Copyright is owned by the Author of the thesis. Permission is given for a copy to be downloaded by an individual for the purpose of research and private study only. The thesis may not be reproduced elsewhere without the permission of the Author.

The Ecology and Evolution of New Zealand's Endemic Alpine Grasshoppers

A thesis presented in partial fulfilment of the requirement
for the degree of

Doctor of Philosophy
in
Zoology

Massey University
New Zealand

Emily Margaret Koot

2018

Acknowledgements

Steve and Mary, there is no way I could have completed this mammoth task without you. Thank you both for your patience, guidance, encouragement and open door policy – I wouldn't have learnt what I have, or achieved what I have, without your mentorship over the last five years. When I accepted a summer internship with you over the summer of 2012/2013, I never could have imagined it would lead to me completing a PhD!

This journey would not have been the same without the Phoenix Lab group and our weekly meetings. Felix, Mike, Briar, Lizzie, Gillian, Simon, Lena, Louisa, Ben, Matt, Julian, Nim (and everyone else who has come and gone). Being able to bounce ideas and problems off you all has been extremely valuable, and I have enjoyed all the milestones we have celebrated together over the years – both academically and in our personal lives.

The Ecology Group has been my second home for the last eight years, and my undergraduate and postgraduate journey would not have been the same without all the amazing people I share this space with (you know who you all are). There's nothing quite like spending your days with likeminded people, and the friendships I have built over this period will last a lifetime. Kat, Katy, Nicki and Felix, thank you especially for your friendship, counsel and willingness to have "low key" nights at the drop of a hat. And of course, the Ecology Group would not function without our lab technicians: Paul, Tracy, Cleland and Sean, and our receptionist Sharon – thank you!

To Louisa, Ben and Briar, my field assistants, thank you for joining me on my hopper hunting expeditions - and trusting me to drive you up questionable mountain roads. I would also like to thank all of the ski fields that permitted me to sample grasshoppers from mountains along the length of the South Island: Rainbow Ski Area, Mt Olympus Ski Field, Mt Hutt Ski Area, Fox Peak Ski Field, Cardrona Alpine Resort and Snow Farm.

Mum and dad, thank you for your love, support and home cooked meals; thank you for letting me and my fur babies move back home so that I could focus on this project. To the rest of my family, thank you for your love and support– and for kindly pretending you know what I do and not asking too many questions about when I will finish and what I will do after.

To Morgan and Hannah, there is a reason we have been friends since we were kids. You both always know the right things to say to keep me going. Thank you for letting me visit whenever I needed to escape Palmy, and for your endless support and encouragement.

Callum, you came into this when I was halfway through, but your support over the last year and a half has been invaluable. I apologise for all the times my stress and hanger got the best of me, and for reading my thesis draft to you on our drive to Auckland. Thank you for being so understanding and encouraging – if you can put up with me through this, then I think that we will be able to get through anything.

This research was supported in part with funding from the Miss E. L. Hellaby Indigenous Grasslands Trust and the Massey University Vice Chancellor’s Doctoral Scholarship.

Abstract

Anthropogenic climate change has stimulated interest in how species distributions are influenced by climate and how they might respond to global warming. The alpine zone is a harsh ecosystem to inhabit, as it experiences climate extremes daily and seasonally, whilst also exhibiting a steep environmental gradient linked to elevation. This makes it a particularly vulnerable environment in light of anthropogenic climate change, but also an informative situation to explore evolutionary ecology. Flora and fauna inhabiting alpine environments are predicted to be most strongly impacted by future climatic changes, when compared with other global ecosystems. The alpine zone of New Zealand stretches the length of the South Island, and is represented in south and central North Island. It is the result of mountain building since the late Miocene, and is home to a diverse array of endemic flora and fauna. As a relatively large component of native New Zealand habitats that has so far been preserved in higher proportion to other systems, the alpine zone will not be exempt from the effects of global anthropogenic climate change. To date, little research has directly investigated the impact worldwide climate shifts might have on this ecosystem.

I investigated the impact that climate change has had, and will have, on New Zealand's endemic alpine short-horn grasshoppers (Orthoptera: Acrididae), as representatives of New Zealand's alpine fauna. Four endemic genera contain 13 endemic species that are all freeze-tolerant, open ground specialists. To assess how these species will be affected by future climate change, it was necessary to examine how they have likely responded to past climatic cycles. Phylogenetic relationships were investigated using high-throughput Next Generation Sequencing. The current classification of 13 species into four monophyletic genera was not supported by this study, and the re-classification of members within this group would be appropriate. The mitochondrial (mtDNA) genomes assembled in this analysis, were combined with mitochondrial genome data of Acrididae species from around the world. This allowed identification of species most closely related to the New Zealand alpine taxa and to estimate the timing of divergence using fossil calibration. New Zealand's alpine grasshoppers form a monophyletic group and share a common ancestor with alpine species from Tasmania. Molecular phylogenetic analysis established that the split of the New Zealand clade from their

Tasmanian ancestor probably occurred ~17–19Mya, which is about 12My prior to alpine habitat being available in New Zealand. Thus, the radiation of New Zealand grasshoppers predates the availability of alpine habitat, suggesting they retained shared ancestral cold tolerance for 12 million years or they independently converged on their alpine adaptations.

Using the current distributions of New Zealand's alpine grasshoppers, potential niche spaces were projected for three times periods (Last Glacial Maximum (LGM), current and future). Ecological niche models predict that suitable niche space has been reduced for most grasshopper species since the LGM, and that with future climate change, the suitable niche spaces of these species will be reduced further still. Fine-scale niche partitioning and population dynamics of species inhabiting five mountains were investigated using field sampling data and population genetics. On a fine scale the presence of particular species of grasshopper was found to correlate with habitat patches (e.g. rock or tussock) and elevation. Each species contained high levels of mtDNA genetic diversity, as expected of large stable populations, but the most common grasshopper species collected had the lowest genetic diversity of the three examined (*Sigaus australis*, *Paprides nitidus, Brachaspis nivalis),* suggesting it may have been more restricted in the past (perhaps due to microhabitat preferences) compared to the other species. The sampled mountain populations of each species have apparently existed in isolation long enough to accumulate unique clusters of mtDNA haplotypes, suggesting very low gene flow between populations. The fact that regional populations are already segregated could make them vulnerable to future climate warming, but might have the opportunity to adapt independently of one another.

The loss of alpine habitat due to climate change is likely to be more pronounced on islands than continental systems. I modelled the expected alpine area lost due to anthropogenic climate warming for eight island systems around the world. In each case the size of the alpine habitat is predicted to shrink, potentially leading to the extinction of species as a consequence of their insularity. The grasshopper species in New Zealand provide evidence that predictions of range shifts require knowledge of current large scale climatic limitations on species distributions and an understanding of fine scale biotic and habitat interactions as well as species specific potential for dispersal.

Table of Contents

Chapter One 1

General introduction: species responses to a warming world 1

Introduction 1

Thesis Outline 13

References 15

Chapter Two 27

Analysis of genes and phylogenetic signal from NGS generated mitochondrial genomes, 45S Ribosomal cassettes and H3 sequences of 16 New Zealand and Australian grasshoppers (Orthoptera: Acrididae) 27

Introduction 27

Materials and Methods 37

Results 43

Discussion 67

References 74

Supplementary Material for Chapter Two 82

Chapter Three 95

The time of divergence of a monophyletic radiation: an alpine radiation before alpine habitat in New Zealand's endemic grasshoppers? 95

Introduction 95

Materials and Methods 103

Results 110

Discussion 123

References 128

Supplementary Material for Chapter Three 136

Chapter Four 143

Ecological niche modelling of endemic grasshoppers to infer climate change effects on New Zealand's alpine fauna 143

Introduction 143

Materials and Methods 150

Results 156

Discussion 182

References 188

Supplementary Material Chapter Four 195

Chapter Five 209

Niche differentiation and population dynamics in the alpine zone; a case study of New Zealand's endemic alpine grasshoppers 209

Introduction 209

Materials and Methods 214

Results 223

Discussion 241

References 245

Supplementary Material for Chapter Five 251

Chapter Six 261

Thesis discussion 261

References 271

Supplementary Material for Chapter Six 278

Appendix One 282

Species Locations 282

References 304

Appendix Two 307

Anthropogenic cause of range shifts and gene flow between two grasshopper species revealed by environmental modelling, geometric morphometrics and population genetics 307