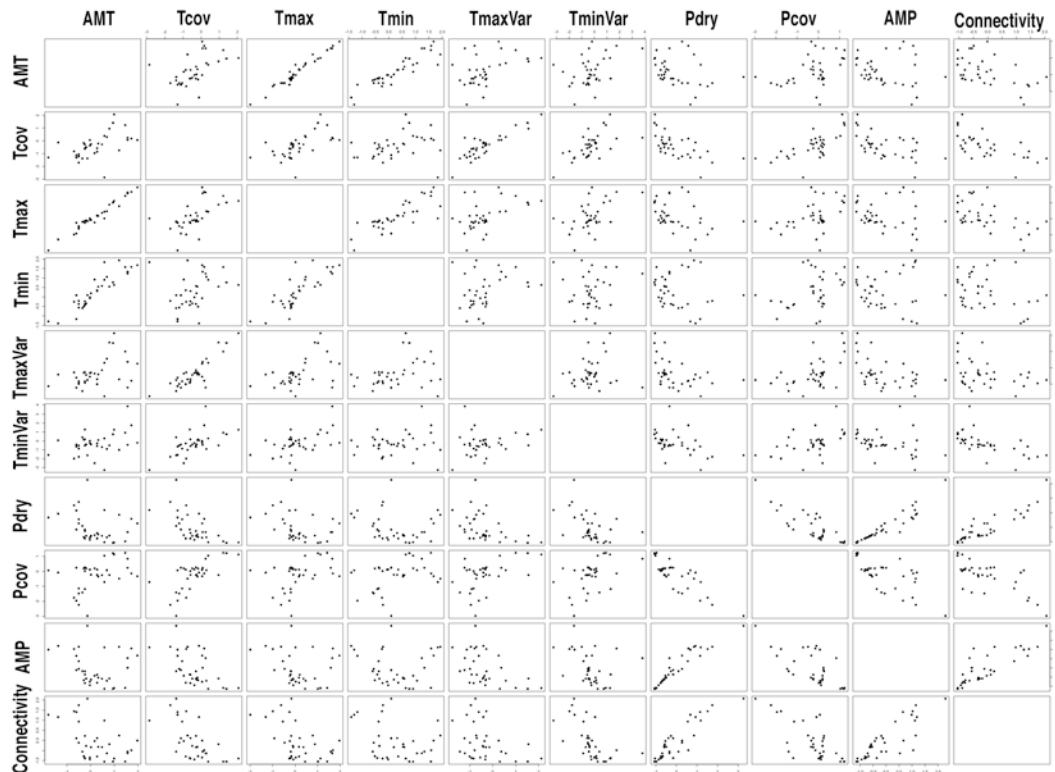


Figure 4.3

Pairwise correlations of environmental variables used in analyses.

Analysis

Our analysis aimed to assess: 1) how traits correlate to environmental variables; and 2) how connectivity affects these relationships with the environment (i.e., the interaction between connectivity and environmental effects). To allow comparison of coefficients across variables, and to make interaction effect-sizes meaningful, all trait and environmental variables were standardized so they had a mean of 0 and a standard deviation of 1. Linear models were run for each pair of environment–trait variables, with all models including the effect of lizard body size and sex, as well as the interaction between environment and connectivity:

$$\text{trait}_i = A + B_{svl} \times \text{SVL} + B_{sex} \times \text{Sex} + B_{env} \times \text{Env} + B_{conn} \times \text{Conn} + B_{int} \times \text{Env} \times \text{Conn} + \text{error}_i$$

Where:

trait_i = trait value of interest (morphological or physiological) from lizard i

A = intercept

B_{svl} = coefficient of SVL

SVL = lizard snout–vent length, to control for effect of body size

B_{sex} = coefficient of Sex

Sex = lizard sex (this species is sexually dimorphic in some morphological traits, e.g., head width)

B_{env} = coefficient of environmental variable

Env = environmental variable (e.g., AMT, AMP)

B_{conn} = coefficient of connectivity

Conn = connectivity index

B_{int} = coefficient of interaction between Env and Conn

error_i = deviation between model and trait value of lizard i

A score for ranking the strength of local adaptation was then calculated as:

$$LA = B_{env} \times B_{int} \times -1$$

If the signs of the two coefficients (B_{env} and B_{int}) are opposite (which indicates an environmental effect being eroded by high connectivity, i.e., evidence for local adaptation), LA will be positive. If the signs are the same (which indicates an environmental effect being enhanced by high connectivity, a situation not consistent with local adaptation), LA will be negative. Thus, higher numbers on this scale equate to stronger evidence for local adaptation in that environment–trait pair. This score can, in theory, range from $-\infty$ to $+\infty$. Once many environment–trait combinations have been assessed, the coefficients for all pairs can be plotted (see Fig. 4.1). As described in the Introduction, in a system dominated by local adaptation, we expect to see a negative relationship between B_{env} and B_{int} (Fig. 4.1B). To assess which type of trait showed stronger signs of local adaptation to the climatic variables tested, ANOVAs were used to compare the size of the coefficient of the environmental effect (B_{env}) and the size of the coefficient of the Conn×Env interaction (B_{int}) between morphological and physiological traits. All analyses were conducted in R v3.2 (R Core Team 2015).

Results

There was substantial variation in the effect of environment (B_{env}) and its interaction with connectivity (B_{int}) across climate and trait variables, with B_{env} ranging from -1.64 to 1.37, and B_{int} ranging from -0.89 to 0.74 (Fig. 4.4). Despite this variation, a clear pattern is evident, with most points in Figure 4.4 appearing in the top-left or bottom-right quadrants: the quadrants in which the two coefficients have opposing signs, and where we would expect points to fall if environment–trait correlations are due to local

adaptation. Across these environment–trait combinations there is a distinct negative linear trend (slope= -0.36, $p < 0.001$). It is especially noteworthy that the environment–trait pairs with the largest coefficients (i.e., those points furthest away from the origin) are in the two quadrants indicative of local adaptation, with the exception of TmaxVar–CTmin which appears at the bottom of the bottom-left quadrant.

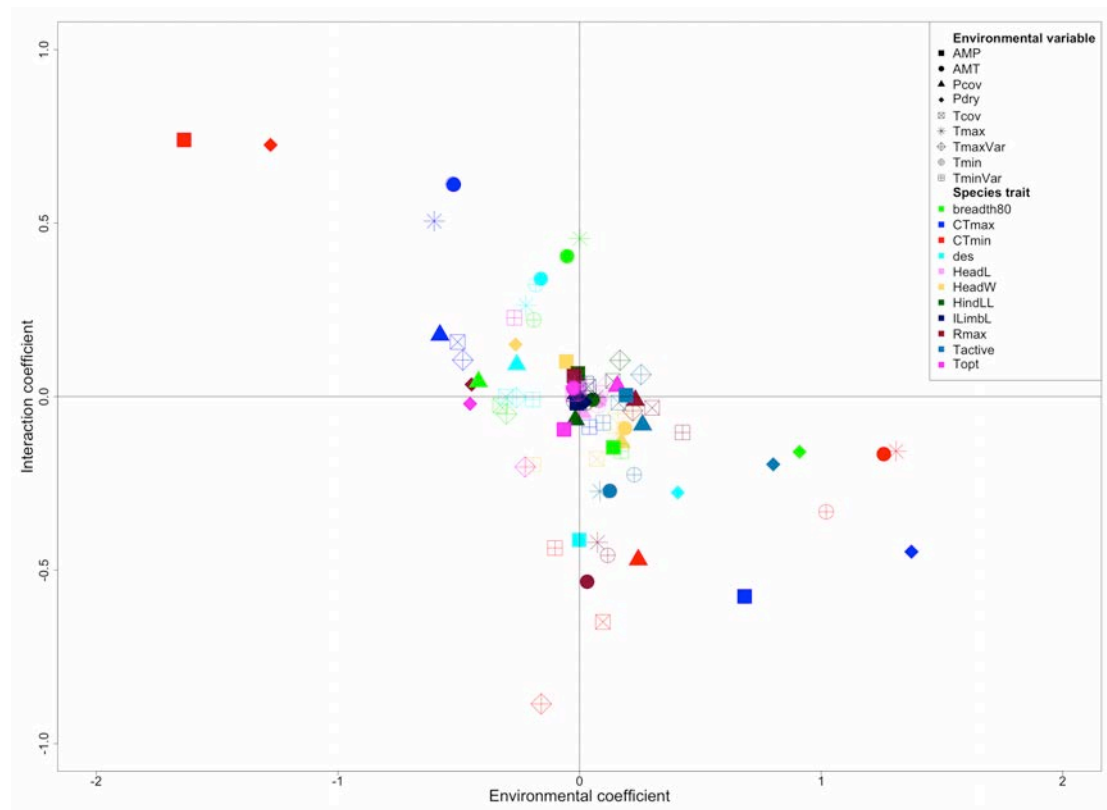


Figure 4.4

Scatterplot showing the results of 99 linear models run to assess the relationship between each pair of environment–trait variables and the environment–connectivity interaction.

Environment–trait coefficients are on the x-axis, and environment–connectivity interaction coefficients are on the y-axis. Local adaptation is suggested in environment–trait pairs that show a strong environmental effect that is eroded by increasing connectivity. Traits (morphological and physiological) are represented by colours, while environmental variables are represented by shapes. Each environment–trait pair on the plot can be identified by its unique shape-and-colour combination.

Overall, physiological traits showed substantially stronger environmental effects (i.e., larger values of B_{env}) than did morphological traits (ANOVA comparing B_{env} for morphological vs physiological traits: $F_{1,97} = 19.6$, $p < 0.001$), with the largest environmental effects being exhibited by CTmin (AMP: -1.64; Tmax: 1.31; Pdry: 1.28) and CTmax (Pdry: 1.37). Physiological traits also showed stronger interactions between environmental effects and connectivity (ANOVA comparing B_{int} for morphological vs physiological traits: $F_{1,97} = 23.89$, $p < 0.001$), again with CTmin and CTmax showing the largest interactions. These trends are apparent when we examine our index of local adaptation. Figure 4.5 shows a heatmap of all environment–trait pairs, ranked via reciprocal averaging according to the strength of their local adaptation index. The environment–trait pairs that show the strongest signature of local adaptation appear at the top-left in red. There is a rough divide, with most of the physiological traits on the left and most of the morphological traits on the right. The exceptions are the physiological traits, Topt and Rmax, which appear at the far right of the figure.

The two environmental variables that produced the strongest effects (topmost rows in Fig 4.5) were both precipitation related: annual mean precipitation (AMP) and precipitation of the driest quarter (Pdry). In our system, AMP and Pdry are both highly correlated with connectivity (see Fig. 4.3). This is expected, because our connectivity index is largely a measure of where rainforest is, and the distribution of rainforest in our study region is driven to a large degree by rainfall.

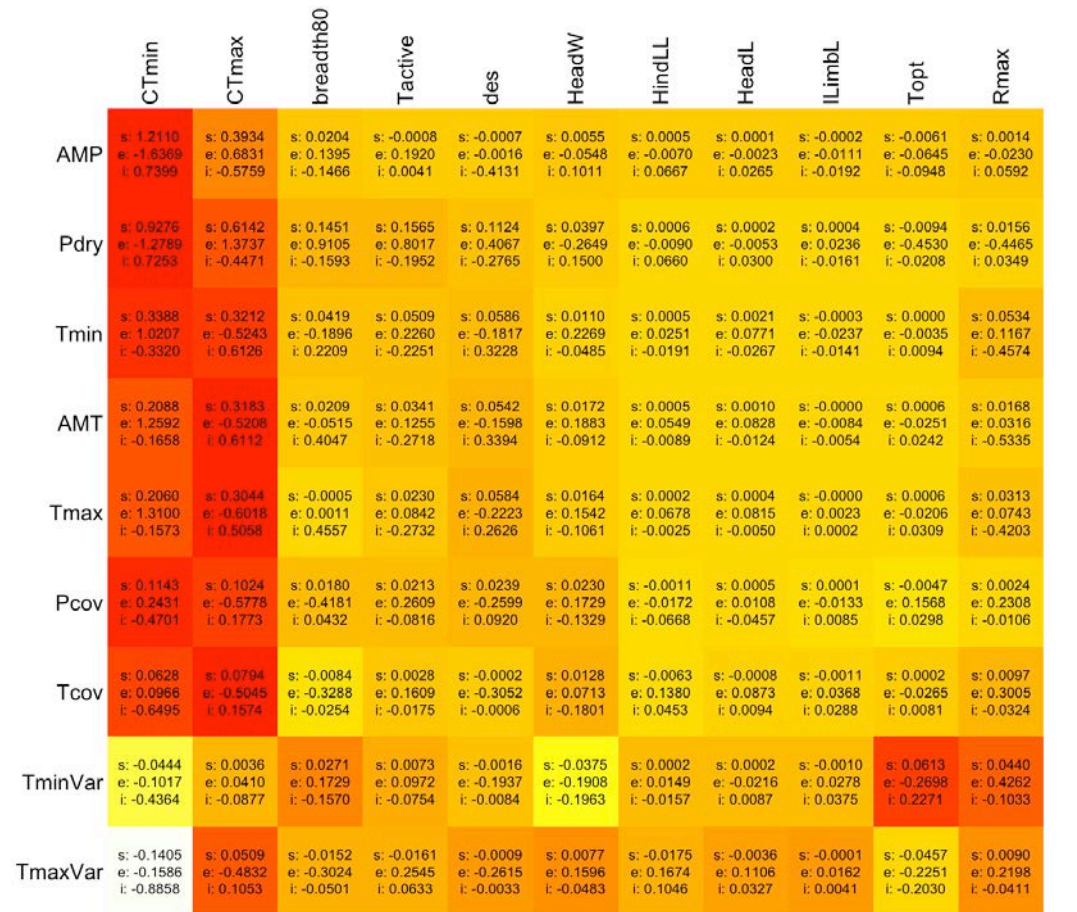


Figure 4.5

Heatmap showing the relative rankings of climate variables (rows) and morphological and physiological traits (columns). The matrix has been sorted (by reciprocal averaging) and coloured according to the strength of local adaptation, with higher values coloured red and being sorted to the top/left. See Tables 4.1 and 4.2 for explanations of the trait and environmental variables used.

s = 'local adaptation' score: $-1 \times e \times i$

e = coefficient of the environmental variable.

i = coefficient of the interaction between the environment and connectivity terms.

Discussion

Understanding environment–trait correlations will help us plan management strategies, such as assisted gene flow (AGF), that can mitigate the impact of climate change on vulnerable species. Numerous studies have looked for (and found) environment–trait correlations (e.g., Bogert 1949; Sandoval 1994; Storfer *et al.* 1999; Wegener *et al.* 2014; Klaczko *et al.* 2015; Llewelyn *et al.* submitted), but the interpretation of these associations is plagued with uncertainty: are they associations due to local adaptation, or plasticity? By acknowledging that gene flow undermines adaptation, we can incorporate connectivity (a proxy for gene flow) into our analysis, and in doing so, separate correlations due to local adaptation from those due to plasticity.

Local adaptation

In the environment–trait combinations we assessed, physiological traits typically showed a substantially stronger effect of environment than did morphological traits, with the largest environmental effects shown in CT_{max} and CT_{min} (Figs. 4.4 & 4.5). Physiological traits also generally showed stronger environment–connectivity interactions, again with CT_{min} and CT_{max} showing the largest interactions. Overall, physiological traits generally showed stronger evidence of local adaptation than did morphological traits. This result is intuitive: we would expect an ectotherm’s thermal physiological traits to be under strong selection from climate (Angilletta 2009; Hoffmann 2010; Clusella-Trullas *et al.* 2011), but the mechanistic links between morphology, climate, and fitness are much less clear. Had we also included some environmental variables that had a clearer link to morphology, we might have detected stronger environment–trait relationships for morphology. For example,

skinks that occur in rockier habitats show various morphological adaptations to that environment (Goodman *et al.* 2008). Including a measure of rockiness in our set of environmental variables, for example, might have allowed us to detect environmental correlations with limb length.

On the environment side, our analysis suggests that precipitation is a very strong driver of local adaptation, even in thermal traits that might not seem obviously related to precipitation (e.g., CTmin, CTmax). Although this may be a surprising result, precipitation has been shown to directly affect growth rate, body temperature, activity patterns, and thermoregulatory opportunities in lizards (Huey & Webster 1976; Stamps & Tanaka 1981; Crowley 1987; Jones *et al.* 1987; Lorenzon *et al.* 1999; Clusella-Trullas *et al.* 2011). Wetter areas also have higher thermal inertia, and therefore lower cyclical thermal fluctuations (Myers & Heilman 1969), and changed environmental variance in temperature potentially has a strong influence on thermal limits (Martin & Huey 2008). Additionally, Bonebrake and Mastrandrea (2010) found that changes in precipitation values can significantly affect modeled fitness and performance curves, and that the inclusion of precipitation in these models produces outcomes that are very different to those from models including only temperature. Finally, comparative analyses also suggest that precipitation can influence thermal traits in many species (Clusella-Trullas *et al.* 2011). Thus, although the mechanisms linking precipitation to thermal limits are diffuse and poorly resolved, they do exist, and our analyses suggest that they are strong drivers of local adaptation.

Our analysis also suggests that temperature is an important driver of local adaptation in this system, but that extremes of temperature (encapsulated in minimum and

maximum temperatures) are at least as strongly associated with local adaptation as is mean temperature. Again, this result is intuitive (natural selection from climate is likely stronger during extreme events than during normal daily temperatures) and agrees with results of empirical studies (Clusella-Trullas *et al.* 2011). Finally, the environmental variables with the weakest signals of local adaptation are Tcov (temperature seasonality), TminVar, and TmaxVar (variance of minimum and maximum daily temperatures, respectively). These variables represent predictable environmental variation occurring within an individual's lifespan and so are variables to which we might expect individuals to develop plastic responses to, rather than adaptive responses (Gilchrist 1995; Kingsolver & Huey 1998; Phillips *et al.* 2015).

System-wide signal of local adaptation

The clear negative linear trend displayed in Figure 4.4 is precisely what we would expect in a set of environment–trait combinations dominated by local adaptation. Migrant load (the negative effect of the immigration of less-locally adapted individuals) scales positively with immigration as well as with the strength of selection [see equation 5 in Polechová *et al.* (2009)]. The reason for this is that, when the strength of selection is moderately high, the environment will have a large effect on relevant traits, and therefore any immigrants coming from differing environments will be particularly maladapted and will therefore have a large and negative impact on the local phenotype. Thus, we expect environment–trait combinations with strong local adaptation to show strong effects of connectivity on the environment–trait correlation (Polechová *et al.* 2009).

We used long-term climatic averages and found strong evidence that local adaptation dominates over plasticity in our system. If we had included conditions the lizards had recently encountered, plasticity may have been of more importance. This is because environmental variables that are similar across generations should lead to local adaptation, while environmental variables that fluctuate within generations should have a strong influence on phenotypic plasticity

Phenotypic plasticity

The importance of accounting for phenotypic plasticity is exemplified in our dataset by the relatively strong effect of precipitation of the driest quarter (P_{dry}) on the temperature at which maximum sprint speed is achieved (T_{opt}) and on maximum sprint speed (R_{max}) itself. On their own, these strong correlations might traditionally be considered evidence for local adaptation. Our analysis, however, suggests that the environmental effect is completely unaffected by connectivity, implying that variation in these traits is due to plasticity. Other work (Llewelyn *et al.* submitted) has shown little temporal variation in T_{opt} (within generations) and this, together with our results, suggests that this trait undergoes developmental plasticity, but is fixed in adult lizards. In principle, this non-effect of connectivity could also arise due to selection that is so strong that it maintains local adaptation despite high levels of gene flow [i.e., immigrants are selected against so strongly that they do not contribute to the effective population (Kawecki & Ebert 2004)]. The environment–trait relationships for T_{opt} and R_{max} are, however, weaker than those for some other traits (e.g., CT_{max} and CT_{min}) that show clear effects of connectivity, so extremely strong selection seems an unlikely explanation for the pattern we see here. It must also be noted that phenotypic plasticity and genetic adaptation are not mutually exclusive:

there can be a genetic basis to the degree to which an organism can alter its phenotype plastically. Indeed, there is geographic variation in the heat-shock response exhibited by our focal skink species that may be adaptive (Phillips *et al.* 2015).

Assumptions and limitations

Our analysis requires an index of population connectivity across the landscape, something that can be calculated relatively easily for many species by using broad scale habitat mapping datasets [e.g., vegetation mapping from DERM (2011)]. Where possible, these measures of connectivity should be calculated at a scale relevant to the scale of dispersal of the species in question (as was ours, using dispersal rate data for *Lampropholis coggeri* from Singhal & Moritz, 2012). For highly mobile species, such as plants or insects that have wind-assisted dispersal and for whom calculating connectivity between populations may be difficult, it is possible our approach will not work. But for many species of animals with relatively low vagility (i.e., the species for which AGF is most needed), our approach should be generally applicable.

Our approach implicitly assumes that traits have a linear response to the environment (at least at the environmental scale across which we are looking). In most instances, this will be a reasonable assumption: it seems unlikely, for example, that a trait such as desiccation resistance would be high in dry environments, low in moderately wet environments, and then high again in very wet environments. The reason our assumption of linear environment–trait relationships bears mentioning is that a limitation of our technique arises when the connectivity index is strongly correlated with one or more of the other environmental variables being used. In our system, for example, AMP and Pdry are correlated with connectivity (Fig. 4.3). Where the

environment–connectivity correlation is very strong, the interaction term in our model (Conn×Env) could be interpreted as a quadratic term for environment (i.e., Env²). In these cases, it is possible that a strong connectivity interaction is, in fact, pointing to a non-linear environment–trait relationship. Thus, for environmental variables that correlate with connectivity (and there will always be some), careful consideration needs to be given to the possibility of a quadratic fitness function between environment and trait. In our case, it remains possible, for example, that the strong influence of precipitation on local adaptation in our system is spurious, and instead reflects non-linear relationships between optimal trait values and precipitation. We can, however, think of no obvious reason why thermal limits should respond quadratically to precipitation, nor why desiccation rates and other physiological traits should also do so. Thus we are inclined to accept the importance of this environmental variable in driving local adaptation in our system.

Finally, our approach, by examining one environment–trait combination at a time, may potentially miss relationships that only appear in multivariate analyses. For example, if two environmental variables are negatively correlated but both have a positive effect on a trait, it is possible that these countergradients can obscure the univariate relationship. Similar problems are encountered when examining response to selection over time Merilä *et al.* (2001), and with our approach may lead us to underestimate the number of important environmental drivers of local adaptation. To minimize this effect, care should be taken in future work to sample environmental spaces in such a way as to minimize correlations between environmental variables. Such an aim can be achieved by, for example, strategically exploiting latitudinal and altitudinal gradients.

Conclusion

There is increasing urgency to identify populations that will act as suitable sources for assisted gene flow efforts in the face of climate change. To identify these populations, we need to know which traits influence sensitivity to climate and are locally adapted. Traditional approaches to unearthing local adaptation (reciprocal transplants and common garden experiments) are time consuming, and often cannot attribute adaptation to any particular environmental driver. Local adaptation is, however, undermined by gene flow, and we can use this fact to sort patterns of local adaptation from patterns with other causes. Here we demonstrate this approach: using connectivity as a proxy for gene flow, and looking for its effect on environment–trait correlations. Our analysis, using a species of lizard from Australia’s Wet Tropics rainforest, suggests local adaptation is the overwhelming signal in the set of environment-trait correlations tested. As well as confirming a strong role for local adaptation, we have effectively ranked environmental drivers of local adaptation, finding evidence that precipitation and temperature are important environmental variables with regard to local adaptation. Our analysis also suggests that some traits exhibit strong plastic responses to the environment, particularly in response to precipitation of the driest quarter and the seasonality of temperature and precipitation. These specific results will likely apply to other species that are phylogenetically or ecologically similar to our focal species, but the methods will apply much more broadly.

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Chapter 5

Identifying source and recipient populations for assisted gene flow: matching locally adapted populations across current and future climates

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Abstract

In the face of rapid anthropogenic climate change, assisted gene flow (AGF) aims to boost the resilience of recipient populations by translocating pre-adapted individuals into the recipient population. This strategy relies on locating populations already adapted to climates that will be more widespread in the future. The magnitude of impending climate change is such that these future climates are likely to be at the extremes of most species' capacity to adapt. Matching the current climate of the source population with the future climate of the recipient population can be done using broadscale climate datasets and future climate projections; however, this matching cannot be done sensibly if we do not understand which aspects of climate are the strongest drivers of local adaptation. Here we demonstrate methods to: 1) identify the climatic drivers of local adaptation; 2) locate locally adapted populations in the extreme parts of the species' current climate space; and 3) identify potential recipient populations to make best use of these adaptive extremes. We demonstrate these methods with a case study from Australia's Wet Tropics Rainforest. By identifying and translocating these extreme variants into recipient populations heading for those climate extremes, we maximize the evolutionary resilience of the species as a whole.

Background

The reality of a warming world is upon us, and while the predictions are dire, there are still ways to mitigate climate change's impacts on biodiversity (Hannah *et al.* 2002; Parmesan & Yohe 2003; Williams *et al.* 2003; Thomas *et al.* 2004; Heller & Zavaleta 2009). One potentially powerful technique is assisted gene flow (AGF), the translocation of pre-adapted individuals to boost the fitness and evolutionary resilience of a recipient population (Weeks *et al.* 2011; Aitken & Whitlock 2013). At the species level, the utility of AGF can be enhanced by careful selection of source populations to capture as much of the species' adaptive variation as possible. As the magnitude of impending climate change will challenge the adaptive capacity of most species, we would be wise to make use of the most extreme adaptive variants found within a species. By capturing these extreme variants into recipient populations heading towards future climate extremes, we maximize the evolutionary resilience of the species as a whole.

Species exist along a continuum of climate: they may be present where climatic conditions are within a suitable range, and they are absent where conditions are unsuitable. When looking for source populations at climate extremes, we need to find a region of climate space in which the species is likely to be present, but only just. We are looking for populations on the edge of climate space. We are also looking for populations that are adapted to their local climate. Local adaptation is widespread, but not ubiquitous (Hereford 2009): small populations and those populations (including sink populations) that experience high rates of maladaptive gene flow may be maladapted to their local climate (Haldane 1956; Kirkpatrick & Barton 1997). Using maladapted populations as sources for AGF would undermine the value of an AGF intervention.

Axes of adaptation

How do we identify such extreme, locally adapted populations, and how do we match them with optimal recipient populations? Figure 5.1 outlines a strategy for answering these questions.

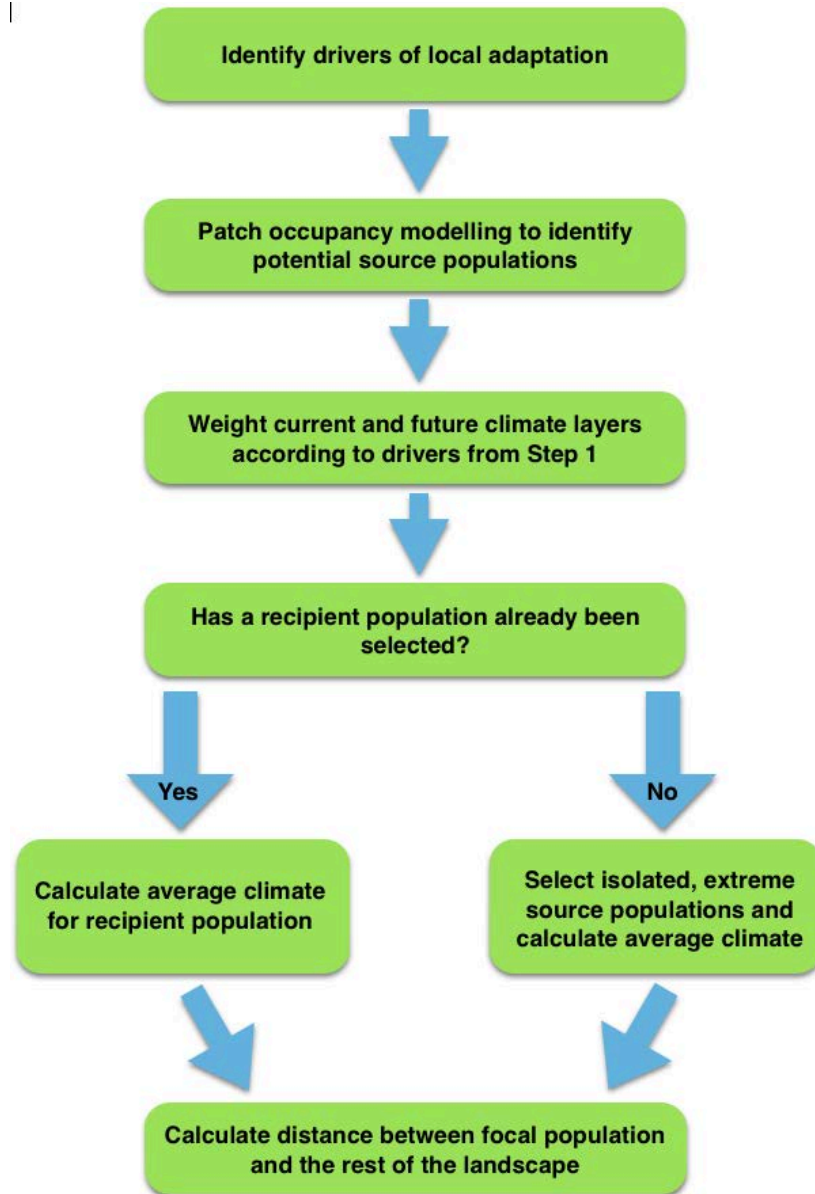


Figure 5.1

A strategy for identifying and matching source and recipient populations for assisted gene flow.

First, we need to know which climate axes are the most important to each species. We need to identify the climate axes along which local adaptation is most strongly occurring. Making this identification is not a trivial undertaking, but it can be done, and here we demonstrate how by using data from a skink species in Australia's Wet Tropics (AWT). The Wet Tropics bioregion is home to a large number of endemic species and communities, many of which are highly vulnerable to climate change (Hilbert *et al.* 2001; Williams *et al.* 2003). Indeed, tropical ectotherms in general may be particularly vulnerable to climate change, because they already exist near their upper critical thermal limits (Huey *et al.* 2009).

Here, we focus on the Rainforest Sunskink (*Lampropholis coggeri*), a small (snout–vent length 45 mm) diurnal scincid lizard that is rainforest-dependent (Wilson & Swan 2010). It is abundant and, because it is active year-round and is typically seen basking in patches of sunlight on the forest floor, is also highly detectable. We collected a sample of these lizards from 35 populations spanning a range of climates, and measured five morphological and seven physiological traits (see Chapter 4 for details). We then examined the strength of the relationship between each trait and each of nine climate variables across the populations. As well as measuring the strength of the relationship between trait and climate, we investigated how strongly habitat connectivity (see Chapter 2 for details on connectivity index) erodes the trait–climate relationship. We did this using an interaction term between climate and connectivity variables. Strong local adaptation is indicated by a strong coefficient for the relationship between trait and climate, as well as a strong interaction in which increasing connectivity erodes the trait–climate association (Chapter 4). We multiplied these two measures (coefficient of the climate term and coefficient of the interaction between climate and connectivity) to generate an index for the strength of local adaptation exhibited by each pair of trait–climate combinations. We then averaged this score over all traits showing local adaptation for each climate variable to generate a local adaptation score for each climatic variable. This process

identified two precipitation variables, annual mean precipitation (AMP) and precipitation of the driest quarter (Pd_{dry}), as being most strongly associated with local adaptation in our study system.

Finding eco-climatic edges

Once we know the axes along which populations locally adapt, we need to find the edge along each axis where adaptation reaches its limit. Occupancy modeling allows us to take the characteristics of sites in which the focal species is known to be present or assumed to be absent (based on survey data), and use these characteristics to predict the probability of occupancy for patches that have not been surveyed. If the occupancy model includes the climate variables we have previously identified as being drivers of local adaptation, we can detect the edge in climate space along which the species still occurs, but is also experiencing extreme climates. It is this edge that should yield the most valuable source populations in the face of climate change. Because we only surveyed under conditions when *L. coggeri* is highly detectable, we assumed perfect detectability at all surveyed locations. Under this assumption, our occupancy model becomes a generalized linear model with binomial errors and logit link function. We fitted this model to create a function predicting the probability of patch occupancy (P_{occ}). The environmental variables used in this model were patch area, plus the highest-ranking, but uncorrelated, climate variables that emerged from the analysis in Chapter 4, viz. AMP, T_{min}, P_{cov}, T_{cov} (Table 5.1). Patch area was used as it is likely to have an effect on population persistence — small patches support only small populations, which are more prone to extinction. Surveys were conducted at 94 sites in 84 patches. *Lampropholis coggeri* was present in 35 out of the 94 sites, and in 26 of the 84 patches. The top two patch occupancy models as judged by AIC_c were: 1) AMP + patchArea + T_{min}; and 2) patchArea + T_{cov} + T_{min} (AIC_c delta = 0.06). All models are presented in Table 5.2, ranked according to AIC_c value.

Table 5.1: Environmental variables used in occupancy modeling and related analyses

LA score = local adaptation score from Chapter 4; Weighting = LA score – min(LA score) + 1.

Variable	LA score	Weighting	Description
CLIMATIC			
Annual mean precipitation (AMP)	0.233	1.205	Average annual rainfall in mm, calculated from 1976–2005 using AWAP data (Jones <i>et al.</i> 2009).
Average minimum daily temperature (Tmin)	0.088	1.06	20-year average (1991–2010) for daily minimum temperature. From data in Storlie <i>et al.</i> (2013).
Seasonality of precipitation (Pcov)	0.034	1.006	The coefficient of variation of precipitation is the 30-year average (1976–2005) of standard deviation of the weekly precipitation estimates expressed as a percentage of the mean of those estimates (i.e., the annual mean).
Seasonality of temperature (Tcov)	0.028	1.0	From ANUCLIM (McMahon <i>et al.</i> 1995).
NON-CLIMATIC			
Patch area	-	-	Area of patch, in m ² .
Connectivity	-	-	A connectivity index for each grid cell of rainforest was calculated by integrating habitat suitability and proximity through space. For full details see Supplementary Material S1 in Chapter 2.

Table 5.2: Model selection results for occupancy modeling.

p-values, based on the z statistic, are shown only for the top model.

Rank	Intercept	AMP	Area	Pcov	Tcov	Tmin	df	logLik	delta	weight
1	2.424	0.6756 (p=0.051)	11.56 (p=0.204)			-1.179 (p=0.001)	4	-43.727	0.00	0.156
2	1.547		8.112		-0.6649	-1.152	4	-43.755	0.06	0.152
3	1.562	0.4712	8.128		-0.4652	-1.303	5	-42.969	0.73	0.109
4	-0.5515	0.5357			-0.6998	-1.526	4	-44.172	0.89	0.100
5	-0.5348				-0.9825	-1.399	3	-45.327	1.01	0.094
6	3.045		14.07			-0.7994	3	-45.725	1.80	0.063
7	1.676		8.562	-0.1689	-0.6199	-1.083	5	-43.657	2.10	0.055
8	2.336	0.7779	11.23	0.1601		-1.275	5	-43.668	2.12	0.054
9	-0.5375			-0.2669	-0.888	-1.28	4	-45.029	2.60	0.043
10	1.432	0.6003	7.645	0.2062	-0.4736	-1.426	6	-42.879	2.84	0.038
11	-0.6117	0.92				-1.413	3	-46.261	2.88	0.037
12	3.13		14.28	-0.3609		-0.6957	4	-45.204	2.95	0.036
13	-0.5502	0.643		0.1578	-0.7029	-1.621	5	-44.117	3.02	0.034
14	-0.6088	0.9967		0.1113		-1.481	4	-46.229	5.00	0.013
15	4.318		18.47	-0.6063			3	-48.256	6.87	0.005
16	4.426	-0.1827	18.92	-0.6955			4	-48.036	8.62	0.002
17	4.508		19.35				2	-50.271	8.76	0.002
18	-0.5843			-0.6222		-0.7751	3	-49.312	8.98	0.002
19	4.363		18.65	-0.6096	0.0353		4	-48.247	9.04	0.002
20	4.328	-0.2631	18.52	-0.7255	-0.1209		5	-47.972	10.73	0.001
21	4.476	0.0462	19.2				3	-50.255	10.87	0.001
22	4.521		19.4		0.01027		3	-50.270	10.90	0.001
23	-0.5564					-0.9786	2	-51.693	11.60	0
24	4.523	0.07652	19.39		0.0535		4	-50.241	13.03	0
25	-0.499			-0.8573			2	-53.809	15.83	0
26	-0.4911			-0.8123	-0.2236		3	-53.370	17.10	0
27	-0.5	-0.03462		-0.8767			3	-53.800	17.96	0
28	-0.4935	-0.3208		-0.9625	-0.4075		4	-52.934	18.41	0
29	-0.4647	0.3817					2	-58.604	25.42	0
30	-0.4688				-0.3795		2	-58.719	25.65	0
31	-0.452						1	-60.142	26.41	0
32	-0.4706	0.2522			-0.2218		3	-58.301	26.96	0

The resulting patch-level probabilities were then thresholded such that $P_{occ} < 0.2$ was considered unoccupied, $0.2 < P_{occ} \leq 0.8$ was considered 'edge' habitat, and $P_{occ} > 0.8$ was considered core habitat. This thresholding identified numerous patches on the eco-climatic edge for our species (Fig. 5.2).

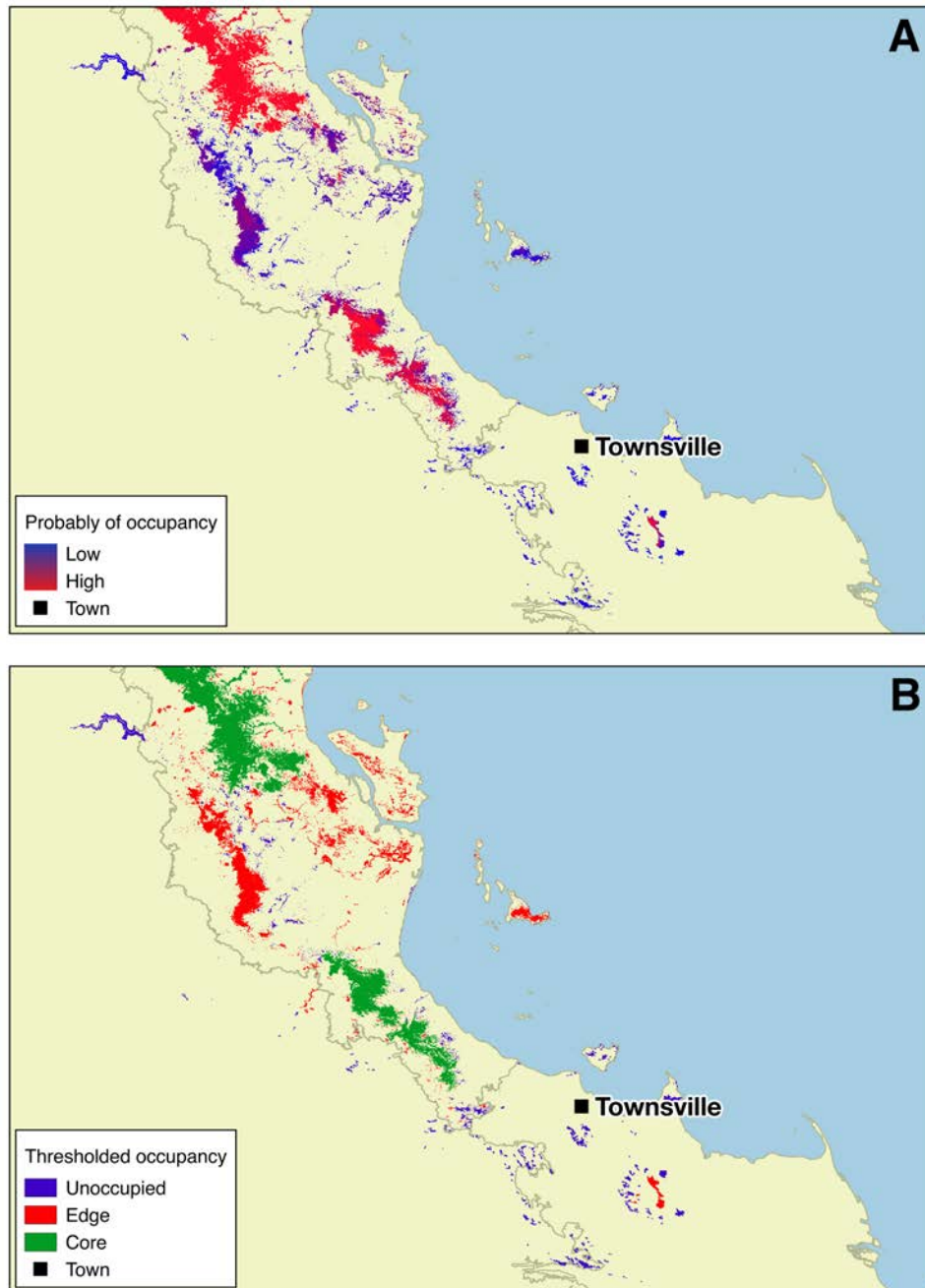


Fig. 5.2

A) Probability of occupancy at the pixel level, from low to high. B) Probability of occupancy averaged at the patch level and thresholded. The red 'edge' ($= 0.2 < P_{occ} < 0.8$) patches are the ones most likely to contain populations of our focal skink species living at their climatic extremes.

The top three models all included patchArea, where the effect was large but not statistically significant. None of the patches in our system were sufficiently small that size affected their probability of occupancy. The scale of the vegetation mapping we used gave us a minimum patch size of one grid cell, or 6400 m², an area that is likely to support a large population of our very small skink species. Had we been able to identify smaller patches, or had we used a larger lizard species, it is likely that patch size would have influenced occupancy (e.g., Hokit & Branch 2003). Given the non-effect of patch size in our system, locally adapted populations are more likely to be found in areas of low connectivity that are shielded from gene swamping (see Chapters 2 & 4), so we then sorted the list of 'edge' patches in order of increasing P_{occ} and increasing connectivity. From this sorted list we can identify the patches that are most climatically extreme (i.e., those with the lowest P_{occ}) and also the most isolated (i.e., lowest connectivity). These source patches are those patches likely to contain populations that are locally adapted to extreme climates.

Weighting axes, and matching source and recipient populations

Now that we have identified places in the landscape likely to contain the most extreme adaptations to climate, we need to match these source populations to potential recipient populations. These populations can be matched easily in an n -dimensional climate space by calculating the distance between the populations along any number of climatic axes (e.g., annual mean temperature, annual mean precipitation, seasonality of precipitation, etc.). This simplistic approach, however, does not account for the differing degrees to which each of the climatic axes drives local adaptation. This is important, because, for example, one unit of change in temperature will not result in the same change in fitness as a unit of change in precipitation. Even if variables are standardized (as ours were), the fitness effects of different variables will not be identical across all climate variables. To find pairs of best-matched populations we should adjust the climate space by scaling the climate axes according to the degree to which they drive local adaptation.

We have already demonstrated a technique that can be used to determine the appropriate weighting for each climate variable (outline above: “Axes of adaptation”; detailed in Chapter 4). The vector of adaptation scores generated for each variable can act as a scaling vector for our climate space. By calculating this score for each climatic variable of interest, we can convert our climate space into an 'adaptation space'. Matching populations in this adaptation space ensures that translocated individuals have maximum fitness in the future climate of the recipient population.

Using the RCP8.5 emissions scenario and the CSIRO Mk3.0 model to generate our future climate space, present and future climate axes were scaled (mean = 0 and SD = 1) and weighted using the adaptation scores developed above. We then calculated the Euclidean distance between the source patch's current average climate and the future climate of every grid cell of southern AWT rainforest. This enables us to identify the areas whose future climates most closely match the current climates of any particular source population. It is to these areas that individuals from the source populations should be translocated. We illustrate this capacity here with an example source patch that was ranked as likely to represent the extremes of local adaptation, and the corresponding recipient localities to which this source patch is best matched (Fig. 5.3).

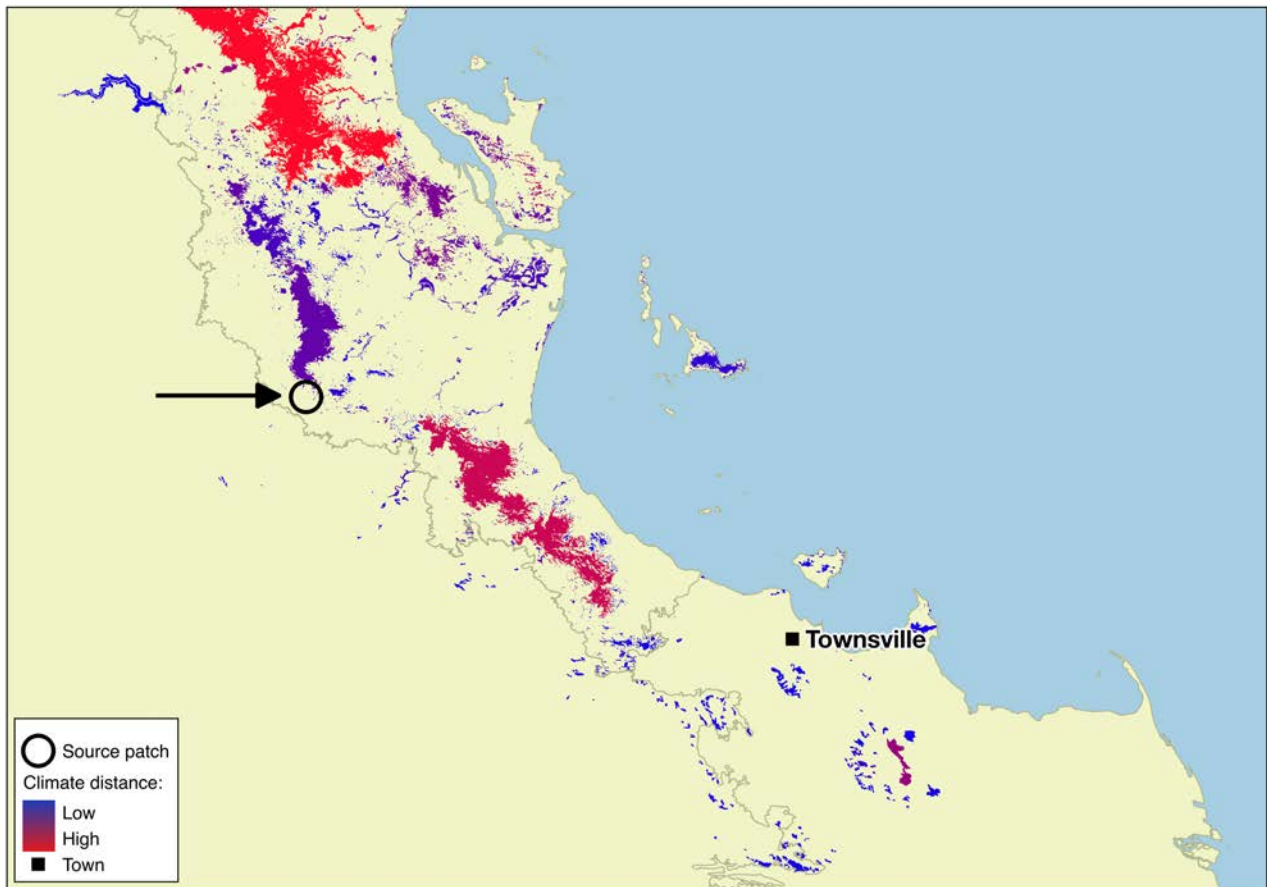


Figure 5.3

A source patch (circled and arrowed) was selected based on its isolation and extreme climate. Colours represent distance in 'adaptation space' (climate space, with axes weighted according to the degree to which they drive local adaptation) from the source patch to all other areas of rainforest in the southern Wet Tropics. This climate space represents the distance from the current climate of the source patch to the future climates of all other patches in the region. It is to the areas of low distance (blue on the map) that individuals from the source population should be translocated in AGF implementations.

Discussion

This study presents the first coherent approach to matching source and recipient populations for assisted gene flow. First, we identify the environmental drivers of local adaptation. We then locate important locally adapted populations in the landscape. Finally, we match these source populations to appropriate recipient populations using a climate space transformed to represent selection pressures. While our approach is an important step, general guidelines for determining the size and timing of any targeted gene flow efforts are yet to be developed (but see McDonald-Madden *et al.* 2011, for an assisted colonisation framework; and Whiteley *et al.* 2015, for a review of genetic rescue, including numbers of migrants reported from various case studies). Translocations that take place too early mean that translocated individuals will not yet match the future climate of the recipient population. Too late, and source populations may already be in decline or extirpated. Translocating early and often is probably a safe approach in the absence of any other data, but determining the optimal size and timing of translocations remains an important unresolved problem.

Generality of approach and results

While we have demonstrated this technique using a model lizard species, the methods detailed above should apply to any taxa for which AGF is a serious consideration, including plants. The results from our particular case study, in terms of the spatial location of best-matched source and recipient populations in the Australian Wet Tropics, will likely apply to other rainforest lizard species in the region. How broadly these specific results apply will depend on how general the effects of climate are. Do AMP and Pdry drive the distribution of, and local adaptation in, other AWT skink species? In birds or mammals? In other habitats? In species outside of Australia? These questions can only be answered empirically: future work using our approach in a wider variety of taxa will determine the generality of our results with regard to the aspects of climate driving local adaptation. For now, however, we would expect that the climatic drivers of local adaptation will be the same in species that are ecologically and/or phylogenetically similar.

Modifications to technique

The lower threshold value for the occupancy model could be altered to suit other systems or for logistical reasons. Our lower threshold of 0.2 means that, in theory, only one in every five patches visited will be occupied by the focal species. If time or budgets are more constrained, increasing the lower threshold value could be an option, though this comes at the price of potentially not finding those most valuable populations that are living on the very edges of suitable climate space.

In our case study, we first identified the most valuable source populations, and then looked to where we could distribute the adaptive diversity they contain across the landscape. This source-focused approach maximizes the adaptive diversity that is captured and redistributed, and increases the chances of persistence for the focal species. An alternative approach – a recipient-focused approach – would first identify one or more valuable recipient populations and then look for the source populations that best match them in the adaptation space. In some situations, particularly when there are few discrete populations or when populations cover a small spatial scale, these two approaches are likely to yield similar results. Where results differ, the choice of approach might be driven by policy/management rather than criteria solely aimed at maximizing conservation outcomes. For example, if particular populations have a high conservation value for cultural or historic reasons (e.g., they fall within a popular protected area) then these populations may be the best recipient populations even if this means they do not make use of the greatest variance in the species' adaptive potential. While a recipient-focused approach might assist particular populations, it is a sub-optimal strategy at the species level because it risks losing source populations that are adapted to the very extremes of climate.

Conservation of peripheral isolates

Somewhat counter intuitively, the very characteristics that make peripheral populations so valuable (i.e., small size, isolation, and climatic extremity) also make them particularly vulnerable to climate change (Chapter 2 this work; Atkins & Travis 2010). Because these populations are already on the edge of climate space, slight changes to climate might tip them over the edge and into extinction. This extreme vulnerability means that identifying and harnessing the adaptive diversity contained within these peripheral populations should be undertaken as a matter of urgency. The techniques detailed above will give conservation biologists the tools they require to locate and exploit such diversity.

Detailed Methods

Surveys and detection probability

Preliminary work showed that the best predictor of *L. coggeri* detection was the activity of other diurnal skink species (Macdonald unpub.). As such, surveys were conducted throughout the year under weather conditions conducive to detecting diurnal skinks (i.e., sunny days). Skinks are a significant and highly visible component of virtually all Australian habitats, especially in the tropics. If few or no skinks of any species were detected in a patch during a survey, the weather conditions were deemed unsuitable and the patch was revisited under better conditions. If *L. coggeri* was not detected in a patch despite the presence of high numbers of other skinks, *L. coggeri* was deemed to be absent from that patch. Once *L. coggeri* had been detected in a patch, 10–20 individuals were captured by hand for morphological, physiological, and genetic studies (detailed elsewhere: Chapter 4 this work; Phillips *et al.* 2014; Phillips *et al.* 2015; Llewelyn *et al.* submitted) and no further presence/absence surveys were conducted at that patch. All individuals were released back at their point of capture. Most surveys were conducted by SLM, but absence data from additional sites were also used from other reliable sources (E. Vanderduys pers. comm. 2012). All procedures involving lizards were approved by the James Cook University animal ethics committee

(projects A1976 and A1726) and by Qld DERM (permit nos: WITK11729912 & WITK10659112).

Occupancy modeling

Given that population-level detectability should be perfect under our sampling design, we used a generalized linear model to relate site and patch characteristics to the presence or absence of our skink species, drawing from a binomial error distribution and using a logit link function. All analyses were conducted in R v3.2 (R Core Team 2015). Site covariates used were patch size (size in m² of the patch in which the site was located) and the following climatic variables: annual mean precipitation (AMP), average minimum daily temperature (Tmin), seasonality of precipitation (Pcov), and seasonality of temperature (Tcov). See Table 5.1 for more details.

An information-theoretic approach was used to assess the contribution of site variables to the occupancy model. Akaike information criterion values (AICc) for all models were calculated, corrected for a finite sample size, with the dredge function from the Multi-Model Inference (MuMIn v1.14) package in R. Model averaging (Burnham & Anderson 2002) was performed using the model.avg function from the same package to generate conditional coefficients for each site variable used in the model (conditional coefficients are the averaged coefficients using only those models in which that variable appears). Model averaging is justified in this case, because all our variables were standardized before analysis and so are always measured on the same scale (Cade 2015). To assess the significance of individual site variables in the top model, likelihood ratio tests were used to compare the best model with the equivalent model with the relevant variable removed.

A probability surface was generated from the fitted *L. coggeri* occupancy model, depicting the probability of occupancy for each pixel of Wet Tropics rainforest. The probability of occupancy (P_{occ}) of a pixel was determined by the following formulae:

$$LP_{occ} = A + \mathbf{B}\mathbf{V}$$

where:

LP_{occ} = logit-transformed P_{occ}

A = intercept

B = vector of model-averaged coefficients for site covariates V

V = vector of site covariates

LP_{occ} was converted to a probability ($0 \leq P_{occ} \leq 1$) with the inverse-logit function:

$$P_{occ} = \frac{e^{LP_{occ}}}{e^{LP_{occ}} + 1}$$

This pixel-level probability was then averaged at the patch level to obtain P_{occ} for each discrete rainforest patch. The resulting patch-level probabilities were then thresholded such that $P_{occ} < 0.2$ was considered unoccupied, $0.2 < P_{occ} \leq 0.8$ was considered 'edge' habitat, and $P_{occ} > 0.8$ was considered core habitat. From this set of edge patches, we then selected the most isolated patches based on our connectivity index.

Connectivity

Our connectivity index is detailed in the Supplementary Materials of Chapter 2. Briefly, our landscape was divided into a grid, and a habitat suitability value assigned to each 80×80m grid cell based on bioclimatic modeling of rainforest distribution (Graham *et al.* 2010). These suitability values were averaged over space with a spatial weighting derived from a species-specific dispersal kernel (Singhal & Moritz 2012). This resulted in high connectivity values assigned to areas of the

landscape that are rainforest and that are surrounded by rainforest, and low values for areas of rainforest surrounded by non-rainforest matrix.

Climate space

Having identified the source patches most likely to contain the most valuable populations, we then placed the average current climate of each source patch in a 'climate space' with axes made up of the four climatic variables used in the occupancy model. Each climatic variable was scaled so that it had a mean of 0 and an SD of 1. We used data layers generated under the RCP8.5 CSIRO Mk 3.0 model to match the current climate of our source patch with the future climate of the landscape. We used the 30-year average, centred on 2085 and downscaled to 250m resolution. To account for the degree to which each climatic variable is driving local adaptation, the local adaptation scores from Chapter 4 were used to weight each climate variable (for both current and future climates). Mean local adaptation scores for climate variables were calculated excluding traits with scores for that climatic variable less than 0. This set of mean local adaptation scores was converted into a vector of weightings by subtracting the set's minimum score from each score and then adding 1 (Table 5.3). This resulted in a weighting of 1 for the climate variable that had the lowest mean local adaptation score, and weightings >1 for all other climate variables. Each of the climatic variables was then multiplied by its weighting to create the scaled and weighted axes in our 'adaptation space'. The Euclidean distance was then calculated between the source patch's average current climate and the future climate of every grid cell across the landscape. Matches are then made between the source patch and the areas in the landscape with the smallest Euclidean distances.

Table 5.3: Individual local adaptation scores used to calculate climate axis weightings

'Mean LA score' is the row-average of all scores greater than zero (scores in italics are <0 and are excluded from the mean LA score).

Each row's weighting is 1 + the row's mean LA score minus the set's minimum mean LA score (=0.028 for Tcov). This gives a weighting of 1 for the lowest-ranking climate variable, and weightings of >1 for all other climate variables.

	CTmin	CTmax	breadth80	Tactive	des	HeadW	HindLL	HeadL	ILimbL	Topt	Rmax	Mean LA score	Weighting
AMP	1.2110	0.3934	0.0204	<i>-0.0008</i>	<i>-0.0007</i>	0.0055	0.0005	0.0001	<i>-0.0002</i>	<i>-0.0061</i>	0.0014	0.233	1.205
Tmin	0.3388	0.3212	0.0419	0.0509	0.0586	0.0110	0.0005	0.0021	<i>-0.0003</i>	0.0000	0.0534	0.088	1.060
Pcov	0.1143	0.1024	0.0180	0.0213	0.0239	0.0230	<i>-0.0011</i>	0.0005	0.0001	<i>-0.0047</i>	0.0024	0.034	1.006
Tcov	0.0628	0.0794	<i>-0.0084</i>	0.0028	<i>-0.0002</i>	0.0128	<i>-0.0063</i>	<i>-0.0008</i>	<i>-0.0011</i>	0.0002	0.0097	0.028	1.000

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Chapter 6

General discussion

With climate change well under way (Meehl *et al.* 2007; IPCC 2014), and catastrophic predictions for much of the world's biodiversity (e.g., Williams *et al.* 2003; Thomas *et al.* 2004), we are already seeing alterations to the distribution and phenology of many species (e.g., Parmesan 1996; Freeman & Freeman 2014). While there is still great merit in reducing our current emissions, it seems the planet is locked into a minimum 2°C increase in global temperature by the end of this century (IPCC 2014). As such, conservation biologists are turning to a variety of techniques to mitigate the impacts of climate change and to preserve biodiversity and productivity. One such technique, and the focus of this thesis, is assisted gene flow (AGF): a technique in which 'pre-adapted' individuals from climatically extreme populations are translocated into a recipient population to boost its climate change resilience.

Given that the planet is rapidly entering climatic conditions that it has not experienced for at least 40 million years (Peters 1994), it is vital that we investigate the climatic limits that species are currently adapted to. The populations occurring at these extremes can then be exploited through AGF to increase the adaptive capacity of the species as a whole. Ideal source populations for AGF will be those that show signs of local adaptation to the climatic conditions that will be more widespread in the future (i.e., generally hotter and more extreme/variable, with changes to precipitation regimes varying geographically). As detailed in Chapter 2, these source populations will often be found in peripheral isolates — small, isolated populations on the edge of a species' range. Their isolation and position on the edge of climate space mean that

these populations are likely to be adapted to the types of extreme climate regimes that will be more common in the future. Somewhat counter-intuitively, the very characteristics that make peripheral isolates so valuable for AGF (i.e., their small size, isolation, and extreme climate) also make them highly vulnerable to climate change. It is therefore imperative that we investigate and harness the adaptive diversity housed within them as a matter of urgency.

The first step in the implementation of an AGF strategy is confirming that the species does indeed show signs of local adaptation to climate, and identifying the particular aspects of climate that appear to be the strongest drivers of that local adaptation. The second step is to match source and recipient populations in a climate space that accounts for the varying degree to which each aspect of climate is driving local adaptation.

Summary of research findings

In this thesis, I have developed a novel technique that uses a connectivity index to identify drivers of local adaptation. These drivers were then used to transform a climate space into a 'local adaptation space', in which source populations can be matched with recipient populations. This general discussion chapter presents the major findings of this thesis in line with the overall aim and questions of the study.

Research aim

To develop techniques for identifying source and recipient populations for assisted gene flow to mitigate climate change impacts.

Why is isolation important and how do we define connectivity?

Chapter 2 used ecological and evolutionary theory to argue that there are three important axes that determine how valuable a population will be in terms of AGF: size, connectivity, and climate. The size of a population will determine its persistence through time (small populations have increased risk of extinction) and the degree of climatic heterogeneity it will experience. Larger populations will tend to be spread out over larger areas, and therefore experience more climatic heterogeneity. This is particularly so in an area such as the Australian Wet Tropics that has high levels of topographical variation. Populations experiencing high levels of climatic heterogeneity are less likely to show tight local adaptation to that climate, due to the effects of intra-population gene flow. Similarly, inter-population gene swamping can erode local adaptation if populations are highly connected to each other. Finally, given that we are looking for source populations for AGF efforts in the face of climate change, the climate that these populations currently experience is of utmost relevance. We want to find populations that currently experience climates that will be more widespread in the future — populations that are adapted to the extremes.

Population size and climate metrics can be readily obtained from broadscale data sets. Calculating connectivity, however, is more involved. I have used habitat suitability data (Graham *et al.* 2010) to develop a connectivity index that accounts for my focal species' dispersal capabilities. This connectivity index was then used to address the remaining research questions.

Do isolated areas experience more extreme climates?

Chapter 3 tests one of the major assumptions of Chapter 1; that more isolated areas of habitat experience more extreme climates. By using broadscale climate data and the connectivity index developed in Chapter 2, I have shown that, in the rainforests of the Australian Wet Tropics, less-connected areas experience more extreme climates.

Importantly, the direction of this extremity is in the direction of climate change; that is, hotter, and more variable. Populations persisting in these environments can tell us about the species' capacity to cope with these extreme conditions. More importantly, these extreme populations may provide the source genetic material needed for AGF strategies hoping to boost climate change resilience across the species' wider range.

How do we detect the environmental drivers of local adaptation?

In Chapter 4, I developed a novel technique for identifying local adaptation without having to conduct lengthy reciprocal transplant or common garden experiments.

Critically, my technique also identifies the drivers behind that local adaptation. My technique relies on the way in which increasing gene flow erodes local adaptation. By looking for correlations between the environment (e.g., climate) and species traits (e.g., morphological or physiological traits), and then assessing the way in which connectivity (as a proxy for gene flow) alters those correlations, I was able to separate environment–trait relationships that are due to local adaptation from those that arise through other processes (such as phenotypic plasticity). This technique enabled me to rank climatic variables according to the degree to which they drive local adaptation. In my focal Wet Tropics-endemic skink, two aspects of precipitation (annual mean precipitation and precipitation of the driest quarter) appeared to be the main drivers of

local adaptation in the set of physiological and morphological traits examined. Additionally, physiological traits generally showed much stronger evidence of local adaptation to the environment than did morphological traits, most likely because the environmental variables were climatic and the physiological traits used were temperature- and moisture-related. While the focus of this thesis has been AGF, the techniques developed in Chapter 4 to identify environmental drivers of local adaptation can be applied much more broadly.

Where will we find adaptive diversity in the landscape?

Knowing that: A) isolation is conducive to adaptation (Chapter 2); B) isolated areas experience the types of extreme climates that will be more common in the future (Chapter 3); and C) my focal skink species shows signs of local adaptation to climate, with different aspects of climate driving local adaptation to differing degrees (Chapter 4), I have defined an 'adaptation space' — a climate space with axes weighted according to the degree to which each climatic axis drives local adaptation — in which source and recipient populations can be matched. Isolated source populations were first identified using the connectivity index (Chapter 2) and occupancy modeling, and then plotted in the adaptation space. This enabled me to identify source patches that are likely to contain a skink population that is adapted to extreme climates, and then highlight the areas in the landscape that will match that climate in the future. It is to these areas that AGF efforts should translocate individuals from the source patch. This process can be repeated for numerous source patches, or reversed so that recipient populations are identified first and then matched with their ideal source patches.

Reflections on a PhD

What worked, what did not work, and what I would do differently

This project originally set out to compare the levels of variation, starting with morphology, in core versus peripheral populations of *Lampropholis coggeri*. In executing that work, I realised the false dichotomy of core vs peripheral and began to think about peripherality as a continuum. This led to the genesis of the idea that environmental effects are eroded by increasing connectivity (i.e., gene flow), which became a central pillar in this thesis. While the original plan for the analysis turned out to be a dead end, in addressing that problem I developed something arguably better. I also planned to compare levels of genetic variation between populations, but logistics prevented me from including that work in this thesis. When that work is conducted, I expect to find lower levels of genetic variation in each isolated population compared with well-connected populations, but that, collectively, isolated populations will represent the bulk of the species' genetic diversity despite occupying less total area (Eckert *et al.* 2008).

The original analysis in Chapter 4 used the best available current climate data to identify the environmental drivers of local adaptation, and produced very strong results. However, when writing Chapter 5, I realised that I needed future (i.e., climate change) versions of all current climate layers, so I returned to the Chapter 4 analysis and substituted the original climate data with other layers that had future projections. While these newer layers still produced significant results that were highly correlated with the previous results, the effect sizes were not as large. In retrospect, I could have

continued to use the best available data in Chapter 4, and then substituted these in Chapter 5. This would have given us a clearer picture of the drivers in Chapter 4, and still enabled me to select the strongest climatic drivers of local adaptation for use in Chapter 5.

Future research directions

This thesis presents the first integrated approach for AGF efforts. There is, however, much more to be done. Future research should address the following:

- Use of genetic tools to validate and/or refine the connectivity index developed in Chapter 2.
- Identifying the particular genes responsible for local adaptation to climate.
- Genetic assessment of potential source populations to assess levels of genetic diversity.
- Simulation work to establish when is the best time to translocate individuals into recipient populations. Translocation needs to occur before the source population is adversely affected by climate change, but after the climate of the recipient population has passed some threshold value to ensure that there is positive selection for the introduced genes. This question has been addressed for assisted colonization (McDonald-Madden *et al.* 2011), but no such work has been undertaken for AGF. My work used only the 2085 climate predictions, but work focusing on *when* could make use of the additional climate prediction data that are available.
- Quantifying, using simulation or empirical work, the ideal number of individuals to translocate.

- Investigating the best type of individual to translocate, as various life-stages of a species may differ in their persistence following translocation (Seddon *et al.* 2015).
- Incorporating climatic niche modeling of the habitat occupied by the focal species so that potential recipient populations can also be ranked by the likelihood of habitat persistence.
- Ways to incorporate phylogeographic information to ensure that translocations only take place between closely related lineages.

Some of the above work is already taking place as part of the ARC Discovery Project that my PhD was a part of.

Concluding remarks

In this thesis, I have developed techniques for locating populations that contain the adaptive diversity required for species to persist in the face of climate change. This work has highlighted small, isolated populations as being of particular importance. The techniques also allowed for source populations to be matched to recipient populations by accounting for the degree to which the various aspects of climate drive local adaptation.

This work contributes significant knowledge to the new field of AGF. While this field is currently young, it will see increasing use in the future. Assisted gene flow is a fairly radical, involved process, but it unfortunately looks like a necessary approach given the sweeping alterations to climate that are underway and/or expected in the future. Assisted gene flow necessarily takes a species-specific approach to

conservation (though there may be ecosystem-wide effects if the focal species is a 'keystone' species). As well as this species-specific approach, conservation initiatives should act more broadly to conserve landscapes, habitats, and communities. Assisted gene flow should be used in concert with other, broader strategies, such as:

- Reduction of emissions
- Habitat restoration to increase community-level resilience
- Assisted colonization (in extreme cases)

It bears repeating that assisted colonization efforts must be very carefully considered (Ricciardi & Simberloff 2009; Ricciardi & Simberloff 2014). The risk of the translocated species causing major problems is very real, and any negative impacts could outweigh the positive conservation outcomes of a successful translocation. It is for this reason that AGF may often be the better choice. Assisted gene flow is akin to habitat restoration using the seedbank that already exists at the restoration site — unlocking the potential of existing resources, rather than trying to build something new from scratch.

The key to any conservation strategy has always been in knowing your species, and this holds true for AGF. By taking key aspects of the work conducted for this thesis and repeating them with other taxa, we will be able to build up a picture of how species have adapted to climate how they may adapt to climate change. This will give us the data needed to effectively implement the AGF strategies that will be required to save species in the future.

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